

Weather, *Eucalyptus* Dieback in New England, and a General Hypothesis of the Cause of Dieback¹

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ABSTRACT: On the New England Tablelands in Australia between 1950 and 1980 very many eucalypts declined and died. This dieback was strongly correlated with a change in the pattern of rainfall. Starting from 1945, trees were more frequently exposed during the growing season to excess of soil moisture followed immediately by a shortage of water. Several species of *Eucalyptus* were affected, but those species which normally grow on poorly drained sites died first and continued, even on better sites, to be the species worst and most frequently affected. Declining trees were heavily and repeatedly attacked by defoliating insects. The same species had declined and died in the same localities approximately 100 years earlier. In this century declines and diebacks in other parts of Australia and overseas showed many similarities to that of eucalypts in New England and to each other. In particular, they have been associated with departure of rainfall from the norm and with insects and fungi attacking mostly old trees and species growing on harsh sites.

It is proposed here that the primary cause of diebacks and declines is a change in the pattern of rainfall which physiologically stresses trees via changes in the availability of water to their roots. Senescing and suppressed trees and those growing on sites most prone to be flooded and dried out will be first and worst affected. Defoliating and cambium-feeding insects and root-killing fungi are secondary, successfully attacking only stressed trees. They may hasten the decline and eventual death of badly stressed trees. Predators are more successful on stressed trees because more of their young survive when they feed on tissues made more nutritious by the release of nutrients during senescence induced by water stress. The extent to which they can attack successfully depends on the frequency and amplitude of stress the trees experience. Thus declines and diebacks are but one extreme of a continuum of response of trees to physiological stress; at the other extreme are small, short-lived increases of predators on one or a few trees. Outbreaks of insects and fungi of varying duration and severity fall between these two extremes.

NEW ENGLAND DIEBACK

The Locality

The New England Tablelands of New South Wales, Australia, are located between latitude 31.1° and 29.0° south and longitude 150.9° and 152.0° east. They extend for some 200 km south from the Queensland border,

following the main dividing range about 100 km inland from the east coast, and with a width of 80 to 100 km. Altitudes range from 800 to 1500 m above sea level. There is a predominantly summer rainfall (60% falls between October and March) with a strong gradient from east (approximately 1200 mm per annum) to west (600 mm per annum). Winters are cold with frosts from April to October. Soil moisture is lowest in late summer and highest during midwinter. Soils are diverse but generally low in nutrients.

The original vegetation varied from open

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grassy woodlands and heaths to wet sclerophyll and rain forests, forming communities closely related to soil water and nutrient supply, the east-west gradient of rainfall, and variations in temperature with altitude. Numerous species of *Eucalyptus* formed intergrading and varied associations within these communities.

From the time of European settlement in the early 1830s the tablelands were grazed by domestic stock and trees were being cleared. This clearing was accelerated after the Second World War so that by the 1960s a large proportion of the tablelands had been cleared and planted to improved pastures of imported grasses maintained by artificial fertilizers. Relatively few trees remained scattered in a park-like effect. But on the higher and rougher parts of the country not suited to intensive agriculture, considerable areas of often quite dense and relatively undisturbed stands of eucalypts remained.

Dieback of Eucalypts

The beginning and subsequent progress of dieback of eucalypts on these tablelands were never accurately documented—probably because the affected trees had no commercial forestry value and because farmers were still clearing trees as they developed the land. But serious dieback was certainly occurring by the mid-1950s, although largely dismissed as an unavoidable effect of development. Decline and death became extensive, especially on the flatter, poorly drained sites, regardless of soil type, and generally above 1000 m above sea level. By the early 1960s many trees were dead, and trees on the lower slopes were being affected. Peppermints (*E. nova-anglica*) on the flats, and to a lesser extent red gums (*E. blakelyi*) and yellow box (*E. melliodora*) on the slopes, were worst hit, but other species were showing symptoms of dieback.

By the mid-1960s fewer trees were dying and some less debilitated trees were showing signs of recovery. But after 1965 dieback became more widespread and severe than before, affecting many more species (especially *E. melliodora* and *E. bridgesiana*) on virtually all sites—decline and death were spreading further and further up the slopes

until the ridgetop associations of stringy barks (*E. caliginosa* and *E. laevopinea*) and white gum (*E. viminalis*) were affected. This process continued through the 1970s and became extreme by 1979 when 22% of all trees recorded as live in a survey in 1977 had died; *E. nova-anglica* with a death rate of 43%, and *E. blakelyi* with 33%, continued to be the worst-affected species (Clark et al. 1981). By 1982–1983, however, deaths were less frequent, remaining crowns were recovering, and a great deal of strong regrowth was apparent, mostly from lignotubers but also some seedlings (Richards 1984). This recovery (if such it is) continued so that by 1985 the countryside was beginning to resume a healthier look.

What is the cause of dieback? Theories are legion (see Marks and Idczak 1973; Old et al. 1981). For New England dieback, most observers implicitly or explicitly assumed that the cause stemmed from development of the pasturelands: “All [theories] depend, ultimately, on the concept that the presettlement equilibria between insect populations, their habitats and predators have been modified by the effects of land clearing . . . the introduction of exotic animals, and pasture improvement” (Mackay 1978: 19).

The major reasons for this assumption were twofold. First, dieback started, and continued to be most severe, on the cleared and improved pastureland, while areas of “undisturbed” forest remained relatively untouched. Second, the trees were heavily and repeatedly defoliated by insects. Therefore some activity or changed condition associated with development had apparently made the trees left as open woodland more susceptible to attack by insects than those left as dense stands, and the insects killed them.

Clark et al. (1981) showed the first—more severe dieback on cleared and improved land—to be due to “a species rather than a density affect.” *Eucalyptus nova-anglica* and *E. blakelyi* are just as heavily defoliated when growing in patches of forest as they are in the open woodland. But they are rare in patches of forest and predominate in open woodland. Other species which predominate in the forest are little defoliated even when they occasionally grow in open woodland. Furthermore, I

would add, the sites where these two susceptible species usually grow happen to be those preferred for clearing and development. The correlation is not cause and effect. (The second point, that of attack by defoliators—and fungi—being the primary cause of dieback, I discuss later in this paper.)

Weather and New England Dieback

The sites where dieback first developed, and was most severe, are flat, poorly drained, and most prone to become stressful to trees growing on them when there are sudden changes in soil moisture (Richards 1984). An excess of rainfall would waterlog the soil. If this happened during the growing season, extensive drowning of feeding roots would result. Should it be followed by a period of much less rain than usual, surviving roots would be unable to maintain an adequate supply of water to the trees. Either one of these events could place the trees under some degree of water stress; a sequence of *both* would produce serious imbalance of the trees' crown/root ratio. They would begin to die back, and at the same time they would become prone to successful attack by defoliating insects. Should such a sequence of events chance to happen over several years, and if the trees on these harsh sites were mostly overmature, continuing decline and ultimate death of many trees would follow. An examination of the recorded rainfall for a locality would reveal patterns which could produce such stressful changes in soil moisture—but only if rainfall for the critical alternating periods during the growing season is inspected, since total annual rainfall will mask such patterns.

To test this hypothesis, a stress index (White 1969) was calculated for Armidale, a rainfall station representative of the New England Tablelands. The stress index (SI) is a measure of the compounded stressful effect on trees of a period of unusually dry weather spanning the time when trees are actively growing. The wetter the wet period and the drier the dry period, the larger the stress index. The SI was calculated as follows.

First, the total rainfalls of the 4-month wet period at the beginning of the growing season

(November to February) and the 4-month dry period at the end of the growing season (April to July) for each year in the New England Tablelands were expressed as standard normal deviates of their long-term means (124 years). The wet and dry periods selected are those most likely to be biologically meaningful in terms of the phenology of eucalypts growing on the New England Tablelands. But calculations of an SI with months added or subtracted in these critical periods in the growing season, or which leave out a "buffer" month between the periods, continue to show the same major changes in the frequency of alternations of wet and dry—as, for example, the wet period of November to February and the dry period of March to June used by Tregonning and Fagg (1984); see the section on "Dieback of Eucalypts in Eastern Victoria" below.

Second, the signs of the standard normal deviates of the dry period were reversed. This means that wet periods wetter than their mean, and dry periods drier than their mean, are positive whereas wet periods drier than the mean, and dry periods wetter than the mean, are negative.

Third, for each of the 124 seasons the standard normal deviates for the wet period and the dry period following it were summed and plotted as an SI for the end of that season (for example, November 1983 to February 1984/April to July 1984, plotted over 1984). (See Figure 1.) On this figure, high positive values of the SI indicate a season of stressful weather; negative values signify an absence of stressful weather. Sudden and large changes from a negative to a positive SI are likely to represent more stressful conditions than lesser and gentler changes; a change from high to low values represents a decline or absence of stressful weather.

Fourth, there is likely to be some "lag" in the system—trees stressed in one season may not show obvious signs of stress until following seasons, and stressful conditions which persist over several successive seasons may result in cumulative and worsening stress of trees over a considerable period. For these reasons, smoothing the annual stress indices by taking running averages of various numbers of seasons may help to reveal longer periods

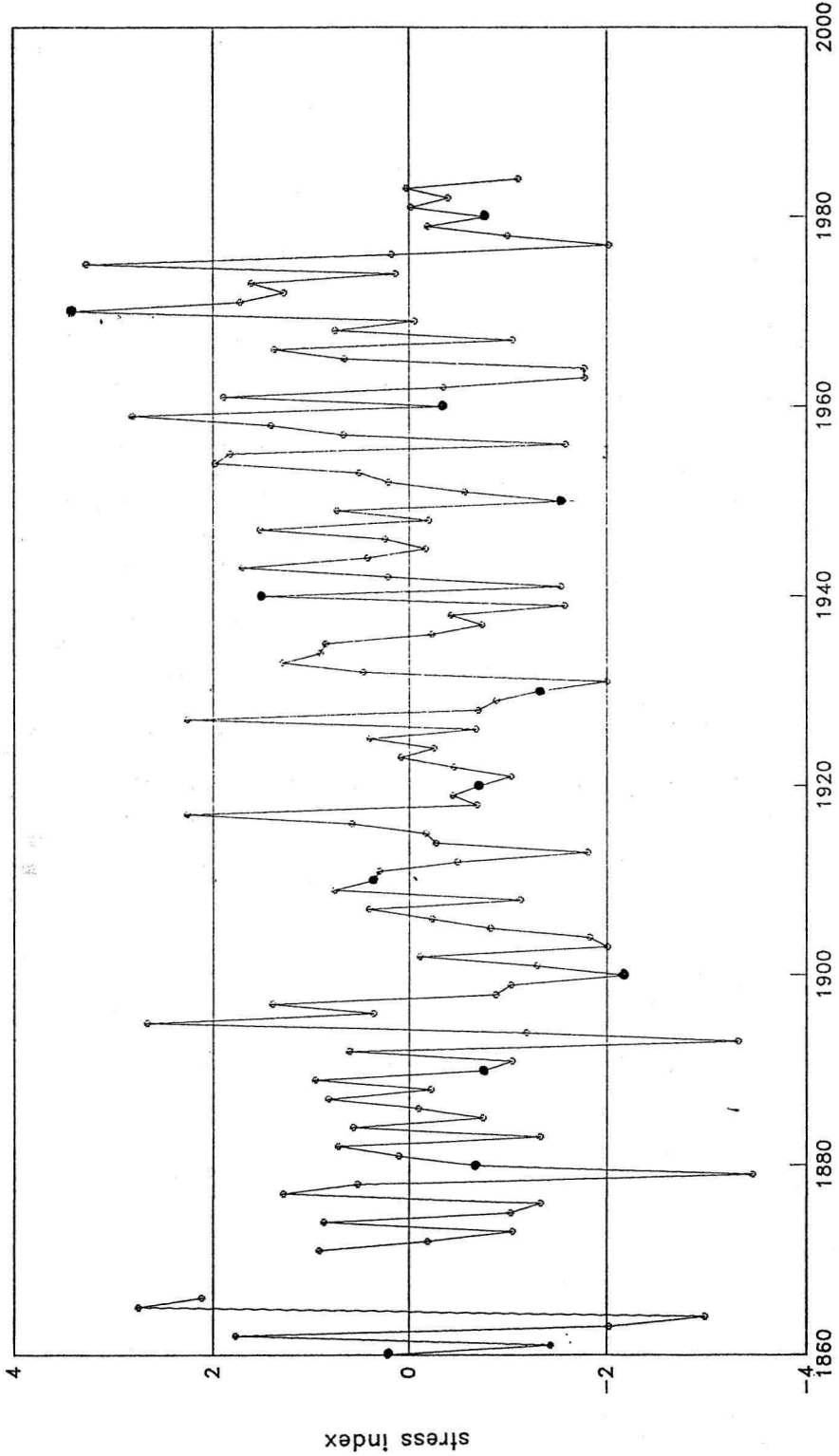


FIGURE 1. Annual stress indices for Armidale (1860-1984). The point for every tenth year is emphasized to aid in reading the graph. See text for the method of calculating stress indices from the deviations from their long-term means of a wet and a following dry period in each growing season.

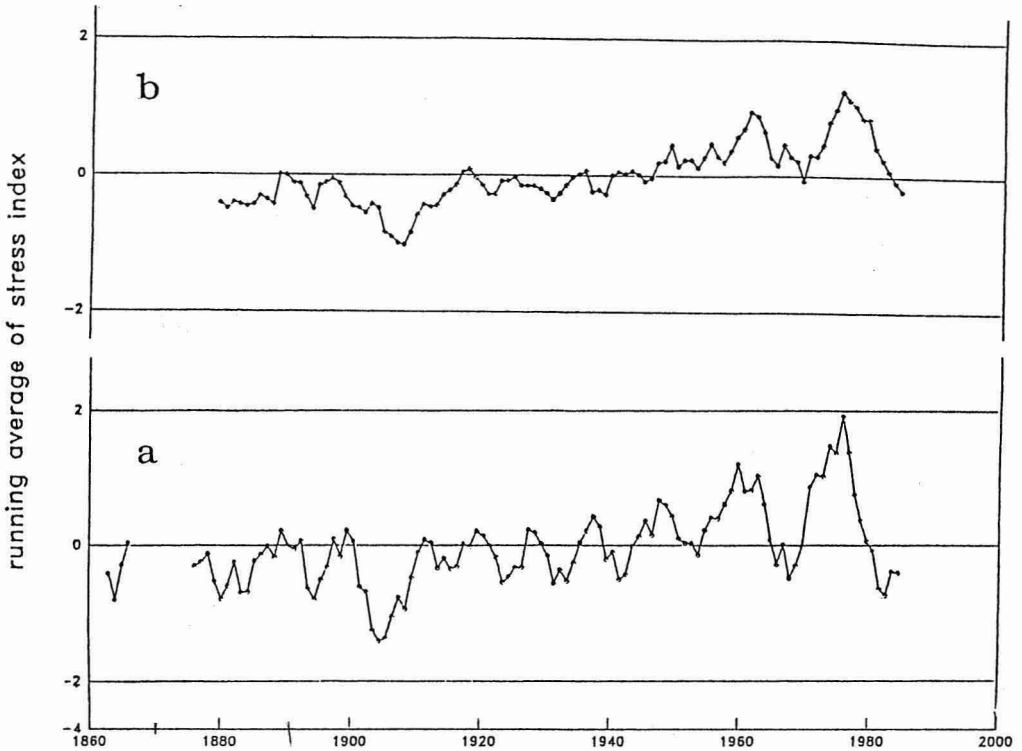


FIGURE 2. Running averages of stress indices for Armidale (1860–1984): (a) three-year running average; (b) ten-year running average. These running averages illustrate the long-term change toward increasingly stressful weather, starting in the 1920s, accentuating after 1945, and culminating in the two major surges of the 1950s and 1970s, which coincide with the extensive dieback of eucalypts on the tablelands.

of persistent stressful weather and long-term changes in patterns of weather (Figure 2).

This SI revealed that just such a sequence of events had occurred (Figure 1). The wet/dry pattern of rainfall in the growing season moved steeply from a nonstressful pattern in 1950 to a point in 1954 higher than it had been for the previous 26 years. The first dieback occurred at this time. The SI then dropped for the next 2 years, but it quickly returned to an even more stressful peak in 1959—the highest since 1895. During this time the extent and severity of dieback increased. But from this high peak in 1959 the SI fell in 1963–1964 to an even lower point than in 1950. The incidence of dieback also declined during this period; by 1965 many trees were refoliating and fewer trees were dying. Then from 1966 to 1967 the SI again became positive, reaching its highest recorded level in 1970. And dieback immediately and rapidly increased and

spread, becoming more extensive and worse than it had ever been. From this peak the SI fell to 1974, surged briefly to its third highest peak of recent times in 1975, and then plunged in 1977 to the lowest point for nearly 60 years. From then until 1984 it remained very low, indicating a period of 7 years when trees would not have experienced stressful changes in the soil moisture. Following the particularly severe phase from 1975 to 1979 the extent and severity of dieback began to decrease. By 1982 the frequency was definitely declining and much new growth was appearing. By 1985 this trend of recovery of the eucalypts was continuing.

The period from 1950 to 1977 represents 30 years when, as well as the very high peaks of stressful weather reached, the pattern of stressful weather during the growing season fluctuated more violently and rapidly than it had for many years. Furthermore, since 1920

there has been a gradual long-term upward trend in the average level of this stressful weather (Figure 2). It has risen in a series of “pulses,” being almost constantly positive since 1945 and culminating in the two great surges of the 1950s and 1970s, each reinforced by following a brief nonstressful period. This trend in the SI matches the general change in the weather patterns of eastern Australia known to have occurred since 1945 (Pittock 1983). On the New England Tablelands in particular, there was an increase in spring and (especially) summer rainfall, little or no change in autumn rainfall, and a decrease in winter rainfall. There was also a steady increase in mean temperature up until the 1970s (Pittock 1983). The SI reveals a long-term trend within these changes which would have subjected trees during the growing season to soil moistures that were increasingly more stressful than those to which they had adapted during the previous 50 years. By the time of the major surge which followed the brief respite in 1951–1952, this trend was sufficient (and the trees were old enough) to generate the extended bout of decline and death which has characterized the last 25 years on the New England Tablelands.

A Repeat of History?

It cannot be predicted whether or not a further (worse?) surge of the stress index will follow. Nor can we tell what effect any level of renewed stressful weather might have on the trees newly established during the past 5 years. But it would appear that all this has happened before.

Norton (1886) observed extensive decline and death of eucalypts in the New England Tablelands and some other districts of New South Wales. He first noticed small patches of dead trees between 1852 and 1857. Soon after that several hundred acres of peppermint gums “died away completely” on flat country between ridges near the town of Walcha. Other species along the borders of these flats were not affected. A few years later 3000 or 4000 acres of peppermints on the western slopes of a nearby low range had died. By 1882 Norton recorded the widespread occurrence of dead trees scattered throughout the bush

and living trees of several different species of gum showing thinning and dieback of their crowns. But by 1886 he reported (p. 16) that on the flats near Walcha “there is now an undergrowth similar to the trees which died out.”

He rejected the idea that defoliating herbivores were to blame. Rather he said (1886: 18) the answer was “partly climatic and partly artificial,” although admitting to being able to offer nothing more than a suggestion,” not knowing the precise times of the onset of death of trees nor having details of the preceding weather patterns. He pointed out that the peppermint gum which was most affected is shallow-rooted and grows on poor, shallow, heavy pipe-clay soils, in a climate which normally has a fairly high and frequent rainfall but which does experience long periods of comparatively dry weather. These trees would therefore not normally experience a shortage of soil moisture, making them particularly vulnerable to periods of drought, especially when interspersed with excessive wet spells which he said commonly follow spells of dry weather. All this was exacerbated, he said (p.20), by the disruption and compaction of these heavy soils by the “excessive stocking . . . commonly practiced in late years.” But it is clear that the flats where the peppermints grew were normally subject to waterlogging so that when dry spells occurred this shallow-rooted species would be the first to be affected by a lack of water. Such weakened trees, he conceded, might well be attacked by possums (MacPherson 1886) or the leaf-eating beetles which, he records, in some seasons swarmed in great numbers and completely defoliated trees. He concluded (p. 22) that he had “attempted to account for the changes which have been going on without involving the assistance of either possums, grubs or beetles” and that if his theory were sound it should be applicable in other districts where trees had sickened and died as they had in many parts of the New England area.

Unfortunately there are no known records of rainfall on the tablelands for the period immediately preceding and during this bout of dieback—other than the tantalizingly incomplete Armidale record. (This record did not start until 1858 and has a 5-year gap from

1867 to 1872, so it is insufficient to enable any conclusions about the likely stressfulness of the weather at that time.) There was extensive dieback in Victoria at the same time, although again there are no rainfall records. MacPherson (1886) reported that from 1862 to 1874 there had been extensive death of trees in the country between Geelong and Ballarat in Victoria. He discussed (and dismissed) various hypotheses put forward to explain these extensive areas of dead and dying trees. These hypotheses are similar to those heard today—flood, drought, bushfire, poor soil, white ants, defoliating and bark-eating insects, fungi, accumulation of sheep manure. He concluded that a population explosion of possums, resulting from the declining number of aboriginal people in the wake of European settlement, was the major cause of death of so many trees. He based this conclusion on observations of the manner in which the foliage on dying trees was eaten, calculations of the number of leaves eaten by possums, and the number of possums eaten by aborigines.

These two papers establish quite clearly that parts of New South Wales and Victoria which today are the sites of extensive decline and death of eucalypts (and of shelter belts of exotic trees) experienced a similar phenomenon almost exactly 100 years ago. In the New England area it is clear from Norton's account that the same species were affected and on the same sites in the same localities. Extensive death of the peppermints on low-lying areas subject to waterlogging was followed by general decline and death of other species on other sites.

These old papers also illustrate that then, as now, most people assumed that human activity had been responsible for changes in the environment and that this activity had been manifest through its influence on the activities of immediate and obvious agents such as Christmas beetles. Few looked deeper for more fundamental causes.

DIEBACK IN OTHER PARTS OF AUSTRALIA

Returning to the present, there have been many cases of dieback of eucalypts in various parts of Australia over the past 30 years, and

these have been extensively studied and reported (see Marks and Idczak 1973; Old et al. 1981). In spite of formal and informal attempts to coordinate such studies, however, most of the work has been piecemeal and has usually sought explanations in terms of attack of the trees by fungi and insects following disturbance of the environment by humans. We turn now to summaries of the published stories of a selection of diebacks in different parts of Australia.

Dieback of Jarrah in Western Australia

The dieback and death of Jarrah trees (*Eucalyptus marginata*) in the dry sclerophyll forests of Western Australia has been extensively studied and reported (Podger 1973). It was first noticed in the 1920s as a few patches of dead and dying trees which gradually increased in size and number, coalescing into extensive areas of dieback. In the 1960s *Phytophthora cinnamomi* was isolated from affected stands and subsequently shown to be consistently present in dieback sites. It was concluded and generally accepted that Jarrah dieback was a disease caused by *P. cinnamomi*, which was believed to have been only recently introduced to Western Australia and spread by logging activities through these forests. However, *P. cinnamomi* was recovered from only about 5% of Jarrah trees sampled, and it would seem premature to conclude that this fungus was killing the trees.

Another discovery of the 1960s—that Jarrah trees cannot tolerate waterlogging—has recently received fresh attention. Davison (pers. comm.) has shown that Jarrah trees grow more slowly on poorly drained sites with perched water tables subject to waterlogging and have died after wet winters (as in 1964) and summers (as in 1982). Shea et al. (1982) found that trees which had died after the exceptional rainfall in January 1982 had been growing in sites where drainage was impeded by a concreted sheet lateritic layer and that *P. cinnamomi* had invaded the phloem of vertical roots where these had penetrated the impeding layer. On well-drained sites trees remain healthy. They also found that sites where extensive mortality of Jarrah had occurred from

1945 to 1965 had similar soil profiles with a concreted sheet lateritic layer near the surface.

Davison and Tay (1985) have also demonstrated that when seedling *E. marginata* are flooded in pots their xylem quickly becomes blocked with tyloses and the plants soon wilt and dehydrate. The roots of these seedlings were much more likely to be invaded by *P. cinnamomi* than those of plants maintained at field capacity.

It seems possible, then, that rather than a newly introduced predator killing the trees, the situation is again one of mature trees, growing on poor, stressful sites, declining and dying when deviations in patterns of weather further stressed the plants. The fungus is then able to attack these debilitated trees successfully, possibly hastening their death. The healthy growth of young *E. marginata* plantations in New Zealand on good sites, but in the presence of high populations of *P. cinnamomi*, illustrate that young trees on sites which do not stress them are vigorous and immune to attack by the secondary pathogen *P. cinnamomi*.

The increase in the incidence of dieback of other species of eucalypts, especially for the 5 to 10 years prior to 1980, and an increase in outbreaks of foliage-feeding insects on trees in both the forest zone and wheat belt of Western Australia (Kimber 1981; Curry 1981), are perhaps not unrelated to the occurrence of Jarrah dieback. Especially would this seem to be so when it is seen that the annual rainfall in the southwest of Western Australia has undergone a slow decline starting in the 1920s and with a more rapid decline in the 10 years prior to 1980 (Kimber 1981; compare with the trend in eastern Australia [Pittock 1983]). Superimpose periods of wet weather such as those of 1964 and 1982 on this trend and trees on poorly drained sites will be severely stressed whereas those on better sites will be only somewhat stressed.

"Gully Dieback" in Tasmania

Palzer (1981) recorded that in northeastern Tasmania in the late 1960s and early 1970s, large numbers of *E. obliqua* trees died in nar-

row strips along the bottoms of gullies where the soils are shallow podzolics and the rainfall ranges from 700 to 1100 mm. In the lower-rainfall areas *E. obliqua* grows only along the bottom of deeper gullies. With increasing rainfall it occurs progressively higher up on slopes. This distribution and its occurrence in patches wherever soil water would be more plentiful (as in runoffs at the foot of cliffs) highlight the availability of water as a major constraint on the distribution of this species in these dry sclerophyll forests. Palzer showed experimentally that *E. obliqua* is much less resistant to drought than *E. viminalis*, which grows as an occasional tree in these otherwise pure stands of *E. obliqua*. In the dieback stands *E. viminalis* trees were often left relatively unaffected when surrounded by dead *E. obliqua*. Palzer found no evidence of attack by viruses, wilts, leaf and twig diseases, or *Phytophthora*. Some dead trees showed sign of infection by *Armillaria luteobubalina*, but it was found in all sites examined and is considered a native and widespread fungus. In the late 1960s the trees had been extensively attacked by leaf skeletonizers. Apparently these insects also defoliated other nearby species which did not subsequently die back, and they have since attacked *E. obliqua* which also did not die—suggesting a response by predators to trees temporarily but less stressed than the *E. obliqua* in gullies.

Returning to drought as the probably primary cause of the dieback, Palzer found that the period January to May 1967 had been the most severe drought recorded for the region, and its geographic center was coincident with the region where the dieback had developed (a rain-shadow zone produced by surrounding ranges). The most conservative estimate of how often such a drought might recur was 250 years.

It seems clear that this localized and relatively sharp and short-lived dieback is a particularly good example of how a departure from the usual pattern of rainfall can stress trees growing on susceptible sites to the extent of killing them. It also demonstrates how fungal and insect predators flourish on their debilitated prey, the degree of their success varying with the extent to which the trees are stressed.

"Regrowth Dieback" in Tasmania

This dieback was first recognized in 1964 in southeastern Tasmania. It was confined to lowland and foothill regrowth stands of 30 to 100+ year old *E. obliqua* and *E. regnans*, regenerated naturally after logging or wild-fires from about 1860 on (West 1979). West recorded that individual trees and patches of trees irregularly distributed among healthy trees were affected. They showed typical dieback symptoms, starting with retarded growth some 10 years before visible symptoms appeared. At the time that visible dieback and epicormic regrowth became apparent they were also being attacked by defoliating chrysomelids and by *Armillaria* root rot. Susceptibility seemed to be independent of age, soil, topography, fire, and logging history of the stands.

Permanent growth plots established in these stands in the 1940s and early 1950s provided West with the measure of growth rate of these trees well before the appearance of dieback. Growth rates had first declined following the start, in 1959, of several years of unusually dry summers and showed subsequent depressions with the droughts of 1967–1968 and 1972–1973. Actual dieback and attack by predators followed. This knowledge plus evidence that these wet forests with their substantial annual rainfall do frequently experience drought stress supported West's (1979) conclusion that the primary cause of this bout of dieback was drought stress, exacerbated by the attack of secondary fungal and insect predators. (Compare this case with that for gully dieback of *E. obliqua*.) West also recognized the similarity of regrowth dieback to the pole blight of western white pine in America. (See the discussion of pole blight later in this paper.)

Dieback of Eucalypts in Eastern Victoria

Eucalyptus dieback in the coastal forests of eastern Gippsland has been attributed to attack by *P. cinnamomi* as a newly introduced pathogen spreading in the area (Marks and Idczak 1977). Dieback was first noticed in early 1950 in these forests comprising species

of *Eucalyptus* known to be extremely sensitive to small variations in climate and differences in soil type. Small patches of trees died back in low-lying areas where the soils are shallow with an impervious layer close to the surface—sites very prone to waterlogging. Sudden death of these trees followed the above-average rainfalls of 1949, 1951, and 1952. Further acute bouts of dieback occurred in 1956, 1966, and 1970–1971. All these produced death of trees after above-average summer rainfall followed by a short period of below-average rain. The dieback was most severe on sites of poor quality with shallow, infertile soils and poor internal drainage—all sites where growth rates were slow and root systems shallow and which are readily prone to waterlogging and yet quickly become excessively dry in quite short periods of drought, conditions guaranteed to place trees under extreme drought stress.

Tregonning and Fagg (1984) have demonstrated that all four recorded bouts of severe dieback occurred after high rainfall in the period November to February was followed immediately by a 3- or 4-month period of low rainfall. They estimated the probability of such a coincidence as less than one in a million. But because there is no record of severe dieback in 1943, a year in which their model predicts it should have occurred, the authors favor the suggestion that *Phytophthora cinnamomi*, as a newly introduced pathogen some time after that date, must have been an additional necessary agent for dieback to occur.

It is possible, however, that most trees in the area had grown since the earlier periods of stress indicated by the model (1888, 1894, 1915), replacing those killed then. They may therefore not have been old enough in the early 1940s to succumb to stress at that time. And the pronounced change to a general increase in the rainfall for this area after 1945 may have provided the small additional stress necessary for the next alternation of wet and dry in 1953 to stress many trees to the point of dieback. And the coincidence of the timing of these bouts of dieback with the New England dieback, and of the virtually identical weather patterns associated with them, would suggest very strongly that increasing stressfulness of

the weather during the growing season was the cause of dieback in both localities.

Dieback of Farm Windbreaks in Victoria

Since late 1983 there has been severe dieback and death of mainly *Pinus radiata* and *Cupressus macrocarpa* trees planted as shelterbelts over a wide area of Victoria from South Gippsland to the South Australian border. The intensity of symptoms varies from the death of single branches to that of a complete windbreak (J. D. Morris, pers. comm.).

The onset of symptoms was sudden and synchronous, in late spring/early summer of 1983—after the prolonged drought of 1982–1983 and wet winter of 1983. Inspection of affected sites revealed poorly drained shallow topsoils overlying ironstone concretions with heavy mottled clay beneath.

Similar dieback of exotic shelterbelt trees occurred following the extremely wet winter of 1946 in western districts of Victoria and again in many places in southern Victoria in the summer of 1960–1961 following the abnormally wet winter of 1960. And there were less extensive bouts of dieback in western Victoria in 1964 and 1969. At the same time severe defoliation and death of windbreaks in the Mt. Gambier area of South Australia were reported. South Australia also experienced extensive death and decline of pines in the Mt. Crawford plantations in 1952–1954 following record rainfall in 1951 and below-average rains in 1949 and 1950.

In the 1950s similar deaths of *P. radiata* and *C. macrocarpa* shelterbelts in New Zealand were widespread and associated with similar weather patterns. *Phytophthora cinnamomi* was attributed as the causative agent for these deaths, as it was for some of the earlier ones in Victoria. *Phytophthora cinnamomi* has not been associated with the 1983 deaths, but there is some suggestion of salt toxicity being involved.

In these Australian examples a general pattern emerges. Dieback first appeared in the 1950s and first affected trees growing on sites most likely to be affected by excess soil moisture and/or drought. And it was associated, to a greater or lesser degree, with patterns of

weather which would subject the trees to periods of flooding or drought or both. Particularly noticeable is the similarity between the dieback in eastern Victoria and that in the New England area. Both occurred in the same period, and both were associated with the same pattern of weather (Tregonning and Fagg 1984). A study of associated weather patterns for other incidents of dieback in Australia may prove rewarding.

But apart from these bouts of actual decline and death of trees, there are numerous recorded outbreaks of defoliating insects attacking eucalypts in many parts of Australia at about the same time without causing very much, if any, dieback. Examples include phasmatids (Readshaw 1965; Campbell 1974); scarabs (Carne et al. 1974); chrysomelids (Greaves 1966); psyllids (White 1969; Clark and Dallwitz 1975); and leaf miners (Wallace 1970; Mazanec 1974). All these outbreaks were associated with similar patterns of stressful weather (White 1969) and attacked first and hardest those trees growing on potentially stressful sites. It would seem probable that all these events have as their basic cause the marked change in the climate which occurred after 1945 (Pittock 1983).

DIEBACK IN OTHER COUNTRIES

There are many records of dieback in other countries in both the northern and southern hemispheres. Most of these occurred around the middle of the century, were associated with deviations of rainfall likely to stress trees, and affected mostly overmature trees and those growing on harsh sites. Some of the more notable and better documented cases are discussed here.

Decline and Mortality of Oaks in North America

In the northeastern United States, decline and death of red and scarlet oaks was observed from about 1951 and continuing into the 1960s (Staley 1965). Numerous trees within extensive areas showed symptoms, and the worst-affected sites appeared to be at the

boundary with northern hardwood or spruce/fir forests. Serious decline of these two species (and to a lesser extent of white and black oak) had also been recorded from a number of localities in the Northeast in 1912–1920 and 1925–1932. Usually these were associated with increasing numbers of insects and fungi attacking the trees. They were likened to similar declines of oaks in Europe, where the general consensus was that defoliating tortricids were causing the decline. During this more recent study Staley (1965) recorded that major symptoms of decline were firstly a marked reduction in radial and terminal growth (commencing some 2 to 7 years before any visible signs of decline) followed by reduced density of crowns, dieback of twigs, and yellowing and aborting of many leaves.

Lammas shoots developed, and up to 30% of rootlets died. At the same time larvae of two species of leaf-rolling tortricids selectively attacked these oaks, often causing severe defoliation. Associated species were not injured except for an occasional light attack on black oak.

A more advanced stage of decline saw whole stems and large branches dying and finally whole trees dying—often quite suddenly at the last and usually in the late summer when stress from lack of moisture in the soil was at its peak. Trees in the advanced stage of decline were attacked by buprestid beetles tunneling in the phloem beneath the bark, and the roots of declining trees were attacked quite early and progressively by fungi—usually *Armillaria mellea*. But both beetle and fungi were found to be secondary, attacking only trees already severely debilitated and dying. The average age of affected trees was 60 years (by contrast with 40 years for adjacent healthy stands).

Sites where decline was most frequent and severe were flat or gently sloping surfaces, benches along valleys in dissected plateaus, or alluvial or colluvial soils in valley bottoms. Where oak decline occurred on steeper slopes the soils were shallow or very rocky and on dry southerly exposures. Usually the soils under stands affected by decline were unfavorable—shallow, infertile, excessively drained, restricting the depth of rooting and

restricting internal drainage—“causing wet soils in spring and droughty soils in summer.”

Patterns of weather experienced by declining and dying oaks showed (Staley 1965:10) “an average deficiency of precipitation during the growing season [which] commonly produces moisture stress” and a “large dormant-season precipitation surplus.” Staley’s calculations of weather data led him to conclude (p. 13) that while drought clearly had some influence, especially on the final death of trees, “the events analyzed . . . cannot adequately explain the initiation of oak decline.” But he failed to consider the influence of the “precipitation surplus” in winter and spring, especially in combination with summer droughts (White 1969). Similarly, when he looked for long-term climatic changes he found no evidence of any, but he had looked only at mean temperature and rainfall in summer. He concluded (p. 15) that “The only primary causal factor . . . is defoliation by the oak leaf roller,” yet he recognized “oak decline as a distinct, and to a large extent site-related disease”—one of several diebacks in the United States influenced by site, soil, and weather conditions similar to those affecting oak mortality in Europe.

Over the same period (1951–1964) stands of red oak in Nova Scotia were exhibiting similar symptoms of decline and death and were being defoliated by an outbreak of the winter moth (Embree 1967). Trees showed a marked decline in growth rate, crowns progressively died back, and many epicormic branches were produced. Growth rates started to decline in 1951; defoliation commenced in 1952 and persisted until 1962. There was repeated and severe defoliation of some stands from 1958 with up to 40% of trees dying. Growth rates were starting to increase by 1959, defoliation gradually subsided after 1961, and by 1964 only a few isolated areas were still affected. Surviving trees recovered their vigor.

Nichols (1968) reported similar dieback of red and scarlet oaks in Pennsylvania during the same decade. He reviewed earlier reports of their decline and mortality, including a 1902 report of serious losses many years earlier and several other more recent and contemporary reports of decline of oaks (includ-

ing Staley's). He concluded (p. 681) that the primary cause of the dieback and mortality he studied was "insect and spring-frost defoliation," an oak leaf-tier being the most important agent. He could find no consistent evidence that age of trees, the soil or sites on which they grew, or the weather contributed to the decline. But his records show that defoliation started *after* the beginning of decline of the trees' growth rates and stopped after growth rates started to recover, not the reverse; that there were 5 other major and 17 minor species of herbivorous insects responsible for the defoliation of the oaks; that "defoliation was greatest on lower slopes and along valley bottoms" (p. 686); that "many such areas served as 'pockets' of infestation from which the insects spread during outbreaks" (p. 686); and that trees which survived severe dieback recovered (albeit slowly) after defoliation ceased. And he looked only at deficits of rainfall in the growing seasons for evidence of an influence of the weather.

Maple Blight in North America

In Wisconsin, Giese et al. (1964) carried out detailed studies of maple blight which was also being experienced throughout the Northeast and North Central states and southeastern Canada. This decline was first reported in Wisconsin in 1957, following (in both time and space) severe defoliation by a complex of insects during 1955, 1956, and 1957. Deaths continued in patches for at least 3 years after defoliation. Symptoms were typical of other recorded diebacks: early loss of branch tips in the upper crown, progressive thinning and dieback of the crown from the top, chlorosis and wilting of leaves, later development of epicormic shoots, and ultimate death.

Mortality was severe—mostly in localized pockets but with dead trees scattered here and there through stands. Pure stands of sugar maple on the poorer, more exposed, and drier sites in areas receiving below-average rainfall were first and most affected. While trees of all ages and all dominance classes died, large overmature trees were hardest hit (80 to 100% mortality) with smaller suppressed trees next (50% mortality). Intermediate trees were usu-

ally vigorous and much less affected (< 30% mortality). Other species growing with maple (especially birch) were also attacked by defoliators and showed symptoms of decline, but they were not usually affected to the same extent.

After artificially defoliating trees, Giese et al. (1964:112) concluded that defoliation by insects was "the primary factor involved in the genesis of maple blight." But they had observed the association of the incidence of blight with other factors such as poor sites and elevated drier locations, and they noted that rainfall in the areas affected by blight had been below normal prior to 1957. They therefore conducted field experiments in which they restricted the supply of water to the roots of healthy dominant trees and at the same time artificially defoliated them. These trees had not previously been defoliated nor shown any signs of decline. Giese et al. decided (1964:127) that "the complete syndrome of maple blight was reproduced by these artificial methods," so they concluded that a reduction of soil moisture "served to increase the effects of defoliation." I would suggest that, once again, the cause of this dieback was climatic stress of old and overmature trees which made them a better source of food for herbivorous insects (and fungi). The large increase in abundance of these insects (several of them had never before been recorded from these forests) pushed these trees more rapidly (and probably more surely) to the point of death.

Dieback of Birch in North America

Dieback or "decadence" of several species of birch became extensive and severe throughout southeastern Canada and northeastern United States from the early 1930s through until the late 1940s (Hawboldt 1952). Symptoms were classic—first the death of the tips of twigs, followed by progressive downward death of the crowns. Significant numbers of feeding roots had died, and radial growth had decreased, prior to visible signs of decline. The trees were attacked by numerous species of defoliators, and eventually fungi and wood borers, prior to the death of many. Overma-

ture trees, those in densely packed stands, and those on poorer, drier sites were affected first. Later younger stands on better sites and even seedlings were affected. By 1948 many trees were recovering, including those with badly debilitated crowns. Certain associated species showed less severe signs of being affected.

Analysis of weather data, tree rings, and old records showed that birch trees had been recorded dying in quite large numbers as early as 1890, with further cases early in the twentieth century. These declines, and the more recent one studied by Hawboldt, were all associated with lowered summer rainfall and rises in summer temperatures. All the evidence pointed to insects and fungi being secondary, only attacking after trees were already debilitated. And their attacks ceased when there was a return to wetter summers from 1938 to 1940. Hawboldt (1952: 19) considered that he was witnessing "a redistribution of birch, accelerated by the secondary contributory factors," as a result of gradual long-term changes in the summer climate of the northeastern seaboard of North America.

Thus during the same 10 years or so, from the early 1950s, there had been a decline of hardwoods in general in the Northeast. In particular losses of oaks, white ash, and sugar maple—three economically important species—had attracted detailed study (Sinclair 1964). While no single cause of the decline and death of any of these species had been identified, there were many points of similarity. The first indications of decline of all were reductions in radial increment and the growth of terminal twigs *several years before visible symptoms appear*. Later, leaves become chlorotic, crowns thin out and start to die back, epicormic shoots develop, defoliating insects attack (often in outbreak proportions), and fungi attack roots and stems. Eventually many trees die.

Comparing the sites and soils on which healthy and declining stands were growing showed that, in general, affected stands occurred on sites more subject to stressful conditions—too much or too little water, low fertility, shallow exposed slopes, and so on. And all were associated with aberrant weather patterns. The growing seasons during the

early 1950s included several successive years of subnormal rainfall. And the radial growth of ash, oak, and maple was related to precipitation during these periods. Various factors were recognized as contributing to the decline and deaths of these species, but all showed the common factor of response (first on the most unfavorable sites) to a pattern of rainfall which would have placed them under severe and continuing water stress.

Pole Blight of Western White Pine in America

A drought from 1916 to 1940—the worst in 280 years—is considered to have been the major factor in the origin of pole blight of western white pine in the northwestern United States and in British Columbia (Leaphart and Stage 1971). This was a period of steadily falling rates of growth of basal area in response to increasing moisture stress, with extreme minima in 1922, 1931, and especially 1936.

Blight was first observed in 1929 in pines growing on sites with shallow soils of low moisture-storing capacity. The susceptible age for attack is approximately 60 years—the pole stage for this species with a life span of nearly 400 years—and attack was on trees in even-aged stands of this age, growing on these sites with severe moisture-stress characteristics. Rootlets of trees on these droughty sites had been deteriorating and dying before any external symptoms of pole blight developed. Decline of crowns was secondary to death of the root systems, but roots continued to die as the disease progressed, until the worst-affected trees were almost devoid of absorbing rootlets. Many trees died.

By the late 1940s to early 1950s there was some recovery of basal growth of surviving pines. But growth was still below normal in 1958, and some young stands still showed symptoms then and again in 1967. By 1970 pole blight was still apparent in stands first surveyed in the early 1950s, and in stands only very lightly blighted in 1956 there was moderate damage and some deaths. But in stands first blighted prior to 1940, the few surviving trees appeared healthy. They had apparently

by then, like the older trees of mature stands, passed the susceptible stage.

Western white pine regenerates readily on areas denuded by fire or other catastrophe if the weather is favorable for germination and survival of seedlings. One such period occurred from 1853 to 1882. It was the 40- to 80-year-old trees in pole stands from that period, growing on sites predisposing trees to moisture stress, which became diseased and died during the drought of the 1920s and 1930s. It is likely that, rather than a single very dry year such as 1922 or 1936, a series of consecutive dry years such as 1935 to 1940 or 1952 to 1957 would be needed to trigger such an outbreak. From their 280-year record of growth and (presumed) weather pattern, and assuming that the climate from 1916 to 1940 did not represent a permanent shift to less favorable conditions for growth, the authors considered (p. 238) the chances were good that "pole blight will not reoccur for many centuries."

Dieback of Metrosideros in Hawaii

Mueller-Dombois (1983 and references therein) discusses the dieback of *Metrosideros polymorpha* in the native rain forests of Hawaii. Severe dieback of *M. polymorpha* occurred on the islands of Hawaii and Maui at the turn of the century. Another severe decline started in the mid-1950s. In the following 20 years dieback and death of this species increased and spread to the point where, by 1975, it was considered to be a "severe disease" probably caused by some newly introduced pathogen and potentially capable of eliminating these forests.

Initially dieback was found on inundated or poorly drained sites and only large upper-story trees were dying. Later other sites were affected, but usually with less extensive and scattered patches of trees, or individual trees, declining and dying. Similar decline of *M. polymorpha* was reported from several of the major Hawaiian islands, but it reached its greatest intensity in the wet windward forests on the island of Hawaii itself. There has been no appreciable spread of dieback since 1977, and except for some stands on richer soils with dense competing vegetation, there is strong

and abundant regeneration of *M. polymorpha* replacing dead trees.

Recent research has demonstrated that *Phytophthora cinnamomi* and a cambium-feeding cerambycid beetle, both early suspects as the primary causative agent, are clearly secondary, attacking only trees which were already declining. It had earlier been concluded (Mueller-Dombois 1980:159) that the dieback of these *Metrosideros* forests was "initiated by a climatic instability which becomes effective through the soil moisture regime." (The "climatic instabilities" were periods of excessive or deficient rainfall.) Mueller-Dombois was later dissuaded from this view when subsequent dieback occurred on dry sites and richer soils. He now recognizes five "dieback types" but does not rule out the possibility that climatic stress could be responsible for them all. (Evenson 1983 has shown that decline and dieback on both wet and dry sites may well be linked to periods of unusually wet and dry weather in the 1950s and 1960s.)

Mueller-Dombois has now proposed a "cohort senescence theory" which says that the dieback of *M. polymorpha* is the result of a chain reaction. The predisposing factor is senescence of a group of trees. Their death is precipitated and synchronized by a "trigger." This trigger may be an internal stress of the trees (heavy flowering, nutrient deficiency) or an external perturbation of the environment (storm damage, drought, flooding). The quality of the site may significantly exacerbate the impact of these triggering perturbations. Diseases and insects are tertiary, but they can hasten the death of already debilitated trees. Mueller-Dombois suggests that other diebacks, such as those of *Nothofagus* forests in Papua New Guinea and New Zealand, may result from a similar chain of events. (See further comment in the "Discussion.")

Dieback of Nothofagus in Papua New Guinea

Arentz (1983) reported decline and death in *Nothofagus* forests in Papua New Guinea. Deaths occurred in patches spreading from one or a few trees, and it was only the large old (150–200 year) senescing trees which were af-

fect. Symptoms are typical: dieback, defoliation, epicormic shoots. The A_1 mating type of *Phytophthora cinnamomi* was thought to be a newly introduced and pathogenic agent responsible for this dieback. But it has now been found to be widely distributed, is not recently introduced, and is unlikely to be the primary cause of the decline. Arentz suggests that these *Nothofagus* forests are a mosaic of even-aged cohorts similar to the *Metrosideros* forests of Hawaii (Mueller-Dombois 1985) and the New Zealand Rata (*Metrosideros*)/Kamahi forests (Stewart and Veblen 1983). They form a self-replicating system of regenerating even-aged patches which follow the death of a group of senescing trees and will in turn senesce and die, making way for a further even-aged patch of regeneration. Arentz concludes by suggesting that the "trigger" needed to stress these old trees to the point of death is an exhaustion of available nutrients. Old trees develop prop roots, and most of their feeder roots appear to be confined to the deep humus layer suspended above the mineral soil. Nutrients would be continually leached from this organic layer and become greatly reduced as the trees mature and the feeder roots become more restricted to this layer. The trees would then be stressed, predisposing them to attack by insects and fungi. I would suggest that another trigger for these trees in such a situation could be a period of drought drying out the suspended humus layer.

Dieback of Nothofagus and Other Species in New Zealand

The Rata/Kamahi forests of New Zealand's high country have been declining and dying for the past 30 years. The introduced Australian possum has been blamed, but recently this conclusion has been challenged. Stewart and Veblen (1983:427) state that "abundant evidence suggests that ... mortality is due to senescence of cohorts ... originated at approximately the same time after ... windthrow and [landslides]. It may be that ... possums hasten the death of trees already susceptible as a result of natural processes." They point out that other, nonpalatable species have also

been dying in these forests, that "mortality ... was evident ... before the buildup of [possums]," and that adjacent young stands are little affected. Most of the mortality has been in even-aged stands of old trees on steep slopes. The abundant and dense stands of young Rata/Kamahi established on scars from landslides and windthrow (and which will eventually produce more old, even-aged stands) are healthy and have few possums in them.

Batcheler (1983), on the other hand, says the possum is the primary causative agent, citing the presence of high numbers of possums in dying forests and low numbers in healthy stands (including the young stands on high steep slopes referred to by Stewart and Veblen and other stands which have remained healthy in spite of 100 years of occupation by introduced mammals). Both authors cite the relative absence of possums from some (mostly young) stands and their high numbers in dying stands in support of their hypothesis. Stewart and Veblen suggest that possums are more abundant in declining stands because they are attracted to feed on the herbaceous species of the understorey in these stands; Batcheler says they are more abundant because the older stands provide nesting sites and other physical aspects of a suitable habitat for them. I suggest a third hypothesis: possums are more abundant in the dieback stands because the old, stressed trees provide them with a better source of food. Folivorous marsupials usually experience a shortage of nitrogen in their food and have evolved mechanisms to increase its availability in their diet (Hume et al. 1984). These mechanisms include the ability to select leaves with the highest levels of available nitrogen in them. Senescent and stressed trees are likely to provide such leaves (White 1984). The end result would be higher survival and greater numbers of possums feeding on such trees, hastening still further their decline and death.

Many of New Zealand's *Nothofagus* forests also have been showing varying degrees of decline and death in recent times. Wardle and Allen (1983) suggest that this dieback is confined to old, even-aged stands of senescent trees and, to a lesser extent, dense over-

crowded stands of young pole-sized trees, which have experienced some form of disturbance stressing them to the point of decline and death. They note (1983:403) that “younger stands or those with a greater mix of age classes are relatively immune.” Damage from snowstorms, earthquakes, drought, and rising water tables are suggested as likely triggering disturbances. They report extensive recent dieback of *Nothofagus* in areas of the South Island after a period of low rainfall, and they list evidence of widespread decline of *Nothofagus* forests in the early days of European colonization and more recently following the 1945–1946 drought and the 1929 Murchison earthquake. Outbreaks of pests and pathogens which follow disturbances are secondary “in response to the stressed condition of the trees,” they note (p. 403). They do not suggest what the stressed condition of the trees might be. I would suggest it is the same as that proposed above for the possums.

Skipworth's (1983) study of dieback of *Nothofagus* forests in the Tongariro National Park demonstrated that the affected stands were even-aged and with an unusually high percentage of old trees. Dieback became evident in 1967 accompanied by attack by fungal diseases. This decline is attributed to stress of these senescent trees triggered by a lowered water table following a period of deficient rainfall in the early 1960s. There is some evidence that this dieback is cyclical, as new even-aged stands regenerate and eventually senesce to the point where any additional environmental stress will kill them.

Jane and Green (1983) report mortality of vegetation in the Kaimai Ranges of the North Island. This dieback is strongly linked to topography and weather. Affected forests are growing in the cloud zone and on soils which are almost constantly waterlogged, resulting in shallow, poorly developed root systems. Such vegetation is extremely sensitive to quite minor droughts. Jane and Green (1983:389) observe: “Correlations with climatic records . . . and dendrochronological climate estimations suggest droughts to be the main contributing factor. Mortality is episodic . . . over several hundred years, with severe droughts implicated as the causative factor.”

DISCUSSION

A Common Cause?

These examples of decline and dieback of many species of trees in many countries have several features in common. In all cases the trees exhibited the same general sequence of symptoms: slowed radial growth, death of roots, progressive dieback from the tips of the crown, epicormic growth, ultimate extensive stag-headedness, and then the death of the whole tree. But some trees recovered from all points along this continuum of decline. Usually the oldest trees were first and worst affected; but in some cases young, densely overcrowded ones declined. Decline started and usually became worst on the harshest sites. These declines and diebacks were associated with changes in the weather which would have placed trees under some degree of water stress (mostly periods of drought but also wet periods and sometimes a sequence of both). And most occurred at a time when there had been a marked shift in the general pattern of rainfall and temperature in both the northern and southern hemispheres. A great variety of leaf-eating insects and either root-invading fungi (the ubiquitous and normally saprophytic *Armillaria* and *Phytophthora*) or cambium-feeding insects attacked declining trees. All of these declines were widespread and unexplained; none was the result of an obvious perturbation of the environment.

These similarities suggest the likelihood that there was a common “natural” cause of all these phenomena—that they were *not* man-made, nor were they diseases, but that they were generated by changes in the weather stressing the trees, very possibly by a series of events similar to those documented at the beginning of this paper for the dieback of eucalypts on the New England Tablelands. Four major factors emerge as being consistently associated with these declines and diebacks: the sites where the trees were growing, the age of the trees, the weather they experienced, and the predators which attacked them.

Hypothesis of the Mechanism of Dieback

Trees grow where seeds happen to fall and germinate. If it is a good site they will prosper and grow. If it is not a good site, depending on how poor it is, and how variable its quality, trees may die soon after germination, or grow to varying stages and for varying times, before the site becomes inadequate—that is, until the stage is reached where the root/shoot ratio of the trees becomes unbalanced.

There are numerous well-documented factors which may contribute to the unsuitability of a site or cause its quality to vary from time to time. Usually they operate by preventing further growth of roots or by killing them. Many have been discussed in this paper. Commonly the most critical are variations in the slope, aspect, altitude, depth of soil, and drainage of a site influencing the amount of water available to the roots. But once the site does become stressful, for whatever reason, trees will respond by reducing the amount of aerial tissue to a level that their root systems can support. They will die back. Houston (1973: 76) makes the point nicely by analogy with the bristlecone pines: "These trees, the oldest living organisms in the world, exist on sites where environmental stress is extreme and continuous. The tenacity of these trees results from their remarkable ability to 'die back' and produce no more energy-requiring tissue than can be supported."

Old trees are more susceptible than young ones to any form of environmental stress, even on adequate sites, and moreso on inadequate ones. However, young trees growing on harsh sites, or if overcrowded, may decline and die long before achieving the normal life span for the species. Trees may reach senescence individually (in mixed tropical rain forests, for example) or en masse (as in North American balsam fir forests and many plantations). But for many trees to decline and die at one time, something must happen to reduce the adequacy of their sites. It is unlikely that all sub-optimal sites in one locality would be equally harsh or that trees growing on them would be of the same age. Even with a stand of trees of the same age, no two will have identical sites

for their roots, and all will differ genetically in their speed of development and longevity. Different species are adapted to grow best in different sites and have different tolerances to changes within the site. But the weather does change synchronously over large areas.

Seasonal fluctuations in the weather may cause the harshest sites to become harsher, but usually not sufficiently harsh, for long enough to seriously affect trees growing there—at least until they were very old. (If so trees would not persist on such sites.) But deviations from an annual or seasonal norm, sometimes for several successive years, can be marked and cause many sites—even those normally most favorable—to become stressful. Especially is this so for deviations in rainfall during the growing season which increase or decrease the amount of water in the soil beyond that to which the root systems of the trees have become adapted. Thus periods of drought or waterlogging—or worse still a succession of both—are likely to make many sites simultaneously harsher in terms of their capacity to accommodate the roots of trees growing on them. When this happens the trees will respond by dying back. First to do so will be those on the already marginal sites, very old trees, and individuals of species least adapted to tolerate changes in soil moisture. This may well mean that large, vigorously growing trees are first and worst hit if they happen to be growing on a site which would experience wide fluctuation in soil water only when the rainfall is extreme.

When a tree is stressed to the point where it will start to die back, but long before any visible signs of decline, chemical changes occur within its tissues. These are invisible but nevertheless real symptoms of senescence and signs of stress in young and old alike. These changes are the basis of the "lowered resistance" of "sick" or old trees. They consist of the breakdown of nutrients in the senescing or stressed tissues and their transport away to sites of storage or new growth. These processes provide an increased level of more readily available—more readily assimilated—food for young defoliating insects feeding on these tissues. In particular there is an increase

in the level of usually limiting nitrogen in the form of soluble amino acids. Then many more young defoliators may survive and grow to maturity than would have been the case had they attempted to feed on the leaves of young or unstressed trees.

In many cases the stressful weather may be only temporary—and short-lived. Then this sequence of events is halted and the trees quickly recover; their secondary predators can no longer successfully attack them. If stress persists over more than two or three generations of the attacking insects, however, an outbreak may result. But it will disappear as suddenly as it appeared once the stress stops, and the trees will quickly grow new foliage. Such events are common all over the world as unexplained outbreaks of varying duration and intensity. It is usually assumed that for unknown reasons the predators of the herbivores were temporarily unable to “control” their prey. The prey then increased in abundance to the point where they defoliated their food plants.

But if stress persists, or if trees are very old, the herbivores are likely to persist and increase on the continued supply of good food. They may completely defoliate the plants, forcing them to mobilize more reserves from storage to grow epicormic foliage. The defoliators will continue to thrive on these highly nutritious epicormic leaves, and at the same time cambium-feeding insects and root-invading fungi may successfully attack the phloem which carries the reserves to these leaves. Like the defoliators, these latter organisms cannot successfully attack a healthy tree, but they may well provide the *coup de grâce* to an aged, wounded, or physiologically stressed one.

CONCLUSION

This explanation is not new. It builds on, extends, and modifies earlier suggestions (Norton 1886; Houston 1973, 1981; Mueller-Dombois 1983). As these have done, it brings together evidence demonstrating that dieback is *not* a disease. While many and diverse

species in many and diverse parts of the world are affected, and while many and diverse organisms attack affected trees, there is nevertheless a common first cause of decline and dieback: changes in the weather.

What I have proposed slightly modifies the most recent and comprehensive hypothesis of Mueller-Dombois (1983) and integrates it with my earlier explanation of outbreaks of herbivores (White 1969, 1973, 1974, 1978, 1984). Mueller-Dombois proposes that the primary and predisposing cause of dieback is synchronous senescence of a number of trees in one place—“cohort senescence.” A sudden perturbation is then needed to trigger and further synchronize their senescence. He suggests a range of factors as possible triggers, including changes in weather patterns which may increase the harshness of the site. Finally he says that insects and fungi are tertiary, serving only to hasten the process of decline and death.

I put the perturbations of weather—especially rainfall—as the first cause, followed by the quality of the site. Senescence (even-aged or otherwise) is one important (but not *necessary*) predisposing factor. For example, young trees in overcrowded stands may decline and die if the site becomes inadequate. And cohorts of even-aged, over-mature balsam fir, which would have died after being defoliated by spruce budworm, when sprayed with insecticide recovered and remained free from attack until the next period of stressful weather. Predators *are* tertiary, depending on the debilitation of the plants for their successful attack. But as the last example illustrates, trees might often survive if freed from their attacks until the stress imposed by the weather has passed.

Decline and dieback of trees are merely one end of a spectrum of symptoms generated when trees are stressed by unpredictable changes in their environment. Minor stress from a variety of agents other than the weather may produce short-lived and often very localized increases in abundance of herbivores (White 1984). Widespread and general stress, normally from changes in the weather, may produce extensive and debilitating out-

breaks (White 1969, 1973, 1974). Should a pattern of weather become so severe and prolonged as to constitute a persisting change in the local climate, then general declines or diebacks like those discussed in this paper may result. If many trees in one locality are even-aged and old, then all may die, as with balsam fir forests attacked by spruce budworm. The recent extensive dieback and death of forest trees in Central Europe ("Waldsterben"), usually attributed to industrial pollution ("acid rain"), may well be another example of the same phenomenon (Schutt and Cowling 1985).

Finally, this is not a cry of doom—an admission that nothing can be done because the weather cannot be controlled. Once these processes are *understood*, much can be done in an environment which is manipulated by human effort. Activity can be directed toward managing and manipulating the trees and the sites on which they grow, rather than chasing will o' the wisp "factors" which was presumed to have stopped "controlling" the *apparent* culprits, the insects and fungi, which are then able to attack and kill the trees. It is unlikely that the effects of unpredictable bouts of stressful weather can be entirely avoided. But control of the age structure, composition, and proportion of species of a population of trees growing in a locality, together with careful selection and amelioration of the sites where they grow, could do much to alleviate the effects of such weather.

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