On the origin of northern and southern hemisphere grasslands

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Abstract

The origin of the grassy habit during the Eocene and the development of C4 grasses during the Miocene/Pliocene boundary are discussed before the origin of primary and secondary grassland in Eurasia and North America are discussed. A comparison shows that both Northern and Southern hemisphere primary grassland originated due to climatic changes to drier conditions during the end of the Eocene, and that modern grassland vegetation types can be traced back to the Oligocene. The Eurasian steppes becomes more fragmented towards the west and south and relicts of primary grassland exists only in the most xerothermic localised habitats in central and western Europe. Secondary grassland clearly due to manmade deforestation, started with the spread of Neolithic husbandry. Southern African grasslands were however not only determined by droughty conditions, but cooler conditions at high altitudes are one of the major driving forces that prevent colonisation by trees of a generally tropical origin.

Introduction

Temperate grasslands in western and central Europe are associated with human activity, and their origin and maintenance are mostly linked to forest clearing and subsequent management such as mowing, grazing by domestic livestock and even fire (Coupland 1979a; Knapp 1979; Pott 1995). These grasslands are therefore considered as secondary and anthropogenic. Although forests were cleared continuously to the mid-twentieth century, secondary, man-made grasslands were in place since the Pleistocene (Pott 1995). Eastern Eurasian steppes are nevertheless considered climatogenic (Numata 1979; Sochova 1979), as a result of increased aridity during the Oligocene (Axelrod 1972; Tiffney 1984).

Although secondary anthropogenic grasslands do occur in southern Africa, these are limited in extent and distribution. Primary grassland originated through climatic change during the Oligocene and became widespread during glacial events when southern Africa was 5 °C colder than present (Scott et al. 1997, Anderson 1999) and the climate was suitable for the replacement of the former tropical and subtropical forests and woodlands (savannas) by grassland.

The main aim of this paper is to summarize the evidence on the origin of Eurasian steppes, western European grassland, and North American Prairies and to investigate and explain the origin of southern African grasslands, referring to other southern hemisphere grasslands. A further aim is to illustrate differences between temperate steppe and tropical grasslands, emphasizing climate (rainfall/aridity versus temperature) and to discuss their implications.

The early history: Pre-angiosperm xeromorphic vegetation

Well before Angiosperm diversification, fossil records of the Middle/Late Triassic show an increasing diversity of gymnospermous seed plants exhibiting specialised xeromorphic, scale-leafed adaptations in conifers, along with thick-cuticled seeds in seed ferns and cycadophytes as adaptations to aridity (Veevers 1989). Macro- and mega-vertebrate herbivory, which is one of the very powerful evolutionary driving forces to the development of the herbaceous growth-form, can also be dated to this time. Records of these adaptations seem to be associated with the maximum devel-

opment of Pangea, when the coalescence into a large land mass had led to the development of a marked continentality, aridity, extreme seasonality, and probably a monsoonal climatic zonation over large areas in the inner regions of this continent (Kutzbach & Gallimore 1989). Along with processes of accumulation of dry biomass during the dry seasons, with consequent easy ignition by lightning, these environmental constrains seem to have triggered the evolution of a herbaceous or shrubby growth habit among conifers, ginkgoaleans, cordaitaleans and pterydophytes, especially at higher latitudes of both Laurasia and Gondwanaland. Herbaceous ferns (Gleicheniaceae and Matoniaceae) may have been major colonists of the open, dry or even nutrient-poor environments during much of the Mesozoic (in particular sphenopsids and lycopsids were only represented by herbaceous forms during the Triassic), forming vegetation analogous to the savannas or grasslands now dominated by herbaceous angiosperms (Coet et al. 1987). These evidences stress the importance of drought as environmental factor selecting for the reduction of stature in plants and for the achievement of a herbaceous habit.

The grassy habit

The earliest pollen similar to Poaceae or related families e.g. Restionaceae and Cyperaceae, have been reported from the Maastrichtian of the upper Cretaceous and the Palaeocene and Eocene of the Cenozoic (Daghlian 1981; Muller 1981; Linder 1986; Crepet & Feldman 1991). Megafossil remains from the Oligocene are the earliest generally accepted evidence of grasses (Thomasson 1987), though Crepet & Feldman (1991) described fossil spikelets inflorescence fragments, leaves and entire plants from the Palaeocene/Eocene boundary of the Wilcox Formation, western Tennessee. Extant tribes of Poaceae apparently established by the early Eocene. During this time grasses might have had a Gondwanaland origin in north-eastern Australia (Simon & Jacobs 1990), and megafossils of grasses of modern shape are known from some fossil floras dating back to the last part of the Eocene of North America (Colorado) (Lauenroth & Milchunas 1992). Small amounts of grass pollen and fossils of grazing faunas reveal that grasses established under droughty conditions, particularly in dry areas of what is now South America and southern Australia, after climatic deterioration in the Eocene. These drought-stressed patches unfavourable environments

of the early Cenozoic within a forested landscape, formed the scenarios of the emergence of the flora of the modern grasslands.

The achievement of the hemicryptophytic life form was crucial for the development of the modern herbaceous flora of the grasslands. The processes triggering the evolution of weedy herbaceous plants commenced from adaptation to lower levels of nutritional supply, which implies both the syndromes of the adaptation to dry habitats and the adaptation to oxygen poor, water saturated, habitats. Having achieved these traits, helophytic angiosperm ruderals and colonisers (*sensu* Grime 1979) could establish, and successfully compete in these habitats.

The achievement of the helophytic structure is supposedly crucial for the development of the monocotyledons and the modern grassy habit (grasses and sedges). Morphology suggests that monocotyledons might have their closest relatives in the magnoliid helophytic dicotyledonous Nympheaceae. While other basal magnoliid angiosperms are woody, the evolutionary pathway leading to at least some of the monocotyledons palaeoherbs might, therefore, have started from phylogenetically related groups of the Nympheaceae or Ceratophyllales (Bremer et al. 1999).

A characteristic trait for the Poaceae is the intercalary meristem. Since the spread of embryonal parenchyma throughout the stem in angiosperms is observed under low oxygen, water and nutrient supply (epicormy, polycormic stems, resprouting stumps, resprouting lignotubers), intercalary meristems can be interpreted as a manifestation of resistance towards the loss of biomass. This trait is likely to be an adaptation to defoliation by herbivores and wildfires and, ultimately extreme environmental harshness.

This nutrient and oxygen-deficiency adapted, or alternatively, drought-adapted life form among angiosperms, seems therefore to precede the development of traits specialised to withstand disturbance. These adaptations to seemingly contrasting habitats, based on a common anatomic structure, are still apparent in modern taxa. Helophytism is common in Poaceae as well as tolerance to intense drought, often among congeneric species (*Bromus, Poa, Festuca, Calamagrostis*). This makes it difficult to detect whether xerophytism or hydrophytism is primary or derived. The hydrophytic Bambusioideae appeared early in the evolutionary history of the grasses. The same pattern can be detected in the sedges where *Carex* is prevalently a genus of waterlogged habitats, but some of its species in western Eurasia are xero-

phytic, tolerate low temperatures at high elevations and thus belong to the climatogenic grasslands.

On the basis of these adaptive traits, grasses became capable of establishing as dominant taxa in the dry treeless inner part of the continents of the Neogene. Other monocotyledons and dicotyledons were able to spread into the same areas, and withstand the same climatic constrains by developing subterranean cryptophytic organs such as bulbs and rhizomes among forbs and lignotubers among phanerophytes. The development of these adaptations followed basically the same evolutionary pathway. From ancestral monocotyledons of water saturated habitats, they separated early from the lineage of the commelinoids, developing larger, mostly insects-pollinated flowers but converging in the achievement of traits adapted to tolerance of nutrient deficiency and water shortage conditions.

Changes in the carbon isotope ratios of fossil tooth enamel from grazing animals indicate that there was a global increase in the biomass of C_4-grasses at the Miocene/Pliocene boundary (Cerling et al. 1997; Ehlinger et al. 1997). This implies an abrupt and widespread increase in C_4-biomass, related to a decrease in atmospheric CO_2 concentrations below the levels favoured by C_3-grasses. This change occurred earlier at lower latitudes, as the threshold for C_3-photosynthesis is higher at warmer temperatures, while C_4-grasses did not expand as effectively in the cooler parts of the world (Cerling et al. 1997; Ehlinger et al. 1997). A further important observation from this time is the replacement of tropical forest adapted mammalian animals by more open woodland/grassland habitat animals in Pakistan and East Africa. The expansion of C4-grasses at the expense of trees and C_3 grasses (Street-Perrott et al. 1997), accompanied by important faunal changes, was a global phenomena, beginning in the late Miocene and persisting to the present day. It is thought that these changes were not solely due to higher temperatures or the development of arid conditions, as the C_4 expansion was triggered by a single global event, interpreted as the low CO_2 concentrations prevailing at that time (Cerling et al. 1997; Ehlinger et al. 1997).

It therefore seems that although aridity, as an ecological factor, is often considered as a major evolutionary force in generating responses in plants to shift to the herbaceous habit and ultimately to an annual growth habit, low CO_2 concentrations also played a role. C_3 plants were at a disadvantage during glacial times, favouring C4 plants (mainly grasses and a few dicotyledons, especially weeds (disturbed sites) or halophytes (saline sites).

Northern hemisphere grasslands

The origin of Eurasian steppes

The evolutionary adaptation to aridity and morphogenetical trend towards the herbaceous habit persisted across major floristic turnovers during geological times. This can partially explain the dramatic floristic change since the onset of the Cretaceous, which lead to the gradual predominance of the angiosperms. By the Early Cretaceous angiosperms achieved some importance at low palaeo-latitudes (Drinnan & Crane 1990), at that time mainly northern Gondwanaland (Scotese 1997; Anderson 1999; Anderson et al. 1999). They only later spread to the higher latitudes, mainly due to the slow evolution of their tolerance to cold (Brenner 1976). Some fossil assemblages suggest an explosion of angiosperm diversity with a large proportion of early successional, weedy, herbaceous plants (up to 80% angiosperm species pollen) at middle and high palaeo-latitudes at the onset of Late Cretaceous, especially in brackish-or fluvio-lacustrine habitats (Spicer & Parish 1990).

Fossil records are therefore consistent with the idea that the radiation of angiosperms in mid-Cretaceous took place in disturbed or ephemeral habitats (riparian corridors, burned areas), where pioneer, weedy angiosperms were seemingly able to compete successfully. Moreover, coincidence with the recorded increase in relative abundance of large herbivores, (hadrosaurid, ornithopods and ceratopsid ceratopsians), suggests for this period an intense process of co-evolution between animals and weedy angiosperms, in which increased productivity in disturbed sites favoured herbivores, inducing a positive selective feed-back on the fitness of weedy angiosperms habitats (Spicer & Parish 1990).

Later, during the Aptian, a marked equatorial-high latitude floristic gradient established. Angiosperms were more frequent and abundant at lower latitudes in a dry (sub)tropical zone, at that time mainly tropical Gondwanaland (Scotese 1997; Anderson et al. 1999), though gymnospermous forests prevailed in wetter climates in the higher latitudes of northern Laurasia and southern Gondwanaland. At mid-latitudes angiosperms still persisted only as pioneers in disturbed riparian sites as late as in Aptian and Albian. In the

Cenomanian they appeared as under-storey in open gymnospermous forests (Spicer et al. 1990).

Unlike forest, primary steppes are relatively new (Numata 1979; Sochova 1979). The herbaceous habit of the monocotyledons and dicotyledons that dominate the physiognomy of present-day steppes, is the result of selective forces of global environmental perturbations at the onset of the Cenozoic.

While the ancestors of the main taxa that today characterise steppes and open dry woodlands in the old world first appeared at the Cretaceous/Paleogene boundary, increasing abundance and diversity of herbaceous angiosperms in the floras of temperate-latitudes are recorded only later in Cenozoic (Axelrod 1972; Tiffney, 1984). The scenario at the onset of the Eocene was still that of an almost totally forested world dominated by evergreen mega- and mesophyllous angiosperms with some gymnosperms at low and middle latitudes. At the end of the Eocene open, grassy vegetation began to develop due to dry conditions in Eurasian landscapes, previously almost completely covered by forests (Pott 1995).

Modern grassland vegetation types are first recorded from the Oligocene (Anderson 1999). Today these climatogenic grasslands occupy a 800 to 1,000 km range from north to south and a 8,000 km range from east to west in the inner part of the Eurasian continent (Lavrenko & Karamysheva 1993). This extensive, climatically (dry) well defined region is situated between 48° and 57° N, and between 27° and 128° E, from the Amur to the Danube. The grasslands of Eurasia form a continuous belt around a core of desert located east of the Caspian Sea.

The southern Eurasian steppe is more fragmented and floristically more diverse than the northern parts. Contiguity with the alpine tundras and alpine deserts of Tibet and the Himalayas and the contact with the monsoon grasslands of southern Asia (at the fringe of the desert areas of Baluchistan, Arabia and north India), provide opportunity for huge intrusions of stocks of plants from other domains and the establishment of transitional communities between grasslands and the other domains. Their floristic composition ranges, therefore, from temperate in the north to nearly tropical in the south, suggesting a complex ontogeny of the Eurasian grassland communities across time and space.

Due to the disjunct distribution of xerothermic grassland vegetation in western and central Europe, the large distance between typical east Eurasian steppe and western and central European xerothermic grass-land and the large present climatic differences between these regions, it is presently almost impossible for eastern steppe taxa to migrate to central Europe. If such a migration took place, it must have occurred previously, when environmental conditions over eastern and central Europe favoured xerothermic taxa (Pott 1995). The disjunct distribution supports the idea that xerothermic grasslands in western and central Europe are post-glacial relics (Pott 1995). These grasslands must be regarded as remnants of a once much larger territory connecting western and central Europe to the southern and eastern Eurasian regions during subarctic times. During the post glacial period the boundary between forest and steppe shifted, and as climatic conditions became more favorable, forest again expanded, though leaving isolated enclaves of xerothermic grassland as relics of the previously widely distributed steppe. Rocky, gravelly and sandy arid areas resulting from periglacial conditions provided many localities where steppe vegetation could remain and gain the upper hand over woodland vegetation (Pott 1995).

From the Egeo-Anatolian area, westwards all across the Mediterranean regions but especially in the Iberian peninsula, clusters of extrazonal enclaves or relics of primary grasslands occur. These clusters were gradually enlarged by the herds of the first domestic grazers of the early Neolithic in the Middle-East, became coalescent across the Irano-Turanian area (Straka 1970), reaching as far as central Anatolia and the coasts of the Mediterranean. These clusters of primary grassland in some cases might have merged with secondary grassland to form the contemporaneous grasslands of western Europe or served as a vast reservoir of species for colonisation of the newly formed human made open spaces in the place of former forest. On the other hand Le Houerou (1993) is of the opinion that no climax grassland occurs in the Mediterranean region, except perhaps the *Stipa tenacissima* steppes of North Africa and Spain.

Contemporary Eurasian steppe

The Eurasian grasslands are, due to their origin, primary climax biomes or secondary where man has cuased their origin (Sochava 1979). This primary characteristic is conspicuous in the north and east. In western and central Europe prevailing human interference has induced the formation of vast expanses of secondary grasslands in the place of former forest biomes.

Natural, primary steppe today dominates the land-scape across a large corridor in Eurasia, from the lowlands of inner Mongolia, to the northern and west-ern coasts of the Black Sea, encompassed by nemoral and boreal forest biomes in the north, and deserts and semi-deserts in the south. Primary grassland mostly occurs either in arid regions or at high altitudes (Nu-mata 1979; Sochova 1979). While the northwestern and northern parts of the grassland belt borders the deciduous forest biome of eastern Europe, the north-eastern part faces the boreal coniferous forest, the Taiga of eastern Siberia. Typical steppe is normally distinguished by greater aridity (Lavrenko & Karamy-sheva 1993), and always indicate a period of drought, that is not the case in the forest zone (Ellenberg 1988).

These patterns of vegetation are due to the effect of the major north-south thermal gradient. Another pattern of floristic change follows the longitudinal (east-west) gradient, with increasing continentality towards the east, favouring the development and main-tenance of steppe, while oceanic conditions to the west favours the development of forests. In this sense the summer-dry Mediterranean gap is, from the phytocli-matical point of view, a western (Atlantic) aspect of the regions of the steppe.

Although steppes can be found in a wide vari-ety of climates they have some climatic features that distinguish them from other vegetation zones (Ripley 1992). They are associated with semi-permanent ar-eas of high pressure, with greater solar radiation than other locations at the same latitude. Annual precipi-tation is intermediate between forest and true desert (160–1,700 mm average 640 mm), with annual dry seasons up to 8 months, precipitation in the form of showers, often with wind and hail. The uneven dis-tribution of precipitation results in water surplus in the rainy season and a deficit during the dry season. Therefore, primary steppes (and desert) occupy the continental regions where temperature amplitude is greater, the summers are hotter but the winters colder than in oceanic regions of the same latitude (Ellenberg 1988). In eastern Europe the forest zone, forest steppe zone and steppe zone are easily distinguished on a cli-matic basis. Chernozem soils typify true steppes and variation within the zonal types of steppe is related to edaphic properties (Lavrenko & Karamysheva 1993).

Surface radiation exchange and continentality are the most important factors in controlling the climatic patterns in Eurasia. Seasonal variations in mean daily temperature can reach 40° C at higher latitudes in grassland areas of Eurasia, while annual mean pre-cipitation lies mostly within the 200–400 mm range. While precipitation is concentrated during winter in the west (in areas contiguous to the Mediterranean regions), in Siberia a strong precipitation maximum is recorded in summertime (Ripley 1992). Tempera-ture is not as critical as moisture, as is evident in the great latitudinal range of north-south distribution of grasslands in Eurasia. Along with a general pattern of great seasonal and daily ranges of temperature in the north mean monthly winter temperature drop down to $-15\,°C$, while summer temperature in the south may exceed 32 °C. Frost can persist for up to 100 days in the north, but the southern regions are without frost. Temperature is important in delineating the temperate and tropical C_4 grasslands (Ripley 1992).

The grasslands above the tree-line on mountains and highlands from eastern Asia to western Europe, are floristically distinct from the previous primary for-mations. Most treeless areas on these summits are primary grassland communities, even if disturbance due to domestic grazing may be locally heavy. Their lower altitudinal limits, on the other hand, depend mainly upon human disturbance, at the expense of the upper belt of a previous forest. These communities contain species restricted to arctic-alpine communi-ties, scattered on major elevations throughout Eurasia, along with specialised orophytes and species of sub-alpine heathlands. These quite heterogeneous aggre-gations are often endemic to the individual mountain groups. In the mountains of Mediterranean Europe, the arctic-alpine taxa decrease, and the floristic similar-ity with eastern European lowland steppe aggregations increases.

Trees and shrubs in Eurasian steppes

The absence of trees in the steppe biome (Walter 1968) seems to be controlled by macroclimatic aridity and poor soil drainage. Furthermore, macro-mammalian herbivory by herds of wild ungulates and wildfires, caused by high frequency of lightning, enhance the competitive ability of herbs and grasses, prevent-ing the establishment of tree seedlings. Tussocks of drought-tolerant Poaceae (*Stipa, Festuca, Agropyron, Poa, Koeleria, Cleistogenes*) along with Asteraceae (*Artemisia, Tanacetum*) dominate the physiognomy of these climatogenic grasslands. This is not necessar-ily the case in southern hemisphere countries where trees are drought and fire tolerant (Bredenkamp & Van Vuuren 1987; Coetzee et al. 1994).

Although trees are nearly absent in the climatogenic steppe, scanty groves are scattered across the districts with semi-humid climate, in the so called meadow-steppes or forest-steppes, which face the borders of the forest biomes, and which cover large areas in the Pontic steppe province, from the Black Sea to northern Kazakhstan, and areas in western Siberia (Sochava 1979).

Quercus robur stands are scattered in the steppe-forest stands of Ukraine and European Russia, in well-drained catchments along the slopes of large rivers, and along the slopes of ravines in the true steppe zone. *Betula pendula, B. pubescens, Populus tremula* grow in shallow depressions in western Siberian forest-steppes and in the hills of central Kazakhstan. *Pinus sylvestris* is scattered along flood terraces and flood-plains throughout the range of the forest steppe and in the low mountain in central Kazakhstan, while *Larix sibirica* and *L. gmelini* are spread more east, throughout the mountain forest-steppes in Transbaykal and Mongolia.

The importance of bushes (suffruticose Chamaephytes and Mesophanerophytes) increases from northwest to southeast where they occur (*Calophaca, Caragana, Spiraea*) in the steppes rich in dwarf half-shrubs and bunch-grasses of the semi-deserts of Trans Volga-Kazakhstan steppe province and northern Gobi.

These extensive forest-free areas are the refugia for the extant herds of some of the ungulates which roamed from the Iberian peninsula to central Asia during the last pleniglacial, some of which became extinct as late as the last few centuries, such as the wild horses in the west, and the wild bovids, ancestors of the modern cattle breeds (sparse populations of the European Bison survive in Poland). This veritable sea of grasses has linked human groups of different lineages, cultures and languages across immense distances. This is the region where the art of riding is likely to have evolved (donkeys, horses, camels,) and where the oldest ancestors of the wheeled chariots took form. Thanks to this, migration routes were early established and tramped by reiterate waves of centrifugal human invasions over thousands of years.

Secondary anthropogenic grasslands of central and western Europe

Unlike the steppe of central Asia and of the Pontic region in Europe, the grasslands covering large areas in central and western Europe, below the tree-line, are secondary. These meadows and pastures developed during millennia of human deforestation, as a consequence of farming and pastoralism, which started with the first spread of Neolithic husbandry in Mediterranean Europe (Pott 1995). A pronounced floristic similarity with the climatogenic steppes of central Asia, at generic or species level, is evident.

The environmental scenario is, on the other hand very different, displaying climatic conditions favourable to forest growth (Ellenberg 1988). Central Europe would therefore be a monotonous woodland had not man produced a colorful mosaic of cultivated land and heath, meadow and pasture and over centuries continually cut back the forest. Without mans impact only dry salt marshes, coastal dunes, steep rocks and screes, avalanche tracks and areas above the climatic timberline, and mires too wet and too poor in nutrients for tree growth, or too exposed, would be free of trees (Ellenberg 1988; Knapp 1979; Pott 1995). Even poor sandy heaths were successfully afforested, and even the steppe-like grasslands of southern central European limestone mountains revert more or less quickly to scrub and woodland if grazing or burning are discontinued. All meadows and pastures are considered as man-made (Pott 1995). Even the xerothermic grasslands, Festuco-Brometea on calcareous and Sedo-Scleranthetea on siliceous substrates are generally considered as manmade and maintained by grazing and mowing. Their conservation became a problem, as when these vegetation types are not managed, woody species immediately start to encroach and the succession to woodland commences. Only where the soil is very shallow on rocks the soil cannot support woody vegetation. Before man began to influence the vegetation of Europe rock heaths and Blue Moorgrass slopes were the last refugia of light-loving steppe plants, which had been very widespread just after the ice receded and before the forest advanced (Frenzel 1968; Ellenberg 1988; Pott 1995). Since the Late Stone Age they have again greatly extended their range. Secondary dry grasslands that have arisen from former woodland, scrub or ploughed land, differ from primary grasslands in species composition. As the stands age these differences gradually disappear. Many plants of the dry grasslands can spread surprisingly quickly into open new sites, such as rock falls, roadsides, burnt areas and fallow land (Ellenberg 1988).

Other Northern hemisphere grasslands – USA prairies

Prairies are very similar to Eurasian steppes, in that they are considered temperate grasslands, probably climatogenic in origin (Walter 1979).

During the late Mesozoic, (the time of the sudden origin of the Angiosperms (Good 1964)) there was a large oceanic embayment from the south, dividing North America into eastern and western parts. This transgression split the arcto-tertiary landscape into two regions of parallel development, with almost no angiosperm tree species common to the eastern and western United States, though almost all main angiosperm genera are common to both regions. The temperate and tropical mesophytic forests that occupied the region during the Palaeocene and Eocene were replaced by vegetation dominated by drought tolerant grasses and forbs (Dix 1962). This replacement is explained by the rapid and substantial global cooling and uplift of Rocky Mountains during the Oligocene, creating a rain shadow in the short-grass steppe region.

Short prairie

Grasses have been the dominant growth form in the short-grass steppe since the early Cenozoic (Lauenroth & Milchunas 1992). Especially during the Pliocene, North America became drier suggesting that there may have been grassland in the central parts, east of the Rocky Mountains, before the Pleistocene (Good 1964). However, contemporary North American temperate grasslands have few endemics, suggesting that they are fairly recent, and indeed the present Great Plain grasslands developed since the last glacial maximum. This area was probably *Picea* forest before glacial times, though these forests could have replaced earlier Pliocene grasslands. After the disappearance of the forests the episodes of continental glaciation, separated by warm interglacial periods, had a substantial impact on the region. Although the short grass steppe was never under ice, alluvium from melting mountain glaciers contributed to shaping the landscape (Lauenroth & Milchunas 1992).

An analysis of the climate of the main body of grassland east of the Rocky mountains (Borchert 1950) shows the distinctiveness of grassland climate and suggested it to be related to the amount and distribution of precipitation, which is mid-continental, strongly seasonal and as low as 300–550 mm. Evapotranspiration exceeds precipitation (Lauenroth & Milchunas 1992). Under these conditions succession of old fields after abandonment takes 20–40 years to reach the climax grassland though this is thought to be optimistic.

The prairies are situated at an altitude of 1,500 m and precipitation decreases from east to west. Tall prairie, mixed prairie and short prairie succeed one another from east to west with increasing aridity. Temperatures rise from north to south and the prairies extend to a latitude of 30 ° before merging into *Prosopis* savanna in the warmer south. Trees can grow in the prairie region, if the competition from grass roots is eliminated (Walter 1979). Where prairie fires do not occur and where human influence is excluded, forest slowly encroaches upon the prairie. Recurrent drought is undoubtedly partially responsible for the absence of trees in the prairie (Weaver 1954).

The current vegetation is a mixture of plants of northern temperate and southern tropical origin and may be divided at the 35 ° N latitude into a temperate and a subtropical portion (Lauenroth & Milchunas 1992).

Tall prairie

Although the evolutionary roots of tall prairie date back to the middle Tertiary, the modern tall prairie, is not older than 11,000 years (Martin 1975), with tree pollen 10,000–20,000 years old indicating the existence of previous forests. Northern tall prairie developed on terrain that had at least one ice sheet, though southern tall prairie developed on ancient land forms derived from sedimentary formations (Kucers 1992). Warming and aridity resulted in the advance of prairie species eastwards. Entry of grassland was rapid replacing *Picea* forest in the northern parts as the latter retreated northwards.

At 5,000 years ago, under more moist conditions, there was a resurgence of forest. Faunal evidence supports this history of prairie. Particularly in the moister eastern sections fire played an important role in preventing forest invasion into the prairie (Bragg & Hulbert 1976; Coupland 1979b), though some authors suggest that prairie was maintained as a stable entity, whether fires occurred or not (Borchert 1950).

The more tropical coastal prairie on the gulf of Mexico is prone to invasion by *Prosopis* and other woody species especially after the settlement of Europeans due to less fire and more grazing (Kucers 1992).

Fescue prairie occurs at the northern more mesic and cooler perimeter of mixed prairie, on foothills of

mountains (Coupland 1992). Further north trees occupy more and more of the landscape while grassland occupies only the drier sites within the forest.

Southern hemisphere grasslands

General overview

Before the separation of Gondwanaland the climate was moist and warm and supported forest in southern Australia, coastal Antarctica and southern South America even far south of latitudes where forests occur today. Africa and India separated from Gondwanaland before the late Cretaceous, though Australia, New Zealand, Antarctica and South America separated only during the late Cretaceous and developed their unique biotas. The total separation of the latter continents during the Eocene-Oligocene resulted in the development of the circum-Antarctic current, which led to a massive drop in temperatures of the high southern latitudes and caused a major increase in the temperature gradient from the south pole to the equator (Siesser 1978; Scholtz 1985; Scotese 1998). During this time the rainfall decreased and a seasonal rainfall pattern developed over large areas of the southern hemisphere continents.

The late Cretaceous vegetation of high southern latitudes was forest dominated by broad-leaved angiosperm trees, both evergreen and deciduous (Anderson 1999; Anderson et al. 1999). Deciduousness developed due to high latitude photoperiods. A variety of gymnosperms, including conifers were also found in these forests.

Areas of dry climate were not yet widespread in the Palaeocene (Aubreville 1970). This is supported by data from the Tethyan sclerophyll vegetation which appeared only later in the Eocene in southwestern Asia and southwestern North America (Axelrod 1975). In all cases the vegetation was derived from subtropical forests that adapted to drier climate. This is true for northern Africa and southern Eurasia, as well as southwestern North America, and also from southern Africa (Rennie 1931; Axelrod & Raven 1978; Scott et al. 1997).

By the Miocene there was also a dramatic effect of continental drying in Africa, with the expansion of drought resistant, open savanna and grassland and even the development of desert vegetation (Scott et al. 1997). Furthermore, Africa was also affected by cooling, with forest giving way to woodland/savanna, which gave way to grassland, which retreated before the spreading desert. In South America a similar trend of vegetation change took place with open savannas being a relatively late development. In Antarctica dramatic climate change caused almost complete extinction of the vascular flora (Anderson 1999).

Later during the Quaternary the climatic fluctuations caused by cycles of glacial and interglacial events strongly influenced the evolution of plant communities and contributed to the development of modern biomes of the southern hemisphere continents. Data on palaeoclimate during glacial and interglacial events are scanty for the southern hemisphere, the last full glacial circle of the southern hemisphere being recorded from the Vostoc Ice Core from Antarctica (Scott et al. 1997). Likewise long term pollen records from the southern hemisphere, and therefore long term history of vegetation are scarce, with fairly detailed records from only from Australia (Kershaw & Nanson 1993). The fairly long pollen record from the Pretoria Saltpan in South Africa is, however, not continuous. These pollen records show similarities in vegetation changes in southern Africa and Australia over the last full glacial cycle. In both continents it is suggested that temperature and moisture changes were not in phase during the Pleistocene. The lack of correlation between moisture and temperature can be expected if the complex influence of orbital forcing on the earth's climate is considered (Scott et al. 1997). A wide diversity of plant community types can therefore be expected.

The extent to which upland grassland vegetation in southern Africa migrated during the last glacial maximum (500 km; Coetzee 1967; Livingstone 1971; Vincens et al. 1993) is comparable with similar trends elsewhere on the globe. The existing data and comparisons with other continents suggest that the late Quaternary vegetation of the southern African subcontinent responded according to patterns of global change (Scott et al. 1997).

Origin of southern African grasslands

Cretaceous

Through continental drift Africa became geographically and floristically isolated from the rest of the Gondwanaland landmasses by mid Cretaceous times (Smith & Briden 1977; Axelrod & Raven 1978). Global climates at this stage were relatively warm (Shackleton & Kennet 1975). Angiosperms were well

established worldwide, and showed considerable diversity (Penny 1969; Axelrod & Raven 1978; Traverse 1988; Coetzee 1993). Though, the fossil record of angiosperm development and angiosperm dominated vegetation during the Cretaceous is scanty and incomplete, probably because the uplift of the continent restricted lowland areas where fossils could be preserved (Burke & Wilson 1972) and the erosion and climate in the highland interior were not favourable for preservation of fossils (Scott 1995).

The available data suggest that the microfloras conform with those from other southern hemisphere continents (Scott 1976a; McLachlan & Pieterse 1978), with *Clavatipollenites* as the first recorded Angiosperm, while *Nothofagus*, present in the late Cretaceous – early Tertiary in other southerly sections of Gondwanaland, is absent in southern Africa (Scholtz 1985).

Northern Africa, lying over the equator during the late Cretaceous, was then covered by tropical rainforest. As East Africa had not yet been elevated, this forest extended from coast to coast in Palaeocene times (Axelrod & Raven 1978). Macrofossils from the late Cretaceous Umzamba beds in the Eastern Cape show different gymnosperms and primitive Monimiaceae and Euphorbiaceae (Madel 1960, 1962; Klinger & Kennedy 1980), while pollen fossils from Namaqualand indicate a vegetation with trees, lianas, epiphytes, mosses and fynbos taxa such as Proteaceae, Ericaceae and Restionaceae, probably as part of a forest understorey (Scholtz 1985; Scott et al. 1997). These records indicate that the forests might have occurred as far south as southern Africa.

Cenozoic

During this time vegetation in southern Africa evolved into equivalents of the modern biomes (Scott et al. 1997).

The origin of Poaceae in the Eocene, was during the same period when grazing herbivore mammals appeared. Dry woodland and scrub, probably with much grass, originated as early as the Eocene in the southwest of Africa where dry sites were available. From these edaphic dry sites (which still today occur in the tropics) dry-adapted taxa could then spread as regional climate became drier (Axelrod 1970, 1972).

By the Oligocene grasslands became a widespread vegetation type in southern Africa (Anderson 1999). The co-evolution of the grasses with grazers, and explosive radiation of Artiodactyls and their dependent carnivores, along with the evolution of grasses during the Miocene is a remarkable case of symbiotic co-evolution. The grasses are well adapted to defoliation by both herbivory and fire: they generally do not have chemical defences while intercalary meristems at base of leaves ensure continued growth after top parts of leaves were removed (Anderson et al. 1999).

During the Neogene (Miocene, Pliocene Pleistocene) southern Africa experienced considerable climatic change. Major tectonism elevated the southern African central Highveld at the end of the Miocene (King, 1963, 1978; Gough 1973; Newton 1974) and further major uplifts raised the interior plateaux to form the high-altitude mountains of the Great Escarpment on the eastern side of the subcontinent and the extensive interior plateaux (1,400–3,000 m) that forms the greater part of the South African landscape (Partridge 1997). This steepened the coastal monoclines by hundreds of meters (Baker & Wohlenberg 1971). This uplift not only modified the topography, but also the climate of the region, bringing cooler and drier conditions. Old stable ecosystems were restricted and then replaced by new ones that were expanding as a broad belt of progressively drier climate spread over areas previously covered with forest and savanna woodland (Axelrod & Raven 1978). Savannas and woodlands replaced forest. The development of rain shadows in the rift valleys favoured the spread of savanna woodland and eventually grassland. Furthermore, Antarctica parted in the late Oligocene (Kennet & Houts 1974), shifted to its polar position, developed an ice sheet, the cold Benguela current commenced and brought cold water to the west coast of Africa. (Shackleton & Kennet 1975; Van Zinderen Bakker 1975; Coetzee 1978a, b). This brought increased drought over the former moist west coast of Africa.

The increasing drought was further intensified by later global changes in palaeogeography which inhibited movement of moist air into Africa, e.g. the destruction of the Tethys sea by the union of Arabia with Iran during the middle Miocene which changed the major latitudinal system of circulation (Crowell & Frakes 1970). These changes together with the closure of the Panamanian portal, the formation of the Mexican plateaux, and the uplift of the Andes and Eurasian Alps caused that the anticyclones in the lower middle latitudes became progressively stronger and more persistent and dry climates increased in area (Axelrod & Raven 1978).

There was therefore an even more intense selection for drought-resistant vegetation, thus restricting forest even further at the expense of savanna, grass-

land and scrub (Axelrod & Raven 1978). These entire ecosystems spread rapidly as dry open environments expanded in the late Pliocene and Pleistocene (Axelrod & Raven 1978). The spread of a seasonally dry climate also confined montane rainforest to sheltered ravines over the interior where there was adequate moisture, causing discontinuous forest.

During this period hominid genera appeared in the African interior (Coetzee et al. 1983; Coetzee & Muller 1984; Hendey 1984; Klein 1984; Vrba 1985; Scott 1995). From the interior summer rainfall plateaux, the present location of the grassland biome, fauna fossils from hominid-bearing breccias of 3 million years of age indicate that the vegetation changed from dense woodland to more open vegetation around Pliocene times (Vrba 1985). Pollen in deposits from Kromdraai and Sterkfontein suggest that open *Protea* savanna occurred (Scott & Bonnefille 1986; Scott 1995), which is quite similar to the *Protea caffra* dominated communities and which are presently widespread on the hills and ridges over the entire range of the Bankenveld (Acocks 1953; Bredenkamp & Theron 1978, 1980; Behr & Bredenkamp 1988; Bezuidenhout et al. 1994). Contamination from modern vegetation can however place a question on some of these results (Scott 1995).

Scott et al. (1997) conclude that the early types of fynbos, semi-arid shrublands and desert vegetation only became established by the end of the Miocene, more or less at the same time as modern communities on other continents.

Quaternary

During the Quaternary marked shifts in modern biomes occurred in response to glacial-interglacial changes in climate. No single palaeovegetation record for the entire Quaternary exists, but shorter pollen profiles confirm this pattern (Scott et al. 1997). Pollen records from Soutpan near Pretoria and Port Dunford suggest that although modern biomes were well established during the Quaternary, and probably before, marked cycles of vegetation change occurred during this period, which resulted in wide shifts in biome composition and boundaries (Scott et al. 1997). These were apparently driven by fluctuations in temperature, precipitation and seasonal distribution patterns of moisture.

During Pleistocene interglacial periods the forest expanded again, pushing sclerophyllous vegetation northwards into the present Karoo and Namib where relicts are still present today. Such a shift parallels the shift of pinyon pine and juniper into the present deserts of western North America during the last glacial (Wells 1966; Wells & Berger 1967).

Pollen data from different parts of southern Africa from deposits between 40,000 and 75,000 years BP provide indications that forests were more widespread under much improved moisture conditions (Scott et al. 1997). During the last Glacial Maximum period, 18,000 years BP, vegetation belts were generally lowered by about 1,000 m in altitude, responding to a drop of about 5 °C. In addition to lower temperatures or glacial aridity, lower CO_2 concentrations during glacial times, in addition to climate, had a significant impact on the distribution of forests on the tropical mountains of East Africa (Street-Perrott et al. 1997), and probably also southern Africa. The ecophysiological effects of this large decrease in the CO_2/O_2 ratio would have disadvantaged almost all trees and shrubs due to increased respiration and physiological drought, while the competitive advantage shifted to C_4 grasses at all elevations in the tropics (Cerling et al. 1997; Ehlinger et al. 1997; Street-Perrott et al. 1997). The Last Glacial Maximum is marked by an abundance of grass pollen, including C_4 grasses, in association with ericaceous shrubs, indicating a treeless grassy heathland (Street-Perrott et al. 1997).

A survey of the distribution of grasses in South Africa shows that C_3 and C_4 species are markedly separated geographically, with C_4 species more abundant over most of the country, indicating warmer conditions, and C_3 species predominant in the winter rainfall region of the Western Cape and also on the summits of the Drakensberg and other mountain ranges (Vogel et al. 1978), indicating that the lower temperatures prevailed at these higher altitudes favouring C_3 species (Cerling et al. 1997; Ehlinger et al. 1997; Street-Perrott et al. 1997).

Studies on isotopes in grazer animal bones indicate that C_3 plants were utilised by animals living in grasslands during the late Pleistocene (Vogel 1983), and this could be related to the lowering of upland grassland, due to colder conditions, or to changes in CO_2 concentrations. Highland Mountain Fynbos at Clarens probably migrated to lower elevations during the last Glacial Maximum (Scott 1989). The spread of cold grassland during glacial periods is confirmed by presence of shrubby fynbos elements among grass pollen (Van Zinderen Bakker 1983; Street-Perrott et al. 1997).

Precipitation rates fluctuated considerably from the end of the Pleistocene (25,000–10,000 years BP), reaching low levels at 18,000 years BP. Though, with cooler temperatures evaporation rates declined, resulting in greater effectiveness of the (low) rainfall. In general temperatures decreased since 14,000 years BP, while precipitation increased. Rainfall declined markedly at the start of the Holocene, but about 7,000 years BP the biomes began to reflect modern conditions, though smaller fluctuations continued until recently.

Evidence from grassland ecotones with other biomes

Grassland-Karoo ecotone

Karoo shrubland seemed to have had a much wider distribution than at present by the end of the Pleistocene, being recorded from the southern Kalahari at 10,400 years BP (Scott 1987). At Aliwal North, in an area presently bordering on grassland, spring deposits show a cycling between grassy and karoo vegetation at the end of the Pleistocene (Coetzee 1967), though with more grassy vegetation. The western boundary of the grassland biome was further west (into the present Nama-Karroo) during the favourable conditions of the late Holocene (4,000–1,000 years BP), when grassland was very well developed in the transitional area at Deelpan and Alexanderfontein in the Free State (Scott 1976b, 1988; Scott & Brink 1992).

Younger Holocene spring deposits at Badsfontein (Scott & Cooremans 1990) and Blydefontein were characterised by relatively low proportions of grassy pollen, but grasses in the vegetation returned by the middle Holocene (Bousman et al. 1988; Scott 1993). Pollen from the Nuweveldberge (Sugden & Meadows 1989) indicate shifts between mountain grassland and karroo.

Hydrax middens from Blydefontein near the Nuweveldberge indicate progressive replacement of grass by shrubby Asteraceae during the last 400 years (Scott & Bousman 1990; Bousman & Scott 1994). This deterioration started before the advent of modern grazing practices and was initiated by climatic change, though overgrazing may have exacerbated the process.

In general palynological evidence suggest that karroid shrublands were well established and more widespread in the interior of South Africa during the late Pleistocene (Scott et al. 1997). More grass occurred in the region since the middle Holocene, but the grass to shrub ratios continued to alternate. Before the arrival of farmers with domestic livestock these shifts were caused by climatic change, though contemporary changes are influenced by both climatic and land management.

Grassland-savanna ecotone

Because of downward shifts of zones during glacial events, Highveld grassland types expanded regularly at the expense of woody vegetation. Pleistocene pollen records from woodland vegetation outside the present grassland biome at Wonderkrater, Equus Cave and Pretoria Salt Pan suggest that grassy vegetation occupied a much greater area to the north during past cooler episodes (Scott 1982b, 1987; Partridge et al. 1993).

During a climatic optimum in the mid-Holocene (7,000 yrs BP) on the northern boundary of the main Highveld region, bushveld vegetation temporarily spread southwards over the edge of the plateau at Rietvlei Dam near Pretoria (Scott & Vogel 1983).

Data suggest that vegetation altered markedly ranging from woodland savanna during warm interglacial phases, to cool open grassland, with fynbos elements, during glacial maxima, and even to mesic woodland with *Podocarpus* forests during some intermediate phases (Scott 1982a, 1982b; Partridge et al. 1993). Charcoal in the Pretoria Saltpan sequence indicates that phases of more intense fire occurred in the bushveld environment in the past (Scott 1995) though since the last interglacial denser bush cover does not coincide with charcoal abundance, suggesting that fire frequency is not dependent on vegetation type (Scott et al. 1997).

Grassland-forest ecotone

Records of forest history in the interior provide evidence of much wider distributions of forest patches during the Pleistocene. After the last interglacial phase *Podocarpus* was very prominent, in contrast to the present situation where numbers of Gymnosperms are low (Van Daalen et al. 1986). Certain periods of favourable climate with increased rainfall and cloudiness in the Late and Middle Pleistocene provided the opportunity for forests to establish on extensive areas on mountains, e.g., the Waterberg, and even at places such as Wonderkrater and Pretoria Saltpan (Scott 1982b; Partridge et al. 1993), now savanna biome. During the last 180,000 years the size of the forest patches fluctuated considerably (Partridge et al. 1993).

Forests were well developed before the last glacial maximum and occurred in areas devoid of forest today (e.g., KwaZulu midlands, Botha et al. 1992). During the Last Glacial Maximum forest patches survived in protected mountain valleys in the interior plateaux. In the high Drakensberg temperatures were too low for their survival, though amelioration of temperatures and moisture after the Last Glacial Maximum forest must have spread up the lower mountain ravines of the Drakensberg range, and must have been more widespread than today. Forests in mountain ravines were reduced during the early Holocene due to aridification (Scott 1982b). Over this time they persisted in more favourable environments (such as Tate Vondo in the Zoutpansberg), and in the late Holocene started to spread again, but never reached the same proportions as during the Middle and Late Pleistocene.

Anthropogenic grassland

Early Iron Age people lived in the north and the east of southern Africa (Maggs 1984; Thomas & Shaw 1991; Hoffman 1997) in the savanna biome. Here they had a great influence on the vegetation where they cut trees for wood fuel for the iron furnaces (Van der Merwe & Killick 1979). This extensive clearing of the bottomland savanna has left its mark on many savanna area of today, especially in KwaZulu-Matal and Mpumalanga Lowveld areas. The wilderness status of KwaZulu-Natal nature reserves has been questioned, since a set of secondary successional pathways may explain the structure and composition of the contemporary vegetation (Feely 1980; Granger et al. 1985). The transition from Early to Late Iron Age towards the end of the first millennium AD is marked by dramatic cultural, agricultural and economic developments, with concomitant changes to the disturbance regime of the savanna and grassland biomes at both landscape and regional scales. Settlements were shifted from bottomland sites to hilltops with greater reliance on stone materials for hut and wall construction (Maggs 1984; Hall 1987). The interior treeless grassland, also those west of the escarpment were colonised for the first time during the late Iron Age. There were clear preferences for savanna/grassland ecotone sites. The sourveld grasslands of the Free State at the base of the Drakensberg were avoided (Maggs 1984).

Anthropogenic influences were mostly concentrated at the lower altitudes below the escarpment, where it was warmer and where trees for firewood were available in the savanna biome. Many of these

sites are now open treeveld with *Acacia sieberiana* or *A. karroo*, and very often is the grass layer dominated by *Hyparrhenia hirta*, a grassveld type often considered to be secondary (Moll 1967; Eckhardt et al. 1996).

The high altitude plateaux contained primary grassland, too cold for the early human inhabitants of southern Africa, already in place in the Pleistocene and already treeless.

Data from different areas (Inyanga mountains in Zimbabwe (Tomlinson 1974), KwaZulu-Natal and Lesotho Drakensberg (Van Zinderen Bakker 1955), central Free State (Van Zinderen Bakker 1989), and Eastern Cape (Bousman et al. 1988; Meadows & Meadows 1988) suggest that the grassland biome occupied roughly the same area during the Holocene as it does today, but some movement of its boundaries is indicated. Apart from temporary boundary shifts (Scott & Vogel 1983), pollen data from several sites support the view that grasslands have essentially been in place throughout the Holocene, and that they were often more widespread during the Pleistocene. The view (e.g., Acocks 1953) that Afro-montane grassland is the result of forest clearance in the recent past is not substantiated (Meadows & Linder 1993). Human influence on grassland as a result of agricultural or forestry activities is restricted to the very late Holocene.

Contemporary southern African grasslands

Most contemporary southern African grasslands are considered to be primary. Climax grasslands are those that remain treeless in the absence of man (Tainton & Walker 1993). Although some authors consider savannas merely as grasslands with trees (e.g., Beard 1953; Moore 1970; Misra 1979), a clear distinction is made between the savanna and grassland biomes of southern Africa (Rutherford & Westfall 1986; Low & Rebelo 1996) mainly on basis of climate and floristic differences. The hypothesis that southern African grasslands were anthropogenically derived and maintained by fire is now generally discounted (Bredenkamp & Van Vuuren 1987; Meadows & Meadows 1988; Ellery & Mentis 1992; Meadows & Linder 1993; Coetzee et al. 1993, 1994).

In South Africa temperature decreases with increasing latitude, but is influenced by the high altitude eastern escarpment and mountains. Rainfall generally decreases from this eastern escarpment where precipitation is > 1,000 mm per year, westwards to the west

coast where desert conditions prevail and the rainfall is 100–200 mm per year. Because natural grassland occurs along a climatic gradient between desert and forest, it has many contacts with various other vegetation types (Coupland 1992). Southern African grassland borders on warm, moist savanna to the north and east and warm, dry savanna to the northwest. To the south and southwest it borders on cool, dry semi-desert karoo scrub. Afromontane forest occurs as isolated islands in sheltered and moist ravines scattered in eastern grassland zone of the Great Escarpment, while Fynbos enclaves occur on the higher mountain summits within the grassland zone (Rutherford & Westfall 1986).

The extent of the grassland biome is limited by climatic factors (Rutherford & Westfall 1986) and is distinguished from neighboring biomes by the number of days with sufficient soil moisture for plant growth, the mean temperature of such days and the mean temperature of days too dry for growth to occur (Ellery et al. 1992; Bredenkamp 1999). Grassland has a longer growing season (higher rainfall) and higher temperatures during the non-growing season than karoo, lower seasonal rainfall than forest and lower temperatures during the non-growing season than savanna. The Fynbos is unique in having a winter rainfall regime, as opposed to summer rains in the entire grassland biome area.

Topography often determines microclimate e.g., cooler higher altitudes, or soil type, e.g., clay soils in bottomlands. Fire and grazing are secondary determinants, not independent from climate.

The distribution of the major grassland types in southern Africa follows an altitudinal (temperature)/rainfall gradient. The high altitude ($> 2,000$ m), low temperature, high rainfall (> 800 mm) eastern escarpment mountains are covered by temperate Afroalpine or Afro-montane grassland (White 1978), with a great proportion C3 grasses and which also shows affinity to European grasslands through the dominance of *Festuca* bunch grasses and many alpine-like cushion plants. These areas are too cold for trees. The eastern and central plateaux of mid-altitudes (1,500–2,000 m) have warmer temperatures but lower rainfall (500–800 mm) and are covered by the widespread *Themeda triandra* dominated grasslands, with almost exclusively C4 grasses. These areas are also too cold for the (sub)tropical savanna trees. The western areas of lower elevation (1,400–1,500 m) are warmer and drier (< 500 mm) and carry open bunchgrass communities dominated by *Eragrostis lehmanniana* or *Stipagrostis*

uniplumis, transitional to Kalahari dry savanna vegetation or karoo, dominated by dwarf scrub (Tainton & Walker 1993; O'Connor & Bredenkamp 1997).

The climate of the Tall Grassland (Acocks 1953) on the continental terrace east of the Great Escarpment, at mid-altitudes (1,200–1,400 m) and high rainfall (850 mm) areas, is suitable for (sub)tropical trees, and this grassland is considered to be secondary. It probably developed under the influence of early Iron-age people who lived in those areas (Feely 1980; Maggs 1984; Thomas & Shaw 1991; Hoffman 1997).

Satellite grasslands are extrazonal patches of grassland within the zones of other biomes, especially savanna to the north and north-east and karoo to the south and southwest. Satellite grasslands in savanna are restricted to distinctive topographic-geological situations with specific soil conditions (O'Connor & Bredenkamp 1997). Grassland occur on plateau summits of hills and ridges, at altitudes too cool for the surrounding zonal savanna (Bredenkamp & Van Vuuren 1987; Coetzee et al. 1994) or they could be edaphically determined, especially in areas that are seasonally flooded or having a seasonally high water table. Examples are the grassland on the black vertic clayey soils of seasonally waterlogged dambos in Zambia (Zieger & Cauldwell 1998), the open parkland on black clays in Tanzania and the grassland communities on black vertic soils derived from gabbro in the Kruger National Park, South Africa (Bredenkamp & Deutschlander 1994). In all these areas the flat plains with black vertic clay soil are covered by grassland while adjacent slightly more elevated areas are not flooded and have deep red sandy loam soils, covered with woody savanna vegetation.

Patches of grassland in karoo occur on higher altitude escarpments where they intercept more precipitation than their surroundings (Palmer 1989), or on areas (Bushmanland) where the (clayey) soil is covered by a Aeolian sand layer (Palmer & Hoffman 1997).

Likewise patches of savanna and karoo can occur as satellites in the grassland biome where local environmental conditions would allow this (e.g., protection against frost or differences in soil types). (Bredenkamp & Theron 1980; Coetzee et al. 1994; Bredenkamp & Bezuidenhout 1990).

Although the role of fire in shaping grassland and savanna communities all over Africa is not denied, and fire indeed played a major role in the evolution of grassland and savanna taxa (Bredenkamp & Van Vuuren 1987), the fire regime does not differ in grass-

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land as opposed to savanna and savanna tree species are adapted to survive fire (Coetzee et al. 1994). Fire frequency and intensity can however cause shifts in the species composition of some grassland and savanna communities (Bond 1997). However, the boundary between grassland and forest communities on the Great Escarpment indicates that fire does play a role in determining forest/grassland boundaries (Midgley et al. 1997).

Grazing by wild herds of antelope and domestic stock influences grassland and may cause deterioration and even a shift in biome boundaries, especially towards the drier karoo biome (Acocks 1953), or to the encroachment of savanna species in areas transitional to savanna, when the grassy layer deteriorates and woody species seedlings get a competitive advantage. These changes seem to be short term and the trend may be reversed when conditions are again favorable for grassland.

Grasslands in southern Africa have an exceptionally high biodiversity. (Cowling & Hilton-Taylor 1994). South African hotspots for biodiversity and endemism include grassland areas in the Wolkberg (Matthews et al. 1993) and large portions of the Great Escarpment (Davis & Heywood 1994). This could indicate that they are quite old, and confirm their primary status.

Why are there no trees in the southern African grassland?

The absence of trees in the Eurasian primary grasslands can be explained by an aridity gradient. Where conditions become too dry, the forest and woodland give way to grassland. Trees are often found in river valleys or flood plains within the steppe zone where the moisture regime is more favourable for tree growth. This is also the case in temperate North American Prairies where the moister tall prairies being prone to invasion of trees from the neighbouring woodland.

In southern Africa the situation is different. Although forest tree species are excluded from the grassland zone due to aridity, the tropical and subtropical savannas contain a large variety of trees that are well adapted to the dry conditions. The rainfall gradients in southern African savannas and grasslands do not differ much, the eastern grasslands being even moister than many of the savanna types. Fire also does not exclude trees from the grassland biome, as the fire regime is similar in the adjacent savannas and grasslands and

savanna trees are well adapted to fire (Coetzee et al. 1994).

It has already been shown that clayey vertic soils seasonally flooded and with impeded drainage can also exclude trees due to swelling, cracking clays that are inimical to tree root growth. This is however a typical azonal situation, found only in limited patchy areas over the grassland biome.

It does however seem likely that the Tall Grassland east of the Great Escarpment is secondary and that the trees were greatly reduced by Iron Age people.

The widespread tropical forests of the Cretaceous and early Cenozoic retreated, not only due to increasing aridity, but also due to strongly decreasing temperatures associated with frost, especially due to the high altitudes resulting from the continental uplift during the Cenozoic. Angiospermous trees in southern Africa are of tropical origin, as are the gymnospermous *Podocarpus*. Other gymnosperms are rare and special cases (Cycadales, *Welwitschia* and *Widdringtonia*). There are no cold-adapted deciduous or evergreen angiosperm or gymnosperm trees indigenous to southern Africa. The angiosperms of the nemoral and boreal zones originated or survived in the northern hemisphere and its elements never occurred wild in southern Africa (Scotese 1997; Anderson et al. 1999).

It seems, therefore, that it is not an aridity gradient that excludes trees from the grassland areas. Altitudinal gradients often show gradients from savanna on the lower lying areas to grassland on the high altitude summits of hills, ridges and mountains. The cooler climates, especially during the non-growing dry season (winter) of the grassland areas exclude the subtropical trees from these higher altitude areas.

Many cold and frost tolerant tree species from the northern hemisphere and Australia do grow well when planted in the grassland areas (e.g., *Betula pendula, Eucalyptus camaldulensis, Platanus acerifolia, Populus alba, Quercus robur*), and some even become encroaching weeds causing serious problems (some *Pinus* spp and some Australian *Acacia* spp e.g., *A. mearnsii* and *A. dealbata*). However, indigenous trees from the savanna or forest biomes do not survive when planted, they are killed by the winter frost. Another important aspect is that this grassland, when not managed, does not at all revert to forest. Successional processes in degraded (ploughed, or overgrazed) grassland are slow, often developing to species poor *Hyparrhenia hirta* dominated secondary grassland, which is totally different from the climatic climax grassland. In transitional areas to the

savanna, degraded grassland may however be prone to encroachment of the woody *Acacia karroo* (Friedel 1987).

Very limited indigenous woody species are able to grow, under certain circumstances, in the grassland biome. *Acacia karroo* is the typical example, which contains a variety of forms (ecotypes) and therefore a variety of genotypes. This species is furthermore considered as a pioneer in the succession of many savanna communities. It seems that this species is a forerunner in the evolution of woody species of tropical origin, to adapt to the colder conditions prevailing in the grassland biome. This species will however not encroach into primary grassland in good condition, though may become established in areas degraded by overgrazing or other human influences (Friedel 1987; Bezuidenhout & Bredenkamp 1990).

Other woody species that may also be forerunners in the evolutionary trend to adapt to the colder conditions are *Cussonia paniculata, Diospyros lycioides, Dombeya rotundifolia, Euclea crispa, E. undulata, Rhus pyroides* and *Tapiphyllum parvifolium.*

It therefore seems that a major difference between temperate steppe of the northern hemisphere and sub-tropical/temperate grasslands of southern Africa is coupled with the causal factors excluding trees. While aridity excludes cold resistant trees from temperate steppe, low temperatures (with frost) exclude trees of tropical/subtropical origin from the high altitude temperate grasslands.

Other southern hemisphere grasslands

South America

The South America Pampas are similar to Eastern European steppes – as opposed to tropical grassland (Walter 1979). The Pampas is situated between 38° and 32° S, with 500–1,000 mm annual rainfall and with quite high temperatures (16.1 °C average in Buenos Aires). This seems to be a marginal climate which appears barely wet enough for forest growth, but due to windy conditions and underestimation of Potential Evapotranspiration may be even drier (Soriano 1979). Soil salinization and formation of pans throughout the Pampas region suggests that the climate may recently have been drier than commonly thought. Burning of the vegetation by early local inhabitants may have tipped the balance towards the tall tussock grassland reported by early European settlers. On the other hand, it may simply be a relict

of drier Pleistocene conditions. Prieto (2000) indicated that late glacial vegetation consisted mostly of psammophytic steppe in large areas of the central and south-western Pampa grassland, associated with a shrub steppe in the southwest, indicating sub-humid-dry to semi-arid climatic conditions. The repacement of dry steppe by humid grassland during the early Holocene suggests a shift towards more humid climatic conditions (Prieto 2000). In tussock grasslands with a negative water balance from 100–700 mm, and with hard, bare ground between the tussocks, it may by difficult for trees to become established. Planted trees grow well. The absence of trees in the Rio de la Plata region is also to be sought in climate, with negative water balance during part of the year and the competitive ability of grasses under these conditions contributing to the dominance of grassland. The fine textured soils and summer drought are further causes for the absence of trees (Soriano 1992).

In southern Brazil the large spatial scale seasonal and annual climate fluctuations cause water deficits that prevent the dominance of forest in some regions. On the small scale water deficit is aggravated or moderated by local heterogeneity in geomorphology and soil. Interactions of water budget with current vegetation cover, fire and grazing explain observed vegetation patterns and grassland-forest boundaries (Pillar & De Quadros 1997). The contemporary Pampas are greatly destroyed and replaced by European grasses as planted pastures.

Savannas of tropical South America are completely edaphic, although they are frequently burned, it is not considered to be the primary causitive factor. Fire is however responsible for the presence of many fire resistant species (Beard 1953).

Grasslands of Australia, New Zealand, Oceania and Subantarctic Islands

In Australia latitudinal effects are modified by concentric zonation of rainfall, and geology from ancient to younger land surfaces from east to west. Moore (1970) classifies the grasslands on basis of temperature (tropical-temperate) and moisture (humid-arid). Specht (1970) showed that grassland tend to be on the more fertile soils and scrub and tree communities on the infertile soils. Vast woodland savannas also occur in Australia.

By the end of the Cretaceous Australia was isolated from the rest of the Gondwanaland elements, so the vegetation has had a long period of evolution in

isolation (Coaldrake 1979). Grasses might have had a Gondwanaland origin in north-eastern Australia (Simon & Jacobs 1990), probably in the Eocene. The major floristic elements were well established by the start of the Cenozoic, and grassland probably became established under the Oligocene, due to increase of aridity and decrease of temperature. Light grazing by marsupials and increased natural fire, also used by primitive man, further influenced grasslands during the Quaternary. Xerophytic hummock grassland (spinifex) became the most extensive. Alpine tussock grassland occur in the south eastern corner of the continent, above an elevation of 1,500 m and extending lower to areas subject to cold air.

Many grasslands now seem to be disclimax, the original dominants e.g., *Chrysopogon* and *Eragrostis* being replaced by *Triodia* under combined influence of increased burning and grazing by domestic livestock. These grasslands may therefore be considered as secondary and succession may revert them back to the climax. Many of the temperate grasslands are now degraded through grazing or converted to pasture through introduction of exotic grasses and legumes and fertilizer (Coaldrake 1979).

Absence of trees are due to fine textured soils, waterlogging or very low temperatures in subalpine areas (Moore 1993). In some cases forest was converted to grassland by Maoris.

The New Zealand vegetation history is also linked to Gondwanaland, and though a persistent temperate to subtropical forest covered the area throughout the Cenozoic, grasses appeared in the Eocene (Mark 1992). Grassland vegetation developed as a combined result of Kaikura orogeny during Pliocene climatic deterioration which culminated in Pleistocene ice ages. The present grasslands occur in Alpine regions or in rainshadow areas. The rainfall in the New Zealand Alps, situated 40° S, is 300 mm. Fire and grazing were the agents causing expansion of this grassland to areas previously occupied by *Nothofagus* forest.

Uncertainty surrounds the origin of the grasslands of Oceania (Gillison 1993). The very long history of human utilization has had a very great influence. Historical climatic fluctuations, especially oscillatory glaciation influenced the establishment and maintenance of grassland. Fire and man have contributed to the spread of grasslands.

Subantarctic Islands are mostly volcanic in origin from Tertiary or Quaternary. The glaciation affected these islands, some are still heavily glaciated. The climate has been constant for about 10,000 years and the floristic composition has been fairly consistent since the last glacial period. There have however been local post-glacial fluctuations in the relative position of the plant communities since the last major warming began (Van Zinderen Bakker 1970). Many of the grasslands in the sub-antarctic convergence are influenced by consistency of cool maritime climate, constant high winds and additive nutrients from sea birds and animals.

Concluding remarks

Southern African grasslands are primary and climatically derived. Tropical forest was replaced by open subtropical woodland (savanna) due to increased aridity and this woodland was replaced by grassland during the Eocene and Oligocene due to decreased temperature caused by continental uplift. In this sense southern African grasslands should be considered as temperate vegetation in a subtropical zone, due to its high altitude, comparable to the European alpine grasslands above the tree-line. The altitude of the tree-line in southern African vegetation varies with latitude, though is about at 1,600–1,800 m in the northern parts (25° S) and at 1,200–1,300 m in the south (31° S). Many endemic species, specialised orophytes, are restricted to primary arctic-alpine communities, scattered on major elevations throughout Eurasia. This is also the case with the high altitude grassland in southern Africa (Matthews et al. 1993).

Grassland, therefore, differs from the subtropical savanna on basis of climate and vegetation. Grassland has lower temperatures than savanna (with severe frost), during the non-growing season (winter). The vegetation of the two biomes differs structurally and especially floristically.

Whereas the absence of trees in the Eurasian steppes (Walter 1968) and North American prairies (Borchert 1950) seems to be controlled by macroclimatic aridity and insufficient drainage in the soil, trees are absent in the southern African grassland due to low temperatures and frost during the dry season. The trees present in the savannas are of (sub)tropical origin, no cold-tolerant trees such as the species of the boreal and nemoral zones of the northern hemisphere occur in southern Africa. Cold resistant tree species from these areas and from Australia do grow well when planted, exemplified by extensive plantations of *Eucalyptus* and *Pinus* in the eastern higher rainfall grassland areas. Trees can grow in the North American

prairie region, if the competition from grass roots is eliminated (Walter 1979). Where prairie fires do not occur and where human influence is excluded, forest slowly encroaches upon the prairie. Recurrent periods of drought are undoubtedly partially responsible for the absence of trees in the prairie (Weaver 1954). The contemporary trees in southern African savannas are well adapted to dry conditions and seasonal rainfall, as these conditions prevail in almost all southern African savanna areas. These conditions would not inhibit their spread into the grassland. Angiosperms were initially important at low palaeo-latitudes (Drinnan & Crane 1990), and only later spread to the higher latitudes, mainly due to the slow evolution of their tolerance to cold (Brenner 1976). This confirms the statement of Good (1964) that in plant geography temperature is more fundamental than rain and the distribution of taxa is predominantly dependent on temperature (frost line). It seems that this slow evolution is also applicable to modern angiosperm trees of the savanna biome. Very few savanna tree species achieved tolerance against the cold, dry conditions prevailing in the grassland biome, one being *Acacia karroo* which is considered as a forerunner in the invasion of trees into the grassland biome area. This invasion, furthermore, only occurs when the grassy layer deteriorates due to overgrazing or other destructive human influences (Friedel 1987), indicating that *Acacia karroo* should be considered as a pioneer woody species, capable of establishing in disturbed areas.

Although trees are nearly absent in the climatogenic Eurasian steppe, scanty groves are scattered across the districts with semi-humid climate, in the so-called meadow-steppes or forest-steppes, which face the borders of the forest biomes. These areas are transitional. In transitional areas between southern African high altitude grassland and lower-lying savanna, a mosaic of grassland and savanna communities are found. Local variations in topography result in a variety of microclimatic conditions representative of both biomes. The exposed sites are covered with grassland and the savanna in sheltered situations, protected against extreme cold temperatures and frost. Studies of the gradients in these transitional zones facilitated interpretations of grassland and savanna determinants (Bredenkamp & Theron 1980; Coetzee et al. 1994). Palynological studies revealed shifts in the boudary between these two biomes, corresponding to changes in temperature during glacial and interglacial times (Scott et al. 1997).

The grasslands that presently occur at lower altitudes are either secondary, e.g., east of the Great Escarpment in KwaZulu-Natal or the Eastern Cape (former Transkei) where they replaced savanna due to human activity, or they represent extrazonal enclaves of grassland in other biomes due to soil differences or flooding. These grasslands are subtropical, dominated by C_4 grasses (Vogel et al. 1978) .

In Eurasia and North America macro-mammalian herbivory by domestic livestock or herds of wild ungulates enhances the competitive ability of herbs and grasses, preventing the establishment of tree seedlings. In southern African savanna the deterioration of the grassy layer due to grazing will enhance the establishment of woody species and will lead to bush encroachment. This is a serious ecological, ranch management and economical problem in southern Africa. Encroachment of *Acacia karoo* into grassland from the adjacent savanna is usually caused by overgrazing and subsequent deterioration of the grassy layer (Friedel 1987). Overgrazing in dry western grasslands bordering on the Karoo semi-desert scrub, inevitably leads to invasion of dwarf shrubs and bushes into the grassland due to man-made drought conditions. However, studies on the dynamics of Karoo vegetation at the Karoo-grassland interface suggest a state and transition model (Westoby et al. 1989; Milton & Hoffman 1994) where the vegetation can be changed to situations of either more grasses or more shrubs by both fluctuations in rainfall and grazing (Palmer & Hoffman 1997).

Fire frequently occurs globally in primary grassland due to high frequency of lightning and high fuel loads. Fire played an important role in preventing forest invasion into the moister eastern sections of North American prairie (Bragg & Hulbert 1976), though some authors maintain that prairie was maintained as a stable entity, whether fires occurred or not (Borchert 1950). Fire also plays an important role in shaping grassland and savanna communities in southern Africa, though the fire regime is similar in grassland and savanna and is therefore not a determinant to distinguish between grassland and savanna. It is nevertheless accepted that regular fire cause the abrupt boudaries between grassland and forest communities along the eastern escarpment area, and that fire inhibits the expansion of the forest into the fire-prone adjacent grassland (Geldenhuys 1994; Midgley et al. 1997). The view (e.g., Acocks 1953) that Afro-montane grassland is the result of forest clearance in the recent past is not substantiated (Meadows & Lin-

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der 1993). Human influence on grassland as a result of agricultural or forestry activities is restricted to the very late Holocene.

An important aspect is that primary southern African grassland, when not managed, does not revert to forest or woodland. Successional processes in degraded (ploughed, or overgrazed) grassland are slow, often developing to species poor *Hyparrhenia hirta* dominated secondary grassland, which is totally different from the climatic climax grassland. This is in complete contrast with western European secondary grassland, which become rapidly overgrown by forest when not managed (Pott 1995).

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