Transcript of The War Between Trees and Grasses

Seminar presented at IBERS Aberystwyth 13 xi 2017

The War Between Trees and Grasses covers the whole of plant and human evolution.

In the time I have, I can only present a selective drone's-eye view of the subject.

As a social media experiment, I've arranged for summary points from the seminar be tweeted at intervals starting about now, hashtag #wartreegrass

Comments using the same hashtag welcomed.

The talk ranges across 500 million years of the planet's history.

If, like me, you're not a geologist, you may find it useful to refer to this scale included on the slides during the first half of this talk.

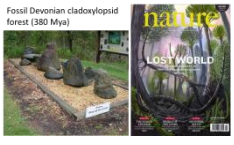
The story begins almost half a billion years ago, with the Gondwana landmass turning green around the edges.

The plants that made the transition from the aquatic to terrestrial environment were small and twiggy, without roots or leaves.

Adaptations to life on land requires the development of structural support and anchorage, waterproofing and the means to acquire and translocate nutrients and water.

In a comparatively short time, geologically speaking, evolution solved these problems.

The result was that the pioneer plants went on to become giants: by the Devonian period the trees had arrived.



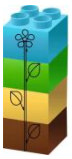
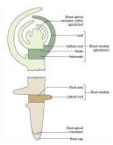
What features define a tree?

Obviously, a tree is big and tough, as a consequence of the fact that most of its cells (more than 95%) are dead.

Programmed disposal of cells, tissues and organs remains the essence of tree development and adaptation in today's forests.

Related to this, trees can indulge in a throw-away lifestyle because of their modular structure.

> Growth and development takes the form of the generation of self-similar, semi-independent units.

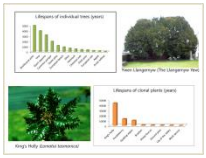
Another defining feature of the tree lifeform is its longevity.

> In this context, can a tree be considered to be an individual organism?

Many (such as yew) develop by what Francis Hallé calls reiterative growth, in which new axes proliferate as hemi-parasitic clones.

> In this respect, a tree is more like a colonial organism, and only differs from other clonal plants in the lack of separation of daughter clones.

Within the broad category of clonal plants, there are some spectacular lifespans.



> It's an amazing thought (well, it amazes me) that the meristems of trees and long-lived clonal plants may have been producing new cells and tissues for a thousand or more years.

It seems that meristems have such extremely robust mechanisms for resisting, purging or adaptively exploiting genetic errors that they may be potentially immortal.

> Thus it was that the tree life-form enabled forests to become the dominant global vegetation type from the mid Devonian (around 380 Mya).

Very few representatives of these early forest pteridophytes exist today.

> One such 'living fossil' is *Ginkgo*.

We now arrive at the time when the flowering plants appear.

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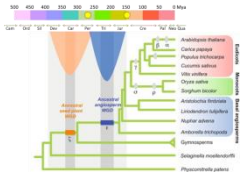
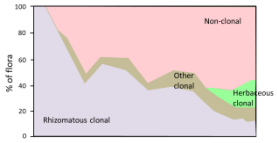
There's uncertainty about when the angiosperms diverged: fossil and other evidence suggest about 160 Mya, molecular clock data put the divergence much earlier.



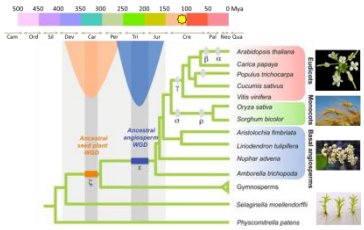
In very general terms, with the appearance of seed and flowering plants came a trend from the long-lived tree and clonal habit to plants obeying the Romano Rule - live fast, die young.



This is an example of the Boop principle.

Betty Boop is the poster child for heterochrony and progenesis: juvenilisation and precocious reproductive development.

Monocots and dicots diverged more than 100 Mya



Monocots are mostly herbaceous, with architectures and adaptive features that differ fundamentally from those of dicots.

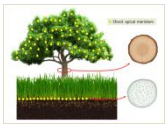
	Monocots	Dicots
Flower parts	Multiples of three	Multiples of four or five
Pollen	Single pore or furrow	Three pores or furrows
Embryo	Single cotyledon	Two cotyledons
Leaf venation	Major veins parallel	Major veins reticulated
Stem vasculature	Vascular bundles scattered	Vascular bundles in a ring
Shoot meristem	Intercalary	Apical
Roots	Produced adventitiously	Developed from a radicle
Secondary growth	Absent	Usually present

Grasses appeared rather late in evolution.

It's possible that they predated the Alvarez meteor catastrophe that wiped out the dinosaurs 66 Mya.

The grass life-form is determinedly as different from that of trees as could be.

In particular, their shoot meristems are at ground-level rather than up in the air, allowing intercalary growth and re-growth, and they don't engage in secondary thickening.

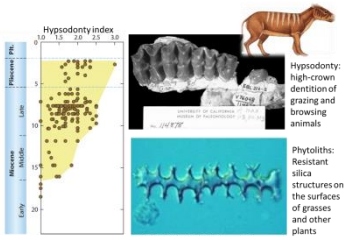


At last we arrive at the outbreak of the war that gives this seminar (and book) its title.

Grass-dominated biomes took on the forests using three potent weapons.

First, herbivory: the distinctive biologies and ecologies of grassland species and grazers were the outcome of antagonistic coevolution.

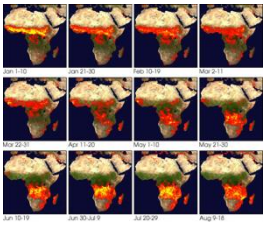
This is exemplified by adaptations such as herbivore dentition and silicification of herbage.



Grasses tolerate - indeed are adapted for - grazing and trampling, unlike trees: the sheep-covered hills of Wales are devoid of woodland.

The abundance of large herbivores tracked the expansion of grassland biomes from about 50 Mya.

Another weapon in the war is fire: William Bond calls fire a 'global herbivore', and it's a natural and essential environmental factor in many regions of the world.



Some trees can survive burning, but in general grasses are far more tolerant of fire by virtue of the same adaptations that allow them to cope with and exploit herbivory.

It's estimated that without the influence of fire, the area of forest across the world would double at the expense of grassland.

So that's herbivory and fire; the third weapon arrived within the last 3 to 7 million years - hominids (including us).

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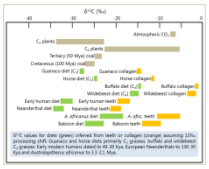
The origins of the relationship between humans and grassland can be seen in the diet of our African hominid ancestors.

We get an insight into diet by analysing the carbon isotope ratios of fossils.



Grasses photosynthesising by the C4 pathway dominate the dry, water-limited grassland environments of Africa (and S America).

As plants, animals and hominids spread out from Africa the C3 grasslands became more prevalent.

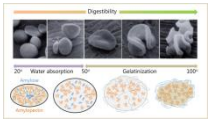
The products of C3 and C4 photosynthesis have different carbon isotope signatures, enabling grassland-based fossil food chains to be recreated.

Thus the *Australopithecus* diet is like that of baboons, wildebeest and buffalo, whereas Neanderthals resemble guanacos and horses.

Ancestors of the grass species that feed the human race today can be traced to the time when the first hominins were beginning to emerge, setting the scene for the rise of agriculture.

What was the key factor in the developing relationship between grassland, and later cereal, species and human evolution?

It was polymerised glucose in the form of starch.



The underground storage organs of grassland species are a stable and abundant source of starch, and observations on our primate relatives provide evidence for the dietary importance of USOs.

Starch provides a high-glycaemic hit and profoundly influenced hominin brain size the form of the skull and digestive tract and, consequentially, behaviour and culture.

The starchy diet has remodelled the genome of humans and domesticated animals.

Starch became airborne as the hominin diet expanded to include seeds, setting in motion the early events in the rise of agriculture.

Starch is only the second most abundant source of polymerised glucose: about half of global biomass is accounted for by cellulose.

Humans can't directly digest and utilise cellulose; but grasslands are extensively populated by animals that can.

Although we think of meat and dairy as primarily sources of protein and fat, in terms of what you might call the 'paleo-diet' their significance is the access they allow to cellulose.

The geological period over which humans co-evolved with the plants that meet their nutritional and energy needs is often called the Anthropocene (Crutzen and Stoemer).

I tend to think of the Anthropocene as the era of human dependence on starch+cellulose.

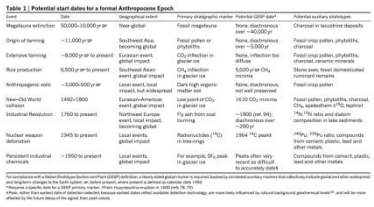
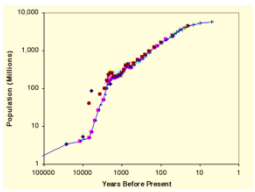


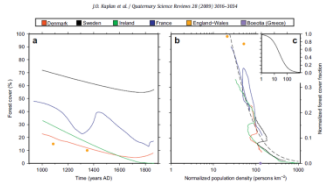
Table 1 | Potential start dates for a formal Anthropocene Epoch

Event	Date	Geographical extent	Primary stratigraphic marker	Potential GSSP date*	Potential auxiliary stratotypes
Megafauna extinction	50,000–10,000 yr BP	Near-global	Fossil megafauna	None, diachronous over ~40,000 yr	Charcoal in lacustrine deposits
Origin of farming	~11,000 yr BP	Southwest Asia, becoming global	Fossil pollen or phytoliths	None, diachronous over ~5,000 yr	Fossil crop pollen, phytoliths, charcoal
Extensive farming	~8,000 yr BP to present	Eurasian event, global impact	CO_2 inflection in glacier ice	None, inflection too diffuse	Fossil crop pollen, phytoliths, charcoal, ceramic minerals
Rice production	6,500 yr BP to present	Southeast Asian event, global impact	CH_4 inflection in glacier ice	5,000 yr BP or CH_4 minima	Stone axes, fossil domesticated ruminant remains
Anthropogenic soils	~3,000–500 yr BP	Local event, local impact, but widespread	Dark high organic matter soil	None, diachronous, not well preserved	Fossil crop pollen
New–Old World collision	1492–1800	Eurasian–American event, global impact	Low point of CO_2 in glacier ice	1610 CO_2 minima	Fossil pollen, phytoliths, charcoal, CH_4, speleothem $\delta^{13}C$, tephra†
Industrial Revolution	1760 to present	Northwest Europe event, local impact, becoming global	Fly ash from coal burning	~1900 (vol. 94); diachronous over ~200 yr	$^{206}Pb/^{207}Pb$ ratio and diatom composition in lake sediments
Nuclear weapon detonation	1945 to present	Local events, global impact	Radionuclides (^{14}C) in tree-rings	1964 ^{14}C peak	$^{240}Pu/^{239}Pu$ ratio, compounds from cement, plastic, lead and other metals
Persistent industrial chemicals	~1950 to present	Local events, global impact	For example, SF_6 peak in glacier ice	Peaks often very recent so difficult to accurately date‡	Compounds from cement, plastic, lead and other metals

The Neolithic Demographic Transition was a population explosion fuelled by starch+cellulose, and it's still continuing.



Humans became dependent on grasses for starch and cellulose, civilisations based on plant and animal domestication emerged across the world, and it was, and still is, bad news for forests.



We've arrived at the time when humans could look beyond simple survival and begin to look around and ask the big existential questions - what's it all about, why are we here, how should we live?

In other words, it's the dawn of the age of ritual and religion, with the three-way relationship of trees, grasses and humans at its centre.

This part of the story is an enormous subject in its own right, and I only have time to glance at a wide and rich panorama.

According to one primal myth, a tree stands at the source of all the world's troubles.

God, it seems, wanted humans out of the forest of paradise so that he could keep an eye on us.

Soon afterwards, we are told, the Curse of Cain was laid upon us, and we became enslaved by the arable and pasture grasses.

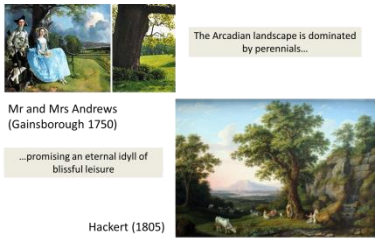
Even today, in the era of mechanised agriculture, farming is a story of relentless and physically demanding toil.

Myths, legends, fairy tales, literature tell of forests as places of fear and madness.

As well as these examples, I'm thinking of Sir Gawain and the Greene Knight, Hansel and Gretel, Tolkien, Dante, Red Riding Hood, Titus Andronicus, the Blair Witch Project…

By the time we reach the Age of Enlightenment, some kind of reconciliation between trees and grass was achieved.

Trees are props in the Arcadian scenery favoured by garden designers (Capbility Brown etc) and artists.



In the Romantic era, forests 'savage, dark and dangerous' represented a sublime thrill.

Trees also took on political significance; Edmund Burke famously invoked the oak as a symbol of English resilience and stability in his denounciation of the French Revolution.

This symbolism lives on in these days of Conservative difficulties with Europe.

The present vogue for so-called New Nature Writing (Robert McFarlane, Roger Deakin, Richard Mabey etc) is essentially in the Romantic tradition.

> Some of us, perhaps most of us here, in our bubble, may revere trees and deplore deforestation and environmental degradation.

But the fact is, the vast majority of humanity doesn't share our attitudes and is merrily slashing and burning for all it's worth.

> To conclude: in the dawn of human evolution, grasses enlisted us as mercenaries in their war on trees, offering a King's Shilling in the form of polymerised glucose.

We remain, and maybe will always be, enslaved by grass - not just as a source of food but for our leisure and entertainment too.

> After all, the most powerful man in the world spends a third of his time chasing a small white ball around on the stuff.