

The Biogeography of the Grasses and Lowland Grasslands of South-eastern Australia

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This paper reviews the evolution of Australian grasslands in a global context, with the aim of defining the main factors dictating the distribution of lowland grasslands in south-eastern Australia prior to human occupation (60+ ka: thousand years before present). A summary of the major human influences on grassland distribution is summarised in a companion paper (Jones, 1999). The climatic history affecting grasslands during the Holocene is also reviewed with a summary of Victorian distribution at the time of European occupation (Jones, 1999). A knowledge of the factors affecting the occurrence and composition of Australian temperate grasslands will contribute to their management and can help identify issues requiring further investigation.

The Palaeobiology of Grasses and Grasslands

Grasses are the most commercially and nutritionally important family of plants to humans, yet while most grass species are preserved, their ecosystems — grasslands — are under global threat. Little is understood about the biological origins of both grasses and grasslands, but if grassy ecosystems are to survive, their biological origins and evolution must be explored.

Clayton and Renvoize (1986) nominate six main sub-families in the family Poaceae, although the origin of these groups, their relationships and even constituent memberships still remain to be determined (Soderstrom et al., 1987). Five of these subfamilies, the Bambusoideae, Pooideae, Arundinoideae, Chloridoideae and Panicoideae are discussed below, while the sixth, Centothecoideae is fairly minor.

Grasses are thought to have had a tropical origin, evolving in the tropical forest-savannah ecotone (Clayton and Renvoize, 1986). Bambusoideae was thought to be the most primitive of the extant groups (Stebbins, 1982; Clayton and Renvoize, 1986), but phylogenetic analysis shows that the sub-families Pooideae, Bambusoideae, Panicoideae and possibly Chloridoideae are monophyletic and may be derived from the polyphyletic Arundinoideae (Kellogg and Campbell, 1987).

Most tribes of grasses are widespread (Hartley, 1964) but the major proportion of genera (76%) are restricted to a single land-mass (Clayton and Renvoize, 1986). This suggests that the major subfamilies named above

had evolved by the early Tertiary and become widespread before the major breakup of the supercontinents during the Tertiary. Grasses continued to radiate throughout the Tertiary period, as shown by the relatively low endemism of grasses compared to other plant groups (Hartley, 1964). Endemism is most common at the southern tips of continents and in restricted environments where relict vegetation has been allowed to survive (Clayton and Renvoize, 1986).

Fossil evidence of grasses and grasslands date back as far as the Eocene (45 Ma) in the Americas (Thomasson, 1987; Crepet and Feldman, 1991) which is supported by faunal associations (Webb, 1977, 1978). Although grass pollen occurs in Africa in the Eocene (Salard-Chebouldaef, 1979) evidence of grassland communities does not appear until the mid-Miocene (14 Ma: Retallack, 1992). The mid-Miocene flora, occurring in Kenya, is of a tropical affinity, probably a wooded grassland (Retallack, 1992). A fauna co-evolved with grasses also dates from this period (Pickford, 1985). Grass pollen in Australia dates from the Oligocene but only in very small percentages, reflecting the limited development of open vegetation at the time (Kershaw et al., 1994).

Grasslands evolved in tropical climates which were developing seasonal aridity, related to the general cooling and break-up of super-continent from the late Mesozoic (Clayton and Renvoize, 1986). This separation altered global circulation systems. Cooling conditions progressed through the Tertiary, with temporary periods of warming, to culminate in the current period of glacial and interglacials during the past 2.5 Ma (Williams, 1984). Grasslands took advantage of changing environments that were inimicable to rainforest

(Retallack, 1992). As environmental conditions became more extreme, temperate and arid grasslands evolved.

The earliest grasslands are interpreted as being subtropical savannahs (Webb, 1977; 1978). These later evolved into temperate grasslands in continental and higher latitude areas. This transition occurred about 15 Ma in South America and 6 Ma in North America (Webb, 1978). A similar process occurred in Eurasia, and at times steppe vegetation was extensive enough to permit faunal migration from Asia to North America (Webb, 1977). North America met South America about 3 Ma, and during cool periods, savannah vegetation allowed a similar exchange of fauna, mainly north to south (Webb, 1978).

The timing of continental separation and collision is critical in unravelling the evolution of grassland flora, but the poor fossil record and uncertain evolutionary relationships between grasses limit any conclusions about the evolution of Australian grasslands. The origin of temperate grasslands in South America during the mid-Miocene occurred well after the breakup of Gondwana. Australia had separated from Antarctica by that stage (Crook, 1981), although Antarctica provided a temperate link between Australia and South America during the early Tertiary (Clifford and Simon, 1981).

Timings for continental separations and collisions are as follows: India separated from Australia and Antarctica about 130 Ma in the Early Cretaceous and continued northward, accelerating after 80 Ma until its collision with Asia about 55 Ma (Powell et al., 1981; Quilty, 1984). Australia had a long history of separation from Antarctica with the formation of shallow seas at about 55 Ma and final separation in the early Oligocene, about 30 Ma.

New Zealand moved east from Australia about 70 Ma and the Tasman Sea opened until about 60 Ma (Quilty, 1984). Land bridges over the Lord Howe Rise may have existed at this time (Crook, 1981). Powell et al. (1981) postulate that Sundaland (South-east Asia and the Indonesian archipelago) may have moved east toward the northward-moving Indian sub-continent, with a near collision with the Australian plate as early as 20 Ma. The Australian plate collided with Sundaland (the Indonesian archipelago) in the Miocene (15 Ma, Powell et al., 1981). South America had links with Antarctica until about 30 Ma (Powell et al., 1981; Kemp 1981).

The major development of grasslands occurred in the mid to late Tertiary, well after the breakup of the super-continent Gondwana and Laurasia (Europe, Asia and North America). The major taxonomic groups of grasses appear to be much older, preceding the evolution of grasslands by many millions of years.

Biogeography of Australian Grasses

Clifford and Simon (1981) discuss the biogeography of Australian grasses with reference to the distribution of genera and continental evolution. They demonstrate that the links between genera in Australia and the other Gondwanan continents (Africa, Indo-Malaya and South America) are more developed than for Eurasia and North America. This supports the contention that these taxa are ancient, pre-dating the break-up of Gondwana.

Clayton and Renvoize (1986) hypothesize that Stipeae and Arundinoideae dominated the early savannahs around the world which were in turn ousted by the C4 sub-families Panicoideae and Chloridoideae; both more efficient in tropical environments. Arundinoideae is a very old group of a heterogeneous character which appears mainly in the southern hemisphere and is thought to have a Gondwanan origin (Conert, 1987).

For example, the tribe Danthonieae which contains the genus *Danthonia*, the only worldwide taxon of this group, has a number of Australasian endemics and is allied with the Arundinoideae (Conert, 1987). *Danthonia* is shown in the tribe Arundinoideae in Table 1, based on the interpretation of Walsh (1994). Table 1 contains a census of indigenous Victorian genera with reference to their broader relationships.

Barkworth and Everett (1987) also ally the Stipeae, another (sub)tribe with Gondwanan affinities, with the Arundinoideae. Kellogg and Campbell (1987) place it at the base of the Pooideae, an interpretation followed by Walsh (1994, Table 1).

Arundinoideae, Chloridoideae and Panicoideae all show a degree of endemism in Australia (Clifford and Simon, 1981; Clayton and Renvoize, 1986; Table 1), while Stipeae have retreated to drier environments world-wide and show a degree of endemism at species level. The Australian Stipeae are thought to be a monophyletic group with a distinct character. The taxonomic label of *Stipa* is attributed to a number of groups that are related on a morphogenetic basis, but not on an evolutionary basis (Barkworth and Everett, 1987). This group is likely to be separated into a number of genera following revision.

Stipa and *Danthonia*, to which *Themeda* grasslands in south-eastern Australia will revert if overgrazed (Moore, 1959) both show a degree of endemism at the species level (Clifford and Simon, 1981) and are part of the polyphyletic Arundinoideae. These taxa both have Gondwanan affiliations although *Poa* is thought to have evolved from Stipeae in the Northern Hemisphere (Clayton and Renvoize, 1986). Total species of Stipeae in Australia number over 60, mostly *Stipa*, and

Table 1. Census of indigenous Victorian grass genera showing subfamily and tribe, with distribution and total species numbers. Data from Walsh (1994).

Subfamily	Tribe	Genera (number)	Distribution, number of species	
Bambusoideae	Ehrharteae	Microlaena (1)	Pacific region, 10 species	
		Tetrarrhena (4)	Australian endemic, 7 species	
Pooideae	Stipeae	Stipa (35)	Temperate world-wide, >300 species	
	Poeae	Festuca (2)	Cosmopolitan, ~180 species	
		Dryopoa (1)	SE Australian endemic, 1 species	
		Puccinellia (1)	Temperate world-wide, ~30 species	
		Poa (26)	Cosmopolitan, ~300 species	
		Austrofestuca (3)	Australia, New Zealand, 3 species	
	Meliceae	Glyceria (1)	Cosmopolitan, ~30 species	
Aveneae	Amphibromus (8)	Australia, New Zealand, South America, 12 species		
	Trisetum (1)	Cosmopolitan, ~75 species		
	Koeleria (1)	Temperate, ~60 species		
	Deschampsia (1)	Cosmopolitan, 40 species		
Bromeae	Heirochloe (3)	Cool-temperate, ~30 species		
	Agrostis (11)	Cosmopolitan, ~200 species		
	Deyeuxia (20)	Temperate Gondwana, ~200 species		
	Echinopogon (3)	Australasia, 7 species		
	Pentapogon (1)	Australian endemic, 1 species		
	Dichelachne (6)	Australasia, 8 species		
	Bromus (1)	Mainly old world, ~50 species		
	Triticeae	Elymus (1)	Cosmopolitan, ~100 species	
Australopyrum (2)	SE Australian endemic, 3 species			
Arundinoideae	Arundineae	Chionochloa (1)	New Zealand, Australia, ~20 species	
		Plinthanthesis (1)	SE Australian endemic, 3 species	
Danthonia (23)		Mainly Gondwanan, ~150 species		
Erythranthera (1)		Australia, New Zealand, 2 species		
Anisopogon (1)		SE Australian endemic, 1 species		
Amphipogon (2)		Australian endemic, 7 species		
Phragmites (1)		Cosmopolitan, 3 species		
Aristideae	Aristida (5)	Tropical cosmopolitan, ~350 species		
Chloridoideae	Pappophoreae	Enneapogon (3)	Warm-temperate & tropical, ~30 species	
	Eragrostideae	Triodia (1)	Arid Australian endemic, 34 species	
Distichlis (1)		North America maritime/saline, 13 species		
Triraphis (1)		African, 10 species		
Diplachne (2)		Cosmopolitan, ~15 species		
Tripogon (1)		Tropical Africa, Asia, 30 species		
Eragrostis (11)		Cosmopolitan, 300 species		
Dactyloctenium (1)		Subtropical, 13 species		
Sporobolus (4)		Warm-temperate & tropical cosmopolitan, ~150 species		
Panicoideae		Cynodonteae	Chloris (2)	Warm-temperate & tropical cosmopolitan, ~40 species
			Enteropogon (1)	Gondwanan, 12 species
	Cynodon (1)		Tropical Gondwanan, ~10 species	
	Tragus (1)		Mostly African, 7 species	
	Zoysia (1)		Maritime cosmopolitan, ~10 species	
	Paniceae	Neaurachne (1)	Australian arid endemic, 7 species	
		Oplismenus (1)	Widespread excepting Europe, 7 species	
		Panicum (3)	Warmer cosmopolitan, 500-600 species	
		Entolasia (2)	Tropical Africa, Australasia, 5 species	
		Eriochloa (1)	Tropical cosmopolitan, 30 species	
Paspalidium (3)		Warm cosmopolitan, ~27 species		
Isachneae	Homopholis (1)	SE Australian endemic, 2 species		
	Digitaria (4)	Cosmopolitan, ~220 species		
	Pseudoraphis (2)	Asia, Australia, 5 species		
	Spinifex (1)	Australia, Asia, 5 species		
	Isachne (1)	Tropical, ~60 species		
Andropogoneae	Imperata (1)	Tropical & warm-temperate, 10 species		
	Eulalia (1)	Tropical & sub-tropical, ~30 species		
	Sorghum (1)	Tropical & sub-tropical, ~60 species		
	Dicantheum (1)	Widespread except Americas, ~15 species		
	Bothriochloa (1)	Tropical & warm-temperate, ~35 species		
	Cymbopogon (2)	Tropical Africa, Asia, Pacific, ~60 species		
	Themeda (1)	Warmer Africa, Asia, Australia, ~10 species		
	Hemarthria (1)	Tropical Africa, Asia, ~10 species		

Danthoneae number over 40, mostly *Danthonia*. Both of these groups show great variation at the genus level and their nomenclature is controversial (Clayton and Renvoize, 1986; Conert, 1987; Barkworth and Everett, 1987).

The most widespread of the endemic Australian grasses are the Triodiinae subtribe of which *Triodia* is widespread in arid environments. This may be a response to the development of aridity in Australia from the Miocene (Bowler, 1982) and evolution in relative isolation, as a number of other plant communities within the arid and semi-arid zones also show endemic and Gondwanan elements (Clifford and Simon, 1981).

Many other grasses appear to have migrated from Asia. Such grasses occurring in the temperate grasslands of south-eastern Australia include *Themeda*, *Dichantheum* and *Bothriochloa* of the Andropogoneae tribe within sub-family Panicoideae. All are tropical grasses which extend into the temperate zone of southern Australia. *Dichantheum sericeum* has a distribution in E. Australia, New Guinea, New Caledonia and the Phillipines (Willis, 1970). *Dichantheum* and *Bothriochloa* are generally grasses of the old world tropics. *Themeda triandra* (syn. *australis*) has a wide distribution in Australia, southern Asia and southern Africa (Hartley, 1964).

Hartley (1964) showed that the Andropogoneae have major centres of distribution in south-eastern Indonesia and India, with a lesser centre in central eastern Africa. Fifty percent of the genera within the tribe occur in Africa and Tropical Asia (Clayton and Renvoize, 1986). This infers that the taxa listed above have entered Australia from the north since its collision with Asia (although Andropogoneae may have existed in Australia before this time). This later migration may have management implications for grasslands, particularly those which are *Themeda* dominated, discussed in a companion paper (Jones, 1999).

Although other members of the Andropogoneae may have entered Australia earlier, it is likely that *Themeda triandra*, migrated from south-east Asia (Hartley, 1964) in the late Tertiary. At some time in the late Tertiary, *T. triandra* also migrated across into Africa and today is widespread in southern Africa.

Poa, another major genus in temperate grasslands, is thought to have a temperate genesis, possibly evolving from Stipeae (Clayton and Renvoize, 1986). The uplands of Europe have a long temperate history and have the highest number of endemic Pooideae genera, centred on central Europe and North Asia (70), compared to S. America (12) and Australia (10). Clayton (1976) shows that the degree of endemism in tropical African

highlands reflects long-standing temperate links between the northern and southern hemisphere.

Biogeography of Australian Grasslands

Kershaw et al. (1994) trace the entry of the Poaceae into palynological records across regional Australia from the first definite records in the Oligocene. Grass pollen first occurs above trace levels in north-western Australia possibly forming open savannah by the mid Miocene. From this region, grasses expanded south-east through central Australia as aridity intensified throughout the Late Tertiary (Kershaw et al., 1994).

Grasses were present in northern and central Australia extending into the Murray Basin in the early to mid Miocene, however the content during these early periods is too small to propose a definite occurrence of grassland (Martin, 1991). The entry of grasses into more southern and eastern areas occurred in the mid to late Miocene and early Pliocene but the proportion of grass pollen to total pollen remained minor. Open vegetation communities developing sclerophyllly began to appear, but did not have a significant herbaceous understorey (Kershaw et al, 1994).

The expansion of open vegetation types accelerated in the Late Miocene, due to increased seasonality as proposed by Bowler (1982). Fires were a part of the ecosystem in the Murray Basin throughout the Miocene, increasing with aridity (Kershaw et al., 1994). Herbaceous communities dominated by Asteraceae and Chenopodiaceae, originally surviving harsh conditions on the coastal fringe, expanded into arid environments during the Pliocene (Kershaw et al., 1994). This flora is now the primary vegetation in central Australia where conditions are too dry for grasses.

By 6 Ma seasonal aridity within central Australia was commonplace, associated with a gradual transgression of seas from coastal areas and inland sedimentary basins, such as the Murray Basin. This is associated with high summer rainfall and deep weathering, with the expansion of the arid zone in central Australia (Bowler, 1982) although conditions at Lake Frome were still dominated by sclerophyll and dry rainforest species (Kershaw et al, 1994).

The period 6–2.5 Ma saw a sequence of sediments in south-eastern Australia largely barren of pollen (Kershaw et al., 1991), perhaps due to winter aridity (Bowler, 1982). This has hampered the reconstruction of grassland evolution; although grasses continued to expand south and east, the fossil record of this process is poor.

A major climatic change in the late Pliocene at 2.5 Ma saw the development of winter rainfall systems as cooling associated with the closing of the Ross Sea intensified (Bowler, 1982). This period is characterised by glacial-interglacial sequences where the climate oscillated between short, warm periods (~10 ka) and longer, cool periods (~100 ka). At the end of an warm interglacial, climate cooled in a series of rapid events punctuated by longer, more stable periods, eventually culminating in a glacial maximum. This was followed by rapid warming and a return to interglacial conditions. The glacial periods last for 80,000–100,000 years while the interglacials are much shorter at 10,000–15,000 years.

The glacial maximum is cool and dry, whereas the preceding glacial episodes are not so cold and oscillate between dry and wet. Interglacials are associated with warm and wet conditions. The Australian fossil record from the Pleistocene is complicated by a lack of preservation, possibly due to the dessication of older records during dry periods.

Herbaceous ecosystems evolving in south-eastern Australia during the Pliocene and oscillating climate of the Pleistocene were dominated by Asteraceae, although Poaceae and Chenopodiaceae were components (Kershaw et al., 1991, 1994). Poaceae achieved further prominence throughout the Pleistocene, mainly at the expense of Asteraceae, and formed open vegetation. These early grasslands oscillated with Casuarinaceae forests which were favoured during the wetter interglacials (Kershaw et al., 1991). Casuarinaceae was more prominent than Myrtaceae (Eucalyptus) during the evolution of these drier forest types (Kershaw et al., 1994), delaying the dominance of *Eucalyptus* in many areas until the Holocene.

It is difficult to interpret these past pollen associations on the basis of current vegetation. The use of modern analogues often breaks down for floras occurring during previous ages with different climates, because taxa have become extinct or their autecology has changed.

For example, Asteraceae and Casuarinaceae pollen types widely occurring in south-eastern Australian cores during the Pleistocene are difficult to interpret as there are no modern analogues and the species involved appear to be extinct (Kershaw et al., 1991). Small grains of *Casuarina*, unlike any today, decline in all cores to disappear only a few hundred years ago at Lake George (Kershaw et al., 1991).

Another disappearing taxon is a spiny pollen of the Asteraceae family that resembles pollen from the genus *Calomeria* (Kershaw et al., 1994), which has only one species in Victoria, *Calomeria amaranthoides*. This pollen also declines during the late Pleistocene, disap-

pearing at Tower Hill by the late Holocene. *C. amaranthoides* is a 2 m tall biennial herb that grows on disturbed sites in wet forest in east Gippsland and the Grampians. *Cassinia arcuata* has also been named as a candidate as parent of this pollen (Kershaw et al., 1994) but neither of these species are considered good analogues for the fossil species.

Early Gondwanan connections may have been responsible for the entry of primitive taxa into Australia, but the later role of Antarctica, before the two continents separated towards the end of the Eocene is unclear. South to north movement cannot be discounted from the Eocene to the Miocene and perhaps later, as recent evidence indicates the coverage of the Antarctic ice-cap was not complete until the late Tertiary.

However, the small proportion of Pooideae present during the evolution of temperate forests replacing rain-forest after 2.5 Ma (Kershaw et al., 1991, 1994) suggests that temperate grasses such as the Pooideae were not well represented in Australia at that stage. The favoured route for these grasses must be from the north via tropical highlands during the Pleistocene ice-ages.

Summary

The evolution of Australian grasslands is summarised in the following:

- Grasses from most, if not all, the major tribes migrated into Australia when it was part of Gondwana. Their habit at this time is unknown. Clayton and Renvoize (1986) state that grasses were more likely to have evolved in open habitats and Retallack (1992) says they were likely to be minor herbs within forested habitats in the early Tertiary. Were upheavals associated with continental rifting a factor in their evolution and distribution? If so, rift areas are geologically very active and preservation is unlikely.
- Grasses were evident in Australia from at least the Oligocene (Kershaw et al., 1994). They continued to evolve in response to cooling from the late Miocene (dominated by Stipeae and other Arundinoideae?), through the Pliocene, first present in sub-tropical savannah (development of Chloridoideae and Panicoideae?) with later adaptation to aridity characterised by *Triodia* in central Australia (Chloridoideae with relict Arundinoideae). Pooideae probably entered in the last few million years.
- The development of grassland is associated with seasonal aridity which began in the north-west of

Australia in the Miocene. Grasses spread into the centre of the continent as aridity intensified, then eventually into the wetter margins of the south-east. Even in areas of the Murray Basin that are now arid to semi-arid, grasslands did not become apparent until at least the Pliocene. The movement further south and east are due to the climatic oscillations of the last 2.5 million years, although it can be shown that the taxa themselves demonstrate much older links.

- In south-eastern Australia where cool temperate Nothofagus rainforest was being replaced by elements of drier rainforest dominated by *Casuarina*, *Auracaria* and Proteaceae, and sclerophyllous vegetation was becoming dominant, warm but drier, temperate elements developed. Early herbaceous vegetation was dominated by Asteraceae and Chenopodiaceae. Grasses did not achieve their current prominence until the Late Pleistocene.
- Pleistocene additions to grassland flora continued to come south from south-east Asia, perhaps taking advantage of low sea levels to colonise large areas of continental shelf. The number of taxa added were not large compared to the pre-existing taxa but the additions of species such as *Themeda triandra* had a major effect on Australian grasslands. Pooideae also became significant during the Pleistocene having migrated southwards from temperate Eurasia. Pooideae elements of some antiquity in tropical highlands (Clayton and Renvoize, 1986) lend some support to this possibility.
- The glacial and interglacial oscillations of the late Pleistocene as described by Bowler (1982) would have contributed to widespread movements in grasslands within Australia as they responded large changes in temperature and precipitation.

Changes associated with the Holocene and human influences are discussed in a companion paper (Jones, 1997).

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