

What controls South African vegetation — climate or fire?

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The role of fire in determining biome distribution in South Africa has long been debated. Acocks labelled veld types that he thought were 'fire climax' as 'false'. He hypothesised that their current extent was due to extensive forest clearance by Iron Age farmers. We tested the relative importance of fire and climate in determining ecosystem characteristics by simulating potential vegetation of South Africa with and without fire using a Dynamic Global Vegetation Model (DGVM). The simulations suggest that most of the eastern half of the country could support much higher stem biomass without fire and that the vegetation would be dominated by trees instead of grasses. Fynbos regions in mesic winter rainfall areas would also become tree dominated. We collated results of long term fire exclusion studies to

further test the relative importance of fire and climate. These show that grassy ecosystems with rainfall >650mm tend towards fire-sensitive forests with fire excluded. Areas below 650mm showed changes in tree density and size but no trend of changing composition to forest. We discuss recent evidence that C₄ grasslands first appeared between 6 and 8M years BP, long before the appearance of modern humans. However these grassy ecosystems are among the most recently developed biomes on the planet. We briefly discuss the importance of fire in promoting their spread in the late Tertiary.

'Temperature and moisture are the two master limiting factors in the distribution of life on Earth'
Krebs (2001)

Introduction

The great German biogeographer, Schimper (1903), observed that global patterns of vegetation were broadly correlated with climate. On different continents, with distantly related floras, similar vegetation formations occurred under similar climatic conditions. The implication is that climatic factors, primarily temperature and moisture, are the main factors controlling the distribution of vegetation. The idea of the primacy of climate in determining vegetation has prevailed for at least a century though soil nutrient status has sometimes also been considered an important secondary determinant of ecosystem characteristics (Beadle 1966, Specht and Moll 1983). In South Africa, ecologists soon became aware that many grassy ecosystems were not at equilibrium with climate but were deflected from their 'potential' by fire (Phillips 1930, West 1969). Acocks tried to identify these fire-dependent veld types by labelling them as 'false' (Acocks 1953). 'False' grasslands still had forests present in facets of the landscape suggesting that climatic conditions (rainfall and temperature) would support forests in these landscapes if fire was excluded. False grasslands occupied vast areas east of the Drakensberg (Acocks 1953,

Ellery and Mentis 1992). Acocks also implied that large areas of fynbos were far from their climate potential and labelled most of the eastern half of the Fynbos Biome as 'False' macchia. In order to explain why such large areas of the country were not at equilibrium with climate, Acocks suggested that forests had been cleared by Iron Age farmers causing their replacement by earlier successional grasslands or 'macchia'. He drew a map of South African vegetation as it might have looked in 1400 AD — just before Iron Age settlement according to the consensus at that time. The map shows a heavily forested eastern half of the country with 'natural' grasslands only occurring in the high country of the interior and in the arid west. Acocks' map was significant for two reasons: first it made an explicit prediction about which areas of South Africa were controlled by fire and secondly it suggested an hypothesis for their origin and extent. In this paper, we first report a test of the extent to which fire, rather than climate, determines South African vegetation. We then discuss the evidence for the age of fire-dependent vegetation. Finally we assemble new evidence for the origin of grassy ecosystems and propose a new hypothesis for the

key role of fire in their spread to mesic areas which might otherwise support forests. We briefly speculate on why fire became important in angiosperm-dominated floras so late in evolutionary history. We focus mainly on grassy ecosystems of the summer rainfall areas though winter rainfall shrublands show many parallels.

Testing the importance of fire vs climate with DGVMs

Until recently, analyses of determinants of vegetation were largely correlative. The distribution of vegetation, or of plant species, was correlated with various climate (or soil) variables using a variety of statistical procedures (e.g. for biomes, see Rutherford and Westfall 1996, Ellery *et al.* 1991, for forest see Eeley *et al.* 1999). These correlative methods cannot be used to disentangle climate versus fire as potential determinants of plant distribution. Recently, mechanistic models for predicting global vegetation have become available. Dynamic Global Vegetation models (DGVMs) are designed to simulate vegetation responses to changing climates. DGVMs 'grow' plants according to well established physiological principles (Woodward *et al.* 1995, Cramer *et al.* 2001). These models generate predictions of the composition and structure of vegetation at any given point in terms of relatively few plant functional types (PFT's, e.g. Woodward *et al.* 1995). The results generally support the primary importance of climate in determining global vegetation.

Disturbance is also important in many regions and DGVMs have begun to include fire modules and drought (Cramer *et al.* 2001). Determinants of fire are complex and the role of fire in shaping the geographic distribution of vegetation is still poorly understood. The occurrence of a fire is conditional on an ignition event, vegetation ('fuel') dry enough to ignite, and continuity of fuels that allow fires to spread (Catchpole 2002). Areas with similar climate (mean temperature and moisture conditions) can have very different fire regimes because of different frequencies of extreme weather conditions (short, hot, dry periods), different lightning frequencies, different fuel properties of the vegetation, or differences in the frequency of natural fire-breaks such as large rivers or barren areas (Bond and Van Wilgen 1996). People have altered fire regimes by adding, or suppressing, ignition, by changing fuel properties, and by altering fuel continuity through construction of roads, fields, and settlements. As yet, no general model exists for predicting fire regimes and the consequences of changing them at a regional or global scale. This means we cannot determine the relative sensitivity of fire regime to changes in climate, extreme weather conditions (lightning, hot, dry periods), distribution of fire-promoting, or fire-blocking vegetation, and physical barriers to fire movement.

Methods

We used the Sheffield Dynamic Global Vegetation Model (SDGVM) to simulate potential vegetation of South Africa. The SDGVM is a global-scale model that simulates carbon and water dynamics and structure of vegetation using input data of climate, soil properties, and atmospheric CO₂ (Woodward *et al.* 1995, Cramer *et al.* 2001, Beerling and

Woodward 2001). The SDGVM includes a fire module that approximates fire frequency in a reasonable manner given the global scale of the model (Woodward *et al.* 2001). No mechanistic model to generate fire on a global scale exists. In the SDGVM, fire is simulated from empirical relationships between moisture content of plant litter (which can be simulated from climate) and fire return intervals. The fire module assumes that ignition is not limiting (Woodward *et al.* 2001). Output of the model has been tested against measured ecosystem properties over a wide range of climates worldwide and gives a satisfactory fit (Woodward *et al.* 2001, Cramer *et al.* 2001). We used the DGVM to investigate the importance of fire versus climate as determinants of vegetation in South Africa. It is particularly useful for this purpose since the model is mechanistic and not based on correlations of existing vegetation with climate. We were therefore able to separate effects of climate from those of fire by 'switching off' the fire module in the simulations. Climate data used in the model were taken from the University of East Anglia global data set. The model incorporates soil depth and texture from a global data base (FAO 1998). It assumes soils are freely drained.

Model output includes ecosystem properties, such as plant biomass, and also the cover of several major growth forms.

Results

Biomass change

Figure 1 shows simulated biomass differences with and without fire for southern Africa. Biomass in the arid western half of the country is, as expected, largely unaffected by fire. In the higher rainfall eastern regions, large changes in biomass are predicted in the absence of burning. To indicate the interaction between climate, fire and potential plant biomass, we show the results of simulations along a gradient of increasing precipitation in summer rainfall regions along latitude 26.75°S (Figure 2). Sites along the gradient do not vary greatly in temperature but rainfall increases from west to east. The simulations predict that exclusion of fire would result in negligible changes in biomass below 300mm in summer rainfall regions. As rainfall increases above 300mm, biomass in the no-burn scenarios diverges strongly from burn scenarios. At the high rainfall end of the gradient the simulation predicts that stem biomass will change from less than 4 000g C m⁻² to 20 000g C m⁻² with fire excluded! DGVM type simulations usually over-estimate forest biomass, in one study by as much as 400% (Jenkins *et al.* 2001), so the model simulations should be seen as indices of potential biomass until further testing and validation. Nevertheless changes of this magnitude suggest a major vegetation shift, equivalent to a change from open savannas to forests (Scholes and Walker 1993, Jenkins *et al.* 2001). The simulation results indicate that the vegetation of the more mesic areas of South Africa could be very different if fires were not a frequent disturbance.

Simulated biomass in winter rainfall shrublands is shown in Figure 3 along a transect from south to north at longitude 18.25°E. The higher rainfall half degree squares in the south

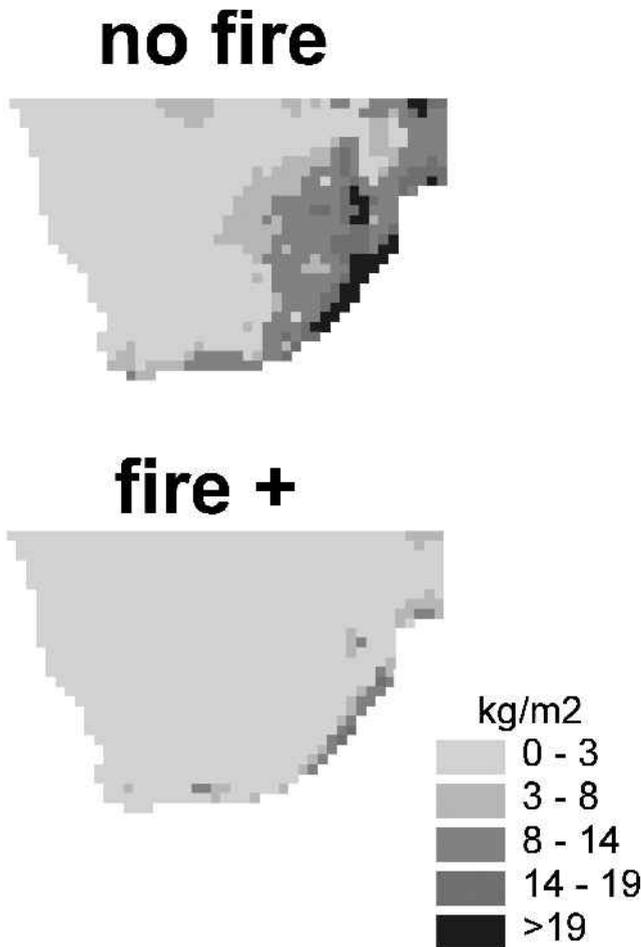


Figure 1: The effect of climate (above, without fire) and burning (below, with fire) on stem biomass in southern Africa simulated with the Sheffield Dynamic Global Vegetation Model (SDGVM). The units listed in the legend are kg C m^{-2}

show a marked increase in biomass in the absence of burning. This suggests that the more mesic parts of the fynbos biome have the climate potential to support a forest. The western Cape has steep climate gradients and areas of potential high and low biomass are closely juxtaposed. Only the narrow high rainfall belt is potentially influenced by fire (Figure 1).

Vegetation change

In Figure 4, we contrast vegetation type, as indicated by the percent cover of trees, with and without fire. The simulations are startlingly different. They predict that most of the eastern half of the country would be covered with trees in the absence of fire. The southern and south-western margins of South Africa (the winter and all-year rainfall regions) are also sensitive to fire. The simulations predict shrublands (fynbos) with fires allowed to burn and tree-dominated vegetation with

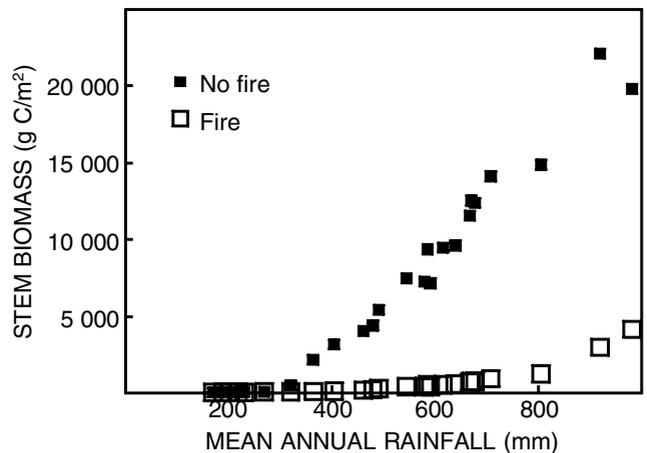


Figure 2: Stem biomass (g C m^{-2}) simulated with and without fire using the Sheffield Dynamic Global Vegetation Model. The simulations are for a transect in summer rainfall areas at latitude 26.75°S

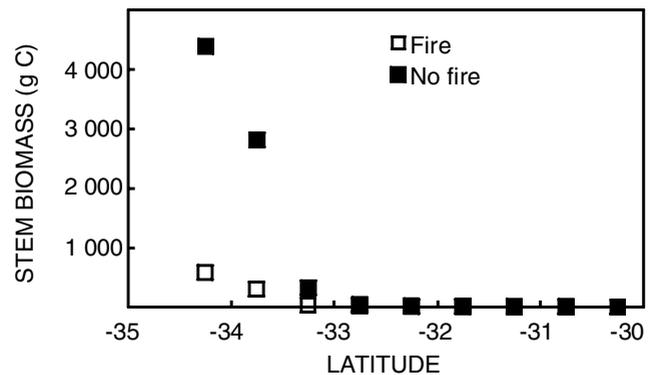


Figure 3: Stem biomass (g C m^{-2}) in winter rainfall areas simulated with and without fire using the Sheffield Dynamic Global Vegetation Model. The simulations are for a transect in winter rainfall areas along longitude 18.25°E . Precipitation decreases from south to north along the gradient

fire excluded in the higher rainfall areas. The arid western region, including the Karoo and grasslands adjacent to them, would be unaffected by fire according to the simulations.

The predicted vegetation change includes those areas called ‘false’ by Acocks, and therefore determined by fire, rather than climate. However the DGVM simulations also predict that the high grasslands of the interior could also be more wooded whereas Acocks considered these grasslands to be ‘natural’.

The SDGVM is designed to simulate global vegetation and only has a limited set of functional types against which to compare native vegetation. Nevertheless, the general pattern of grass-dominated ecosystems in the east shown in Figure 4 is a surprisingly good fit to general vegetation patterns seen in South Africa (Acocks 1953, Low and Rebelo 1996). Most of the higher rainfall south-western and eastern parts of the country, it would seem, owe their current vegetation to fire.

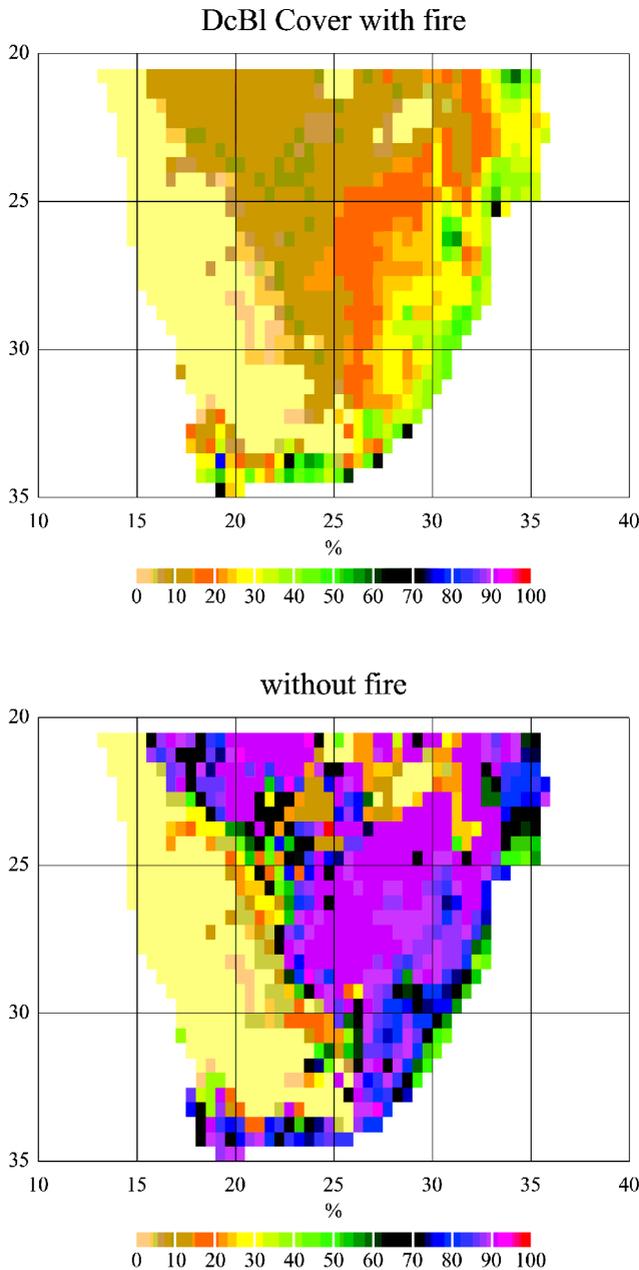


Figure 4: Tree cover simulated with and without fire using the SDGVM

What limits trees in grassy vegetation?

Alternative hypotheses

Though vegetation predicted by the SDGVM 'plus fire' simulation is largely consistent with what we observe, is fire really the culprit? Several alternative hypotheses, of which fire is but one, have been suggested for the scarcity of trees in the grassland regions of South Africa (for an excellent review see O'Connor and Bredenkamp 1997). Acocks (1953) suggested that frost was a major factor excluding trees in highveld grasslands. Correlative models, designed to predict vegetation change in response to global warming, have also

predicted invasion of trees into these grasslands in response to warmer temperatures (e.g. Ellery *et al.* 1991). However much of the tree-less grassland to the east of the Drakensberg is frost-free casting doubt on the importance of frost (O'Connor and Bredenkamp 1997). It is also noteworthy that *Rhus* spp. and *Acacia karroo* both occur in frost-prone areas near Bloemfontein in the Free State. Non-native species of *Acacia* and *Eucalyptus* from Australia have invaded highveld areas near Gauteng also suggesting that frost is not the factor limiting trees in the highveld. Unfortunately there is a remarkable dearth of experimental work on frost sensitivity of South African tree species, despite its supposed ecological importance. Experimental studies are needed to determine which elements of our flora, if any, are frost limited. Perhaps slower growth of saplings under cooler conditions is enough, for savanna trees of sub-tropical origin, to prevent their emergence from frequently burnt grassland.

A second hypothesis for the tree-less nature of many of our grasslands is that many soils are seasonally waterlogged (Tinley 1982), or have a duplex nature which inhibits tree growth (Feely 1987). Seasonally waterlogged sites are common features of soil catenas in much of Africa, including the miombo woodlands of south-central Africa. However only the lower slopes and bottomlands within a landscape are tree-less in these mesic savannas and freely drained upland soils bear tall woodlands. Many landscapes in the grasslands east of the Drakensberg have duplex soils with the potential for seasonal water logging but at least some of these soils are dry enough for long enough for trees to invade. Titshall *et al.* (2000) reported that fire exclusion experiments in grasslands on plinthite (seasonally waterlogged soils) were invaded by trees. As is the case for frost, there are no experimental studies on the importance of seasonal water logging or the presence of hard pans in limiting trees in grasslands. One possibility may be to use explosives to alter soil properties. San Jose and Farinas (1983) experimentally demonstrated an increase in South American savanna tree densities when an indurated iron pan was cracked using dynamite.

Fire

Our SDGVM simulations incorporate modules that determine growth, and functional type, responses to low temperatures, snow and frost. The results of the no-fire simulations (Figures 1 and 4) support Acocks' concept of 'true' grasslands for arid areas but not for mesic but cold areas. These areas are not cold enough, on a global scale, to exclude trees. The SDGVM assumes freely drained soils and cannot address the impeded drainage hypothesis for the absence of trees in grasslands. However the model clearly supports the hypothesis that fire is a major factor limiting woody plant cover in cool, mesic areas of South Africa.

Methods

It is possible to test these simulations, at least qualitatively, because of the many long term fire exclusion experiments and observations that have been conducted in South Africa. We have summarised the results of fire exclusion experiments known to us in Table 1 and Figure 5. If fire is the main

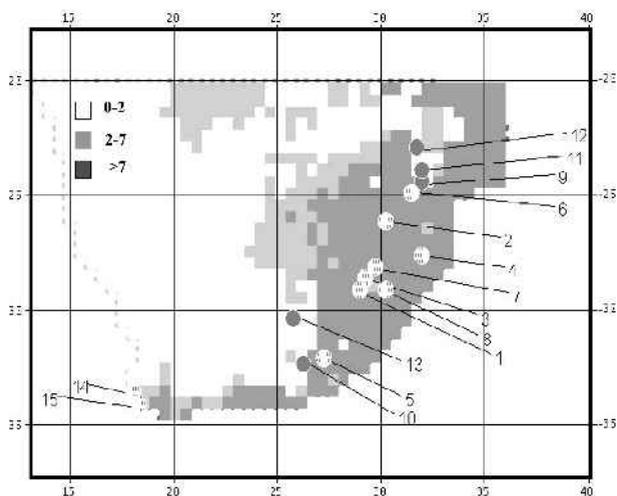


Figure 5: Successional trends in long term studies of fire exclusion. Studies showing a successional trend to fire-intolerant forest or thicket species are hatched. Studies with no evidence for such a compositional change are dotted. Site numbers refer to further information on each study in Table 1. The unshaded parts of the map have a simulated stem biomass, without fire, of $<2\text{kg C m}^{-2}$; lightly shaded = 2 to $<7\text{kg C m}^{-2}$ and heavily shaded = $>7\text{kg C m}^{-2}$

determinant of vegetation, then we would predict successional tendencies to greater biomass of woody species in more mesic sites but negligible change in biomass in more xeric areas. Unfortunately data to test biomass predicted from the 'fire-off' simulation are usually not available from these experiments. Results have mostly been reported as changes in cover or density of trees and other growth forms, rather than changes in biomass. It may also take many more decades of fire exclusion before woody plants reach the equilibrium biomass predicted by the DGVM for a given site. From the data available, the effects of fire exclusion are best measured qualitatively as a tendency for increased woody cover. Three qualitative outcomes can be expected from long term fire exclusion experiments (long term is >10 years in grasslands, >20 years in savannas, >50 years in fynbos):

- no change (climate limited)
- increased density or size of woody plants but no change in species (climate-limited, fire modified)
- increased density and size of woody plants and successional tendency to forest with invasion of fire-sensitive trees and shrubs (fire-limited)

The third case indicates that the vegetation is meta-stable with alternate fire-dependent or climate-dependent states.

We summarise the results of a number of studies, mostly experimental but also observational, on long term fire exclusion in Figure 5. Most of the studies have been published but we have included unpublished observations in some instances (Table 1). The figure indicates whether exclusion treatments resulted in compositional changes (FDE) or merely structural or no change (CDE) as defined above.

Results

Two studies from winter rainfall regions in the western Cape reported successional trends from fynbos to forest with long-term fire exclusion (Table 1). This, together with the SDGVM simulations, suggests that, at least in the more mesic areas, fynbos is an FDE and that much of the region could support a forest or thicket (strandveld).

In summer rainfall areas, all eight sites with annual rainfall $>650\text{mm}$ showed successional trends to forest with fire exclusion. All five sites with $<650\text{mm}$ annual rainfall showed no changes in composition to fire-intolerant forest or thicket species over the study period. However most of the drier sites showed an increase in tree density relative to treatments with frequent burns (usually annual to triennial). In the mesic sites, the rate of successional change varied greatly among sites. It was generally fastest on south-facing aspects and slowest on north-facing aspects (see e.g. Titshall *et al.* 2000). Rate of change is also likely to be influenced by distance to nearest source of propagules of forest or thicket species. However tree species colonised exclusion plots far from the nearest source in some studies (Titshall *et al.* 2000). Several sites were colonised by alien trees but all exclusion sites had at least some native shrub or tree invasives. A common feature of many grassland exclusion experiments is the increased abundance of shrubs of fynbos affinities with forest species taking longer to invade an area. This suggests that the climate is suitable for much more extensive areas of shrublands and that the grassy appearance of sourveld areas is a product of frequent burning. The shrublands tolerate fire but at lower frequencies and are, in turn, displaced by forest in the long absence of burning.

The SDGVM simulated biomass without fire is also shown in Table 1. Simulated biomass is for averaged climate in a 0.5 degree square 'pixel'. Because of the hilly topography and steep climate gradients in the eastern half of the country, it would be better to run the simulations on actual climate data at each experimental site where suitable records are available. Six of the sites which shifted towards forest had simulated biomass $>10\,000\text{g C m}^{-2}$, but three were $<10\,000$ to $>7\,000$. Four of the five sites showing no compositional change had simulated biomass without fire $<2\,000\text{g C m}^{-2}$. One site, the fire exclusion experiments at Fort Hare, would be expected to shift to thicket or forest from the simulations ($>8\,000\text{g C m}^{-2}$). However there are steep topographic and rainfall gradients in the area and the averaged climate data for the 0.5 degree square may not be representative of the experimental site.

Discussion

How old are the fire-dependent ecosystems?

The SDGVM results broadly support Acocks' view that many veld types are not at equilibrium with climate — they are 'false'. However the extent of 'false' vegetation is much greater, at least according to the DGVM predictions, than mapped by Acocks. Acocks suggested that the current extent of flammable vegetation owed much to human activities, especially forest clearing by Iron Age settlers. At the

Table 1: Results of long-term fire exclusion experiments and observations in grassy ecosystems and fynbos ranked by rainfall. A result of 1 = colonisation of fire-sensitive forest species; 2 = increased tree density or basal area, no trend to forest; 3 = no change in composition or woody plant invasion. Methods include: expt = fire exclusion compared to fire maintained; photo = photographic evidence, fire history not well documented; farmer = L Howell, Hillside, reported by Sue van Rensburg; obs/expt = changes in areas of known fire history, including long-term fire exclusion. Authors are listed in the references. Acocks = Acocks veld type number. Rainfall is from the original publication of Schultze 1997. Period is as listed in the publication or when observations were made for unpublished observations. Trends in KNP (Kruger National Park) are unpublished observations of Bond (2001). Biomass is simulated biomass for the closest 0.5 degree square using the no fire SDGVM simulation

No.	author	veld type	Acocks	location	long	lat	rainfall mm	method	period y	result	Biomass g C m ⁻²
GRASSY ECOSYSTEMS											
1	Everson, Breen	sourveld	44	Drakensberg	29	29.1	1 000	expt	32	1	7 000
2	Titshall <i>et al.</i>	sourveld	63	Athole	30.32	26.32	992	expt	45	1	16 989
3	Westfall <i>et al.</i>	sourveld	44a	Thabamhlope	29.31	29.12	900	expt	42	1	12 987
4	Skowno <i>et al.</i>	<i>A. karroo</i> savanna	6	Hluhluwe	32.08	28.05	800	photo	25	1	13 419
5	Titshall <i>et al.</i>	sourveld	44b	Dohne	27.25	32.31	762	expt	34	1	13 351
6	Unpublished	<i>Terminalia</i> mesic savanna	9	KNP	31.15	25.1	750	expt	50	1	8 920
7	Hoffman, O'Connor	<i>Acacia</i> savanna	23	Weenen	30	28.5	700	photo	45	1	16 280
8	Titshall <i>et al.</i>	sourveld	65	Ukulinga	30.24	29.4	694	expt	49	1	14 256
9	Unpublished	<i>Combretum</i> savanna	10	KNP	31.3	25.06	650	expt	50	2	1 127
10	Trollope	<i>A. karroo</i> veld	21/22	Fort Hare	26.53	32.47	590	expt	29	2	8 789
11	Unpublished	<i>A. nigrescens</i> savanna	11	KNP	31.5	24.23	550	expt	50	2	580
12	Unpublished	<i>Colophospermum</i> savanna	15	KNP	31.2	23.4	450	expt	50	2	570
13	Van Rensburg	arid grassland	50	Free state	26	30	450	farmer	50	3	288
FYNBOS											
14	Manders <i>et al.</i>	fynbos	69	Jonkershoek	18.55	33.57	>1 500	obs/expt	50	1	4 391
15	Masson, Moll	fynbos	69	Cape Peninsula	18.2	34.05	1 227	obs	100	1	4 391

time (1954), these farmers were thought to have began settling in South Africa from about 1400 AD. We now know that Iron Age farmers first entered South Africa about 1 000 years earlier (see e.g. Hoffman (1997) for a review of human activity in South Africa). However despite the greater time this would allow for forest clearance, the growing consensus has been that the current distribution of grasslands (and fynbos) pre-dates intensive farming activities by thousands of years (Ellery and Mentis 1992, Meadows and Linder 1993, O'Connor and Bredenkamp 1997). Of course fire was used by humans long before agriculture was invented. The earliest association between fire and hominids is dated at about 1.8 million years (Brain and Sillen 1988) but regular domestic use of fire may only have commenced about 100 000 years ago based on the frequency of hearths in the archaeological record (Deacon and Deacon 1999). We discuss evidence below that grasslands appeared millions of years before anthropogenic fires became a significant factor in Africa or elsewhere.

Is the current distribution of grassy ecosystems determined by past anthropogenic activities?

Ellery and Mentis (1992) and Meadows and Linder (1993) challenged Acocks' view that South Africa's grasslands are of anthropogenic origin. There is now a diversity of evidence that the grasslands are ancient.

1) Palaeo evidence

Dated pollen cores from a number of sites show that grassland dominated most of the summer rainfall in montane areas throughout the Holocene (Meadows and Linder 1993).

Grasslands were even more extensive in the last glacial (Scott *et al.* 1997, Scott 1999). Savanna trees disappeared from South African grasslands as far north as Wonderkrater (24°30'S) (>40 000yr BP to 12 000yr BP). Vegetation resembling the current savanna woodlands is less than 10 000 years old (Scott 1999). Charcoal evidence from Tswaing crater indicates that fires have been burning for 160 000 years with no obvious sign of an increase with the appearance of farmers in the last millennium (Scott 2002b). The palaeo-record implies that South Africa was even more treeless before agricultural settlement. The implications of the tree-less state of most of South Africa over the last glacial have yet to be assimilated by ecologists. What happened to the large mammal savanna fauna? Is colonisation of grasslands by savanna trees still in progress?

Carbon isotopes can be used to distinguish between grassland or wooded vegetation because of their different isotopic signals. Most summer rainfall grasslands are dominated by grasses with a C₄ photosynthetic pathway (Vogel *et al.* 1978). Organic matter derived from these grasses has a carbon isotope signature quite distinct from trees, shrubs and forbs which have a C₃ signal. Isotopic changes at different depths in the soils can be used to indicate past shifts in vegetation from C₄ grasses to C₃ plants. The depth of the organic matter in the soil is a surrogate of age. There is no evidence, from analyses of carbon isotope signals in soil organic matter, that grasslands have been replaced by forests. On the contrary, in Hluhluwe, in eastern Kwa-Zulu Natal, forests have replaced an earlier grass-dominated vegetation (West *et al.* 2000). An extensive analysis of carbon isotope composition of soil organic matter in the Transkei (Foord 1999) and Kwa-Zulu Natal (Foord 2001)

also found no support for recent expansion of grasslands at the expense of forests. On the contrary, more sites showed evidence of forest expansion than forest retreat. Unfortunately, switches in vegetation recorded in soil organic matter are difficult to date so we cannot date these changes with any precision.

2) The history of grasslands: biological indicators

If flammable vegetation was recent, and had spread due to anthropogenic fires, we would expect the vegetation to have low diversity and low endemism of both fauna and flora. The grasslands occupying vast areas of the western side of Madagascar are an example. They are thought to post-date human settlement of the island some 2000 years ago. The grasslands are dominated by very few grass species and the few trees that survive the frequent fires also occur in forests (White 1983). In contrast, South African grassland floras are rich in species including many endemics (Cowling and Hilton Taylor 1997). This is true not only for plants but also for the fauna. Eleven globally threatened bird species have major centres in the grassland biome and five of these are entirely restricted to the biome.

Iron Age settlers might, indeed, have had an influence on the extent and current distribution of grasslands and shrubland formations of the winter rainfall regions. However their effects appear to be local and there is no evidence to support the massive impact suggested by Acocks.

Attributes of climate dependent grassy ecosystems (CDEs) vs fire-dependent ecosystems (FDEs)

In this section we discuss the attributes of climate-dependent grassy ecosystems (CDEs) versus fire-dependent ecosystems (FDEs). Contrary to Acocks we suggest that CDEs are limited to arid environments. There are no mesic grasslands where trees are excluded by cold. Highveld grasslands are well below global tree-line and could support trees. This is readily evident in the invasion of many such grasslands by alien trees including conifers and wattle *Acacia mearnsii*. Only the highest grasslands of the Drakensberg (*Themeda-Festuca* veld) may be true cold-limited grasslands and genuinely above tree-line. Though fire burns in both CDEs and FDEs, its effects are different. In arid savannas, fire influences tree densities but does not change ecosystem type (Table 1, Figure 5). In FDEs frequent fires prevent succession to closed forest or thicket that is too shady to support a grassy understorey. The distinction is readily apparent in the 50 year fire experiments at Kruger National Park (the results of these experiments are currently being analysed by a number of researchers but published information is still sparse). Fire exclusion has resulted in the colonisation of fire-sensitive forest species at the most mesic sites near Pretoriuskop (750mm rainfall p.a.) on sandy granite soils (WB, personal observation). There is no comparable invasion of forest species at the Numbi site on similar granite substrates but at lower rainfall (c. 650mm p.a.). Nor is there any sign of invasion of forest or thicket species in the exclusion plots on basalt soils at Satara (*Acacia nigrescens/Sclerocarya* woodland; 550mm rainfall p.a.) or in *Colophospermum mopane* woodlands (450mm

p.a.) (Gertenbach and Potgieter 1979). However there are significant differences in tree densities and sizes of the dominant species in the arid savanna sites (Shackleton and Scholes 2001 for Satara, Bronn and Smit 2002 for mopane). The Kruger experiments suggest that the lower rainfall limit for forest invasion in the absence of fire is c. 700mm on sandy soils, and presumably somewhat higher for clay soils. As a first approximation, then, CDEs predominate at sites with rainfall <650mm and FDEs above this threshold in South Africa. This is consistent with similar divisions of grassy ecosystems into arid versus mesic savanna and sweetveld versus sourveld (Bond 1997, Huntley 1984). It is interesting to note that 'rainforests' in Australia, a fire-intolerant vegetation type similar to our forests and thickets, also has a lower rainfall limit of about 650mm. In Australia, too, these communities are rare in most landscapes which are dominated by flammable (FDE) vegetation (Bowman 2000).

Floristic and functional differences between CDEs and FDEs

Grasses

Grasses of the C₄ photosynthetic pathway dominate almost all South Africa's summer rainfall grasslands and savannas (Vogel *et al.* 1978, Schulze *et al.* 1996). However there is apparent specialisation, at sub-family level, for arid versus mesic areas (Gibbs Russell 1988). The Chloridoideae dominate in regions with <600mm of rain outside the tropics and <500mm of rain in tropical regions. They form the dominant component, in terms of proportion of species, of the CDEs. Typical genera include: *Chloris*, *Cynodon*, *Enteropogon*, *Eustachys*, *Perotis*, *Tragus*, *Eleusine*, *Eragrostis*, *Dinebra*, *Trichoneura*, *Sporobolus*, and *Fingerhuthia*. In contrast, the Andropogoneae form the largest percentage of the grass flora in mesic summer rainfall areas, the FDEs. They include the dominant genera of sourveld and mesic savannas: *Themeda*, *Heteropogon*, *Hyparrhenia*, *Hyperthelia*, *Andropogon*, *Trachypogon*, *Cymbopogon*, *Tristachya*, *Schizachyrium*, and *Sorghastrum* (Kellogg 2000). Paniceae, including the variable genus *Panicum*, reach their highest percentage of the grasses in arid summer rainfall regions (Gibbs Russell 1988). This specialisation of grass groups to CDEs or FDEs also occurs in North America where Andropogoneae dominate in mesic areas of the east and south-east and Chloridoideae in the arid south-west (Barkworth and Capels 2000). Similar patterns have been reported at a global scale (Hartley 1958, Hartley and Slater 1960). The key group capable of displacing forests from mesic areas is thus the Andropogoneae and it is members of this group that constitute the dominant cover of FDEs world-wide.

Functionally, there are a number of features of Andropogoneae that may help promote fire. All the species have the NADP-me (malate) enzyme for C₄ photosynthesis (Kellogg 2000) which has the highest quantum yield (leaf level ratio of photosynthetic carbon gain to photons absorbed, Ehleringer *et al.* 1997). They are highly productive grasses capable of producing in excess of 10 tons ha⁻¹ in a single season's growth under suitable climatic conditions (Scholes and Walker 1993) and therefore able to sustain

intense burns on an annual basis under suitable climatic conditions. Andropogoneae are the dominant constituents of 'sourveld' and lose their nutritional value towards the end of the growing season. The low nutritional value reduces decomposition rates and un-decomposed litter accumulates in successive growing seasons producing a highly flammable fuel. Tannin-like substances (TLS) accumulate in the leaves of many sourveld species and are a common feature of Andropogonoid grasses (Ellis 1990). They are much less common in sweetveld grasslands. Ellis (1990) suggested that they might function to reduce herbivory and may inhibit nitrification in the soil by reducing microbial activity. Similarly, TLS might act to reduce decomposition rates, promoting fuel build-up. TLS varies within species and among populations (Ellis 1990) suggesting that tannin concentrations are under active selection and that selection pressure varies in different areas. More research on the function of TLS is needed.

A by-product of slow decomposition is that some of the commonest grasses in FDEs have an obligate dependence on defoliation, usually by fire. This is because they produce basal tillers which makes them susceptible to shading by old undecomposed material persisting from previous growing seasons (e.g. Everson *et al.* 1988, O'Connor and Bredenkamp 1997). In the absence of burning, the dominant grasses often rapidly decline in importance. *Themeda triandra*, for example, drops from 70% cover to <10% after only three years of fire exclusion in the Midlands of Natal (Tainton and Mentis 1984, Le Roux 1989, Uys 2000). Similar rapid decline of dominant Andropogonoid grasses in the absence of burning has been reported in North American prairies (Hulbert 1969), South America (Silva and Castro 1989), Australia (Morgan and Lunt 1999) and south-east Asia (Stott 1988).

Grasses dominating CDEs typically have the NAD or PCK form of C_4 photosynthesis (Ehleringer *et al.* 1997, Gibbs Russell 1988). They remain palatable in the dry season and might be expected to show higher rates of litter decomposition than andropogonoid grasses and therefore less 'carry-over' from one growing season to the next. However there is very little information on 'carryover' and its effect on fuel properties for any South African grasses. CDE grasses have variable morphology (FDEs are typically tufted 'bunch' grasses in South Africa) including forms with laterally spreading runners, and aerial tillering is common in frost-free areas (Van Rensburg 2002, pers. comm.). They are tolerant of long fire-free periods and may be less prone to becoming moribund in the absence of burning or grazing (Tainton and Mentis 1984).

Trees

There are distinct differences between the trees of FDEs and CDEs with the former equivalent to 'broad-leaved savanna' and the latter 'fine-leaved savanna' (Scholes and Walker 1993). Members of the Caesalpinioideae dominate in FDEs in the tropics while Mimosaceae, and especially *Acacia* dominate in CDEs (White 1983). This distinction breaks down in South Africa where few caesalpinoids reach mesic savannas in the east and south-east (Pooley 1993). Instead a few species of *Acacia* dominate in these areas (e.g. *A. karroo*, *A. sieberiana*, *A. caffra*, *A. davyi*). The lack of tropical FDE taxa in southern parts of South Africa might

reflect younger, more nutrient-rich soils, delayed dispersal following the elimination of savanna trees from most of the country in the last glacial (Scott 1999) or physiological intolerance of freezing — experimental work is needed! *Colophospermum mopane* is a remarkable exception to the general pattern. Though it is a caesalpinoid it is dominant in vast nearly mono-specific stands in many arid savannas (Acocks 1953, White 1983, Low and Rebelo 1996).

The tree flora of grassy CDEs and FDEs appears to be phylogenetically distinct from species of closed forests. Taxa differ at family, generic and species level (Acocks 1953). However we know of no formal analysis of floristic affinities and differences between trees of grassy fire-prone ecosystems and forest or thicket formations which are intolerant of burning.

Adaptations of trees to FDEs, as opposed to arid savannas or forests have been very little studied in southern Africa. Frost (1984) provides one of the few accounts of fire 'adaptations' in savannas. In fynbos and other fire-prone shrublands, there is clear evidence for fire-adapted features, especially features associated with fire-stimulated reproduction (Le Maitre and Midgley 1992, Brown 1993, Bond and Van Wilgen 1996). Fires are so frequent in mesic savannas, and grass regrowth so rapid, that it is unlikely that savanna trees would have evolved fire-stimulated recruitment traits. Indeed there is very little evidence for obligate dependence on fire to stimulate germination of savanna trees. Many species show reduced germination after heating and, unlike species of flammable shrublands (e.g. Brown 1993), there are no reports of an obligate dependence of savanna tree seeds on fire for germination (Okello and Young 2001, Bond 1997).

We suggest that a distinctive feature of many savanna trees is the ability to recruit into grasslands. Trees of forest, thicket or 'bush clump' savannas, such as those of the eastern Cape, appear to lack this ability. Tolerance of very frequent fires, especially in the juvenile stages, is a key requirement for savanna trees recruiting into the grass stratum of FDEs. Many species appear to have saplings with a pole-like form promoting rapid height growth, and a lignotuber which stores reserves to subsidise vigorous post-burn sprouting (Boaler 1966, Bond and Van Wilgen 1996, Gignoux *et al.* 1997, Maze 2001). *Acacia karroo* is an interesting species because it is highly plastic in form and occurs across a wider range of environments, including CDEs and FDEs. Archibald and Bond (in press) showed that *A. karroo* had saplings with a pole-like form in frequently burnt savannas. In contrast, it had a broadly spreading, cage-like architecture in arid shrublands, and in coastal dune forests that do not burn but where browsing pressure is high. Archibald and Bond suggest that selection for fire survival over-rides selection against herbivory since spines and structural defences were weakly developed in populations subjected to frequent burning. Functional interpretations of savanna trees are still in their infancy and there is great scope for comparative studies of tree form and function in FDEs, and CDEs where browsing may be heavier. Selective pressures in both types of savannas should differ strongly from trees growing in forests where light is a major limiting factor.

Forbs

There is very limited information on the floristic or functional differences between forbs of CDEs and FDEs. Many forbs of sourveld areas seem characterised by large underground storage organs enabling them to resprout and flower very rapidly after burning (Bayer 1955, Hilliard and Burt 1987, Uys 2000). These growth forms are extremely resistant to frequent grass fires but decline in the absence of fire (Uys 2000). There are few, if any, annual forb species in mesic grasslands and seedbanks appear to be very rare (Uys 2000, Mativandlela 2001). In contrast, underground storage organs appear to be the exception among dicot forbs in CDEs but species with dormant seedbanks appear common. Annuals are common and emerge when the grass cover is broken by grazing or drought (Uys 2001, pers. comm., Mativandlela 2001). The very preliminary work available suggest that the functional types may be very different in the two grassland types with fire-tolerant sprouting species in mesic grasslands and many more annuals or short-lived perennials in CDEs. The floristic affinities of the forb elements have not been studied but we would predict different phylogenetic relationships for arid versus mesic grassland and for both groups compared to forest forbs.

On the origins of grassy FDEs

The origin of South Africa's grasslands is only a small part of a global story of the evolution of grasses which has begun to unfold over the last ten years. The appearance of grasslands can be traced from hypsodont (high-crowned) dentition of fossil herbivores (reviewed in MacFadden 2000). The appearance of C_4 dominated grasslands can be traced from their distinctive carbon isotope signature which can be detected in palaeosols and in the bones of grazers (Cerling *et al.* 1997). These markers together help us to trace the appearance of grassland as a vegetation while pollen and macro-fossils provide evidence for the origin of grass taxa. The results of such studies have been recently reviewed (Jacobs *et al.* 1999). The earliest undisputed fossil evidence for grass is in the Palaeocene, some 65M yr BP. The earliest evidence for dentition adapted to a grass diet is from South America some 35M yr BP. Grazers on other continents only appeared in the mid Miocene, c. 15M yr BP, or later (MacFadden 2000). Grasslands had begun to spread on all continents by the late Miocene, based on a variety of evidence (Jacobs *et al.* 1999).

Between eight and six million years ago, isotope evidence from fossil tooth enamel and palaeosols indicates an abrupt appearance of C_4 grasslands in Asia, Africa, North America and South America (Cerling *et al.* 1997). The change from preceding C_3 communities to C_4 grasslands first occurred at lower latitudes from which C_4 grasses spread. The speed of change is startling, as is its parallel development on different continents. The remarkably rapid dispersal of C_4 grasses around the planet has yet to be explained. How, for example, did *Themeda triandra* spread to Africa, India, south-east Asia and Australia, across ocean barriers in the latter case, in the brief seven million years of C_4 grassland emergence? Why are there such close phylogenetic relationships among the grass taxa but very different phylogenetic affinities of

savanna trees on each continent (Bond and Van Wilgen 1996)?

The early history of grasslands in South Africa is still poorly documented. For most of the Tertiary, the vegetation appears to have been broad-leaved forests, thickets and strandveld-like assemblages. Several Miocene sites in the arid western half of the country show evidence for forests (Scott *et al.* 1997). For example, some 12M yr BP, forests occurred in the Orange River Valley in an area that is now desert and forest and closed woodlands were still dominant at Langebaan Weg some 5M yr BP (Scott *et al.* 1997). In the summer rainfall areas, cheetahs were present at Makapansgat by 3M yr BP suggesting that grassy ecosystems occurred there at that time (Turner 1985). A large turnover of bovids occurred at about 2.5M yr BP in sub-Saharan Africa which has been attributed to a spreading of open grassy formations (Vrba 1985). Taken together, the evidence suggests that C_4 grasslands and savannas are of Plio/Pleistocene origin in South Africa. The C_4 grassy biomes, here and elsewhere, are among the most recent vegetation formations in earth history, appearing long after the continents had drifted to their current position.

There has been no attempt, as yet, to separately trace the origins of arid versus mesic-adapted grasslands. However sub-families of grasses can be identified from phytoliths and preliminary work suggests that Chloridoideae can be separated from Andropogoneae and other groups in sediment cores (Scott 2002a). It may, in future, be possible to reconstruct the history of FDEs as distinct from CDEs in order to trace the origins of FDEs and their effects on forests, independently of aridity impacts. Indeed a start has already been made on Late Pleistocene reconstructions on Mount Kenya where the evidence suggests expansion of Andropogonoid grasses in the last glacial, increased fire, and the retreat of forests. Forest re-colonised the grasslands in the Holocene (Wooller *et al.* 2000). Over longer time scales, Herring (1985) reported that charcoal fluxes analysed from deep sea sediment cores in the Pacific increased by more than an order of magnitude from 10M yr BP to 1M yr BP. Bird and Cali (1998) reported charcoal also from marine cores off the coast of West Africa over a million year period. Their results suggested a marked increase in charcoal for the last 200 000 years of the record. Late Tertiary charcoal deposits from marine cores have not yet been analysed from the South African coast. The interpretation of carbon in sediments is controversial and an active area of research so that earlier results, such as those of Herring (1985) should be treated with caution (Schmidt and Noack 2000). Nevertheless carbon analysis off the shores of South Africa offers a promising tool for detecting when fires began to burn and when FDEs began to spread.

Why did FDEs come into being?

Fires have occurred since the Devonian, some 400M yr BP (Scott 2000) and long before hominids first used fire in Africa. However fire-prone angiosperm-dominated vegetation appears only to be of late Tertiary origin. Why did these flammable formations begin to spread and carve out the ancestral forests so late in earth history? Given the long his-

tory of fire it seems unlikely that natural ignition sources, chief of which is lightning, were ever limiting for large regions for long periods of time. It is interesting to note that fynbos, an FDE, burns from lightning strikes even though lightning flash densities in the western Cape are far lower than in the montane grasslands of the Drakensberg (Edwards 1984). Seasonally dry climates are often considered to be a prerequisite for fire. However large fires have occurred recently in humid tropical rainforests, usually following logging (Nepstad *et al.* 1999). The occurrence of fire depends on weather, not climate. Two or three weeks of dry weather is all that is required to dry out suitable fuels and permit burning (Nepstad *et al.* 1999). The availability of suitable fuel is an important requirement. Afro-temperate forests burn much less readily than fynbos (Van Wilgen *et al.* 1990) because of the spatial arrangement of potential 'fuels'. Did fires begin to burn when new, flammable, growth forms evolved? It seems unlikely since grass pollen has been found in the Palaeocene, some 50 million years before grasslands emerged as a new vegetation type. Why did grasses take so long to spread as FDEs given their early origin?

One possible explanation is linked to changing atmospheric CO₂. There has been considerable recent interest in the potential importance of low atmospheric CO₂ in promoting the spread of C₄ grasslands. Atmospheric CO₂ is thought to have declined through the Tertiary (Berner 1997). C₄ grasses have a photosynthetic advantage over C₃ grasses at low CO₂ and at higher growing season temperatures (Ehleringer *et al.* 1997). Ehleringer *et al.* (1997) have argued that the rapid appearance of C₄ grasses c. 7M yr BP is coincident with CO₂ levels dropping below 500ppm, the concentration at which C₄ grasses would first have gained a photosynthetic advantage over C₃ grasses at equatorial latitudes. CO₂ levels dropped even lower in the Pleistocene falling to 180ppm during glacial periods (Petit *et al.* 1999). At such low CO₂, C₄ grasses should have gained a photosynthetic advantage over C₃ grasses over a wide range of growing season temperatures. Ehleringer *et al.* (1997) noted that C₄ grasses expanded in many tropical areas, including on Mount Kenya, during the last glacial and attributed the increase to their relative photosynthetic advantage at low CO₂ concentrations. The implication is that C₄ grasses, and therefore fire-dependent grassy ecosystems, might have evolved as an indirect response to low atmospheric CO₂ in the late Tertiary and Quaternary.

Low CO₂ might also be implicated more directly in the spread of flammable vegetation (Bond and Midgley 2000). This is because low atmospheric CO₂ could reduce post-burn recovery rates of trees relative to flammable growth forms such as grasses or shrubs. Slow recovery rates at low CO₂ would favour the spread of grasses and reduction of trees. Simulation analyses support these predictions showing that savanna trees would have been eliminated from representative South African sites under growing conditions of the last glacial CO₂ (Bond, Midgley, Woodward in press). The simulations show trees present, but at low densities, for interglacial concentrations of CO₂ (270ppm). CO₂ has increased by a third following increased industrialisation and the use of fossil fuel and is currently higher than at anytime for at least the last half million years (Petit *et al.* 1999). Simulated tree densities under current CO₂ concentrations

(360ppm) increase sharply because of the fertilising effect on tree growth, a pattern possibly reflected in widespread bush encroachment in many South African grasslands (Bond *et al.* in press). Bond *et al.* (in press) suggest that fire, interacting with low CO₂, might have promoted the spread of FDEs because of the slow recovery rate of trees and that this mechanism might have contributed to the spread of FDEs from the late Tertiary.

Conclusions

The appearance of FDEs, including both grassy ecosystems and fire-prone shrublands, from the late Tertiary has received remarkably little attention in the literature. In their review of grass evolution, Jacobs *et al.* (1999) do not mention the fact that grasslands burn and that fire might have promoted their spread. Stebbins (1981) has been widely cited for the hypothesis that grazers co-evolved with grasslands. However a careful reading of this paper shows that he argued that herbivores evolved in response to the appearance of grasslands and that only a few grasses, low spreading forms, might have evolved in response to herbivores. Cerling *et al.* (1997) point out that C₄ grasses should generally be less palatable to grazers than C₃ grasses. They note that herbivore diversity fell with the spread of C₄ grasses and that the composition of grazing faunas suffered a major turn-over of species. In South Africa, there are very few mammal grazers restricted to sourveld and these are thought to have occurred in small herds or as migratory groups that moved seasonally to more rewarding winter grazing (Huntley 1984). In contrast, large herds of grazers were (and still are) supported in sweetveld (CDE) areas. Fire, not grazing, seems the key agent of disturbance in mesic C₄ grasses and burning, unlike grazing, is known to promote the spread of these ecosystems at the expense of woody plants.

Acocks was too astute a field biologist to miss the importance of fire in shaping the vegetation of the higher rainfall eastern parts of South Africa. However, like most ecologists of the time, he had difficulty in accepting the importance of fire in shaping regional vegetation long before humans mastered fire for domestic purposes. At least we now know that fire is of great antiquity (Scott 2000). A full appreciation of its evolutionary and biogeographic significance in South Africa and elsewhere is long overdue.

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References

- Acocks JPH (1953) Veld types of South Africa. *Memoirs of the Botanical Survey of South Africa* 28: 1–192
- Archibald S, Bond WJ (in press) Growing tall vs growing wide: Tree architecture and allometry of *Acacia karroo* in forest, savanna, and arid environments. *Oikos*

- Barkworth ME, Capels KM (2000) Grasses in North America: a geographic perspective. In: Jacobs SWL, Everett J (eds) *Grasses: Systematics and Evolution*. CSIRO, Melbourne, pp 331–350
- Bayer AW (1955) The ecology of grasslands. In: Meredith D (ed) *The Grasses and Pastures of South Africa*. CNA, Union of South Africa
- Beadle NCW (1966) Soil phosphate and its role in molding segments of the Australian flora and vegetation with special reference to xeromorphy and sclerophylly. *Ecology* **47**: 992–1007
- Beerling DJ, Woodward FI (2001) *Vegetation and the Terrestrial Carbon Cycle: Modelling the First 400 Million Years*. Cambridge University Press, Cambridge
- Berner RA (1997) The rise of plants and their effect on weathering and atmospheric CO₂. *Science* **276**: 544–546
- Bird MI, Cali JA (1998) A million year record of fire in subsaharan Africa. *Nature* **394**: 767–769.
- Boaler SB (1966) The ecology of *Pterocarpus angolensis* in Tanzania. Overseas research Publication 12, Ministry of Overseas Development, London
- Bond WJ (1997) Fire. In: Cowling RM, Richardson D (eds) *Vegetation of Southern Africa*. Cambridge University Press, Cambridge, UK, pp 421–446
- Bond WJ, Midgley GF (2000) A proposed CO₂-controlled mechanism of woody plant invasion in grasslands and savannas. *Global Change Biology* **6**: 1–5
- Bond WJ, Midgley GF, Woodward FI (in press) The importance of low atmospheric CO₂ and fire in promoting the spread of grasslands and savannas. *Global Change Biology*
- Bond WJ, Van Wilgen BW (1996) *Fire and Plants*. Population and Community Biology Series 14. Chapman and Hall, London
- Bowman DMJS (2000) *Australian Rainforests: Islands of Green in a Land of Fire*. Cambridge University Press, Cambridge.
- Brain CK, Sillen A (1988) Evidence from the Swartkrans cave for the earliest use of fire. *Nature* **336**: 464–466
- Bronn AvZ, Smit GN, Potgieter ALF (2002) Effect of long term fire regime and herbivory on the structure of the woody component of the *Colophospermum mopane* shrubveld in the Kruger National Park. In: Seydack AHW, Vorster T, Vermuelen WJ, Van der Merwe IJ (eds) *Multiple use management of natural forests and woodlands: policy refinements and scientific progress*. DWAFF, Forestry, Pretoria, pp 155–163
- Brown NAC (1993) Promotion of germination of fynbos seeds by plant-derived smoke. *New Phytologist* **122**: 1–9
- Catchpole W (2002) Fire properties and burn patterns in heterogeneous landscapes. In: Bradstock RA, Williams JE, Gill AM (eds) *Flammable Australia: the Fire Regimes and Biodiversity of a Continent*. Cambridge University Press, Cambridge, pp 49–76
- Cerling TE, Harris JM, MacFadden BJ, Leakey MG, Quade J, Eisenmann V, Ehleringer JR (1997) Global vegetation change through the Miocene/Pliocene boundary. *Nature* **389**: 153–158
- Cowling RM, Hilton-Taylor C (1997) Phytogeography, flora and endemism. In: Cowling RM, Richardson D (eds) *Vegetation of Southern Africa*. Cambridge University Press, Cambridge, pp 43–61
- Cramer W, Bondeau A, Woodward FI, Prentice IC, Betts RA, Brovkin V, Cox PM, Fisher V, Foley JA, Friend AD, Kucharik C, Lomas MR, Ramankutty N, Sitch S, Smith B, White A, Young-Molling (2001) Global response of terrestrial ecosystem structure and function to CO₂ and climate change: results from six dynamic global vegetation models. *Global Change Biology* **7**: 357–373
- Deacon HJ, Deacon J (1999) *Human Beginnings in South Africa: Uncovering the Secrets of the Stone Age*. David Philip, Cape Town, South Africa
- Edwards D (1984) Fire regimes in the Biomes of South Africa. In: Booysen P de V, Tainton NM (eds) *Ecological Effects of Fire in South African Ecosystems*. Springer-Verlag, Berlin, pp 19–38
- Eeley HAC, Lawes MJ, Piper SE (1999) The influence of climate change on the distribution of indigenous forest in KwaZulu-Natal, South Africa. *Journal of Biogeography* **26**: 595–617
- Ehleringer JR, Cerling TE, Helliker BR (1997) C₂ photosynthesis, atmospheric CO₂, and climate. *Oecologia* **112**: 285–299
- Ellery WN, Mentis MT (1992) How old are South Africa's grasslands? In: Furler PA, Proctor J, Ratter JA (eds) *Forest Savanna Boundaries*. Chapman and Hall, London, pp 659–682
- Ellery WN, Scholes RJ, Mentis MT (1991) Differentiation of the grassland biome of South Africa based on climatic indices. *South African Journal of Science* **87**: 499–503
- Ellis RP (1990) Tannin-like substances in grass leaves. *Memoirs of the Botanical Survey of South Africa* **59**: 59–77
- Everson CS, Everson TM, Tainton NM (1988) Effects of intensity and height of shading on the tiller initiation of six grass species from the Highland sourveld of Natal. *South African Journal of Botany* **54**: 315–318
- Everson CS, Breen CM (1983) Water stress as a factor influencing the distribution of the ericoid shrub *Phyllipia evansii* in the Natal Drakensberg mountains, South Africa. *South African Journal of Botany* **2**: 290–296
- Feely JM (1987) *The early farmers of Transkei, southern Africa before AD 1870*. Cambridge Monographs in African Archaeology 24 BAR International Series 378, Oxford
- Food and Agriculture Organization of the United Nations (1998) *World reference base for soil resources*. FAO, Rome. <http://www.fao.org/ag/agl/agll/prtsoil.stm>
- Foord J (1999) *Transkei Grasslands: Recent or Ancient?* Honours project, Botany Department, University of Cape Town, Cape Town, South Africa
- Foord J (2001) *Palaeo-distribution of Afromontane Forests in KwaZulu-Natal*. MSc thesis, Conservation Biology, University of Cape Town, Cape Town, South Africa
- Frost PGH (1984) The responses and survival of organisms in fire-prone environments. In: Booysen P de V, Tainton NM (eds) *Ecological Effects of Fire in South African Ecosystems*. Springer-Verlag, Berlin, pp 273–309
- Gertenbach WPD, Potgieter ALF (1979) Veldbrandnavorsing in die struikmopanieveld van die Nasionale Krugerwildtuin. *Koedoe* **22**: 1–28
- Gibbs Russell GE (1988) Distribution of subfamilies and tribes of Poaceae in southern Africa. *Monographs in Systematic Botany, Missouri Botanical Garden* **25**: 555–566
- Gignoux J, Clobert J, Menaut JC (1997) Alternative fire resistance strategies in savanna trees. *Oecologia* **110**: 576–583
- Hartley W (1958) Studies on the origin, evolution and distribution of the Gramineae. I. The tribe Andropogoneae. *Australian Journal of Botany* **6**: 116–128
- Hartley W, Slater C (1960) Studies on the origin, evolution and distribution of the Gramineae. III. The tribes of the subfamily Eragrostoideae. *Australian Journal of Botany* **8**: 256–276
- Herring JR (1985) Charcoal fluxes into sediments of the North Pacific Ocean: The Cenozoic record of burning. In: Sundquist ET, Broecker WS (eds) *The Carbon Cycle and Atmospheric CO₂: Natural Variations Archaean to Present*. *American Geophysical Union Geophysical Monograph Series* **32**: 419–422
- Hilliard OM, Burt BL (1987) *The Botany of the Southern Natal Drakensberg*. National Botanic Gardens, Cape Town, South Africa
- Hoffman MT (1997) Human impacts on vegetation. In: Cowling RM, Richardson D (eds) *Vegetation of Southern Africa*. Cambridge University Press, Cambridge, UK, pp 507–534
- Hoffman MT, O'Connor T (1999) Vegetation change over 40 years in the Weenen/Muden area, KwaZulu-Natal: evidence from photo-panoramas. *African Journal of Range and Forage Science* **16**: 71–88
- Hulbert LC (1969) Fire and litter effects in undisturbed bluestem

- prairie. *Ecology* **30**: 874–877
- Huntley BJ (1984) Characteristics of South African Biomes. In: Booysen P de V, Tainton NM (eds) *Ecological Effects of Fire in South African Ecosystems*. Springer-Verlag, Berlin, pp 1–18
- Jacobs BF, Kingdon JD, Jacobs LL (1999) The origins of grass-dominated ecosystems. *Annals of the Missouri Botanical Garden* **86**: 590–643
- Jenkins JC, Birdsey RA, Pan Y (2001) Biomass and NPP estimation for the mid-Atlantic region (USA) using plot-level forest inventory data. *Ecological Applications* **11**: 1174–1193
- Kellogg EA (2000) Molecular and morphological evolution in the Andropogoneae. In: Jacobs SWL, Everett J (eds) *Grasses: Systematics and Evolution*. CSIRO, Melbourne, pp 149–158
- Krebs CJ (2001) *Ecology: the Experimental Analysis of Distribution and Abundance* (5th edn). Benjamin Cummings, San Francisco
- Le Maitre DC, Midgley JJ (1992) Plant reproductive ecology. In: Cowling RM (ed) *The Ecology of Fynbos: Nutrients, Fire and Diversity*. Oxford University Press, Cape Town, pp 135–174
- Le Roux CJG (1989) Die invloed van brand en maai op onbeweide langrasveld in Natal. (The effect of burning and mowing on ungrazed tall grassveld of Natal). *Journal of the Grassland Society of South Africa* **6**: 59–64
- Low AB, Rebelo AG (1996) *Vegetation of South Africa, Lesotho and Swaziland*. Department of Environmental Affairs and Tourism, Pretoria, South Africa
- MacFadden BJ (2000) Cenozoic mammalian herbivores from the Americas: Reconstructing ancient diets and terrestrial communities. *Annual Review of Ecology and Systematics* **31**: 33–59
- Manders PT, Richardson DM, Masson PH (1992) Is fynbos a stage in succession to forest? Analysis of the perceived ecological distinction between two communities. In: Van Wilgen BW, Richardson DM, Kruger FJ, Van Hensbergen HJ (eds) *Fire in South African Mountain Fynbos*. Ecological Studies 93, Springer Verlag, Heidelberg, pp 81–107
- Masson PH, Moll EJ (1987) The factors affecting forest colonisation of fynbos in the absence of fire at Orange Kloof, Cape Province, South Africa. *South African Forestry Journal* **143**: 5–10
- Mativandilela S (2001) *The Effects of Frequency and Season of Clearing on Species Diversity and Species Richness in Grassy Patches*. Honours thesis, Botany Department, University of Venda, South Africa
- Maze KE (2001) *Fire Survival and Life Histories of Acacia and Dichrostachys Species in a South African Savanna*. MSc thesis, Botany Department, University of Cape Town, South Africa
- Meadows ME, Linder HP (1993) A palaeoecological perspective on the origin of Afrotropical grasslands. *Journal of Biogeography* **20**: 345–355
- Morgan JW, Lunt ID (1999) Effects of time since fire on the tussock dynamics of a dominant grass (*Themeda triandra*) in a temperate Australian grassland. *Biological Conservation* **88**: 379–386
- Nepstad DC, Verissimo A, Alencar A, Nobre C, Lima E, Lefebvre P, Schlesinger P, Potter C, Moutinho P, Mendoza E, Cochrane M, Brooks V (1999) Large-scale impoverishment of Amazonian forests by logging and fire. *Nature* **398**: 505–508
- O'Connor TG, Breidenkamp GJ (1997) Grassland. In: Cowling RM, Richardson D (eds) *Vegetation of Southern Africa*. Cambridge University Press, Cambridge, pp 215–257
- Okello BD, Young TP (2001) Effects of fire, bruchid beetles and soil type on germination and seedling establishment of *Acacia drepanolobium*. *African Journal of Range and Forage Science* **17**: 46–51
- Petit JR, Jouzel J, Raynaud D, Barkov NI, Barnola JM, Basile I, Bender M, Chappellaz J, Davis M, Delaygue G, Delmotte M, Kotlyakov VM, Legrand M, Lipenkov VY, Lorius C, Pepin L, Ritz C, Saltzman E, Stevenard M (1999) Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature* **399**: 429–436
- Phillips JFV (1930) Fire: its influence on biotic communities and physical factors in South and East Africa. *South African Journal of Science* **27**: 352–367
- Pooley E (1993) *The Complete Field Guide to Trees of Natal, Zululand and Transkei*. Natal Flora Publications Trust, Natal Herbarium, Durban
- Rutherford MC, Westfall RH (1986) Biomes of southern Africa — an objective categorisation. *Memoirs of the Botanical Survey of South Africa* **54**: 1–98
- San Jose JJ, Farinas MR (1983) Changes in tree density and species composition in a protected *Trachypogon* savanna, Venezuela. *Ecology* **64**: 447–453
- Schimper AFW (1903) *Plant Geography on a Physiological Basis*. Clarendon Press, Oxford
- Scholes RJ, Walker BH (1993) *An African Savanna: Synthesis of the Nylsvley Study*. Cambridge University Press, Cambridge
- Schmidt MWI, Noack AG (2000) Black carbon in soils and sediments: Analysis, distribution, implications, and current challenges. *Global Biogeochemical Cycles* **14**: 777–793
- Schulze RE (1997) *South African atlas of agrohydrology and -climatology*. Water Research Commission Report TT82/96, Pretoria, South Africa
- Schulze E-D, Ellis R, Schulze W, Trimborn P, Ziegler H (1996) Diversity, metabolic types and $\delta^{13}\text{C}$ carbon isotope ratios in the grass flora of Namibia in relation to growth form, precipitation and habitat conditions. *Oecologia* **106**: 352–369
- Scott AC (2000) The Pre-Quaternary history of fire. *Palaeogeography, Palaeoclimatology, Palaeoecology* **164**: 297–345
- Scott L (1999) The vegetation history and climate in the Savanna Biome, South Africa, since 190 000 KA: A comparison of pollen data from the Tswaing Crater (the Pretoria Saltpan) and Wonderkrater. *Quaternary International* **57–58**: 215–223
- Scott L (2002a) Grassland development under glacial and interglacial conditions in Southern Africa: review of pollen, phytolith and isotope evidence. *Palaeogeography, Palaeoclimatology, Palaeoecology* **177**: 47–57
- Scott L (2002b) Microscopic charcoal in sediments: Quaternary fire history of the grassland and savanna regions in South Africa. *Journal of Quaternary Science* **17**: 77–86
- Scott L, Anderson HM, Anderson JM (1997) Vegetation history. In: Cowling RM, Richardson D (eds) *Vegetation of Southern Africa*. Cambridge University Press, Cambridge, pp 62–90
- Shackleton CM, Scholes RJ (2000) Impact of fire frequency on woody community structure and soil nutrients in the Kruger National Park. *Koedoe* **43**: 75–81
- Silva JF, Castro F (1989) Fire, growth and survivorship in a Neotropical savanna grass *Andropogon semiberbis* in Venezuela. *Journal of Tropical Ecology* **5**: 387–400
- Skowno AL, Midgley JJ, Bond WJ, Balfour D (1998) Secondary succession in *Acacia nilotica* (L.) Savanna in the Hluhluwe Game Reserve, South Africa. *Plant Ecology* **145**: 1–9
- Specht RL, Moll EJ (1983) Mediterranean-type heathlands and sclerophyllous shrublands of the world: an overview. In: Kruger FJ, Mitchell DT, Jarvis JUM (eds) *Mediterranean-Type Ecosystems: The Role of Nutrients*. Ecological Studies 43, Springer Verlag, Berlin, pp 41–65
- Stebbins GL (1981) Coevolution of grasses and herbivores. *Annals of the Missouri Botanical Garden* **68**: 75–86
- Stott PA (1988) The forest as Phoenix: towards a biogeography of fire in mainland South East Asia. *Geographical Journal* **154**: 337–350
- Stott PA, Goldammer JG, Werner WL (1990) The role of fire in the tropical lowland deciduous forests of Asia. In: Goldammer J (ed) *Fire in the Tropical Biota*. Ecological Studies, 84, Springer Verlag,

- Berlin, pp 32–44
- Tainton NM, Mentis MT (1984) Fire in grassland. In: Booysen P de V, Tainton NM (eds) *Ecological Effects of Fire in South African Ecosystems*. Springer-Verlag, Berlin, pp 115–148
- Tinley KL (1982) The influence of soil moisture balance on ecosystem patterns in southern Africa. In: Huntley BJ, Walker BH (eds) *Ecology of Tropical Savannas*. Springer Verlag, Berlin, pp 175–192
- Titshall LW, O'Connor TG, Morris CD (2000) Effect of long-term exclusion of fire and herbivory on the soils and vegetation of sour grassveld. *African Journal of Range and Forage Science* **17**: 70–80
- Turner A (1985) Extinction, speciation and dispersal in African large carnivores, from the late Miocene to recent. *South African Journal of Science* **81**: 256–257
- Trollope WSW (1984) Fire in Savanna. In: Booysen P de V, Tainton NM (eds) *Ecological Effects of Fire in South African Ecosystems*. Springer-Verlag, Berlin, pp 149–176
- Uys RG (2000) The Effects of Different Burning Regimes on Grassland Phytodiversity. MSc thesis, Botany Department, University of Cape Town, South Africa
- Van Wilgen BW, Higgins KB, Bellstedt DU (1990) The role of vegetation structure and fuel chemistry in excluding fire from forest patches in the fire-prone fynbos shrublands of South Africa. *Journal of Ecology* **78**: 210–222
- Vogel JC, Fuls A, Ellis RP (1978) The geographical distribution of Kranz grasses in South Africa. *South African Journal of Science* **74**: 209–215
- Vrba ES (1985) African Bovidae: evolutionary events since the Miocene. *South African Journal of Science* **81**: 263–266
- West AG, Bond WJ, Midgley JJ (2000) Soil carbon isotopes reveal ancient grassland under forest in Hluhluwe, Kwa-Zulu Natal. *South African Journal of Science* **96**: 252–254
- West O (1969) Fire in vegetation and its use in pasture management with special reference to tropical and subtropical Africa. Mimeographed Publication No. 1, pp 1–53. Commonwealth Bureau of Pastures and Field Crops, Hurley, Berkshire
- Westfall RH, Everson CS, Everson TM (1983) The vegetation of the protected plots at Thabamhlope Research Station. *South African Journal of Botany* **2**: 15–25
- Whelan RJ (1995) *The Ecology of Fire*. Cambridge University Press, Cambridge
- White F (1983) *The Vegetation of Africa*. UNESCO, Paris
- Woodward FI, Lomas MR, Lee SE (2001) Predicting the future productivity and distribution of global vegetation. In: Jacques R, Saugier B, Mooney H (eds) *Terrestrial Global Productivity*. Academic Press, New York, pp 521–541
- Woodward FI, Smith TM, Emanuel WR (1995) A global land primary productivity and phytogeography model. *Global Biogeochemical Cycles* **9**: 471–490
- Wooller MJ, Street-Perrot FA, Agnew ADQ (2000) Late Quaternary fires and grassland palaeoecology of Mount Kenya, East Africa: evidence from charred grass cuticles in lake sediments. *Palaeogeography, Palaeoclimatology, Palaeoecology* **164**: 223–246