

## OVERVIEW OF THE GRASSLANDS OF OCEANIA

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### INTRODUCTION

The grasslands of Oceania are distributed in fragmented units over a region extending some 105 degrees longitudinally [from Australia (120°E) to Pitcairn Island (135°W)] and 78 degrees latitudinally [from the Northern Mariana Islands (23°N) to the sub-Antarctic islands (55°S)]. Within this vast territory, the land area of approximately 8 509 400 km<sup>2</sup> supports a human population of about 25 060 000, the area per head ranging from nearly 0.3 ha in Tuvalu and Nauru to 14 ha in Papua New Guinea and 44 ha in Australia. Although the proportion of land which has been converted to grassland tends to vary directly with population pressure, direct relationships are con-

founded by variation in climate, soils, terrain, island size and patterns of land use. Some of the land areas treated here are outside Oceania *sensu stricto* and include "outliers" such as Hawaii, the Philippines and the sub-Antarctic islands. These have been included to provide a more appropriate regional biogeographic framework. A broad indication of the regional distribution of major grass tribes is given in Table 12.1.

Comparative studies of grasslands within Oceania are made complex by extreme variation in physical environments: although semiarid Australia contains extensive areas of "pure" grassland, the south-west Pacific island grasslands are mostly fragmented mosaics distributed along locally variable — often steep — physical environmental

TABLE 12.1

Composition of the grass flora (% contributed by each major tribe) in selected localities in and near Oceania, compared with the global average<sup>1</sup>

Locality	Agrostaceae	Andropogoneae	Aveneae	Eragrostaceae	Festuceae	Panicaceae	Others
Hawaii (below c. 1300 m)	5.7	11.4	6.8	8.0	17.0	35.2	15.9
Luzon, Philippines	2.3	33.7	1.1	7.4	2.9	33.7	18.9
Papua New Guinea	5.5	29.6	4.6	8.3	7.4	22.2	22.2
Kimberley Dist., W. Australia	—	28.2	10.9	9.1	3.6	29.1	19.1
De Grey, Western Australia	1.1	15.7	10.1	22.5	—	27.0	23.6
South-western Queensland	4.4	10.6	8.0	21.3	1.8	18.6	35.3
Southern S. Australia	10.4	4.5	12.3	2.0	26.0	9.7	35.1
Tasmania	21.2	3.0	14.1	2.0	27.3	4.0	28.4
South-western New Zealand	25.3	—	29.3	—	30.7	—	14.7
Average	8.4	15.2	10.8	9.0	13.0	19.9	23.7
Normal distribution spectrum (global)	8.2	11.9	6.3	8.1	16.5	24.7	24.3

<sup>1</sup> The values used are from Hartley (1950), except for New Guinea, which are based on lists of grass genera extracted from Henty (1969). Hawaii and the Philippines are not parts of Oceania *sensu stricto*, but are of interest for biogeographic comparison.

gradients which may be variously associated with woody species. Similarly, in the sub-Antarctic islands, grasslands are components of ecosystems rather than ecosystems in their own right.

The following four chapters are concerned with the grasslands of Oceania: Australia (Chapter 13), New Zealand (Chapter 14), the sub-Antarctic islands (Chapter 15) and the south-west Pacific (Chapter 16.)

## ORIGINS AND AFFINITIES

Uncertainty surrounds the origins of grassland in Oceania. Whatever the pre-human evolutionary determinants, the close interaction between man and grassland in both Australia (up to 40 000 years or more with fire) and Papua New Guinea (at least 9000 years with slash-and-burn agriculture) suggests it is logical to include humans as a "natural", albeit recent, evolutionary component for these areas (Gillison, 1972).

As with large areas of south-eastern Asia and the Philippines, in recent times many grasslands have been initiated by slash-and-burn agriculture and by fire-based hunting practices. In Australia, before the arrival of European man in the 1780s, aboriginal hunters manipulated the spatial extent and structural and floristic composition of many woodland savannas and grasslands by "patch"-burning in order to concentrate groups of grass-eating animals such as kangaroos and wallabies. Although the use of fire for hunting is also widespread in Melanesia and Polynesia, there is no parallel in Australia for aboriginal slash-and-burn subsistence agriculture.

This background, together with the uncertain origin of many so-called exotics, also creates problems in defining "naturalness". There is continuing debate about the origins of the New Zealand alpine and grassland biotas that have developed only recently and continue to evolve rapidly (see Chapter 14). The New Zealand grassland vegetation developed following a major orogeny in the Pliocene and Late Tertiary and was later subject to limiting climates under Pleistocene glaciation. The general lack of drought in New Zealand, and the relatively cool oceanic climate, distinguish it from the continental environment of Australia and give it a closer affinity with Tasmania and the sub-

Antarctic islands. In the tropical Pacific, on the other hand, the closest affinities of New Zealand are with the upper montane and subalpine formations of New Guinea.

Partly because of a sparse fossil record, the origin of the gene pool from which Oceanic grasslands have been derived is unclear. Takhtajan (1969) and others have argued a case for likely centres of origin for the Angiosperms, one focal area being north-eastern Australia — a hypothesis which tends to be supported by the more recent findings of Audley-Charles (1987). A numerical analysis of world grass genera by Simon and Jacobs (1990) postulates that, with the exception of the Poaceae, the currently recognized groups of the Poaceae are Gondwanan in origin. The analysis by Simon and Jacobs (1990) has demonstrated close affinities between the tropical Pacific grasses and those of the cold temperate (mesotherm/microtherm) oceanic islands, whereas grasslands of microtherm/mesotherm Australia and New Zealand have closer ties with Hawaii and the Antarctic zone. The affinities of the sub-Antarctic island grasslands with South America (Gremmen, 1982; see also Chapter 15) are also reflected in the findings of Simon and Jacobs, where, at the generic level, there are evident links between tropical Asia, Australia and parts of the western Pacific.

Although providing a useful focus for regional geographic studies, phytogeographic analyses of grass genera alone are inappropriate for ecological interpretation. There is a need to take into account variability in environment as well as in plant functions and floristics in order to provide clearer insights into evolution and development and into responses to environmental change. Throughout Oceania there are "grasslands" which are closely associated with, or sometimes dominated by, cyperaceous or other graminoids. The pervasive distribution patterns of these graminoids and their close ecological ties with true grasses suggest that they should be included in studies involving grasslands.

Instead of concentrating solely on grass taxa (e.g. genera), some of the questions concerning grassland origins may be better focused using multivariate analytical techniques involving identifiable, response-based attributes of graminoids as a whole. Functional groups in graminoids can be

characterized in part by specific forms of acid decarboxylation and associated enzymic pathways (Prendergast, 1989) and by other functional characteristics (Gillison, 1988). By examining the spatial and temporal distribution of these functional groups along defined physical environmental gradients, potentially useful models could be derived which would assist in interpreting graminoid origins. For Australia and the larger islands (New Zealand, New Guinea) and parts of the sub-Antarctic, various authors have argued that historical climatic fluctuations, and in particular oscillatory glaciation, have profoundly influenced the establishment and maintenance of grasslands. Periglacial activity in parts of the sub-Antarctic (e.g. Macquarie Island) also affects the establishment of grasses (Löffler et al., 1983; see also Chapter 15). These processes fuel speculation about grassland origins. Apart from geomorphic processes, grassland domains have a broad history of expansion and maintenance by man-made fire, except perhaps in the sub-Antarctic islands. In New Zealand it is argued that the origin of grasslands following the arrival of early Polynesian settlers over 1000 years ago may have been accompanied by climate change, and not be purely pyrogenic. In Papua New Guinea, the connection of lowland with upper montane and subalpine grasslands through the agency of man-made fire has facilitated the spread of lowland graminoids and associated introduced plant and animal species. Little is known about the likely origins of sub-Antarctic grassland. Although the earliest vegetation is recorded from the Tertiary and Quaternary, there is some evidence in the Îles de Kerguelen of loss in overall floristic richness since the

Miocene. For the islands in the sub-Antarctic convergence it is likely that the climate has remained relatively constant over the past 10 000 years (see Chapter 15).

## VEGETATION

### Bioclimate classification

Within Oceania, present-day climates range from extremes of seasonal tropical lowland on the one hand and alpine on the other to cold non-seasonal regimes in the sub-Antarctic. Because there are broad climatic similarities between high-altitude/low-latitude and low-altitude/high-latitude domains, the use of terms such as "tropical" and "temperate" can mislead when comparing grassland climates between regions (Oliver, 1979).

The bioclimatic framework used in Chapter 16 (see also Gillison, 1983) to compare the grasslands of the south-west Pacific has been extended in the following discussion to apply to Oceania as a whole. This is based on broad categories of optimal growth responses of the whole plant to defined thermal domains. The use of a response-based approach of this kind makes possible more meaningful ecological comparisons between grassland regions with broadly similar climates than can be obtained with other, more arbitrary methods (see Nix, 1983, and Table 12.2). Nix's approach has made possible a simplistic but relatively uniform comparison between grasslands in high and low latitudes with similar bioclimates. Although there are broad similarities in such contrasting

TABLE 12.2

The bioclimatic classes used by Nix (1983)

Bioclimatic class	Photosynthetic pathway	Optimum temp. (°C)	Lower temp. threshold (°C)	Upper temp. threshold (°C)
Megatherm	C <sub>4</sub> and CAM	30–32	10	46
Megatherm	C <sub>3</sub>	26–28	10	36–38
Mesotherm	C <sub>3</sub>	19–22	5	33
Microtherm	C <sub>3</sub>	12–14	0	25
Hekistotherm	C <sub>3</sub>	6–8	–10	25

climates of the sub-Antarctic convergence and tropical alpine areas, significant differences exist in rainfall seasonality, solar radiation intensity, day-length and wind. These differences are reflected in different plant functional characteristics expressed in the same (poid) genera; the sub-Antarctic grasses are mesomorphic and the tropical alpine grasses xeromorphic. Other functional characteristics related to the photosynthetic pathway of grasses reveal a strong concentration of C<sub>4</sub> acid decarboxylation types (especially andropogonoid taxa) towards the megatherm seasonal bioclimate and a converse increase in the proportion of C<sub>3</sub> types along a decreasing thermal cline to complete C<sub>3</sub> (poid) dominance in the sub-Antarctic. In applying this classification, a bioclimate domain is defined as "seasonal" if the coefficient of variation in annual rainfall during the year exceeds 60%.

### Megatherm grasslands

In general terms the strongly seasonal megatherm grasslands include many CAM- and C<sub>4</sub>-based vegetation types. For grasslands this domain is dominated by C<sub>4</sub> Andropogoneae (cf. Johnson and Tothill, 1985). In northern tropical Australia, perennial, chloroid "spinifex" hummock grasses, especially *Plectrache schinzii* and *Triodia basedowii*, occupy the drier seasonal interior north of 22°S, whereas in areas with more than 1200 mm mean annual rainfall there tends to be a divergence into "seasonal" and "perennial" andropogonoids, for example within the genus *Sorghum*. Some of the most extensive tussock grasslands within this Australian zone are those on cracking clays dominated by *Astrelia* spp. (Mitchell grass). These are relatively pure grasslands where the botanical composition is strongly influenced by rainfall seasonality. Like the spinifex-dominated grasslands of the more arid interior, they are unique within Oceania. It is not surprising that, in northern megatherm seasonal Australia, graminoids with Indo-malesian affinities occur towards the warmer, more humid extremes. These include in particular, members of the tribes Andropogoneae (*Arthraxon*, *Capillipedium*, *Chrysopogon*, *Dichanthium*, *Eulalia*, *Heteropogon*, *Imperata*, *Ischaemum*, *Saccharum*, *Sorghum* and *Themeda*) and Paniceae (*Alloterop-*

*sis*, *Brachiaria*, *Cenchrus*, *Digitaria*, *Melinis*, *Panicum*, *Pennisetum* and *Setaria*). In this region, semi-permanent to permanent swamp formations commonly contain indigenous oryzoid C<sub>3</sub> "wild-rice" genera (*Leersia* and *Oryza*) and arundinoid *Phragmites*.

Two andropogonoid C<sub>4</sub> grasses *Imperata cylindrica* and *Themeda triandra* (formerly *T. australis*) typify much of the humid Australian and Papua New Guinean megatherm grasslands. For this reason their presence in southern mesotherm/microtherm Australia, where C<sub>3</sub> grasses predominate, is difficult to explain on functional grounds. In seasonally or permanently moist environments, members of the andropogonoid sub-tribe Saccharinae (*Miscanthus* and *Saccharum*) are conspicuous. It is puzzling that, although *Miscanthus* is widespread throughout the south-west Pacific, it is not indigenous to Australia despite the presence of an apparently suitable bioclimate. As with some other grass genera, the distribution of *Miscanthus* may be due largely to historical trading activities (cf. Simon, 1988). Maritime megatherm grasslands are the norm for many south-west Pacific islands, often with *Imperata cylindrica*, *Ischaemum* spp. and tall rottboellinoid species of *Rottboellia* and *Ophiuros*. Deliberate annual firing of these grasslands by man is common.

The seasonal megatherm woodland savannas of southern and south-western Papua New Guinea are characterized by *Eucalyptus* spp. and *Melaleuca* spp. This reflects a structural and floristic continuum with the savannas of Cape York Peninsula in Australia. These mixed grasslands are unique within Oceania. In New Caledonia where *Melaleuca* ("Niaouli") savannas occur without *Eucalyptus*, taxa (including *Melaleuca quinquenervia*) which are common to both Australia and New Caledonia exhibit much wider environmental amplitude. The structure and floristic composition of grasslands in the smaller islands of the south-west Pacific reflect the combined effects of oceanic climatic buffering, relatively lower floristic richness in the island domains, increased vulnerability to invasive exotics, and varying and often intense land use.

The fragmented nature of many megatherm grasslands makes difficult their comparison within the region. Apart from localized, repetitive patterns of mid-height to tall grasslands (typically

of species of *Heteropogon*, *Miscanthus*, *Themeda* and members of the Rottboellinae), there are non-grass graminoid components which occur repeatedly throughout the region. Apart from typical herbaceous cyperaceous elements, these are woody, rosulate graminoids represented mainly by Pandanaceae (*Pandanus* spp. and *Sararanga* spp.) and palms, especially *Livistona*. Whereas Pandanaceae are distributed throughout Indo-malesia and the megatherm Pacific generally, they appear to be particularly well developed in south-west Pacific grasslands. The genus *Sararanga* is restricted to the Philippines, the Solomon Islands and the New Ireland Province of Papua New Guinea where it occurs in typically humid habitats. *Pandanus* ranges across a wide spectrum of physical environments from seasonal megatherm (Figs. 16.3, 16.10, 16.19 and 16.24) to cooler mesotherm situations.

The broad-leaf fan palm *Livistona* is represented in Papua New Guinea by *L. brassii* (Fig. 16.10), and another ten species (approximately) occur in Australian savannas. The distribution pattern of this palmoid grassland formation is repeated in similar environments around the megatherm seasonal tropics in various, presumably functional, analogues (e.g. *Borassus*, *Mauritia* and *Sabal*). As with *Pandanus*, the global distribution of this grassland type has yet to be studied in detail. Another feature of Australian and south-west Pacific grasslands is the frequent association of other woody rosulate growth forms and, in particular, their distribution along thermal gradients. In the lowland megatherm grasslands these are represented by the genus *Cycas* (*C. media* and *C. rumphii*) (Fig. 16.11) and in montane, mesotherm/microtherm grasslands by tree-ferns of the genus *Cyathea* (Figs. 16.14, 16.15 and 16.16). Apart from the *Cyathea* association which appears to be unique to New Guinea, the *Cycas* association is pantropical; yet its ecological connection with grassland does not appear to have been examined in a global context.

### Mesotherm grasslands

Within the warmer part of the mesotherm range there is considerable spatial overlap between grasses with mesotherm and cooler megatherm growth optima. Whereas the latter tend to

be dominated by C<sub>4</sub> andropogonoid and panicoid groups, in semiarid Australia the largest proportion of grasses is represented by the chloridoid xerophytic hummock (*Plectrachne* and *Triodia*) and tussock (*Astrebla*) grasses, which otherwise are megatherms. Within this broad region, soil type is a critical determinant in grassland distribution. This is especially evident in respect to species of *Astrebla* (see Chapter 13).

There is an evident climatic correlation with vegetation change throughout most of the area of mesotherm/megatherm overlap. The "semi-arid crescent", which stretches from south-western Western Australia through to the rain shadow west of the Great Dividing Range to northern Australia, lies within this area. This constitutes an ecotone between the arid shrublands and grasslands too dry for arable agriculture and the higher-rainfall temperate and tropical woodlands in which crops can be grown. The drier boundary of the crescent in southern and eastern Australia approximates the limit for introduced pasture species (see Chapter 13).

Towards the cooler mesotherm region there is a gradual change from C<sub>4</sub> to C<sub>3</sub> grasses (especially Arundineae, Stipeae and Aveneae). In lowland semiarid southern Australia these may be variously associated with halophytic chenopod shrubs — the saltbushes (*Atriplex* spp.) and bluebushes (*Maireana* spp.) — often with scattered mallee-form *Eucalyptus* spp. (Chapter 13; Carnahan, 1990). These southern xerophytic grasslands are often invaded by Mediterranean annuals (e.g. *Hordeum leporinum* and *Medicago* spp.). In Australia, temperate (mesotherm) short-grass vegetation occurs between 27° and 42°S, with the proportion of Arundineae, Pappophoreae and Stipeae varying inversely with mean annual air temperature. In the montane and upper montane grasslands of Papua New Guinea, there is a parallel development in C<sub>3</sub> groups — especially Aveneae (*Anthoxanthum*, *Deyeuxia*, *Dichelachne*, *Hierochloë*), Arundineae (*Chionochloa*) and Isachneae (*Isachne* species). The "trunked" nature of some grasses, such as *Chionochloa archboldii*, is conspicuous in moist environments that are fired episodically. This trunked habit has some structural and possibly functional affinities with rosulate semi-ligneous plants [*Cyathea* spp. (Fig. 16.15) and *Pandanus* spp.] associated with up-

per montane and subalpine grasslands. Although the adaptive aspects of this form require further study, there are clear implications for adaptive convergence in a wide range of taxa — including grasses — in other tropical high mountains in the world (such as Africa and South America).

Other montane mesotherm grasslands in the south-west Pacific are relatively few. But where they exist — for example on Mount Tabwemasana (1800 m) in Espiritu Santo in Vanuatu — they are typically C<sub>4</sub> megatherm types with tall grasses (Rottboellinae) and andropogonoid *Imperata cylindrica* and *Themeda triandra* (see Fig. 16.8). On the island of Savaii in Western Samoa, *Imperata cylindrica* occurs on montane lava flows with a short herb and moss layer, as well as on a montane cinder cone and ash plain. Other associated species are *Oplismenus compositus* and *Paspalum orbiculare* (Whistler, 1978). The apparent elevational “depression” of vegetation in these smaller islands may be related to the Massenerhebung effect<sup>1</sup>.

The New Zealand mesotherm grasslands resemble in floristic and structural profile the southernmost temperate short grasslands of Australia (cf. Chapter 13). Differences derive from the predominantly oceanic climate of New Zealand and the less buffered continental climate of Australia. Whereas in the North Island precipitation is relatively non-limiting, within the South Island of New Zealand there is a marked rainfall gradient, which decreases to the east in the form of a rain shadow from the Southern Alps. This exerts a major influence on the structure and composition of grasslands and associated vegetation types. Drought is not a feature of New Zealand vegetation, “desertic vegetation” being the only major plant formation absent from the two islands. Below the New Zealand alpine grasslands lie mesotherm tussock or bunch grasses dominated by species of Poaceae (*Festuca* and *Poa*), which reflect the growth forms of tropical mesotherm and sub-Antarctic microtherm grasses.

### Microtherm/hekistotherm grasslands

These grasslands are restricted to very small areas of the high mountains of southern Australia, and the New Zealand and New Guinean alpine and subalpine zones. The close bioclimatic affinities between the hekistotherm sub-Antarctic grasslands and the essentially microtherm grasslands of these alpine and subalpine areas suggest they should be treated as one entity. The broader-ranging microtherm grasses (mainly C<sub>3</sub> arundinoid and pooid groups) are common to the alpine, subalpine and high-montane zones of Australia, New Zealand and New Guinea. These form tussock formations of varying height (0.2–1.2 m), and their growth form and cover are influenced by soil and aspect (this is not always so in Papua New Guinea — see Smith, 1977). Although the ecological affinities of the high-altitude New Guinean grasslands are with high-latitude (30° to 55°S) southern Oceania, they contain woody elements — especially Ericaceae (*Rhododendron* spp.) — which have strong biogeographic links with the Himalayas.

Although there are closely overlapping thermal ranges, the only grass genera common to microtherm Australia, New Zealand and Papua New Guinea are the C<sub>3</sub> pooids, *Agrostis*, *Festuca* and *Poa*. Despite the apparent climate similarities between the sub-Antarctic islands and the alpine grasslands of the other areas, the rolled, xeromorphic leaves of the New Zealand pooids suggest closer affinities with the high-montane New Guinean tussock grasses rather than with the mesomorphic forms of the sub-Antarctic species, with their broad, flattened laminae. Limited studies of shoot/root ratios indicate that these are much higher in tropical alpine zones than elsewhere (cf. Chapter 15). Other features of the sub-Antarctic islands, that are unique in Oceania, are the large-leaved forbs associated with grassland. On Macquarie Island these are represented by *Pleurophyllum hookeri* and *Stilbocarpa polaris* and, on the Îles de Kerguelen, by *Pringlea antiscorbutica*. It is worth noting the convergence in form between the rhizomatous *Stilbocarpa polaris* (Macquarie Island cabbage) and *Rheum rhabarbarum* (domestic rhubarb) which is widespread in Iceland. Another large forb common in Arctic and sub-Arctic Fennoscandia is *Archangelica*. Al-

<sup>1</sup> “Massenerhebung effect” refers to situations on large islands where vegetation, occurring at high elevation inland, also occurs at increasingly lower elevation towards the coast (see Chapter 16, p. 437).

though large forbs are absent from New Guinea microtherm grassland habitats (except *Gunnera* spp. along forest edges in moist sites), they occur in alpine and subalpine areas of Africa and South America (e.g. *Lobelia* and *Espeletia*, respectively).

Despite some similarities in tropical alpine and sub-Antarctic climates, there are significant differences (see Chapter 15). Radiation loads are considerably less in the sub-Antarctic zone, and photoperiodic amplitude is much wider. In the sub-Antarctic islands, precipitation is non-limiting for plant growth and relative humidity is always high. There are also strong year-round winds arising from anti-cyclonic high-pressure systems which exert a dominant effect on the aspect of vegetation (Löfller et al., 1983). Although winds reach gale force in the high mountains of New Guinea, they are without the same intensity or persistence as those in the sub-Antarctic convergence. A notable feature of the sub-Antarctic climate is its relative stability throughout the year. Although Hnatiuk (Chapter 15) comments that tropical alpine areas of Papua New Guinea also show little climatic variation, the high-montane, south-eastern extremities of the main cordillera of Papua New Guinea (e.g. Mount Suckling at 3300 m elevation) do exhibit distinct seasonality (personal observation).

### Grassland productivity

There are no comparative studies of grassland production within Oceania. Most productivity data are available in different forms, which complicates cross-tabulation. The data presented in Chapters 13 to 15 (summarized in Table 12.3) indicate regional bioclimatic trends in herbage production in defined grassland types. Despite the paucity of data, the mesotherm natural and introduced grassland species appear to out-perform their megatherm and microtherm counterparts.

Natural nutrient input varies with bioclimate and geographic location. Nutrient inputs appear to increase away from megatherm seasonality towards the highly buffered, oceanic, microtherm/hekistotherm environments. This may be due mainly to nutrient input in the latter from marine animals and sea birds and to increased atmospheric deposition of nutrients, especially nitrogen

and phosphorus from ocean-borne nutrients. Significant atmospheric transfers of nutrients from the sea to the land — through aerosols and precipitation — occur in oceanic climates. Manuring by animals and sea birds also contributes significantly, especially in the sub-Antarctic zone. Some limited studies suggest that there also may be significant nitrogen input to the soil by blue-green algae. Nutrient pathways have been little studied, but, due to the paucity of vertebrate herbivores in some areas, energy may be channelled directly through the detritus food chain (Chapter 15). Nutrient transfers from vegetation to soil are reduced in the megatherm seasonal environments, where annual burning of grassland removes significant amounts of labile nutrients — especially nitrogen, potassium and sulphur — whereas phosphorus and other macronutrients tend to be lost in ash run-off. In New Zealand, earthworms play a significant role in soil-nutrient mobility (Chapter 14). The conspicuous presence of earthworm casts in seasonally flooded grasslands of the Sepik Plains in Papua New Guinea and on the north-east coast of Queensland also suggests that these invertebrates play a significant role in nutrient relationships, where the store of soil nutrients is otherwise impoverished.

Despite this apparent range of nutrient inputs, a limited set of productivity data of annual herbage production from grassland types across a range of bioclimates (Table 12.5) indicates that mesotherm grasslands are the most productive.

### Effects of humans and other animals

In recent times man has exerted a powerful influence in the conversion of forest to grassland by fire and agriculture. In the south-west Pacific the rate of spread of anthropogenic grasslands is increasing with population pressure and forest removal.

In Oceania humans have been major agents in extending and maintaining grassland. Influences range from primitive slash-and-burn agriculture throughout the south-west Pacific, to purposive firing to drive game or else modify vegetation for subsistence (e.g. firing to increase productivity of the edible fern *Pteridium esculentum* by Maori). In some areas — such as highland Papua New Guinea — as population pressure has increased,

TABLE 12.3

Net annual herbage production ( $\text{g m}^{-2}$ ) in various grassland types in selected bioclimates within Oceania<sup>1</sup>

Region	Bioclimate	Grassland type	Production
Australia	megatherm seasonal	tropical tall grass	
		<i>Themeda triandra</i>	112–170
		<i>Themeda/Sorghum</i>	120
		<i>Heteropogon contortus</i>	250–750
	megatherm	xerophytic tussock ( <i>Astrelba</i> spp.)	128–188
	megatherm/ mesotherm	xerophytic hummock grass <i>Triodia pungens</i>	94
	mesotherm	“Mediterranean” pasture (+ <i>Trifolium subterraneum</i> )	594
New Zealand	mesotherm	short tussock grass	
		<i>Chionochloa crassiuscula</i>	949
		<i>C. pallens</i>	718
		<i>C. rigida</i>	539
		<i>C. macra</i>	346
		<i>C. oreophila</i>	180
		tall tussock grass <i>Chionochloa</i>	750–1042
Sub-Antarctic: <sup>2</sup>			
Marion Is.	microtherm	tussock grass <i>Poa cookii</i>	465
South Georgia	microtherm	<i>Poa flabellata</i>	6025

<sup>1</sup> Based on assumed total above-ground production in one growing season.

<sup>2</sup> Based on total above- and under-ground estimates in one growing season (data from Moore, Ch. 13; Mark, Ch. 14; Hnatiuk, Ch. 15).

slash-and-burn agriculture has changed to sedentary methods with accompanying replacement of tall grasses by relatively short grasses (e.g. *Imperata cylindrica* and *Themeda triandra*) — and often with increases in invasive weeds and overall loss in plant production.

In Australia, the extent of grassland has increased and undergone modification since the arrival of Europeans in 1788. Carnahan (1990) has estimated some of these changes (Table 12.4), of which the conversion to graminoid crops (cereals and sugar cane) and pasture with introduced species is the most significant. Introduced grazing animals in both New Zealand and Australia have had a major impact on grassland. Vast tracts of semiarid Australia have been modified under grazing pressure over the last century (see Chap-

ter 13). In New Zealand, deer (*Cervus elaphus*) are three times as efficient in energy use as sheep (Chapter 14). The impact of feral deer species in New Zealand has been greatly reduced in recent years by culling for meat. In southern Papua New Guinea the population of introduced rusa deer (*Cervus timorensis*) has risen to a point where it is competing significantly with the indigenous agile wallaby (*Macropus agilis*) for a highly seasonal grassland food resource. In a Hawaiian coastal grassland, Mueller-Dombois (1981) reported results from a grazing enclosure where, after one decade he identified four dynamic categories of plant responses. One form (“persisters”) could be divided into stable and oscillatory types. The latter can be compared with species showing similar behaviour in Mitchell grass (*Astrelba*) lands in



TABLE 12.4

Extent ( $10^3$  km<sup>2</sup>) of Australian grassland formations — past and present<sup>1</sup>

Structural form	Before 1780 <sup>2</sup>		At present	
	area	% <sup>3</sup>	area	%
<b>NATURAL GRASSLANDS</b>				
Hummock grassland	45	0.6	45	0.6
Closed grassland/sedgeland	14	0.2	25	0.3
Tussock grassland/sedgeland	359	4.7	326	4.2
Open tussock grassland	115	1.5	348	4.5
Sparse grassland	14	0.2	15	0.2
Subtotal	547	7.2	859	9.8
<b>GRASS UNDERSTOREY IN WOODLANDS</b>				
Hummock grasses	2045	26.9	2065	26.8
Tussock grasses	2385	31.0	2308	30.0
Subtotal	4430	57.9	4373	56.8
<b>ARTIFICIAL GRASSLANDS</b>				
Sown pasture	0	0.0	436	5.6

<sup>1</sup> From Carnahan (1990).<sup>2</sup> That is, before the arrival of European settlers.<sup>3</sup> % of total land area.

semiarid megatherm/mesotherm overlap areas of Australia.

The influence of native animals on vegetation in the sub-Antarctic islands is far more benign, as none is a herbivore and most (e.g. seals and penguins) contribute significantly to the nutrient resource. The introduced animals tell a different story. Mostly introduced as a source of food by early sealers and whalers, these are many and varied, including cattle, cats, horses, mice, mules, pigs, rabbits, rats, reindeer, sheep, and flightless rails (wekas). Whereas some populations have been reduced, others persist. As with mainland Australia, on Macquarie Island rabbits have created profound changes in grassland floristics and structure, and a concerted program of eradication using a myxoma virus has been under way for several years.

### Vulnerability to exotic species

As a general rule, the relative impact on indigenous biota by invasive exotics increases with decreasing island size and distance from mainland sources. In this respect, at least for plants, the sub-Antarctic islands are no different to the

islands of the tropical south-west Pacific. In the former, 32 species of invasive plants have become persistent or naturalized (Chapter 15). Of these, *Acaena magellanica* continues to spread with disturbance and grazing by introduced animals, especially rabbits. In the south-west Pacific (Chapter 16), apart from introduced weeds, which also increase under grazing pressure by cattle, continual firing and removal of woody vegetation by logging or gardening have paved the way for invading exotic grasses. The two most significant are *Pennisetum polystachyon* and *Panicum maximum*. The former continues to spread rapidly (Figs. 16.7 and 16.26) with increasing land degradation. Associated with these grasslands are two conspicuous woody weeds, *Leucaena leucocephala* (Fig. 16.7) and *Psidium guayava*, which, together with *Muntingia calabura*, rapidly occupy overgrazed and frequently fired lands.

Although many exotic species have invaded the "natural" grasslands of New Zealand, the richer and more diverse flora in Australia has rendered the grasslands less subject to the entrance of invaders. However, the massive invasion of prickly pear (*Opuntia* spp.) in the early 1900s is an exception to this pattern, and more recently other

TABLE 12.5

Summary of tribes in Australia with more than 1% of the total number of grass entities<sup>1</sup>, showing the relative proportion of naturalized exotics (in descending order)<sup>2</sup>

Tribe	Native entities		Naturalized entities	
	No.	%	No.	%
Paniceae	187	68.8	85	31.2
Eragrostideae	154	88.0	21	12.0
Andropogoneae	130	88.4	17	11.6
Danthonieae	107	95.5	5	4.5
Agrostideae	76	77.6	22	22.4
Aristideae	64	100.0	0	0.0
Stipeae	61	92.4	5	7.6
Poeae	55	55.0	45	45.0
Chlorideae	30	75.0	10	25.0
Pappophoreae	20	100.0	0	0.0
Sporoboleae	16	76.2	5	23.8
Phalarideae	15	60.0	10	40.0
Aveneae	8	21.6	29	78.4
Micraircae	8	100.0	0	0.0
Triticeae	4	16.7	20	83.3
Bromeae	1	4.0	23	96.0

<sup>1</sup> Entities include species and infra-specific taxa.

<sup>2</sup> From Simon (1981).

invaders have appeared (Chapter 13). Although Australian grasslands have suffered invasion by native woody weeds, there are some conspicuous exotics. The grasslands of northern Australia are currently being invaded by the Madagascan rubber vine (*Cryptostegia grandiflora*), and in swampy areas in the north-west by *Mimosa pigra*, for which urgent control measures are being sought. Simon (1981) has provided an analysis which shows the relative proportion of the existing grass flora that is made up of naturalized exotics (Table 12.5).

### CONCLUDING REMARKS

The future for grasslands in the region is not promising given the present and likely continuing levels of disturbance. To develop better management tools, a more comprehensive and spatially referenced regional data base is required for inventory and monitoring. This should include response-based models built from a basic knowledge of how grasslands respond to environmental change along local as well as regional gradients.

In this respect a minimum set of biophysical attributes using attributes of plant function as well as structure and floristics should be developed which can be directly related to temporal and spatial changes in the physical environment.

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