LONG TERM CLIMATE CHANGE AND THE EVOLUTION OF TREES IN AUSTRALIA

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INTRODUCTION

Trees form a major part of the living biota on Earth. They are often very large, long-lived, stationary and majestic. Despite their prominence in the landscape, or perhaps because of it, we rarely ask the question “Why do trees exist at all?”, and yet that is fundamental to our understanding of the way vegetation has evolved on land since its appearance there hundreds of millions of years ago.

The first land plants were extremely simple, with no leaves. They were only a few centimetres tall, and the equal dichotomous branching and terminal sporangia contributed to a bushy habit and restricted vertical growth. However, it did not take long for plants to evolve to a greater height, with more complex branching patterns allowing for the development of a main stem and the evolution of vascular conducting tissue allowing for the transport of water from the soil to the aerial parts of the plant at a much greater height than is possible using positive turgor pressure alone. It is intrinsically interesting to know how plants overcame the problems involved in growing taller in what is essentially a hostile environment, but this does not tell us what advantage plants gained from doing so. There seem to be at least two logical reasons why plants should grow taller. Firstly, it is of great assistance in dispersing propagules. Early land plants had terminal sporangia that literally rotted on the plant, passively releasing the spores. With the plants very close to the ground it was difficult to get very much spore dispersal at all with the result that plants became locally crowded. Plants that were, by chance, taller were able to spread their spores further and their offspring had a greater chance of survival, and thus evolution favoured this taller growth strategy. Secondly, once plants made the transition onto land, there would have been immediate competition for light. Shade is a very major disadvantage for photosynthesis and growth, and an obvious solution for each individual plant is to be as tall as possible. This has the capacity to develop in an uncontrolled way, and we see the result today – trees have had to evolve some very sophisticated mechanisms in order to achieve great height to get their foliage into unshaded light.

Amongst the earliest plants to achieve the status of trees are some groups that we do not think of as trees at all today, for example, relatives of living *Equisetum* and *Lyopodium* were large and prominent trees for long periods of time in the past, even though there is no sign of that habit in their living relatives today.

The Major Constraints on Tree Growth at High Southern Latitudes in Gondwana

It is generally understood that a major constraint on tree growth is temperature, and in the Northern Hemisphere in particular this is most easily demonstrated by the often obvious tree-line on mountains. However, this also works on a latitudinal basis, although the demarcation is not as obvious as it is on mountains because temperature declines much more slowly with increasing latitude than it does with increasing altitude. It therefore comes as a surprise to see evidence of extensive forests on Antarctica during much of the past. Some of the earliest evidence of this is *in situ* tree trunks from about 200 million years ago and this kind of evidence extends until about 80 million years ago and trees were present on Antarctica much more recently than this. While Antarctica has not always been as close to the South Pole as it is now, it certainly was polar during much of the time when conifers and later angiosperms made up forests of substantial trees there. Given that trees very likely grew under the same physiological constraints then as they do now the only rational conclusion to draw from this is that at the time Antarctica was much warmer than it is today, and there is abundant independent evidence to support that hypothesis. Interestingly, two of the major reasons to believe Antarctica was warmer at times in the distant past than today are a much higher atmospheric carbon dioxide level (possibly around 10 times current levels) and a major difference in oceanic circulation brought about by the existence of the supercontinent Gondwana, centred over the South Pole and blocking the formation of a circum-antarctic ocean current. The circum-antarctic ocean current that is in place today traps vast amounts of sea water at very high latitudes, circulating constantly around Antarctica. This water is very cold because the sun is always low in the sky and hence the radiation from it has to pass through a large volume of atmosphere before it reaches the surface and in the process much of it is lost to reflection, absorption and re-radiation. The relatively small amount that does reach the surface of the sea does not heat the sea to any great extent. On the other hand, when Gondwana was in place, the major ocean circulation patterns moved water from polar to equatorial latitudes on a regular cycle. When ocean circulates from the equator to the pole, the water is heated at the equator by the sun that is directly overhead for much of each day and has a relatively small volume of atmosphere to penetrate. This warm water then circulates to high latitudes, and, due to the high specific heat of water, transfers a lot of stored heat to those latitudes, leading to a relatively small temperature gradient between the equator and the pole, a relatively warm planet, and polar forests. If this is coupled with a very high atmospheric carbon dioxide level and the associated greenhouse warming, conditions for tree growth were extremely favourable in most terrestrial environments.

In today's world there are no polar forests and so we have no living comparison to make with these ancient forests of Antarctica. This is not the only unusual feature of these forests, because as well as dealing with what we would consider as unusual temperatures, they also had to cope with very unusual photoperiods. Forests within the Antarctic Circle would have experienced some total winter darkness, possibly for months, and in summer a sun that did not set for a prolonged period. However, even though the sun did not set, it also never rose high in the sky and circled around horizon during each day from a relatively low angle. This means that trees in these forests must have had their canopies cascading down the sides of the trees, rather than on top as is usually seen in tropical forest trees, and the tress probably need to be quite widely spaced to avoid excessive shading. Some of the living relatives of the species that we know grew in these Antarctic forests retain this shape in modern, much lower latitude forests. An excellent example is seen in all extant species of *Araucaria* (Figure 1).

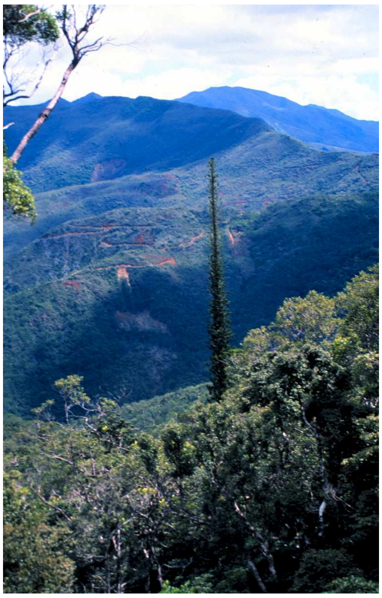

Figure 1. Extremely tall and thin *Araucaria* tree in New Caledonia. Note the positioning of foliage down the side of the tree.

The Weddellian Biogeographic Province

Flowering plants (angiosperms) first appear in the fossil record around 120 million years ago and reached high southern latitudes several million years later. Angiosperm diversity and dominance slowly rose in Antarctica over the next few tens of millions of years, and sometime around 80-100 million years ago a remarkable but poorly understood set of evolutionary events took place. This occurred in what is now known as the Weddellian Biogeographic Province, which encompasses the region made up by southern South America, the Antarctic Peninsula and associated parts of eastern Antarctica, New Zealand and south-eastern Australia. Some remarkable members of the living Southern Hemisphere flora and fauna had their genesis at this time and in this place. Amongst the flora, this includes iconic southern families like the Casuarinaceae, Nothofagaceae and Proteaceae, as well as some of the better known conifer genera. The explosion of information that has accompanied the breakthrough in analysing DNA from living species and using the results to estimate the evolutionary relationship amongst them has revealed some relationships that had not been previously anticipated from morphological research. For example, the living genus *Nothofagus*, now assigned to its own family, the Nothofagaceae, is closely related to the Betulaceae, which is now restricted to the Northern Hemisphere; the Proteaceae are closely related to the Platanaceae and the Casuarinaceae are closely related to the Ticodendraceae and Betulaceae. There is some macrofossil and pollen evidence to suggest the presence of these now Northern Hemisphere families at high southern latitudes during the Cretaceous, but there is no fossil record to demonstrate how these remarkable transitions may have taken place. What we do know is that by the time we see the first macrofossil record of each of the Southern Hemisphere families, the fossils look very much like living members of their respective families. These fossil records are at least 55 million years old, suggesting that there has been very little evolution within these families during that time, and yet sometime during the previous 30-40 million years dramatic change took place that is so far unrecorded. This remains one of the major unsolved problems of Southern Hemisphere plant evolution.

The Early Migration of Angiosperms in the Southern Hemisphere

The first angiosperms in the fossil record, from the Early Cretaceous, appear to have filled an early successional niche. These plants were small and herbaceous, but before too long trees had also evolved to fill an early successional niche. When angiosperms began to spread through the Southern Hemisphere, there is evidence to suggest that they migrated through the rift valleys that developed as Gondwana began to separate into smaller land masses. These rift valleys must have had high levels of volcanic activity, earthquake and landslip, providing massive opportunities for early successional plants, including trees. Australia is now relatively free of these types of disturbance, but that isn’t true of South America, New Zealand and Papua New Guinea. On these land masses volcanoes are relatively common, as are earthquakes and landslips and many tree species are well adapted to regenerate in these conditions. Species of *Nothofagus* are notable for this, and a great deal of research has been done on the need for relatively frequent major land disturbance for their seed germination and seedling establishment. *Nothofagus* in Australia has developed a slightly different regeneration strategy, but this seems to be an exception.

The First Modern Forests in Australia

The Cretaceous Period ended with a massive extraterrestrial impact about 65 million years ago. While the full significance of that impact is still not completely understood, darkness prevailed for months or years, interfering with normal photosynthetic production and forest fires raged as incendiary particles returned to Earth from the ejecta thrown up by the impact. Forests must have been devastated on a global scale, although Australia was on the other side of the world from the impact point and may have escaped some of the more dramatic effects. In the aftermath of this impact event, the forests that established looked much more like modern forests than anything that had preceded them. Angiosperms were common in these forests and the general “tropical rainforest” nature of the vegetation increased until it peaked at about 45 million years ago. By this time forests that resemble today’s dense tropical lowland rainforests dominated even very high latitudes, with warm and very wet conditions prevailing. Mangrove swamps occurred at 70°S and large, broad-leaved species dominated the complex forests.

It is worth considering the conditions that allowed the development of such forests at high altitudes. There are three major issues:

1. An extinct climate prevailed where there was only a relatively small temperature gradient between the equator and pole, with polar regions being relatively warm, and everwet conditions were common. The main driver for this climate may have been the placement of the southern continents, since, as noted above, Australia and South America were still connected to Antarctica, blocking the formation of the circumantarctic ocean current. The presence of large volumes of warm oceanic water at high southern latitudes not only decreased the temperature gradient from the equator to the pole, but also increased evaporation and led to a very wet climate.
2. A very different photoperiod for these forests at high latitudes, leading to forests where trees were quite widespread, and hence a very diverse understorey of shrubby plants may also have and enough light to develop.
3. Atmospheric carbon dioxide levels were considerably higher than at present. It is widely reported that atmospheric carbon dioxide levels are currently rising and there is a very strong inference that this is a result of the changes brought about by the increasing human population

and the impacts of the industrial revolution (Figure 2). There is no doubt that atmospheric carbon dioxide levels are at their highest point for the last 160,000 years at least, but even though methods of measurement are less precise, it appears that levels may have been as much as 10 times higher than present levels 45 million years ago. This is particularly interesting from a botanical perspective because increased atmospheric carbon dioxide has at least two impacts on plants – it is a greenhouse gas and hence may contribute to a warmer climate, and it is a fuel for photosynthesis and hence may lead to much increased rates of photosynthesis. At present there is no simple way to test the impacts of such high carbon dioxide levels.

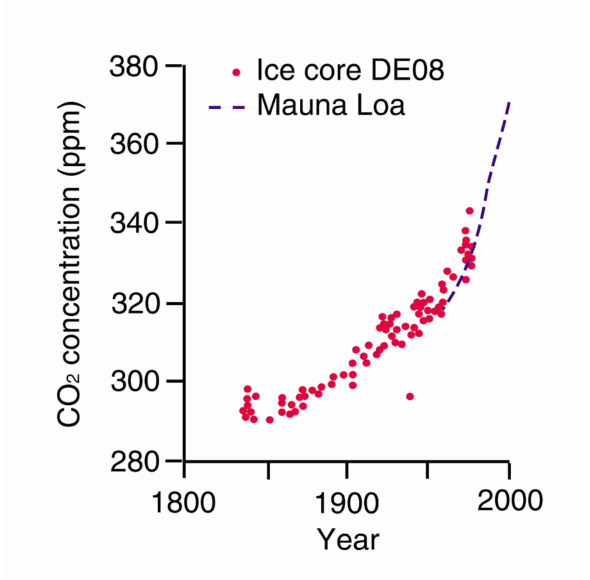

Figure 2. Atmospheric carbon dioxide levels measured from atmospheric readings (Mauna Loa) and from gas bubbles trapped in ice cores (DE08).

Long term climate change

When Australia separated from Antarctica a complex set of interactions were set in place that resulted in a change in climate, including a decrease in temperature at high latitudes, a decline in water availability, and eventually the evolution of the arid zone that dominates Australia today. When Australia separated from Antarctica, southern Australia contained diverse forests that included tree species with nearest living relatives that now occur from Tasmania to New Guinea, and even southern China, and from South America to New Zealand. As the climate cooled and dried these rainforests simplified and broke up into smaller patches, eventually resulting in the disjunct distribution that prevailed even before human occupation of the continent and the consequent decimation of rainforest.

Aridity began to develop towards current conditions from about 20 million years ago and has more recently gone through cycles of increasing and decreasing dryness as part of the glacial cycles of the last million years or more. A recent manifestation of these cycles of increasing and decreasing aridity is the presence of some tree species in small oases amongst vast arid areas (e.g. the palms and cycads in Palm Valley in central Australia). An even earlier manifestation of the impact of increasing aridity was the interesting interaction between plants and low nutrient level soils, and in particular low soil nitrogen and phosphorus, which is common in Australia and has led to the characteristic scleromorphic ("heath") vegetation. The evolutionary response to low soil nitrogen and phosphorus occurred quite early in the history of the Australian vegetation (there are fossils with a scleromorphic response from 55 million years ago, Figures 3,4), and those plants that adapted to these low nutrients were well placed to thrive as the climate dried out. This is because the morphological responses to low soil nitrogen and phosphorus may pre-adapt the plant to low water levels, and the transition of plants from low soil nutrients to low soil water conditions is apparent from about 30 million years ago in south-eastern Australia. There are few other examples of the evolution of arid zone vegetation in the Australian fossil record, because plants rarely fossilise well in dry conditions, but there is some evidence that the arid zone tree genus *Callitris* had its origins in wet forests in south-eastern Australia about 35 million years ago.

Figure 3. Fossil *Banksia*-like Leaves from about 55 million years ago in southern NSW.

Figure 4. Cast of a *Banksia* cone from about 45 million years ago in north-western Western Australia.

As the climate dried, leaf litter began to build up and dry out, and when ignition sources were available fire became an important part of the environment. There is evidence for regular pre-human fire in south-eastern Australia from about 25 million years ago, although it probably had a relatively low natural frequency, since it occurred among species that are often killed by fire and rely on released seed to produce a new generation of adult trees (Figure 5). Notable for their absence from the forests were *Eucalyptus* trees, which began to appear in sporadic fashion on the east coast of Australia at about 20-25 million years ago (Figure 6). Although eucalypts appear to have primarily evolved in response to high fire frequencies, they do not become common in the Australian vegetation until relatively recently (last 50-200,000 years) and appear to have responded strongly to a combination of climate change and fire management of the vegetation by the newly arrived aboriginal people.

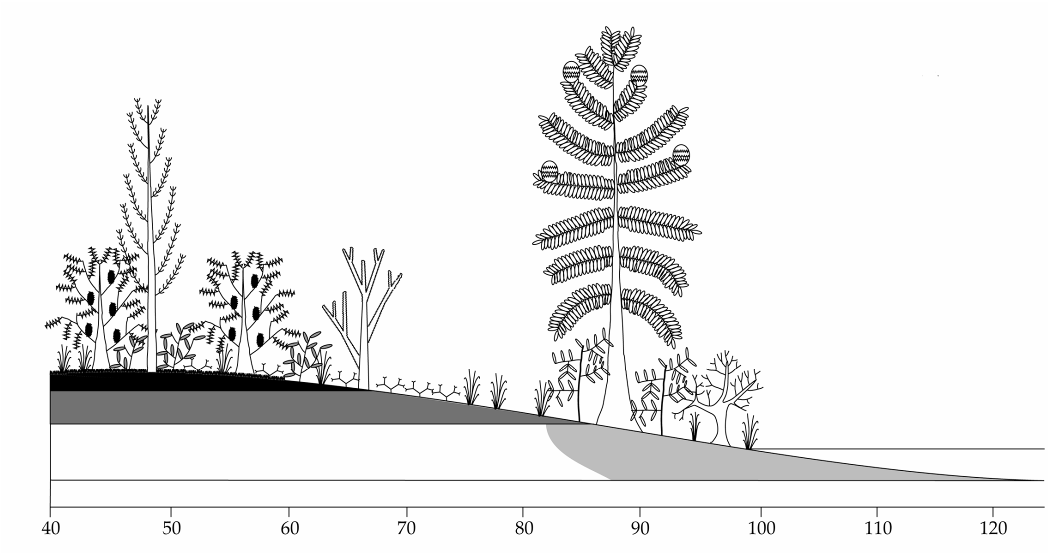

Figure 5. Reconstruction of vegetation that formed the Latrobe Valley coal in south-eastern Victoria about 20 million years ago. There is open water on the right of the figure, and as the land surface rises above the water table from right to left, the recorded fire frequency increases, with the vegetation at the left hand side, including *Banksia*, *Callitris* and Casuarinaceae, suffering the highest fire frequency.

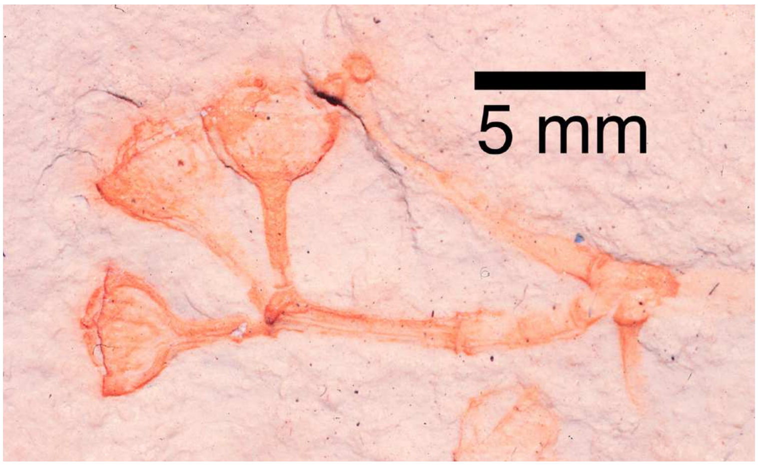

Figure 6. Fossil fruits of *Eucalyptus* from eastern NSW about 20 million years ago.

CONCLUSION

The vegetation we now recognise as truly unique to Australia is a relatively modern phenomenon, but its genesis extends back many tens of millions of years. The history of individual genera and species contains surprises, with well known, and sometimes controversial introduced trees like *Platanus* and *Betula* figuring prominently in the history of the native Australian flora. Climate change has been critical to the evolution of the Australian vegetation for a very long time and it provides some important lessons for what may happen in the future with human-induced climate change. The world is change dramatically, and this will pose many challenges, not least of which will be what we do about plants, both native and introduced. Many species will survive and the vegetation will recover from whatever shocks are imposed on it. However, the issue for us is that the recovery will be too slow to be relevant for human timescales, and the ultimate challenge for us is to minimise the changes and to plan very carefully to provide the best adaptive responses possible.

FURTHER READING

Hill, R.S. (ed.) 1994. *History of the Australian Vegetation: Cretaceous to Recent.* Cambridge University Press, Cambridge. 433pp.

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