

CHAPTER 10 THE ROLE OF NUTRITION

As a generalization, eucalypts are opportunistic users of nutrients. They are able to survive under conditions of low soil nutrient status yet are able to respond to the addition of nutrients with increased growth (Pryor, 1976). The most significant example of opportunism is the increased growth rates of seedling eucalypts in sites which have recently been burnt (Cremer et al., 1978). Increased availability of nutrients, particularly phosphorus, is central to this response, though microbial factors are possibly also important (Renbuss et al., 1972).

Eucalypts are dominant throughout much of Australia over a vast range of soil types. Nutritional factors appear to be important in delimiting the ranges of many species, e.g. the demarcation between wet sclerophyll forest and dry sclerophyll forest was found to be associated with the concentration of available phosphorus (Beadle, 1954, 1962). Intraspecific differences in the capacity of eucalypts to tolerate particular edaphic conditions may also be significant (Ladiges and Ashton, 1977). Despite these considerations, overseas plantings have shown that many eucalypts, in particular members of the sub-genus *Symphomyrtus*, grow well in a range of soil fertilities in the absence of eucalypt-feeding insects (Pryor, 1976).

A number of studies concerning nutrient fluxes in eucalypt forests have been carried out (Bevege, 1978; Australian Forest Nutrition Workshop, 1981). However knowledge is severely

restricted in a number of areas including the role of root systems in mineral cycling and the quantities of nutrients added to the system through the weathering of primary minerals. Some information concerning nutrient fluxes in subalpine woodlands is available (see Bevege, 1978 for sources), but there is a deficiency of knowledge concerning mineral cycling in Australian woodlands. In contrast to woodlands, mineral cycling in grasslands has been relatively well studied (Fissel, 1978, Till, 1979).

The Northern Tablelands contains a variety of soil types (see Section 3.1)., Table 10.1 gives examples of the range of soil fertility. The influence of soil fertility on the distribution of eucalypts in the Northern Tablelands has been discussed by Williams (1963) and Beadle (1961) [also see Section 3.2].

Possible nutritional problems of trees can be classified into: (a) deficiencies, (b) toxicities and (c) indirect effects favouring or disfavouring associated animals, plants or microbes. Since eucalypts affected by rural dieback are indigenous to the area, any possible nutritional problems must relate to changes in the nutrient status of the soil, to an altered physiological condition or nutritional demand of the trees, or to competitive interference from pasture plants.

10.1 Influences of livestock and clearing

The tendency of sheep to regularly camp in the same place leads to an uneven distribution of urine and faeces which has caused significant redistribution of nutrients within paddocks. Hilder (1969) estimated that the rate of movement of major nutrients into sheep camps is more than 4 times the rate of loss through the removal of animal products. Concentration of potassium in soil from sheep camps has been found to be up to 100 times that of non-camp areas and variations in the concentration of phosphorus have been found to be almost as great. There is considerable loss of nutrients from urine or dung through volatilization (e.g. nitrogen compounds) and leaching and, in the case of cattle, concentration of dung into pads is also a problem. Trees themselves also influence soil properties (Story, 1967) including the spatial distribution of mineral nutrients (Ward, 1979). Thus, it is possible that situations involving both deficiencies and excesses of nutrients could develop in the same paddock. It is not certain whether there is a link between the changes to the distribution of nutrients caused by grazing patterns and tree vigour, but the data from 'Kiparra' (see Section 3.6) indicate that *E. blakelyi* on the sheep camp were markedly more vigorous than *E. blakelyi* elsewhere on the property.

Clearing of land usually affects tree-grass interference and water balance more directly than it affects soil fertility. However, where subsoil salinity is high, reduced tree cover with a consequent reduction in removal of excess water from the

subsoil may lead to an upward movement of the watertable and subsequent accumulation of salt higher in the profile. Salination has had very little effect on pastoral production in the Northern Tablelands but there are some sodic soils in broad valleys in central parts of the Tablelands. *Eucalyptus nova-anglica*, the eucalypt species most affected by dieback, formerly dominated many of the lower lying areas most prone to salt accumulation. Hence attention to the concentrations of salt in these soils and determination of the sensitivity of *E.nova-anglica* to salting is recommended.

10.2 Pasture improvement

For over two decades pasture improvement programmes on the Northern Tablelands have commonly involved broadscale aerial spreading of superphosphate and clover seeds (see Section 3.3). Nitrogen fixation by the clover allows soil nitrogen levels to build up. Such pastures may then be fully improved by the sowing of introduced grasses such as phalaris, ryegrass and cocksfoot. Fodder crops such as oats are relatively rare on the Tablelands.

Major changes to the soil are initiated by pasture improvement. They include: building up of soil organic matter, increased levels of organic phosphorus and nitrogen, increased soil acidity, and as a consequence, increased cation exchange (Williams and Donald, 1957). In soils tested on the Southern Tablelands, much of the phosphate and sulphur added as superphosphate could be accounted for in the increased organic

matter in the surface layers of the soil, even many years after application (Donald and Williams, 1954).

On the Northern Tablelands a folklore linking eucalypt dieback with the use of superphosphate has developed. Duggin (1981) noted that the results of a survey which collated information from graziers showed some association between the observed onset of extensive dieback and the time superphosphate was first applied extensively. In contrast there are reports of marked growth responses by seedlings of woodland eucalypts, such as *E.melliodora*, to phosphate fertilizers (F.R. Humphreys, pers. comm.). It is difficult to separate the effects of application of superphosphate from the other effects of pasture improvement. There is substantial evidence linking pasture improvement with dieback at a macroscale (see Sections 3.4, 3.5) but the situation is less clear with respect to the application of superphosphate to individual paddocks (Sinden et al. 1983; also see Section 3.4).

Phosphate poisoning has been reported in some eucalypts after the addition of superphosphate to soils. However, these reports are confined to areas with nutrient poor soils of low buffering capacity (Mullette, et al., 1974; Specht et al., 1977). Most eucalypt species which show symptoms of rural dieback on the Northern Tablelands are growing naturally on a range of soil types whose differences in soil phosphorus status are greater than the changes of soil phosphorus expected to result from the application of fertilizers at commonly used rates (J.L. Charley, pers. comm.). Thus, except perhaps on very

nutrient poor soils, e.g. soils derived from leucoadamellite in areas which originally contained dry sclerophyll forests the occurrence of phosphate toxicity is unlikely on the Tablelands.

Since the ratios of concentrations of major macronutrients in the organic component of the soil remain fairly constant in semi-improved pastures (Williams and Donald, 1957), it is also unlikely that development of any nutrient imbalances of macronutrients severe enough to affect trees, would be widespread. Any link between superphosphate and eucalypt dieback must be more subtle.

A number of more subtle responses to superphosphate have been reported. Gulliford (1976) reported that aerial application of superphosphate at the time of a honey flow could stop the flow abruptly. Some farmers have also reported leaf scorching of eucalypts following aerial application of superphosphate but this has not been confirmed. Mycorrhizal activity can be suppressed at higher levels of available phosphorus (Ratnakjake et al., 1973). This may be important in a number of ways, including reduction of the effective absorptive area of the tree's root system (see Section 6.5). Increased levels of available phosphorus and nitrogen lead to a reduction of the root /shoot ratio of pasture plants (Davidson, 1969). A similar response is possible in eucalypts. Addition of superphosphate was also reported to have caused premature ageing of heathland plants (Specht, et al., 1977).

The development of lignotubers is suppressed in some species of eucalypts when the concentration of available phosphorus is high (Beadle, 1968). Since lignotubers are important storage organs in eucalypts, it would be interesting to ascertain the effect of phosphorus fertilizers on the total carbohydrate storage capacity of eucalypts. Another possible effect of the use of superphosphate is the development of toxicities resulting from impurities such as cadmium. Cadmium is normally present in concentrations ranging between 2 and 200 ppm in superphosphate (Foy et al., 1973). Symptoms of cadmium toxicity include stunting and chlorosis. The significance of toxicity problems in pasture plants due to trace elements in superphosphate has been discussed by Williams (1977).

Increased soil acidity following pasture improvement has resulted in changes in the relative availability of trace elements. Williams and David (1976) found that soils which had been under continuous improved pasture for 30 years had increased availability of manganese, aluminium, iron and zinc, but little change in the availability of molybdenum. Plants vary greatly in their tolerance of high concentrations of manganese and aluminium. Concentrations of available manganese vary between seasons and were found to be higher during hot dry conditions in summer or when soils were waterlogged (Siman et al., 1974). There are some reports of the occurrence of chlorotic leaves in eucalypts associated with a low Fe/Mn balance; the symptoms disappeared when the eucalypts were treated with iron chelates (Andrew and David, 1959; Winterhalter, 1963; Stewart et al,

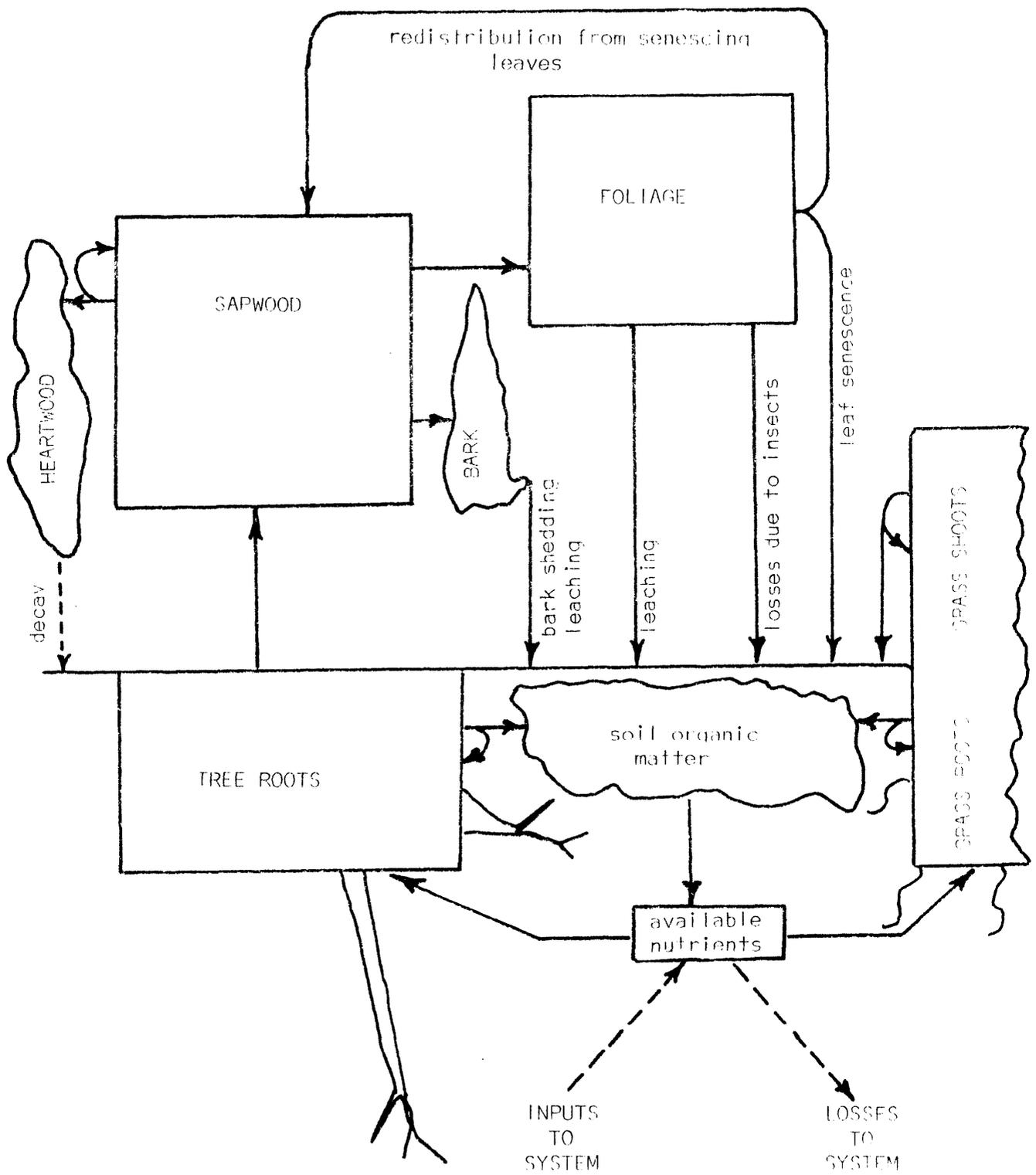


Figure 10.3.1 Simplified representation of the pathways of mineral nutrient transfer in the tree-grass system.

1981). Though this form of toxicity may occur in parts of the Tablelands, chlorotic leaves are not a common symptom of rural dieback and it is unlikely that manganese toxicity would be an important factor. Little is known about the occurrence of aluminium toxicity in eucalypts, though Mullette (1975) found that *E.gummifera* growing in the Hawkesbury Sandstone region was tolerant of relatively high concentrations of available aluminium. Other longterm effects of increasing soil acidity may include: increased leaching of calcium and magnesium ions, breakdown of soil structure, and the creation of more favourable conditions for the development of fungal diseases (Lee, 1980).

Side-effects of pasture improvement practices influencing leaf-feeding insects and possibly root pathogens or other components of the ecosystem are discussed elsewhere. However, mention of some of the possible nutritional consequences of competition between trees and grasses is necessary here.

10.3 Tree-grass competition

Where pasture improvement has encouraged the growth of denser grass swards, usually with an altered species composition, the pathway of mineral cycling in trees may be disrupted. If grass roots dominate the surface layers of the soil the nutrients recycled through leaching, leaf fall and insect frass will be more readily available to grasses than to trees (see Fig. 10.3.1).

Nutrients locked into the biomass of grasses or excluded from trees by interference from grass roots are likely to become available to trees if the quantity of grass (both shoot and root) is reduced, e.g. during drought. The deeper roots of trees and their network of lateral roots from which feeding roots are borne give trees a competitive advantage when fluctuations of soil moisture severely affect grasses.

The deeper roots of trees also facilitate greater access to nutrients available deeper in the soil profile (see Section 9.2). In addition to precipitation inputs, most nutrients (e.g. calcium, magnesium, phosphorus) are partly supplied to plants through chemical breakdown of mineral constituents in the soil. Nitrogen not added to the system in precipitation is circulated to plants through the breakdown of organic matter. Thus the supply of nitrogen or a mineral constituent particularly deficient in the soil parent material (e.g. phosphorus) is likely to be most affected by disruption of the normal pathways of nutrient cycling.

Little is known about the effect of tree-grass competition on the availability of trace elements to trees. Boron is a trace element with a vertical distribution closely following the distribution of humus (Aubert and Pinta, 1977, p. 8), i.e. mostly near the soil surface. Dieback of eucalypts in Southern Africa has been attributed to boron deficiency (Savory, 1962). However, the symptoms involved crinkling and discolouration of the unfolding leaves in the apical bud. Boron deficiency was found to limit the growth of subterranean clover in soils from 3

out of 17 sites tested on the Northern Tablelands (Spencer and Barrow, 1963). Work to ascertain the role of boron in eucalypt nutrition is required.

10.4 Links between tree morbidity and nutritional status

Since eucalypts showing severe dieback usually have a degenerate root system, it is probable that consequent reductions in nutrient absorption have led to the development of nutrient deficiencies. In Tasmania, assessment of foliage mineral nutrient status of *E. obliqua* showing symptoms of gully dieback failed to demonstrate any significant difference in the concentrations of the 10 nutrients tested compared with controls (Neilsen and Palzer, 1977). There has been no attempt to ascertain the nutritional status of eucalypts showing rural dieback. To be successful such a study requires careful calibration and a rigorous sampling approach. Perhaps sampling the nutrient content of young stem tissue instead of foliage would provide a better indication of nutrient status.

Excessive insect grazing of foliage and leaching of nutrients from damaged leaves would further increase the possibility of nutrient deficiencies developing.

Insect grazing most severely affects the cycling of the nutrients that are usually internally redistributed within the tree. About 40-60 % of phosphorus and 50-60 % of nitrogen (Attiwill, 1981) is recovered directly from senescing leaves;

these nutrients are lost from the plant if defoliation occurs.

Figs. 10.4.1 and 10.4.2 illustrate likely changes to nitrogen flow resulting from insect induced defoliation of 40 % per annum. This was the average rate of defoliation of *E.blakelyi* determined in a study near Canberra (Journet, 1981) and falls within the range of rates of defoliation determined in other Australian studies. The model assumes: (1) a leaf life expectancy of two years if insect damage is absent, (2) that leaves consumed by insects are replaced within the year, and (3) that only leaves less than one year old are consumed by insects. The proportions of nitrogen utilized for bark and heartwood production are estimates. For simplification only the net incorporation of nitrogen in the heartwood is given so that redistribution of nutrients during heartwood formation (Beadle and White, 1968) need not be considered. These assumptions determine that 70% of leaves are consumed by insects whereas only 30% senesce naturally. In addition, 40% extra nitrogen is required to replace the lost foliage. The total nitrogen demand of the tree is increased by 87%. If it is assumed that the rate of defoliation is independent of leaf age the total increase of nitrogen demand is reduced to 75 % (instead of 87 %). Quantities of nitrogen in the various pools are taken from Turner's (1980) study of *E.dalrympleana* and *E.radiata*. in dry sclerophyll forest near Tumut, N.S.W. His data showed that foliage contained 32% of the nitrogen and 13% of the phosphorus in the living parts of the tree above ground level, but proportions of phosphorus varied significantly between species. Sapwood contained 35% of the

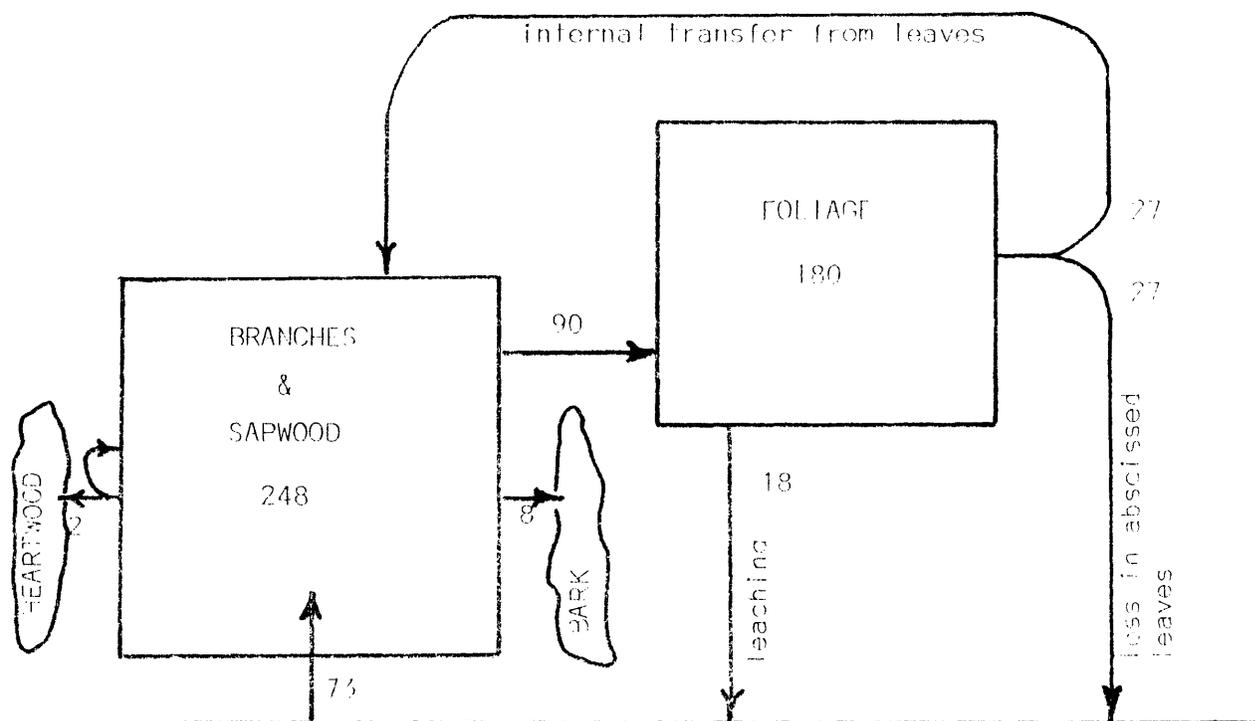


Figure 10.4.1 Flow of nitrogen through a tree expressed in terms of percent movement through sapwood and branch pool. No insect defoliation.

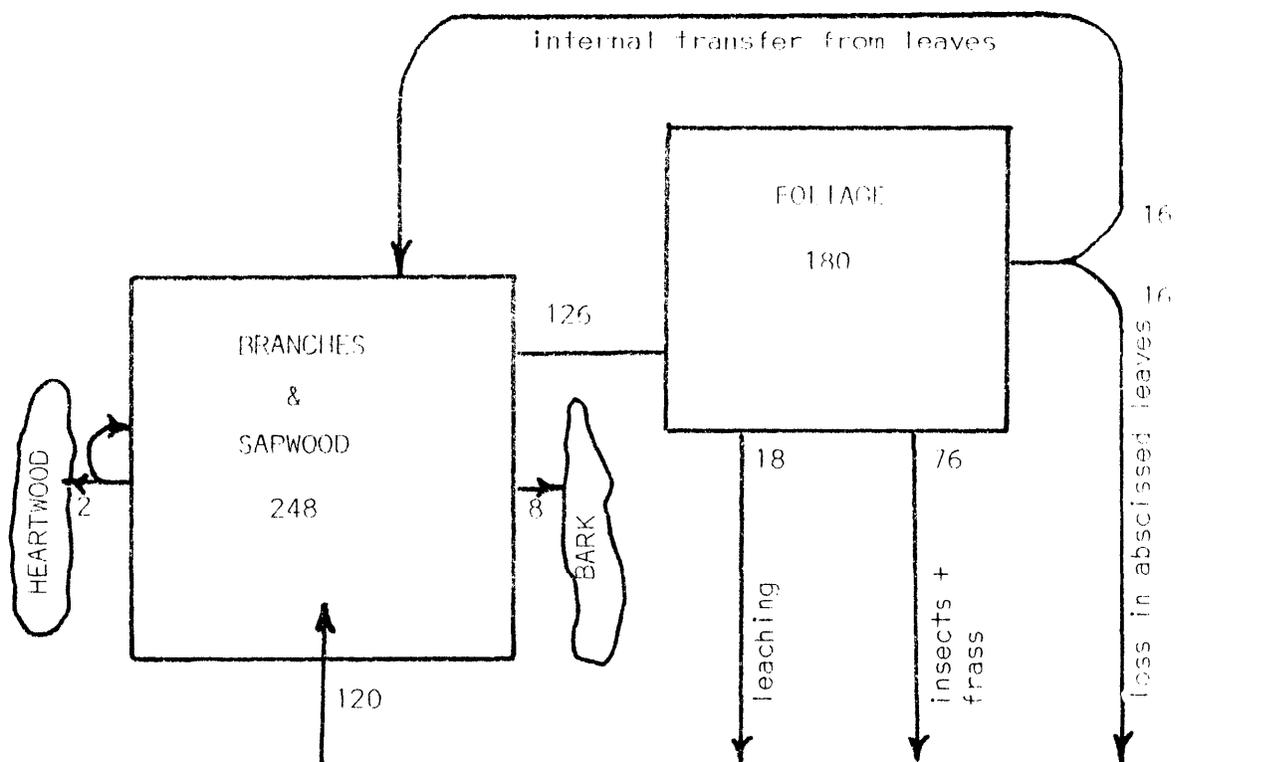


Figure 10.4.2 Changes to system shown in Fig. 10.4.1 due to 40% insect induced defoliation per annum.

nitrogen and 56% of the phosphorus.

Eucalypts have the ability to replace their crowns using reserves stored in the sapwood, e.g. after fire or massive insect attack. Replacement foliage is usually richer in mineral nutrients, so much so that phosphorus toxicity symptoms have been induced in eucalypts simply by pruning (J.L. Charley, pers. comm.). If tree-grass competition for nutrients was intense nutrient reserves in the sapwood could be depleted by chronic insect defoliation. Deficiency symptoms are unlikely to appear in the leaves before the mobile reserves in the sapwood have been depleted. Turner's data concerning the distribution of nutrients within the aerial parts of eucalypts indicate that nitrogen in particular could be drained from the system relatively rapidly.

The problems of nutrient supply brought about by excessive insect grazing would be exacerbated if the condition of the tree had deteriorated, particularly if the carbohydrate supply to the roots became critical, affecting root function.

10.5 Conclusion

There are several nutritional problems which might affect eucalypts growing on certain soil types on the Northern Tablelands and require investigation. These include: salting, boron deficiency and acidity induced problems. Closer attention to the effects of superphosphate fertilizers on rural eucalypts would probably also be worthwhile.

Though the concentrations of macronutrients in soils has generally increased under improved pastures little is known about the relative nutritional status of eucalypts remaining in these pastures. Competition with grasses and increased nutritional demand caused by insect grazing in combination with deteriorating tree condition could easily disrupt the nutrient supply. In the absence of secondary ramifications, e.g. increased insect activity, eucalypts that have been defoliated by insects would be expected to respond positively to the application of mineral nutrients which have been depleted. In particular, the supply of nitrogen could easily be affected.

Possible effects of altered tree nutritional status and soil nutritional status on insect populations is discussed in Sections 13.3 and 13.1 respectively.

CHAPTER 11 THE AGE STRUCTURE OF EUCALYPT POPULATIONS AND DIEBACK

The age structure of natural eucalypt populations ranges from uniform aged stands, in which the recruitment of seedlings is usually prevented by the density of the standing vegetation until a catastrophic event (typically fire) destroys the whole population, to mixed-age stands in which there is continual loss and replacement of individual trees (Cremer et al. 1978). Uniform aged stands in tall open-forests are usually dominated by fire sensitive species, e.g. *Eucalyptus fastigata* and *E. nitens*. More xeromorphic communities, including open-forests and woodlands, usually have some variation in tree ages. In particular, lignotuberous advanced growth (i.e. eucalypts that consist of a number of shoots arising from a basal lignotuber and that remain of seedling size often for extended periods until conditions suitable for development into saplings occurs) is critical in the replacement of individuals that have died.

A discussion of the links between the age structure of eucalypt populations and dieback is important because the response of eucalypts to particular stresses varies with age and because the survival of eucalypt populations affected by dieback depends on the age structure of the population.

11.1 The life system of eucalypts

As Cremer et al (1978) have reviewed most of the published information relating to reproduction and establishment of forest eucalypts this treatment concentrates on the woodland eucalypts. Fig 11.1.1 summarizes the major processes in the development and reproduction of eucalypts.

Seed production. Only trees with a relatively high vigour rating were found to initiate the production of quantities of flower buds (see Section 4.2). Initiation of flower buds may occur annually, biannually or irregularly depending on the species and internal and external conditions. In some species, e.g. *E. diversicolor*, the variations of flowering intensity between seasons is much greater than the variation of initiation of flower buds (Longeragan, 1979). Insects and weather related stress both contribute to the loss of flower buds. *E. blakelyi* generally has a biannual reproductive cycle with flower buds being initiated every two years (Clark and Dallwitz, 1974).

Both Griffin (1980) and Ashton (1975a) investigated the flowering phenology of *E. regnans*. The flowering period of individual stands usually lasts about 90 days with adjacent trees flowering synchronously. Individual flowers last about one week. Near Canberra *E. blakelyi* usually flowers between late November and mid January (Clark and Dallwitz, 1974). The flowering of *E. melliodora* trees, near Armidale, that were monitored as part of the present study appeared to be less

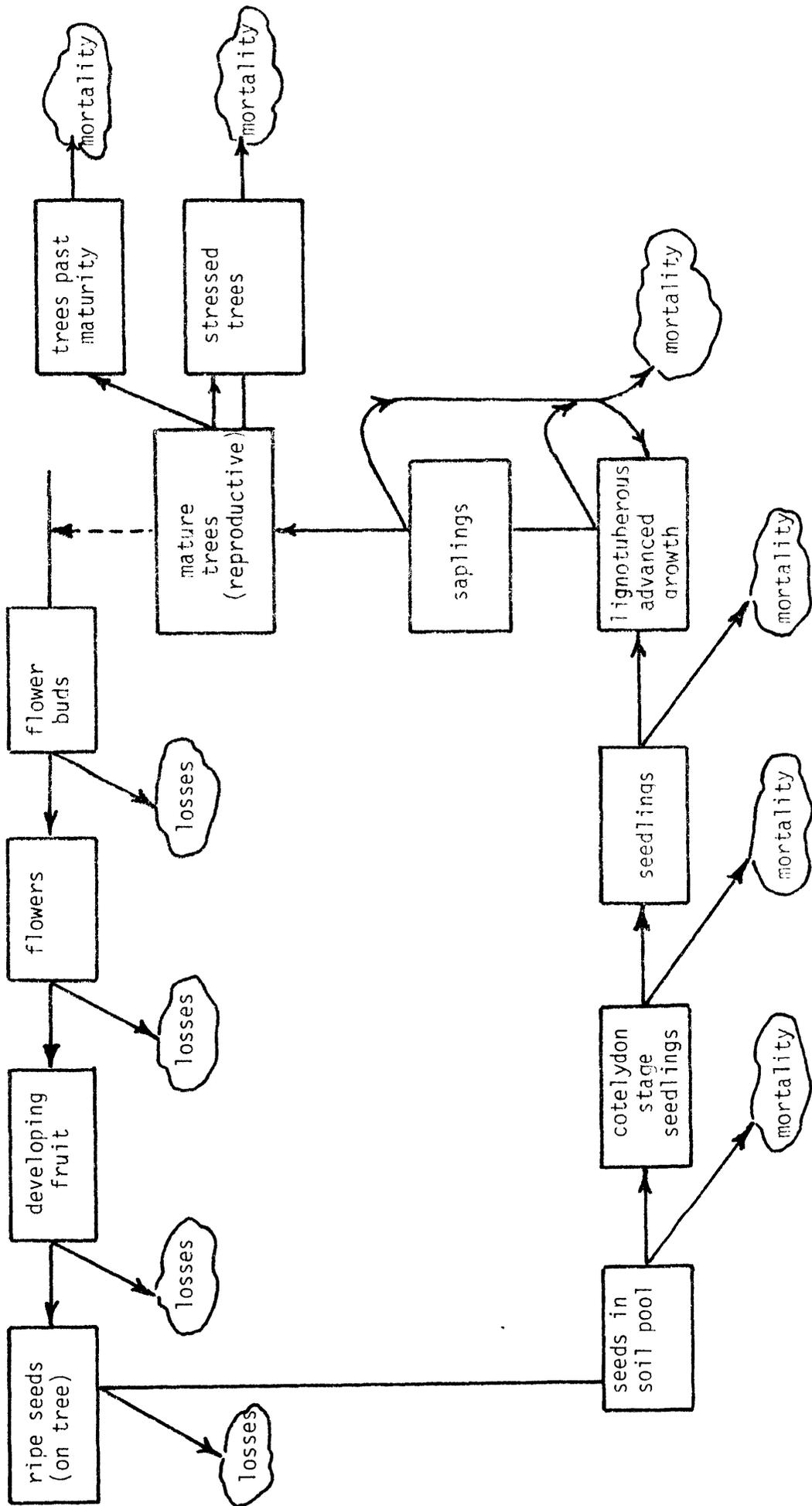


Figure 11.1.1 The life system of woodland eucalypts.

restricted by season: flowers were noted in late winter, spring (heaviest set) and summer (see Section 4.3). However, the unusually dry conditions may have affected the phenology.

The time between initiation of flower buds and the ripening of seeds varies from about 6 months in *Angophora floribunda* (personal observation) to over 4 years in some *Monocalyptus* eucalypts and *E. diversicolor* (Cremer et al, 1973). Most eucalypts appear to be intermediate. Seed fall in *E. camaldulensis* commences about 9 months after flowering (Dexter, 1967). The period between flowering and the ripening of seeds is also significantly less than one year in both *E. blakelyi* and *E. melliodora* (personal observations).

Though the proportion of unripened seeds lost due to consumption by seed feeding insects and to other factors is usually high, the annual production of seeds by a single mature tree with a healthy crown is in the order of 5,000 to 100,000 (Cremer et al, 1973).

Seed dispersal. The capacity of trees to store seeds in their crown varies between species. As a generalization, *Monocalyptus* species retain seed in their crowns for longer periods than other eucalypts (J.B. Williams, pers. comm.). *E. camaldulensis* (in *Symphyomyrtus*) sheds its seeds over the entire year, though most seeds fall in spring and summer and some seeds remain in the capsules for over one year (Dexter, 1967). Viable seeds are usually shed within about a week after a fire or an injury that causes the eucalypt's canopy to

wilt (Cremer et al, 1978; personal observation).

Most seed that is released from mature capsules falls within a distance of equal to the height of the tree and few seeds fall at a distance greater than twice the height of the tree (Cremer, 1977). Some branches carrying capsules with ripe seed are blown further from the tree, but this is unlikely to account for more than a small proportion of regenerating seedlings. For example, when Onans and Parsons (1980) investigated the regeneration of mallee vegetation after clearing they found no eucalypt seedlings more than 10 m from a seed source.

Germination. Seed-feeding ants usually remove a large proportion of the seed released from eucalypts unless fire causes a mass release of seed (Ashton, 1979; Drake, 1981; Wellington, 1981).

Most eucalypts have no special germination requirements and their seeds will readily germinate within a few weeks. However, some species from cold areas, e.g. *E. pauciflora* ssp. *niphophila*, have a weak dormancy and require stratification at near freezing temperatures to ensure high germination rates (Scott, 1972). The exposure of the seeds of some temperate eucalypts to high temperatures may also induce a secondary dormancy in a proportion of the seeds. Thus the rate of germination of seeds during the summer months is restricted and some seeds are able to survive in the soil till the following spring (Cremer et al, 1978). Mild water stress

may also retard germination. The germination rate of *E. camaldulensis* placed in a mannitol solution with an osmotic potential of as low as -0.2 MPa was markedly less than the germination rate in pure water, while *E. regnans* only showed reductions of germination rates at water potentials of -0.6 MPa or less*. However, since periods of heavy rainfall are frequent on the Tablelands and the long-term survival of eucalypt seeds in storage is affected by moisture, it is unlikely that eucalypt seeds ever survive in the soil pool for significantly more than one year.

Establishment of seedlings. Factors contributing to the mortality of newly emergent seedlings include: damping-off fungi (see Section 6.1), damage by herbivores (decapitation at the cotyledon stage is fatal), dehydration, prolonged absence of adequate light, and frost injury. Light is a critical factor limiting the recruitment of new seedlings in relatively dense vegetation (Cremer et al, 1978).

The growth of establishing eucalypts may be further restricted by allelopathic substances from mature trees (see Section 6.6) and by the availability of mineral nutrients (see Section 10.0). The central role of fire in the creation of conditions that facilitate the survival and growth of eucalypt seedlings has already been mentioned (Sections 8.5, 10.0). However, fire is not essential for the establishment of eucalypts. Dexter (1967) found that the survival of *E. camaldulensis* seedlings was greater on cultivated soil than

* Edgar (1977)

on an uncultivated ashbed.

Bryant (1969) observed a progressive increase in the density of *E. pauciflora* seedlings under conditions that did not involve any significant disturbance of the community during the period of study. The vegetation studied consisted of snowgum woodlands with a shrubby understorey containing snowgrass and other herbs on a shallow alpine humus soil. However, several other workers considered that mechanical disturbance was necessary to facilitate the establishment of artificially sown seed of *E. pauciflora* in snowgrass communities (reported in Noble, 1980). Noble (1980) presented evidence that accorded with the hypothesis that the presence of the grass tussocks reduced the vigour and the survival rate of neighbouring *E. pauciflora* seedlings. The characterization of the seed bed conditions required for the establishment of eucalypts in woodlands needs further study.

Jacobs (1955) suggested that conditions suitable for the establishment of eucalypts in savanna woodlands only occurred infrequently. He observed that during the 27 year period between 1928 and 1954 there were only two periods of significant regeneration in savanna woodlands near Canberra, 1934-36 and 1948-52; they were associated with unusually wet spells. Jacobs considered that eucalypts require about 3 favourable years (in terms of moisture regime) to become established. However, the resilience of eucalypt seedlings rapidly increases with age. In a direct-seeding trial carried out in a mulched seedbed near Armidale in the summer of 1982/3

the *E. viminalis* seedlings that had survived after the third month were mostly still alive one year later despite several dry spells during late summer and autumn (Curtis, in preparation). Dexter (1967) found that woody stemmed *E. camaldulensis* seedlings over 15 cm high were able to recover after shedding all their leaves when moisture stress was severe. Potted seedlings of *E. nova-anglica*, *E. blakelyi* and *E. melliodora* of a similar size also had this capacity (personal observation). It is likely that many eucalypts growing on the Tablelands could become well established in a single season.

Juvenile eucalypts with multiple shoots arising from a basal lignotuber have the capacity to survive severe disturbances, e.g. fires that kill their aerial parts. Their importance in the regeneration of most eucalypts has already been stressed. Lignotubers that are suppressed, chronically damaged, or lack the metabolic reserves necessary for the transition into a sapling form may survive in a dwarf state for extended periods.

Establishment of saplings. The likelihood that establishing saplings die back repeatedly before they finally become established has already been mentioned (see Section 2.1, Jacobs, 1955). Jacobs (1955) considered that many of the juvenile eucalypts that were established in the Canberra region in the 1934-36 period only succeeded in developing into saplings in the second favourable (moist) period, from 1943 to

1952. However, numerous juvenile eucalypts successfully developed into saplings in the Northern Tablelands in the relatively dry years between 1981 and 1983 (personal observation). So it is probable that the development of established seedlings on the Northern Tablelands is not limited by below average rainfall. Factors such as grazing by insects or livestock and competition with grasses are probably of more importance. Establishment of saplings never occurred on sites where grazing by livestock was intense (see Section 8.1).

The vulnerability of developing saplings to shoot dieback has already been mentioned (see Section 2.1). Where stands of developing eucalypts are dense, resources are utilized rapidly (see Section 9.3), the competition between saplings becomes intense, and suppression and mortality of individuals occurs.

Maturation. Jacobs (1955) described the changes in the form of trees associated with the development from sapling to mature tree. The time required for woodland eucalypts to attain reproductive maturity has not been systematically monitored but is probably well over one decade.

Longevity. Eucalypts are not especially long-lived trees. Dating studies that have been carried out suggest that *E. camaldulensis*, or other large eucalypts such as *E. regnans*, rarely live for more than 400 years (Ogden, 1978). Gill (1971) estimated the age of one *E. camaldulensis* to be 950

years using radiocarbon dating but no other estimates of eucalypt age have approached this figure.

Kile et al (1980) estimated that woodland eucalypts in south-eastern Australia rarely live more than 200-300 years.

The factors associated with the decline of ageing trees is discussed in Section 11.3.

11.2 The age structure of eucalypts in rural areas on the Northern Tablelands

Partly because of technical problems associated with the lack of correlation between tree size and age (Jacobs, 1955) and the unreliability of age determinations using ring counts [see Odgen (1978) for a discussion], there have been no systematic studies on the Northern Tablelands aimed at determining the age structure of eucalypt woodlands.

A historical account of the broad changes in the character of the vegetation was included in Section 3.3. However, the available information is sketchy: pioneer squatters seldom commented on the structure of eucalypt communities.

The reported "parkland-like appearance" (Section 3.3 and Norton, 1971) of some of the gentle slopes and shallow open valleys of the New England Plateau is characteristic of woodlands on soils of at least medium fertility and dominated by mature trees. It is probable that individual ageing or

moribund trees progressively died and were replaced by lignotuberous advanced growth, so that denser patches of regenerating saplings were sparse. If this impression is accurate then within the period preceding settlement by Europeans in the areas described it is probable that there had been no widespread occurrences of dieback: such occurrences would have involved mortality of stands of eucalypts and their eventual replacement by dense stands of saplings.

However, the density of vegetation on ridgetops in the same general area was considerably greater. This difference probably related to topographic and lithological factors but it is possible that the trees on the ridges were regrowth populations that had replaced populations of trees that had recently died out.

Given the intensity of clearing and the profuse regeneration in the late 19th century (see Section 3.3) it is probable that the great majority of trees in rural areas on the Northern Tablelands are less than 100 years old (also see Section 3.4).

Both the recruitment of new seedlings and the survival of lignotuberous advanced growth appear to have been deleteriously affected by pasture improvement. Probably increased browsing (see Section 8.1) and increased competition with grasses are responsible. Consequently, in many areas there has been no recruitment of new seedlings since the 1950s.

In some areas juvenile eucalypts have been completely eliminated by cultivation, and the only juveniles remaining are in stock reserves.

Dieback of eucalypts during the 1970s caused greater mortality of saplings, immature trees and trees past maturity than of mature trees. This has further reduced the range of tree ages within eucalypt populations.

Thus, since settlement, a large proportion of older eucalypts have been eliminated from most rural areas, and juvenile eucalypts have been eliminated from some areas. However, management has varied from area to area so there are, for example, properties where only overmature eucalypts remain and properties where young regrowth is dominant.

11.3 Dieback and tree age

There are two plausible explanations for saplings and over-mature trees being more severely affected by dieback than mature trees (see Sections 3.6, 3.4):

(i) the different age classes of trees were stressed to different degrees;

(ii) the different age classes of trees responded to stress in different ways.

Mortality in saplings. It is plausible that saplings are generally more severely stressed and, in particular, are

defoliated to a greater extent than mature trees. M. Lowman (pers. comm.) found that defoliation of mature eucalypts by insects was greater near ground level than in the crowns of mature trees. Therefore it is probable that saplings are defoliated more than taller trees. Also, juvenile eucalypts differ from mature trees with respect to their chemical composition and physiology (see Section 9.3). Other forms of stress that will generally affect saplings more than mature trees include competition with grasses and competition with other trees.

It is also probable that the metabolic reserves of saplings are generally not as extensive as the reserves of well established trees.

Mortality in ageing trees. The capacity of trees that are past maturity to withstand stress diminishes with time. It is sometimes difficult to distinguish the effects of old age from the effects of severe stress. The rate of ageing of trees appears to depend as much on the conditions under which the trees are growing as on their chronological age. The processes of growth are intrinsic to trees and other perennial plants because their organs and tissues, including leaves, xylem (see Section 9.4) and phloem, have finite functional life-spans. In addition, the supportive tissues, including heartwood, are subject to decay. Factors influencing the initiation of heartwood decay include structural injuries to the tree and the presence of wood-boring insects; the actual

resistance of wood to decay is probably an important determinant of tree ageing (Jacobs, 1955).

The major factors involved in the onset of old age in trees are:

1. the increasing difficulty of maintaining a favourable ratio of assimilatory surfaces to respiring surfaces as the dimensions of the tree increase;
2. wood decay leading to the development of structural weaknesses;
3. increasing stem resistance to water flow as the branching pattern of the tree becomes more complex after successive replacement of broken limbs and damaged roots (Hinkley et al, 1978) ; and
4. loss of juvenility (Kramer and Kocilowski, 1978).

Ultimately mortality associated with old age usually relates to shortages in the supply of energy and nutrients within the tree leading to a reduced rate of replacement of senescent parts and finally to a breakdown in the tree's life-support system.

The process of breakdown is analagous to the situation where chronic insect infestation directly reduces the tree's energy reserves and leads to a decrease in the ratio of photosynthetic surface to respiring surface. The death of the tree is again related to the accumulation of an energy

deficit. Since both processes are related in this way, death due to chronic insect attack is not independent of age and vice versa. Ageing trees are more likely to die from insect infestation than mature trees that generally have a more positive energy balance. Also, trees that are chronically affected by insects are likely to suffer from old age prematurely since their capacity to maintain their original ratio of assimilatory area to respiring area is impeded by degeneration of the root system and insufficient replacement of conductive sapwood during the period of infestation.

11.4 The survival of eucalypt populations and dieback

The following discussion assumes that dieback in Tableland areas occurs in discrete periods (e.g. the 1970s) followed by periods of recovery (e.g. the early 1980s). Several points that were discussed in Section 11.1 and 11.2 are vital for assessment of the capacity of eucalypts to survive periods of dieback:

1. Moribund or overmature eucalypts do not produce seed, and even in healthy trees new crops of seed are not produced every year.
2. The seeds of the majority of eucalypts (*Symphyomyrtus*) do not remain on the tree for more than about one year, and storage of seed in the soil appears to be limited (though this is not certain).

3. Seeds are only dispersed in the immediate vicinity of the tree, so areas devoid of trees are generally not recolonized.
4. With the possible exception of skeletal soils some form of disturbance is generally required for high recruitment rates of seedlings.
5. The recruitment of seedlings in woodlands appears to be infrequent and affected by seasonal factors.
6. Establishment of seedlings and the development of saplings is generally not possible unless the seedlings are protected from livestock or the stocking rates are low.
7. Once established, juvenile eucalypts are able to persist for extended periods and to survive stresses such as destruction of their aerial parts and severe moisture deficits, while retaining the capacity to develop into saplings when the conditions for growth become optimal.
8. Saplings are more vulnerable to mortality than mature trees and must develop for many years before they become reproductively active.

From these points it is apparent that lignotuberous advanced growth is critical for the survival of eucalypt populations through periods of dieback. When dieback begins

to affect tree vigour then the recruitment of new seedlings is prevented. In the absence of lignotuberous advanced growth, if a large proportion of the trees is killed the lack of dispersal of seeds from the surviving trees would limit the recolonization of the site. Where lignotuberous advanced growth is present protection of juvenile eucalypts from livestock is necessary for some time following the period of dieback to enable the juvenile eucalypts to develop into saplings. Even then the survival of the eucalypt population is not assured if there is another period of dieback before the trees have reached reproductive maturity and successfully replaced the population of lignotuberous seedlings. Eucalypts (particularly *E. nova-anglica*) have already been eliminated from some localities where lignotuberous advanced growth had been destroyed (see Section 3.5). Though there are Tablelands areas where there are sufficient vigorous trees to facilitate the regeneration of new seedlings from natural seedfall, management techniques to ensure the successful recruitment of new seedlings have not been fully worked out for the local conditions.

CHAPTER 12 SYNTHESIS: THE PROCESS OF DIEBACK

Stress becomes critical to the survival of a tree when it reaches a level that interferes with the functioning of the tree as an integrated organism. To describe possible breakdowns in the functioning of a tree it is convenient to divide the tree into discrete functional systems (see Horsfall and Cowling, 1978). Functions which need to be successfully carried out in every part of the tree are: (1) supply of photosynthates (energy); (2) supply of water; (3) supply of mineral nutrients; (4) maintenance of structural integrity; (5) defence against invasion by foreign organisms; and (6) hormonal regulation. Hormonal regulation, if successful, organises the growth and development of the tree in a manner that allows optimal achievement of the other functions. Successful reproduction is also necessary for the long-term survival of the species, but not all parts of the tree, nor even all individuals, need to reproduce.

12.1 The determinants of injury

Defoliating insects, especially paropsine and scarabaeid beetles, are the most obvious stressing agents of rural eucalypts (Sections 2.2, 4.3, 4.4). Artificial defoliation experiments have shown that excessive defoliation can induce: (a) carbohydrate starvation, (b) increased susceptibility to fungal root pathogens (Section 5.2), and (c) disfunction of growth regulation (in ash type eucalypts). Damage of terminal buds (e.g. by paropsine beetles) retards the replacement of

leaves, aggravating the damage due to defoliation. Though the activities of insects could account for the intensity of dieback and both the temporal and spatial patterns of its incidence, the central importance of the role of insects in the syndrome has not been proven beyond doubt (Section 5.4).

No strong microbial pathogens have been found in association with declining trees, but, given the limited scope of the pathological investigations carried out as part of this study, it is not yet possible to rule out the possibility of a strong pathogen being found in the future. Weak fungal pathogens, such as *Phytophthora cryptogea*, might place some stress on trees under some circumstances (Section 6.3) though there is no evidence of this actually occurring in the field (Section 4.4). Wood decay fungi and connective tissue feeding insects are able to colonize moribund trees, thereby contributing to the process of senescence.

It is unlikely that drought-induced damage has severely affected more than a small proportion of woodland trees (Sections 2.2, 9.2), and the proportion of trees that could have been adversely affected by waterlogging is also probably relatively small (Sections 3.5, 9.2). However, most eucalypts in the process of dying have some intact leaves that wilt on the tree - so water stress might to be critical in the final stages of tree decline (Section 2.2).

The supply of mineral nutrients does not appear to be sufficiently critical to cause visible deficiency symptoms in the great majority of eucalypts. However, it is likely that the supply of nutrients is a factor limiting the growth of most trees (Chapter 10).

The combination of tree morbidity and enhanced pasture growth (due to pasture improvement practices) could limit both the supply of water (Section 9.3) and the supply of mineral nutrients (Section 10.4) to trees. The allelopathic effects of the pasture plants have not been quantified (Section 6.3).

Other factors have contributed to the decline of individual trees or to the decline of trees in individual localities. These factors include: infestation by mistletoes (Section 6.6), old age (Sections 11.2, 11.3), damage attributable to human activity (Sections 3.2 to 3.5), windthrow and other injuries caused by wind (Section 7.2), hail (Section 7.3), frost (Section 7.1), girdling by cattle (Section 8.1), and possibly salt toxicity (Section 10.2).

12.2 The dieback process

On the basis of the information available it appears likely that excessive rates of defoliation by insects has been the major form of stress responsible for the development of dieback. Defoliation has major effects on both the production and available resources of photosynthates (Section 5.2); the quantities of nutrients stored in the tree

are also reduced (Section 10.4). Thus the demand for both nutrients and photosynthates is increased.

It appears that in the absence of excessive defoliation or other unusual stressing factors most mature eucalypts growing in areas that became affected by eucalypt dieback had supplies of water and mineral nutrients that were adequate for survival. It is also probable that only weak fungal pathogens were present and that a vigorous tree would be able to restrict the damage induced by these pathogens.

Fig. 12.1 illustrates the effect of defoliation on the flow of photosynthates within a tree. For simplicity of presentation, the system is divided into 3 component subsystems: foliage, secondary tissue, and primary roots; the reproductive system has been excluded. All the energy input is from photosynthesis. The total primary production of a tree is influenced by the environmental conditions, including: temperature, availability of water and mineral nutrients, and wind. The flow of photosynthates is also linked with the successful operation of the other functional systems. Trees in an extreme environment have difficulty maintaining a carbon-balance even in the absence of defoliation (Tranquillini, 1979). A thorough analysis of the effects of given rates of defoliation on plants requires a detailed understanding of the plants' productivity in the environment in which they grow (e.g. see Fetcher, 1981). It is probable that environmental changes (especially those associated with clearing, see Chapter 7) have affected the

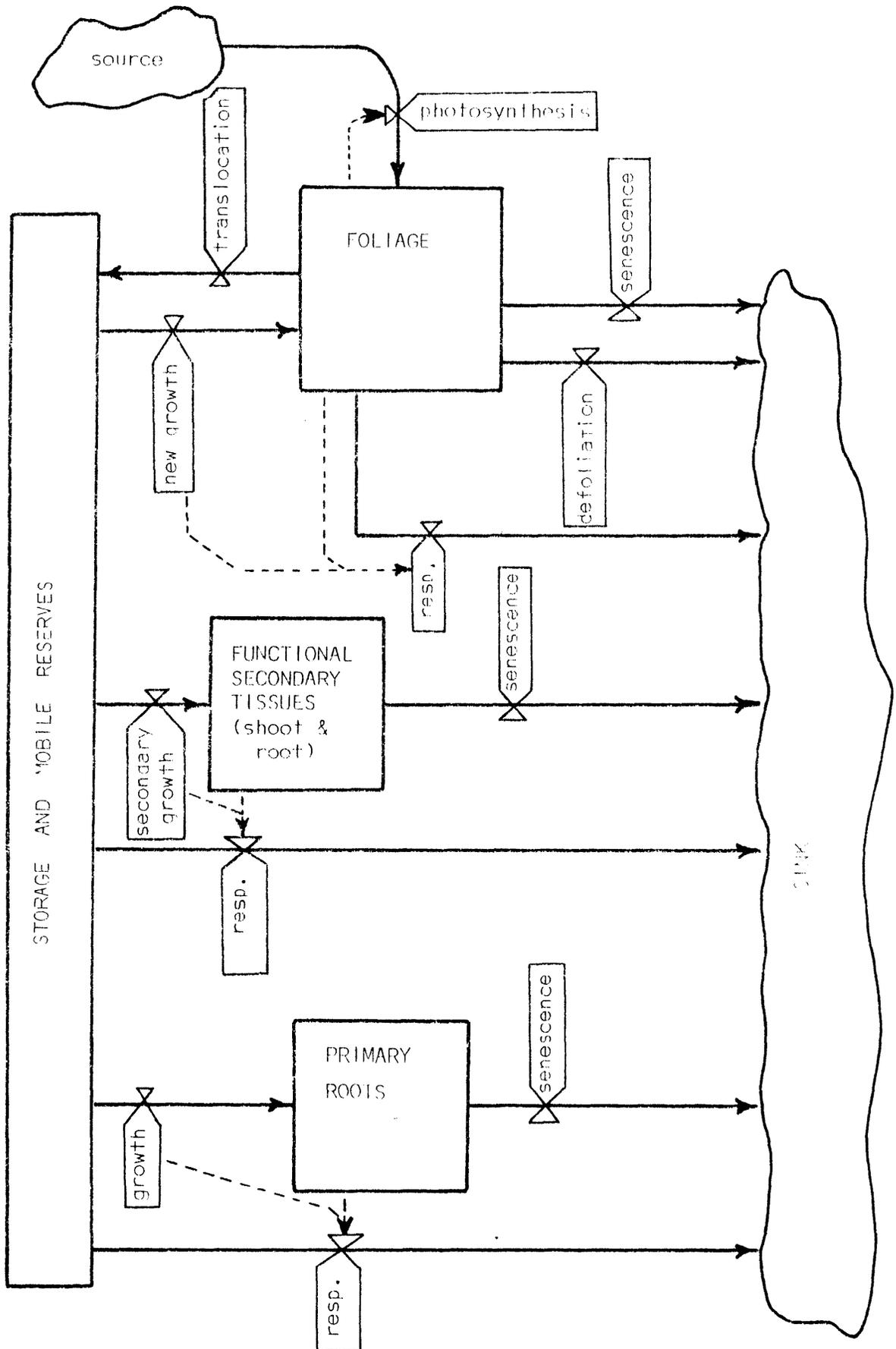


Figure 12.1 A simplified model of the flow of photosynthates in a eucalypt. Feed back mechanisms controlling senescence and growth have been excluded for simplicity (see text for details). Solid lines indicate material flows, dotted lines indicate flow of information.

productivity of eucalypts on the Tablelands. However, for simplicity, the flow diagram (Fig 12.1) only considers the role of defoliation in a constant environment.

Respiration presents a continuous drain on the supply of photosynthates and (ignoring temperature effects) the rate of respiration is related to the amount of living tissue within each component of the tree. Newly-formed meristematic tissue respire more than mature tissue (so respiration can be considered to be proportional to surface area rather than volume). Estimates of the proportion of gross primary production used for respiration vary from 33% in an 8 year old apple tree to 58% in 14 year old lobboly pine, while older trees probably use a greater proportion of energy in respiration (Kramer and Kozlowski, 1979). Growth is discontinuous and is regulated by hormonal links between the 3 subsystems and by the supply of resources. The rates of senescence are partly predetermined by ageing processes, but may be altered by environmental factors or by hormonal regulation. The immediate response to defoliation is compensatory growth of new foliage (Section 5.2), while root growth and woody growth are restricted, apparently by hormonal action (Kozlowski, 1969). Compensatory growth usually facilitates rapid replacement of the crown. However, if defoliation continues to be excessive for an extended period then the reduced replacement of functional roots, and (at a later date) the reduced replacement of secondary connective tissue, will limit the supply of water and mineral nutrients

to the foliage. This is additional to the increased demand for mineral nutrients that is directly attributable to replacement of lost foliage (Section 10.4). There is a constant, hormonally mediated readjustment of root/conductive tissue/shoot relationships.

If the total primary production of the tree is less than the losses (senescence + defoliation + respiration) then the loss of tissue (foliage, absorptive roots and connective tissue) will exceed its replacement, and the net reserves of photosynthates will decrease. If this net reduction of living matter continues then the ratio of assimilatory surfaces to respiring surfaces will decrease, further compounding the negative energy balance (cf. Section 11.3).

The senescence of ageing branches that have ceased to function in an efficient manner (and are not net exporters of photosynthates) is a natural feature of eucalypt growth habits (Jacobs, 1955). Assuming that growth regulation processes are still functioning in a manner optimal for the survival of the organism, then induction of the senescence of the limbs (and roots) that are functioning least efficiently could restore the balance between production and consumption. A process such as this appears to actually occur in declining eucalypts (Section 2.2).

If the simultaneous senescence of a large number of roots and branches is not associated with efficient compartmentalization of decay then the tree may be subject to

penetration by fungal and other pathogens (Sections 2.3, 6.1).

If excessive defoliation (or insufficient production) continues then the life-support system ultimately collapses. In eucalypts that are severely affected by dieback the form of the final collapse of the life-support system probably varies. Possible disfunctions include: carbohydrate starvation (Clark et al, 1981); inability to cope with increasing moisture stress (Section 9.4); invasion by wood rotting organisms (e.g. as in *Eucalyptus bridgesiana*, Section 2.3); damage by insects feeding on connective tissue; and breakdowns in hormonal regulation that may involve the accumulation of growth inhibitors (Section 5.2).

The interactions between the functional processes are important, e.g. sudden water stress or the presence of weak fungal pathogens could kill a tree that would otherwise survive.

It is worth noting that the process of decline is not greatly altered if the type of injury leading to decline involves chronic destruction of primary roots (Hepting, 1945; see Section 5.2). The replacement of the lost roots drains part of the tree's reserves of photosynthates and the tree's productivity is affected by the reduced capacity of damaged roots to supply resources to the foliage. Such interactions partly explain the similar patterns of decline shown by eucalypts affected by various types of chronic injuries (see Section 1.2).

PART 3

THE UNDERLYING PROBLEM

CHAPTER 13 POSSIBLE REASONS FOR INSECT OUTBREAKS

Here it is assumed that the observed levels of defoliation during the development of dieback (Section 5.3) were due to increased insect abundance rather than decreased leaf replacement and that eucalypt-grazing insects were of critical importance in the syndrome (see Chapter 12 for a discussion).

Numerous insect species appear to be involved in defoliation of eucalypts on the Northern Tablelands (see Table 2.2.1); all being indigenous. There are several introductory reviews describing the major groups of insect pests of eucalypts (Neumann and Marks, 1976; Hadlington and Johnson, 1977; Carne and Taylor, 1978). Near Armidale, chrysomelids appeared to be the most significant group of insect feeders on saplings of *Eucalyptus viminalis*, *E. caliginosa* and *Angophora floribunda* in the summer of 1979-80; several species were involved (S.C. Cairns, unpublished). Seasonal activity of insects varies, with chrysomelids apparently important from spring to autumn, scarabaeids in summer, leaf skeletonizers in late summer and winter; and sawflies in winter. No systematic study has been undertaken to determine the distribution of eucalypt-grazing insects in the region but it is probable that the relative importance of particular insect groups varies over the region and with time.

The biology of most of the major groups of insects involved is well understood. Scarabaeids have been studied in detail on the Northern Tablelands (e.g. Davidson et al., 1979) and records from a light trap in the CSIRO Research Station at Chiswick have been kept since 1962-63 (Roberts et al., 1982a). Scarabaeids differ from other eucalypt-grazing insects in that their larvae feed on roots of pasture plants and soil organic matter (Davidson and Roberts, 1966) and only the adults of some species feed on eucalypt leaves. The eucalypt-grazing scarabaeids include Christmas beetles, *Anoplognathus* spp., and smaller *Sericestis* spp. (Roberts et al., 1979). Other insect groups which have been intensively studied include: chrysomelids (Carne, 1966; Greaves, 1966; Steven, 1973; Tanton and Khan, 1978), gregarious sawflies (Carne, 1969), psyllids (Clark, 1964; Clark and Dallwitz, 1974), scale insects (Patel, 1971) and leaf skeletonizers (Campbell, 1962; Morgan and Cobbinah, 1977).

Increased insect activity in rural areas during recent times may be associated with:

- i) changes to the habitat of the defoliating insects;
- ii) decreased effectiveness of biological control;
- iii) changes to the food quality of foliage; and/or
- iv) the prevalence of weather conditions that favour breeding and survival.

13.1 Changes to the habitat of defoliating insects

Prevalence of eucalypt dieback is usually associated with pasture improvement and the gross environmental changes which accompany it (see Section 3.5). Direct effects of these changes on insect abundance would be expected to be most readily apparent in insects with life stages separated from the tree. Scarabaeids are the most significant example of foliage-feeding insects that do not feed on eucalypts for their entire life cycle.

Jacobs (1955) warned that foliage-eating scarabaeids were likely to become a problem when the relative proportion of trees declined as a result of clearing. In addition, Davidson et al. (1979) stated that it was irrefutable that the total population of scarabaeids had increased since the 1950s on the Northern Tablelands as a result of pasture improvement. Factors favouring the growth of scarabaeid larvae in improved pastures included: the greater availability of grass roots, increased soil organic matter and a greater population of micro-organisms in the soil. However, during dry spells pastures sown to improved grasses tended to dry out more than native pastures, causing significant mortality to scarabaeid larvae. The larvae are also sensitive to high soil temperatures: temperatures in excess of 32.5 degrees C were found to cause extensive mortality. Under drought conditions, when soil moisture is critical and improved pastures are closely cropped allowing soil temperatures to increase, the normal trend of

scarabaeids being more abundant beneath improved pastures may be reversed. In these cases, native pastures carry greater populations of scarabaeids than improved pastures.

There is some evidence that the relative abundance of particular scarabaeid species has changed in recent years. About 7500 *Anoplognathus porosus* were caught in the light trap at Chiswick during the 1962/3 season, but only a few hundred were caught during 1973/9 and 1979/80 while the abundance of some non-tree-feeding scarabaeids and *Sericestis geminata* had increased (R.J. Roberts, unpublished data; Roberts et al, 1982a). The relative decline of the Christmas beetle at Chiswick may be partly related to reduced tree cover. Trenbath and Smith (1981) suggested that where the relative proportion of trees to pasture fell below a critical level, the population of scarabaeids would decrease. Their model is based on the untested assumption that eucalypt-grazing scarabaeids are obligatorily dependent on eucalypts for reproduction. A reduction in the ratio of eucalypt-grazing to non-feeding scarabaeids has been observed amongst the larger scarabaeids in totally cleared areas. Yet at least some of the smaller foliage-feeding scarabaeids, *Sericestis* spp., appear to be able to reproduce in the absence of eucalypts and there is a trend towards dominance by smaller scarabaeids where trees are scarce (Roberts et al, 1982b). However, severe damage to eucalypts by *Sericestis* has been noted (Section 4.3). If these foliage-feeding scarabaeids can reproduce in the

absence of eucalypts it is possible that some semi-cleared woodlands are supporting greater populations of scarabaeids than the trees can sustain. Hence it is uncertain whether the system could eventually equilibriate in favour of the eucalypts.

Many insects that feed exclusively on eucalypt foliage have resting stages during which the insect leaves the tree to pupate or to over-winter, e.g. chrysomelids (Carne, 1966) and the sawfly, *Perga affinis affinis* Kirby (Carne, 1969). Small changes in the availability of shelter or altered soil strength could easily affect insect survival. For example, Carne (1969) found that extensive mortality of final instar sawfly larvae occurred during dry springs when soils became harder and larvae found it difficult to burrow and find protected sites for pupation. Basic questions about how pasture improvement has affected the availability of protected sites for the resting stages of insects remain to be answered.

There has recently been some speculation suggesting that the greater availability of light in semi-cleared woodlands stimulates the activity of insects such as chrysomelids (Old et al., 1981). However, the influence of increased light and other micro-climatic changes within tree canopies that have resulted from clearing need to be critically evaluated before these speculations can be substantiated.

13.2 Decreased effectiveness of biological control

There is substantial evidence suggesting the importance of predation (including parasitism) in the regulation of insect populations. Lawton and McNeill (1979) categorized the evidence into (a) circumstantial evidence based on the results of attempts to control insects by the introduction of natural enemies, and (b) evidence from the life-tables of insects that have been intensively studied. DeBach (1974) listed 120 attempts at biological control of insects. At least a third of these were described as completely successful, with varying degrees of success in other attempts. Thus, at least in some instances, biological agents appear critical in the regulation of insect populations.

A review by Podoler and Rogers (1975) draws attention to the prominence of natural enemies in life-tables. Detailed investigations of the population dynamics of 13 herbivorous insects were reported in their review. In 5 cases natural enemies were the key-factor influencing populations. In other cases natural enemies were usually responsible for at least some mortality of the insects and clear-cut key-factors unrelated to natural enemies were only evident in 4 cases.

Natural enemies of insects usually respond to fluctuations in the prey's population. This sensitivity to prey density provides a mechanism by which natural enemies

regulate the insect's population (Stubbs, 1977; May, 1982).

Clearing and other changes within woodland ecosystems associated with agricultural development have drastically affected many of the parasites and predators of eucalypt-grazing insects. To facilitate this discussion, the natural enemies of insects that feed on eucalypt foliage are classified into: (a) vertebrate predators, (b) invertebrate predators, and (c) invertebrate parasites. Disease-inducing agents, including viruses, fungi, bacteria and protozoa, can also affect insect populations but they are not included in this discussion since there is as yet no evidence that the incidence of insect-disease has been affected by agricultural development.

(a) Vertebrate predators

Birds are the most obvious predators of insects. Ford (1981) reviewed the available information concerning the capacity of birds to control the major eucalypt-grazing insects. There was no direct proof that birds influence populations of eucalypt-grazing insects significantly, but the available information suggested that birds have the basic requirements necessary to exert a controlling influence on insects. Firstly, a variety of birds prey on the major eucalypt-grazing insects; and secondly, birds are generally opportunistic feeders and will concentrate on a particular food which is abundant. Thus, although bird populations are relatively stable in comparison to insect

populations, birds are able to converge on an area (within their range) that has a greater than usual abundance of insects. Otvos (1979), in a review chiefly concerned with bird-insect relations in the Northern Hemisphere, concluded that regulation of insect populations by birds was likely to be most effective when insect populations were small.

The relative stability of bird populations on the Northern Tablelands between seasons (Ford and Bell, 1982) makes it likely that the impact of birds on insect populations (excluding scarabaeids) would be greatest during the winter months when the populations of over-wintering insects are low.

After an extensive study of the psyllid, *Cardiaspina albitextura*, Clark (1984) concluded that density dependent feeding by birds was a major factor in population regulation. In addition, P.B. Carne (unpublished) suggested that birds were probably the major predators of adult paropsine beetles.

Ford and Bell (1982) found that bird densities on 4 sites near Armidale appeared to be strongly associated with the density of remaining trees. Bird densities varied from about 22 birds/ha in Eastwood State Forest (200-300 trees/ha), to 10 birds/ha on a site with slightly over 100 trees/ha, and about 2 birds/ha on a site with severe eucalypt dieback and few remaining live trees (less than 100 trees/ha). A site consisting of open grassland contained

less than one bird/ha. Reduced tree density was associated with a dramatic reduction in species diversity. Small insectivorous birds and honey eaters appeared to be more seriously affected by reduced tree density than other species (Ford and Bell, 1982).

The most common small bird remaining in the intermediate site (10 birds/ha), the Striated Pardalote (*Pardalotus striatus*), used hollows in the standing trees as nesting sites. Small insectivorous birds were virtually absent from the sites with fewest trees and larger, predominately ground-feeding birds, such as the Australian Magpie and Eastern Rosella, were most common amongst the remaining species. The few trees still standing appeared to be important as nesting sites and roosting platforms for the remaining birds. The Noisy Miners and Gray Butcherbirds, which only occurred in the site with few remaining live trees, could have actively excluded smaller birds from that site.

The major trends reported in this study suggest that, since the Northern Tablelands was formerly mainly tree-covered but is now predominately cleared (see Section 3.4), the species diversity and density of birds has almost certainly been seriously depleted in most areas. H.A. Ford (unpublished data) has also noted that bird populations appear to be adversely affected by prolonged dry periods.

A range of native mammals also feed on insects. These mammals include: bandicoots, marsupial mice (*Antechinus* spp.), other dasyurids, various rodents, bats, gliders and occasionally possums.

Records indicate that there have been dramatic changes in the abundance of native mammals on the Northern Tablelands (Rolls, 1969; Jarman and Johnson, 1973), though most records refer to species which are potential pests. Cameron (1975) reported the changes in the wildlife observed since the establishment of his family's properties in the Waterloo Valley near Glen Innes during the 1860's. By 1930 kangaroo rats, koalas, tiger cats, dingoes and native cats had completely disappeared from the area and possums and gliders had become very rare on the property. Other animals such as bandicoots have also completely disappeared from most parts of the Tablelands.

Sugar gliders in Victoria were found to feed on insects during summer and on plant exudates (mainly wattle gum, eucalypt sap and eucalypt nectar) during the winter months when insects were less common (Smith, 1982). Such behaviour could allow sugar gliders to remain sufficiently abundant to influence insect populations. Surviving populations of sugar gliders still persist on the Tablelands (A.P. Smith, pers. comm.). The Yellow-footed Antechinus (*A. flavipes*), is also predominately arboreal (Ride, 1970), but it is more common in dry sclerophyll forest than in woodland (Dickman, 1980).

Ground-feeding insectivores may also be of significance. Blackhall (1979) found that the Eastern Native Cat, *Dasyurus viverrinas* (Shaw), predominately a ground feeder, consumes the chrysomelid *Paropsis dilatata*. The insect is more frequently consumed in spring and winter than in summer even though only remnants of the population would persist through winter, in leaf-litter and under bark. It is likely that other small mammals also consume over-wintering chrysomelids. If predation significantly reduced the quantity of adult beetles^{*} which survived winter then the population buildup during spring would be greatly retarded.

Amongst ground-feeding mammals, long-nosed bandicoots consume quantities of scarabaeid larvae (Ride, 1970) while echidnas consume scarabaeid larvae and other beetles in addition to their principle diet of ants and termites (Griffiths, 1968).

H.F. Heatwole and B. Crome (unpublished report) investigated the potential of lizards to regulate eucalypt-grazing insects. They found that the lizards were predominately ground-feeding rather than arboreal; ants appeared to be a major component of their diet and they did not consume large quantities of eucalypt defoliating insects.

(b) Invertebrate predators

* &pupae

There is a diverse range of invertebrate predators that attack insects which feed on eucalypts. These include spiders, centipedes, mites, ants, lacewings and predatory bugs and beetles. Coccinellids (Coleoptera) and pentatomoid bugs are the most prominent predators of eggs and larvae of *Paropsis atomaria* (Chrysomellidae) (Tanton and Khan, 1976). Carne (1966) found that mortality of *P. atomaria* eggs attributable to predation ranged between 51 and 74% in a study near Canberra during 1961/2. Mathews (1976) reported that large numbers of predatory insects, particularly carabid beetles, shelter under the exfoliating bark of eucalypts. Most of these insects feed at night and it is likely that they consume phytophagous insects.

There is a lack of information concerning long term changes in the populations of predatory insects and whether their abundance is influenced by landuse.

(c) Invertebrate parasites

Parasites may cause significant mortality in foliage-insect populations. Some degree of parasitism is evident in most species of foliage-feeding insects that have been studied including: chrysomelids (Tanton and Khan, 1976), scarabaeids (Ridsdill Smith, 1971), sawflies (Carne, 1968) psyllids (Clark, 1964, 1964a; Clark and Dallwitz, 1974) and the gum tree scale (Patel, 1971). Most parasites are included in the orders Hymenoptera and Diptera but there is a large number of parasitic species within these orders;

for example, Riek (1962) classified 53 species of parasites and hyperparasites of psyllids within the genus *Psyllaephagus* (Encyrtidae: Hymenoptera) as well as mentioning 6 other genera which contained psyllid parasites.

The importance of parasites as mortality factors varies temporally, spatially and according to species: rates of parasitism of *Paropsis atomaria* of over 90% have been noted on the Northern Tablelands (A.J. Campbell, unpublished data). Ridsdill Smith (1970) noted that *Hemithynnus hyalinatus* a thynnid parasite of scarabaeids, was usually active within 200 metres of a source of nectar or a substitute carbohydrate such as manna. However, the rates at which it parasitizes scarabaeids is relatively low and there is no evidence to suggest that this thynnid has an important role in population regulation (Ridsdill Smith, 1971). It is likely that many other parasites have similar requirements for nectar or other plant exudates.

(d) Conclusions

Amongst vertebrates, it appears that birds and possibly mammals have some potential as regulators of insect populations. However, more work is needed to quantify their impact on insect populations. In contrast, the influence of invertebrate parasites and predators on the mortality rates of eucalypt-grazing insects has already been demonstrated. Invertebrate parasites and predators almost certainly reduce the buildup of insect populations during the season. Thus,

the development of conditions unfavourable to these parasites and predators could facilitate the buildup of insect infestations.

There have been substantial reductions in the density and species diversity of insectivorous birds and mammals in most parts of the Tablelands since the arrival of European settlers. Similar changes in the density and species diversity of invertebrate parasites and predators have not yet been demonstrated, but it is likely that at least some invertebrate predators and parasites have been affected by the changes which have affected vertebrates.

Factors responsible for reductions in predator control.

The factors responsible for reductions in the density and species diversity of vertebrate insectivores include: destruction of the animals' habitats, depletion of food reserves, and direct destruction of the animals. The habitats of many native mammals have been effectively destroyed by: clearing, displacement of tussock grasses by prostrate grasses, periodic overstocking, changes in the fire regime, and the intentional removal of shrubs (which provided shelter for rabbits). The availability of shelter, nesting sites, roosts and potential hiding places was reduced. The availability of food for animals which feed primarily on arboreal insects was restricted by the isolation of trees into small clumps or individuals. Supplementary sources of food (e.g. the supply of nectar

and fruit from native herbs and shrubs) were adversely affected by grazing management. Findings concerning the role of nectar in the distribution of thynnid wasps (Ridsill Smith, 1970) indicates that supplementary food sources are also necessary for invertebrate parasites. Shortages in the supply of nectar may be more critical than indicated by the distribution of trees and shrubs because flowering of shrubs within paddocks is reduced by browsing damage and, perhaps more importantly, during periods of dieback very few eucalypts flower (see Section 4.3).

Amplification of food shortages during the periods of drought may have been catastrophic to many species of vertebrate insectivores. So if vertebrate insectivores are important regulators of insect populations (during non-outbreak periods) the association of the 1965-6 drought (see Section 9.1) with insect infestations during the 1970s might have been more than coincidental.

Direct destruction may have been responsible for the decline of some insectivores. In the past some of the larger insectivores, such as bandicoots were intentionally hunted (Rolls, 1969). It is likely that large numbers of native animals have been killed by baits, primarily 1080 (sodium fluoroacetate) aimed at rabbits and dingoes. The destruction of smaller birds and mammals by feral cats may also be significant.

Simulation models of predator-prey interactions provide further insight into the decline of insectivores, and the decline of the effectiveness of biological control, in areas developed for pastoral production. A number of articles relating spatial heterogeneity of the environment to population stability have recently been published (Lawton and McNeill, 1979; Lomnicki, 1980; Stenseth, 1980; Pimm and Rosenzweig, 1981). A variety of simulation models predict that, where population dynamics are primarily regulated by predators (or parasites), reduced heterogeneity of the environment (i.e. reduced availability of hiding places for the prey) will enable the predator to deplete the prey's population to lower than usual levels. Consequently the predator's population will decline dramatically enabling resurgence of the prey's population to higher than normal levels. Spatial heterogeneity, in terms of measurable components such as plant species diversity, range of tree sizes, etc. is reduced in areas prone to eucalypt dieback (G. Morgan, unpublished data; Section 3.4). Any reduction in the population stability of eucalypt-grazing insects is more likely to lead to the development of a situation in which eucalypt-grazing insects reach a population level sufficient to damage eucalypts.

13.3 Changes in the food quality of foliage.

To assess the possibility that changes in the quality of foliage have influenced the development of insect outbreaks on the Tablelands it is necessary to determine:

(1) whether variations in food quality affect the population dynamics of the insects; and

(2) whether the food quality of foliage was likely to have improved in the periods during which insect population buildups occurred.

Factors affecting insects' nutritional intake.

The long co-existence of plants and foliage-feeding insects has resulted in the evolution of an array of barriers that restrict herbivory, while herbivores have evolved mechanisms for overcoming these barriers (Feeny, 1976; Harborne, 1978). This co-evolution has led to a large diversity of herbivores with specialized adaptations enabling them to survive on a restricted range of plants, and usually the diets of these herbivores are further restricted to specific parts of the plants. However, some barriers still reduce the availability of food to specialist herbivores that are feeding on the hosts to which they are adapted (Lawton and McNeill, 1979), and, even without these barriers, foliage is often a nutritionally inadequate foodsource (White, 1973).

Features limiting the nutritional value of leaves include: physical barriers such as thickness of the cuticle and leaf toughness; low availability of nitrogen; secondary metabolites that are directly toxic or inhibit digestibility; and insufficient water content (Edwards and Wratten, 1980; Scriber and Slanky, 1981).

The availability of nitrogen appears to be a critical factor limiting both the rates of insect development and the rate of survival (McNeill and Southwood, 1978; White, 1978). A variety of adaptations compensating for the general shortage of nitrogen can be found in insect herbivores. These adaptations include: facultative predation; the capacity to seek foliage likely to have a higher nitrogen content; adjustment of phenology synchronizing stages when the insects' demand for nitrogen are maximal with periods when nitrogen is most readily available from the tree; and adjustment of feeding rates to compensate for the low nitrogen concentrations (McNeill and Southwood, 1978). Where feeding rates have been preadjusted to compensate for the low nitrogen concentrations on the host, higher than normal concentrations of nitrogen in leaves may have no influence on insect growth rates or survival (Fox and Macauley, 1977).

There is a diversity of secondary metabolites that may affect potential herbivores. Feeny (1976) classified these agents into: (1) qualitative defense agents, which are directly toxic to most generalist herbivores but usually

innocuous to specialized herbivores possessing the metabolic apparatus for detoxification; and (2) quantitative agents, which act through decreasing the digestibility of plant tissue. Qualitative defences are predominant in ephemeral plants or ephemeral plant parts, while quantitative defences are predominant in plant tissues that are both abundant and long lived, e.g. the mature leaves of forest trees (Feeny, 1976; Swain, 1978). Feeny (1976) considered that this pattern was the result of quantitative defences being more difficult for specialist herbivores to circumvent. Swain (1978) suggested an alternative explanation: that qualitative defence agents are usually highly volatile aromatic compounds with a short half-life and that more stable quantitative defence agents (e.g. tannins) are probably more efficient in long-lived tissues.

The food quality of eucalypt leaves and insects. The applicability of the above generalizations to insects which feed on eucalypt foliage has only been experimentally tested for a few insects (see below). However, the importance of leaf age as a determinant of the food quality of eucalypt leaves is evident from many studies.

As leaf age increases: leaf toughness increases; concentration of nitrogen decreases (see Lamb, 1976; Journet and Cochrane, 1978); water content decreases; and the composition of secondary metabolites changes (Kramer and Kozlowski, 1979). Surprisingly, the concentrations of

phenolics in eucalypt leaves are just as high in newly formed leaves as in older leaves (Macauley and Fox, 1980).

Most eucalypt-grazing insects appear to be dependent on particular age classes of leaves. Adult chrysomelids (e.g. *Paropsis atomaria*) may survive on all age classes of leaves, but new leaves are essential for larval survival and oviposition is delayed until new shoot growth appears (Carne, 1966). Among the Tablelands scarabaeids, *Anoplognathus porosus* and *A. hirsutus* favour fully expanded leaves that formed during the preceding spring; they do not appreciably damage older leaves or leaves that are not fully expanded (personal observation; and see Carne et al, 1974). At least one species of psyllid, *Cardiaspina albitextura*, can develop on older leaves when fully developed new-season leaves are absent (Clark, 1963) but most of the species that have been studied favour fully developed new-season leaves (Clark and Dallwitz, 1974) and their survival rates are reduced if they are transposed to older leaves (Journet, 1980). In general, although different insect species vary in their leaf age preference, few insects actually prefer older leaves.

The first attempt to isolate the biochemical factors determining the food quality of eucalypt leaves was by Fox and Macauley (1977) who compared the growth rates of *Paropsis atomaria* (Chrysomelidae) on newly-formed leaves from 13 species of eucalypts. Growth rates and the efficiency of nitrogen use were positively correlated with

the concentrations of nitrogen. The concentrations of condensed tannins appeared to have no clearcut effects on larval growth or rates of food intake. However, the chemical nature of condensed tannins is likely to have varied between the species and the authors did not test the capacity of the tannins to precipitate proteins (cf. Martin and Martin, 1982).

Morrow and Fox (1980) also found that the growth rates of *P. atomaria* were more closely associated with leaf nitrogen concentrations than with concentrations of essential oils.

Miles et al (1982) carried out some further experiments on the effects of food quality on the growth of *P. atomaria*. They used only one species of host, *E. camaldulensis*, but subjected some of the plants to water stress. The leaves of the stressed plants had greater concentrations of amino acids (especially proline), greater concentrations of total nitrogen, smaller concentrations of phenolics, and a reduced water content. The growth rates of the chrysomelid were the same on both stressed and unstressed plants. They considered that the contrast between their result and Fox and Macauley (1977) was probably related to the (unusually) high nitrogen concentrations in the *E. camaldulensis* foliage [ranging between 1.8 and 4.4%; cf. a maximum of 1.85% in the foliage used by Fox and Macauley (1977)]. They inferred that nitrogen no longer limited insect growth. However, the relative differences in water content and other unmeasured

biochemical changes could have also accounted for the result.

Farr (1983) carried out a similar experiment, subjecting *E. camaldulensis* to waterlogging, drought and normal watering regimes, and using the gum leaf skeletonizer, *Uraba lugans* (another common defoliating insect on the Northern Tablelands), as the test animal. She found that although the growth rates and survival of the insects were unchanged, their potential fecundity (a factor not measured by Miles et al, 1982) was greater on both droughted and waterlogged plants.

Cobbinah et al (1982) attempted to identify some of the factors affecting insect (*U. lugans*) growth on various species of eucalypts by using artificial diets and adding extracts from eucalypt foliage or purified nutrients to assess the larval feeding responses. The factors responsible for food plant selection were retained in prepared leaf powder; extraction of organic fractions showed that the most unfavourable eucalypt tested, *E. platypus*, contained both feeding-inhibitors and substances that promoted feeding. The substances that were most clearly associated with positive feeding responses on artificial media were sucrose, fructose and ascorbic acid, though a number of other substances tested, e.g. most of the amino acids, acted synergistically with the stimulants. These experiments emphasise the complexity of feeding responses in insects.

Further work, also incorporating the use of artificial diets, to test the effects of nitrogen sources on the growth and development of *U. lugans* is in progress (J.D. Farr, unpublished).

Possible changes in the food quality of eucalypt foliage

The 3 factors most likely to be associated with changes in the food quality of foliage within the region are: (1) changes in the age structure of leaf populations; (2) the imposition of stress; and (3) changes in soil fertility status.

Chrysomelid larvae feed on new foliage and scarabaeid beetles feed on leaves of an intermediate age. Foliage more than one year old is unsuitable for either insect. Defoliation usually stimulates the production of new leaves, and the life-expectancy of leaves that have been damaged by insects is reduced (Section 5.2). Therefore, if insects which feed on young leaves cause severe defoliation during successive years then the older leaves will eventually senesce while few of the younger leaves are retained for a full 2-3 years. Thus the proportion of leaves susceptible to damage by the insects will increase.

The Ministerial Working Group (1979) surmised that during the period in which dieback became severe an annual sequence of insect infestations recurred: chrysomelids attacked the new flush of shoot growth in spring; scarabaeids damaged the remaining newly-formed leaves in

summer; and there was further damage of the replacement shoot growth by chrysomelids in autumn. Repetition of such a cycle would cause the average age of leaves to decline, and a greater proportion of the crown to be suitable food for the insects.

White (1969) suggested that outbreaks of eucalypt-grazing psyllids usually coincided with periods of moisture stress. He discussed evidence indicating that plants subjected to moisture stress usually have increased concentrations of nitrogenous compounds in solution within their tissues - and that increased concentrations of nitrogen should be favourable to insects. White supported this contention by constructing a "stress index" on the basis of differences between summer and winter rainfalls. Both of the *Cardiaspina* outbreaks that occurred in White's study area since the 1900s coincided with periods of "high stress" [though the first *Cardiaspina* outbreak apparently began before the period of "high stress" (Fig 1, White, 1969)]. White also found links between other reported psyllid outbreaks and "high stress" as measured by his index. Later White extended this hypothesis to explain outbreaks of some other animals (White, 1976).

Clark and Dallwitz (1974) examined the population dynamics of 4 species of psyllids with respect to White's hypothesis. They found that, although the quality of leaves as a foodsource appeared to be a critical determinant of psyllid abundance, high psyllid populations were associated

with favourable moisture conditions rather than the reverse. However, drought in the preceding year was associated with greater abundance of at least 2 of the species of psyllids. Clark and Daliwitz suggested that this trend might have been related to increased mineralization of nutrients after a dry spell (Simpson, 1962).

Recent findings, discussed in the preceding subsection, provide some evidence that the concentrations of nitrogen in leaves could influence the rates of increase of insect populations, and that both water-stress and water-logging could influence the populations of at least one species of insect via the host.

Other types of stresses which affect plants might also influence insect populations, e.g. Carne and Taylor (1978) reported that trees of *E. grandis* that were stressed by competing grasses were more likely to be attacked by the chrysomelid, *Chrysophtharta cloelia*. The stress was associated with changes in the composition and yield of essential oils.

The production of epicormics following various types of stress, including defoliation, might also influence the populations of some insects. Leaves derived from epicormic shoots are usually richer in nutrients than normal mature leaves (Section 10.4). Landsberg and Wylie (1983) found that foliage from trees affected by dieback was richer in nitrogen than foliage from adjacent trees. *U. lugans*

prefers to lay eggs on epicormic shoots on the lower crown of the host tree (Campbell, 1962). Such epicormic shoots are more prevalent in stressed trees. Stress might also stimulate defensive reactions in plants. A number of recent studies have shown that in some plants the concentrations of chemicals that interfere with potential herbivores are increased in response to defoliation (Haukioja, 1980; Schultz and Baldwin, 1982; Edwards and Wratten, 1983). In one case the observed changes appeared to be in response to defoliation of nearby plants (Baldwin and Schultz, 1983). The only evidence of such defensive responses to leaf damage in eucalypts is from the study by Miles et al (1982). They found that in well-watered plants at temperatures below 25 C, phenolic compounds increased and nitrogenous compounds decreased in damaged leaves, compared with undamaged leaves on the same plant.

The importance of predisposing stress as a factor influencing populations of leaf-feeding insects on the Northern Tablelands is unknown. There is no evidence that dry spells on the Tablelands have been associated with insect outbreaks, but periods of excessive precipitation might have resulted in some trees being stressed by waterlogging (Section 9.2). Stimulation of pasture growth during the wet spells might also have affected some trees. During the recent period of relatively severe dieback the most direct source of stress on trees growing in the Tablelands has probably been previous damage by the insects

themselves.

The buildup of soil fertility due to pasture improvements (Section 10.2) might have resulted in some changes in the concentrations of nutrients within eucalypt leaves, but this has not been confirmed. Cromer et al (1981) reported the results of an extensive investigation of the responses of seedling eucalypts, mainly *E. globulus*, to applications of various combinations of nitrogen, phosphorus and potassium fertilizers. They found a marked growth response to applications of nitrogen and/or phosphorus, but there was little change (and sometimes negative change) in the concentrations of nitrogen and phosphorus within leaves. However, the nitrogen:phosphorus ratio changed substantially, depending on the balance between the two elements.

Food quality and insect populations.

The review has provided an indication that increases in the food quality of foliage are likely to lead to: increased growth rates (reduced periods of development), increased survival rates, and/or increased fecundity. In a population not limited by density dependent factors, any of these increases will cause the rate of increase of the population (r) to increase. If the proportion of leaves accessible to insects is increased, e.g. by changes in the age structure of the leaf population, then the maximum sustainable population of insects (K) will be increased.

Mathematical models, although necessarily oversimplified, are of benefit in facilitating understanding of the behaviour of complex biological processes (May, 1974). Lawton and McNeill (1979) have reviewed dynamic models predicting the effects of changes in the quality and abundance of food (increases in r and K) on population regulation by density-dependent predators (or parasites). In brief, a range of mathematical models describing the population dynamics of host-predator systems with closely coupled interactions predict that the populations will either tend to a stable equilibrium or tend to a stable equilibrium cycle of a given magnitude. An increase in r would both increase the equilibrium population and decrease the stability of the system. Thus a stable equilibrium might become a stable equilibrium cycle and a stable cycle would become a stable cycle of increased amplitude, i.e. the population would tend to fluctuate to a greater extent. The models predict that relatively small changes in r could produce relatively large changes in the equilibrium population. The effects of changes in r on the population dynamics would be less when predator populations were not closely linked with the populations of the host (e.g. as in the case of generalist predators such as birds), but large increases in r would still increase the instability of the system. Lawton and McNeill (1979) suggested that an increase in K would simply lead to a proportional increase in the equilibrium population.

Not enough is known about changes in r resulting from nutritional factors, about the nature of host-predator interactions, or about the influence of complicating factors such as weather (see Section 13.4) to know to what extent the populations of eucalypt-grazing insects on the Tablelands are actually affected by these processes.

13.4 Weather conditions that favour insect breeding and survival

Weather is an important determinant of insect abundance (Andrewartha and Birch, 1954). Elements of weather directly affecting insects include: temperature, relative humidity, rainfall and, to a lesser extent, wind. The build up and decline of the populations of most insects on the Tablelands occur within the framework of the seasonal cycle, e.g. chrysomelids in the Canberra district generally overwinter as adults or pupae and have 2 generations per season (Carne, 1966). Particular conditions are often critical at particular stages during the seasonal cycle: early frosts in autumn are associated with high mortality of over-wintering insects; cold weather in spring both delays the growth of new leafy-shoots and suppresses the reproductive activity of adults (Carne, 1966).

The rate of chrysomelid development is increased at higher temperatures, but temperatures (and moisture conditions) also affect the host plant and the predators of the chrysomelids (Carne, 1966; P.B. Carne, unpublished).

Therefore, temperature-mediated increases in the intrinsic rate of population increase of the herbivore are likely to be compensated by temperature mediated increases in the rate of increase of density-dependent predators. However, (at least in the case of psyllids) the synchronized development of parasites and their prey can be affected by changes in temperature (Carne and Taylor, 1978). So, while prediction of some of the factors that would result in a population collapse of chrysomelids is possible, prediction of the optimal conditions that favour population increase is difficult.

There has been more success in the prediction of scarabaeid populations from weather (East, 1979; Davidson et al, 1979; Carne, 1981). The implications of weather as a factor complicating the influences of pasture improvements on scarabaeid populations has already been mentioned (Section 13.1). Moist, mild weather, especially in summer, generally favours scarabaeids (Davidson et al, 1979; Hassan, 1975). With the exception of one dry year (1974-5) the 1970s upto 1979 were relatively moist (Fig 9.2.1).

13.5 Conclusions

There are a number of factors likely to have contributed to the increases of insect populations in the period when dieback became severe. These factors can be classified into: (a) long term changes associated with changes in landuse, (b) the occurrence of weather favourable

to the breeding and survival of the major insect defoliators, and (c) exacerbating factors associated with the response of eucalypts to chronic defoliation.

Long term changes. From the review it appears that the effects of pasture improvement have been directly beneficial to scarabaeids, but the direct benefit of pasture improvement on other insects is questionable. However, there is some evidence of a long-term population shift amongst scarabaeids from a dominance of larger eucalypt-grazing scarabaeids to a dominance of smaller eucalypt-grazing scarabaeids and/or non-eucalypt feeders.

Both the diversity and abundance of vertebrate insectivores have been reduced since settlement, and the general abundance and diversity of invertebrate predators and parasites are also likely to have decreased. Factors responsible for this include: direct destruction (of vertebrates) by humans, removal of habitat and, in some cases, removal of alternative food sources, e.g. nectar-producing native shrubs and herbs.

Simulation models of insect population dynamics predict that decreased heterogeneity of the ecosystem, which has resulted from grazing management, could further reduce the effectiveness of biological control leading to abnormally high populations of insects, followed by population dramatic population declines. In addition, the equilibrium populations of the insects would be higher.

Weather. Weather affects populations of eucalypt-grazing insects both directly and indirectly. Adverse weather may cause substantial, or even catastrophic, mortality or may retard the growth and development of insects. Indirectly, weather can influence: (1) the condition and phenology of the host plant, (2) the activities and abundance of predatory or parasitic animals, and (3) the incidence of insect-diseases.

In the case of scarabaeids, although pasture improvement has improved their normal breeding conditions, it has also resulted in scarabaeids beneath improved pastures becoming more susceptible to extremes of weather such as drought. Relatively little is known about the overall influence of weather on chrysomelid populations on the Northern Tablelands.

Exacerbating factors. Three factors increase the likelihood of chronic outbreaks of defoliating insects continuing once the condition of eucalypts has been affected:

i) the average age of leaves on eucalypts will be reduced (and a greater proportion of young succulent leaves will be available);

ii) stress due to previous defoliation is likely to increase the nutritional value of foliage; and

iii) flowering of the eucalypts will be prevented and the production of nectar (required by parasitic insects and many

vertebrate insectivores) will cease.

Increased proportions of young leaves would increase the size of the maximum possible population of insects; increases in the nutritional quality of foliage would increase the intrinsic rate of growth of the population; and lack of nectar would decrease the effectiveness of biological control. The increase in the intrinsic rate of population growth could further destabilize population regulation by density-dependent predators.

It is possible, under some circumstances, eucalypts that have been defoliated could invoke defensive reactions against herbivorous insects, but this has not been confirmed.

Summary. Given the destabilizing effects of the changes to the eucalypt-pasture ecosystems of the Northern Tablelands since settlement, and the existence of factors that further destabilize the system during periods of stress, severe and protracted outbreaks of eucalypt-grazing insects are likely to recur. However, it is not yet possible to predict the likelihood of the recurrence of weather conditions necessary for the development of such protracted insect outbreaks.

CHAPTER 14 RECOMMENDATIONS

The aim of this chapter is to outline possible remedial actions that can be taken to reduce the incidence and impact of dieback, and to suggest some ideas for future research.

14.1 Possible remedial action

There are a number of measures that can be taken to reduce the likelihood of eucalypts being affected by dieback, or to assist the recovery of woodlands following dieback. The feasibility of such measures needs to be assessed in terms of the value landholders place on their eucalypts, and on the willingness of the community to financially subsidize actions that the farmer cannot afford. The tangible benefits of trees on farms have been discussed by Lade (1981) and Breckwoldt (1983), and the importance of eucalypts as a component of the habitat of fauna that contribute to the biological regulation of pasture pests has been emphasized by Loyn and Middleton (1981) and Davidson (1982, 1982a).

Avoidance of direct damage.

Trees that are chronically defoliated are less able to cope with additional injuries. Direct damage to eucalypts resulting from human activities have been responsible for substantial mortality of trees in many areas. Common, easily avoided injuries include:

- chemical injuries, e.g. from spraying weedicides too close to trees or in windy conditions;
- earthmoving that results in the burial or exposure of surface roots;
- mechanical injuries to the trunk, leaving exposed wounds that allow decay fungi to penetrate;
- damage to tree roots (and lignotuberous advanced growth) by cultivation
- injection of insecticides into trees in dry weather, or otherwise not according to instructions;
- constriction of tree trunks with wire; and
- girdling of trees by livestock.

The prevention of girdling of trees by livestock sometimes requires the physical separation of the livestock from trees. Other means of preventing this sort of damage (e.g. by the provision of food supplements) require investigation.

Assisting the recovery of trees.

Supplementing the supply of mineral nutrients to trees by the application of fertilizers is a standard method of assisting the recovery of trees after defoliation (Hadlington and Johnson, 1977). However, no tests on the efficacy of such treatments have been carried out on the Northern Tablelands.

Measures to keep the cover of pasture plants beneath trees to a minimum might also be expected to assist the recovery of trees (Section 10.4), but the relationship between tree vigour and grass growth has yet to be investigated.

Insecticides.

The technique of trunk injection was clearly designed as a last resort measure to save trees that are of special value. Both the high concentrations of toxic chemical handled during application and the labour involved in sealing injection wounds, restrict the general usefulness of the technique. It is the author's experience that some attempts by property managers to adapt the technique for extensive use have resulted in shortcuts that have either endangered the people applying the chemicals or damaged the trees. In addition, the side effects and longterm implications of the technique (e.g. on biological control) have not been fully investigated: tree injection is not a registered use of monocrotophos.

Facilitating regeneration.

The longterm survival of eucalypts in a particular area (with or without dieback) depends on the recruitment of seedlings and the survival of lignotuberous advanced growth. Lignotuberous advanced growth is critical to the survival of eucalypt populations during periods of severe dieback. Even during a period when few insects are grazing on eucalypts, the activity of livestock in the vicinity of the seedlings needs

to be minimal if the establishment of trees is to be successful. These aspects were discussed in Section 11.4.

Replanting.

Where lignotuberous advanced growth is not present, direct replanting of eucalypt seedlings is likely to be necessary. Techniques for establishing eucalypts are well known (Borough and Cameron, 1981).

Eucalypt species must be selected to suit the local conditions (e.g. soil fertility, drainage conditions, degree of exposure to frost). Eucalypts growing in unsuitable conditions have tended to be less tolerant of insect damage (personal observations).

In the absence of other information, the species of eucalypts that originally grew on the site could be expected to be a suitable choice of species. However, some sites have been altered, e.g. by clearing and pasture improvement, to the extent that the original species are no longer the most appropriate. Successful re-establishment of eucalypts is most likely to succeed where changes have not been so drastic, i.e. existing woodlots should be extended rather than isolated trees planted in exposed sites (see Section 7.1).

The investigation found that real differences exist in the preference of individual species of eucalypt-grazing insects for individual species of eucalypts. For example, some *Anoplognathus* were found to prefer feeding on *Eucalyptus*

blakelyi rather than *E. melliodora* (Section 4.3). However, with the exception of one study that mainly involved eucalypts not endemic to the area (Roberts et al, 1981), there has been no systematic attempt to ascertain the relative importance of the various species of eucalypt-grazing insects in the development of dieback on the Northern Tablelands.

In addition, total reliance on eucalypt species (or cultivars) resistant to the set of eucalypt-grazing insects that are currently abundant is dangerous because:

(a) the only long-term records available (Roberts et al, 1982a; see Section 13.1) indicate that there are important shifts in the relative abundance of different types of scarabs (which prefer to feed on different species of eucalypts); and

(b) reports of the relative incidence of dieback among different species of eucalypts indicate that it has varied with time (Section 3.4).

Both these changes have occurred in a time span much less than the life-expectancy of individual trees. Maintenance of genetic diversity in eucalypt populations is a necessary precaution against such changes. The importance of interspecific (and intraspecific) differences in resistance to particular insects should not be overstated, e.g. where dieback was intense all eucalypt species present were affected by dieback (see Section 3.5).

Encouragement of biological control.

Arguments were presented in Section 13.2 which suggested that the effectiveness of biological control might have been reduced since settlement by Europeans. The changes to the environment likely to have contributed to this reduction include: the loss of the habitat required by many animals that feed on insects, and a reduction in the spatial heterogeneity of woodland ecosystems (e.g. loss of diversity in the understorey, and a loss of diversity in tree sizes). The corollary of these arguments is that the effectiveness of biological control could be improved if these changes were reversed. In fact, by ecological engineering, it should be possible to sustain greater densities of predators and parasites than were present in pristine conditions.

At this stage, only the specific habitat requirements of some vertebrate insectivores have been studied and, with few exceptions, the specific habitat requirements of arthropod parasites and predators are not well known. However, adherence to a number of general principles should enable the provision of habitat that would support a wide variety of native animals, including arthropods, that contribute to biological control. These principles include:

1. maximizing the density of small trees and shrubs that provide cover for birds;

2. providing a range of native flowering plants that produce nectar during various times of the year; and
3. retaining features, such as standing dead trees (especially hollow trees) and fallen logs, which provide protection and cover for animals.

Enrichment planting of woodlots, accompanied by the restriction of livestock activity within the woodlots may be required to achieve these objectives. At this stage the possibility that eucalypt dieback could be prevented by such ecological engineering is only an untested hypothesis, but it is probably worth testing experimentally on a large scale.

14.2 Recommendations for further research

Eucalypt dieback is a periodic event that is difficult to study unless it is actually occurring. However, a major limitation to the progress in the development of an understanding of eucalypt dieback on the Northern Tablelands has been the lack of a detailed understanding of how woodland ecosystems function under normal conditions. Projects aimed at remedying these deficiencies would probably be more productive than another retrospective investigation of dieback. Particular deficiencies in basic knowledge that have caused difficulty in the understanding of dieback include:

- Lack of knowledge concerning the taxonomy and basic biology of many of the organisms, e.g. woodrotting fungi,

root-feeding insects and parasites and predators of eucalypt-insects, which live on or within eucalypts.

- Lack of knowledge of the nature of eucalypt-grass interactions, e.g. the nature of competition for water and mineral nutrients, and the significance of chemical interference.

- Lack of a sound understanding of how the populations of important eucalypt-grazing insects (e.g. chrysomelids) vary and how their population size is governed.

The literature review uncovered many other deficiencies in our knowledge of eucalypt woodlands.