

Natural and Human Influences on the Distribution and Extent of Victorian Lowland Grasslands

Roger Jones

Indigenous Flora and Fauna Association

Lowland temperate grasslands are the most threatened of Australia's major temperate ecosystems. Since European settlement, the lowland grasslands and woody grasslands of Victoria have contracted from an area covering 35% of the state to less than 1% (Lunt, 1991). This vulnerability is due to a number of historical factors, both natural and human. These factors intertwine in a complex history of geology, biology, climate, and Aboriginal and European culture, that together, have influenced the evolution, and the more recent destruction, of lowland grasslands.

The merging of natural and human history into a single discipline to determine the long term interactions of society and the environment is termed biohistory (Boyden, 1990). The disciplines of natural and human history have traditionally been practised quite separately, preventing the required synthesis needed to describe the continuum between the pre-human and historical realms. Consequently, natural history must reach forward into contemporary issues, and conventional history must reach back, beyond the written record.

Australian history has been entwined with natural ecosystems since people first arrived. Humans have played a role in the "natural" history of grasslands, in their removal, and as will be argued later in this paper, should have a continuing role in shaping the future of grassland conservation. Applying the principles of ecological sustainability to threatened ecosystems, such as lowland grasslands, requires a knowledge of their historical ecology.

The continental and climatic influences on Australian grasses and grasslands from their origins to the Pleistocene era are reviewed in a companion paper (Jones, 1999). This paper examines the natural and human influences on Victorian grasslands from the Pleistocene to the early European era.

The discussion is presented in three parts: part one summarises the known influences until the beginning of the Holocene period at 10 ka (thousand years before present). Part two examines Western and Northern Victorian grasslands in more detail, where new data on Holocene climate change in western Victoria is presented. Part three summarises the effect of the early period of European occupation on those grasslands.

Part One — Pre-Holocene Influences

Climate

Historically, the natural distribution of temperate grasslands has been classified according to climate, mainly due to observations from the northern hemisphere, where steppe grassland communities were matched with particular climatic zones (cf. Koppen, 1918). This led to the theory that grasslands occur as a climatic climax; i.e., left undisturbed, a particular area will revert to grassland, each community occurring within a unique range of temperature and rainfall (McNaughton et al., 1982).

Early attempts to classify grasslands in Victoria reflect these attempts; both Sutton (1916) and Patton (1935)

identify the grasslands of the basalt plains of Victoria as having steppe characteristics while not being true steppe. A further development, is the proposal of a deterministic model, where distribution can be determined within a climatic envelope (eg. Coupland, 1992).

However, climate does not adequately explain regional grassland distribution (Moore, 1964; Anderson, 1982), the way it does rainforest. For example, if rainfall is high enough and relatively uniform, rainforest will grow on many soils and across many topographies. In contrast, the presence of a particular temperature and rainfall is not sufficient to support the presence of grassland (Eyre, 1968; Beadle, 1951).

The test of falsification (Popper, 1972) is the simplest way to test how valid climatically determined models are for the prediction of grassland distribution. The first

step is to determine the limits of climate covering a region of biologically related grassland communities, then see whether other vegetation types exist in that same climatic envelope. Such a model would fail in most areas of temperate Australia, even if a large number of climatic indices are included in the analysis.

For example, western Victorian grasslands receive rainfall ranging between 450–850 mm pa, with a seasonal distribution that is fairly uniform or with a late winter peak, and has average monthly temperatures ranging from 7–22 °C. This climate is typical of Victoria south of the Great Dividing Range and the diverse vegetation communities therein. Therefore, the presence of grasslands within this climatic envelope is not unique, and other factors must also dictate its distribution. Even sophisticated and complex climate models, such as those presented in Coupland (1992), fail in this regard.

Climate models can predict whether a grassland can potentially exist within a region, but cannot predict its presence at a particular locality. For instance, Anderson (1982) observes that grasses are adapted to periodic drought, which is important to the overall ecology of grasslands (Anderson, 1982), but periodic drought does not necessarily dictate the presence of grassland. Therefore, climate models should be used as a guide, not an *a priori* reason, for the presence of grasslands.

Soil, fire and topography are other factors which are just as influential. In south-eastern Australian lowland grasslands, these factors may collectively be more dominant than climate and are vital to any analysis that attempts to explain grassland distribution. Long-term climate changes also affect grassland distribution and have played a major part in grassland evolution (Jones, 1999). Rather than being described in a separate section on climate, long-term climate changes are discussed in context with other factors such as soil, fire and grazing.

Soils

Soil-type is critical to the presence of grasslands: without a suitable soil, other vegetation may result. For instance, Eyre (1968) characterises a prairie soil as one where the upward movement of soil solution (evapotranspiration and capillary movement) predominates over downward movement. Such soils typically have some inherent fertility and contain CaCO_3 in the B horizon, as the limited infiltration of water leads to the deposition of calcium solutions. This process is largely controlled by available precipitation and clay content of the soil, as both limit leaching processes. Soils in moister climates which are more acidic and have no

CaCO_3 may also carry grassland, although they are still characterised by a high clay content and available fertility.

A characteristic of grassland soils in the Northern Hemisphere is their homogeneity and widespread distribution. These soils are derived from several sources:

1. Eurasia and North America have a parallel zonation of soil, vegetation and climate (Weaver, 1968) due to widespread and fairly homogeneous glacial and loess soils. Loess are aeolian sediments deposited mainly in the northern hemisphere during glacial periods, as deposition from wind-blown sediments created homogenous soils over wide areas.
2. The mid-west of the United States also has large areas of clay-rich and/or calcareous sediments deposited in shallow marine waters, and these weather to form prairie soils.

The close association of climate with grassland that has evolved in the Northern Hemisphere, and has given rise to the many models relating climate to grassland presence, is largely a function of the geological and climatic history that formed the underlying soils. The different geological and climate history of Australia and its resultant influence on soil formation explains why the links between grassland and climate here are not so straightforward.

The northern hemisphere loess and glacial soils are generally less than 18,000 years old, and are deep, fertile and extensive. Comparable soils in southern Australia are alluvial and have a much patchier distribution. While the Murray Basin contains widespread grasslands on alluvial soils <10,000 years old, elsewhere they occur on less extensive and older soils derived from basalt, limestones and sedimentary rocks.

In summary, the general characteristics of typical grasslands soils of south-eastern Australia include:

- age; soils tend to be young (although usually much older than their northern hemisphere counterparts). Older soils become leached over time, even in drier climates. Grasslands tend not to occur on lateritic and leached infertile soils which are more often occupied by heath or other sclerophyllous vegetation.
- the parent material is capable of generating a soil dominated by clay minerals.
- soils contain clay minerals that swell and shrink under changes in water content, restricting root growth and water availability. Most grassland soils have a high water content, but relatively low water availability due to small pore spaces and hydrostatic forces which bond water to clay particles.

- a history that favours deposition or in situ weathering rather than erosion.
- a reasonable level of fertility
- soil structure and/or soil chemistry unfavourable to the growth of trees, such as soils dominated by sodium common in northern Victoria.

Fire

Fire is a vital factor in the occurrence of grasslands (Anderson, 1982; McNaughton et al., 1982; Eyre, 1968) but the relationship between fire, humans and grassland distribution is controversial (eg. Horton, 1982; Flannery, 1990). The role of anthropogenic fire in grassland formation is often emphasised (Moore, 1966; Harlan, 1982) but naturally occurring fires shaped grassland evolution before humans were present (Recher and Christensen, 1981). The evolution of fire resistant trees in wooded grasslands in Australia and Africa also provides evidence for regular long-term burning before the advent of anthropogenic fire (McNaughton et al., 1982).

Nor is grassland the sole result of regular fire. Evidence from southern Australia indicates that sclerophyllous vegetation evolved on the margins of rainforest in the presence of fire without significant grass populations (Martin, 1991; Kershaw et al., 1994) whereas on other continents savannah was forming on rainforest margins (Webb, 1977, 1978; Retallack, 1992). As discussed in Jones (1999), it is possible that while sclerophyllous vegetation was prominent in southern inland Australia as seasonal aridity became a factor, savannah was forming on the north-west margins in similar conditions.

Fire is also affected by topography: small depressions in grasslands in both North America and the European steppes are treed, whereas the plains above allow fires to pass freely, burning out seedlings if other factors permit their growth (Eyre, 1968). For grasslands to persist, grassfires must occur within a certain frequency and they must be able to burn freely across suitable topographies.

Unless connected with significant changes in climate, such as those before and after the last glacial maximum (25–18 ka), grassland formation is invariably interpreted as being due to human influence (Diamond, 1992; Flannery, 1994). While true for grasslands in New Zealand and Papua New Guinea (Flannery, 1994), evidence from western Victoria and the ACT indicates that more complex relationships have occurred.

A core from Lake George (ACT), over 2.5 million years old, contains significant quantities of grass pollen during glacial periods, showing that grassland communities were favoured by periods of climatic stress due to

aridity and cold (Kershaw et al, 1991). Asteraceae and Casuarinaceae were prominent during the greater part of the sequence but decline in favour of *Eucalyptus* and Poaceae during the late Pleistocene and Holocene (McEwen-Mason, 1991). This change has been dated at about 130 ka (Singh and Geissler, 1985) and has been used as evidence of Aboriginal burning, but the dating is uncertain and the relative tolerances of *Eucalyptus* and Casuarinaceae to fire are still being debated (Head, 1989).

Several cores from maar swamps in Western Victoria contain long sequences of pollen extending back to about 120 ka (D'Costa et al, 1991; Kershaw et al., 1994). This region is significant, as heavy clays, associated with the Western Victorian grasslands, occur to the north. Around the maars are clay loams that will carry trees in wetter climates, but at the time of European occupation, were wooded grasslands or woodlands with a grassy understorey. To the south are calcareous clays which carry forest in today's climate.

Nothofagus appears in the early part of the core at Lake Terang, suggesting cooler and wetter conditions during the early part of the last glacial (<110 Ka; Kershaw et al., 1991). During most of the last ice-age from 110–15 ka, the climate was cooler than today, with both wet and dry periods. Poaceae is present throughout the Terang core, becoming more significant towards the Holocene which is characterised by a regional presence of grassland and grassy woodlands.

The cores from Lake Wangoom and Tower Hill show a lesser influence of grasses over the last 100,000 years (D'Costa et al, 1991; Kershaw et al., 1994), but these sites are volcanic outliers separated from the main basaltic areas of the western plains, and may show influences of vegetation colonisation from more forested areas. In general, fossil pollen indicates that vegetation communities during this period resemble those during the Holocene.

Interpretation of all cores older than 40 ka is limited by dating problems. Despite the increase in fire at 130 ka at Lake George, archaeological evidence has not located the entry of humans into south-eastern Australia, so the transition between natural and anthropogenic fire regimes is still under debate. This period is complicated by a number of climatic changes involving both temperature and precipitation. Changes in fire frequency also have an effect on the presence and species composition of grasslands which may not become apparent in the fossil pollen record.

The clay loams surrounding the western Victorian maar lakes and swamps are not likely to support grasslands except under conditions of frequent fire. During the Holocene these tuffs supported open woodland with a

grassy understorey (Dodson, 1974; Dodson, 1979), whereas the more open soils on scoria cones such as at Tower Hill were well forested (D'Costa et al., 1991). Whether natural frequencies were high enough to maintain grasslands in these areas before Aboriginal burning began is difficult to ascertain.

The complex history of soils, climate, fire and humans cannot be unravelled until better dated evidence from more sites becomes available. While not wanting to downgrade the importance of Aboriginal fire on the Australian landscape, the evidence shows that rather than grassland being created, existing grassy ecosystems were modified and ecosystem boundaries shifted. Evidence from western Victoria during the Holocene presented in part two looks at this point in more detail.

Grazing

Fossil evidence shows that grazing animals have co-evolved with grasslands on most continents (Webb, 1977, 1978). How influential this co-evolutionary role has been in Australia remains unclear, due to a paucity of fossil sites detailing the evolution of both flora and fauna. While strong relationships between megafauna and grasslands have been documented in Africa, Eurasia and North America, the Australian evidence is less definitive.

Although Africa is the only continent where megafauna still co-exists with grasslands, all other continents with grasslands, including Australia, maintained populations of large herbivores until the Late Pleistocene (Flannery, 1990; 1994). The megafaunal extinctions of the Late Pleistocene would have totally altered the grazing regimes of Australian grasslands: Flannery (1990) estimates that 20 of the 50 species which became extinct at that time were grazers, leaving *Macropus spp.* as the largest grazing mammals by the Holocene. The remainder were browsers, so the alteration in the ratio of grazers to browser would have affected differential pressures on grasslands and shrublands (Flannery, 1994).

Flannery (1990; 1994) proposes that the megafaunal extinctions and subsequent hunting pressures on the survivors caused an increase in standing fuel, resulting in hotter and larger fires, eliminating fire sensitive species from unprotected areas. This prompted a greater use of fire-stick farming by Aborigines (Jones, 1969) altering vegetation patterns formed under earlier natural fire regimes.

Flannery's proposed sequence of events (1994; pers. comm.) is summarised as follows. Predation of a browsing megafauna led to rapid extinctions. The reduction in grazing pressure led to an increase in standing fuel

which in turn led to wildfires. The changed fire regime then altered the nature of open vegetation. Palynologists have identified a dry rainforest vegetation type existing throughout the Pleistocene that may have formed the overstorey of a savannah throughout inland Australia (Kershaw et al., 1994). Flannery's hypothesis has this vegetation being altered from dry rainforest shrubland and savannah to grassland dominated by *Eucalyptus* and *Acacia*, as the fire-sensitive elements were removed by repeated burning. The key element in this theory is the removal of large, browsing animals.

Repeated burning also controls the amount of standing fuel and attracts grazing animals, as the regrowth is more palatable and nutritious than mature growth (Dyer et al., 1982). This evolved into the intimate relationship between Aboriginal people, fire and the landscape that existed during the Holocene.

Flannery's model has implications for grassland formation, because it describes a sequence where modern grasslands arose out of overhunting and species extinction. It is also a very linear sequence, where the pre-existing vegetation was so dependent on the megafauna, that their removal led to a cascade of subsequent changes.

Several obstacles limit the acceptance of the hypothesis. There is no direct archaeological evidence of megafauna being hunted, the extinctions are not well dated (ie. how long after humans entered Australia did the megafauna become extinct and how is this related to vegetation change?) and the pollen evidence does not give a clear picture of vegetation change. Despite these unknowns, Flannery's hypothesis (1990; 1994) offers a framework around which long-term ecological change can be investigated.

Summary

The available evidence for the evolution of grasslands in south-eastern Australia describes two processes: the progressive dominance of grasses in herbaceous ecosystems and the strengthening of aridity, allowing those ecosystems to spread into south-eastern Australia from central Australia (Jones, 1999). This evolution may not have been gradual. Successive ice-ages led to alternating warm and cool periods. Sometime during the last glacial period, but before the glacial maximum, humans changed both fire frequency and predation patterns on herbivores. Human pressure on herbivore populations may have also led to feedback effects, permanently altering vegetation.

The long-standing inter-relationships between fire, grasslands and herbivores observed in other continents

may not have as long a history in Australia. Despite this, the presence of a complex marsupial fauna in central Australia requiring frequently fired habitats (Latz, 1995) indicates that the relationship between grassland, fire and fauna may be several million years old.

During the Tertiary, fire promoted the development of sclerophylly in Australia (Kershaw et al., 1994). Progressive aridity promoted herbaceous vegetation dominated by Chenopodiaceae and Asteraceae rather than savannah, although grasses were present in Australia from the early Tertiary, and in the northwest, prominent from the Miocene (Kershaw et al., 1994). Grasses may not have dominated herbaceous ecosystems in south-eastern Australia until the Pleistocene (Kershaw et al., 1994), despite the growing prominence of sclerophyllous vegetation which progressively replaced rainforest during the mid to late Tertiary (Martin, 1981).

Temperate lowland grasslands are a product of the Pleistocene era which is typified by cyclic glacial-interglacial periods. With a history of widely oscillating climates, it is very difficult to trace the evolution of Pleistocene ecosystems. One method is to compare an ecosystem with a similar ecosystem from an earlier period with an equivalent climate. The last climate comparable to the Holocene (10–0 ka) is the last interglacial (125–115 ka) but there are too few pollen sites to determine whether vegetation distribution shows similar influences (Kershaw et al., 1991). Many sites from earlier warm and wet interglacials that may be compared with modern vegetation have been desiccated during the intervening and much longer cold and dry periods.

Poor dating further complicates the human influence on grassland evolution. The advent of humans in Australia is viewed through a window of speculation that ranges from about 60–120 ka in the north and at least 35 ka in the south. The few deposits which display evidence of grassland formation are not conclusively dated (Carbon 14 dating fails before about 40 ka), so any conclusions as to the early interactions between humans and grassland must remain speculative.

Part Two — Holocene Influences.

Climate Change in Western Victoria

The last great expansion and contraction of grassland areas surrounded the last glacial maximum which was most intense at 18 ka. Grassland expanded at the ex-

pense of forest as conditions became cooler and drier between 25 and 18 ka, then contracted between 18 and 10 ka. A concurrent but opposing trend occurred in central Australia: grasslands contracted in favour of Chenopodiaceae–Asteraceae shrublands during the drier periods then recovered when conditions became wetter.

The post-glacial succession from the drought and cold adapted communities of the glacial maximum is recorded by fossil pollen cored from crater lakes in western Victoria (Dodson, 1974, 1979; D'Costa et al., 1989). A sequence of late Pleistocene and Holocene vegetation from Lakes Keilambete and Bullenmerri at Terang and Camperdown respectively is summarised in Figs. 1a & b. The Lake Bullenmerri record dates from 16–8 ka and the Lake Keilambete record extends from 10 ka to the present.

During the glacial maximum, the overstorey from the surrounding woody grasslands, woodlands and open forests retreated to refugia in the sheltered valleys of the Otway Ranges and elsewhere. The grasslands surrounding the lakes were high in Asteraceae and Chenopodiaceae (Fig. 1b) indicating alpine affinities, but were also adapted to low rainfall conditions. Reconstruction of this vegetation is hampered by the lack of modern analogues for low rainfall/low temperature vegetation in Australia. The closest analogue would perhaps be Patagonia.

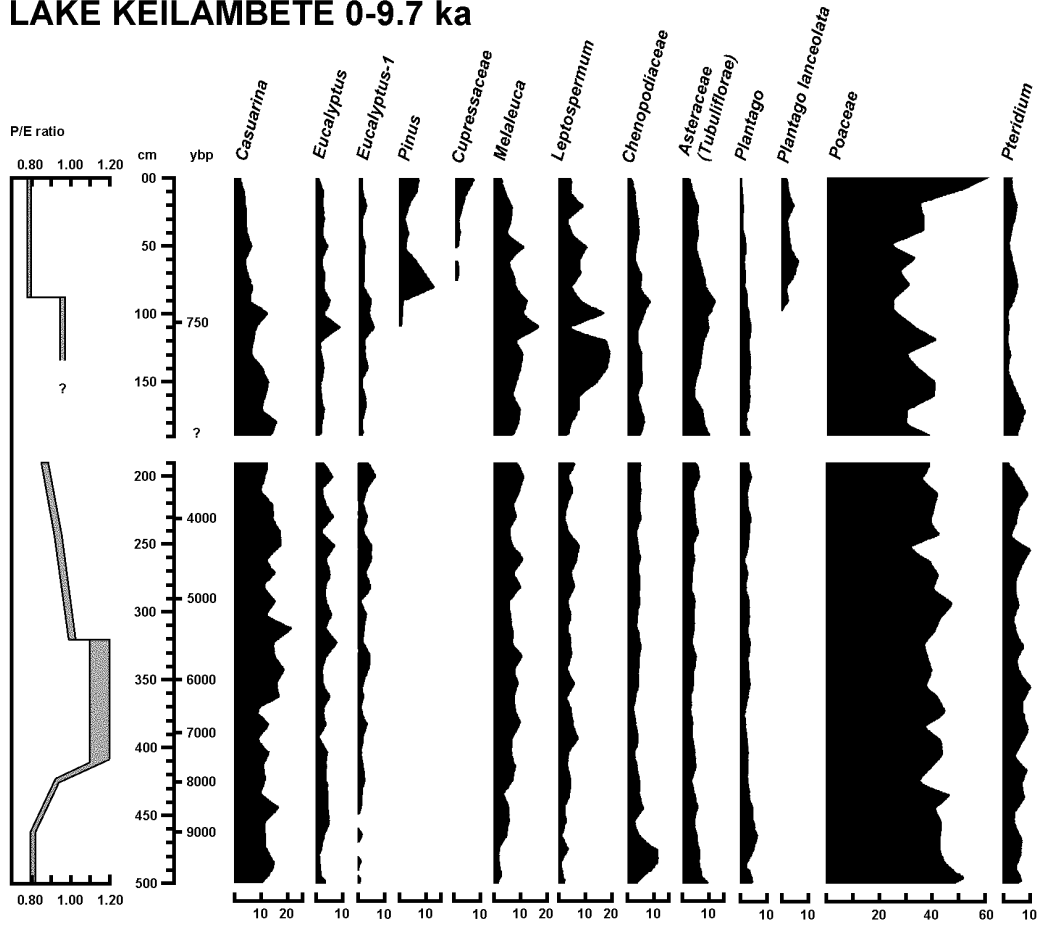
Trees and shrubs are used as climatic markers in the following summary, as most herb and grass fossil pollen taxa are only identified to family level.

Following the glacial maximum, temperature and rainfall increased from 16–10 ka (Jones, 1995). As the vegetation adapted to more temperate conditions, Asteraceae and Chenopodiaceae declined (Dodson, 1979). *Callitris* was present in trace amounts at Lake Bullenmerri during this period (Dodson, 1979) and now occurs as restricted remnants on the Werribee and Keilor Plains today, an area that averages about 200 mm pa less rainfall than Lake Bullenmerri (820 mm pa).

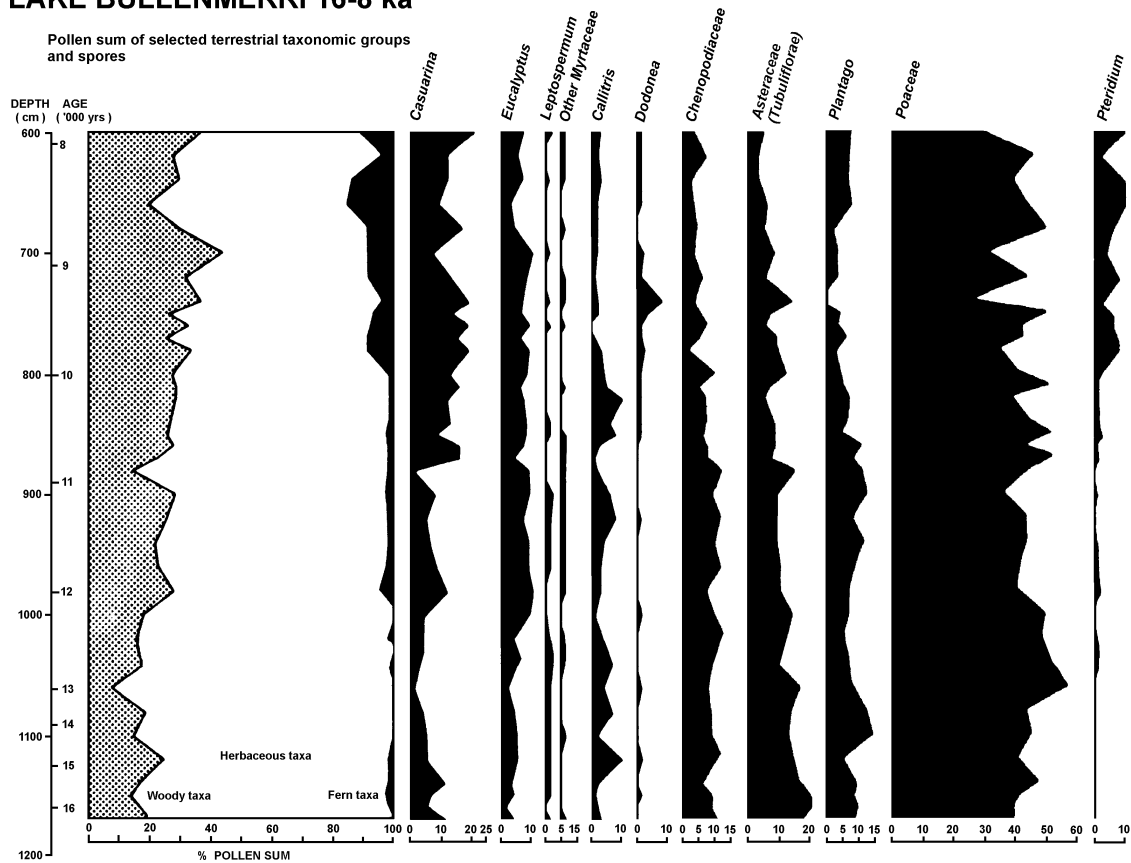
From about 16–14.5 ka, the average temperature was 2–3 °C cooler than today and rainfall was within the range of 350–550 mm (Jones, 1995). The current limits of *Callitris*' range in Victoria and Tasmania occur at cold/wet and warm/dry extremes; neither combination is analogous to the cold/dry period before at least 12 ka. The species of *Callitris* present may have been *C. rhomboidea* (Jones, 1995).

From about 14.5 ka evaporation increased slightly faster than rainfall, so the moisture balance was drier than that at the glacial maximum. These dry conditions persisted until rainfall rose substantially at about 10.5 ka (Jones, 1995). *Casuarina* (probably *Allocasuarina stricta*) ap-

LAKE KEILAMBETE 0-9.7 ka



LAKE BULLENMERRI 16-8 ka



Figs 1a & b. Pollen sums of selected terrestrial taxonomic groups and spores from Lakes Keilambete and Bullenmerri. Pollen diagrams redrawn from Dodson (1974, 1979). The chronology in Fig. 1a is re-interpreted from Dodson (1974) and Bowler (1970). P/E ratio in Fig 1a from Jones (1995).

peared at Lake Bullenmerri from 10.5 ka, as both rainfall and temperature rose. *Pteridium* became common from about 10 ka, although occurring in trace amounts earlier (Dodson, 1979). *Dodonea* is intermittent in the Lake Bullenmerri core, peaking with *Acacia* between 9.6–9.2 Ka (Dodson, 1979), indicating a warm climate with a pronounced seasonality and low summer rainfall. *Dodonea viscosa ssp. cuneata* is found today on the Keilor plains on drier and warmer sites than those in south-western Victoria.

The period from 10.5 ka marks the beginning of the Holocene, the modern interglacial period, in southern Victoria. Rainfall and temperature in the Camperdown area were close to the modern values of about 800 mm pa and 13 °C.

The overall succession of climate in the region during the glacial, post-glacial and interglacial Holocene periods was cold/semi-arid, warming to a Mediterranean climate between 16–10.5 ka followed by a sub-humid cool temperate climate which persisted throughout the Holocene.

The regional vegetation during the Holocene appears to have remained fairly constant (Jones, 1995; Fig. 1a). There is some variation of woodland species during the early Holocene, but this is due to the delay in the outward colonisation of woody species from their ice-age refugia. Grassland species spread much faster than longer-lived woody plants, so apart from the overstorey, vegetation patterns in the region appear to resemble their pre-European state by about 10.5 ka. In general, the variation of tree and shrub pollen during the Holocene is minimal and related to edaphic, rather than climatic change.

Throughout the entire period from 16ka to the present, the vegetation of south-western Victoria was dominated by grassland, although the types of grassland that existed cannot be determined from the pollen diagrams. The overstorey changed in response to climate, and the ground flora obviously did as well, but grassland persisted in one form or another. This shows that factors other than climate dictate the regional presence of grassland.

During the Holocene there were further large changes in climate, yet the pollen sequence from Lake Keilambete (Fig. 1a) shows little variation. A high resolution sequence of precipitation/lake evaporation (P/E) ratio has been produced for 16 ka to the present by modelling the past levels of Lakes Bullenmerri, Gnotuk and Keilambete (Fig. 2; Jones, 1995). P/E ratio is a measure of atmospheric moisture balance, and does not indicate absolute values of rainfall and evaporation (or temperature). For instance, vegetation shows that both temperature and rainfall increased substantially between 16–10 ka but P/E ratio changed by only a small amount (Jones, 1995).

The current P/E ratio for these lakes is 0.79, at a precipitation of 815–825 mm pa and a lake evaporation of 1,030 mm (Jones, 1995). During the Holocene the moisture balance of the region was extremely variable (Fig. 2) while the major elements within the palynology remained largely unchanged (Fig. 1). P/E ratio varied between 0.80 and >1.10, a range of over 30%.

Although there is little evidence, temperatures during the Holocene probably did not vary by much more than ± 1 °C. There is some evidence for evaporation changes due to altered radiation patterns (Jones, 1995), but it is unlikely that evaporation varied by much more than $\pm 10\%$. If that is so, most of the variation in P/E ratios during the Holocene was due to precipitation change. The following calculations, therefore, establish the minimum precipitation ranges needed to produce the P/E variations seen in Fig. 2.

Three values of lake evaporation were used ($1,030 \pm 10\%$). The driest and wettest P/E ratios of 0.80 and 1.20 were chosen, and were multiplied with evaporation to estimate precipitation. The resultant matrix of values is shown in Table 1.

A variation of 0.80–1.20 in P/E ratio during the Holocene would produce a total possible variation in rainfall of 370–450 mm with evaporation rates held constant (Table 1). From Table 1, if evaporation varied fully between the limits of $\pm 10\%$, then the maximum possible precipitation range during the Holocene is 620 mm (740–1,360 mm pa) and the minimum range is 200 mm (910–1,110 mm pa). Even if evaporation was 10% lower than today, with

Table 1. Possible ranges of precipitation in western Victoria during the Holocene with lake evaporation held to $\pm 10\%$ of its current value.

Evaporation (mm pa)	Precipitation (mm pa)		
	P/E = 0.80	P/E = 1.20	Range
1,030 + 10%	910	1,360	450
1,030	820	1,240	410
1,030 - 10%	740	1,110	370

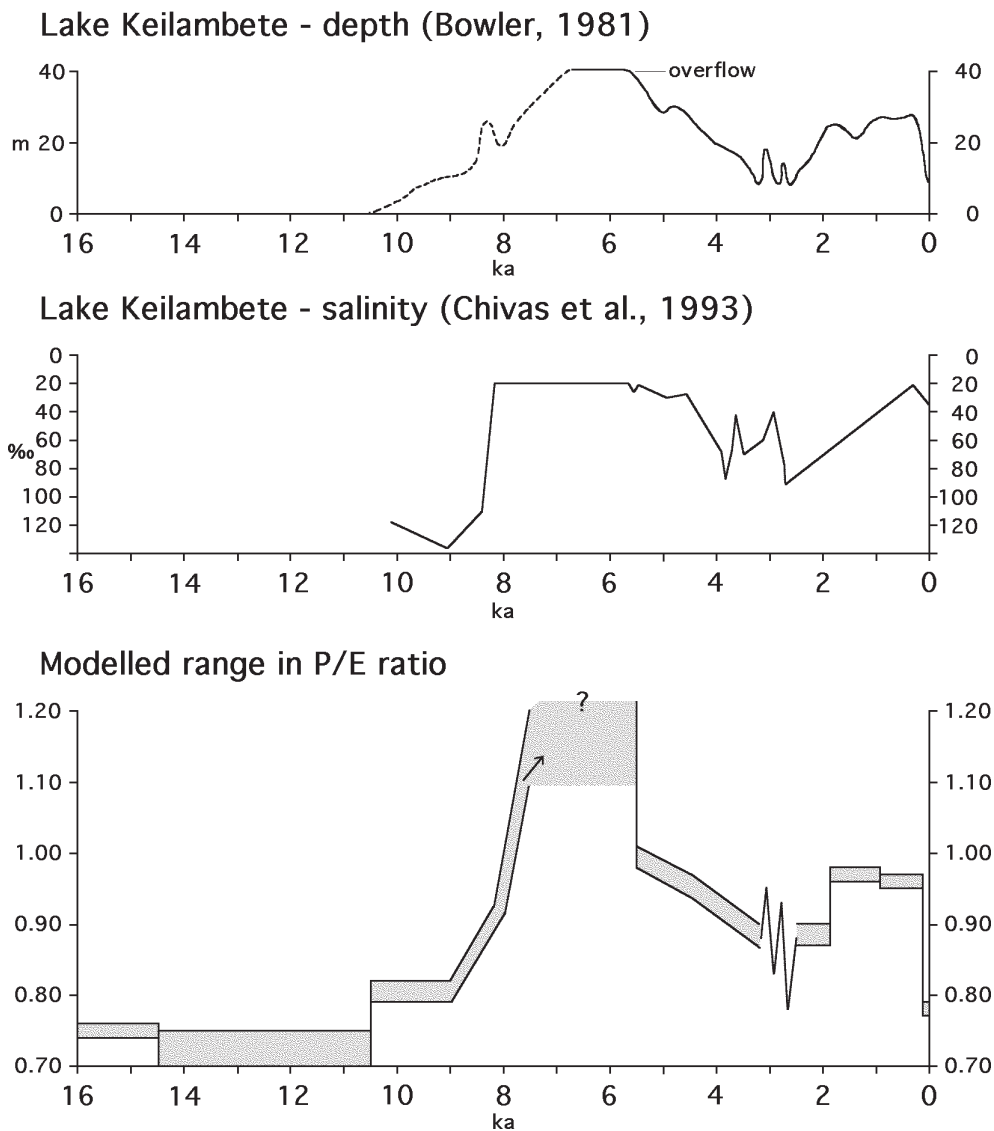


Fig. 2. Lake levels (Bowler, 1981), salinity (Chivas et al., 1993) and modelled precipitation/evaporation ratio (Jones, 1995) at Lake Keilambete 16 ka to present, showing substantial variations in climate.

a P/E of 1.2 during the wettest part of the Holocene, rainfall would have to be 1,110 mm pa. This means that precipitation has ranged at least between the current value of 815–825 mm pa and 1,110 mm pa. This is a variation of at least 300 mm pa or nearly 40% of current annual precipitation.

These large ranges in precipitation contrast dramatically with the minor changes to vegetation shown in Fig. 1. Vegetation shows few variations compared to climate, demonstrating that the overall structure of grasslands and grassy woodlands surrounding the maar lakes in western Victoria is fairly insensitive to climate change. This result is expected given the wide distribution of average annual rainfall across the basalt plains.

This finding accentuates the dominance of soil and fire over climate on grassland distribution within the basalt plains. It also applies for the rest of the state, as it is possible to map regions of grassland and grassy woodland from geomorphic zones, rather than climatic zones. For instance, the distribution of grassy ecosystems shown in Lunt (1991) is derived from the geomorphic zones of Jenkin (1988; Lunt, pers. comm.).

The relationship between soil and fire is geographically and historically complex. Was Aboriginal burning a feature of the plains throughout the period shown in Figs 1a&b? Unfortunately, the archeological evidence is not complete enough to supply an answer, although the matter will be discussed later in this paper. Soil-vegetation relationships are summarised in the next section.

Soils and Topography in Western Victoria

The dominant geology of western Victoria is volcanic, giving rise to its other name, the basalt plains region, having formed from the Newer Basalts which have erupted over the past 4.6 million years (Price et al., 1988). Vegetation structure in western Victoria is closely related to soil-type which in turn derives from the underlying geology. Open grasslands are typical of the thinner soils on unbroken plains, whereas trees and woodlands usually occur on deeper, more friable soils and on stony rises containing open fractures.

The broad distribution of vegetation is influenced by following major soil systems:

1. Deep weathered red-brown earths on Pliocene basalt

Red-brown earths have developed on basalts of Pliocene age south of Hamilton (Gill, 1973) where deep weathering proceeded under a seasonally wetter climate than today. Other areas occur around Lake Elingamite, south of Camperdown. This soil type did not carry open grassland, although open forest with a grassy understorey was common in some areas. Towards the west of the state where annual rainfall approaches 800+ mm pa soils generally become better and *Poa* tussock grassland gains in prominence. Much of the far south-west was forested at the time of settlement with *E. viminalis* and *E. obliqua* being common (eg. Gibbons and Downes, 1964).

2. Clay soils on Pleistocene basalt

Most of the widespread basalts on the plains are approximately 2.5–0.5 Ma in age. They are younger than the Hamilton basalts and form a wide variety of soils depending on their age, position and weathering history. Most carry duplex soils: loams and clay loams overlying a tough clay horizon. Often the soils in a small area may vary widely depending on the local drainage history affecting the process of soil formation (eg. Leeper, 1982). Therefore, the degree of soil development is not necessarily a guide to the age of the underlying basalt. The better drained soils were more likely to have a tree or shrub cover, although virtually all duplex soils carried some form of grassland vegetation. Grassland communities range from sub-humid grasslands on drier sites to sedgeland and ephemeral wetlands.

3. Stony rises.

Stony rises may cover large areas, such as the Stony Rises west of Lake Corangamite and between Portland and Hamilton, or are local rises of small extent. The stony rises tend to be some of the youngest formations and often carry skeletal soils. The presence of open fractures in the rises allows free percolation of water, and thus allows tree growth. The larger areas typically carry *E. viminalis* forest. Smaller rises often carry a band of tree and shrub vegetation in otherwise open grassland, so are ecologically important.

4. Pyroclastics

Tuffs and scorias typically carry dark loams which grade into a clayey subsoil. These soils always carry some tree cover, ranging from *E. viminalis* forest with a grass and shrub understorey on scoria cones, grading into *E. camaldulensis* grassy woodland in drier areas. The major area of pyroclastics is a region of maars and scoria cones surrounding Camperdown.

Landforms also influenced the type of vegetation community present. Common landforms include: eruption points, stony rises, lava collapses and flow features, incised streams, lakes, lunettes and geological inliers.

1. Eruption points

Although there are over 400 eruption points on the basalt plains, consisting of basalt, scoria and tuff, they are of limited areal extent. Usually they carried woody vegetation, with a varying density of cover. Often they were the only treed point in a wide expanse of grassland (eg. Mt. Elephant). Most of the cones have been cleared or had their vegetation highly modified.

2. Drainage patterns

The basalts were erupted onto a fairly level landscape, flows generally only becoming >10–20 m deep in old stream valleys. They have created a fairly chaotic landscape, where the old shapes of flows, lava collapses and different eruptions combine to form a great deal of shallow relief which contains numerous wetlands ranging from ephemeral swamps to fresh and saltwater lakes. These carried a large number of aquatic and semi-aquatic plants; close to half the species documented by Willis (1964) are aquatic.

Closed basins are generally saline. Shallow salt lakes in lava depressions are often associated with halophytic (saltbush) communities which show little variation. The freshwater communities, whether temporary or permanent were much richer. Ephemeral lakes, swamps and pools that dried out completely in summer would support a large number of plants, amphibians and invertebrate fauna during the wetter months.

A number of water-courses deeply incised into the landscape allowed different vegetation to thrive in the more sheltered conditions. The incised valleys also exposed earlier rock types, such as Tertiary sediments, Older Volcanics, Palaeozoic sediments and granitic rocks. The cliffs found in these valleys often contained ferns and other small plants which did not occur elsewhere, especially in amongst the cracks of rocky escarpments.

3. Sedimentary processes

Alluvium from streams occurs in the wider valleys. Aprons of colluvial (hillside) material occur washed from surrounding hills extending out onto the plains. There are also lacustrine (lake) sediments, as well as deposits of aeolian (windblown) origin including lunettes (crescentic clay dunes) on the eastern shores of lakes and rare sand dunes in the northern part of the plains. These allowed less characteristic plant species to grow onto the basalts, adding to the species richness and often creating local oddities. Many of these individual occurrences have since been wiped out.

4. Heterogeneity

Although the Newer Basalts are extensive, they do not form a continuous sheet over the plains. Tertiary sediments outcrop on the southern edges of the plains, north and west of Geelong and near Melbourne. These areas would have consisted of open forest with grassy understoreys and have mostly been cleared also. Near Melbourne, these areas tended to be open *E. camaldulensis* or *E. microcarpa* forests with a grassland understorey.

5. Topography and climate

Two areas of rainshadow containing drier vegetation types occur on the basalt plains: the Lake Bolac-Lismore region and the Werribee Plains. The western rainshadow is shadowed by the Grampians and the Otways, while the eastern rainshadow is affected by the Otways, You Yangs, and the Wombat-Macedon Ranges.

Many early accounts described the basalt plains grasslands as species poor (Sutton, 1916; Barnard, 1925; Patton, 1934), but it may be possible that this was an artefact of the early period of European occupation. Some historical and contemporary material is indicating that the plains may have been richer than earlier thought. This is discussed in Part 3 of this paper.

Northern Plains

The northern plains of Victoria once supported extensive grasslands. Reconstructions have proved difficult for the following reasons:

- Grazing by ungulates altered the species mix on the grasslands very quickly.
- Climatic variability, with chemically and physically hostile soils meant that the grasslands did not recover from overgrazing.
- Irrigation leads to dryland vegetation being outcompeted by exotic weeds.
- Salinity caused by rising watertables has altered the soil hydrology of much of the region.

The northern plains are made up of dark clays and clay loams of variable salt content and structure. The clays were deposited under low energy as floodwaters from northflowing rivers such as the Loddon spread out over the very flat plains (Macumber, 1983) forming the Shepparton Formation. The floodwaters evaporated, leaving clays and salts. The highly evaporative climate and heavy clay content of the soils prevented much of this salt from leaching past the subsoil, leading to sodic soils in many areas. Some of the salt content within soils may also persist from past climate related periods of high water tables.

Silty soils occur along streamlines and forming narrow sinuous bands known as string sands. String sands are associated with both present and prior streams and usually carry some woody vegetation. Prior stream soils are also associated with red sandy loams or clays marking the course of older, higher energy watercourses. Occasional sand dunes associated with point bars or beaches occur along existing and ancestral streams and are known as blow-outs. These carried vegetation with affinities to Mallee and Wimmera plant communities.

Most lakes in the region have lunettes, clay dunes formed from pelletised clays blown from lake beds, on their western shores. Like a number of other topographical features in the area, they were formed under the influence of climatically induced conditions when high water tables persisted throughout the region (Bowler, 19??).

The earliest descriptions of the region come from Mitchell (1838) who was rather more interested in grasslands for their pastoral qualities than for their botanical qualities. Although he had a useful knowledge of botany, he often neglected to identify the vegetation present; less common species were often named while the major grass species went unremarked.

The northern plains of Victoria were well grassed in the winter of 1836 when Mitchell's party traversed them, although the Lachlan River further north was in the grip of a drought (Mitchell, 1838). Mitchell travelled into Victoria at the Murrumbidgee-Murray junction, went south-

east through Swan Hill, Kerang, Pyramid Hill and Cohuna, then turned south-west towards the Loddon River and Korong Vale. The famous descriptions of Australia Felix come from the Cohuna area where Mitchell praised the lush growth of grass, comparing its lushness to grasslands in the Bathurst Region, but failed to identify its dominant species (Mitchell, 1838).

Mitchell (1838) mentions *Danthonia* at Pyramid Hill, an area dominated by heavy black clays. Further west, towards the Loddon, *Themeda triandra* is named, probably associated with red clay loams of prior streams running parallel to the river. Similar soils are widespread on the northern slopes and occurs more commonly in the Goulburn region to the east. *Themeda* still occurs on the red clay loams bordering the Riverine Plain and the Mallee.

In 1841, Edmund Curr squatted in the Tongala area and travelled regularly towards Swan Hill. He mentions tussocks occurring throughout the region which, under pressure of grazing, were replaced by a grass sward (Curr, 1882). He also mentions salt bush (probably *Atriplex nummularia*) 8–10 feet high, 30–40 feet apart in the Pyramid Hill area. Curr's full description is presented in the next section.

The northern plains grasslands were adapted to highly variable climate. The interstices between tussocks were covered by salsolaceous plants such as pigface and prostrate chenopods which became prominent during drought years as the grasses failed (Curr, 1882).

The plains were largely treeless on the heavier soils away from the streamlines. The eucalypts, *E. camaldulensis* and *E. largiflorens*, occurred along streams and in regularly flooded areas. The string sands and blow outs were covered by *Callitris*, *Casuarina*, *Acacia*, *Cassia* and smaller shrubs of Mallee heaths and the Wimmera as indicated by the collections of Mitchell (1838). Some of the shrubs he identified are now restricted to areas of the Wimmera near the Little Desert.

The grasslands of the Goulburn region were generally on better soils ranging from clays to sands. There was a more extensive tree cover consisting of *E. microcarpa* and *Allocasuarina stricta* with *Callitris* on sandy areas. *E. camaldulensis* remained the tree of regularly flooded areas.

The Wimmera region is dominated by *Allocasuarina leuhmannii* grassy woodlands and grasslands on black self-mulching soils. These soils are high in calcium giving them an open structure. Consequently they dry quickly in summer but moisten fairly quickly in winter, and have a better structure than most other grassland soils when wet. They have similarities to the Darling Downs in eastern Queensland (Leeper, 1982) which

forms the northernmost limit of warm temperate grassland in Australia. *Themeda* would have been the dominant grass on the better soils of the Wimmera and northern Victoria and also occurred on open areas in the central hills such as Korong Vale (Mitchell, 1838; Joyce, 1969).

Little is known of the northern plains grasslands and associated grasslands in the Wimmera. McDougall et al. (1993) were restricted to nominating three communities on a regional rather than floristic basis on the Riverine Plains in Victoria and New South Wales, and were unable to distinguish significant regional variation within those communities. Recent interest in the region has uncovered a number of remnants in the area, and new vegetation communities are being proposed on the basis of further survey (E. Jones, pers. comm.).

Part Three — European Occupation

Early Contact

As mentioned in the last section, a significant obstacle to our knowledge of grassland ecosystems at the time of European occupation is the speed at which they were altered. A further obstacle is the lack of adequate descriptions before alteration occurred. The following example, taken from the period of the first official British landfalls in Victoria illustrates this point in several ways.

Europeans visited Victoria a number of times before parties led by the Henty brothers, John Batman and John Fawkner settled at Portland and Port Phillip in 1835–6. Several parties surveyed Port Phillip in 1802–3, before a short-lived settlement was made at Sorrento on the basis of a report from Flinders (Shillinglaw, 1973). The years 1802–3 were El Nino dominated drought years (Nicholls, 1988) and the survey reports differed as the drought intensified.

Flinders arrived in 1802 when the country was in good condition. He described a country that had:

a pleasing and in many parts a fertile appearance, and the sides of some of the hills and several of the valleys are fit for agricultural purposes. It is in great measure a grassy country and capable of supporting much cattle, though better calculated for sheep. Indented Head at the northern part of the western peninsula had an appearance particularly agreeable.

Grimes' report, some 10 months later was less enthusiastic than Flinders. The country was dry due to poor winter rains, although his gardener Flemming recognised the good quality of the soil.

In October 1803, Collins arrived after 18 months of drought and was far less complimentary:

The land in general round Port Phillip at a short distance from the shore carries a deceitful appearance of a Rich Country. The soil is, however, for the most part Sandy and very thinly wooded. Some light black mould is found on the Heights and in the Vallies, but neither in quality or Quantity sufficient for cultivation to repay the cares of the Husbandman. The best soil is found in Western Bay, chiefly consisting of Marle, covered with a light black Mould. Good water is found in many parts of the Eastern coast of the Harbour, but the Western appears a dried-up Country, seeming not to possess sufficient moisture for the smallest Cultivation.

Flinders, Grimes and Flemming, and Collins were describing exactly the same country but observed it as a drought intensified. In only 18 months, the Bellarine Peninsula changed from being *particularly agreeable* to a *dried-up country*.

The first limitation of these early descriptions is that the observers rarely understand what they were describing. They had no prior knowledge of the natural history, climate or the inhabitants. The second limitation is that they were usually describing pasture, timber and water as resources, while today we also require an idea of vegetation structure and species composition. Very rarely was this information supplied. Even the botanists accompanying Flinders collected plant specimens with little regard to their ecological context.

In 1824, Hume and Hovell travelled from New South Wales to Port Phillip and back. They travelled down from Mount Disappointment, through the Beveridge area, to Bulla, across to the Werribee River and down to Corio Bay (Andrews, 1982). Hovell describes (using Hume's bushcraft) open grassland on the plains and on the lower slopes of basaltic volcanoes (the lower, squat peaks north of Melbourne). Occasional woodlands of around 500 acres were also noted (Andrews, 1982), being gum and box woodlands on Tertiary inliers, such as the *E. microcarpa* forest at Tullamarine Airport. Their descriptions provide a number of interesting details whose exact localities may be revealed by careful research. Examples include a description of gilgai soils north of Campbellfield and the appearance of particular peaks such as Bald Hill.

Almost all early Europeans commented on the amount of previously burnt country. Burning occurred regularly and frequently in both grasslands and woodlands on either side of the bay. The resemblance of the woodlands surrounding Port Phillip to parkland was mentioned constantly. Arthur's Seat, was so named because it resembled a similar hill near Edinburgh (Austin, 1974).

Undergrowth was limited, the density of trees apparently being restricted by regular fire.

Sea voyagers report seeing fires burning in all months from spring to autumn. The lush pastures often commented upon in journals were usually regrowth from an earlier burn. Mature grassland was described less often, although Gellibrand reports waist-high grasses travelling from Melbourne to Geelong in 1836 (Billot, 1979).

Occupation

The settlement of Port Phillip started a land rush. Suitable grazing land was becoming scarce in Tasmania and there was a great deal of pressure on the Port Jackson administration to open up the land north of Bass Strait. European settlement had a swift and irreversible effect on all parts of the grasslands: flora, fauna and human.

The early growth in sheep numbers was exponential, which helps explain the speed of alteration of grasslands easily traversed from the coast. The first sheep arrived in Port Phillip in October 1836. By May 1837 there were 26,500 sheep, 177 Europeans, 100 horned cattle, 57 horses and 60 acres under cultivation. By September 1837 there were 41,322 sheep, 224 Europeans, 155 cattle and 75 horses (Billot, 1979).

The number of sheep continued to rise as squatters took up open country. Sheep were transported by sea from Van Dieman's Land and Sydney, landing at Portland, Geelong and Port Phillip, and were soon followed by treks overland from the north. The discovery of wetter grasslands meant that cattle soon followed.

Our current knowledge of the pre-European climate is minimal, but it appears that a major drought began in 1837–38 and persisted until about 1842 (Critchett, 1990; Jones 1995). This drought is largely undocumented in historical records, but may have gone unremarked as a lack of climate knowledge meant that comparisons with normal conditions could not be made.

During the drought, lakes such as Bolac and Bookar, which are shallow lakes in lava depressions, dried up (Clark, 1990) and the Hopkins, Leigh and Barwon Rivers only flowed for short periods. In August 1837, Lake Burrumbeet near Ballarat was brackish; by January 1838 it was a few inches of intensely salt water (Learmonth in Bride, 1898). Chirnside (in Bride, 1898) describes water in the upper Hopkins River in 1839 as unfit with other local watercourses carrying no water. The drought persisted until 1843, as good winter rains are not recorded during the period 1837–42 (Russell, 1935).

Lake Bolac is a large lake of about 1,400 ha in central western Victoria that overflowed into Salt Creek during the wetter months. Robinson (Clark, 1990) describes 800 to 1,000 Western District Aborigines gathering annually to fish at the lake where they would catch eels moving down the outlet on their return to the sea (Dawson, 1881). The lake dried in 1841 and Chirnside (in Bride, 1898) observed sheep feeding in its centre during the summer of 1842. By 1850 or 1851 the lake had refilled to a depth of 15 feet (4.6 m) near the lake shore (Chirnside in Bride, 1898). The lake has not dried since.

This drought heralds the beginning of the driest climate for at least 2,000 years (Jones, 1995). Until early last century the crater lakes of western Victoria, described in the last section, maintained high levels which have declined since the 1840s. Until that time, the lakes were at equilibrium with climate, at a modelled P/E ratio of 0.94–0.96, whereas since 1860, the climate has maintained a P/E ratio of 0.79 (Jones, 1995). The entry of humans into Victoria, therefore, coincides with a major climate change, probably involving both a reduction in rainfall and increase in temperature (Jones, 1995).

The recovery of the land during the 1850s following the drought coincided with the establishment of grazing, leading to the observation that sheep grazing actually improved the condition of native grasslands (Bride, 1898). Such observations led to the belief that placing stock on native grasslands led to an increase in grassland productivity, a belief which lasted well into this century.

1837–1842 is also the period of major expansion across the open grazing lands of Victoria, and by 1842, most of the grasslands of Victoria, excepting Gippsland, were occupied. Critchett (1990) describes the conquest of the western plains during the drought as follows: squatters moved outward from the centres of expansion, Port Phillip and Portland, occupying the few major sources of fresh water as they went. The loss of water led to the rapid displacement of the local Aborigines, separating them from basic amenities such as water, then shelter and food, as they were semi-sedentary and their shelters were quickly destroyed.

Within the space of a few years, the major habitation areas in Western Victoria had been occupied by Europeans (Critchett, pers. comm.). This pattern was repeated in other areas of Victoria, as the best and more permanent areas of fresh water were taken up by the earliest squatters, removing Aborigines from reliable sources of fresh water.

A further factor, was the introduction of exotic pasture species, which proceeded from the earliest contact. Exotic seed was planted by Grimes' party in 1802, Hume and Hovell in 1824 (Andrews, 1982) and by many of the

squatters that followed after 1835. Subsequent overgrazing led to the conditions where these exotics were free to spread. These factors combined to provide the basis for the rapid alteration of lowland grasslands in Victoria.

There are a number of accounts which describe these early alterations. Two of the most noteworthy come from Western Victoria (Robertson in Bride, 1898) and Northern Victoria (Curr, 1882). They are worth quoting comprehensively to give some idea of the scope and rapidity of the changes. Robertson squatted on land in the Wannon region in May 1840, and in 1853 had this to say:

*When I arrived through the thick forested land from Portland to the edge of the Wannon country, I cannot express the joy I felt at seeing such a splendid country before me where my little all that I was driving before me was to feed. The whole of the Wannon had been swept by a bush fire in December, and there had been a heavy fall of rain in January (which has happened, more or less for this past thirteen years), and the grasses were about four inches high, of that lovely dark green; the sheep had no trouble to fill their bellies; all was eatable; nothing had trodden the grasses before them. I could neither think nor sleep for admiring this new world to me who was fond of sheep. I looked amongst the 37 grasses that formed the pasture of my run. There was no silk-grass (*Vulpia bromioides*; Moore, 1960), which had been destroying our V.D.L. (Van Diemens Land) pastures, where I had watched its progress with uneasiness, and I wrote to my friends there that I had never been able to detect any of this noxious grass. The fire had been so great that one could not get as much grass as would thatch our hut; we were obliged to take the large cut tail-grass out of the waterholes. The sheep thrived admirably, and with a little care were clean from the scab, and I did not know there was such a thing as clean sheep.*

*The few sheep at first made little impression on the face of our country for three or four years; the first great change was a severe frost, 11th November 1844, which killed nearly all of the blackwood trees that studded the land in every sheltered nook - some of them really noble, 20 or 30 years old; nearly all were killed in the one night; in the same night a beautiful shrub that was interspersed amongst the blackwoods (Sir Thomas Mitchell called it *acacia glutinosa*) was also killed. About three weeks after these trees and shrubs were all burnt, they now sought to recover as they would after a fire. This certainly was a sad chance; before this catastrophe all the landscape looked like a park with shade for sheep and cattle.*

Many of our pasture plants began to disappear from the pasture land; the silk-grass began to show itself at

the edge of the bush track, and in patches here and there on the hill. The patches have grown larger every year, herbaceous plants and grasses give way for the silk-grass and the little annuals, beneath which are annual peas, and die in our clay soils in a few hot days in spring, and nothing returns to supply their place until later in the winter following. The consequence is that the long deep-rooted grasses that held our strong clay hill together have died out; the ground is now exposed to the sun, and it has cracked in all directions, and the clay hills are slipping in all directions; also the sides of precipitous creeks - long slips, taking trees and all with them. When I first came here, I knew of but two landslips, both of which I went to see, now there are hundreds found within the last three years.

A rather strange thing is going on now. One day all the creeks and little watercourses were covered with a large tussocky grass, with other grasses and plants, to the middle of every watercourse but the Glenelg and Wannon, and in many places of these rivers; now that the only soil is getting trodden hard with stock, springs of salt water are bursting out in every hollow or watercourse, and as it trickles down the watercourse in summer, the strong tussocky grasses die before it, with all other. The clay is left perfectly bare in summer. The strong clay cracks; the winter rain washes out the clay; now most every little gully has a deep rut; when rain falls it runs off the hard ground, rushed down these ruts, runs into the larger creeks, and is carrying earth, trees, and all before it. Over Wannon country is now as difficult a ride as if it were fenced. Ruts, seven, eight, and ten feet deep, and as wide, are found for miles, where two years ago it was covered in tussocky grass like a land marsh. I find from the rapid strides the silk-grass has made over my run, I will not be able to keep the number of sheep the run did three years ago, and as a cattle station it will still be worse; it requires no great prophetic knowledge to see that this part of the country will not carry the stock that is in it at present - I mean the open downs, and every year it will get worse, as it did in V.D.L., and after all the experiments I worked with English grasses, I have never found any of them that will replace our native sward. The day the soil is turned up, that day the pasture is gone forever as far as I know, for I had a paddock sown with English grasses, in squares by itself, and mixed in every way. All was carried off by the grubs, and the paddock allowed to remain in native grass, which returned in eight years. Nothing but silk grass grew year after year, and I suppose it would be to the end of time. Dutch clover will not grow on our clay soils; and for pastoral purposes the lands here are getting less of value every day, that is, with the kind of grass that is growing in them, and will carry less sheep and far less cattle. I now look forward to fencing my run with wire as the only chance of keeping stock on my run.

Robertson's account, while not being the first to describe salinity, is the first to describe salinity induced by land degradation resulting from European occupation. His account of soil erosion is just as stark. While the latter part of this passage has often been quoted to illustrate land degradation, the earlier description of the disappearance of grasses is often omitted but is just as important.

A contemporary account comes from Curr (1882) who settled near Tongala in Northern Victoria in 1841, and who travelled widely throughout the region:

In the greater part of Australia, indeed nearly all over it, the grass originally grew in large tussocks, standing from two to twenty feet apart, depending on circumstances. Gradually as the tussocks got fed down by sheep and cattle they stooled out; and the seed got trampled into the ground around them, and in the absence of bush fires grew, so that presently a sward more or less close resulted, such as we see at present. Constant feeding has now cultivated their propensity, and year by year the grass is more inclined to stool. Originally also, in conjunction with a little grass, large proportions of the continent were covered with salt-bush and pigs-face. In places, for instance around Mt Hope and the Terricks in Victoria, the salt-bushes occasionally attained the height of 12 feet, standing 20 or 30 feet apart; in other localities a dwarf variety of this plant prevailed, and grew so close as to almost crowd out the grass entirely. With this class of vegetation great changes have occurred, and at Mt Hope (as in country where generally it grew), stocking has almost entirely destroyed it. The pigs-face, once general in that country, has also disappeared, a luxuriant growth of grass having taken its place. The same may be said of cotton bush and similar plants. Then again, throughout the continent the most nutritious grasses were originally the most common; but in consequence of constant overstocking and scourging of the pastures, these, where not eradicated, have very much decreased, their places taken by inferior sorts and weeds introduced from Europe and Africa.

He also described land management as practised by the Koories.

I refer to the fire-stick; for the blackfellow was constantly setting fire to the grass and trees, both accidentally, and systematically, for hunting purposes. Living principally on wild roots and animals, he tilled his land and cultivated his pastures with fire; and we shall not, perhaps, be far from the truth if we conclude that almost every part of New Holland was swept over by fierce fire, and on average, every five years.

Curr (1882) also refers to an increase in runoff, and the addition of fertility through the dung of stock changing

the baked, calcined and indurated condition of the ground so that the pasture was of higher productivity but lower quality. This increase may also be due to higher rainfall following the 1837–42 drought, concurrent with an increase in weediness; the introduced grasses producing pastures higher in nitrogen, hence lower quality feed for wool production.

Both Robertson's and Curr's accounts demonstrate the devastating effect that grazing had on Victorian grasslands. Such widespread changes so early in the period of written records also casts doubt on many of the subsequent records concerning grasslands. One example is the assumption that grasslands, most notably western Victoria, were species poor.

In 1925, the editor of the *Victorian Naturalist*, a sympathetic commentator, wrote on the flora of Victoria in a conservation book called *Save Australia*:

A fourth soil division consists of the western basaltic plains, on which, however, little of special interest grows. (Barnard, 1925)

Few botanists and naturalists would agree today.

Historically, botanists tended not to focus on the area west of Melbourne. Von Mueller (the famed 19th century botanist) seldom visited the area. It was not until 1916 (Sutton) that the flora was reviewed and then only the Keilor Plains. Other articles followed in 1935 (Patton) and in 1963 (Willis). By the time of Stuwe's review in 1986, he was only dealing with 0.15% of the original area of *Themeda* grasslands.

Much earlier, in November 1836, Alexander Norcock described Port Phillip from Hobson's Bay with enthusiasm:

the country here is enchantingly beautiful – extensive rich plains all around with gently sloping hills in the distance, all thinly wooded and having the appearance of an immense park. The grasses, flowers and herbs that cover the plains are of every variety that can be imagined...

Were the plains always species poor, or is the *little of special interest* (Barnard, 1925) an artefact of grazing?

One example that illustrates this trend is myrnong (Yam Daisy). Myrnong was a very important food plant of the Aborigines and was extremely common in marshy areas. Baskets of the tuberous roots were collected in the spring, the plant being replaced after root collection to regenerate (Dawson, 1881; Gott, pers. comm.). Myrnong became a favoured plant of sheep and rabbits, and if grazed heavily in late spring when still green and palatable, may not regenerate in the dry conditions of sum-

mer during the plant's dormancy period. Consequently, myrnong has gone from being one of the state's most widespread plants to one of the rarest. This process was rapid, as many early graziers note the preference of sheep for the more palatable herbaceous plants.

Orchids have suffered a similar fate. Although not common over large areas, they were locally abundant, suffering great depredation due to overgrazing. Other plants have gone the same way: peas, lilies, daisies and many plants of the ephemeral wetlands.

Even though grassland remnants remain, we cannot assume that they are representative of pre-European grasslands until careful historical research and close survey confirm their affinities. Given the history of degradation outlined above, the traditional conservation model of maintaining ecosystems in their pristine condition, or as close to pristine as possible, may not be possible for Victorian lowland grasslands.

Discussion

This paper is a biohistorical treatment of Victorian lowland grasslands. The first two sections summarise the mainly scientific evidence describing the pre-human evolution of grasslands. New evidence describing the relationship between the structure of grassy woodlands in western Victoria and climate during the Holocene is presented.

The last section describes the early history of the grasslands with reference to the vegetation at the time of European occupation and the speed of its alteration. Many of the topics addressed in this paper may not seem relevant to the short-term problems of grassland conservation, such as saving the rapidly disappearing remnants. What is the point in discussing inconclusive evidence of grassland evolution dating back 60,000 years if the product of that evolution may not exist in 6 years?

However, our knowledge of the past affects the way we view ecosystems and that, in turn, influences their management. Without biohistorical assessment we have the formal, but largely separate, disciplines such as history and biology. Knowledge that links the two and relates them to other disciplines (such as earth science) tends to fall between the cracks of the formal disciplines. Also lying in this no-man's (grass)land are the cultural characteristics that have allowed grasslands to be reduced to less than 1% of their former extent with very little consideration or afterthought. These characteristics harbour assumptions that do not survive examination within a broader, biohistorical context.

One such assumption is the distinction of native and exotic grassland into unimproved and improved pasture, as in the board-game *Squatter*. This creates a management imperative to clear native pasture and replace it with exotic pasture. Is exotic pasture really an improvement to the land? Production does increase, although often at the expense of wool quality in sheep (eg. Curr, 1882). Biologically, exotic grasslands have proved disastrous, yet for many years, the reseeded of native pasture has been accepted agricultural practice. In this context, “improved” and “unimproved” are value judgements that need to be redefined.

Another example, the origin of which was discussed earlier, is the myth that stock grazing leads to an improvement in the productivity of native grasslands. The first observations that led to this truism were due to the recovery from land from drought at the same time as it was being stocked, so was actually a misinterpretation of natural climate variability.

Many such interpretations are based on a melange of historical misconceptions and scientific “assumptions”. Grasslands will continue to be at risk if these assumptions are not examined thoroughly.

The continuing role of humans in grassland evolution is one area where great care must be taken. Did Aboriginal burning lead to the formation of modern grasslands? Should they be conserved as highly managed systems or should they be just reserved and preserved? The biohistorical approach provides a framework in which some of these questions can be addressed.

For instance, this paper shows that the notion of grassland forming a climatic climax can be discarded. Climatic models cannot determine regional grassland distribution, which is more influenced by factors such as soil and fire. Grasslands cannot be managed solely under the influence of climate. Other factors must be addressed.

There are characteristic grassland soils associated with all the major grasslands in Victoria. This was alluded to in part one of this paper and described in part two. Furthermore, different soil types carry different grassland communities and these soil types may vary over even short distances. This infers that the fragmentation of grassland systems has led to much of the original complexity being lost.

Natural fire is also important to grasslands. Whether variations in local fire regimes were important, and whether different fire regimes were maintained by humans to sustain particular resources, depends on the role of Aboriginal burning, discussed later in this section.

Despite the rejection of a climatic climax, long-term climatic change has affected grasslands. The gradual cooling and drying of the Australian continent throughout the Tertiary has largely determined the long-term evolution of grasslands and grassland taxa (Jones, 1999). The more recent entry of taxa from the north has also been significant; these include species such as *Themeda triandra*, *Poa spp.* and others (Jones, 1999). And while the variations in Holocene climate in western Victoria did not affect the overall structure of grasslands within the region, they would have influenced the composition and distribution of grassland communities, as spatial variations in climate do today.

How much of a part did humans play in the formation of the grasslands described in the latter part of section two? The answer depends on the evidence furnished by palynology and archaeology. Evidence regarding the role of fire during the late Pleistocene, its origins and its influence on grassland is patchy and not well dated. The much later relationship between humans, climate and grasslands following the last ice-age is also uncertain. For this reason, archaeology has not been summarised within the body of the paper, but a brief overview follows.

In southwestern Victoria, palynology and hydrology show that although vegetation changes from 16–10 ka can be ascribed to gradually warmer and wetter conditions, grassland structure during the Holocene was relatively stable. Was this stability due to continuous Aboriginal burning? Did human burning occur during the entire period from post-glacial times to just before European occupation or was it intermittent with other factors taking precedence?

Only two archaeological sites in southwestern Victoria date earlier than 10 ka, at 12.5 and 11.5 ka (Lourandos, 1983) although occupation at Keilor to the east is older than 31 ka (Flood, 1983). There is little archaeological evidence of occupation throughout the Late Pleistocene, but Holocene dates are much more common. According to that evidence, intensification of human activity occurred during the Holocene with its highest level occurring after about 2,500 ybp (years before present; Lourandos, 1983, Williams, 1988).

Aborigines most likely both the aridity and cold of the glacial maximum in western Victoria, as this environment was less climatically hostile than southwestern Tasmania which was continually occupied during the ice-age. Human ignition may have been a dominant part of grassland ecology in Victoria from before 16 ka, after which we have some confidence in the reconstruction of vegetation patterns.

The origins and continuity of Aboriginal burning within grasslands is extremely important. The debate concern-

ing the role of Aborigine fire in the distribution of Australian vegetation generally, has generated much heat and not very much light, including in the anthropological literature (cf. Horton, 1983).

Much of this heat is generated around the perceived need to determine whether Australian vegetation systems are natural or whether they are human artefacts. There revolves around the issue of whether Aborigines were intrusive or non-intrusive managers of the landscape. Ecological evidence is often used to promote both arguments, but a better ecological understanding is very rarely the result. As such, these debates probably tell us more about western culture than they do about Aboriginal land management, as they are usually harnessed to justify or reject the modern uses of natural resources.

This tendency to divide the environment into natural and unnatural or “manmade” components has affected grasslands more than any other major ecosystem. Viewpoints become polarised, resulting in either/or arguments as to whether grasslands evolved naturally or are an artefact produced by anthropogenic burning. Such arguments can be summarised as follows:

- grasslands are naturally evolved ecosystems where Aboriginal people adopted or slightly modified the existing fire regimes.
- grasslands are an artefact produced by repeated burning by humans. Left alone, grasslands will revert to other forms of vegetation.

Neither point of view is completely true, at least for Victoria. Although human intervention played a part in the distribution of grasslands during the Holocene, certain areas would have supported grasslands before anthropogenic fire was introduced. One such area is the Werribee Plains in the rain shadow formed by the Macedon and Wombat Range, Brisbane Ranges and the You Yangs.

This rain shadow is an area of basalts over 2 million years old covered by relatively thin soils. Most are clays with a parna topsoil, containing windblown dust deposited during arid periods. The thin soils in this area reflect a history with few trees, poor rainfall and little infiltration. Even during wetter periods, these plains would have received little extra rainfall due to their position within a rain-shadow, thus remaining a core area of grassland throughout most climate regimes. Naturally ignited fires would have burned freely across the grassy plains, except where the few river valleys formed barriers. Forested areas and wetlands were not common enough to slow these fires down.

Other such areas can be nominated. The northern plains south of Kerang, where sodic soils and heavy clay would have limited tree growth under most conditions is one. Another possible core area is the western slopes and plains of New South Wales, where miles of open country covered by clay soils contain grasslands with few breaks that promote widespread fires. These would have carried significant areas of grassland when rainfall remained below about 800 mm.

The role of humans in the geologically Recent evolution and distribution of lowland grasslands cannot be fully explained. Historical evidence shows that lowland grasslands were regularly burnt 200 years ago, but when this burning started, whether it continued throughout the glacial maximum (when conditions inland were fairly inhospitable to humans but grasslands were widespread), and how much influence this had on the vegetation communities encountered by the first Europeans remains unclear.

Like most arguments that are highly polarised, both of the extremes detailed above contain some truth. Examples of grasslands, both as naturally evolved ecosystems and artefacts, can be found in Australia. However, the misuse of ecological information in mythologising will feed the wrong signals into the political and social arena. Points of view can be made, but the reasoning behind those assertions must be transparent rather than based on evidence used to promote a particular ideology.

Lowland grasslands contain evolutionary elements dating from before and after the introduction of humans. Any management ethic would be wise to incorporate the full range of these elements. Research must endeavour to determine what the various influences are, and quantify them if possible. Lunt (1995) is notable in this regard, showing how two different historical management styles have produced two very different types of grassy ecosystems.

The legacy of the European era to our understanding of grasslands is very important. This paper shows that the changes to grasslands after 1835 were so rapid, that modern, or even historical, survey data does not give a true idea of their character under Aboriginal management. Further historical information will be found, and every effort should be made to use primary historical material whenever possible.

The western ideal of wilderness also promotes misinterpretation (cf. Flannery, 1994), because it rests on the incorrect notion that the natural character of vast areas was formed in the absence of humans. This powerful ideal excludes grasslands; having been burnt by Aborigines, then cleared by Europeans, grasslands have no wilderness qualities. Conservation models based on

wilderness tend to exclude grasslands because most grasslands occurred on fertile soils readily used for agriculture.

Furthermore, a hands-off approach to management is not possible, due to the removal of antecedent conditions from grasslands (eg. Aboriginal and natural burning), followed by their fragmentation. Grassland management can not be left up to nature, as pre-European, or “natural”, conditions no longer exist. Grasslands have been farmed and fragmented, and are further threatened by changed fire regimes, environmental weeds, climate change and intensive development.

This paper shows that grasslands are complex ecosystems with a complex history. They cannot be easily reproduced, nor can all species that make up a grassland be preserved outside grassland ecosystems. For all species to survive independently of grasslands, all grassland taxa must occur in other ecosystems and those ecosystems must be sustained. The growing list of grassland endemics (Carr, this volume) and threats to allied ecosystems renders this possibility unlikely.

The biohistorical approach shows that an understanding of the long-term influences of an ecosystem is critical to its future management. New models of grassland management must be constructed through an understanding of their history integrated with contemporary ecological survey and research.

Conclusions

The lowland grasslands of south-eastern Australia have formed from flora with Gondwanan affinities and more recent Asian additions that entered Australia in successive waves throughout the Tertiary. Temperate grasslands formed relatively recently in Australia’s geological history, probably during the past 2.5 million years. The Australian elements come from savannah and desert ecosystems, while the Asian components are from old world savannah ecosystems. Temperate elements, originating in tropical highlands, probably entered Australia during successive glacial periods (Jones, 1999).

The use of fire by Aboriginal people has played a major role in the more recent evolution of grasslands, but the existing evidence points to the widespread occurrence of grasslands before humans entered Australia. Although there appears to be a reduction in the range of fire sensitive species following human occupation, there is little solid evidence as to how anthropogenic burning

affected large-scale ecosystems such as temperate grasslands.

The link between Aboriginal people and grasslands was more complex than it was for most other ecosystems. Grasslands supported higher human populations than forest, for example, and fire was much more widely used. The Holocene history of grasslands in western Victoria shows that despite wide fluctuations in climate, major elements within the vegetation were largely unchanged. This points to the pervasive influence of both soil and fire during this period. Archaeological evidence also shows large changes in living patterns during the late Holocene (Lourandos, 1983; Williams, 1988), yet the vegetation and consequently, the use of fire remained prominent.

The associations between Aboriginal people and grasslands in western Victoria may be one of the longest unbroken associations between a particular people and ecosystem on the planet. It shows that the relationship between people and temperate Australian grasslands was dynamic in the evolutionary sense. Endemism was undoubtedly operating within the flora (Carr, this volume) and the human-ecosystem interactions were ecologically sustainable throughout the Holocene. It is impossible to determine the continuity of the relationship prior to this time due to large climatic changes and a lack of archaeological evidence.

The European occupation of Victoria coincided with a climate change that probably involved both a reduction in rainfall and an increase in temperature (Jones, 1995). The modern era is the driest for at least 2,000 years and possibly 9,000 years, since the early Holocene. At the same time, a cascade of changes were wrought by the introduction of grazing by ungulates, altering grasslands before they could be accurately recorded. The removal of botanic interest in grasslands, and their continuing utility, have led to a situation where they have been reduced to real estate. Their exclusion from conservation mythology has led to a situation where, until recently, grasslands have been ignored.

The structure, distribution and processes that existed within grasslands at the beginning of the modern era remain a useful point to establish a benchmark for management. It is clear that a great deal more information is needed to understand the links operating before European occupation. It is important to understand their long-term evolutionary history in addition to short-term management imperatives, to implement a conservation model that will allow a continuity of both the ecosystem and its contingent species.

References

- Anderson, R.C. (1982) An evolutionary model summarizing the roles of fire, climate and grazing animals in the origin and maintenance of grasslands: an end paper, in J.R. Estes, R.J. Tylr and J.N. Brunken eds. *Grasses and Grasslands, Systematics and Ecology*. University of Oklahoma Press, Norman, 297–312.
- Austin, K.A. (1974) *Matthew Flinders on the Victorian Coast*. Cypress Publishing, Surrey Hills, 64 pp.
- Bride, T.F. (1899) *Letters from Victorian Pioneers*. Trustees of the Public Library, Melbourne, 325 pp.
- Barnard, F.G.A. (1925) The Flora of Victoria, in J. Barrett (ed.) *Save Australia*, McMillan and Co., London, 45–53.
- Billot, C.P. (1979) *John Batman and the founding of Melbourne*. Hyland House, Melbourne, 330 pp.
- Boyden, S (1990) *Patterns in Biohistory*. Oxford University Press, London.
- Clark, I.D. (1990) In quest of the tribes: G.A. Robinson's unabridged report of his 1841 expedition among Western Victorian Aboriginal tribes, Kenyon's 'condensation' reconsidered. *Memoirs of the Museum of Victoria: Anthropology and History*, **1**, 97–130.
- Coupland, R.T. (1992) *Natural Grasslands: Introduction and Western Hemisphere*, Elsevier, Amsterdam, 469 pp.
- Critchett, J. (1990) *A distant field of murder*. Melbourne University Press, Melbourne, 303 pp.
- Curr, E.M. (1882) *Recollections of Squatting in Victoria*. Robertson, Melbourne.
- Dawson, J. (1881) *Australian aborigines: the languages and customs of several tribes of aborigines in the western district of Victoria*. George Robertson, Melbourne.
- D'Costa, D.M., Edney, P., Kershaw, A.P. and De Deckker, P. (1989) Late Quaternary paleoecology of Tower Hill, Victoria. *J. Biogeogr.*, **16**, 461–482.
- Diamond, J. (1992) *The Rise and Fall of the Third Chimpanzee*. Vintage, London, 360 pp.
- Dodson, J.R. (1974) Vegetation and climate history near Lake Keilambete, western Victoria. *Aust. J. Bot.*, **22**, 709–717.
- Dodson, J.R. (1979) Late Pleistocene vegetation and environments near Lake Bullenmerri, Western Victoria. *Aust. J. Ecol.*, **4**, 419–427.
- Dyer, M.I., Detling, J.K., Coleman, D.C. and Hilbert, D.W. (1982) The role of herbivores in grasslands, in J.R. Estes, R.J. Tylr and J.N. Brunken eds. *Grasses and Grasslands, Systematics and Ecology*. University of Oklahoma Press, Norman, 255–295.
- Eyre, S.R. (1968) *Vegetation and Soils: A World Picture*, Edward Arnold, London.
- Flannery, T.F. (1990) Pleistocene faunal loss: implications of the aftershock for Australia's past and future, *Archaeology in Oceania*, **25**, 45–67.
- Flannery, T.F. (1994) *The Future Eaters*. Reed Books, Chatswood, 423 pp.
- Gibbons, F.R. and Downes, R.G. (1964) *A study of the land in southwestern Victoria*, Soil Cons. Auth. Vict., T.C. 3.
- Gill, E.D. (1964) Rocks contiguous with the basaltic cuirass of Western Victoria, *Proc. R. Soc. Vict.*, **77**, 331–355.
- Head, L. (1989) Prehistorical Aboriginal impacts on Australian vegetation: an assessment of the evidence, *Australian Geographer*, **20**, 37–46.

- Hodgkinson, K.C. and Griffin, G.F. (1982) Adaptation of shrub species to fires in the arid zone. In W.R. Barker and P.J.M. Greenslade (eds.) *Evolution of the Flora and Fauna of Arid Australia*. Peacock Publications, Adelaide, 145–152.
- Horton, D.R. (1982) The burning question: Aborigines, fire and Australian ecosystems, *Mankind*, **13**, 237–251.
- Jenkin, J.J. (1988) Geomorphology, in J.G. Douglas and J.A. Ferguson (eds.) *Geology of Victoria*, Geological Society of Australia, Victorian Division, Melbourne, 401–419.
- Jones, R. (1969) Fire-stick farming, *Australian Natural History*, **16**, 224–228.
- Jones, R.N. (1995) *Modelling hydrologic and climatic controls of closed lakes, Western Victoria*. Unpublished PhD Thesis, University of Melbourne.
- Jones, R.N. (1997) The biogeography of the grasses and lowland grasslands of south-eastern Australia. In R.N. Jones (ed.) *The Great Plains Crash: Proceedings of a Conference on Victorian Lowland Grasslands and Grassy Woodlands*, *Advances in Nature Conservation*, **2**, 11–18.
- Joyce, A. (1969) *A Homestead History: being the reminiscences and letters of Alfred Joyce of Plaistow and Norwood* (ed. G.F. James). Oxford University Press, Melbourne, 206 pp.
- Kershaw, A.P., D'Costa, D.M., McEwen Mason, J.R.C. and Wagstaff, D.E. (1991) Palynological evidence for Quaternary vegetation and environments of southeastern Australia. *Quaternary Science Reviews*, **10**, 391–404.
- Kershaw, A.P., Martin, H.A. and McEwen-Mason, J.R.C. (1994) The Neogene - A period of transition, in R. Hill (ed) *History of the Australian Vegetation: Cretaceous to Recent*, Cambridge University Press, 299–327
- Koppen, W. (1918) Klassifikation der klimate, nach temperatuer, niederschlag, und jahreslaf, *Geogr. Mitt.*, **64**, 243–248.
- Latz, P.K. (1995) *Bushfires & Bushtucker: Aboriginal plant use in Central Australia*, IAD Press, Alice Springs, 400 pp.
- Leeper, G. W. (1982) *Introduction to soil science*. Melbourne University Press, Carlton, 253 pp.
- Lourandos, H. (1983) Intensification: a Late Pleistocene–Holocene archaeological sequence from Southwestern Victoria. *Archeol. Oceania*, **18**, 81–94.
- Lunt, I.D. (1991) Management of lowland grasslands and grassy woodlands for nature conservation: a review. *Vict. Nat.*, **108**, 56–66.
- Lunt, I.D. (1995) Management of remnant grassy forests and woodlands in South-eastern Australia, *Vict. Nat.*, **112**, 239–249 (reprinted in this volume).
- Macumber, P.G. (1984) *Interaction between groundwater and surface systems in Northern Victoria: as reflected by hydrochemistry, hydrodynamics and geomorphology*. Unpublished PhD Thesis, University of Melbourne.
- Martin, H.A (1991) Tertiary stratigraphic palynology and palaeoclimate of the inland river systems in New South Wales, in M.A.J. Williams, P. De Deckker and A.P. Kershaw (eds.), *The Cainozoic of the Australian Region: a Reassessment of the Evidence*, Geological Society of Australia, Sydney, 181–194.
- McDougall, K., and Kirkpatrick, J.B. (1994) *Conservation of Lowland Native Grasslands in South-eastern Australia*. World Wide Fund For Nature, Australia, 187 pp.
- McDougall, K., Barlow, T. and Appleby, M. (1994) Western Basalt Plains, Lake Omeo, Murray Valley riverine plains and the Wimmera, in McDougall, K. and Kirkpatrick, J.B., *Conservation of Lowland Native Grasslands in South-eastern Australia*, World Wide Fund for Nature Australia, 44–112.
- McEwen-Mason, J.R.C. (1991) The palaeomagnetism and preliminary palynology of sediment cores from Lake George, southeastern Australia, in M.A.J. Williams, P. De Deckker and A.P. Kershaw (eds.), *The Cainozoic of the Australian Region: a Reassessment of the Evidence*, Geological Society of Australia, Sydney, 195–209.

- McNaughton, S.J., Coughenour, M.B. and Wallace, L.L. (1982) Interactive processes in grassland ecosystems, in J.R. Estes, R.J. Tylor and J.N. Brunken eds. *Grasses and Grasslands, Systematics and Ecology*. University of Oklahoma Press, Norman, 167–193.
- Mitchell, T.L. (1839) *Three expeditions into the interior of eastern Australia : with descriptions of the recently explored region of Australia Felix and of the present colony of New South Wales*. T. & W. Boone, London, 2 vols.
- Moore, C.W.E. (1964) Distribution of grasslands. C. Barnard ed. *Grasses and Grasslands*. MacMillan, London. pp. 182–205.
- Moore, R.M. (1959) Ecological observations on plant communities grazed by sheep in Australia, in A. Keast, R.H. Crocker and C.S. Christian, eds. *Biogeography and Ecology in Australia*, Dr W Junk, The Hague, 500–512.
- Nicholls, N. (1988) More on early ENSOs: evidence from Australian documentary sources, *Bull. Am. Meteorol. Soc.*, **69**, 4–6.
- Patton, R.T. (1930) Ecological studies in Victoria; Part IV – Basalt Plains Association. *Proc. Roy. Soc. Vict.*, **48**, 172–190.
- Price, R.C., Gray, C.M., Nicholls, I.A. and Day, A. (1988) Cainozoic Volcanic Rocks, in J.G. Douglas and J.A. Ferguson (eds.) *Geology of Victoria*, Geological Society of Australia, Victorian Division, Melbourne, 439–452.
- Popper, K.R. (1972) *The Logic of Scientific Discovery*, Hutchinson, London.
- Recher, H.F. and Christensen, P.E. (1981) Fire and the evolution of Australian biota, in A. Keast (ed.) *Ecological Biogeography of Australia*, Dr W Junk, The Hague, 137–162.
- Retallack (1992) Middle Miocene fossil plants from Fort Ternan (Kenya) and evolution of African Grasslands, *Palaeobiology*, **18**, 383–400.
- Russell, G. (1935) *The Narrative of George Russell of Golf Hill*. Oxford University Press, London, 469 pp.
- Shillinglaw, J.J. (1972) *Historical records of Port Phillip. The first annals of the Colony of Victoria*. Heinemann, Melbourne.
- Singh, G. and Geissler, E.A. (1985) Late Cenozoic history of fire, lake levels and climate at Lake George, New South Wales, Australia, *Phil. Trans. R. Soc.*, **311**, 379–447.
- Stuwe, J. (1986) *An Assessment of the Conservation Status of Native Grasslands on the Western Plains, Victoria and Sites of Botanical Significance*. Tech. Rep. Series No. 48, Dept. Conservation, Forests and Lands, Melbourne.
- Sutton, C.S. (1916, 1917) A sketch of the Keilor Plains flora. *Vict. Nat.*, **33**: 112–123, 128–143.
- Weaver, J.E. (1968) *Prairie Plants and their Environment*. University of Nebraska Press, Lincoln, 276 pp.
- Webb, S.D., 1977, A history of savanna vertebrates in the New World. Part I. North America. *Annual Reviews of Ecology and Systematics*, **8**, 355–380.
- Webb, S.D., 1978, A history of savanna vertebrates in the New World. Part II. South America and the Great Interchange. *Annual Reviews of Ecology and Systematics*, **9**, 393–426.
- Williams, E. (1988) *Complex hunter-gatherers: late Holocene example from temperate Australia*. Oxford, B.A.R., 319 pp.
- Willis, J.H. (1964) Vegetation of the basalt plains in Western Victoria. *Proc. Roy. Soc. Vict.*, **77**, 397–418.

