# FOREST RESEARCH INSTITUTE WESTERN REGIONAL STATION KEIMSCOTT, W.A.

## RESEARCH PROJECT W.A.4 - THE CAUSE OF JARRAH DIEBACK

# PROGRESS REPORT NUMBER 2 DROUGHT AS A POSSIBLE CAUSE OF JARRAH DIEBACK.

This report is the second in a series which examine some of the hypotheses which have been advanced by earlier workers as possible explanations of the cause of jarrah dieback. In the first report, Progress Report Number 1, possible causes which could account for the disease syndrome as it was known in 1960, were reviewed. Hypotheses of site deterioration in terms of decline of nutrient capital and soil toxicity due to the accumulation of excess ions in the soil, were examined and rejected.

In this report drought is examined as a possible cause.

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#### FOREST RESEARCH INSTITUTE

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#### PROJECT W.A.4

#### PROGRESS REPORT NUMBER 2.

Kramer (1962) has stated that "it seems probable that every process occurring in trees is more or less affected by water deficits" and concludes that tree growth is controlled directly by the internal water balance or degree of turgidity which, in turn, is controlled by the relative rates of absorption and water loss. Maintenance of cell turgidity is necessary for plant health and growth so that continued water loss in excess of absorption will lead to physiological malfunction. If this malfunction is protracted, then, by definition, disease follows.

Imbalance in the relative rates of absorption and water loss leading to water stress may occur as a result of change in the following factors:-

- 1. Incidence and/or distribution of rainfall.
- 2. Incidence and degree of atmospheric stress.
- Rate of water loss following changes in the composition and biomass of vegetation.
- 4. Available water storage capacity of the solum.
- 5. Ability of the vegetation to explore and exploit the available water in the solum.

Reports of such changes causing disease in forest trees are common in the literature.

The importance of rainfall deficit and high atmospheric stress

for the health of forest crops has been stressed by Boyce (1948).

Hepting (1963) has drawn attention to the significance for forest health of an apparently worldwide trend to warmer climate through the period 1895 to 1945. He has suggested that "weather changes of many years' duration" have had a role "in a number of recent and important forest tree diseases throughout the United States of America".

Acute drought stress occasioning serious damage and often large scale mortalities, may occur during "major periods of below normal precipitation often accompanied by above normal temperatures" (Copeland 1960). Copeland refers to accounts in the literature of such damage to five Pinus species, to Abies grandis (Dougl), Abies concolor (Gord and Glend) Lindl, Quercus coccinea Muenchh, and Larix occidentalis (Nutt), in the United States of America and notes that "nearly all reports emphasize the shallow depths or low water holding capacity of soils that support the stands suffering greatest damage". Boyce (1948) lists, in addition to the above genera, examples for Thuya and for Tsuga and names six major periods in the interval 1913 - 1934 in which severe injury to trees occurred over extensive areas of the United States. Croxton (1966) suggests that recent dieback of Fraxinus in New York State may be related to three Day (1960) describes dieback of Pinus major droughts there since 1950. nigra on the island of Cyprus and relates the condition to soils of limited moisture holding capacity. Pook, Moore and Costin (1966) and Cremer (1966) have described the effects of a severe drought in 1965 on dry sclerophyll forests of Eucalyptus rosii R.T.Baker and H.G.Smith, and Eucalyptus macrorhyncha F. Muell. Pook, et al (1966) showed the damage was generally restricted to shallow stony soils of low moisture

holding capacity on northerly and westerly aspects.

Similarly, there are chronic diseases of forest trees which have been attributed to water deficits and correlate with dry sites and years of deficient rainfall. A widespread dying of Shorea robusta in the Utta Pradesh and Bihar States of India, has been attributed to cumulative water deficits over a number of years (Seth et al 1960).

Other examples are Top Dying of Norway Spruce (Picea abies - Karst) in Britain (Murray 1957), Sweetgum Blight of Liquidambar styraciflua L. (Toole and Broadfoot 1959), Pole Blight of Western White Pine (Pinus monticola Dougl.) (Leaphart 1958) and Dead Top of Pinus radiata D.Don in Australia (Johnston 1964).

When climatic conditions which are favourable for the growth of a given forest community persist for a number of years, biomass may build up to levels which are beyond the capacity of the site to sustain in subsequent periods of drought stress. Zahner (1958) has shown that dense stands of understorey hardwoods so depleted soil moisture reserves under an overstorey of southern pines in the southeast of the United States that the Pine suffered drought stress. Toole and Broadfoot (1959) have suggested that Sweetgum grows well on a variety of soils under favourable conditions, but that during periods of soil moisture stress it apparently recedes from less favourable sites. Havel (personal communication) has shown that plantations of Pinus pinaster. Ait on deep sands of the Swan Coastal Plain in Western Australia deplete subsoil moisture reserves to much greater depth than does the indigenous dry sclerophyll woodland. He has shown that high levels of stocking or biomass result in early season depletion of deep reserves with an attendant risk of drought damage during the long dry summer typical of

the region. He advocates earlier and more intensive thinning in order to maintain the biomass at levels which will not deplete these deep reserves.

Changes which reduce the moisture storage capacity of the solum may also lead to drought stress. The limited moisture storage of eroded old field soils of the Appalachian Piedmont is considered to be an important factor in the aetiology of the Littleleaf Disease of Pinus echinata Mill and P. taeda. L., a disease in which the root pathogen Phytophthora cinnamomi Rands is also important (Copeland 1964). Copeland describes two similar diseases, Spot Die-Out in Pinus taeda L. and Red Pine Malady in Pinus resinosa Ait which are associated with adverse physical factors including low moisture storage capacity. Toole and Broadfoot (1959) suggest that deaths of Sweetgum on article-ially drained bottom land sites is due to lowering of the water table from which Sweetgum drew part of its moisture requirements.

Plant water stress may develop in forests growing on soils of more favourable moisture holding capacity where other physical or biological soil factors limit root development. Excessive soil moisture for long periods may induce severe root damage and lead to imbalance of absorption and water loss (Kramer 1949). Hopkins (1964) has described how low soil temperatures may reduce absorption by Eucalyptus species and lead on clear days to plant water stress when transpiration exceeds absorption. On the other hand, Redmond (1955) has shown experimentally that an increase of soil temperature of 3.6°F. for 100 days caused a marked increase in the rate of rootlet mortalities in Betula lutea Mich x.f. seedlings and suggests this may be significant in the Birch Dieback

disease. Broadfoot and Toole (1959) have demonstrated significant correlation between disease index in Sweetgum Blight and several soil properties which adversely affect moisture absorption.

It is apparent that the symptoms of malfunction generally referred to as "physiological drought" may arise from effects of a variety of factors ranging from simple rainfall deficiency to complex interactions involving unfavourable soil conditions, pathogenic organisms and abnormal atmospheric stress.

## An hypothesis of drought cause consistent with the disease syndrome as defined by Wallace and Hatch.

A number of features of the jarrah forest environment and of the disease syndrome were considered in 1960 to be consistent with the hypothesis that drought was the cause of jarrah dieback.

Symptoms in Jarrah.

The symptoms in individuals are consistent with drought stress. Variation in the response of individual jarrah trees ranged from sudden death of the whole crown to a gradual dying from the top down and outside in, sometimes with temporary epicormic replacement of the crown. Similar symptoms have more recently been described (Cremer 1966) for another rough barked eucalypt, E. macrorhyncha F. Muell following drought stress. These symptoms are also consistent with Boyce's (1948) description of typical drought response. The gradual death and chlorosis of many of the trees is consistent with Kramers (1948) description of moisture stress symptoms, viz. "premature senescence of leaves, reduced leaf area, disturbed nitrogen metabolism......". The presence of healthy major roots observed in rapidly killed jarrah trees is considered to be typical of

acute drought stress in other species (Boyce 1948, Day 1960).

Incidence of Dieback in relation to climate.

Hamilton (1951) had pointed out the low incidence of dieback in southern areas and related this to the less severe climatic conditions. Until 1960 only 5 or 6 small areas of dieback were known in the area south of the Blackwood River and each of these occurred on shallow and very gravelly soils. The climate of this region, which has higher incidence of rainfall and cloud during the summer months, is regarded by Loneragan (1962) as more suitable for the growth of jarrah.

The low incidence of dieback in the lower rainfall areas east of the main belt of prime forest is, at first sight, inconsistent with drought cause. Reference to the climatograms of figure 1 shows, however, that there is little difference in the total dry (December to March) season rainfall between eastern and western stations in areas away from the influence of the south coast. Thus, the decline in total rainfall eastwards is due almost entirely to reduction in the intensity of winter rainfall. Another reason which had been suggested for the low incidence of dieback in eastern areas was the generally higher proportion of "fine fraction" in the soil.

### Evidence of the sensitivity of jarrah to water deficits.

If jarrah dieback is caused by soil moisture deficiencies, then it should follow that species such as E.calophylla and E. wandoo are more resistant to water stress than species such as E.marginata and Banksia grandis.

Variation in adaptation to water stress and its ecological significance has long been recognised. Warming (1895) delineated three

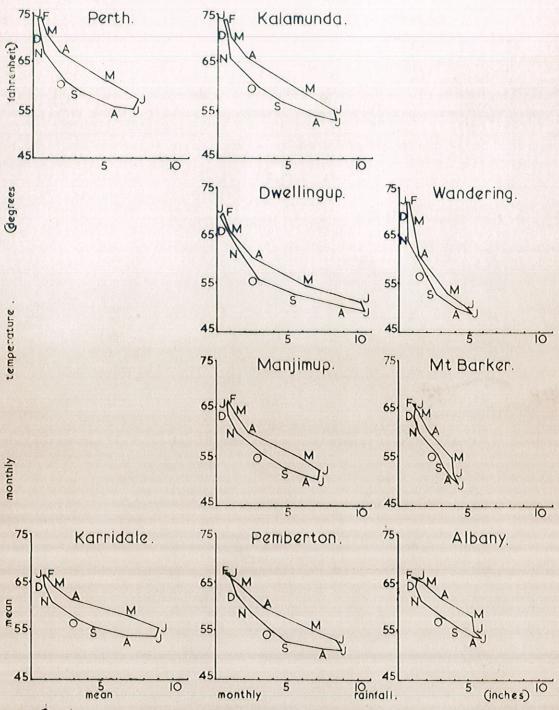


Fig 2 .1. Climatograms for nine stations within or at the margin of the continuous distribution of Eucalyptus marginata. Arranged in west-east order (left to right) and north-south order (top to bottom)

classes of plants on the basis of the moisture relations of their habitats. Although there has since been an enormous volume of work on the significance of variation in morphological and physiologic characters in relation to drought resistance, Daubenmire (1959) concludes that "perhaps no part of ecological literature contains so many fallacious atatements as that concerned with the adaptations of plants to endure drought". No single morphological or physiological character may be taken as indicating a greater or less resistance to drought. Evaluation of the relative tolerances to drought of a group of species therefore should be based only on a consideration of the whole plant in its natural environment. In such considerations it is necessary to take into account each of the two distinct classes of adaptation to water stress which have been recognised by Levitt, Sullivan and Krull (1959). These are a first, drought avoidance or the ability to reduce water usage and so avoid permanent wilting; and second, drought tolerance or the ability to tolerate or resist dessication while in the wilted condition.

Eucalyptus in mixed species stands in Victorian foothill forests (Hopkins 1964). "Both interspecific and intraspecific adaptation of possible importance to plant water availability, in respect to both drought avoidance and resistance to dessication, have been found to exist in Eucalypt species." Hopkins concluded that his studies provided support for the observation of the extreme sensitivity of eucalypt growth and distribution to site-water relations in mixed species forests.

Although no comparable studies have been made for Western Australian eucalypts the evidence available, which is summarised below,

is consistent with the hypothesis that the reactions of the various species in dieback areas are related to their drought resistance.

The distribution in relation to rainfall, of the three physiognomic dominants of the jarrah forest, i.e. E.marginata.

Banksia grandis and E. calophylla, supports the hypothesis. The most susceptible to jarrah dieback of the three, B.grandis, has the most limited eastward distribution; E.marginata is slightly less sensitive and extends a little further eastward, whereas E. calophylla, the most resistant, extends even further into the dry areas.

The apparently anomalous northern extension of <u>B.grandis</u> is on deep, slightly more fertile, sands with better ground water storage than the lateritic gravelly soils to which jarrah is almost entirely restricted.

Evidence that E.marginata is highly sensitive to relatively small changes in rainfall at the dryer end of its range, has been deduced by D.M.Churchill (in preparation). He has noted that the most easterly outliers of E.marginata are some 90 miles beyond the eastern margin of continuous distribution in areas receiving only 3" of annual rainfall less than forest at the eastern margin of continuous distribution. He suggests that an increase in annual rainfall of 3" would allow extension of the continuous distribution on to suitable soils to include all existing outliers.

In field studies on the physiology of water use in local species of dry sclerophyll, Grieve (1956) has shown that E.calophylla has much more effective control of water loss and thus drought avoidance capacity, than E.marginata which he regards as "prodigal of water".

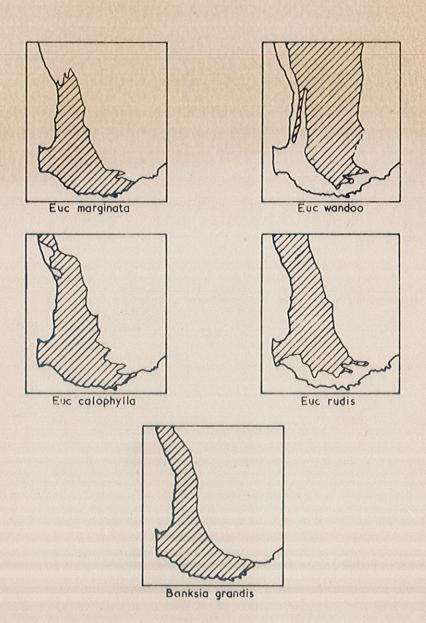


Fig. 11. Continuous distributions of Banksia grandis and four Eucalypt species in south western Australia.

(from data of Churchill and Storr reported in Lange 1960.)

There was thus some ground for concluding that the symptoms and occurrence of dieback are generally consistent with drought effects and that the hypothesis was consistent with what was known of the relative sensitivity to moisture stress of at least the physiognomic dominants. Hamilton (1951) and Loneragan (1962) suggested several mechanisms by which drought stress may be increased above the level to which these forests were adapted in their undisturbed stage. Two further influences may be considered. These are climatic change and the marked increase in the density of understorey in much of the cutover forest. Evidence of increased climatic stress.

Gentilli (1952) has presented evidence for a long term but slight increase in summer temperatures at Perth and of changes in the incidence of winter rainfall. The temperature changes are very small but could be of significance for survival in plants which make most rapid foliar growth during months of maximum atmospheric stress. Both E.marginata and Banksia grandis make rapid shoot extension as the spring rains retract. Leaf extension follows during the hottest and dryest months of the year (Loneragan 1962). These phenomena are reported to be common to a number of species in dry sclerophyll formations in southern Australia (Specht 1957). Water deficits during active radial growth or shoot growth have more deleterious effects than at any other time (Fraser 1962). Although the jarrah forest is adapted to this apparent out-of-phase relation between moisture demand and moisture supply, it might be expected that a lower than normal incidence of summer rainfall, or a delayed arrival of winter rains, could initiate severe drought stress. Evidence of possible increases in biomass and water demand.

One of the most striking results of cutting in the virgin jarrah

forests has been the subsequent marked increase in the density of understorey species, particularly Banksia grandis (Wallace, personal communication). Although basal area stockings of jarrah regrowth and understorey are often of the same order as that in the original apparently less vigorous virgin forests, the biomass is probably greater. Although no direct data are available to support the view, foresters with a long experience in these forests, believe that older regrowth stands now have a more dense leaf cover than did the original stands. This is supported by data of Hatch (1964) who found litter fall over a two year period in a pole stand much greater than in a virgin stand. It is possible therefore, that there has been an increase in the biomass during favourable years and that there is a greater interception of summer showers and would place a greater water demand on the site which would aggravate the stress.

On the other hand, two facets of the disease syndrome which are not readily accounted for by the drought hypothesis are the apparent spread of dieback patches and the failure of jarrah to recover after the thinning out of the stand resulting from the earliest deaths. A possible explanation in terms of drought, is that the initial deaths occurred on limiting microsites only and that these deaths opened the floor at the edges of the surrounding stand to increased insolation and subtle erosion. According to Wallace and Hatch (1953) these patches did not extend indefinitely and the disease did not develop on sites other than those marginal for the growth of jarrah. The failure of jarrah to regenerate might be similarly explained by accelerated site deterioration, exposure and the possible operation of a climatic trend to more severe conditions.

It seemed reasonable therefore, to attribute jarrah dieback to critical plant water deficit in drought sensitive species. These deficits could be induced by deterioration of the soil moisture holding capacity of some sites and an increase in the biomass beyond tolerable limits in others, intensified by a climatic trend to summers of slightly greater severity. These effects could be expected to be most severe on the poorest soils.

At this point it was necessary to consider how the validity of the drought hypothesis might be tested experimentally.

Approaches to the evaluation of drought as a cause of disease.

Attempts to evaluate the validity of hypotheses of drought induced disease in forest trees have been numerous and a variety of methods have been used.

Indirect parameters of plant moisture stress have been correlated with arbitrary indices of disease severity in individual stands and for "disease years". Estimates of atmospheric stress and rainfall deficit have been used, for example, in the work on Pole Blight of Pinus monticola (Wellington 1954). Leaphart and Stage (cited in Hepting 1963) investigated the relationship of severity of Pole Blight to climate as indicated by growth ring width. Others, including Zahner (1958) and Seth et al (1960) have correlated growth or mortality with soil moisture deficits in soil moisture budgets. Others, working on moisture stress in relation to growth, have measured the period for which soil moisture tension exceeds prescribed values (Hopkins 1964).

Another widely used approach is study of the association of site factors, or combinations of factors, with an index of severity.

This approach has been used in studies of tree growth in relation to site factors as exemplified by the work of Coile and in a study of a disease index of Sweetgum Blight in relation to factors affecting soil moisture availability (Toole and Broadfoot 1959). These last authors recognise the limitations of this method in stating:

"None of these correlation methods are really satisfactory measures of the order of moisture stress."

More direct measures have been advocated by Kramer (1962) who concludes that "the only reliable method of evaluating the water balance of a tree is to measure the internal water stress, preferably in terms of diffusion pressure deficit, although measurements of relative turgidity are useful". Pook, Costin and Moore (1966) measured relative turgidity of leaves and moisture content % of bole and branchwood of E. rossii and E. macrorhyncha and found that relative turgidity of the foliage may be low before signs of water stress are obvious. Hopkins (1964) has suggested that the difficulties inherent in the use of leaves of tall trees may be overcome by measurement of stem shrinkage at breast height. This method provides a convenient measure of the onset and duration of water stress.

Any of the above approaches might be used in a study of jarrah dieback in relation to plant water stress. However, the validity of the hypothesis rests, inter alia, on establishment of a greater drought resistance in the non-susceptible associates than in jarrah. Because of the marked differences in susceptibility of jarrah and its eucalypt associates a simple test of the hypothesis is available. Test plants of jarrah should succumb to drought more rapidly than the resistant associated species.

The difficulties of working with large plants under natural conditions are widely recognised and most approaches in this field have been made using seedlings, larger container grown plants, or detached shoots.

This approach would appear to be valid at least for determining relative differences of a major order since, under natural forest conditions, the success or failure of species is determined primarily in the seedling stage. In established formations of woody perennials seedlings are likely to be more highly sensitive to the effects of drought than are later stages (Daubenmire 1959). Hopkins (1964) who examined the relative drought resistance of a range of foothill eucalypts in Victoria, had reviewed approaches in this field and concluded that the use of seedlings is a satisfactory technique for demonstrating gross differences in response to water stress. The use of seedlings in this present study would seem also to be appropriate since relative susceptibilities to dieback of the various tree species were generally observed to be of the same rank in the seedling stages as in the later stages.

The hypothesis was subjected to test by comparing the response to drought of the seven eucalypt species most common in the jarrah forest. All except E. accedens were known to occur in at least one dieback area. Its inclusion in this experiment was due to an error of identity with E. laeliae, now recognised as a new species. (Podger and Chippendale in preparation).

#### Experiment 1.

Method:

Test plants were obtained in August 1962, from two sources.

wilding seedlings of E.marginata, E. calophylla, E. patens, E.megacarpa and E. rudis were collected on ashbeds at the ecotone between an E.marginata - E.calophylla community and a swamp fringing community of E.megacarpa - E. patens with occasional E. rudis near reference CR60.

The seedlings, which were 15 months old when collected, originated from natural seed fall on ashbeds created by the severe fires of January, 1961. Twelve month old seedlings of E. accedens and E. wandoo species were selected from routine 4" potted stock raised in the Dryandra Forest Nursery. Test soil was obtained from the first mentioned locality in the top six inches of the profile, screened to pass 3/10" mesh, and steamed for 45 minutes. The gravelly sandy loam was taken from an area on which seedlings of each of the first five species co-occurred. The remaining species, E. wandoo and E. accedens, occur further eastward on similar surface soils.

The seedling root systems were washed of soil, the tops leaf pruned to reduce transpiration. The seedlings were then reported, three to a one-gallon container, with free drainage through the bottom. They were then raised under 50% shade with weekly applications of Aquasol and watered daily if required with tap water.

In January 1963, twelve pots of each species were selected for uniformity and randomly assigned three replicates to each of four treatments in a randomised block layout.

#### Treatment:

Three replicates of each species were subjected to one of four droughting treatments. Plants were watered from below until the entire soil volume was saturated, allowed to drain and then set out,

one replication of each species x treatment combination to each of three blocks. The plants were visited three times daily and the time of wilting recorded for each pot. The four droughting treatments were:-

- (a) 24 hours drought after wilting before rewatering from below.
- (b) 48 hours drought
- (c) 96 hours drought, and
- (d) 192 hours drought.

The pots were then watered as required, or at least once daily, to maintain soil moisture near field capacity by rewatering from below and draining.

During the course of the experiment a continuous record of air temperature and humidity at one location among the test plants was made. From this data saturation defects each hour were calculated and a saturation deficit curve prepared.

Fourteen days after the last drought treatment was completed the experiment was terminated and mortalities recorded. For each pot the number of days to wilt, and the area under the saturation deficit curve (a) from start to wilt and from wilt to the end of treatment, was measured.

#### Results:

There was considerable variation between species in the time to develop the first symptoms of wilting.

Since the humidity and temperature conditions were not controlled, comparisons of the stress tolerated before wilting were made using the area beneath the saturation deficit curve as an index of atmospheric stress. These data (table 1) relate to the first of Levitt, Sullivan and Krull's (1959) two aspects of drought resistance, i.e. the ability to

reduce water loss and so avoid permanent wilting.

Table 1. Mean number of hours and mean stress index (Area under the saturation deficit curve) required to wilt seven eucalypt species.

Constant	ů.	Starra Odrana Tadam	3
Species	Mean Hours to Wilt	Mean Stress Index tolerated before wilt.	
E. rudis	123	9.34	13.0
E. wandoo	128	9.77	13.0
E. accedens	132	10.50	Buch
E. megacarpa	159	13.14	ts-i
E. calophylla	172	14.63	u·g
E. patens	180	15.16	15-1
E. marginata	208	16.55	h b

The second aspect of drought resistance, as defined by Sullivan et al., is tolerance of dessication. Differences in the ability of the various species to tolerate dessication may be examined by a comparison of the greatest level of stress tolerated before substantial mortalities occur. A level of 66% has been taken as representing substantial mortality; stress tolerated by each of the species before this arbitrary level of mortality occurred, is shown in table 2.

Table 2. Drought stress index tolerated after wilting before 66% of plants died (in each of seven species of Eucalyptus.

		Block 1	Block 2	Block 3	Mean.
E	. accedens	2.74	2.75	2.50	2,66
E	. megacarpa	4.80	1.91	2.43	3.05
E	• patens	7.72	3.73	3.72	5.06
E	. wandoo	5.13	9.24	5.13	6.50
E	. merginata	5.08	7.57	9.34	7.33
E	. rudis	10.77	18.00	18.18	15.68
E	. calophylla	19.05	17.91	17.91	18.29

Drought resistance in the field is, however, determined by the capacity of a plant to delay drought and then to tolerate dessication. The stress tolerated before death may be expressed by the addition of the data of tables 1 and 2.

Table 3. Mean drought stress index tolerated before 66 percent mortality in seven Eucalypt species.

E. accedens	13.16
E. megacarpa	16.19
E. wandoo	16.27
E. patens	20.22
E. marginata	23.88
E. rudis	25.02
E. calophylla	32.92

Relative drought resistance of the seven species in this experiment was also measured by a comparison of the number of plants among nine seedlings of each species which died after drought treatments of 1, 2, 4 and 8 days' duration.

Table 4. <u>Number of plants of each of seven species which</u> died after four periods of drought.

	Days droughted wilting					
	1	2	4	8	Total	
E. megacarpa	0	6	9	9	24	
E. accedens	0	8	6	9	23	
E. wandoo	0	3	7	9	19	
E. patens	1	0	6	9	16	
E. marginata	0	0	3	9	12	
E. rudis	0	0	2	5	7	
E. calophylla	0	0	0	1	1	

#### Discussion:

In each of the aspects examined above, <u>E. marginata</u> was less sensitive to water deficiency than <u>E. patens</u>, <u>E. megacarpa</u> and <u>E. wandoo</u>, all of which are field resistant to dieback. <u>E. marginata</u> did not, however, tolerate drought as well as <u>E. calophylla</u> although their relative abilities to delay wilting are comparable. This last response is surprising in view of Grieves' (1957) findings, 'though Grieve worked with detached shoots which may not transpire as entire plants. The pattern of sensitivity to drought in most of the species

examined was consistent with their apparent site requirements. In the field each of the drought sensitive species, with the exception of E. accedens, occur in water gaining situations. The only species occupying dry sites are E.marginata and E. calophylla and where clay subsoils occur E. wandoo and E. accedens. E. rudis is normally restricted to riparian sites and seasonally flooded soils; its high relative tolerance to drought is therefore surprising. This species was the earliest to wilt, but all plants shed their leaves shortly after wilting and passed most of the dessication phase of the experiment in a deciduous condition. These defoliated plants produced new epicormic shoots on the lower stem and developed normally when regular watering was reintroduced. This apparent drought escape mechanism may have prevented further dehydration of tissues.

the six other eucalypts to drought is not consistent with their relative susceptibility to jarrah dieback and hence with the hypothesis that the deaths of E.marginata in dieback are due to soil moisture deficits per se. This hypothesis is also unable to account for the extensive development of dieback in the climatically milder southern forests in the last four years; a period in which rainfall has been higher than average through most of the forest region. Some other primary cause than drought must be responsible for the symptoms of physiological drought in individual jarrah trees. Such symptoms are not, in fact, specific to disease due to water deficiency in the environment, since most diseases, whatever their cause, result in disturbance of the water balance of the host (Subramanian and Saraswathi-Devi 1959).

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