

CLIMATE CHANGE IN PERSPECTIVE - VEGETATION RESPONSES TO GLOBAL CLIMATE CHANGES OF THE PAST.

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ABSTRACT

There is a high probability that climates of the future will show similar patterns to those of the past. Several distinct elements of the palaeoclimatic record of the past 12,000 years have been correlated to the regional expansion or contraction of particular types of vegetation, including families which today are of economic value. However, increasingly reliable climatic data now extend back to the very origins and evolution of most flowering plants covering the last 100 Ma (million years) of geological time, during which some 120 extant families have appeared in the fossil record. This paper focuses on two families of particular significance to tropical and temperate agriculture and to weed science, the Asteraceae (Compositae) and Poaceae (Gramineae). Both appear in the record relatively recently, in the Oligocene, from about 30 Ma ago. Within a relatively short time these families, and particularly the grasses, began to form extensive ecosystems where they replaced the retreating tropical and warm temperate forests. The expansion of both families coincided with a number of major shifts in climate patterns. These include changes, globally, in the partial pressure of CO₂, O₂, rainfall, sea-levels, air and sea temperature as well as in the form, position and elevation of major continents. Evidence is presented for the expansion of grass and composite floras in areas which were increasingly subjected to seasonally distributed rainfall, against a background of cooling temperatures, widespread drought and the greatest regression of the sea. Into these environments, the Poaceae and Asteraceae expanded to form the temperate grasslands, savannas, dry scrub to semi-arid vegetation systems of today. Severe limits to the expansion of these ecosystems occurred during the subsequent development of wetter climates. The environmental conditions which favoured expansion and dominance of the Poaceae and Asteraceae, were associated largely with restricted access to water, whether due to periodic patterns of precipitation, to increased evapo-transpiration in seasonally high temperatures or restriction in ground-water availability due to seasonally low temperatures, possibly to fire, but not to temperatures *per se*. A brief mechanistic explanation is provided of the outstanding molecular attributes of these two families which might again favour their success and perhaps expansion under future drier climates.

INTRODUCTION

Global climate change is not new. Over the past 450 Ma, throughout the periods covered by land plant evolution, climates have differed markedly from those of today. Coinciding with the most significant changes in palaeoclimates, there have been major alterations in the structure and composition of global vegetation; some of these changes have led to the great extinctions of the past, others to the evolution of new plant forms. Less dramatic, but of particular interest in the context of contemporary concerns over climate, are the changes in the distribution of particular plant communities, often well marked in the fossil record. In recent years it has become possible to link these changes in vegetation composition and distribution with long-term alterations to global, and sometimes regional, changes in temperature, sea level, rainfall and atmospheric gas compositions and in atmospheric and oceanic circulation patterns. With varying degrees of certainty, it has been possible to provide reconstructions of climate zones for all of the periods covering angiosperm evolution (e.g. Frakes & Kemp, 1972). Extensive data sets showing global temperature changes over the past 50 Ma are now available from oxygen-isotope analyses of deep-ocean cores. From wind-borne dust sediments in deep-ocean cores, estimates of climate dryness, atmospheric circulation and of wind strength can be derived (e.g. Rea, Leinen & Janecek, 1985). Data on sea levels, recording global regressions and inundations are available for even greater lengths of geological time (e.g. Vail & Hardenbol, 1979) exposing the existence of oscillatory cycles.

From the considerable body of fossil data, from spores, pollen and other plant parts, detailed records can be built up of past vegetation, itself a reflection of changes in earlier climates. Much we do not know, however. While there is good agreement that the major components of the global vegetation of the late Cretaceous 80 Ma ago was composed, quantitatively, of ferns, cycads, conifers and angiosperms in that order, we have no commonly agreed *environmental* explanation for the almost complete reversal of that order within a mere 20 Ma. The point should be made that natural selection can release evolutionary forces way beyond the apparent magnitude of the particular selective push that triggered the change. We have to accept that the events that marked the end of the Cretaceous were so catastrophic as to turn the composition of the global flora on its head.

Putting this great body of palaeoclimatic data to use in order to predict the effects of future climates on particular plant communities is possible. The more closely defined the vegetation, however, the more it is necessary to know something of the physiology of the component species under different environments. Fortunately this too can be achieved and this review concentrates on two of the major flowering plant families, the grasses and the Asteraceae (Compositae). These families today, have a cosmopolitan distribution, but are significant components of the cool temperate through to sub-tropical zones, including drylands and, in the case of the Asteraceae, the semi-arid regions (see Hendry, 1993). Grasses, including graminaceous crops, now contribute significantly to or dominate between one-quarter and one-third of the world land surface in the vegetation of the savannas, long and short grasslands as well as cultivated lands and contribute to about one-quarter of the global primary

productivity (Table 1). The quantitative significance of the Asteraceae, globally, is less certain, though the family is extensively cultivated in certain areas, particularly in horticulture and market gardening.

Table 1. Type, area and productivity grass-dominated vegetation, globally

Vegetation type	Area 10 ⁶ km ²	% world land area	Primary productivity 10 ⁹ dry tonnes/yr
Global land mass	149	100%	117
Savanna	15-25	10-17	13.5
Temperate grassland	7-12	5- 8	5.4
Cultivated land	14-15	9-10	9.1
Total grass-dominated land	36-52	24-35	27.0
% Global total			23%

(Data: World Conservation Monitoring Centre (1992))

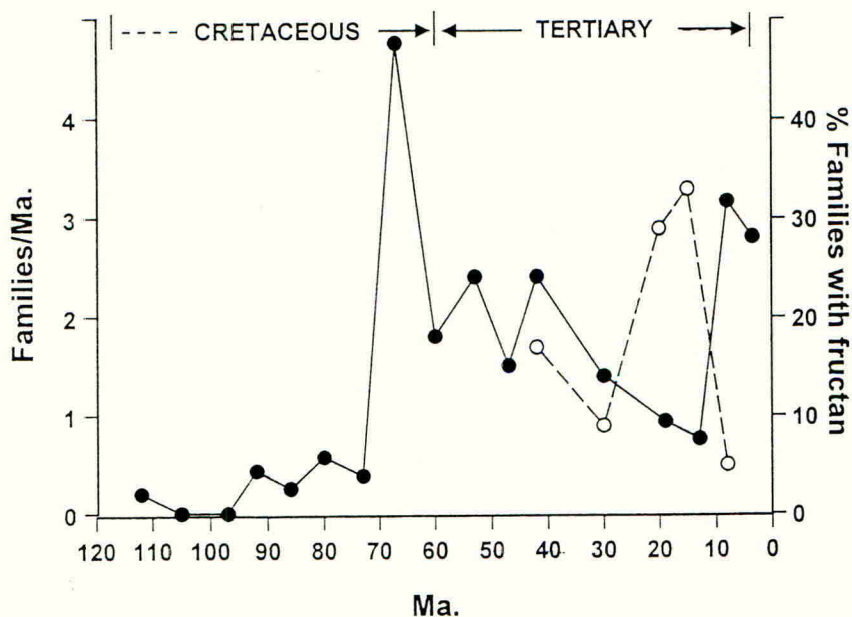
These present day grass-dominated regions (or nearest geographic equivalents) 70 Ma ago were dominated by an extensive tropical forests or by a fern-rich flora in drier areas. By 30 million years ago, the contribution made by grasses to global vegetation cover, to biodiversity or to global productivity would have been little, probably insignificant. By 20 Ma ago grasslands were becoming a notable though minor element in global vegetation, particularly where accompanied by the retreat of the tropical forests world-wide. By 10 Ma ago several elements of the global vegetation had a significant grass component, by 5Ma more so. The question we address here is what were the environmental conditions which brought about this major change in vegetation? This review explores the environmental origins of the grasses and attempts to pinpoint those aspects of the changing physical environmental which are repeatedly associated with the expansion and, at times, contraction of grasslands.

In addition, this review also considers the climatic origins of the largest of the dicot families, the Asteraceae (Compositae) both as a comparison with the Poaceae (Gramineae) and, in the context of this conference, as a family containing many weeds of economic significance. By focusing attention to the particular climatic conditions likely to have had a marked effect on the distribution of grasses and composites, we can attempt to discern the prospect for global grasslands in climates of the future.

THE ORIGIN OF THE ANGIOSPERM VEGETATION - A GRASSLESS WORLD.

The angiosperms appear to have originated in the early Cretaceous, 130-140 Ma ago, or even earlier in the upper Jurassic. From the fossil evidence, however, it is unlikely that the angiosperms made any significant contribution to plant speciation much before the mid-Cretaceous (90-85 Ma ago). From about this time there was a rapid increase in the number of recognisable angiosperm families (figure 1).

Figure 1. The rate of appearance in the fossil record of extant angiosperm families (solid line) (data derived from Muller, 1981) together with the percentage of evolving families which today store fructan as the principal storage carbohydrate (dotted line) (data from Hendry & Wallace, 1993).



However, the quantitative impact of flowering plants, measured as vegetation cover, may not have been great until much later. A glimpse of the vegetation at a single warm-temperate site towards the end of the Cretaceous about 70 Ma ago has been provided for the Big Cedar Ridge flora (central Wyoming) by Wing *et al*, 1993. There, angiosperms, largely dicots, constituted only 12% of the vegetational cover, though making up over 60% of the total number of species. By contrast, 50% of the cover was provided by ferns, another 25% by one species of palm.

It was this or a similar world which experienced the mass extinctions at the end of the final phase of the Cretaceous, the Maastrichtian, eliminating the last of the dinosaurs, 50% of marine animal spp. (Raup, 1986) and many terrestrial animal groups, perhaps 80% of the gymnosperms and, incidentally, a significant element of the recently evolved angiosperm flora (Hickey, 1981). Immediately following the Cretaceous the vegetation consists almost entirely of ferns from sites in New Mexico (Pillmore *et al*, 1984), Montana (Smit & van der Kaars, 1984) and elsewhere. The initial cause of the mass extinctions is the subject of continued debate (e.g. Robin *et al*, 1993) but appears to have been associated with a brief but severe climatic deterioration. It was into this world that the angiosperms rapidly achieved dominance.

THE ORIGIN AND RISE OF THE GRASSES AND ASTERACEAE

From the end of the Cretaceous, the following 40 Ma saw the development and geographic expansion of an increasingly modern-looking angiosperm flora. By 15 Ma ago a recognizably modern-day flora was in place and included now familiar plant communities such as extensive savanna, prairie and other dry grasslands. The flora of 5 Ma ago bears strong similarities to contemporary floras often of the same present-day region if not locality (see examples in Axelrod, 1985).

The origins of the grasses and Asteraceae, from the fossil evidence, go back at least to the Palaeocene and Oligocene respectively. Grass-like fossils have been reported from the mid-Palaeocene 50 to 55 Ma ago and include Stipa-like florets (Muller, 1981). However, the great expansion in speciation and distribution of the grasses occurred considerably later and probably not before the Oligocene 30 Ma ago. In North America grass pollen becomes appreciable from the mid-Miocene 20 Ma ago and abundant in the upper Miocene from 12 Ma ago (Chaney & Elias, 1936). This explosion of grasses was accompanied by a rapid expansion of herds of large grazing mammals, particularly the horses and bovines. A brief summary of the global palaeoclimates from the end of the Cretaceous, covering the Tertiary, is shown in Table 2 but discussed in greater detail below.

Table 2. Summary of global palaeoclimates and palaeobiology of the Tertiary

Epoch (Ma ago)	Global climate and vegetation	Mammalian Herbivores
Palaeocene (65-56)	Warm -temperate to sub-tropical forests to high latitudes with no extremes of seasons	Rise of proto- and paeno- ungulates
Eocene (55-34)	Warmer than present. Rain-bearing winds from extended Pacific Ocean.	Browsers with fibrous diet
Oligocene (32-25)	Slowly declining temperatures. Retreat tropical forests. Evidence of seasonal vegetation	Increase body size bovids, deer and horses
Lower Miocene (24-15)	Drier. Distinct seasons. Retreat of temperate forests. Expansion dry vegetation. Mountain uplifting	Development of foregut. Large herds bovids
Upper Miocene (14-5.1)	Cool, intense drought. Expansion dry grasslands. Rainshadows with low rainfall and arid regions	Extinction many tree/scrub browsers
Pliocene (5-2)	Further cooling. Poles ice-up, glaciers on low-latitude mountains. Widespread dry-arid vegetation	Bovid-equid geographic expansion

(Data on climate and vegetation adapted from Hendry, 1993; on mammals from Janis & Jarman, 1984)

The rise of C4 terrestrial plants in the late Miocene, dated from palaeosols and palaeodiets, indicate a rapid expansion of C4 biomass in both the Old and New World starting 7 Ma ago and lasting for about 2 Ma (Cerling *et al*, 1993). Although this is thought to be due to a short-lived expansion of tropical savanna, perhaps warm temperate grasslands and semi-arid regions, in this particular case the expansion of C4 vegetation may have been more related to the lower atmospheric CO₂ concentrations of the late Tertiary. Why at this moment is not clear; the decline in CO₂ concentrations had been in train for at least the past 30 Ma, if not throughout the whole of the Tertiary (see Table 3 below).

THE TERTIARY CLIMATES

Global generalizations on palaeoclimates can be highly misleading and rarely do justice to the wealth of hard-won data on which they rest. A great deal is now known of climates of the past, often with considerable precision in scale, in time and in locality. The evidence extends to detailed information on past atmospheres, including CO₂ and O₂, to rainfall patterns, to sea levels, to temperatures both terrestrial and marine, as well as to physiographical changes, mountain building and, with increasing precision, the influence of changes in the earth's orbital geometry. Studies of particular localities, in North and South America, Europe, Middle East and East Africa have enabled the construction of climatic zones over considerable periods of geological time. Despite this one has to repeat the warning that extrapolations from site-specific climatic and other physical data to a regional, let alone global, scale in the form of generalized statements inevitably result in gross distortions and are plagued with exceptions. With this warning, the following summary of global climate change during the rise of the grasses is given. Many more detailed accounts are available and include those of Frakes, 1979; Tallis, 1991 and Retallack, 1992.

The Tertiary lasted from 65 to approximately 2 Ma ago and was accompanied by climatic deterioration from relatively warm to sub-tropical temperatures at high latitudes, with no extensive areas of low rainfall, through to the extreme aridity of the late Miocene and Pliocene and a world-wide decline in temperatures, heralding the onset of the Pleistocene ice-ages (see Table 2 above). Following the global catastrophe at the end of the Maastrichtian and the slow recovery through much of the early Palaeocene, the vegetation was dominated by tropical to sub-tropical forests, reaching their maximum extent in the early to mid-Eocene (55-40 Ma ago), an epoch described as climatically benign (Tallis 1991). From the end of the Eocene through to the end of the Miocene the changing patterns of climates, the regression of the sea, the late Miocene phase of mountain building and the appearance of extensive semi-arid areas opened up what Tallis calls new ecospace; extensive new habitats or biomes which developed from the changing climates and led to the foundation of new types of plant communities. The essential point is that the global ecospace of the Eocene was limited while the ecospace of the Miocene was diverse. From the Oligocene, and particularly the Miocene, the drier climates and the opening up of the forested areas are associated with the radiation and geographical expansion of herds of large-bodied bovids, deer and horses. The extent to which these mammals influenced the shift in vegetation types is conjectural but towards the end of the period it is highly likely that extension of the grasslands were influenced by increasing grazing pressures.

Rather more detail of the physical climate is provided in Table 3 which shows that, apart from the 60 Ma-long drift downwards in temperature, there was a decline in atmospheric CO₂ and O₂ and changes both in frequency and amplitude in dryness, in extent of seasonality and in sea level. What the table cannot do is to illustrate the speed of specific changes occurring even in quite extensive areas. For example, the rainfall patterns of the Eocene and Oligocene are described in Table 3 merely as 'wetter than now' and 'less wet'. The detailed summaries provided by

Retallack (1992) indicate that annual rainfall of the present Great Plains of North America was in excess of 1000mm at 38Ma, 500-900 by 32Ma, down to 450-500mm by 30.5Ma and 250-450mm by 29.5Ma. This represents a 2 to 4-fold decline in rainfall in a short timescale for evolution and would constitute a rapid imposition of a strong selective pressure.

Table 3. A generalized summary of Tertiary rainfall, temperatures, atmospheric composition and sea-levels (for greater detail see references below)

Tertiary epoch (Ma ago)	Precipitation and dryness	Relative temperature	CO ₂ x now	O ₂ kPa at sea level	Change in sea level
Palaeocene (65-56)	wetter than present	subtropical to warm	x2.5	27-26	rising with minor falls
Eocene (55-34)	wetter than now	warm to subtropical	x2	25-24	minor fluxes
Oligocene (33-25)	less wet seasonal	warm to temperate	x2	24-23	great regression
Miocene (25-5.1)	dry to arid seasonal	temperate to cool	x1.5	23-21	rising then long regression
Pliocene (5-2)	dry and seasonal	cool	x1	21	rapid rise and fall

(Data derived from: Precipitation - Frakes, 1979 and Rea *et al*, 1985; Temperature - Axelrod & Bailey, 1969 and Tallis, 1991; CO₂ - Berner, 1991; O₂ - Berner & Canfield, 1989; sea level - Vail & Hardenbol, 1979 modified as in Summerhayes, 1986)

WHAT KIND OF CLIMATE FAVOURED THE EXPANSION OF GRASSES AND ASTERACEAE?

As long ago as 1950 Sauer pointed out that simple links between climate and grassland are hard to establish - for every climate that has been recognized in which grasslands dominate, the same climates elsewhere are associated with forests or scrub. Because grasslands are to be found chiefly where there are dry seasons and on smooth to rolling plains - he argued that the one common factor which separated forested areas

from grasslands was not climate directly but a secondary aspect, fire. Recurrent fire suppresses woody vegetation. A similar argument says that conditions which suppress fire result in recolonization of woody vegetation. However, on a global scale, compared with previous periods, fire risk actually decreases throughout the latter half of the Tertiary with the decline in partial pressures of O_2 from a highly flammable 30kPa or more at the beginning of the Tertiary (Berner & Canfield, 1989) (Table 3).

Axelrod (1985) has provided a summary of the central north and west American palaeo-floras, from the mid-Miocene onwards, covering the region from Saskatchewan and Alberta to central Mexico and from Illinois-Indiana across to California. Of the many points which emerged from this and his later studies, the following summary is particularly relevant. By the mid-Miocene, although forested areas were extensive in the region, sufficient openings must have been present to account for the appreciable amounts of grass and Asteralean pollen, particularly in drier or well-drained sites. More open, parkland, vegetation appears to have developed in the late Miocene, in a climate still warmer than at present. The uplifting of the Rockies in the late Miocene would have intercepted the cool moisture-laden winds from the Pacific leading to a drier climate. Throughout the region the trend towards relatively low rainfall with increasing dry seasons coincided with what has been described as an outburst of fossil grass speciation (Axelrod, 1985) at the end of the Miocene (6-5Ma ago). The pattern of patchy grasslands in a dominant forest was reversed to leave patchy forest and woodlands scattered over the extending grasslands, particularly on the drier sites.

The fragmentation of woodland and its replacement by grassland by the Pliocene suggests one or a few widespread environmental pressures which favoured grass over trees. Among these pressures would have been drought, the activities of the previously large herds of browsing mammals and, thirdly, fire. If, as seems likely, drought conditions were exerted seasonally, there is an immediate link between the annual dry season and relatively frequent episodes of fire. Axelrod (1985) has pointed out that, for North America, by the Pliocene the relatively flat Great Plains were subject to dry seasons and to southerly and westerly winds, including dry warm fohn winds, conditions favourable to the spread of fire north and east. Following the passage of fire the production of a new generation of seed is possible within one or two years in the case of grasses and forbs with short life-cycles while woody vegetation takes several years to become seed-producing. Breaks in the regular patterns of fires, on obliteration of dry seasons and increases in precipitation would, presumably, reverse this development allowing the development of scrub, shrub and tree cover. The rapid and opportunistic spread of Asteraceae and Poaceae in the north of the Great Plains at about this time is considered to be linked to the presence of charcoal horizons (Axelrod, 1985). The converse seems to have occurred, much later during the Holocene, in the wetter climates of west Europe 7000 years ago and in south east Europe 5000 years ago; in both cases the expansion of the oak forests was matched by a contraction of grass pollen (Hendry 1993). It should be added, however, that the evidence that natural as opposed to man-made fire played any significant role in the reduction in area of western European forests from 4000 years ago is by no means clear. On the Great Plains, however, the incidence of fire as a result of

natural causes, particularly in periods of drought and fohn winds, have been well described by Komarek, 1968. In addition to fire, the grazing-browsing pressures of the large herbivores from the late Miocene-Pliocene through to historic times would have helped further to open up parkland-savanna into grassland particularly under conditions of drought. Grasslands, however, can become unstable when in contact with woody vegetation. From the evidence of the expansion and contraction of the European oak forests during the Holocene, the singly most likely climatic promoter of expansion of the forests and simultaneous contraction of extensive grasslands was increased rainfall (Hendry, 1993). Temperature, in these mid-latitudes, seemed to have played little part in this perpetual tilt between forest, scrub and grasslands.

The changes in vegetation from the early to the late Tertiary were associated with well documented changes in the number and species of large-bodied grazing mammals. The fossil remains from the first half of the Tertiary showed the radiation, particularly in the northern hemisphere, of herds of equids (and other odd-toed ungulates) whose diet was fibrous and woody plant material, reflecting presumably the predominately forest vegetation. By the mid-Tertiary the dominance of the odd-toed ungulates passed to the bovids and deer whose numbers, and body sizes, increased rapidly with the development of the foregut. The Miocene saw the explosive radiation of the ruminants, particularly among the large bovids. From the analysis of Dix (1964), the adaptive changes that produced the modern horses and other herbivores suggest that the widespread establishment of grasslands had occurred by the late Miocene 12 Ma ago, formed under mild, frost-free climates (Thomasson, 1979). Such areas as the Great Plains did however, support a regular association of browsing and grazing mammals well into the Pliocene and suggests a much more patchy environment with extensive woodlands and localized grasslands (MacGinitie, 1962).

So what part did temperature play in these developments? Crowley *et al* (1986) have argued that regardless of how cold it gets in winter, it is not possible to initiate ice cap formation if it gets too hot in summer. The consequence is that quite severe changes in the seasons would be required to allow formation of polar ice. Ice-free states may have been due more to high summer temperatures rather than year-round warmth. They argue that cool non-glacials may have prevailed for as much as one-third of the last 100 million years. We cannot then explain the spread of grasslands 8 Ma by the onset of severely cold seasons. Instead the one element of climate change, as presented in Table 3, which consistently appears to be associated with grasslands in time, space and in quantitative effect, is seasonal rainfall. Of course, at low or high latitudes, the annual imposition of a season of water-stress may be due less directly to low rainfall, and more to increased evapo-transpiration under high temperatures or to ground-water freezing at low temperatures. But for mid-latitudes, the alternation of wet and dry seasons is the key.

WHY GRASSLAND? MOLECULAR MECHANISMS FAVOURING THE POACEAE AND ASTERACEAE

The Poaceae and the Asteraceae, together with five other families (Hendry &

Wallace, 1993), are unique among the flowering plants. Whereas most other families store starch or sucrose as the principal storage carbohydrate, the Poaceae and Asteraceae store fructan. In the case of the grasses, in one of the six sub-families, the Pooideae (or northern grasses), the fructan concentrations in the *vegetative* tissues greatly exceed any starch present. In the other five more tropical sub-families, fructan may be less significant, at least in unstressed environments. Throughout the Asteraceae, as far as we know, fructan is the main, if not sole, storage carbohydrate, particularly in below-ground storage organs.

Fructan unlike starch is water soluble, at least to the low degree of polymerization found in most species (Table 4). It is also stored in the vacuole to exceptionally high concentrations. Hendry, (1987) and Brocklebank and Hendry (1989) in an extensive survey of native British species showed that the range of concentrations to which fructan was stored generally exceeded that of starch or sucrose, by several orders of magnitude. Amounts of fructan as high as 50% or more of the dry weight of the plant are not exceptional among grasses and Asteraceae (see examples in Housley & Pollock, 1985 and Edelman & Jefford, 1968).

Table 4. Molecular differences between fructan, starch and sucrose

Attribute	Fructan	Starch	Sucrose
Composition	Fructose	Glucose	Glucose + fructose
Major subcellular location	Vacuole	Amyloplasts Chloroplasts	Vacuole
Solubility	high	low to nil	high
Mol. wt x 10 ³	0.5 to 50	300 to to >30,000	0.36
Degree of polymerization	<30 (rarely >200)	2000 to >200,000	2

High concentrations of a soluble carbohydrate stored in the vacuole will have strong regulatory effects on the osmotic potential of the cell. Estimates of vacuolar concentration in eight cool temperate region fructan-rich spp. ranged from 31 to 450mM, under winter conditions (Hendry, 1987). All eight species were able to

sustain growth throughout periods of low temperatures and low water availability. Although similar data are not yet available for warm or tropical species under water stress, there is much evidence from the life history patterns of fructan-rich species of semi-arid regions including Australia, the Brazilian Cerrado and Argentinian Chaco that the osmotic potential exerted by fructan plays a similar key role in survival of these families under seasonal water stress in warm temperate to dry sub-tropical climates. It is this attribute, the ability to draw in water and to store it in vacuoles against a water deficit which distinguishes starch-rich from fructan-rich species.

The origins of fructan in the angiosperms are relatively recent. Most fructan-rich families appear in the fossil record 20 and 10 Ma ago (see figure 1), coinciding with the increasingly severe Miocene droughts. Their global success, particularly in the Poaceae and Asteraceae, is a reflection of their ability to overcome the problems of the seasonal availability of rainfall and to survive during the intervening water-limited season.

THE FUTURE

We can now pinpoint with some confidence, the climatic conditions which most markedly influenced the expansion or contraction of grasslands and grassland communities in the past. The evidence from palaeoclimatic and fossil records strongly confirm that episodes of water shortage, of weeks or several months duration on a predictable annual cycle favoured the expansion of grass-dominated vegetation in warm to cool temperate regions whereas climatic condition characterized by relatively high rainfall or low evapo-transpiration with no strongly marked season bias favoured the extension of woody species and, in time, forest communities.

For the future, the key to predictions rests on establishing good estimates of the amount of rainfall and its spread over the year. For the fructan-rich Poaceae and Asteraceae, temperature does not appear to play a significant *direct* role in determining distribution, (other than as a component of evapotranspiration calculations), outside the extremes of the tropics and polar regions. If we are to make predictions on the future of natural grasslands and the status of communities and individual species of Poaceae and Asteraceae in grassland and cultivated land, we need more reliable estimates not just on likely levels of rainfall, but most particularly on the timing and *duration* of seasonally wet and dry periods. This is so particularly in the mid latitudes, the zones covering the temperate grasslands, savannas, semi-arid to desert regions and the greater part of the cultivated lands.

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