THE ROYAL SOCIETY

Origins of the southeastern Australian vegetation

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Australia is an ancient continent with an interesting geological history that includes a recent major shift in its position, both globally and compared with neighbouring land masses. This has led to a great deal of confusion over many years about the origins of the Australian biomes. The plant fossil record is now clarifying this, and it is clear that the ancient Gondwanan rainforests that covered Australia while it was still part of that supercontinent contained many of the elements of the modern vegetation. However, major climatic sifting, along with responses to other factors, including soil nutrient levels, disturbance regimes, atmospheric CO_2 levels, fire frequency and intensity, glaciations and the arrival of humans, have had profound impacts on the Australian vegetation, which today reflects the sum of all these factors and more. The origins of Australian vegetation and its present-day management cannot be properly understood without an appreciation of this vast history, and the fossil record has a vital role to play in maintaining the health of this continent's vegetation into the future.

Keywords: Australian vegetation; palaeobiology; Cenozoic; Cretaceous; Gondwana

1. INTRODUCTION

Australia is an old, flat, highly weathered continent. It is the driest continent apart from Antarctica, and it is well known for its arid interior and the stark beauty that comes partly from the sparseness of the vegetation there. However, a closer inspection reveals a wide variety of vegetation types and regions of astonishing species richness, ranging from arid grasslands to semi-arid scleromorphic shrubland, alpine shrub- and herblands and tropical rainforests. This complex range of living vegetation has its origins in the supercontinent Gondwana, with the most important influence in shaping the modern vegetation being the arrival of the angiosperms from the Early Cretaceous (*ca.* 120 Myr ago). However, important additions to the vegetation since Australia rifted away from Gondwana have complicated any historical reconstruction. Recent phylogenetic studies have helped clarify the origin and history of present-day plant lineages (Crisp *et al.* 2004) and palaeobotanical studies are essential for the calibration and interpretation of the molecular phylogenetic evidence.

The modern vegetation of Australia has its roots in the Late Cretaceous (*ca.* 98–65 Myr ago) forests of the Weddellian Biogeographic Province, a region covering southern South America, western Antarctica, southeastern Australia and New Zealand, when all these land masses were connected. Little is known about events in this region during the Late Cretaceous, but we do know that it was an environment that is totally foreign to us today, and it spawned some remarkable plant and animal groups that help characterize the living Southern Hemisphere biota. This review will begin in this region and at this time, and consider the main factors driving the formation of the living vegetation of southern Australia. The southeastern quarter of Australia will be the focus, because this provides the overwhelming majority of the plant macrofossil record for the past 80 Myr (figure 1). Although the impact of the physical environment is the major thrust of this review, it is important to acknowledge the profound, but largely unknown, impact on the vegetation of the arrival of humans into Australia. Little will be said about that here, but recent research suggests that our impact may have been much more significant than is usually acknowledged. Similarly, there is no doubt that many taxa have been added to the Australian vegetation over the past 40 Myr through long-distance dispersal, but with few exceptions the fossil record does not assist in illustrating this, except in a negative sense.

2. THE PHYSICAL ENVIRONMENT

Australia has been profoundly altered by its movement through *ca.* 20° of latitude since its initial rifting from Antarctica *ca.* 40 Myr ago (figure 1). This movement had major climatic implications, both directly, as Australia moved through broad climatic zones, and indirectly, as Australia's movement influenced other events with a climatic outcome. Other land masses were also moving relative to each other, altering ocean currents with dramatic climatic consequences, and atmospheric CO_2 levels were changing, with consequent, but poorly understood, greenhouse effects. As Frakes (1999, p. 173) noted, Australia passed through a variety of climatic zones, ranging from tropical to polar as a result of motions of the Australian tectonic plate. However, the general thermal state of the Earth has also undergone changes. He concluded 'At times, one or the other of these influences has been in the

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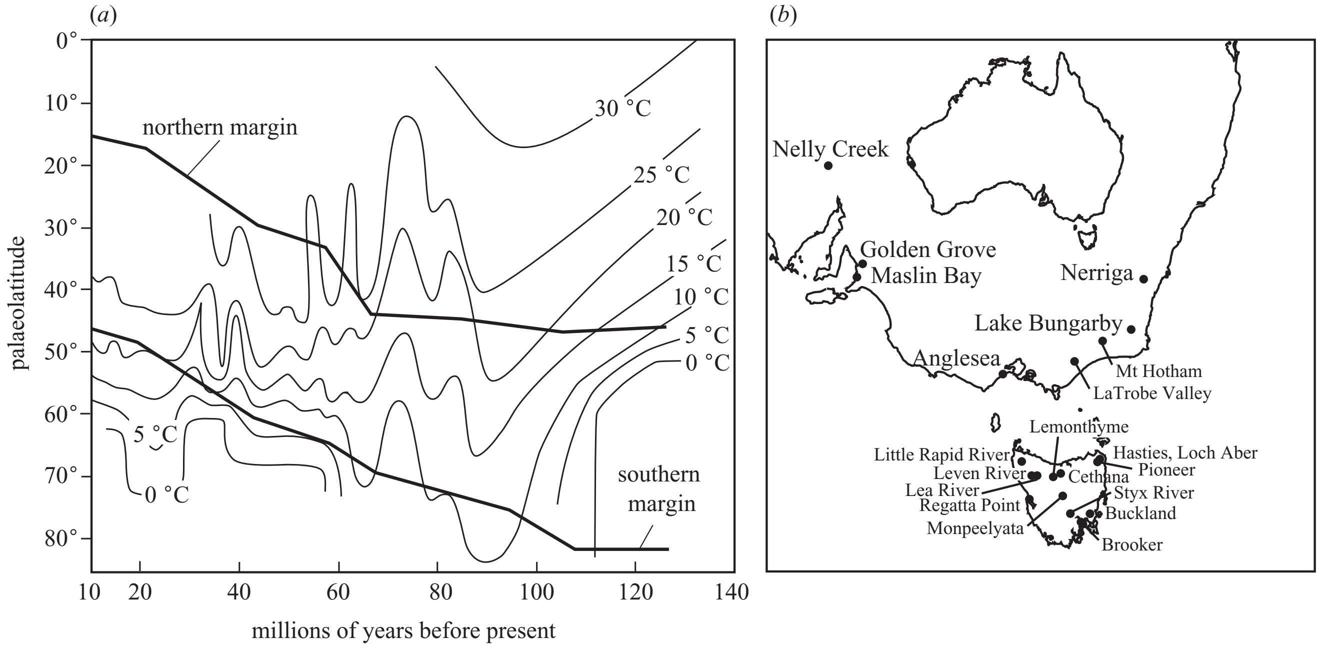

Figure 1. (*a*) Estimated global palaeotemperatures for continents from the Cretaceous to the Middle Miocene plotted over thick diagonal lines that represent the approximate northern and southern margins of Australia (modified from Frakes 1999). (*b*) A map of Australia drawn to scale. The expanded map of southeastern Australia shows the major plant macrofossil localities. (Lake Bungarby: Late Palaeocene; Mt Hotham, Regatta Point, Styx River, Buckland, Brooker: Early Eocene; Nelly Creek, Golden Grove, Maslin Bay, Nerriga, Anglesea: Middle Eocene; La Trobe Valley: Eocene–Miocene; Hasties, Loch Aber: Late Eocene; Little Rapid River, Lea River, Lemonthyme, Cethana, Leven River: Early Oligocene; Pioneer, Monpeelyata: Late Oligocene–Early Miocene; Regatta Point: Early Pleistocene).

ascendancy, but the widest swings in the continental climate have resulted when the effects have been additive towards either warming or cooling' (figure 1).

(a) *The Late Cretaceous environment*

Australia's separation from Antarctica began *ca.* 97 Myr ago, with initial seafloor spreading, substantial volcanic activity, and marine incursion into the southeast. Before this, Australia was connected to eastern Antarctica along a broad front that today comprises the Australian south coast. Antarctica has moved very little since that time, and so southern Australia was then well inside the Antarctic circle. An obvious consequence for the veget-ation is that it had to survive prolonged winter darkness, and a summer season when light was continuous, or almost so. However, the sun was always low in the sky, and sweeping around the horizon during the day, so that incoming light was effectively from all directions over each 24 h.

The connection of Australia and South America to Antarctica meant that the Circumantarctic ocean current, which so dominates the Southern Hemisphere today, did not exist, and there is abundant evidence that the major ocean currents circulated water through tens of degrees of latitude (Quilty 1994). The impact of this on climate was dramatic. The Circumantarctic current today restricts a vast amount of oceanic water to very high latitudes. This water is very cold, contributing to the massive Antarctic ice cap, and there is a very large temperature differential between the equator and the poles. However, when oceanic currents were circulating water across latitudinal belts, the water was warmed at low latitudes, and retained much of this energy when it returned to high latitudes. The impact of this was that, compared with today, the temperature differential between the equator and the poles was much reduced, and there was little or no polar ice cap. However, it is likely that the long dark winters were still severe, and frosts may have been common (Hill *et al.* 1999).

A particularly interesting feature of the Late Cretaceous environment was the atmospheric CO_2 level. Some estimates place this at 10 times or more above current levels (greater than 4000 p.p.m.). This is extraordinary, not just because of the direct impacts on climate, but also because of the largely unknown impact on photosynthesis. In summary, during the Late Cretaceous, southern Australia was likely to have had a very seasonal climate, with at least mild summers, with long days and probably reasonably reliable and high rainfall (as a result of warm oceanic waters leading to high evaporation rates and then condensation at high latitudes). Winters were cold, but probably not extremely so, with the very high atmospheric CO_2 levels and probably high humidity assisting in reducing low temperature extremes.

(b) *The Cenozoic environment*

Despite abundant evidence for a catastrophic event at the end of the Cretaceous (*ca.* 65 Myr ago) from around the world (Keller *et al.* 2003), this event is not well recorded in Australia. The major impact on the environment that is well established in southern Australia was the increase in the rate of rifting from Antarctica. This proceeded from west to east, so that Tasmania, including the South Tasman Rise, was the last land connection between the two continents. The vast, warm, marine inlet between Australia and Antarctica was in place for many millions of years before Tasmania finally separated, allowing free flow of ocean currents between Australia and Antarctica.

A period of global warming before this separation is clearly reflected in the vegetation of southern Australia. The relatively high temperatures must have been accompanied by abundant year round rainfall, again presumably originating from the relatively warm ocean waters at very high latitudes. Australian Cenozoic climates were significantly influenced by the rapid movement of the continent to lower latitudes, and by progressive global cooling and drying episodes (Frakes 1999). The Early Cenozoic climate was globally unique, with high humidity and temperatures at middle to high latitudes. A marked worldwide cooling at the end of the Eocene (*ca*. 35 Myr ago; Frakes & Kemp 1973) had a very significant impact on Australia, which was still at relatively high latitudes and had experienced warm and wet climates for most of the previous 25 Myr. For example, the temperature dropped from *ca*. 20 °C to *ca*. 13 °C in southern Victorian marine sites, although regional humidity remained high (Frakes 1999), and Macphail *et al.* (1993) provided evidence for a Tasmanian glaciation *ca*. 35–30 Myr ago. This cooling event may have been a result of major shifts in ocean currents and changes in atmospheric circulation patterns that were forced by the opening of a seaway between Australia and Antarctica, but other factors may also have contributed, for example a decline in atmospheric CO_2 (DeConto & Pollard 2003). Despite this cooling event, the region remained very wet, and rainfall must have been distributed quite evenly throughout the year. The evidence for this comes directly from the vegetation, and will be considered in detail later.

After its separation, Australia moved rapidly northwards, at a rate of up to 7 cm per year (Hill *et al.* 1999). Over millions of years this equated to *ca*. 20° of latitude through to the present day. Coincident changes in the light regime had a major impact on forest structure, and the physiological response of individual species. However, a more critical impact on the vegetation was the change in both the amount of rainfall and its distribution through the year. The drying of the Australian continent probably began between 35 and 24 Myr ago (Frakes 1999). Abundant central Australian lake deposits suggest relatively high rainfall persisted from *ca*. 28–11 Myr ago followed by further widespread drying (Truswell 1993). Bowler (1982) proposed that the steepening equator–south pole temperature gradient between *ca*. 15 Myr ago and the present resulted in a major northerly shift and intensification of anticyclonic high pressure cells. Therefore as Australia drifted north it was overtaken from the south by equatorward compression of circulation belts with consequent general development of arid conditions from south to north. Short intervals of increased rainfall in southern Australia occurred between 5 and 1.8 Myr ago, but continent-wide conditions first approximated the present by *ca*. 2.5 Myr ago (Bowler 1982; figure 2).

Major climatic oscillations began with the onset of repeated Quaternary glacial cycles, with associated biotic impacts that are complex to interpret. The snowline has been as much as 1000 m lower than now, corresponding to a 6–7 °C temperature drop (Hope 1994) and fluctuating temperatures caused major sea-level shifts, reflecting the amount of oceanic water locked up as ice. Compared with today, sea level ranged from -120 to -140 m during maximum ice formation, to +5 to +8 m in the warmest interglacials (Hope 1994). This led to the appearance and disappearance of wide continental shelves, including land bridges between mainland Australia, Tasmania and New Guinea.

3. CRETACEOUS VEGETATION

Prolonged winter darkness impacts on vegetation. Some living Southern Hemisphere woody plant species can survive long dark periods, especially under cold conditions, when respiration is reduced (Read & Francis 1992). Cretaceous gymnosperm wood from more than 70° S palaeolatitude has large, well-defined annual increments, suggesting good spring and summer growth (Truswell 1991), perhaps boosted by high prevailing atmospheric CO_2 levels (Creber & Chaloner 1985). Trees in one Early Cretaceous Antarctic site are spaced 3–5 m apart, which is sparse enough for them to have intercepted sufficient illumination from the low angle sun to produce the observed growth, provided the trees were relatively tall and with foliage arranged down the sides of the tree (Creber & Chaloner 1985). In central Australia during the Early Cretaceous, a conifer (Araucariaceae and Podocarpaceae) canopy grew over an understorey of pteridosperms, cycads, bennettitaleans and cryptogams (Hill *et al.* 1999). Sometimes *Ginkgo* occurred in the canopy and its probable deciduous habit may have been advantageous during prolonged winter darkness. These forests probably surrounded river and lake systems, but in coastal regions they were replaced by cheirolepidiacean woodlands (Dettmann 1994). Vegetation may reflect prevailing climatic zones that ranged from cold winters at times in the southeast to much warmer climates in the west (Frakes 1999).

The first angiosperms entered Australia *ca*. 120 Myr ago and occupied lakeside and riverine habitats, and broad coastal plains in southern and eastern Australia (Dettmann 1994). Throughout the Cretaceous, angiosperms became more widely distributed and diverse, and vegetation became more regionally defined (Dettmann 1994). A later Cretaceous angiosperm diversification was coincident with regression of the central and eastern Australian sea, and widening of the southern rift valley floodplain (Dettmann 1994). The high disturbance level associated with marine regression and the early successional nature of many early angiosperms (Wing & Tiffney 1987) may explain the Australian diversification seen at this and later times (Hill & Brodribb 2003).

The transition from gymnosperm- to angiosperm-dominated vegetation was associated with these environmental changes. The first macrofossil evidence for this occurs in the Cenomanian (96–92 Myr ago) Winton Formation of central Queensland, where abundant leaves of eight hamamelid angiosperm species, possibly all with betulaceous and fagaceous affinities, occur among a diverse array of ferns, *Ginkgo*, conifers and *Taeniopteris* (McLoughlin *et al.* 1995).

Important components of extant austral floras (e.g. the conifers *Lagarostrobos*, *Dacrydium*, *Dacrycarpus* (Podocarpaceae) and among the angiosperms, the early Proteaceae) were introduced into southeastern Australia *ca*. 94 Myr ago (Dettmann 1994). Angiosperm diversity increased steadily and podocarp and araucarian forests probably had canopy angiosperms by 86–84 Myr ago. *Nothofagus* (Nothofagaceae) was introduced after 84 Myr ago and Proteaceae

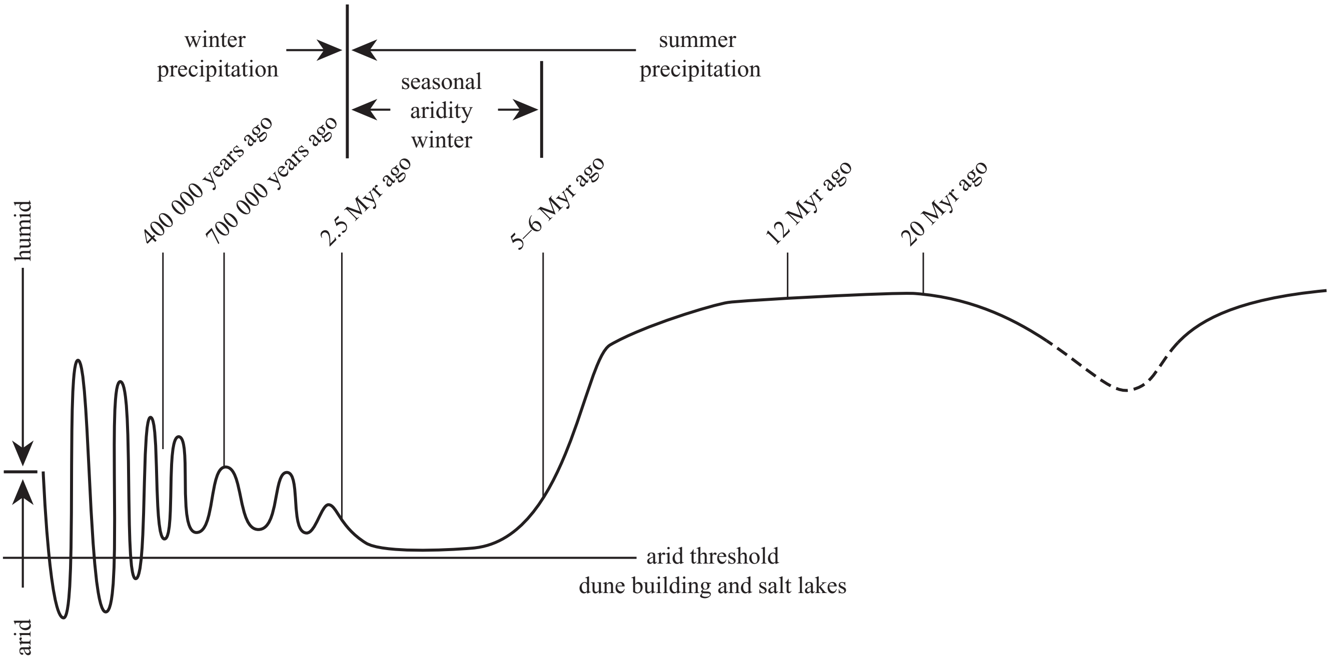

Figure 2. Diagrammatic summary of changes in humidity experienced by the southern arid and semi-arid regions of Australia since the Early Miocene. (Modified from Bowler 1982.)

further diversified to include canopy and understorey taxa as well as scleromorphic communities on forest fringes and/or nutrient-deficient soils (Hill *et al.* 1999).

Some of these Cretaceous angiosperm introductions pose an evolutionary problem that at present has no satisfactory resolution. The Weddellian Biogeographic Province, mentioned earlier, seems to have been the site of many major evolutionary innovations during the Cretaceous. Three angiosperm examples illustrate this well. The families Casuarinaceae, Nothofagaceae and Proteaceae all first appear (although at quite distinct times) in this region. They are first recognized from their excellent fossil pollen records, but this tells us nothing about the overall form of the plants bearing the pollen. When these families first appear as macrofossils (Late Palaeocene (60–55 Myr ago) for all three) they look very similar to living representatives, with the possible exception of Nothofagaceae, which has a confusing early history for reasons that will be explained at the end of this discussion. That is, for Casuarinaceae and Proteaceae at least, there has been little change in the morphology of the plants over the past 55 Myr. According to recent molecular phylogenies, the sister families for Casuarinaceae and Proteaceae are families now centred in the Northern Hemisphere (e.g. Manos & Steele 1997; Hilu *et al.* 2003). These families are very distinct morphologically and such close relationships had never been predicted previously. This suggests that the Casuarinaceae and Proteaceae evolved, possibly quite quickly, during the Late Cretaceous at very high latitudes, and have changed relatively little since. Nothofagaceae, containing the single extant genus *Nothofagus*, is less clear. This is because *Nothofagus* has broad leaves that are superficially similar to some extant broad-leaved Northern Hemisphere families, including one of its probable extant sister families, the Betulaceae. It is possible that *Nothofagus* has not altered its morphology compared with its sister family, as much as Casuarinaceae and Proteaceae. Many fossil leaves in the Southern Hemisphere are placed in *Nothofagus* for no other reason than they are in the right place at the right time (Hill 2001*b*) and many are probably not *Nothofagus*. A closer investigation of these fossil records, especially the older fossils from the Antarctic Peninsula and southern South America, may shed some light on the early evolution of this key southern family, and possibly also on the early history of Casuarinaceae and Proteaceae as well.

Many Late Cretaceous taxa have close relatives surviving today in closed Australasian rainforests. Although rarely dominant, some taxa are emergent above the general canopy and have slender, conical crowns. Perhaps as Australia drifted into lower Cenozoic latitudes, gaps between Cretaceous forest canopy trees were filled by trees with spreading, dome-shaped canopies that maximized solar absorption in mid- to low latitudes (Dettmann 1994).

4. PALAEOGENE RAINFORESTS

Palaeocene (*ca.* 65–55 Myr ago) vegetation is sparsely represented in Australia. Conifers dominated the southeastern highlands, with broad-leaved angiosperms also present. About 40 macrofossil species of angiosperms and conifers occur at one site, suggesting complex temperate rainforest with some mesothermal and scleromorphic taxa (Hill *et al.* 1999). Minor differences in lowland southeastern Australia suggest little altitudinal zonation (Macphail *et al.* 1994).

Major meso-megathermal rainforest developed in southern Australia in the Early Eocene (*ca.* 55–49 Myr ago) (Macphail *et al.* 1994). Megathermal rainforests are now confined to the lowland tropics with mean annual temperatures of more than 24 °C. In the Early Eocene, high moisture levels probably moderated high latitude seasonal effects to allow these forests to occur so far south. Contrasting the Palaeocene, angiosperms were highly diverse and dominant, except in some Tasmanian locations. Mangroves had their southernmost expansion to western Tasmania (Truswell 1993; Pole & Macphail 1996).

Middle to Late Eocene (*ca*. 49–35 Myr ago) vegetation of coastal southeastern Australia was compared with living lowland megathermal rainforest in northeastern Queensland (Christophel *et al.* 1987), but an important difference is the presence of winter deciduous species in the Eocene (Scriven *et al.* 1995), which was probably a response to high latitude winter darkness. Tasmanian vegetation was more temperate with a lower angiosperm diversity but much higher conifer diversity (Hill & Brodribb 1999). Very high epiphyllous fungal loads on fossil leaves from this time strongly suggest high rainfall with no dry season during the year. Around the Early to Middle Eocene boundary, *Nothofagus* pollen increased markedly across southern Australia, particularly the extant tropical subgenus *Brassospora*.

A Middle Eocene central Australian macrofossil site (Christophel *et al.* 1992) contains a more scleromorphic and possibly xeromorphic vegetation than the southeast, although more recent examination suggests that larger, broad-leaved forms are present in this site, but were missed in the earlier study because of the sample preparation technique employed (R. S. Hill and R. Paull, unpublished data).

One interesting feature of early Palaeogene vegetation in southern Australia, while the region was still at very high latitudes, is the presence of some plants that appear to be distinct in their form and/or function compared with any species in the living Australian vegetation. Three examples demonstrate this. A poorly dated, but probably early Palaeogene site in southern Tasmania contains good impressions of one almost complete *Ginkgo* leaf and several fragments of the same taxon (Hill & Carpenter 1999). This is the last Australian record of this genus, which was relatively common in the Cretaceous. The single living species of *Ginkgo* is winter deciduous, and it is therefore usually assumed that all fossil species of this genus were as well. There is no particularly compelling reason to believe this, because many extant genera contain both deciduous and evergreen species, but in this case it provides a good explanation for the demise of this fossil taxon. When Australia was at very high southern latitudes, winter deciduous taxa were more common than they are today. The reason for this is almost certainly that this is a competitive strategy when occurring in a region with winter darkness. Physiological experiments by Read & Francis (1992) demonstrated that evergreen species could also survive winter darkness, provided the winter was cool enough, but the rapid movement of Australia into lower latitudes during the Cenozoic may have made the winter deciduous habit less competitive and led to the local extinction of *Ginkgo* there.

The second example is an extinct genus of cycad, *Pterostoma*, which has been recorded from several southern Australian Eocene localities (Hill 1980; Hill & Pole 1994). The best preserved material of this genus is found in the Middle Eocene sediments at Anglesea, in southern Victoria (Hill 1980). The holotype is a near complete frond, and fragments of fronds are very common. The unusual feature of *Pterostoma* at this site is that it is also represented by many frond bases, which have a clearly formed abscission layer. No extant cycad sheds its fronds cleanly, although there are reports of one northern Australian species that may do so in extreme drought. Why did *Pterostoma* do so, and why is it now extinct? It is tempting to conclude that *Pterostoma* may have been a winter deciduous cycad, shedding its fronds each year to minimize dark respiration during winter at the very high latitudes where it grew. This would represent a major nutrient loss for the plant, but perhaps for carbohydrates at least, this was not a serious problem because the extremely high prevailing atmospheric CO_2 levels may have allowed for higher-than-extant photosynthetic rates when fronds were present, so that reserves were laid down more quickly. As Australia moved northwards during the Cenozoic, this strategy would have become less competitive, and deciduous taxa in general became extinct. The problem with this scenario is that we have not yet found a way to determine whether *Pterostoma* shed its fronds annually or whether the abscission zone was part of a strategy to allow for the loss of evergreen photosynthetic units when they reached the end of their productive lifespan.

The third example is an extinct genus of the Araucariaceae, *Araucarioides* (Bigwood & Hill 1985; Hill & Bigwood 1987). This genus is common as leaf remains in the extensive Early Eocene (55–50 Myr ago) sediments that surround Macquarie Harbour on the west coast of Tasmania. No complete leaf of *Araucarioides* has ever been recovered, but the apex clearly tapers very gradually into an acute tip, and the blade begins to narrow towards the base, but the basal end is always broad enough where it ends to suggest that it probably had no petiole, but was broadly attached like extant *Araucaria* and *Wollemia* leaves. The striking feature of *Araucarioides* is its extremely thick leaf cuticle, many times thicker even than living Araucariaceae, which themselves have relatively thick cuticles. It is likely that *Araucarioides* is common among leaf fossils from the Cretaceous of southeastern Australia, but it has been placed in a form genus and its araucarian affinities remain unrecognized. Some of the Cretaceous fossils that appear to be related to *Araucarioides* have extremely thick cuticles, reaching *ca*. 0.5 mm. Why would plants have such a thick cuticle? There is no suggestion that the region they grew in was ever drought-prone, and even in the driest environments today such cuticle development is unknown. Possibly this cuticle development was a deterrent to herbivores, especially in an environment where extremely high atmospheric CO_2 may have allowed for high photosynthetic rates and hence the synthesis of massive amounts of otherwise unproductive cuticle. Whatever the reason, there is no evidence that *Araucarioides* extended past the Early Eocene, whereas other members of the Araucariaceae remained prominent in the region for tens of millions of years, and had a very modern morphology even when they coexisted with *Araucarioides*.

5. ORIGINS OF THE SCLEROMORPHIC VEGETATION

A relatively poorly dated Palaeogene southwestern Australian macroflora contains diverse scleromorphic Proteaceae and Myrtaceae, and is distinct from southeastern macrofloras (Hill & Merrifield 1993). This highlights a significant trend within the Palaeogene macrofossil record. In several fossil localities across southern Australia, leaves are preserved that demonstrate typical scleromorphic characteristics (e.g. thick leaves, high vein density, well-defined areoles, etc.). These fossil leaves occur with a suite of fossils that clearly represents closed forest growing under very high rainfall conditions, suggesting that scleromorphy, especially as preserved in the Proteaceae, is a response to low soil nutrients, and in particular low phosphorus and nitrogen. There has been ongoing debate about the role of low water availability as a primary forcing factor in the evolution of these leaf forms, but the fossil record clearly demonstrates that this is a secondary response (Hill 1998). The oldest records of scleromorphic plants in Australia are Late Palaeocene (*ca*. 60–55 Myr ago) leaves placed in the genus *Banksieaephyllum*, and clearly related to the living *Banksia*. Unequivocal xeromorphic characters first appear in the Late Eocene (*ca*. 41–36 Myr ago) in southwestern Australia and the Early Oligocene (*ca*. 36–28 Myr ago) in the southeast (Hill 1998; Hill & Brodribb 2001), and become increasingly more common through time as the continent dried out. It has been possible to distinguish between plants that are scleropmorphic but not xeromorphic and those that are both scleromorphic and xeromorphic by concentrating on morphological adaptations to protect the stomata against excessive water loss: the former do not have these adaptations, the latter do (Hill 1998).

6. RAINFOREST VEGETATION IMMEDIATELY AFTER AUSTRALIA SEPARATED FROM ANTARCTICA

Early Oligocene to Early Miocene (*ca*. 36–20 Myr ago) sediments preserve a variety of habitats and distinctive plant communities. For example, there were lowland peat swamps in the southeast, developing alpine vegetation in New South Wales and Tasmania, lowland rainforests in Tasmania, and widespread and complex riverine plain vegetation in the Murray Basin (Hill & Brodribb 2003).

Tasmanian Oligocene sediments are relatively common, and contain a high diversity of beautifully preserved macrofossils. These have now been quite well studied and provide a detailed cross-section of vegetation at an important time just after the separation of this part of Australia from Antarctica. These sediments contain mixtures of plants with living affinities ranging from low altitude rainforests at low latitudes, to high altitude shrublands at high latitudes. The evolution of living vegetation involved a long, climate-induced sifting of these Oligocene rainforests, in conjunction with other complex selection pressures.

Hill (1990) separated the fossil taxa in these Oligocene rainforests into five groups according to the fate of their nearest living relatives. Since that time there has been a significant increase in the number of fossils from these sites that have been identified and these groups can now be updated, although the broad groupings remain the same.

(i) Fossil taxa that have not left descendants in the region, but have migrated (or been restricted in range) northwards, and currently occur in low latitudes rainforest (usually, but not always, in the mountains of Papua New Guinea). There are many taxa in this group and examples include the gymnosperms *Agathis*, *Araucaria* (Araucariaceae), *Dacrycarpus*, *Dacrydium*, *Falcatifolium*, *Podocarpus* (large-leafed) (Podocarpaceae), *Papuacedrus* (Cupressaceae), and the angiosperms *Gymnostoma* (Casuarinaceae), *Caldcluvia*, *Vesselowskya* (Cunoniaceae), Lauraceae (several undetermined genera), Myrtaceae (soft-fruited genera), *Nothofagus* subgenus *Brassospora* (Nothofagaceae) and *Quintinia* (Saxifragaceae).

(ii) Fossil taxa that have migrated northwards (or been restricted in range) to temperate rainforests in the mid-east coast region of Australia (New South Wales, southern Queensland), but have left descendants in place in southeastern Australia that uniformly have much smaller leaves than their fossil precursors or their living relatives to the north. The two examples here that are strongly supported by fossil data are the extant species pair *Nothofagus cunninghamii* (southeastern Australia) and *N. moorei* (mid-east coast of Australia), which have an abundant fossil record, especially in Tasmania (Hill 1983, 1991*a*, 1994) and the three extant *Eucryphia* species, *E. moorei*, *E. lucida* and *E. milliganii*, which also have a good fossil record (Hill 1991*b*; Taylor & Hill 1996; Barnes & Jordan 2000). In all cases the older fossils in southeastern Australia most closely resemble the northernmost living species in leaf size (see table 1). For those living species listed here where phylogenetic research has been performed (e.g. *Nothofagus* and *Eucryphia*), the living species listed are very closely related, suggesting that this is an example of *in situ* evolution, rather than an invasion of existing species into Tasmania to replace an older vegetation.

(iii) Fossil taxa that are found today at similar latitudes to southeastern Australia (in New Zealand or southern South America), but are extinct in Australia and Papua New Guinea. Examples include the fern *Lophosoria* (Lophosoriaceae, extant in South America), the gymnosperms *Araucaria* (Araucariaceae, extant in South America), *Austrocedrus*, *Fitzroya* (both extant in South America), *Libocedrus* (extant in New Zealand) (Cupressaceae), *Dacrycarpus* (extant in New Zealand, Podocarpaceae), and the angiosperms *Weinmannia* (extant in South America, Cunoniaceae), *Nothofagus cethanica* (extant in New Zealand) and *N. lobata* (extant in South America) (Nothofagaceae). It is difficult to explain the persistence of these taxa in other land masses at similar latitudes while they have become extinct in Australia. However, it is worth noting that the rainforests of Tasmania today are very species poor, and the accumulating impacts of dramatic cyclic climate changes, the barrier imposed by Bass Strait (Tasmania is an occasional island, but when Bass Strait has been dry land during recent glaciations it has been relatively arid), and the major impact of aridity and fire on mainland Australia, have combined to decimate Tasmania's rainforests. Such impacts may not have been as severe in South America, where continuous land for migration exists, and in New Zealand, where the recent history has been less arid and fire-dominated than in Australia. It is possible that some of the living taxa involved here achieved their current distributions as a result of long-distance dispersal. This is very likely to be true for some of the extant New Zealand taxa.

(iv) Fossil taxa that have remained more or less unchanged in southeastern Australia through tens of millions of years, and do not occur outside the region. There are few of these, but there certainly are some taxa that in leaf form at least appear to be unchanged, possibly even at the species level, since the Early Oligocene. In the living vegetation, examples include

Table 1. Genera in the living vegetation that have at least one species in southeastern Australia (Tasmania and Victoria, the southern species) and one on the central east coast (New South Wales, the northern species).
(In each case the northern species has by far the largest leaf area, and where fossil evidence exists, it most closely resembles the Oligocene form in southeastern Australia (data modified from Hill & Read 1987).)

	field grown plants	glasshouse grown plants
Acradenia euodiiformis (NSW)	9817 (3424)	—
A. frankliniae (TAS)	756 (338)	—
Anopterus macleayanus (NSW)	13846 (3326)	9662 (1603)
A. glandulosus (TAS)	3420 (1664)	5342 (2622)
Eucryphia moorei (NSW)	2278 (1024)	1908 (526)
E. lucida (TAS)	405 (140)	340 (108)
E. milliganii (TAS)	75 (33)	83 (30)
Nothofagus moorei (NSW)	1649 (692)	1421 (652)
N. cunninghamii (VIC)	130 (59)	108 (36)
N. cunninghamii (TAS)	83 (36)	86 (26)

the gymnosperms *Athrotaxis selaginoides*, *Diselma archeri*, *Microstrobos niphophilus* (Cupressaceae), *Phyllocladus aspleniifolius* (Podocarpaceae), and the angiosperm *N. gunnii* (Nothofagaceae: Australia's only winter deciduous species). In all cases there are Early Oligocene leaf species that are either assigned to the extant species or are extremely similar in form but are assigned to an extinct fossil species.

(v) Fossil taxa that are extinct either in the Southern Hemisphere or globally, and have no close relatives in the region. This group consists entirely of gymnosperms. However, that may be an artificial distinction, because it is relatively easy to determine whether a fossil gymnosperm has close living relatives, whereas if a fossil angiosperm has no close living relatives that can be quite difficult to determine, especially when the fossil material available has well preserved leaves, but not reproductive organs. Examples include *Coronelia*, *Smithtonia*, *Willungia* (Podocarpaceae) and *Austrosequoia* (Cupressaceae).

It is important to understand that these groups do not always have clear boundaries, nor do they have simple explanations. For example, at least one member of the Lauraceae was still in Tasmania in the Pleistocene (Jordan 1997*a*), but today the family is extinct there and is found from mid–low latitudes along the east coast of mainland Australia, north to Papua New Guinea (and throughout the tropics). This taxon is placed in group (i) above, but other members of that group were clearly extinct in Tasmania well before the Pleistocene, even though they are lumped together here.

These Tasmanian Oligocene sediments provide the first extensive evidence for cool temperate rainforest. All four extant *Nothofagus* subgenera are present, including, until recently, the only macrofossil records of subgenus *Brassospora* species, which occurred in nearby vegetation. These subgenera are now separated by thousands of kilometres, latitudinally and longitudinally, and their combined presence in Oligocene Tasmania indicates extinct climates, and most probably extremely wet conditions, that in turn eliminated temperature extremes (Read *et al.* 1988). The pollen record clearly demonstrates the sifting and migration that occurred among the subgenera of *Nothofagus* in eastern Australia and Papua New Guinea throughout the history of this genus (figure 3). A significant decline in leaf size through time, probably in response to cooling climates, occurs in the *Nothofagus* subgenera *Lophozonia* (Hill 1994) and *Nothofagus* (Scriven & Hill 1996). Deciduous *Nothofagus* species were more diverse in Oligocene southern Australia than now, where *N. gunnii* is now the only Australian winter deciduous species. Living *Brassospora* species have a lower tolerance to temperature extremes than other *Nothofagus* subgenera (Read *et al.* 1988), and, if their fossil ancestors had a similar tolerance, they probably became less competitive as southern Australia cooled and temperature extremes widened. Presumably similar forcing factors impacted on other, less well known, fossil taxa in the region.

Conifers were extremely common in Oligocene southeastern Australia (Hill & Brodribb 1999) and some demonstrate trends in leaf size and stomatal distribution in response to climate change (Hill & Carpenter 1991). In Tasmania during the Early Eocene, *Dacrycarpus* had relatively large leaves in flattened shoots, but by the Early Oligocene small-leaved imbricate shoots predominated, suggesting *Dacrycarpus* moved from the understorey to the well lit forest canopy (Brodribb & Hill 1998), similar to its extant niche. *Dacrycarpus* leaf size probably reached a minimum in the Early Pleistocene (1.8–0.75 Myr ago), just before its Australian extinction. These small-leaved, imbricate shoots had stomata restricted to the appressed leaf surface (Jordan 1994), possibly indicating that a reduction in water availability may have been involved in the extinction as well as lower temperatures, because this stomatal positioning restricts water loss from the leaf (Brodribb & Hill 1997). The species diversity of conifers in some deposits is extremely high (table 2). The best documented, and probably most diverse site recorded, is at Little Rapid River in northwest Tasmania. This very localized outcrop of fossil-bearing sediment, which cannot have contained input from more than a few hectares (1 hectare $= 10^4\ \mathrm{m}^2$) of forest, contains 26 macrofossil species of conifers, across all three extant Southern Hemisphere families (Araucariaceae, Cupressaceae and Podocarpaceae). This is, as far as has been determined to date, the most diverse conifer representation in a single localized vegetation ever recorded, living or fossil. Given the extreme sensitivity of many of these conifers to lack of water (Brodribb & Hill 2003), it is likely that Tasmania had a very high rainfall,

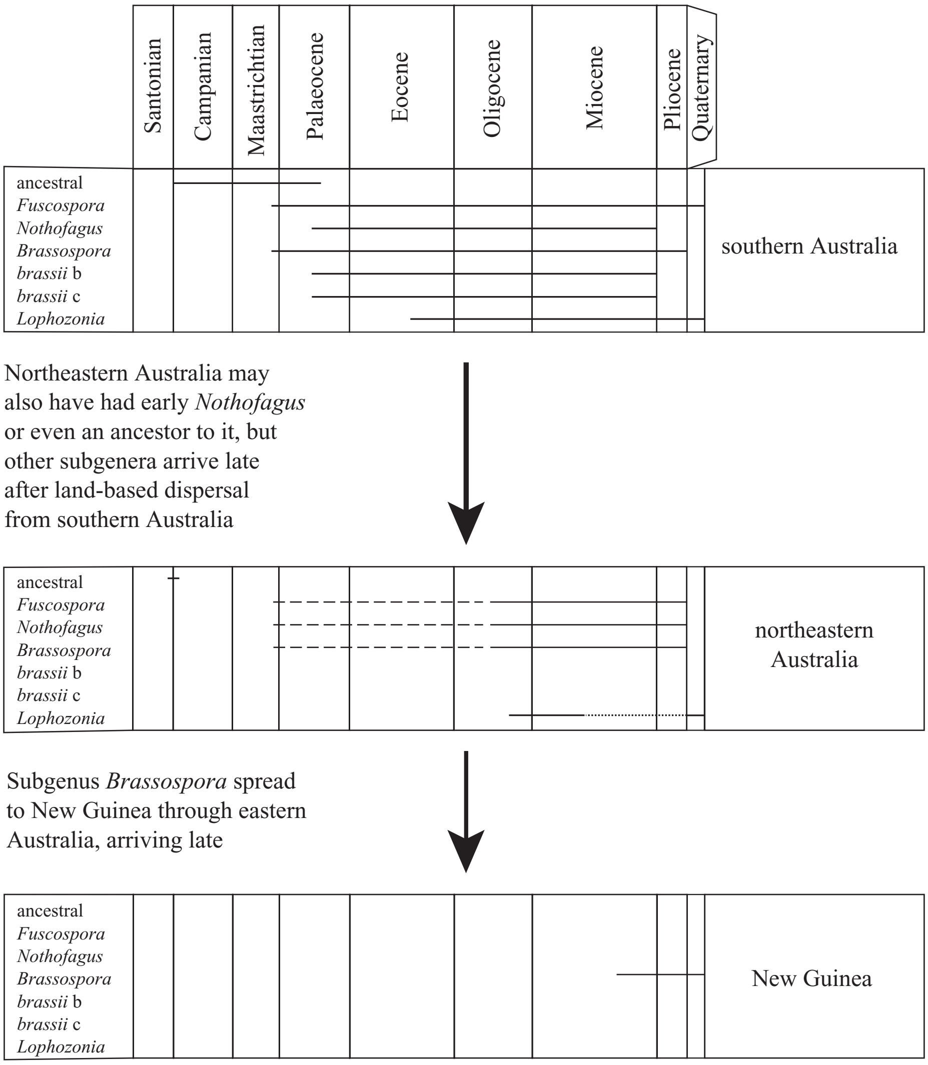

Figure 3. Pollen ranges of the major *Nothofagus* pollen types in eastern Australia and Papua New Guinea throughout their complete stratigraphic range. Modern subgeneric names have been used where appropriate. The arrows indicate the most likely migration route. (Adapted from Hill 2001*a*.)

spread across the year during the Oligocene, and conifers declined as this climate deteriorated. The extinction of many of these conifers from southeastern Australia later in the Cenozoic was probably driven by declining water availability. Those taxa that are now extinct in Australia, or very limited in their distribution to wet environments, are clearly intolerant of low water availability (figure 4). This is one of the clearest reasons for extinction that we have in the plant fossil record of Cenozoic Australia.

7. THE ORIGINS OF THE ALPINE VEGETATION

The earliest macrofossil evidence for the origins of the Australian alpine vegetation comes from a Late Oligocene–earliest Miocene (*ca.* 25–20 Myr ago) site in central Tasmania (Hill & Gibson 1986; Macphail *et al.* 1991). These sediments contain a diverse array of extremely microphyllous remains. The lake sediments have abundant macrofossils and megaspores of *Isoetes*, which suggest *in situ* deposition (Hill 1987). The well-preserved macrofossils include abundant and diverse conifers, some identified angiosperms, including one evergreen and two deciduous *Nothofagus* species, all with very small leaves, many unidentified angiosperm leaves, all extremely small, and one piece of wood suggestive of a small tree trunk, *ca.* 15 cm in diameter. It is possible that this high altitude (*ca.* 900 m above sea level) site represents the earliest evidence of Australian vegetation beginning to adapt to lower temper-atures. The present altitude of the site has changed little since the sediments were deposited, and is in a very exposed region topographically. However, the presence of a small tree trunk or branch in the sediments demonstrates that it was below the tree-line. Nevertheless it is likely that it is a precursor of the alpine vegetation of Tasmania, where intermittent snowfall allows for a highly diverse perennial and evergreen shrub vegetation above the tree-line.

8. THE BREAK-UP OF RAINFORESTS AS THE CLIMATE DRIED

The Early–Middle Miocene (*ca.* 24–11 Myr ago) section of the southeastern Australian Latrobe Valley coals demonstrates cyclic succession from open water and swamp communities through rainforest associations to drier scleromorphic and xeromorphic communites. This occurred as peat accumulated above the water table, and there is an associated fire interaction (Blackburn & Sluiter

Table 2. Cenozoic macrofossil conifer species from southeastern Australia.
(Data from Hill & Brodribb (1999) with new data added as appropriate. The numbers of genera are given in parentheses.)

site	age	Araucariaceae	Cupressaceae	Podocarpaceae	total
mainland Australia					
Lake Bungarby	Late Palaeocene	3 (2)	4 (3)	6 (4)	13 (9)
Hotham Heights	Early–Mid Eocene	1 (1)		5 (4)	6 (5)
Anglesea	Middle Eocene			5 (4)	5 (4)
Maslin Bay	Middle Eocene	1 (1)		1 (1)	2 (2)
Golden Grove	Middle Eocene			2 (2)	2 (2)
Nelly Creek	Middle Eocene	1 (1)		2 (1)	3 (2)
Berwick Quarry	Late Oligocene–earliest Miocene	1 (1)		1 (1)	2 (2)
Latrobe Valley	Oligo–Miocene	3 (2)	1 (1)	5 (4)	9 (7)
Tasmania					
Buckland	Early Eocene		1 (1)	7 (4)	8 (5)
Regatta Point	Early Eocene	5 (2)	1 (1)	5 (4)	11 (7)
Hasties	Mid–Late Eocene	2 (1)		10 (7)	12 (8)
Loch Aber	Mid–Late Eocene	1 (1)		4 (4)	5 (5)
Cethana	Early Oligocene	4 (2)	2 (2)	10 (6)	16 (10)
Lea River	Early Oligocene	2 (2)	5 (4)	6 (4)	11 (8)
Little Rapid River	Early Oligocene	3 (2)	4 (3)	19 (9)	26 (14)
Monpeelyata	Late Oligocene–earliest Miocene	3 (1)	3 (3)	2 (2)	8 (6)
Pioneer	Late Oligocene–earliest Miocene	2 (2)	5 (4)	7 (5)	14 (11)
Regatta Point	Early Pleistocene		2 (2)	5 (5)	7 (7)

1994). Species diversity at this time is much greater in the Murray Basin than in the southeast, probably because of the great variety of habitats. In the Murray Basin *Nothofagus*, or Casuarinaceae and gymnosperms, usually dominate, halophytes (e.g. Chenopodiaceae) are common, and *Acacia* occurs from the Early Oligocene onwards (Truswell 1993). In the Late Oligocene to Early Miocene, drier rainforests dominated by Myrtaceae and Casuarinaceae replace *Nothofagus* dominance (Macphail & Truswell 1989). These rainforests could have expanded from dry parts of central Australia, or they could be new associations that developed with Mid-Cenozoic seasonal dryness.

This shift to drier rainforests also marks the first widespread occurrence of *Eucalyptus* on the Australian east coast (Hill *et al.* 1999). *Eucalyptus* macrofossils are absent from several older southeastern Australian macrofloras and Archer *et al.* (1991) suggested that early koalas were relatively rare in Oligo–Miocene rainforests because of the rarity of eucalypts there. Current evidence favours Lange's (1980) hypothesis that Mid-Cenozoic Australian continental margins supported only mesic, non-eucalypt vegetation, whereas eucalypts contributed to more xeric central Australian vegetation. The weakness in testing this hypothesis at present is the poor stratigraphic control on the extensive fossil-bearing silcretes in central Australia, which probably are the key to determining the early history of *Eucalyptus*. With increasing central Australian aridity, eucalypts were displaced to the continental margins. The early history of *Eucalyptus* is distinct from many of its now coexisting species, and, given its exceptional fire-promoting and fire-surviving adaptations, it probably involved environments with high natural fire frequencies (Hill 1994).

During the Late Miocene (*ca.* 11–5 Myr ago), *Nothofagus* declined even further in central New South Wales and the subgenus *Brassospora* disappeared. Myrtaceae increased again, including rainforest taxa and eucalypts, and fire increased, probably under reduced precipitation and more seasonal rain (Hill *et al.* 1999). This probably reflects wet sclerophyll communities, possibly with a myrtaceous canopy above an understorey including some rainforest taxa, similar to living vegetation bordering north Queensland rainforests.

The trend from closed forests to open vegetation accelerated in the Pliocene (*ca.* 5–1.8 Myr ago), probably in response to large climatic swings. Substantial Poaceae pollen suggests Early Pliocene savannah vegetation in northwestern Australia, although associated trees are poorly understood (Kershaw *et al.* 1994). A dramatic shift from temperate rainforest to Asteraceae and Gramineae (Poaceae) dominance in a landscape with very few trees occurred in the Late Pliocene at Lake George near Canberra. Conditions may have been cool and dry, reflecting this region's first winter rainfall communities (Hill *et al.* 1999).

9. THE INTERACTION BETWEEN THE SOIL NUTRIENTS, CLIMATE AND FIRE

The Latrobe Valley coals demonstrate an early impact of fire on the Australian vegetation. Blackburn & Sluiter (1994) demonstrated a clear correlation between vegetation type and amount of pyrofusinite (fossil charcoal) in a successional sequence where the driest vegetation was also the most fire-prone. There must have been sufficient build-up of fuel in these dry environments to support occasional fires when an ignition source occurred. Although it is difficult to calculate the frequency of fires in these coal-forming communities, it is probable that they were relatively infrequent. This is especially so because many of the plant species involved do not have short term mechanisms for recovery after fire. For example, species of

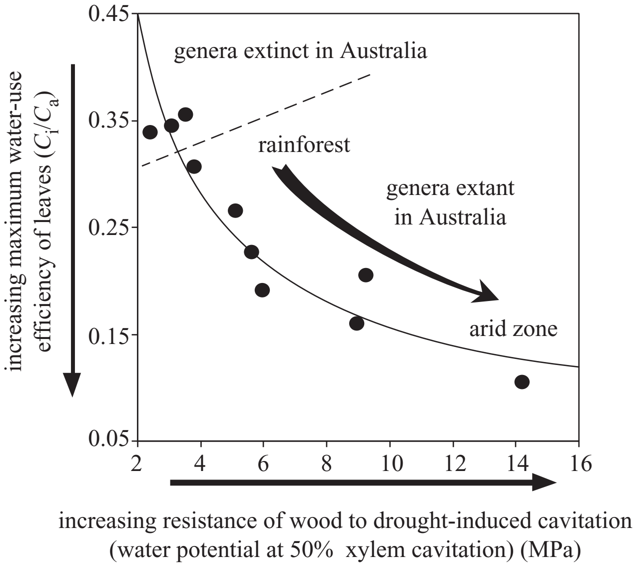

Figure 4. The relationship between maximum leaf water-use efficiency and stem xylem resistance to cavitation by water stress in 10 species of Southern Hemisphere conifers. The minimum drought resistance is in the top left corner, with increasing resistance moving towards the bottom right-hand corner. The three species above the dashed line are from genera that became extinct in Australia during the Mid–Late Cenozoic, while the species below the dashed line are all extant in Australia. The three extinct genera appear to fall outside the physiological range of conifers found in Australia today, exhibiting a lower drought tolerance than even the wet-forest conifers from Tasmania. This suggests that decreasing rainfall was an important factor contributing to their disappearance from Australia. (Modified from Hill & Brodribb 2003.)

Banksia and Casuarinaceae have their seeds enclosed in woody protective structures that preserve them from excessive heat from fires, and after a fire the seeds are released onto a relatively high-nutrient ash bed. However, the parent plants often die as a result of the fire and if another fire occurs before the new seedlings have grown to reproductive age the species involved are vulnerable to local extinction. This suggests an average of several years between fires.

However, *Eucalyptus* can survive more frequent fires, because of the capacity of many of its species to recover vegetatively. As fire frequency increases, the prominence of eucalypts in the Australian vegetation usually increases, except at the very dry end of the climate range. *Eucalyptus* has not been common in the Australian vegetation until quite recently, and this can be strongly correlated to an increase in fire frequency, probably both natural and human-induced.

10. QUATERNARY VEGETATION

The Quaternary plant fossil record is quite patchy, and relies heavily on pollen, and even this is unreliable in arid areas (Hope 1994). During full glacial conditions in southeastern Australia, open steppe grasslands with annual and perennial geophytes and drought deciduous shrubs predominated (Hope 1994). These communities were probably also extensive at times of rainforest expansion, although they were excluded from wetter mountains by forests or shrublands (Macphail 1986). Many extant open forest types were probably favoured by wet glacial conditions, but reduced in area during the cold, dry maxima (Hope 1994). At the last glacial peak (18 000 years ago), mountains were arid as well as cold. Treeless vegetation dominated by Asteraceae and Gramineae extended across most of southeastern Australia, reaching sea level in places, and eucalypts were scattered or restricted to sheltered positions.

Kershaw (1984) reviewed evidence for Quaternary plant extinctions and range retreats and reported only a few clear losses, and several range retreats, such as the conifer *Phyllocladus* (Podocarpaceae) from Victoria and *Nothofagus* from southern New South Wales, with the onset of the last glacial peak (*ca*. 30 000 years ago), or in the rapid warming approaching the start of the Holocene. However, Jordan (1997*b*) provided evidence of many more angiosperm and conifer extinctions in western Tasmanian Pliocene and Pleistocene sediments, suggesting that Australian Quaternary plant extinctions were much more extensive than previously thought. This apparent discrepancy is a result of Kershaw relying on pollen data for his conclusions, whereas Jordan used plant macrofossils. Pollen grains are often much more generalized in form, making it difficult to detect species extinctions. The causes of these plant extinctions are unknown.

Humans probably arrived in Australia between 60 000 and 40 000 years ago (Flannery 1994) and occupied all available niches by 35 000 years ago (Dodson 1992). At the time when humans arrived, Australia supported a megafauna of large browsing and grazing animals that generally occupied niches in open communities. The megafaunal extinctions may have ranged from *ca*. 50 000 to 30 000 years ago for the largest species, continuing to the end of the Pleistocene for the smaller species (Hope 1994), although this is a point of major contention, with some arguing for a much more rapid extinction. Although there is still major debate about the cause of the megafauna extinction in Australia, its impact on the vegetation is worth considering.

Flannery (1994) presented a hypothesis integrating Aboriginal behaviour, the megafauna, fire and vegetation that has apocalyptic ramifications. He concluded that Aboriginal hunting was directly responsible for the megafaunal extinction, and that this had far-reaching consequences. Explicit in Flannery's hypothesis is that fire increased after the arrival of Aborigines and there is good evidence for this. The usual explanation for this increase is that after their arrival, Aborigines began lighting fires and by increasing the fire frequency, they encouraged the growth of fire-loving plants (e.g. Singh *et al.* 1981; Kershaw 1988; Jackson 1999). However, Flannery concluded that the amount of fuel limits fire in Australia, not ignition sources, and Aborigines could directly alter the latter but not the former. He argued that the consumption of plant matter by fire could only increase by increasing the fuel load, and the most probable mechanism for this is megaherbivore extinction. The consequent spread of fire led to increased dominance by fire-adapted scleromorphic plants and reinforced the effects of the El Niño – Southern Oscillation and nutrient-poor soils, further impoverishing Australian environments.

In the extreme case, Australia's climate may have been altered as a result of fire after megafaunal extinction. Miller & Magee (1992, in Flannery (1994)) concluded that when the northern Australian monsoon is strong enough, rainfall extends far enough south to fill Lake Eyre. However, 11 000 years ago was anomalous because the lake remained dry during favourable monsoon conditions. This may be because of a changeover in vegetation over much of northern Australia, from 'dry' rainforest to eucalypt woodlands. Flannery argued that this change resulted from a changed fire regime, which, in turn, resulted from megafaunal extinction. After rain, water drains rapidly away, because the plants and thin soil cannot hold it, and without the significant evapo-transpiration produced by broad-leaved 'dry' rainforest plants, rainfall does not normally penetrate far enough south in sufficient quantity to fill the drainages that flow into the lake. This hypothesis awaits testing, because no relevant sedimentary cores containing pollen and charcoal have been discovered in northern Australia.

11. CONCLUSION

Australia has a remarkably dynamic past, and as we discover more about the fossil record our appreciation of just how complex it is increases. Australia has a unique history, involving long periods of isolation during which climate changed dramatically. However, it is not so complex that we cannot hope to understand it. Australia is a stable landmass and much of it has been relatively unchanged for a very long time. This makes it an ideal place to examine the impacts of long-term climate change. We still know little about some parts of the continent, and especially those areas that have been dry for a long time, making fossilization rare, and potentially destroying any fossils that exist from earlier times. Despite this, we now know the broad picture of a drying climate set against a background of nutrient-deficient soils and massive latitudinal shift and the major changes these have made to the vegetation. There has been a transformation from extraordinarily diverse rainforest biomes across most of the continent in the early Cenozoic through to predominantly desert biomes today.

The most valuable contribution of Australian palaeobotany has been to define the important ecological questions that must be asked if we are to better understand the interactions and origins of the living vegetation. The challenge of interpreting the impact of climate change, fire history, nutrient-deficient soils and recent invasive elements (most notably *Homo sapiens*) is now clear. The challenge lies in new, multidisciplinary approaches to take this understanding to a new level so that we can live on the Australian continent in a relatively non-destructive way.

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