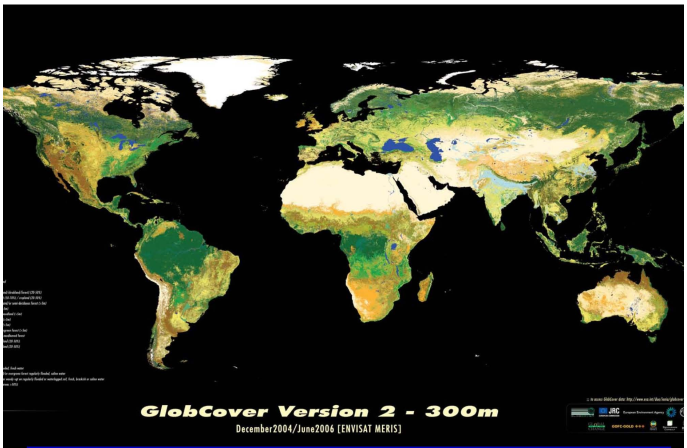
Fire and the angiosperm revolutions

William Bond
Botany Department
University of Cape Town
South Africa
With the help of Andrew Scott, Royal Holloway, UK

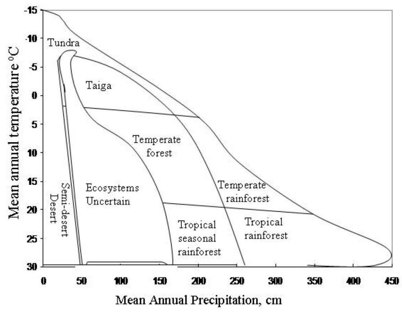


Globally, vegetation is organised into 'biomes' characterised by major growth forms:
TREES: Broad leaved (angiosperm), narrow-leaved (conifer), deciduous, evergreen
SHRUBS, GRASSES (C3 or C4)

What determines the distribution of major biomes

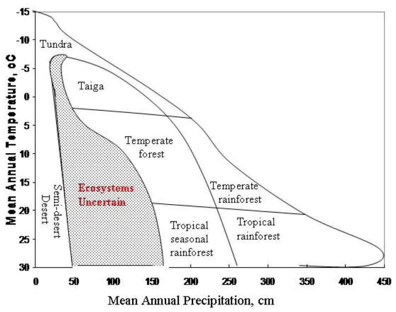
- In the present
- The past
- The future?

CLIMATE: THE USUAL SUSPECT

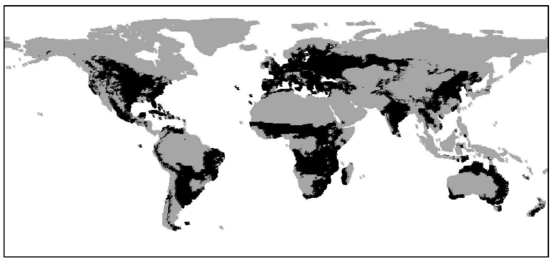


World biome distribution in relation to climate. Whittaker 1975

"Ecosystems uncertain" climate envelope
Mosaics of very different biomes in the same climate
WARMER AREAS (low to mid-latitudes)
NOT TOO DRY, NOT TOO WET



World biome distribution in relation to climate. Whittaker 1975



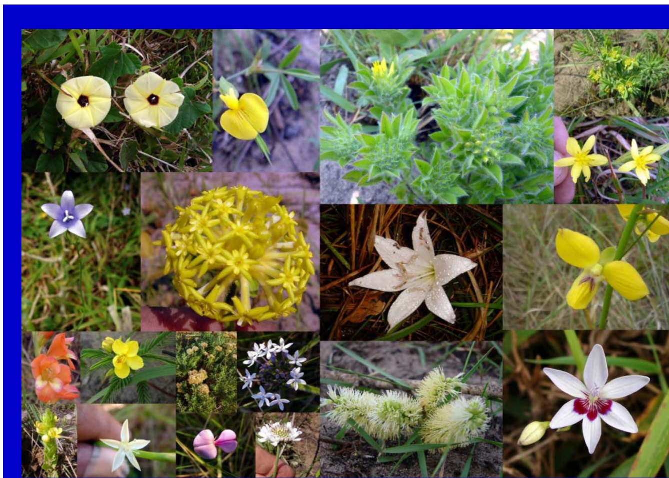
The geographic extent of "Ecosystems uncertain" is VAST. Includes grasslands, savannas, fynbos at low to mid-latitudes (>33% of global biomes)

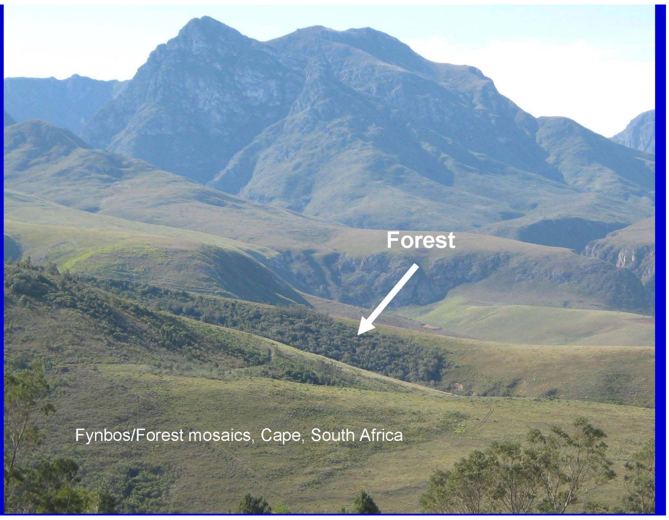
Bond 2005 J Veg Sci

Topical lowland forest/C4 grassland mosaic, Gabon, Africa

Forest-grasslands mosaic, Kansas, USA

Sub-tropical forest-C4 grass mosaic, St Lucia, South Africa





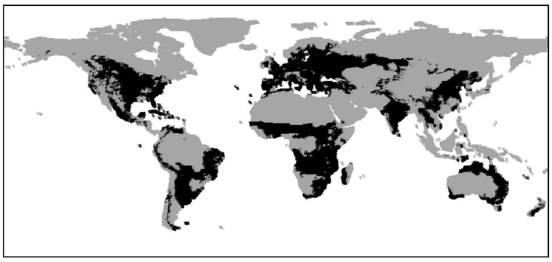
Fynbos/Forest mosaics, Cape, South Africa

Uncertain ecosystems are mosaics of very different vegetation states

- ***'Open'*** ecosystems (typically low biomass)
  - shade-intolerant plants dominate the surface layer
  - Canopy trees, if present, allow enough light for shade-hating Understorey plants
  - grasslands, shrublands, woodlands, savannas
- '***Closed'*** ecosystems (typically high biomass)
  - Canopy trees cast too much shade for shade-intolerant understorey plants to dominate

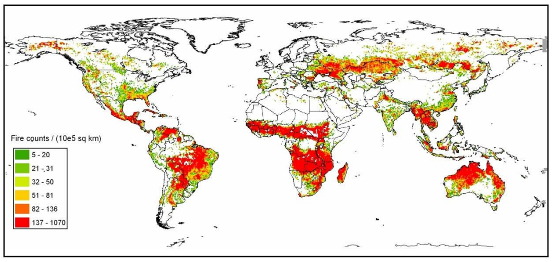
What maintains open ecosystems?

- 'Early successional' so should be replaced by trees which shade out grasses/shrubs
- Forest trees excluded by:
  - Competition from grasses/shrubs
  - Disturbance sufficiently frequent and intense to maintain 'permanent' early successional state
  - Main agents of disturbance are
    - Vertebrate herbivores
    - FIRE



The geographic extent of "Ecosystems uncertain" is VAST. Includes grasslands, savannas, fynbos at low to mid-latitudes (>33% of global biomes)

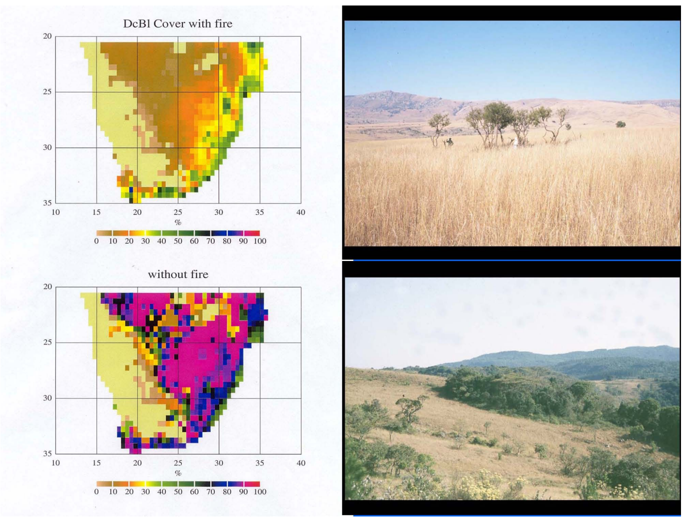
Bond 2005 J Veg Sci

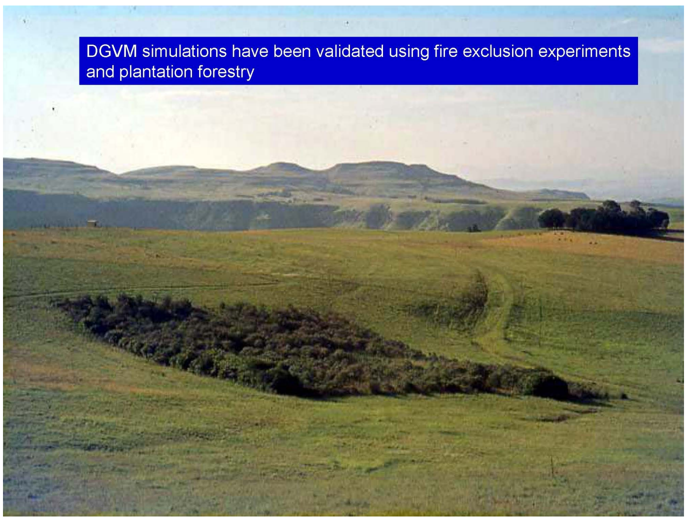


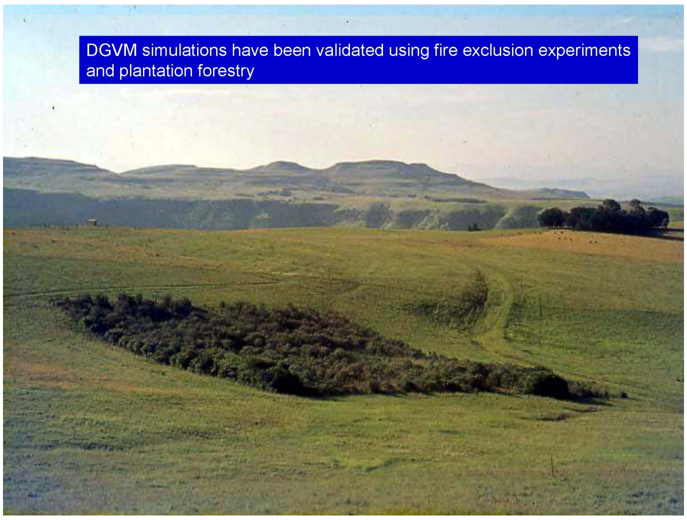
These areas burn more frequently than all other biomes

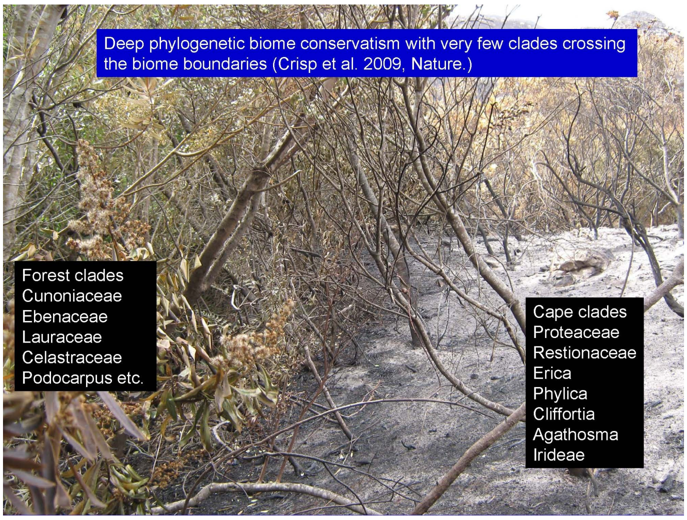
Fire effects on biomes can be predicted

- Dynamic Global Vegetation Models use physiological principles to predict climate potential vegetation
- Several DGVMs include fire modules
- Most also model CO_2 effects on global vegetation









What determines the proportions of closed vs. open ecosystems within 'uncertain ecosystem' climate space?

- The frequency and severity of fire (disturbance)
- The rate of forest colonization and recovery post-burn

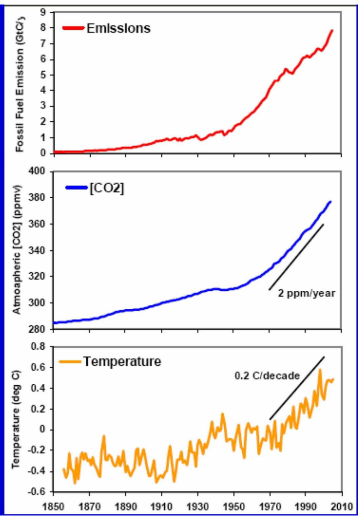
The frequency and severity of fire

- External factors
  - Dry enough to burn
  - Lightning frequency
  - Topography
  - (Oxygen)
- Intrinsic (biological) factors
  - Productivity of flammable biomass

The rate of forest tree colonization and recovery post-burn

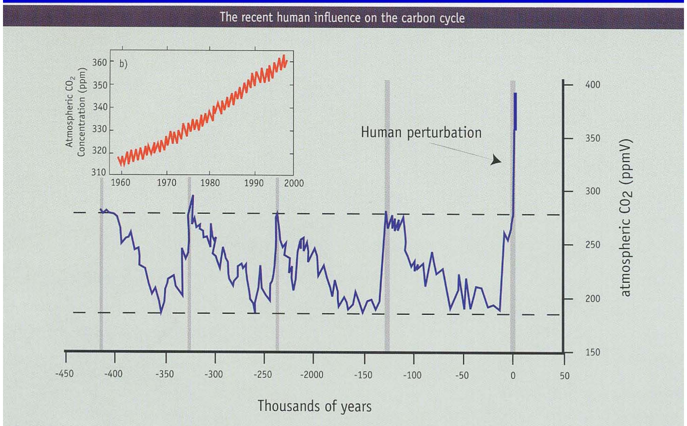
- External factors
  - Climate (warm, wet)
  - Soils
  - CO_2
- Intrinsic factors
  - Sprouting ability, RGR

The CO_2 factor



>35% increase

The history of CO_2

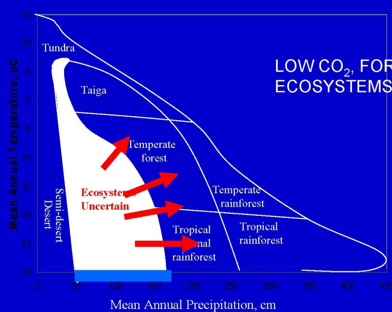


SUB-AMBIENT CO_2

- Array of open top chambers
- Plant species – *Acacia Karroo*, *Acacia sieberiana*, *Terminalia sericea* and *Sclerocarya birrea*

Increasing CO_2 is promoting woody plant increase in savannas

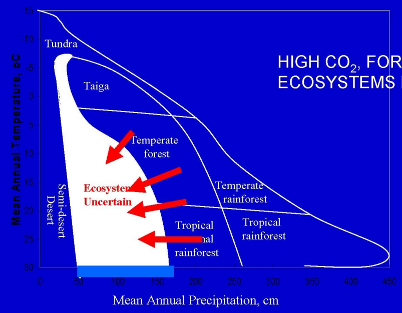
Is the “Ecosystems uncertain” climate envelope CO_2 dependent?



LOW CO_2, FORESTS RETREAT, OPEN ECOSYSTEMS EXPAND

World biome distribution in relation to climate. Whittaker 1975

Is the "Ecosystems uncertain" climate envelope CO_2 dependent?



HIGH CO_2, FORESTS EXPAND, OPEN ECOSYSTEMS RETREAT

World biome distribution in relation to climate. Whittaker 1975

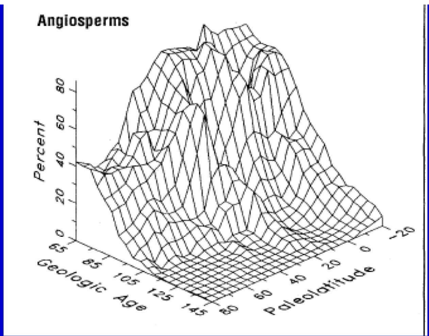
WOODY PLANTS ARE INCREASING IN MANY PARTS OF THE WORLD
WE THINK RISING CO_2 IS AN IMPORTANT CONTRIBUTOR

What does the past tell us about environmental conditions and the extent of open ecosystems?

- In low to mid-palaeo-latitudes most likely to fall within 'uncertain ecosystem' climates
  - Did low CO_2 + high fire - >> open veg
  - Did high CO_2 + low fire - >> closed forests?

The rise of the flowering plants: an open ecosystem success story?

See Bond and Scott. 2010. New Phytologist



From: Crane & Lidgard, Science 1989

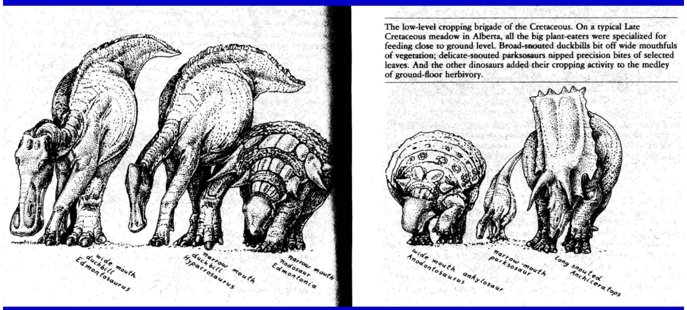
~135 My : 1st angiosperms, early Cretaceous
~100 My : rapid spread from low latitudes
~ 65 My: dominant in low latitudes, coexisting with conifers, ferns higher latitudes

During their Cretaceous spread angiosperms were

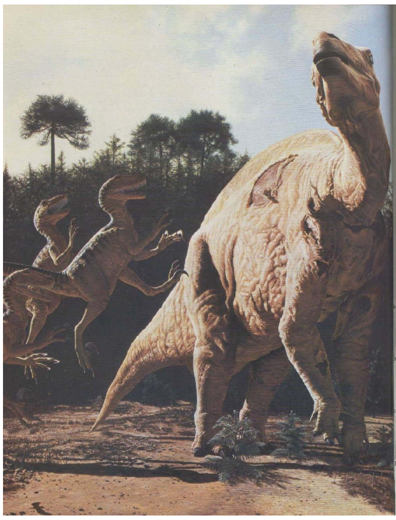
- Small: short trees, shrubs, herbs
- High *maximum photosynthetic rates in open sites with plenty of nutrients*
- Fast reproductive rates, early maturation
- Small seeds, passively dispersed

These are the attributes of WEEDY species: How did weeds (open habitat specialists) take over the world?

DID DINOSAURS OPEN UP CRETACEOUS FORESTS CREATING REGENERATION GAPS FOR WEEDS?


The low-level cropping brigade of the Cretaceous. On a typical Late Cretaceous meadow in Alberta, all the big plant-eaters were specialized for feeding close to ground level. Broad-snouted duckbills bit off wide mouthfuls of vegetation; delicate-snouted parksosaurs nipped precision bites of selected leaves. And the other dinosaurs added their cropping activity to the medley of ground-floor herbivory.

Bakker 1987. Short-necked dinosaurs evolved in the Cretaceous. They browsed tree-fall gaps favouring fast growing ‘weedy’ angiosperms and eliminating slow-growing gymnosperm trees . *But see McElwain, Willis 2002; Butler et al., 2009*



‘Dinoturbation’:

Direct effects of dinosaurs on trees would have opened up woodlands in a manner analogous to elephants today.

Ex: John Gurche from J. Reader The ‘Rise of Life’

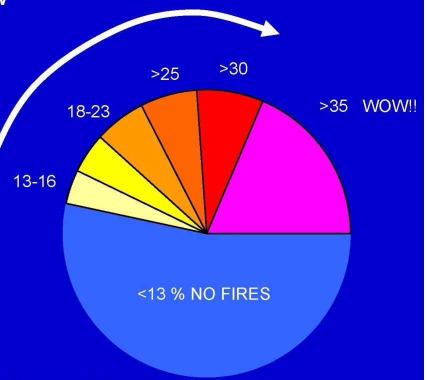
Fires in the Cretaceous

- Physical conditions favoured fire
  - High Oxygen
  - Greenhouse world
  - Seasonally dry climates
- ‘Weedy’ angiosperms promoted fire
  - high productivity created flammable fuels
  - Low CO_2 from 100 Ma favoured early shrubby angiosperms relative to low latitude trees
- A flower/fire cycle long before the modern grass/fire cycle?

The fire window

13 - ~30% Oxygen

Atmospheric Oxygen %
<13 No vegetation fires
13-16 Fires rare, only very dry fuel
18-23 Same as present. Moist. Extinc. 35%
>25 Fires widespread burning high moisture content fuels
>30 Fires active globally wet and dry



>35% Plants burn whether wet or dry
Fires would not go out until large areas were ash

See Belcher et al. 2010. PNAS for latest

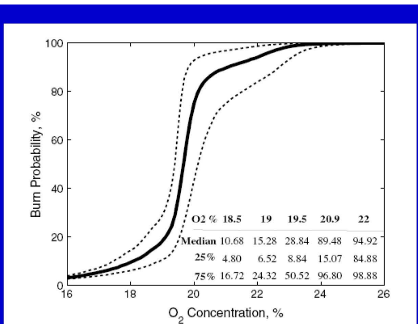


Fig. 4. Model output of the probability of burning according to O_2 concentration. Inlaid table shows the median probability of burning (%) and the 75 and 25% quartiles for O_2 concentrations 18.5–22%.

From: Belcher et al. 2010, PNAS

The probability of vegetation fires igniting and burning estimated from studies of fire spread in sphagnum moss at different atmospheric Oxygen content

From Belcher et al. 2010, PNAS

Oxygen %	18.5	19	19.5	20.9	22
P burn %	11	15	29	89	95

Current atmosphere has 20.9 % O_2.

Cretaceous conditions

- Oxygen 25% + (vs. PAL 21%)
- Fires would burn fuels with much higher moisture content than today

Long-leaf pine savanna: south-eastern US: Burnt **every 3 years** for 50 years

Surface fires burning a long-leaf pine stand.

Direct evidence of Cretaceous fires

- Inertinite (charcoal content of coal) shows high fire activity in mires
- Charcoalified fossil angiosperms are common in Cretaceous deposits in N. America and Europe

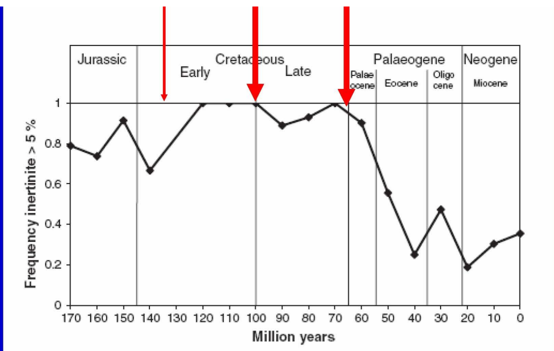


Fig. 1 Frequency of localities with inertinite exceeding 5% of coal macerals over time. The 5% threshold approximates the average charcoal content of contemporary mires. Data are sparse (< 10 records) from 140–125 million years ago (Ma) and 115–95 Ma. Data ex Glasspool & Scott (2010). **31**

Charcoal traps Chaparral landscapes

Crown-sprouting chaparral: Arctostaphylos: Note charcoal

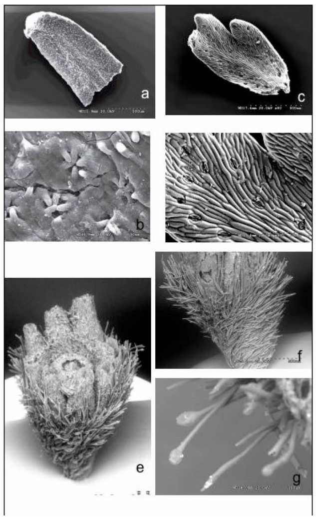
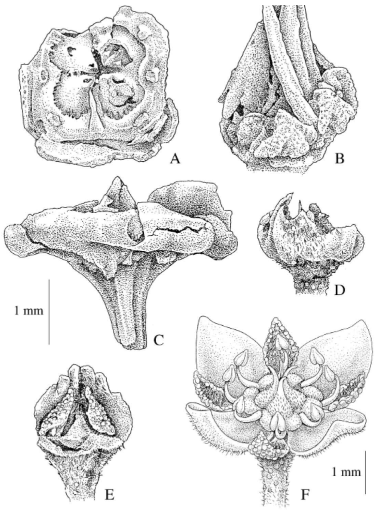


Figure 5. Scanning electron microscopy of fossil charcoalified plants: a) charcoalified conifer ~315 Ma, Illinois, U.S.A.; b) detail showing stomata with over-arching papillae; c) charcoalified pteridosperm leaf from ~325 Ma, Scotland; d) detail showing leaf surface with stomata; e-g) charcoalified ovule from the Mississippian (315-360Ma) of Scotland; e) whole ovule showing ovule lobes and glandular hairs; f) showing spirally arranged glandular hairs; g) detail of glandular hairs.

Ex. Scott, AC. 2009.
a.scott@gl.rhul.ac.uk

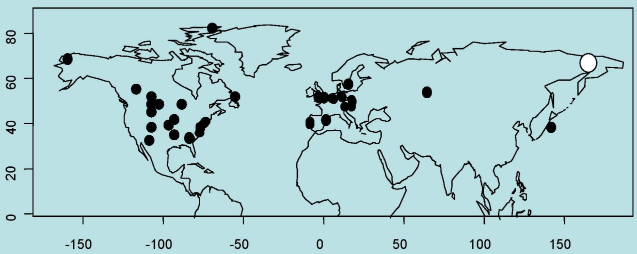


Platydiscus peltatus (Cunoniaceae), charcoalified flowers from the Late Cretaceous of Sweden. Friis et al. 2006. Palaeo3, 232: 251– 293

Vegetation fires were common in the Cretaceous

- Angiosperm flowers at many sites in N. hemisphere, rare in S. hemisphere.
- **Fine detail preserved as CHARCOAL**
- Charcoalified mesofossils produced by low intensity shrubland type fires

Fires were widespread in the Cretaceous



Cretaceous sites with charcoal, including charcoalifed mesofossils, angiosperm flowers etc. Mire fires (inertinite) not included

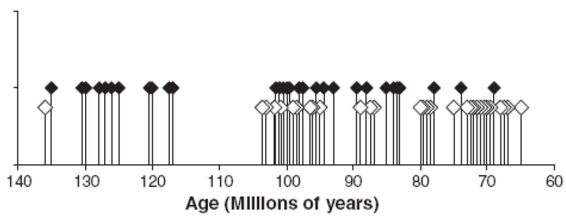


Fig. 3 Ages (millions of years) attributed to Cretaceous sites with evidence of wildfire. Closed symbols, sites with charcoalified mesofossil flowers and vegetative organs; open symbols, general charcoal. See Supporting Information Table S1 for sources.

The first angiosperm-dominated forests

- Large flowering trees were rare until the late Cretaceous
- No fossil evidence for broad-leaved forests leaved forests until the Paleocene 60 Ma (Wing et al. 2009. PNAS)
- Forests became widespread in the Eocene according to fossils (50-35 Ma)

Eocene environments

- Climates warm and assumed to be wet
- Fires 'switched off' (O_2 = PAL)
  - Inertinite record of fire in mires very low
  - Charcoal markers of fire rare/absent
- CO_2 reached highest levels in the last 65 Ma
- *Low fire, high CO_2, favours closed forest ecosystems*

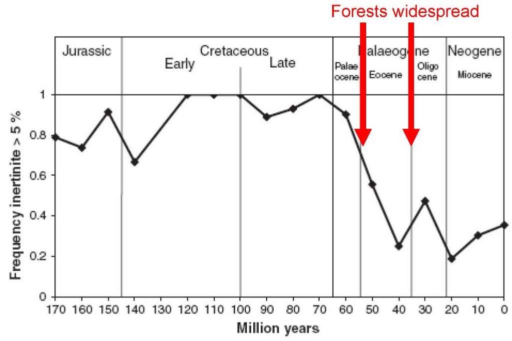
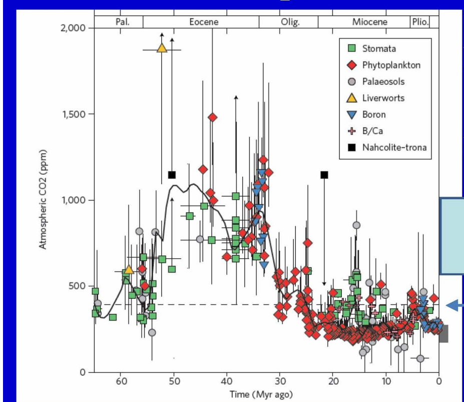


Fig. 1 Frequency of localities with inertinite exceeding 5% of coal macerals over time. The 5% threshold approximates the average charcoal content of contemporary mires. Data are sparse (< 10 records) from 140–125 million years ago (Ma) and 115–95 Ma. Data ex Glasspool & Scott (2010).

31

CO_2 paleohistory



Eocene was warmest period with highest CO_2 from K/T to the present

Are we returning to Eocene Conditions?

IPCC (2007)
CO2 scenarios

Beerling and Royer Nature Geoscience July 2011

The spread of c4 grasses:
another 'weedy' success story

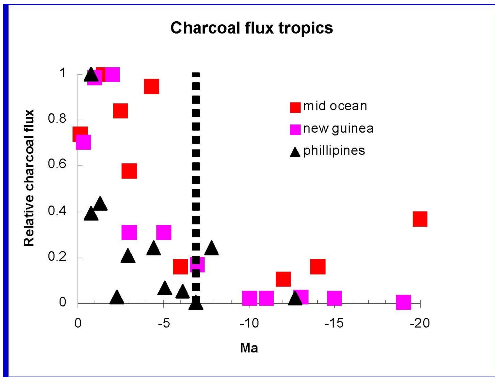
Keeley & Rundel 2005, Ecol Letters
Osborne 2008, J. Ecol
Edwards et al. 2010. Science

The spread of c4 grasses:
another 'weedy' success story

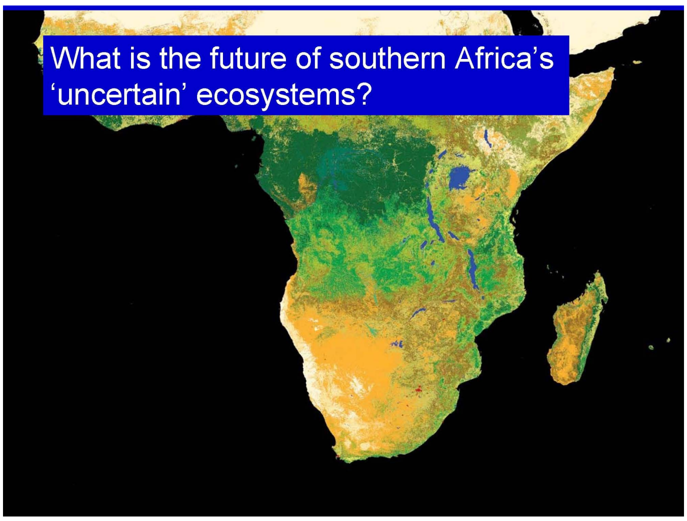
Keeley & Rundel 2005, Ecol Letters
Osborne 2008, J. Ecol
Edwards et al. 2010. Science

Mio-Pliocene environments

- Climate cooling, and assumed to be drying
- Fires 'switched on' (O_2 = PAL)
  - Marine Charcoal record shows explosive increase (Herring 1986)
- CO_2 low to very low in Pleistocene
- C4 photosynthesis efficient at low CO_2
- High fire, low CO_2, favours open ecosystems



Marine cores in N. Pacific show exponential increase in charcoal in Neogene coinciding with C4 grassy biome expansion (Herring 1986; Keeley and Rundel 2005)



The past suggests:

- High CO_2 favours increased trees, decreased fire
- Savannas and grasslands likely to shrink
- Fynbos prone to invasion by trees that grow rapidly on low nutrient soils
- Good for C sequestration?
- But what are the net effects on
  - Biodiversity
  - People and the resources they use
  - Earth-atmosphere feedbacks caused by
    - Changes in albedo
    - Reduced fire activity

We need a far better understanding of ‘uncertain ecosystems’

- In the present
- the past
- To better manage our futures
- UCT’s Botany Department is working at it

Thanks to

- Andrew Scott, Royal Holloway, UK
- David Beerling, Ian Woodward, Sheffield, UK
- Jon Keeley, CJ Fotheringham, UCLA
- Dave Bowman (UTAS) and the NCEAS working group on fire in the earth system
- Erika Edwards, Caroline Stromberg, Colin Osborne and the C4 working group
- Caroline Lehmann, Sally Archibald, Bill Hoffmann and the ARC working group on savannas
- Mike Cramer, Jeremy Midgley, Guy Midgley, Cape Town
- Pete Linder for asking the critical questions in the 1st place