# The ecology of a stressful site: Mount Towrong, Central Victoria 1967-1997

D.H. Ashton[1] and D.K. Spalding[2]

Botany Department, Melbourne University, Parkville, Victoria 3052
Present addresses: [1]92 Warrigal Rd, Surrey Hills, Victoria 3127
[2]534 Monbulk Rd, Monbulk, Victoria 3793

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## Summary

Species on Mt Towrong are distributed along soil moisture gradients which are dictated chiefly by aspect, altitude, soil depth and proximity to drainage lines. On the warm and dry western aspect large areas of shallow, rocky soils alternate with bands of deeper soils. On the cooler eastern aspect, soils are relatively deep throughout. Drought damage has occurred on the rocky soils of the western aspect six times in the last 25 years, whenever the annual rainfall was less than about 50% of the long-term mean. Fires are also recurrent perturbations that are most severe in drought years, especially when accompanied by hot NW winds. The fire of 1983 caused severe damage over the whole western aspect of Mt Towrong. Damage on the eastern lee slope was much less severe. An assessment of relative recovery of tree species from these perturbations was based on various combinations of species pairs growing in close proximity to one another. The rank order of drought resistance was *Allocasuarina verticillata* > *Eucalyptus goniocalyx* > *E. radiata* > *E. obliqua* (= *E. viminalis*) which was the reverse of that in relation to fire+ drought, that is, *E. obliqua* > *E. radiata* = *E. goniocalyx* > *Allocasuarina verticillata*. Seedling regeneration of tree species in the inter-drought periods was meagre but nevertheless the most mesic species, *E. obliqua*, consistently dispersed onto adjacent dry rocky sites, only to be killed in each of the ensuing drought periods. After fire, seedling regeneration of eucalypts (especially *E. obliqua* ) was generally prolific, although the vigour and density of seedlings was patchy and related to the pattern of redistributed nutrient-rich hillwash. After 10-12 years, survival of the best seedlings was evident only in gaps in the reconstituted canopy.

On this stressful site the indigenous species have been resilient to serious perturbations of the environment. It seems likely that, for the retention of species on a site, frequencies of fires and droughts may be more critical than the occasional exceptionally severe event.

*Keywords:* forest ecology, drought, fire, regeneration, *Eucalyptus obliqua*, Victoria, Australia

## Introduction

Drought and fires occur over much of Australia every few decades. In the wetter coastal climates droughts usually last less than one year but the effects on vegetation may be catastrophic. Whalley (1973) has pointed out that native species are adapted to severe droughts and may avoid or resist these conditions. Although fires may occur whenever there is sufficient fuel in the presence of hot, dry and windy conditions, severe fires in wetter climates usually occur only in periods of great water stress. Droughts in the last 50 years in southern Victoria have affected the vegetation of Mt Towrong and on some occasions have been accompanied by severe fire. The effects of these disturbances on the vegetation, and the manner in which species have recovered and community composition changed, have been the focus of study in this area for the last 30 years (e.g. Spalding 1987).

## General environment, variation and site quality

Mt Towrong terminates a short, southern spur from the Great Dividing Range in Central Victoria (lat. 37˚25’S, long. 144˚38’E) at a maximum altitude of 792 m (Fig. 1). It forms part of an Upper Devonian dacite massif which rises to an altitude of 1011 m and, because of its location and topography, receives a reliable, seasonally well distributed mean rainfall of 1085 mm per annum (CV =22%). Its slopes are relatively steep (25-33˚), and in summer the rocky, western aspect receives full insolation in mid-afternoon and can be very dry.

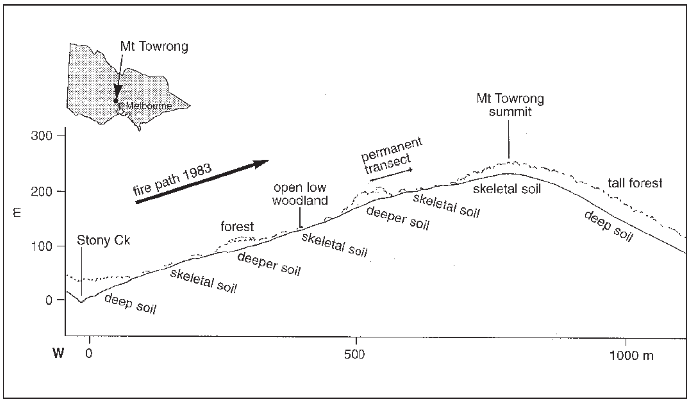

**Figure 1.** Topographic profile of Mt Towrong

Over ten times in the last fifty years the annual rainfall has been more than one standard deviation below the mean. In the very dry years of 1938-39, 1967-68 and 1982-83 when annual rainfall was only about 50% of the long-term mean, droughts were severe enough to cause severe damage to eucalypt forest on shallow soils (Ashton *et al*. 1975). Damage also occurred in 1985, 1993 and 1997 because, although the annual rainfall in the general area was not particularly low, the local distribution was variable, and on this site, it was deficient.

Fire, like drought, is a well-known recurrent perturbation in eucalypt forest (Mount 1969), and in wetter climates tends to occur in very dry years (Ashton 1981; Gill 1993, 1998). At this site, severe fires occurred in 1939 and 1983. Although there may be severe damage, most vegetation is resilient and regenerates from seedlings, or vegetatively from epicormic buds or below-ground organs. Hence the vegetation on various parts of this mountain has suffered periodic damage from drought with or without concurrent fire.

The main factors controlling site quality are aspect, proximity to drainage lines, altitude in relation to cold front cloud bases (i.e. fog drip), the occurrence of massive rock outcrops and the variable depth and available volume of exploitable soil (Ashton *et al*. 1975). There is, therefore, great variation in the size and stocking of trees on Mt Towrong. Drought damage is clearly most severe in low sclerophyll eucalypt forest and open woodlands on shallow soils in and around large rock outcrops. Three such areas occur step-wise up the western face, separated by diagonal bands, 30-50 m wide, of deeper soil carrying taller eucalypt forest (Fig. 2). These bands of forest were undamaged by drought (Fig. 3) and are almost certainly associated with better moisture conditions along major joint planes in the dacite bedrock. Little damage occurred on the summit of the mountain above 600-700 m where, although the soils were rocky and shallow, moisture stress was presumably alleviated in summer by frequent fog drip from low cloud. No drought damage occurred on deeper krasnozemic soil on the cooler, eastern aspect.

**Figure 2.** The western face of Mt Towrong after the 1991 drought showing the damaged, lighter-toned vegetation on rocky areas and darker diagonal bands of taller intact forest

During the most severe droughts the normally permanent stream at the foot of the mountain has run dry and some of the highly stocked wet sclerophyll forest has suffered damage, presumably because the capillary fringe of the watertable had fallen below the root zone of the trees. The altitudinal range of the study site from Stony Creek at the foot of the slope to the summit is 238 m which, based on the regional relationship of annual rainfall to altitude represents an increase in precipitation of about 198 mm (Ashton 2000). From hydrological research in central Victoria (Brookes and Turner 1963), fog drip in forest on the summit of Mt Towrong could add a further 200 mm to the annual precipitation.

In this region fires are usually driven by strong north to west winds, which in summer are invariably hot and dry. Therefore, the steep western slopes in such years suffer not only drought but the brunt of any advancing fire. By contrast, the lee slope is not only cooler but is less drought prone and normally subject to fires of lesser intensity.

**Figure 3.** The typical sharp boundary between shallow, rocky soil and deep soil on the mid-western face of Mt Towrong

## The effect of repeated droughts

### The drought of 1967-68

Towards the end of the severe, prolonged 10-month drought of 1967-68, large patches of vegetation on the western slope of Mt Towrong below 700 m appeared as if they had been scorched. Death of eucalypts occurred not only on the shallowest soils but also on deeper soils where tree stocking was relatively high. Recovery of tree species, which began soon after heavy autumn rains in 1968, was monitored in five categories based on the maximum height above ground level of regenerating epicormic buds. The ranking of species was achieved by comparing the stages of recovery where combinations of species grew within 1-2 m of each other on various sites (Ashton *et al.* 1975; Kirkpatrick and Marks 1985). The most drought resistant tree species was *Allocasuarina verticillata*[1] (she-oak) followed by *Eucalyptus goniocalyx*, *E. radiata* and *E.obliqua* (= *E. viminalis*). Damage was most severe in sites where the volume of rocks in the upper 30 cm of the soil profile exceeded 30% (Ashton *et al*. 1975). Although this order of resistance was evident in the field, based on the distribution of species along moisture gradients, *E. goniocalyx* suffered the greatest damage because it was the only eucalypt able to grow and persist in the driest rocky sites at lower altitudes.

After the drought, conspicuous seedling regeneration of *E. obliqua* developed on the western face from where seed was shed from relatively unaffected trees growing on the diagonal bands of deeper soils. Seedlings of this species also dispersed up to 50 m (or 1.4 times tree height) onto adjacent rocky sites occupied by stunted, open woodland of *E. goniocalyx*. After five years the latter seedlings had reached heights of 2-3 m. Seedlings of *E. radiata* occurred less frequently, whilst those of *E. goniocalyx* were relatively rare.

Species composition of communities was assessed at eight intervals along a transect from Stony Creek at the foot of the western slope, to the summit and down the eastern slope. A vegetation profile from a mid-slope forest (25 m tall) of *E. obliqua* on deep soil, to a low, open woodland (2-3 m tall) of

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[1] Nomenclature follows Walsh and Entwhistle 1994, 1996 and 1999

*E. goniocalyx*, on skeletal soil, was drawn at intervals over 24 years to record the 'ebb and flow' of invasion by *E. obliqua* onto the xeric site (Fig. 4).

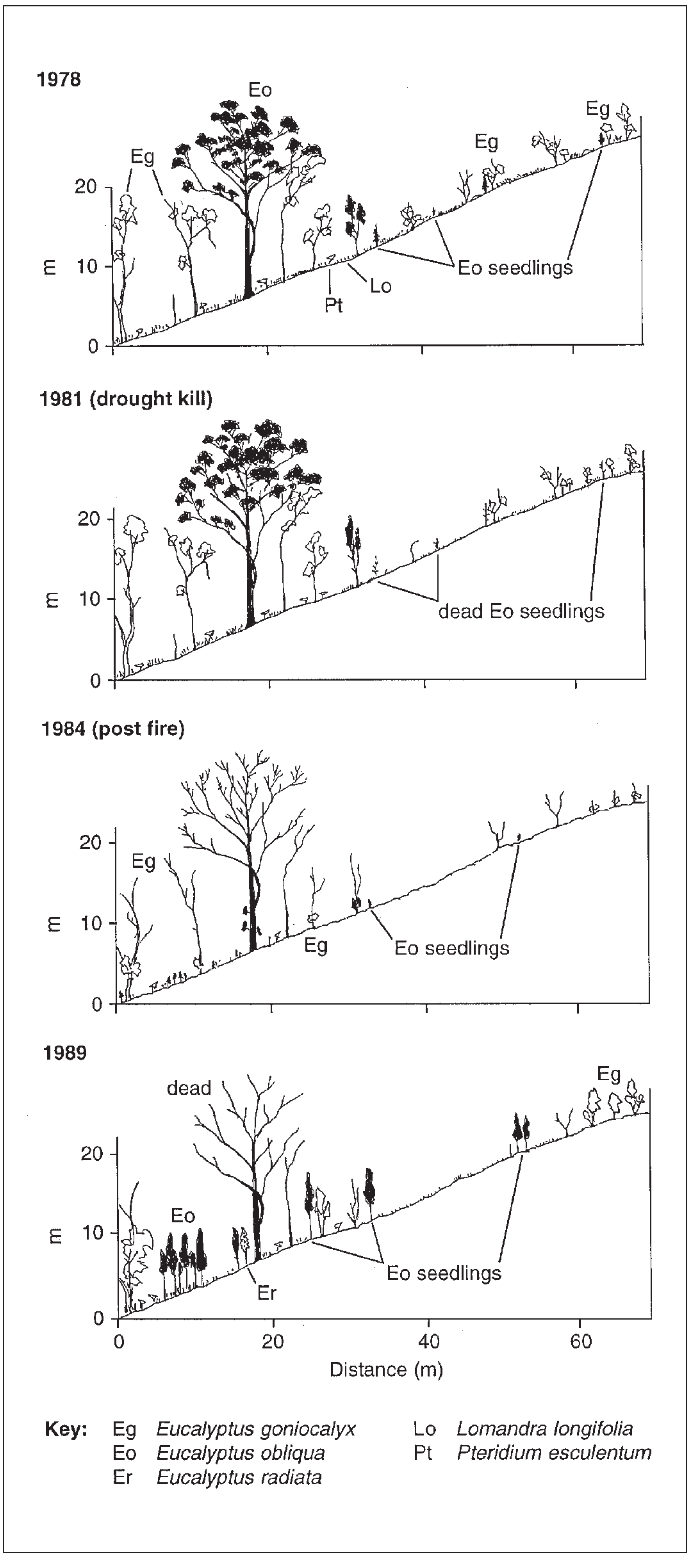


**Figure 4.** Profile drawings of vegetation along a transect across a zone of deeper soil to skeletal soils on the western face at different times from 1978-1989

## The drought of 1972-73

During this drought all the *E. obliqua* invasion of dry sites since 1968 was killed. The dry season ended in February 1973 with the fortuitous arrival of a moist monsoonal air mass and very heavy rain. Following good subsequent rain the invasion of rocky sites by this species was repeated and accompanied by regrowth of lignotuberous coppice of *E. goniocalyx*. Over the following ten years *E. obliqua* seedlings developed conspicuous apical dominance and reached heights of 3 m which equalled the height of the resistant, coppiced trees of *E. goniocalyx* on rocky open woodland.

## The drought of 1982-83

This extremely dry season was, like other such droughts, presaged by a very dry winter, so that little replenishment of sub-soil moisture occurred. Death and damage of trees on the western slopes was widespread, especially on skeletal soils. As before, all *E. obliqua* saplings invading the dry sites since 1973 were killed. This drought was also associated with the devastating fire of late summer 1983.

## The drought of 1985

In this drought, damage was restricted to the shallow soils, but particularly those at lower elevations where annual precipitation is lower. As in other droughts, saplings of *E. obliqua* invading rocky sites were killed (Fig. 5).

**Figure 5.** Dead sapling of *Eucalyptus obliqua* (centre) in rocky soil after drought of 1985

## The drought of 1991

This drought was as severe as that in 1967-68, with widespread death of seedlings and trees on shallow rocky soils on N, NW, W and SW aspects as well as in dense stands which had regenerated after the 1983 fire on the E aspect. This drought was relatively localized since scattered rains during summer in this region did not occur at Mt Towrong which, as a consequence, suffered a five-month rainless period.

## The effect of the fire of 1983

### Effects on vegetation and soil

On 16 February 1983, when air temperatures reached 43˚C, a gale-force westerly wind drove a fire up and over the summit of Mt Towrong. All vegetation on the western slope, much of which was already drought-stressed, was either killed or severely damaged by the radiant and convective heat of the crown fire. Humus and lichens were burnt off exposed dacite rocks, the surface layers of which were patchily exfoliated. On the eastern slope the fire intensity diminished to a surface fire in which most tree crowns were severely scorched and all understorey species were burned to the ground.

Topsoil on the western slopes was rendered strongly hydrophobic by the heat of the fire. This resulted in the fertile upper 5-10 cm of soil (including ash and charcoal) being washed downhill by the first heavy rains of autumn. Such hillwash accumulated at sites of local slope reduction, against obstacles such as logs, large rocks and tree butts, or in the basements of burnt-out houses. In other places in central Victoria massive soil movement resulted in mud slides (Leitch *et al*. 1983).

### Ranking of vegetative recovery

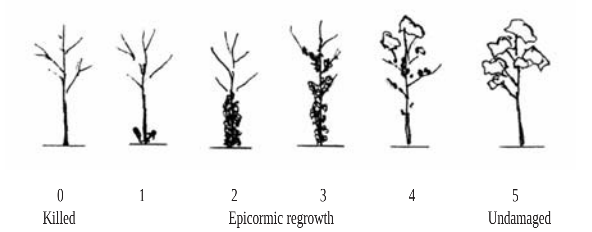
Recovery of tree species after one year was ranked in five categories similar to that used in drought recovery, by measuring the maximum height above ground of epicormic shoot emergence. Thus where damage was light, epicormics occurred on secondary branches in the crown and, where severe, shoot regrowth occurred only as basal coppice. As this is related to bark thickness (Gill and Ashton 1968), young stems and young plants are the most susceptible. Of the tree species, *E. obliqua* was the most resilient and *Allocasuarina verticillata* the most sensitive (Table 1). However, exceptions occurred where 10-15 cm of amorphous humus had accumulated at the base of large old trees, and smouldered long enough for the heat front to kill or severely damage the cambium (Cremer 1962). Some trees showed initial recovery only to be killed later by pathogenic, wood rotting basidiomycete fungi. *E. goniocalyx* occurred on a range of soil depths and showed greatest fire damage on the skeletal soils where drought stress was greatest (Table 1).

*Allocasuarina verticillata* and *Acacia dealbata* regenerated commonly from root suckers up to 1-2 m from the trunk whereas many of the lignotuberous shrubs, such as *Olearia argophylla*, coppiced. Rhizomic lilies and ferns recovered rapidly as did tussock grasses and tree ferns with protected growing points.

### Density of seedling regeneration

Germination of seed followed autumn rains in 1983. Seed of eucalypts and she-oak was dispersed from persistent woody fruits in the scorched crowns, whereas understorey species regenerated from the soil seed bank or from aerial dispersal outside the area. Soil seed bank germination was responsible for carpets of herbs such as *Viola hederacea*, *Geranium potentilloides* and *Gonocarpus tetragynus*, whereas wind dispersal probably contributed to the populations of numerous compositae, both native (*Senecio quadridentatus*) and introduced (*Sonchus oleraceus*).

**Table 1.** Recovery values for tree species at Mt Towrong one year after fire in the drought year 1982-83



| Stand location and species | Mean recovery scores | | | | |
|---|---|---|---|---|---|
| | Tree girth at breast height (m) | | | Weighted mean score score | Weighted mean score as fraction of max. of 5.0 (%) |
| | 0-1 | 1-2 | 2-3 | | |
| Bands of deeper soil (little drought damage) | | | | | |
| *E. obliqua* | 2.26 | 3.30 | 3.67 | 2.76 | 55 |
| *E. viminalis* | 1.14 | 2.22 | 3.67 | 2.21 | 44 |
| *E. radiata* | 1.06 | 2.22 | 3.00 | 1.33 | 27 |
| *E. goniocalyx* | 1.46 | 1.94 | - | 1.38 | 28 |
| Rocky soil, lower slope (severely droughted) | | | | | |
| *E. goniocalyx* | 1.08 | 1.57 | - | 1.14 | 23 |
| *Allocasuarina verticillata* | 0.40 | 0.50 | - | 0.54 | 11 |

Eucalypt seedlings were generally prolific not only in moist gullies and deeper soils but also on the rocky summit of the ridge. Stocking after one year ranged from 93 220 to 218 stems ha$^{-1}$ depending on the site and the distance from seed source (Table 2). Most seed fell from persistent fruits up to one to two tree heights from the parent tree, although some *E. viminalis* dispersed up to five tree heights from the source in gullies - due probably to reduced wind resistance in defoliated but capsule-bearing crowns (Ashton 1986). *E. obliqua* was the commonest tree species in the seedling cohort (Table 3), accounting for 87% of total eucalypt regeneration in 1986. Over the mountain it accounted for 40% of tree stocking and 57% of basal area. Although the relative tree stocking of *E. goniocalyx* was similar to that of *E. obliqua*, its relative basal area was low and its seedling contribution meagre. Pattern analysis, using geometrically enlarged contiguous quadrats (Kershaw 1964), showed a strong statistically significant peak in seedling stocking under canopy and in large gaps in the canopy.

### Growth of *E. obliqua* seedling regeneration

In densely regenerated sites, competition was intense and within three years seedling crown closure caused the differentiation of the populations into dominant, co-dominant, intermediate and suppressed crown classes. By 1987, patches of *E. obliqua* seedling regeneration showed marked variation in growth both under the regenerating tree canopy and in large gaps. The vigour of these patches was arbitrarily classified by the height of dominant plants as good (>3 m), moderate (2-3 m) and poor (<1 m) (Table 4). At least five patches of each class were selected at random and, if covering an area with a diameter >5 m, were assessed for stocking using 2 x 2 m quadrats. All seedling canopies were classified into crown classes and their height measured. Five four-year-old *E. obliqua* seedlings from good, medium and poor patches in gaps and under the regenerating forest canopy were harvested to ground level. Ring growth of stems was analysed at 10 cm intervals to determine the rate of height growth since germination.

In 1987, light intensity across gaps one tree height in diameter was determined using a fish-eye camera to estimate the percentage of both diffuse and direct sunlight (Anderson 1964). Diffuse light in gaps and under canopy was 43% and 32% of full light, respectively, and was statistically correlated with height growth of regeneration. The tallest seedlings, however, were not distributed centrally in gaps but displaced towards areas of better direct sunlight to the south. At the southernmost end of such gaps seedlings would also have been competing with the root system of the adjacent trees (Fig. 7).

**Table 2.** Density and mean height of trees (1983) and tree seedlings of all species on different sites at Mt Towrong three years after the 1983 fire

| Site | Trees 1983 | | | Seedlings 1986 | |
|---|---|---|---|---|---|
| | Stocking | Fraction dead | Mean height | Stocking | Mean height |
| | (stems $ha^{-1}$) | (%) | (m) | (stems $ha^{-1}$) | (m) |
| Gully | 411.3 | 14.3 | 29.0 | 93 220 | 1.88 |
| Western tree bands | 434.3 | 9.5 | 14.3 | 26 050 | 1.55 |
| Western rocky sites | 445.5 | 33.4 | 5.4 | 218 | 0.95 |
| Summit | 381.1 | 7.2 | 24.8 | 88 000 | 0.45 |
| Eastern slope | 459.1 | 14.5 | 28.0 | 19 500 | 1.47 |

**Table 3.** The relative contribution of tree species to overstorey stocking in 1983, and seedling regeneration in 1986, three years after the fire. The percentage contribution was calculated from pooled data from all eight sites on Mt Towrong (including root suckers of *Allocasuarina*).

| Species: | Fraction of all trees 1983 (%) | | Fraction of all seedling regeneration 1986 (%) | Seedlings (1986) per tree (1983) |
|---|---|---|---|---|
| | Stocking (no. stems) | Basal area | | |
| *E. obliqua* | 40.4 | 57.2 | 87.2 | 134.8 |
| *E. viminalis* | 16.2 | 8.1 | 7.1 | 71.4 |
| *E. radiata* | 8.1 | 14.3 | 3.5 | 27.3 |
| *E. goniocalyx* | 45.0 | 20.1 | 1.4 | 2.0 |
| *Allocasuarina verticillata* | 0.1 | 0.3 | 0.6 | 28.3 |

Table 4 shows the wide range in height of regeneration at seven years (both upper quartile and total) across the vigour classes – from 4.5 m for regeneration of good vigour within gaps to 1.1 m for regeneration of poor vigour under the canopy. The growth of seedlings classified as 'poor' was significantly less than that of other classes, even in the first year of growth, and irrespective of the presence or absence of a canopy (Fig. 6). A profile drawing across a gap in *E. obliqua* dry sclerophyll forest is shown in Figure 7. At seven years, both stocking and height of regeneration in gaps were greater than those under the, by then, reconstituted canopy. The good growth patches maintained a vigorous growth rate typical of post-fire eucalypt regeneration.

**Table 4.** Demography of seven-year-old *Eucalyptus obliqua* seedlings arising after the 1983 fires at Mt Towrong North, in gaps and under the regenerated canopy of adjacent *E. obliqua* forest, showing stocking and mean height of total seedlings as well as those in the upper quartile of frequency distribution (* also compare a', c', b'' c''.)

| Vigour class | Site | Stocking per 10 m2 | Mean height (m) | |
|---|---|---|---|---|
| | | (no. stems) | Upper quartile* | All |
| Good | Gap | 110.2 a | 4.46 a' (17.9%) | 2.66 a |
| | Under canopy | 94.5 a | 3.49 b" (17.9%) | 2.36 b |
| Moderate | Gap | 77.5 a | 2.72 c' (19.4%) | 1.65 c |
| | Under canopy | 69.5 a | 2.61 c" (16.4%) | 1.55 c |
| Poor | Gap | 28.5 b | 1.18 d (15.1%) | 0.67 d |
| | Under canopy | 19.5 b | 1.07 d (15.4%) | 0.63 d |

Seedlings of *E. obliqua* were commonly attacked severely by leaf-spotting fungi, particularly *Aulographina eucalypti*. In better growing conditions eucalypts outgrew such attacks each year, but under canopy this did not occur and heavily infected plants eventually succumbed after 10-12 years. Under the reconstituted canopy of *E. obliqua* forest, growth of *E. obliqua* seedlings was also impaired by dense, vigorous regrowth of *Acacia verticillata*.

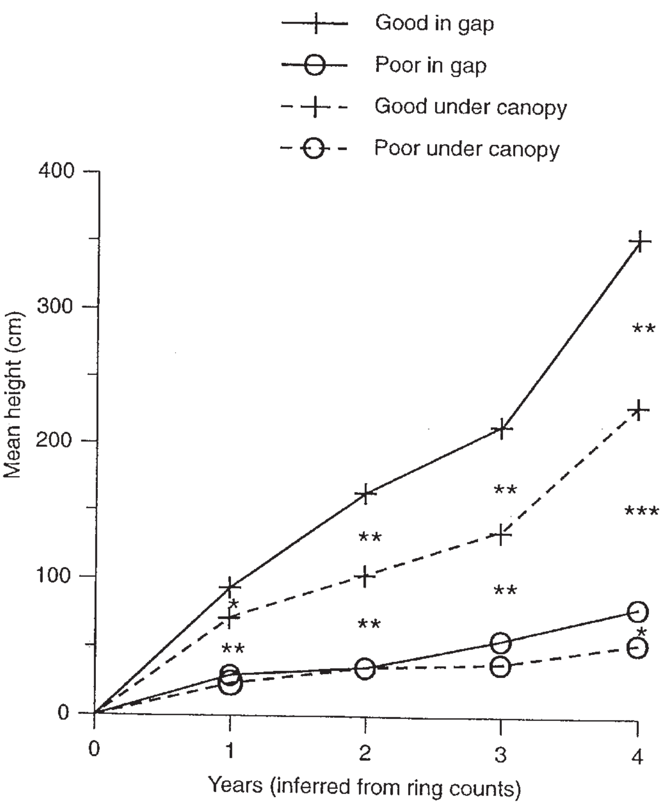


**Figure 6.** Reconstructed growth curves of four-year-old *Eucalyptus obliqua* regeneration on good and poor soil patches

A bioassay, based on the growth of *E. obliqua* seedlings in pots 12 cm in diameter (n=10) in topsoil from good and poor seedling patches, five years after the fire demonstrated the greater fertility of the good patch soils in gaps. Under canopy such differences in fertility appear have abated. Analysis of topsoil collected one year after the fire indicated that good patch soil was higher in available P ($HCO_3$ extract) and total N than soil from poor patches (Table 5). Three years after the fire, the N content of foliage collected from good patch seedlings (>2 m high) was significantly higher (1.47%) than from poor patch seedlings (<1 m) (1.14%) at $P<0.05$ (Student's *t* test). The response of seedlings in various soil patches is consistent with observations on the removal or accumulation of nutrient-enhanced topsoil after the fire.

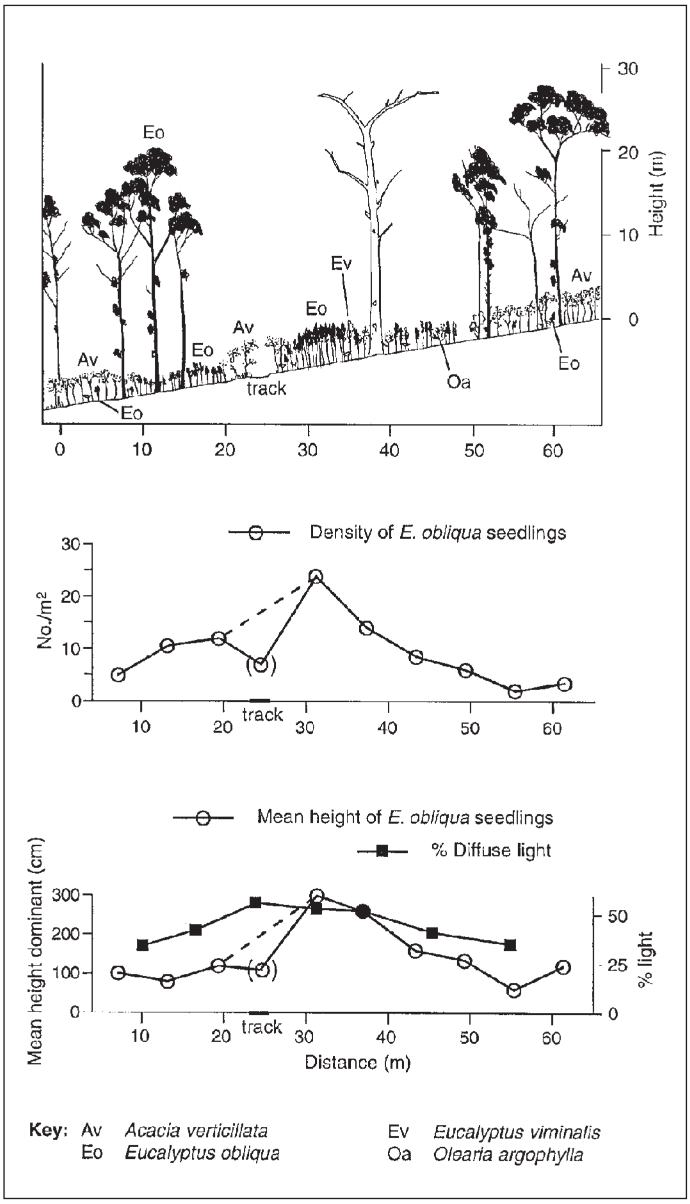


**Figure 7.** Profile drawing across a gap in *Eucalyptus obliqua* dry sclerophyll forest at Mt Towrong North in 1990, together with estimates of light intensity

**Table 5.** Bioassay in glasshouse using *Eucalyptus obliqua* seedlings in soils (0-15 cm) from various microsites, 1988; plants harvested after three months. Different letters against values in each row indicate statistical significance at $P<0.05$ (Student's *t* test).

| Seedling indicators | In gaps | | Under canopy | |
|---|---|---|---|---|
| | Good patch | Poor patch | Good patch | Poor patch |
| Average plant biomass (g) | 6.1 a | 1.8 b | 2.5 b | 2.2 b |
| Height (cm) | 27.5 a | 8.4 b | 15.4 b | 10.0 b |
| Shoot:root (biomass) | 2.5 | 1.9 | 2.4 | 2.0 |
| N (mg per plant) | 66.8 | 27.4 | 35.3 | 29.3 |
| P (mg per plant) | 7.6 | 1.4 | 3.3 | 1.6 |

## Discussion

Drought and fires are major factors affecting vegetation on Mt Towrong. Drought damage is strongly associated with skeletal soils, particularly those on the warm north to west aspects. Similar findings were reported by Pook *et al.* (1966) near Canberra and Kirkpatrick and Marks (1985) near Hobart. Typically, drought imposes a slow sustained stress over many months, whereas fires in this region are typically rapid and inflict greatest damage on the hotter, windward slopes where vegetation is also drier and more flammable. Thus fire has inflicted very severe damage on trees on the stony soils on Mt Towrong. In general, fire severity and damage is mainly dependent on aspect and slope, wind speed and the availability of dried fuel (Luke and McArthur 1978). It is well known that fires are worst on windward slopes, which in this area are usually the hotter north to west aspects.

### Vegetative recovery

The relative severity of both drought and fire damage was based on the maximum height above ground at which epicormic shoots appear after the onset of autumn rains. Resistance to fire is related primarily to the thickness of bark which itself is dependent on stem diameter and therefore age of the stem (Gill and Ashton 1968; Ashton and Martin 1998). Resistance to drought is related to the water content and water potential generated in the meristematic tissues. Since there is a marked gradient of water potential in trees with height above ground (Legge and Connor 1977), it is likely that the uppermost issues will suffer death before those close to the ground. Pook *et al.* (1966) indicated that droughted eucalypts often showed a significant decrease in tissue moisture with height from the lower trunk to the leaves and twigs of the canopy. Shorter-term droughts may permit considerable recovery from older parts of the tree, but in sustained severe droughts trees may dry out completely, resulting in the separation of wood and bark and subsequent complete death. The lignotuber of eucalypts or the legacy of the bud-bank so produced at ground level is an important feature affecting survival after stressful events.

Because the vegetation in 1982-83 was almost certainly damaged by drought, it was impossible from our study to separate drought and fire damage. The ranking of species recovery in 1984 was therefore a resultant of both perturbations in 1983. This was clearly different to that of drought alone in other years.

Because of the differing morphological and physiological responses between the main tree species, the rank orders of resistance to drought and fire + drought were different. *E. obliqua* was the most drought-sensitive tree species and normally occurs in the most mesic sites. In marginal sites it was severely damaged or killed by drought. It was, however, the most resistant to fire since it possessed the thickest bark. If the outer layers of bark are removed by repeated fires, however, such an advantage may be negated. *Allocasuarina verticillata* was by far the most drought-resistant tree and, although readily killed by fire, recovered vegetatively from root suckers and coppice. These results are generally similar to those found by Kirkpatrick and Mark (1980) near Hobart in droughts of 1976-83, and by Martin and Specht (1962) and Sinclair (1980) in the Mt Lofty Ranges near Adelaide. Understorey species also often recovered from damage from both fire and drought by means of lignotubers (*Olearia argophylla*), rhizomes (*Pteridium esculentum*, *Cheilanthes austrotenuifolia*, *Tetrarrhena juncea*) and hemicryptophytic buds (tussock grasses, *Poa labillardierei*). The apical bud of tree ferns (*Cyathea australis*) was resistant to fire but not to prolonged drought.

### Seedling regeneration

Canopy storage of seed in woody fruits is a feature of both eucalypts and she-oak. Seed fall occurs between spring and autumn after drying out of the fruit either following abscission layer development (Cremer 1962), or the death of subtending branches. In drought periods, seed may lie on the ground for some time and be susceptible to harvesting by insects such as ants and bugs (Cunningham 1960; Ashton 1979). Seedling regeneration therefore may be sporadic and subject to severe competition from surrounding species. After fire, capsules are dried by the rapid passage of the fire front and all surviving seed falls soon afterwards onto ash, charcoal and bare soil. Germination in autumn is prolific since predator demand tends to be satiated (O'Dowd and Gill 1984 ). Establishment is usually good since light, soil moisture and soil nutrient supplies are enhanced considerably. Most understorey species regenerate abundantly from the soil seed bank, producing carpets of dicotyledonous herbs (*Viola hederacea*, *Geranium potentilloides*, *Hydrocotyle hirta* and *Gonocarpus tetragynus*). Grass seedlings of species of *Poa*, *Danthonia*, *Stipa*, *Tetrarrhena* and *Microlaen*a may be locally abundant, together with vegetative regeneration.

### Pattern of vigour of *E. obliqua* seedlings after the 1983 fire

Within three years of the fire, marked variation in the vigour of *E. obliqua* was evident in patches of one to several square meters. Initially it was thought that all patches of seedling regeneration would have been stimulated by the 'ash bed effect' of the fire (Pryor 1963) and that later differentiation would have occurred as a result of adjustment to competitive factors exerted by the redeveloping canopy. However, the same variation in vigour occurred in both gaps and under the developing tree canopy. Ring-count growth analysis of seedling regeneration in 1987 indicated that the differentiation of good and poor growth patches had existed from the first year. It was found to be correlated with the local erosion and accumulation of hillwash in discrete patches. Topsoil from good patches was higher in N and P than poor patches, and bioassay growth trials confirmed differences in top soil fertility.

After 10-12 years seedlings in good growth patches in gaps continued to develop as vigorous saplings, while those under the reconstituted tree canopy became suppressed. Seedlings in poor growth patches became increasingly affected by fungal leaf spots (especially *Aulographina eucalypti*), and were unable to maintain adequate growth and succumbed. In addition, dense stands of *Acacia verticillata* under eucalypt canopy appeared to have been detrimental to the growth of *E. obliqua* seedlings, in spite of any advantage bestowed by nitrogen fixation.

### The frequency of perturbations

Over the last three decades, droughts have recurred at intervals of two to six years. This has had the effect of repeatedly damaging species on shallow soils and killing mesic species which had dispersed onto them in the intervening periods. Such perturbations could also eliminate species with relatively long juvenile non-flowering periods. Jacobs (1955) pointed out succinctly that a series of favourable years may be a prerequisite for regeneration of some eucalypts on marginal sites. It is probable that repeated stress at short intervals could weaken trees (Chapman and Ronaldson 1958) and result in tree death from secondary causes such as fungal or insect attack. A similar argument could be made for repeated fires. At Mt Towrong fires have occurred at long intervals (50-60 years) but have left a legacy of dense even-aged eucalypt stands or, where damage has been less severe, multi-aged stands. Although severe fires are usually associated with dry years, the area disturbed is generally discrete and controlled by aspect and slope. Undoubtedly the nexus of drought and fire paths has exacerbated the damage inflicted on the north to west slopes. There is little doubt that the frequency of severe fires has increased since European times (King 1963). Even so, the species dominating and persisting in the various niches on Mt Towrong are remarkably resilient to the regime of disturbance imposed today.

On Mt Towrong the tree species appear to conform to those plants with stress-tolerant strategies (Grime 1979), although there is considerable variation in such tolerance. Grubb (1998) has sharpened concepts relating to plant survival strategies and has referred to eucalypts as 'superplants' with switching strategies from seedling to adult stages. Eucalypts characteristically have dimorphic foliage which shows differences in shade tolerance (Ashton and Turner 1979) and water use (Ashton *et al*. 1969). *E. obliqua* is the most mesic of the eucalypts present and transpires rapidly, whereas *E. goniocalyx* readily curtails water loss through both leaves and young stems and in stressful periods rapidly sheds juvenile foliage. The drought resistance of juvenile *E. radiata* is similar to juvenile *E. goniocalyx* but the behaviour of adult foliage is similar to that of *E. obliqua*. *Allocasuarina verticillata* is both xeromorphic and xerophytic. Its water use is severely curtailed in drought and it withstands low water potentials (Ashton *et al*. 1969). In this area it occurs on the driest sites where shading and competition from eucalypts is reduced.

An important feature of this study is the resilience of tree species to repetitive stress, and the question that may be asked is 'how severe does an environmental perturbation have to be before a species is removed from a site?'. Trees species on Mt Towrong have recently endured three decades of perturbation and remained on site. It has been inferred from pollen analyses that the distribution of most vegetation communities in southern Australia has changed during the climatic fluctuations of Quaternary times (Kershaw 1998). Precisely how the weather conditions associated with such climate changes have affected vegetation is yet to be understood. Bryant (1997) noted that at least in North America, Greenland and the Antarctic, climatic changes at the end of the last glacial period were completed in decades after periods of considerable oscillation (Daansgard-Oeschler Oscillations). If such rapid fluctuations had occurred in southern Australia, they could have tested species survival on marginal sites such as on Mt Towrong. Climate change from a so-called 'greenhouse effect' is prophesied, but whether this will be manifest by a gradual deterioration of conditions or an increase in the frequency and duration of lethally extreme events is not known. The precise character of the climatic changes which trigger the removal of vegetation from a site is likely to depend on the severity and rate of such change, the adaptive capacity of the species involved and the variability of their collective gene pool.

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