

# THE EFFECT OF LOW ROOT TEMPERATURES ON THE GROWTH OF MOUNTAIN FOREST EUCALYPTS IN RELATION TO THE ECOLOGY OF *EUCALYPTUS NITENS*

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To compare the response of four montane eucalypts to low soil temperature, seedlings of *Eucalyptus regnans*, *E. delegatensis*, *E. fastigata* and four provenances of *E. nitens* were treated for 100 days in a glasshouse. Mean ambient air temperatures varied between 15°C and 29°C while temperatures within the root zone were held in the vicinity of either 5°C or 10°C.

All species grew significantly better at the higher temperature for all variables measured. Differences in stem diameter, root length, root and shoot dry weight were consistent between species at both temperatures. Growth of *E. regnans* and *E. nitens* was similar overall. For most variables both species grew significantly better than *E. delegatensis*, which grew significantly more than *E. fastigata*. For height growth there was a highly significant interaction between species and temperature. At both temperatures, *E. regnans* made significantly better height growth than all other species. At the higher temperature, *E. fastigata* grew significantly taller than *E. nitens* and *E. delegatensis* but, at the lower temperature, *E. nitens* grew significantly taller than *E. delegatensis* and *E. fastigata*. Comparing the difference in height growth, *E. fastigata* and *E. delegatensis* were reduced substantially more than *E. nitens* by the cool root environment.

*Eucalyptus nitens* has a restricted distribution for a species with outstanding vigour. This may be related to a fire regime which also encourages the development of rainforest understoreys, and cool, heavily shaded soils. The implications of topography and fire regime on understorey type and soil temperature are discussed in relation to the ecology of *E. nitens*.

FOUR TALL forest eucalypts in the mountain forests of southeastern Australia have overlapping distributions in regions with mean annual rainfall exceeding 750 mm. *Eucalyptus delegatensis* R. Baker and *E. regnans* F. Muell are dominant species over extensive highland areas of Tasmania and Victoria (Eldridge 1972, Boland & Dunn 1985). *E. delegatensis* extends into southern New South Wales, replacing *E. regnans* above 1000 m over the greater part of its range. *E. nitens* (Deane & Maiden) Maiden and *E. fastigata* Deane & Maiden occupy similar latitudes in northern New South Wales (Sherry & Pryor 1967, Tibbits & Reid 1987). Both species extend south into East Gippsland, Victoria, while scattered stands of *E. nitens* also occur westward along the Great Dividing Range and into the Central Highlands. The elevation range of both species is influenced by latitude but, in Victoria, optimum development occurs at or near the lower limit of winter snow.

The growth rates of *E. nitens* are recognised as being greater than those of *E. regnans* in plantations up to 15 years (Pederick 1976), and planting trials indicate that *E. nitens* can be successfully grown in cool mountain areas receiving an annual rainfall of over 1000 mm (Turnbull & Pryor 1978). Despite this, the natural distribution consists mainly of small, disjunct stands (Pederick 1979) that may be enclaves of formerly more widespread populations.

Three broad regional forms of *E. nitens* have been recognised on the basis of leaf shape (Shepherd et al. 1976). The northern New South Wales form occurs near Mt Ebor and Barrington Tops. The southern New South Wales and West Gippsland forms both occur in Victoria. They differ in their morphology and vigour (Pederick 1979) and in some aspects of their physiology (Pederick & Lennox 1979, Tibbits & Reid 1987). The West Gippsland form is fast growing with strongly glaucous juvenile leaves and occurs



predominantly in the Central Highlands. The southern New South Wales form is less glaucous, less vigorous and has marginal glands on its mature leaves. The major occurrence of this form is on Errinundra Plateau. It also occurs intermixed with the West Gippsland form on the western slopes of the Baw Baw Ranges and on the Toorongo Plateau; however, the West Gippsland form does not occur naturally in East Gippsland.

In the Victorian Central Highlands, *E. nitens* is often found in association with or in close proximity to the cool temperate rainforest species *Nothofagus cunninghamii* (Hook.) Oerst. and *Atherosperma moschatum* Labill. Mixed forest associations with *Elaeocarpus holopetalus* F. Muell and *A. moschatum* replace *N. cunninghamii* in East Gippsland beyond the natural range of that species. In areas where the understorey consists of a dense growth of *A. moschatum*, *E. holopetalus* and associated cool temperate closed forest species, an almost complete dominance of the site by *E. nitens* is often apparent. In northern New South Wales, mixed forest reoccurs with associations between *E. nitens* and *Nothofagus moorei* (F. Muell) Krasser (Pederick 1977).

The development of cool temperate closed forest understoreys has been associated with crown die-back in mature *E. delegatensis* forest in Tasmania (Ellis 1964, 1971, Ellis et al. 1980) although associated *E. dalrympleana* Maiden was unaffected. Ellis et al. (1980) concluded that depressed root temperatures due to the encroachment of closed forest may be important in the "decline" of *E. delegatensis*, as the deterioration could be reversed by cutting or burning

the understoreys. A mean annual soil temperature below 7°C was identified as the critical point at which the growth of *E. delegatensis* deteriorated (Ellis 1971). Although healthy and unhealthy stands differed little in winter soil temperatures, unhealthy stands had summer temperatures below 10°C. This suggested that soil temperature could be an important factor influencing the natural distribution of eucalypts (Ellis 1971).

The strong topographic and floristic similarities between the declining *E. delegatensis* forests of Tasmania and the apparently unaffected *E. nitens* forests of Errinundra Plateau suggested that *E. nitens* might be more tolerant of low soil temperatures than *E. delegatensis*. This factor might also influence the distribution of *E. regnans* and *E. fastigata* in eucalypt-rainforest associations in Victoria. The aim of this study was to test this experimentally under controlled conditions.

## METHOD

To investigate the effect of lowered root temperatures on eucalypts occurring in the montane zone and likely to form an association with a rainforest understorey, seedlings of four common montane eucalypts were grown at temperatures near that identified by Ellis (1971) as critical to the onset of die-back. Seedlings for the trial were grown from provenances listed in Table 1. Seeds of *E. nitens* were collected from several trees at each provenance and care was taken to distinguish between the southern New South Wales and West Gippsland forms at Mt Toorongo. Seeds of *E. delegatensis*, *E. fastigata* and *E. regnans* came from bulked seed lots and

Species	Locality	Latitude	Longitude	Elevation (m.a.s.l.)	Form
<i>E. nitens</i>	Royston River, Central Highlands	37° 25'	146° 53'	1000	West Gippsland (CR)
<i>E. nitens</i>	Mt Toorongo, Central Highlands	37° 50'	146° 07'	1200	West Gippsland (CT)
<i>E. nitens</i>	Mt Toorongo, Central Highlands	37° 49'	146° 07'	1000	Southern NSW (ET)
<i>E. nitens</i>	W Errinundra, East Gippsland	37° 19'	148° 52'	1000	Southern NSW (EE)
<i>E. delegatensis</i>	Delegate River, East Gippsland	37° 17'	148° 50'	1000	East Gippsland
<i>E. fastigata</i>	Delegate River, East Gippsland	37° 17'	148° 50'	1000	East Gippsland
<i>E. regnans</i>	Nunnet, East Gippsland	37° 14'	148° 05'	1000	East Gippsland

Table 1. Eucalypt species and provenance.



would have included a greater number of parent trees.

A selection of uniformly large seeds was germinated on moist plugs of sterile rock fibre. *E. delegatensis* was sown after 6 weeks stratification at 4°C. Because of greater growth rate of seedlings, seeds of all other species were sown one month later. Five seeds were sown in each plug. After germination each plug was placed on the top of a 250 mm length of 60 mm diameter PVC pipe filled with clean river sand. The seedlings were kept moist in a shade house by spray irrigation and fertilized every third day with 10 mL of water and 10 mL of Duralite Hysol, a complete hydroponic nutrient solution. Once established, the seedlings were thinned to leave one plant within each growth tube.

After 115 days from the first sowing, the plants were transferred to an empty glasshouse where they were temporarily stored on the floor. After measuring plant height, ten individuals of each provenance were randomly chosen for initial dry weight and root length determination. At this stage the *E. nitens* seedlings developed a light infection of powdery mildew. All plants were elevated on benches and given two applications of TILT (Ciba-Geigy), a wide spectrum Triazole derivative systemic fungicide at a five day interval. Within ten days there was no evidence of active infection. The plants were given a further 20 days to recover and acclimatise to the glasshouse before the cool root treatment was applied. During this period all seedlings were showing healthy and apparently unaffected new growth. The *E. delegatensis* seedlings were therefore 145 days old at the commencement of the experiment.

Two root temperatures were replicated three times, in six forced air coolers. Mean warm root temperatures were maintained between 8.5°C and 10.5°C while mean cool root temperatures were maintained between 4.5°C and 6.5°C. Temperatures were measured using mercury thermometers inserted to a depth of 75 mm at both

ends of the cooler. The treatments were arranged down the centre of the glasshouse so that the different root temperatures were adjacent. Five plants of each of seven provenances were allocated at random to each of the six coolers. The plants were evenly distributed with their centres 110 mm apart.

The growth tubes were suspended through a false lid so that the roots in each tube were surrounded by fan-circulated air at controlled temperature, while the aerial parts of each plant were exposed to the ambient temperature of the glasshouse. A small temperature gradient of approximately 1°C existed across each cooler, and small differences in the operation of thermostats meant that the regulation of root temperature differed slightly between coolers. To compensate, lids were moved between coolers and turned once through 180° within each cooler so that, as far as possible, all plants experienced an equivalent root and shoot environment.

Temperature control in the coolers was adequate to ensure that clear differences existed between treatments and that similar temperatures were maintained between replicates (Table 2). Some difficulties were experienced in adjusting the thermostat in cooler 1 and the cooler was replaced after 16 days. Cooler 6 failed over a weekend and was replaced the following Wednesday. Typically, temperature fluctuates in the upper soil horizons both diurnally and annually, and lags behind air temperature. Experimentally maintained constant temperatures do not mimic most natural situations, although they may be more typical of soils protected by dense, rainforest vegetation. Watson (1980) considered that soils above 400 m elevation of the Great Dividing Range of Victoria are likely to have a mean annual temperature between 8°C and 15°C. On Errinundra Plateau at mid morning in mid November, soil temperatures of 7–8°C were obtained using a mercury thermometer at 130 mm depth, beneath dense rainforest vegetation. It is therefore conceivable that the experimental

Treatment Temp (°C)	Cooler	Period			
		May/June (°C)	July (°C)	Aug/Sept (°C)	May/Sept (°C)
10°C	1	9.8–12.5	8.6–9.5	8.9–9.6	9.1–10.5
	3	9.6–10.7	8.2–9.4	8.5–9.6	8.8–9.9
	5	9.4–11.8	8.5–9.4	8.8–9.9	8.9–10.4
5°C	2	4.8–6.3	4.5–6.7	4.8–6.1	4.7–6.4
	4	5.1–6.1	4.4–5.0	5.0–6.0	4.8–5.7
	6	6.2–7.4	4.6–5.5	4.4–5.8	5.1–6.2

Table 2. Mean minimum and maximum soil temperature in each cooler.



temperatures could be experienced naturally by the species involved in the trial.

The root medium was washed with water and the plants fertilized to excess every second or third day, initially with 60 mL of nutrient solution, then with 120 mL as they increased in size. Glasshouse temperature and humidity were monitored by a continuous recording thermo-hydrograph. Occasional roots extending beyond the growth tubes were clipped and stored in an alcohol and formalin mixture. Fallen leaves were collected for dry weight determination.

The trial ran for 100 days after which plants were measured for diameter at the harvest point (Dia) and total height (Ht). After harvest, the roots were placed on a fine wire mesh and washed free of sand by a gentle spray and hand teasing, with final cleaning of attached sand grains by forceps. They were stored in an alcohol/formalin mixture for root length determination. Total root length (RL) was determined using a Comair Rootlength Scanner (Richards et al. 1979). Root lengths estimated to be greater than 100 m were partitioned for separate measurement. Roots and shoots were held at 65°C for five days and dry weights of root and shoot (Dwt(r), Dwt(s)) were determined after stabilising for 1 hour at room temperature.

## RESULTS

Mean monthly air temperature and relative humidity in the glasshouse during the trial (Table 3) were uniform, with a diurnal fluctuation in mean maximum and minimum temperature of 10°C and in relative humidity of

approximately 20–30%. Absolute maximum and minimum temperatures of 37.7°C and 11.2°C were recorded.

Increment in growth was obtained by subtracting initial values for each plant in the case of height, and means of an initial sample for root length and dry weight of roots and shoots. An analysis of variance showed all variables to be significantly affected by temperature (Table 4), with growth reduced at the lower soil temperature, as expected.

Height was the only variable for which a temperature  $\times$  species interaction was significant and this was highly significant (Table 4). At the higher temperature, height growth of *E. regnans* and *E. fastigata* was significantly greater than *E. nitens* and *E. delegatensis* ( $p < 0.01$ ) which were not significantly different from each other. At the lower root temperature, height growth of *E. nitens* was significantly greater than that of *E. delegatensis* or *E. fastigata* ( $p < 0.001$ ). At 5°C, height growth of both *E. delegatensis* and *E. fastigata* was ca. 60% less than that at 10°C. In contrast the height reduction in *E. regnans* and *E. nitens* was ca. 30% or less (Table 5). *Eucalyptus regnans* achieved much better height growth at both temperatures at this age than all other species (Table 5). At both temperatures, the southern New South Wales form of *E. nitens* grew significantly better than the West Gippsland form ( $p < 0.01$ ), and within forms there was no significant difference between provenances.

A comparison of shoot to root ratios at the two temperatures (Table 6) suggests that *E. nitens* and *E. regnans* differed from *E. delegatensis* and *E. fastigata* in their ability to maintain stronger shoot growth relative to root growth at the lower

Period	Mean Temperature (°C)		Mean Relative Humidity %	
	Maximum	Minimum	Maximum	Minimum
May–June	26.5	16.5	67.0	43.1
July	27.2	17.6	67.3	46.4
Aug–Sept	29.1	15.1	72.7	40.6

Table 3. Mean monthly air temperatures and relative humidities in the glasshouse.

Variable	Height	Diameter	Root Length	Dry Weight Shoot	Dry Weight Root	Dry Weight Total
Temp.	0.007	0.023	<0.001	0.011	0.005	0.009
Temp. $\times$ Species	<0.001	0.353	0.433	0.893	0.342	0.822

Table 4. Probability values from analysis of variance testing the effect of soil temperature and temperature/species interactions. The main effect of species was significant at  $p < 0.001$  for all variables.



Species	Mean Height Increment (mm) Soil Temperature		Percentage Reduction in Height Growth with fall in Soil Temperature
	5°C	10°C	
<i>E. nitens</i> CR	299	440	32
<i>E. nitens</i> CT	277	403	31
<i>E. nitens</i> EE	364	500	27
<i>E. nitens</i> ET	395	481	18
<i>E. regnans</i>	436	630	31
<i>E. delegatensis</i>	160	406	61
<i>E. fastigata</i>	204	546	63
Least Significant Difference	67	66	

Table 5. Comparison of mean shoot height increment (mm) during the experimental period at two soil temperatures.

Species	Shoot(g)/Root(g) Soil Temperature			Shoot (mm)/Root (m) Soil Temperature		
	5°C	10°C	Difference	5°C	10°C	Difference
<i>E. nitens</i> CR	4.5	4.0	0.5	2.8	2.5	0.3
<i>E. nitens</i> CT	4.9	4.6	0.3	5.2	4.1	1.1
<i>E. nitens</i> EE	4.5	4.7	-0.2	5.2	4.7	0.5
<i>E. nitens</i> ET	4.2	3.9	0.3	5.1	4.1	1.0
<i>E. regnans</i>	5.2	4.6	0.6	6.9	4.9	2.0
<i>E. delegatensis</i>	3.8	4.2	-0.4	2.5	3.9	-1.4
<i>E. fastigata</i>	3.6	4.1	-0.5	6.8	7.2	-0.4

Table 6. Ratio of mean shoot to root dry weight growth and increment in length, and their differences at the two soil temperatures.

temperature. Comparatively low and high root lengths were responsible for the high and low length ratios for *E. fastigata* and the Royston provenance of the West Gippsland (CR) form of *E. nitens* respectively.

For those variables where there was no significant interaction between species and temperature, the data from the different temperatures were combined to determine the significance of difference between species (Table 7). *E. nitens*

overall grew significantly better ( $p < 0.05$ ) than *E. delegatensis* for all variables, and the growth of *E. delegatensis* was significantly greater than *E. fastigata* for all variables ( $p < 0.001$ ). The West Gippsland form of *E. nitens* from Royston (CR) grew significantly better than *E. regnans* and the other provenances of *E. nitens* for all variables. *E. regnans* was significantly better than *E. delegatensis* for all variables except root length and basal stem diameter.

Variable Temp°C	Basal Stem Diameter (mm)			Total Root Length (mm)			Shoot Dry Weight (g)			Root Dry Weight (g)			Total Dry Weight (g)		
	5°	10°	Mean	5°	10°	Mean	5°	10°	Mean	5°	10°	Mean	5°	10°	Mean
<i>E. nitens</i> CR	0.54	0.60	0.57	108	173	141	5.97	8.77	7.37	1.33	2.20	1.77	7.31	10.96	9.14
<i>E. nitens</i> CT	0.43	0.54	0.48	53	99	76	3.40	5.89	4.65	0.70	1.27	0.99	4.10	7.16	5.63
<i>E. nitens</i> EE	0.46	0.55	0.51	70	106	88	4.73	6.97	5.85	1.05	1.48	1.27	5.79	8.45	7.12
<i>E. nitens</i> ET	0.51	0.57	0.54	77	117	98	5.09	7.31	6.20	1.20	1.87	1.54	6.29	9.19	7.74
<i>E. regnans</i>	0.44	0.52	0.48	63	129	84	4.57	7.63	6.15	0.87	1.66	1.28	5.44	9.30	7.44
<i>E. delegatensis</i>	0.38	0.51	0.45	64	103	84	2.98	5.64	4.31	0.79	1.33	1.06	3.77	6.97	5.37
<i>E. fastigata</i>	0.27	0.40	0.33	30	76	53	1.46	3.53	2.46	0.41	0.87	0.63	1.88	4.40	3.10
Least Significant Difference			0.04			17			0.80			0.21			0.98

Table 7. Mean growth at each soil temperature for variables in which the species  $\times$  temperature interaction was not significant, and combined temperature means for each species.



## DISCUSSION

Although the effect of low root temperatures has been widely researched in horticulture (e.g. Cooper 1973, Nielsen & Humphries 1966), the implications of low soil temperatures on growth have received little consideration in the study of natural ecosystems. Low soil temperatures influence the formation of mycorrhizal associations (Theodorou & Bowen 1970) and increase the resistance to the uptake of nutrients (Kramer 1969). In particular, phosphorus is absorbed much more slowly at low than at high temperatures (Sutton 1969). Paton et al. (1979) observed the effect of root temperature on dehardening of four species of eucalypts and found that root temperature in the range 0.5–1.0°C delayed the dehardening response of warm shoots. In general, below the optimum temperature, height growth, root length and dry weight production show a broad sigmoidal increase with increasing temperature to an optimum, beyond which further temperature increase causes a decline in productivity. In most trials of horticultural or agricultural species, the optimum band of root temperature differed between species but was between 20–30°C. In this trial, root temperatures were probably well below optima for all species.

The significant interaction between species and temperature for height growth in this trial was not evident for the other variables tested. Eucalypts that compete with vigorous shrub growth in the early stages of establishment must make rapid, early height growth if they are to survive. In contrast, diameter growth changes little, particularly during the seedling stages. Thus height growth of seedlings may be more sensitive to the different root temperature regimes than the other variables tested. A similar discrepancy between height growth and dry weight production was recorded for *Pinus radiata* and *Pinus contorta* by Sweet & Wareing (1968). Dry weight of their second year seedlings was almost identical for the first eight months, despite more than 30% difference in height growth. In the following months, when the height growth of both species was negligible, dry weight production continued at a reduced rate and clear differences were finally evident in the partitioning of dry weight between root and stem. For the eucalypts tested in this trial, soil temperature appeared to influence this ratio with the response of *E. regnans* and *E. nitens* differing from that of *E. fastigata* and *E. delegatensis*.

The height growth of the southern New South Wales form (EE and ET), which was significantly better than the West Gippsland form (CR and CT), emphasises the difficulties associated with using seedlings as a guide to growth in later stages (Table 5). Pederick (1979) found ranking of provenances according to height growth changed after planting in the field. The Errinundra provenance which was initially the tallest had become the shortest within three years. Thus the growth of seedlings in containers is at best a poor guide to the response of mature to over mature trees growing in the natural environment.

Major Victorian occurrences of *E. nitens* are on plateaus. At the time of European settlement the most extensive populations of *E. nitens* occurred on Errinundra Plateau and Toorongo Plateau. Where the species occurs amongst more steeply dissected land forms, it is often confined to depressions, gully heads or on moderate slopes, in contrast to forests of surrounding species, eg. Connors Plains, Mt Useful Spur, headwaters of Snobs Creek, Moroka, Royston, Rubicon, Little and Taggerty Rivers, Torbreck Range (Pederick 1977) and slopes below the Baw Baw Plateau, e.g. Christmas Creek.

Plateau topography affects at least two factors that influence the vegetation. The undulating landform may increase the severity of frosts through cold air drainage, and by influencing the rate of fire spread, plateaus may reduce fire intensity and frequency.

Where the effect of frost is regular and pronounced it may delimit the tree line (Moore & Williams 1976). Rare but exceptionally severe frosts may influence the segregation of species (Davidson & Reid 1985), particularly amongst lower growing species. For tall growing eucalypts, frost effects are likely to be most severe during early establishment stages. Superior frost resistance combined with good growth rate has led to the increasing significance of *E. nitens* as a plantation species in Tasmania (Tibbitts 1986) and in other countries (Tibbitts & Reid 1987). High frost frequency on Errinundra Plateau could be at least partly responsible for that extensive occurrence of *E. nitens* (Featherstone et al. 1987), although a comprehensive study of variation in frost resistance indicated that the southern New South Wales and Errinundra provenances of *E. nitens* were least frost hardy (Tibbitts & Reid 1987). Damage due to frost would be most pronounced during early regeneration stages, particularly if regeneration occurred as even aged stands without the pro-



tection of an overwood. Since 1967, 4800 ha of forest have been logged by clear felling on Errinundra Plateau. Because of limited seed production, it has not been possible to regenerate these stands with pure *E. nitens*. Various mixtures of *E. nitens*, *E. delegatensis* and *E. fastigata* have been used, with extensive areas regenerated by a seed mixture containing equal proportions of all three. To date regeneration of all three species has occurred without a particular problem due to frost.

Because fire intensity is exponentially related to slope (McArthur 1967) fires burn less intensely on plateaus, and possibly less frequently. The multi-aged stands observed in Tasmania (Webb et al. 1983) are favoured on plateaus because fires create favourable seed bed conditions but have less tendency to destroy the overwood, particularly where this consists of mature trees. Forests with these structures have been observed over a long period in *E. regnans* and *E. delegatensis* forests in Victoria and Tasmania (Lindenmayer et al. 1990). Similar structures have been recorded in mixed stands of *E. nitens* and *E. delegatensis* in the headwaters of the Rodger River (Chesterfield et al. 1983), and in *E. nitens* on Errinundra Plateau. Fires in 1939 burnt the margins of Errinundra Plateau and, at one point where the regrowth occurred amongst a scattered stand of *E. nitens*, the multi-aged structure is clearly evident (Chesterfield et al. 1988). More recently, during burning of logging debris on Errinundra Plateau, approximately one hectare of mature forest recovered after complete defoliation by heat scorch. Thus, provided adequate gaps occur, the formation of multi-aged stands is not an improbable event.

The modification of the fire regime by plateau topography that favours the formation of multi-aged eucalypt stands also protects and encourages the development of rainforest in areas where soils and rainfall are adequate. In Victoria, *Atherosperma moschatum*, *Nothofagus cunninghamii* and *Elaeocarpus holopetalus* are important constituents of the *E. nitens* environment and, in the absence of fire, produce heavily shaded soils at maturity. Forests with similar composition and structure occupy similar environments in Tasmania. Here somewhat uneven aged stands of *E. delegatensis* first declined in the early 1960s, following a period of approximately 140 years without fire. Die-back was associated with the development of dense, closed forest understoreys. Trees of all age classes and canopy positions were affected and the onset of die-back was influenced by elevation.

Below 750 m, stands with a similar understorey were unaffected. After studying soil chemical factors, Ellis & Graley (1987) concluded that the small differences were more likely to be the result rather than the cause of successional changes. Ellis (1971) initially proposed that temperature changes in the root environment were a possible explanation. Over a two year period he recorded mean annual soil temperatures at a depth of 450 mm which were 2–3°C higher under grass in comparison with the rainforest understorey. After considering the environmental lapse rate he calculated that the rainforest invasion was equivalent to an altitudinal increase of 335–520 m, placing stands at 915 m, well above their altitudinal limit. Although the cause of die-back has not been ascertained with any certainty, the results for height growth in this study support the hypothesis that low soil temperatures may be a factor contributing to the decline in *E. delegatensis*. The natural post fire succession in this forest type is toward understoreys that are open at maturity and dominated by grasses, forbs, and ferns over the greater part of their range. Heavily shaded soils associated with a closed forest understorey are rarely present.

The similarities between the vegetation, fire regime and successional changes that have occurred on the elevated montane plateaus of Victoria and Tasmania are striking, with the exception that in Victoria, in areas where the rainforest understorey is dense, die-back of the *E. nitens* overstorey has not been observed. It is recognised that *E. nitens* can tolerate the incursion of rainforest species for longer periods than either *E. delegatensis* or *E. regnans* (United Nations Food and Agriculture Organisation 1979).

In the montane forests of southeastern Australia, fires over a wide elevation zone extending above and below the snow line have been sufficiently frequent to favour eucalypt species capable of producing regular and reliable seed crops. Although *E. nitens* has proven to be of equal or superior vigour to most of its competitors in growth trials, it is an unreliable and poor seed producer (United Nations Food and Agriculture Organisation 1979, Turnbull & Pryor 1978, Boland et al. 1980), particularly when compared to *E. regnans*, *E. delegatensis* and *E. fastigata*. Therefore, as the frequency of fire increases, the proportion of *E. nitens* in mixed stands is likely to decline, as noted in the Rodger River (Chesterfield et al. 1983).

The role of fire in the natural distribution of *E.*



*nitens* may resemble that of *E. grandis* Maiden, another eucalypt that associates with rainforest genera (Cromer 1960). The natural distribution of *E. grandis* is restricted to moist gullies or tablelands (Turnbull & Pryor 1978) due to its extreme sensitivity to fire (Pryor 1972). In the event of a change in fire regime to provide greater protection, the range of *E. grandis* may be readily extended into adjoining sites. Conversely, an increase in the frequency and intensity of fire would cause a contraction of the range. Ashton (1981) considered that during the Pleistocene fires may have been much rarer events than at present, and that the wet sclerophyll forests may have been relatively scarce ecotones between rainforests and the more drought resistant eucalypt forests or woodlands. As fire increased with increasing aridity during the early Quaternary, the contraction of rainforest may have enlarged the ecotone as fire reduced or modified rainforest over the greater part of its range. Some species of *Eucalyptus*, *Tristanopsis* and some rainforest genera adapted to regenerate following disturbance, or on marginal sites, e.g. *Araucaria*, *Flindersia* (Cromer & Pryor 1942), may have dominated this ecotone. The co-existence of eucalypts with cool temperate closed forest has been suggested in areas of Tasmania where fire is infrequent but sufficiently frequent (intervals less than 350 years) to maintain the eucalypts (Gilbert 1959). Thus the fire regime during the early Quaternary may have contributed to vegetation with similar structure to the mixed forest surviving on Errinundra Plateau, and in other isolated montane and coastal forests of southeastern Australia.

After the arrival of the Aborigines, a sudden and dramatic increase in fire frequency may have allowed eucalypts to expand into moister sites that they had not formerly occupied (Smith & Guyer 1983). In southeastern Australia, species belonging to the subgenus *Monocalyptus* are frequently best adapted to such sites (Florence 1981). Their more recent evolution on uniform, regularly watered sites may explain a tendency to form monospecific stands in tall open-forests, lower tolerance to prolonged water stress and their restriction to higher rainfall zones in the south-east and south-west of the continent. The expansion of fire-adapted species may have seen a contraction of rainforest and mixed forest dominated by eucalypts adapted to long intervals between fires. The contraction would have occurred last in the most fire protected localities. In some areas of Victoria,

elevation and topography appears to have been important for the survival of *E. nitens*.

At elevations below the limit of permanent winter snow, *E. nitens* is in competition with *E. regnans* and *E. fastigata* and at higher elevations with *E. delegatensis*. In general, its competitors produce reliable, heavy seed crops and regenerate prolifically after hot fires. In contrast, *E. nitens* produces light and irregular seed crops, and over a long period a series of hot fires could be expected to cause a progressive diminution in its abundance. In competition with *E. regnans*, a species of comparable vigour, the decline in *E. nitens* would be appreciable after each regeneration phase. The ability of *E. nitens* to compete with *E. delegatensis* is limited by the dormancy characteristics of its seed. The stratification requirement of *E. delegatensis* seed indicates an adaptation to an environment where snow may lie for extended periods during winter (Boland et al. 1980). Without this adaptation, the mortality of *E. nitens* germinants would be high, restricting the upper limits of natural establishment to elevations where snow generally persists for less than several weeks. This environment coincides with the extremes in distribution for *E. delegatensis* and *E. regnans*, allowing *E. nitens* to exploit the ecotone where both its competitors are at the limits of their range. The occurrence of plateau land form at this vulnerable point in the elevation gradient of both *E. regnans* and *E. delegatensis* may have protected the niche available to *E. nitens* by a modification of the fire regime. On plateaus, fires occur less intensely and probably less frequently, favouring the development of multi-aged stands. In forests with this structure, poor seed production would have been much less critical to species survival, and competitors promoted by fire less invasive. The fire regime occurring on plateaus also favours the development of rainforest understoreys. An ability to co-exist at various times for extended periods in this association, may have been a factor in the survival of *E. nitens* on plateau and gully topography in Victoria.

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