Ghosts of the Past: Where does Environmental History Begin?

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SUMMARY

The present environment of Australia represents a palimpsest which records a history of past climates, nutrient poor soils, burning, and increasing aridity. The details of the history are not readily disentangled.

The weathering profiles and the nutrient-poor soils associated with their surficial expression may be of great age. Adaptive responses of plants to the nutrient status of the soils may be contemporaneous with and of the same age as the weathering, leaching and initial leached soil formation. Adaptations that developed initially in response to one selective force, e.g., nutrient-poor soils, may subsequently have been co-opted to another purpose such as sclerophylly in resisting wilting during drought, or lignotubers in surviving drought, grazing and burning. The sclerophylly developed by plants in response to nutrient-poor soils makes them fire-prone in the sense of Mutch (1970) which is an adaptation in so far as it promotes sterile ash beds on which seeds germinate free from fungal attack.

Present observations cannot readily be used to interpret past environments. In order to infer the nature of past environments it is necessary to consider geological, climatic and weathering histories as well as the physiological development of the structures being used as evidence to infer past environmental conditions.

It is argued that the origins of fire adaptations may pre-date the arrival of Aborigines, whose influence on the biota may then have been to produce the patterns observed by the early settlers and to eliminate or winnow out those fire sensitive species unable to cope with their cultural practices. Aboriginal use of fire in cultural and hunting practices has only influenced the biota for about 50,000 years which is too short a time to have influenced the biota other than to eliminate, or winnow out, those elements unable to cope with the fire regimes imposed by their cultural practices.

Environment and History **2** (1996): 97-114

INTRODUCTION

The Australian and the Western Australian environment is characterised by high summer temperatures and variable rainfall. High rainfall leads to prolific plant growth while drought predisposes the vegetation to burning. These conditions follow each other so that recurrent destructive fires lit by arson, accident or lightning are potentially of frequent occurrence. Such fires not only destroy native vegetation in nature reserves but also endanger life and property on adjacent settled areas. The issues and dangers have been well portrayed by Pyne (1991).

The risk of fire with its attendant losses has inspired legislation which specifies management actions to be taken in order to minimise fire risks. Management centres on hazard reduction burns, which are planned to be at regular intervals with the goal of ensuring that fuel loads are not so great that burning would lead to uncontrollable fires. An extensive literature has grown around bushfires, their control by hazard reduction burning and the effects of regular and repeated hazard reduction burns on the native biota, especially that within conservation reserves (McArthur [1968], Luke and McArthur [1978], Gill et al. [1981], Ford [1985]).

It is a matter of observation that many elements of the biota, particularly plants, tolerate fire and recover as populations shortly after burning. Seeds of some plants germinate following scorching by fire and generally there is a post-fire sequence of plant growth until the community can again carry a fire.

Gardner (1957) expressed the opinion that many of the traits exhibited by plants were to be interpreted as adaptations to periodic burning extending back over a very long period, and inferred that the periodicity was imposed by the hunting and other practices of the Aborigines. As evidence in support of his interpretation Gardner (1957) cited the large woody fruits of some species which shed seeds after being scorched by fire, the germination of seeds in the mineral ashbeds provided by fire and the presence of lignotubers and other underground perenniating organs from which plants resprout following burning. This interpretation has been accepted in a broader sense by James (1984) who interprets sprouting after injury from a swollen base, rootstock or lignotuber as an evolved reproductive strategy in response to frequency and severity of disturbance, for example fire. Gardner (1957) supposed that repeated burning eliminated those species unable to tolerate fire.

Wallace (1966) considered only the jarrah (*Eucalyptus marginata* Sm.) forest and the natural resistance of this species to fire. In particular he emphasised that prior to settlement it was likely that long burning, low intensity fires such as he had witnessed in virgin forests may have completely burned through the forest every 2-4 years. Merrilees (1968) discussed drought and the burning of vegetation by Aborigines as contributing to the extinction of the large marsupials at the close of the Pleistocene. Hallam (1975) built on the foregoing and after reviewing an extensive literature on Aboriginal occupancy of the continent concluded that natural fires as a result of lightning strikes were less significant than man-made fires in selecting and shaping plant ecology and the adaptations to burning that were apparent at the time of European settlement.

Hallam (1975, 1985) emphasised the regularity of Aboriginal burning practices and inferred that firing of the bush must have been an important factor in establishing and maintaining the vegetation patterns. Gill (1981) discussed the adaptations to burning in detail and concluded that while the structures and biology allowed plants to tolerate or resist fires and were in this sense adapted to fire this should not be interpreted as indicating that the adaptions arose as an evolutionary response to fire. Recher and Christensen (1981) interpret adaptations as being to regimes characterised by season, frequency and intensity of burning. Hingston (1985) points out that the biological processes that sustain the ecosystem evolved with fire which had been used by Aborigines for thousands of years thus shaping the composition of the flora.

These views have influenced the attitudes of managers to reserve management as well as to hazard reduction burns. Burbidge (1985) when discussing the loss of mammals from the desert reservations advocates that the best form of management would be to mimic Aboriginal burning, which has now been implemented, (Burbidge et al 1987, Burrows and Thompson 1990). Hopkins (1985) extended this reasoning by interpreting fire as a recurrent disturbance which triggers regenerative processes. He argues that if the conservation of communities depends on the maintenance of disturbance regimes then it may be necessary deliberately to apply the earlier Aboriginal regime in order to conserve the biota by maintenance of the processes associated with that type of fire. The draft management plan for the West Cape Howe National Park specifically identifies prescribed or hazard reduction burning as the analogue of Aboriginal burning practices (Anon. 1992). Thus, notwithstanding that there is no consensus on the significance of fire and arguments have been advanced against the practice of repeated burning because of its effect on the composition of the biota (Good,1985, and Tingay,1985), present management is predicated on an interpretation of environmental history beginning with the arrival of Aborigines and their burning and husbandry practices. An unstated corollary of this belief is that since the biota was rich and diverse when Europeans displaced Aborigines a continuation of their burning practices will not lead to loss of elements of the biota. However, it is possible that past environmental influences have been more complex and extended over a longer time than Aboriginal influences. The question is whether is it is prudent to ignore environmental influences of the distant past by asssuming, for the purposes of management, that environmental history began with the arrival of Aborigines.

It is the purpose of the present paper to explore the possibility that traits which are now of selective advantage in the present fire-prone environment could have arisen in response to past selection pressures different from those imposed by the fire disclimax resulting from Aboriginal burning practices. This is done by reviewing the geological history of the continent, past climates and the effect that these have had on the flora and fauna, especially as the responses appear to contribute to supposed fire adapted traits.

GEOLOGY AND GEOLOGICAL HISTORY

The present land mass of Australia is composed of very ancient rocks, the ages of which can be used to divide the continent into three parts. The western part is Archaean, the central third is Proterozoic and eastern third is Phanerozoic. With the exception of the eastern and south-eastern parts the landscape is of low relief. None of the ancient mountain belts of the Archaean or Proterozoic are now conspicuous topographic elements, and the area has been stable for a very long period.

During the Palaeozoic Australia was part of Gondwana from which it separated after India and Africa in the late Cretaceous / early Tertiary. At the time of separation the present southern edge of the continent was approximately 70 degrees south latitude. In the Jurassic, prior to the fragmentation from Antarctica, there were widespread fresh water lakes. During the early Cretaceous the crustal thinning and down warping which preceded the final fragmentation of Gondwana led to the development of extensive epicontinental seas which divided Australia into several islands. These seas had withdrawn by the late Cretaceous (BMR Palaeogeographic Group 1990). Apart from some vulcanism along the eastern and south eastern seaboard throughout the Cainozoic the continent appears to have remained unchanged until the present and many of the present drainage channels, particularly on the Archaean and Proterozoic rocks of the continent are recognised as being of early Cainoizoic origin (van de Graaf et al.,1977).

REGOLITH

The regolith consists of those transported or residual rocks, whether unconsolidated or indurated, which blanket older rocks. In Australia the regolith is commonly highly silicified iron and aluminium rich laterite or iron poor silcrete. These rocks commonly overlie a deeply weathered zone which may extend for several tens of metres and is commonly termed the pallid zone. The formation of deep weathering profiles requires high rainfall and efficient leaching. Silcrete and laterite are precipitated under seasonally arid environments as the result of the transport in an aquatic solution of iron, aluminium, and silica to the surface where they are precipitated when the water evaporates. Silcretes, as distinct from laterites, are found in the more arid environments but both laterites and silcretes depend on a deep weathering profile from which the silica can be leached and precipitated during repeated wet and dry cycles. The presence of deep weathering profiles, laterites and silcretes thus have important implications for interpretations of environmental history.

The low relief and subdued topography of much of the continent has meant low rates of erosion. When erosion has occurred the old indurated land surface has been left as residual capping to mesas and butes which are often separated by extensive areas from which the duricrust has been stripped so exposing the pallid zone clays. These stripped or etched land surfaces (Finkl and Churchward 1973) are characterised by the very low nutrient status of their soils.

Despite the wide-spread early Permian glaciation some land surfaces have been identified as being as old as the Cambrian (Stewart et al. 1986). Bird and Chivas (1988) used oxygen isotope dating of minerals developed during deep weathering-lateritisation processes to estimate the ages of clays from such intensely weathered profiles of the regolith and concluded that minerals of three ages could be identified, namely, pre-late Mesozoic; late Mesozoic to early Tertiary; and post-mid Tertiary clays. These observations suggest that some of the land surfaces are of great antiquity with leached, nutrient-poor soils, of similar ages.

CLIMATES

Past climates have been inferred from the presence of fossils, palynomorphs, deep weathering profiles, lacustrine deposits such as dolomites (Callen and Tedford 1976) and sand dunes.

The palaeoclimates and palaeogeography of Australia during the Phanerozoic have been reviewed by Frakes and Rich (1991), Kemp (1981) and Galloway and Kemp (1981). Frakes and Rich (1991) tabulate and summarise the literature on the latitudinal movement of the continent during Tertiary time as well as other environmental and biotic events. Kemp (1981) reviewed the evolution of the Australian environment and particularly the development of the present atmospheric circulation. Galloway and Kemp (1981) review the late Cainozoic environments of Australia and concluded that dryness has been a marked feature of Australia since the mid-Miocene. The broad climatic picture that emerges is one of a mild moist climate associated with an ice-free pole and warm oceanic waters at the commencement of drift to a climate dominated by the present extensive Antarctic ice sheet and very cold circum-Antarctic ocean waters. During this time Australia moved from high latitudes to its present position across the tropic of Capricorn, a total of about 40 degrees of latitude.

The climatic changes recorded in the stratigraphic record show a trend from early warm wet equable climates to the present arrangement of mesic environments around an arid or semi-arid core. The causes of these changes have been attributed to the latitudinal changes (Beard 1977). However, an alternative interpretation has been advanced by Flohn (1978) and Bowler (1978,1982). These authors base their interpretation on the changes in the strength of the atmospheric circulation. This followed from a steepening of the tropic to pole temperature gradient (Kemp 1981) in both the atmosphere and oceans after the opening of Drake passage, the development of the circumpolar current and the Antarctic ice sheet (Flohn 1978). These changes accentuated the intensity of the subtropical high pressure cells which are associated with the development of the present central Australian deserts (Bowler, 1982).

The present rainfall pattern of southern Australia developed after late Miocene/Pliocene. This event was associated with a fall in temperature.

VEGETATION

Records of past vegetation can be reconstructed from plant fossils and pollen preserved in the stratigraphic sequence. The Eocene record is more complete and wide spread than for other parts of the Tertiary (Truswell and Harris 1982). However, the preservation of material depends a great deal on chance, and those growing in drier locations will not be preserved. Nevertheless, despite the fragmentary record it is apparent that the plants present in the early Tertiary are now restricted to wetter cooler parts of the eastern coast, and plants typical of modern floras are poorly represented in the fossil record. This has been reviewed by Lange (1982) for the Tertiary and Kershaw (1981) and Singh (1982) for the Quaternary.

Closed forest elements such as *Podocarpus, Nothofagus* and *Cyathea* persisted in Australia until about the mid Miocene when typical Australian, non-rainforest, trees and shrubs occur in the fossil record (Lange 1982). Lange (1982) reviewed published work interpeting silicified casts of myrtaceous and eucalyptus-like fruits as being evidence of the emergence and radiation of the Myrtaceae and the evolution of eucalypts (*Eucalyptus*), teatrees (*Leptospermum*), paperbarks (*Melaleuca*), and bottlebrushes (*Callistemon*). The age of these fossils was uncertain but could be as old as Eocene or as young as Miocene. Lange (1982) argued that even if these deposits were of Miocene age the degree of specialisation shown by the fossils suggest that the lines emerged at least by the end of the Oligocene. Truswell and Harris (1982) argue for a Miocene age of these fossils but emphasise dating problems and the inability to reconcile macrofossils with the palynological record. Despite these constraints it is clear that by the middle Tertiary Myrtaceae were present allied to genera now commonly found growing in fire-prone woodlands, heathlands and shrublands on low nutrient status, severely leached soils (Specht 1979). Also closely associated with heathlands are the Proteaceae, and the presence of pollen with affinities to modern genera in the early Tertiary of central Australia (Martin, 1982) suggests that components of the present heathland floras were present throughout the Tertiary but perhaps occurring in soils and situations where fossilisation was less likely. This suggestion tends to be confirmed by the description of a fruiting cone of a modern-looking *Banksia* species from sandstones of the Eocene of Western Australia (McNamara and Scott 1983).

FAUNA

The megafauna were large to very large animals ranging up to 1500 kg in weight and a height of two to three metres (Murray 1984), and included large macropods in the genera *Macropus, Protemnodon, Sthenurus* and *Procoptodon*; large quadrupeds such as the monotreme *Zaglossus* (30 kg); the diprotodontids, *Palorchestes, Zygomaturus, Diprotodon*; koalas, *Phascolarctos*; and wombats, *Phascolonus*. Terrestrial bird such as emus were more diverse and the size range greater than in present-day members of the species (Rich and Van Tets, 1984). The large extinct mirihung birds ranged in size from about the size of emus to the largest bird known to have existed. The last of these (*Genyornis newtoni*) survived until at least 26,000 years ago (Rich 1979, Rich and Van Tets 1984). Reconstructions and maps of fossil distribution are given in Murray (1984), Horton (1984), and Rich and Van Tets (1984). Anatomical reconstructions suggest that in feeding habits the megafauna ranged from tall browsers to cursorial grazers; some may have lived in flocks or herds in moist woodlands while others occupied drier more open areas. Many possibly had trunk-like appendages and browsed on shrubs or trees. The heavy claws and nasal bones of others suggest a soil-disturbing, pig or tapir-like, feeding mode (Murray1984). Predators such as *Thylacinus* and *Thylacoleo* (75-100kg) appear to have been widespread.

Fossil assemblages represent accidents of preservation and not the numerical abundance of species in an environment, and give no indication of what was present in places where fossilisation was not possible; nevertheless it is clear that in Australia, before the extinction of the megafauna, there was a fauna capable of browsing and grazing above- and below-ground parts of plants of all ecosystems. Such a comprehensive pattern of disturbance ranging from canopy destruction to soil disturbance must have afforded many opportunities for maintaining a diverse flora adapted to regenerate in disturbed patches of various sizes. Even more significant was the potential for browsers of all sizes to affect the structural composition of any post- disturbance, (including post-fire), regeneration that occurred.

Notwithstanding the faunal losses referred to above, the pollen record indicates that most of the plant species of the biotic environment persisted after the extinction of the megafauna. However, in the absence of trampling, grazing and browsing by the megafauna it would seem that plant densities and abundances would be much higher with correspondingly more abundant litter. All these factors would contribute to more intense fires whenever plant material was burnt.

FIRE

Palaeontological evidence for fire and burning is very fragmentary. Fusain has been found in Australian Tertiary coals (Kemp, 1981). Martin (1990) in a review of Tertiary climate and phytogeography in southern Australia has documented the increase in charcoal abundance in the Miocene which has continued to the present. Taken at face value this evidence indicates an increase in burning coincident with the climatic changes which followed the opening of Drake Passage between Antarctica and South America and the development of the circumpolar current in the Miocene.

Martin (1990) believes that the climatic changes recorded in her studies are typical of southern Australia and that burning of vegetation has been an environmental factor for a long time. Elsewhere late Tertiary environments in which fire could occur have been documented by Callan and Tedford (l976) at a site in lower central Australia. In the Miocene, the area experienced high rainfall, temperatures higher than at present and, at times, seasonal dry periods became part of the weather pattern. This pattern continued until the lakes and swamps of the Tertiary disappeared during the Pleistocene. By the late Pleistocene the drainage and aspect of the landscape resembled the present.

FIRE AND THE MEGAFAUNA

From the Miocene to the end of the Tertiary the terrestrial vertebrates increased in size so that at the end of the period they were very large (see above). The sthenurine macropods were up to 3 metres in height and from 2-300 kg in weight and were browsers (Murray 1984). Browse would be abundant and of high nutritional value in the plant regrowth following burning. Grazing herbivores eat grasses or other monocotyledons, the present distributions of which are limited by climate, soils or fire. Whatever the details might be it seems that the evolution of large marsupials was ultimately associated with the environmental changes set in train in the Miocene and the droughts and fires associated with the drying of the continent. The aboriginal practice of burning areas to which herbivores would be attracted by the post-fire regrowth mimics this earlier pattern.

FIRE IN HISTORICAL TIMES

Early travellers and explorers all record burning by Aborigines. Hallam (1975), Pyne (1991), Clark (1983) and Kimber (1983) have reviewed this literature. When burnt the oil rich plants always provide abundant dense smoke and even in less intense fires it is difficult to interpret observations of burning vegetation without knowing the context and experience of fires that the observers interpreting the actions of the Aborigines possessed.

Nevertheless most observers record, sometimes with surprise, how readily the vegetation recovered from burning. These observations led to the interpretation that the vegetation was adapted to burning by Aborigines (Hallam 1975). Gill (1981) accepted that the ready recovery of vegetation implies adaption but used Dobzhansky's (1956) definition of adapted as 'An adaptive trait, then, is an aspect of the developmental pattern which facilitates the survival and/or reproduction of its carrier in a certain succession of environments'. Such a definition relates to present functions. It does not have connotations relating to origins and so cannot be used to infer the role of fire in environmental history. If, however, a definition of adaptation required that its origins must relate to selection for the present function then any trait which satisfied the definitiion could be used to infer a role for fire in past environments. With the exception of Gill (1981) it is often not clear in which sense many authors use the term 'adaptive traits', though Gardner (1957) seems to infer selection over a long period to produce them. However, should traits be specific adaptations to burning (Gardner 1957, Hallam 1975) and not have arisen in any other way, then they can be used to infer a long history of environments subject to burning. The traits considered by Gill (1981) to be adaptive in this sense were: soil protection of buried buds; bark protection of aerial buds; bud survival and sprouting; fire stimulated flowering; fire triggered dehiscence of fruits; and on-plant seed storage. Gill (1981) was careful to avoid implying that fire was the only selective agent capaple of producing the observed traits and pointed out that the traits must also enable survival and reproduction to take place during the stresses imposed by other selective agents.

ABORIGINES AND BURNING

That Aborigines used fire more or less as a husbandry practice has been advanced by Hallam (1975) and Jones (l969) coined the term 'fire stick farming' for such activity. Haynes (1985) describes the Aborigines' objectives and different management practices between seasons and points out that in north central Arnhemland late in the dry season control of fires is no longer possible and very extensive areas may be burnt. However, areas to be burnt in the dry season were usually delimited by fire breaks burnt early. Nicholson (1981) also emphasised that Aborigines used fire as a common tool within a cultural framework derived from centuries of experience in gaining a living from their land. Kimber (1983) emphasised that in central Australia Aboriginal fires were not accidental but meant many things such as hunting, signalling, ceremonies, the hearth, clearing and improvement of the country. The end result everywhere was a network of fire-scars of different ages resulting from past fires of different intensities and extent.

It is easy to understand the rationale for using fire as the Aborigines did. No reasonable people would let vegetation become so dense that it would become difficult for bare footed people to traverse or escape from wildfire. The cultural patterns and sacred beliefs held ensured that appropriate actions were certainly taken to ensure future food supplies and avoidance of incineration by wildfire. Whether the people understood the less obvious consequences of their actions is doubtful. Hughes and Sullivan (1986) point out that burning practices had a significance beyond whether the biota could persist in the face of repeated burning and demonstrated that soil deposition in rock shelters increased following Aboriginal occupancy. They interpret these observations as resulting from up-slope erosion caused by heavy rains following burning. The extent of erosion resulting from burning practices is not clear. Many other cultures have continued degrading practices long after traditional exploitation was affecting the environment. Moreover, the Aborigines could hardly be expected to distinguish the changes which followed their exploitation from climatic and other environmental variables.

Insofar as Aboriginal burning practices had an impact on plants it was the way the composition of the flora was affected through the elimination of fire sensitive species which could not persist, flower, fruit or seed and regrow between burns in the new fire regime. In part the difficulties that sensitive species experienced in persisting can be related to two factors. First, the fire frequency or fire regime: fires may have been lit at seasons which satisfied the needs of the Aboriginal economy but be quite unrelated to natural burns started from lightning strikes and so unrelated to the biology of the sensitive species. A further complication is that lighting strikes are associated both with convective thunderstorms and with thunderstorms associated with squall lines. Convective thunderstorms occur when humid air lies above hot land surface. Heating and the resultant convection leading to thunderstorm development occurs late in the day and even if no rain develops from the storm any fires tend to die out during the night. Exceptions to this generalisation occur in late summer when vegetation is very dry and once ignited tends to burn extensive areas. Late season fires lit by Aborigines would resemble such extensive fires.

In many ways fires resulting from lightning strikes on squall lines are different. They are associated with air masses of contrasting physical properties, can occur at any hour of the day or night, often occur along a line associated with the boundaries between air masses and are accompanied by strong squally winds. The wind characteristically blows from the north-east and then north as the squall line approaches and then quickly swings to the south west as the squall line passes. The thunder storms and lightning strikes may be associated with any of these winds. Those strikes which ignite fuel when the winds are northerly or north westerly have a characteristic course: from the origin the fire is blown down wind gradually widening as the head fire extends; as soon as the front passes the wind swings to the south-west and the fire then spreads from its former eastern flank to the north-east and continues to burn in that direction until the cool of the evening or until rain falls. As with other late summer lightning strikes it is possible that the fuel will be so dry that the fire will not go out and extensive areas are burnt. Even when fires are extensive the intensity varies over different topographies and at different times of the day, with the result that areas suffer different fire intensities and many areas completely escape being burnt. Such areas become refugia from which biota can re-invade the burnt areas.

The long-term consequences of fires originating from lightning strike was a complex mosaic of burnt and unburnt patches of various sizes and post-fire ages. Following the arrival of the Aborigines these patches were supplemented by fire scars which resulted from their burning regimes centred on hunting, living and ceremonial space.

PLANT GROWTH

Wild (1958) showed that Australian soils were nutritionally poor, and Beadle (1963, 1968) demonstrated that the sclerophylly of some Australian plants was a response to low nutrient levels, particularly phosphorus, in the soil. Other workers (Kerr 1925, Chattaway, 1958) showed that another response was for seedlings to develop tissue proliferation and multiple buds in stem swellings above and below the cotyledons. This swelling or lignotuber contains storage tissue and when development is possible provides the resources for rapid growth when, for example, light is provided through canopy removal. The development of lignotubers is associated with nutrient poor soils and has been interpreted as a response to stress. However, once developed, lignotubers survive drought, fire, and grazing. Regrowth readily develops from the profuse supply of buds present. Such growth forms are common in many myrtaceous genera. When it occurs in eucalypts they grow as mallees. In the absence of fire or stress the plant grows one or few trunks and a tree results. Lignotubers, in the current environment, are an adaptation to fire in the sense of Dobzhsansky (1956), but they were not necessarily selected initially as a fire adaptation.

MODERN VEGETATION AND FIRE

Following fire, eucalypts and other species regenerate profusely from seeds in the soil seed bank or from seeds that have been shed from the scorched canopy on to the bare sterile ashbed. *Nothofagus* will regenerate after fire, but should the fire interval be less than about 250 years sclerophyll forest dominated by eucalypts becomes established (Gilbert 1958, Jackson 1968). Mount (1964) concluded that all eucalypts regenerate abundantly after fire, and some cannot regenerate without it. He concluded that they depend on fire for their present distribution. Florence and Crocker (1962) showed that *Eucalyptus pilularis* seedlings grew vigorously when grown on forest soil that had been dried for several months or freshly sampled soil held for two days at either 32 or 70 degrees Celsius prior to seeding, or after irradiation; they conclude that this success was due to the death of micro-organisms antagonistic to seedling establishment. Jackson (1968) expressed the opinion that eucalypt seedlings could not grow when shaded or in litter because they were susceptible to fungal attack. Mutch's (1970) hypothesis that fire dependent plant communities burn more readily than non-dependent communities because natural selection has favoured characteristics that make them more flammable is supported by the high oil content and flammability of even green eucalypt foliage, which when burnt satisfies the need for a sterile seed bed. Westman (1978) concluded that there was evidence for a distinct evolutionary history of canopy and understorey in eucalypt forest-heath alliances from the Cretaceous. Many of the genera of the heath and understorey are of the families Proteaceae, Myrtaceae and Casuarinaceae; and Christophel et al. (1992) have identified these extant families among megafossils in a middle Eocene flora from South Australia. Should a sterile seed bed be a prerequisite for seedling establishment then it would seem that even in the Eocene some vegetation types were burnt.

Among the Proteaceae the large woody fruits and follicles (e.g. *Hakea* and *Banksia*) which remain on the plant and do not open to shed seeds until scorched or burnt are also interpreted as being adaptations to fire (Gill, 1981). However, Hocking (1982) showed that nutrients accumulated in the developing fruits were later transferred to the seeds, which then are extraordinarily rich in nutrients (see Kuo et al. 1982). Should large woody fruits or follicles be a consequence of the need to accumulate nutrients near to the developing and ripening seed then any fire adaptedness that such fruits or follicles possess would be a secondary consequence of the co-option of the woody structure to a purpose additional to the primary one of providing seedlings with nutrients so that they can establish in the nutrient-poor soil on which these plants grow.

DISCUSSION AND CONCLUSIONS

In the introduction it was pointed out that many Australian plants can withstand burning and drought. These observations can be interpreted in two senses, first as an evolutionary adaptation to fire and drought (Gardner 1957, Hallam 1975) and secondarily as a trait which allows for survival under a vigorous fire regime but not necessarily selected for by that regime (Gill 1981). Should the first sense be true then traits showing adaptations to fire provide useful guides to environmental history and management practices.

However, drought and fire are only two components of the environment. The literature reviewed has shown that lignotubers and sclerophylly are possibly consequences of the low nutrient status of the soils. Moreover, the nutrient loss follows from an intense and deep weathering of the surface so that laterite and silcrete over a leached pallid zone or saprolith have been a characteristic of the regolith since the Mesozoic. It is possible that traits such as scleromorphy, lignotubers, large persistent woody fruits and lignotubers originated by natural selection in response to the stresses imposed by the nutrient status of the soils. Fossil evidence demonstrates that plant families in which these traits are well developed were present long before evidence for drought and fire appears in the fossil record. The presence of fossils of woody fruits suggests that these had originated prior to the beginning of the modern atmospheric circulation in the Miocene. The evidence of charcoal suggests that fires were present long before the arrival of the Aborigines and that widespread burning may have originated after the modern atmospheric circulation began to develop in the Miocene.

In conclusion, it is possible that lignotubers, woody fruits and sclerophylly were early responses to nutritional stress in seedlings. Subsequently the morphological structures were co-opted as traits having survival value in the presence of drought (resprouting and resistence to wilting) and fire (lignotubers and resprouting) when they became common environmental factors. Thus inferring past environments on the assumption that drought and fire-adapted traits solely represent the products of past selection by these factors in environments prone to drought and fire is not valid.

When discussing the megafauna, it was suggested that the browsers exploited the forage provided by post-fire plant regeneration. Any fire regime will produce a burn mosaic varying from severely to lightly burnt. If the landscape is burnt at intervals then over a period of years the vegetation will be composed of a series of patches of different post-fire ages and stages of regeneration which produce the pattern and structure observed by the early settlers and interepreted by Hallam (1975) as the product of Aboriginal husbandry. The literature reviewed indicates that fire has been a part of the environment for a long period prior to the arrival of Aborigines, but the pattern and structure imposed by them on the vegetation is likely to be unique and different to that of the prior period when the megafauna and lightning lit fires controlled pattern and structure.

Moreover, some of the traits permitting persistence of plants in the presence of repeated burning may have arisen in response to other selective forces, e.g. large woody fruits storing nutrients adjacent to the developing seeds or lignotubers storing nutrients for the rapid growth of the juvenile plant, while some traits, e.g. dependency on fire for a sterile seed bed, may have arisen because of the sensitivity of seedlings of some species to microbial and fungal attack. It is clear from the literature that selection for the traits exhibited by the biota arose long before the arrival of Aborigines. In this sense interpretations based on environmental history need to consider a longer time span than is customary, and to recognise that selective forces unrelated to burning history have influenced the biology of species. These are the ghosts whose presence must be acknowledged before an adequate environmental history of the biota can be established. Interpretation of the natural environment must be based on more than information related solely to the present and immediate past. Environmental history begins when it is certain that ghosts of the past can no longer affect interpretations.

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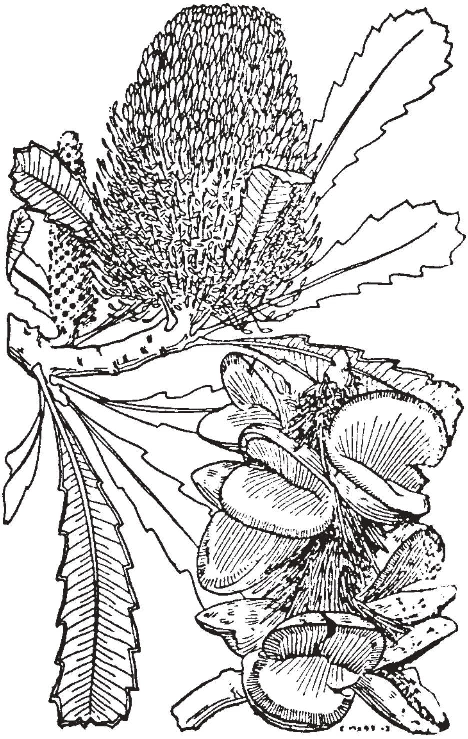

Banksia serrata (drawing by Eirene Mort from Florence Sulman, *A Popular Guide to the Wildflowers of N.S.W.* Sydney: Angus and Robertson, 1913-14)