DOES ELEVATED CO_2 PLAY A ROLE IN BUSH ENCROACHMENT?

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Abstract

Bush encroachment is a widespread phenomenon occurring in southern Africa and many other parts of the world. Its causes are still poorly understood. Changes in tree abundance have been attributed to deeper rainfall penetration into the soil, favouring deeper-rooted trees. Alternatively, tree abundance might vary depending on the disturbance regime and how this influences recruitment of seedlings or release of saplings. Saplings may be prevented from growing to maturity by frequent fires. We suggest that changes in atmospheric carbon dioxide can influence sapling growth to maturity potentially affecting tree abundance in savannas. We simulated growth of saplings and grass at different atmospheric CO_2 levels using a Dynamic Global Vegetation Model. We incorporated these results into a model simulating the demography of savanna trees and fire. The results show that tree cover is sensitive to atmospheric CO_2 with large decreases at low CO_2 level, and massive increases from pre-industrial conditions to today's levels. The results are consistent with palynological data for the last glacial, a time of low CO_2, and with the widespread increase in tree cover seen over the last century. The simulations suggest that elevated CO_2 could be having a widespread and pervasive effect on savanna vegetation by tipping the balance in favour of trees.

1. Introduction

Bush encroachment is the phenomenon of increasing tree density and biomass in grassy ecosystems. It is occurring in many parts of South Africa and also in other parts of the world, including North America and Australia (Scholes and Archer, 1997). Rapid shifts in tree densities following favourable years, and in localised areas, have probably occurred in savannas throughout their history. However the wide and pervasive extent of the bush encroachment phenomenon seems to be a problem that has emerged only in the last century or so. Bush encroachment is often perceived to be "bad" by livestock farmers because of the reduction of grass for grazing. However whether it is "good" or "bad" depends on local circumstances and the objectives of land users.

The causes, and methods of controlling encroachment have been researched for nearly a century. Yet there is still no clear consensus nor any standard method of controlling bush encroachment despite this long history of research (Scholes and Archer, 1997). Is this because different processes in different settings all produce similar results? Tree/grass coexistence in savannas forms part of the general problem of explaining coexistence of competing species. Heinrich Walter, a German biogeographer, first suggested that trees and grasses compete for different resources and, depending on the availability of those resources, this allows them to coexist (Walter, 1971). The idea, first explored formally by Walker and Noy-Meir (1982) is that trees and grasses draw resources at different depths in the soil with trees having deeper roots and grasses shallow roots. If this is the case, then tree abundance should vary depending on how much water gets past grasses to the deep rooting layer accessible only to trees. There has been a great deal of work on this idea in different parts of the world with some studies finding support for the idea of different rooting depths and others finding complete overlap between grass and tree roots (Scholes and Archer, 1997).

An alternative idea has recently been presented by Higgins, Bond and Trollope (2000). This argues that tree abundance varies depending on demographic bottlenecks at the seedling recruitment or sapling release stage. Most of the time, conditions are hostile for juvenile trees preventing an increase in density to the point where they form woodlands or forests. Occasional favourable episodes occur, though, and it is during these episodes that tree populations increase. The hypothesis clearly requires a variable environment (if conditions were always good for young trees then grasses would not get a chance, if they were always bad, then savannas would change to grasslands). Another key requirement of the hypothesis is that trees live long enough to straddle successful episodes of population increase.

Demographic bottlenecks might occur at several distinct stages in the life of a savanna tree (Midgley and Bond, 2001). The first hurdle is seedling establishment. In arid savannas, there may be few years with enough rainfall for seeds to successfully produce established seedlings. Even if seedlings do establish successfully (surviving, say, for two growing seasons), they may fail to produce saplings because of damage from fire, herbivory, or competition from grasses. Even if seedlings do survive to form saplings, saplings still have to have suitable conditions to be **released** into mature adult trees. In mesic savannas, for example, it is not uncommon to find enough saplings to produce a dense woodland yet they are burnt so frequently that the saplings fail to recruit to adult trees - they are caught in a "fire trap". There is an analogous problem in areas with high browsing pressure which might also prevent young trees from growing tall enough to become adults and begin to produce fruits. The recruitment bottleneck might differ in different savannas, perhaps partly accounting for our failure to understand the bush encroachment problem in a general way. In arid savannas, rain may be too little or too intermittent for successful tree seedling establishment. In mesic savannas, seedling establishment may be much more frequent but the higher rainfall is likely to produce higher grass biomass and more frequent fires. Saplings can be stuck for decades in the fire trap in such situations and sapling release is more likely to be the key bottleneck.

Trollope (1984) has studied the importance of fire intensity in keeping saplings stuck in the fire trap. High fire intensities cause "topkill" of the saplings so that they have to start sprouting from the root crown after a fire. If intervals between intense burns are long enough, allowing trees grow to heights of 3 - 4m, saplings escape the trap and become mature trees. The sapling release process has been modelled using relationships derived from Trollope's work to explore the necessary conditions for trees to coexist with grasses (Higgins *et al.,* 2000). The frequency of escape events is controlled by fire intensity (which varies with weather conditions and amount of grass to burn) but also strongly affected by resprouting and stem growth rates to escape height. Small differences in rates of stem growth can have very large effects on tree densities, according to the simulation model. The simulations predict that the same proportional change in stem growth rates would have much larger effects on tree populations than equivalent changes in grass biomass production. Unfortunately, there is very little data from South African savannas on the critical variable of stem growth rates to escape height or how this might be influenced by, say, rainfall variation from year to year or differences among species.

2. Carbon dioxide

Carbon dioxide is an essential requirement for pant growth obtained from the earth's atmosphere. Recent studies have shown that CO_2 levels in the atmosphere have fluctuated between 180 ppm during glacial conditions to 280 ppm in interglacials over the last half million years (Petit *et al.*, 1999). Changing values of CO_2 over time have been recorded in gas bubbles trapped in ice and recorded by taking deep ice cores from the Antarctic. The last glacial ended about 12 000 years ago and CO_2 levels rose to 280 ppm by *ca* 10 000 y and remained at that level until a century or two ago when people began to use fossil fuels to drive the industrialisation process. Today, CO_2 levels are about 370 ppm, higher than they have been for at least the last 430 000 years and probably several million years!

Recently Bond and Midgley (2000) suggested that changes in atmospheric CO_2 might also affect sapling growth rates therefore potentially influencing tree densities in savannas.

We have now explored the CO_2 effect quantitatively using physiologically based simulation models coupled with the demographic bottleneck model (DBM) described above. We were particularly interested in how trees might have responded to low CO_2, such as during the last glacial. We wanted to explore the effects of low CO_2 to give us a perspective on what conditions trees have had to cope with in the past to better understand how they might be responding to current and future high CO_2 concentrations in the atmosphere. CO_2 is expected to double (or more) in this century.

Changes in CO_2 can affect the growth of plants in at least two ways. At low CO_2 plants have to open stomata wider to "feed" (take up CO_2 from the atmosphere). The result is greater transpiration rates so that, for the same rainfall, low CO_2 means effectively drier conditions for plant growth. A recent Dynamic Global Vegetation Model (DGVM) simulation of South African savanna vegetation indicates that 500 mm of rainfall under current conditions would have been equivalent to about 300 mm of rainfall at a CO_2 concentration fo 180 ppm (Bond, Midgley & Woodward, 2002). Low CO_2 alone would have had the effect of almost halving the rainfall in the last glacial according to these simulations. The current high CO_2 levels have the reverse effect, creating effectively moister conditions. For the root niche hypothesis of tree/grass abundance, this means deeper infiltration of rainfall allowing the supposed deeper rooted trees to benefit (Polley, 1997).

Changes in CO_2 also directly effect growth rates by altering photosynthetic rates. Growth rates of juvenile trees to sizes at which they can resist damage to stems may be sensitive to CO_2 concentrations. This is because trees, unlike grasses, need to invest carbon into woody structure to attain height – this large carbon demand can be met much more efficiently (Drake *et al.*, 1997) and quickly (Ceulemans *et al.*, 1995) under elevated CO_2 conditions. So changes in atmospheric carbon dioxide could affect very directly the probability of woody plants growing to fire-resistant size and therefore alter the tree/grass balance. CO_2 effects are likely to be particularly influential for plants recovering from disturbance since light, water and nutrients are least likely to be limiting growth after a burn, thus facilitating maximum CO_2 responsiveness of photosynthesis and carbon fixation. The different responses of trees and grasses to CO_2 are driven mainly by differences in carbon demand for structural allocation, not differences in carbon gain between C_4 grasses and C_3 trees. The potential interactive effects of CO_2 and fire on trees would operate regardless of whether the grasses were C_3 or C_4 (Bond & Midgley, 2000; Bond, Midgley, & Woodward, 2002).

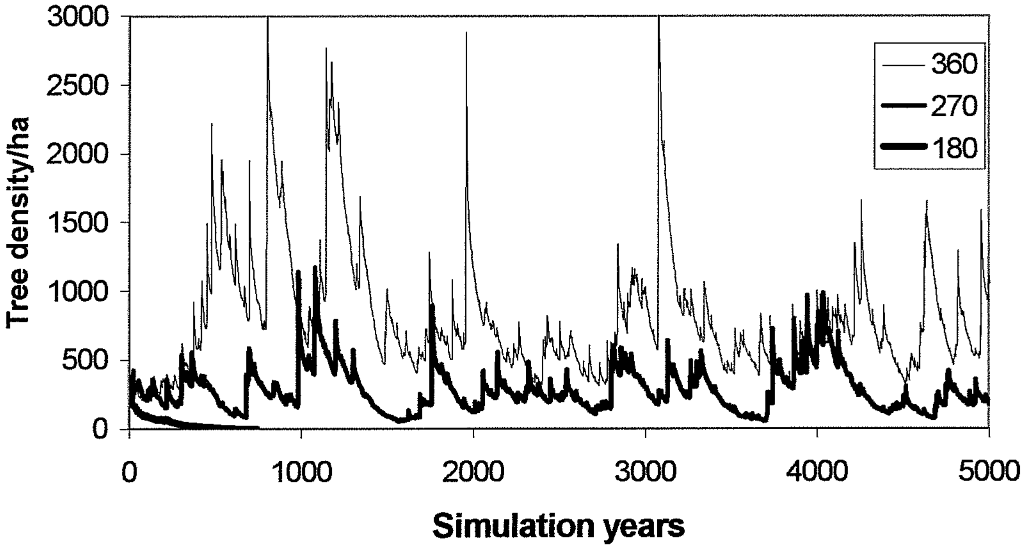
3. Methods

We tested these ideas using the Sheffield DGVM (see Cramer *et al*, 2001 for more infomration on DGVMs) to simulate stem growth rates and Net Primary Production (NPP) at different CO_2 levels but holding climate constant to determine the effects of CO_2 on savanna tree and grass growth. The simulations used climate data for three South African sites representing a rainfall gradient from arid to mesic (see Bond, Midgley & Woodward, 2002 for detail).

4. Results

Table 1 shows simulated growth rates of grasses and trees for the three rainfall scenarios and different CO_2 concentrations. We then used these values to simulate tree demography using Higgins *et al.* (2000) demographic bottleneck model.

Table 1. Growth rates of saplings (stem height, cm y^{-1}) and grass (kg $ha^{-1}mm^{-1}$ rain) simulated for different rainfall and CO_2 scenarios used in the savanna demography (DBM). Values are based on field estimates (Higgins et al 2000) modified according to SDGVM simulations of NPP under each CO_2 scenario relative to current CO_2 (360 ppm)



CO$_2$ (ppm)	Grass (kg ha^{-1} mm^{-1} rain)	Stem growth cm y^{-1}		
		Arid	semi-arid	Mesic
180	2.36	13	19	29
270	2.86	22	35	41
360	3.37	35	45	50
700	4.45	65	71	62

The results of a simulation run for 5000 years and for three CO$_2$ levels is shown in Figure 1. Simulated tree densities are very variable through time depending on the frequency of intense fires. To summarise the simulations, Figure 2 shows median tree densities for the three CO$_2$ scenarios. The results imply that:

- No mature trees would have survived in the last glacial (180 ppm),
- trees would occur, but at low densities, at pre-industrial (270 ppm) CO$_2$ levels, and
- large increases in tree density should be occurring from pre-industrial to today's CO$_2$ levels.

Interestingly enough, the largest responses occur from pre-industrial CO$_2$ to current conditions. Projected future CO$_2$ levels (700 ppm) do not greatly change tree densities relative to simulations of current conditions (results not shown).

Figure 1. **Simulated tree densities for a mesic savanna at four CO_2 concentrations representing last glacial (180 ppm), pre-industrial (270 ppm) and current (360 ppm) conditions. The simulations used a demographic model (Higgins *et al.*, 2000) developed for South African savannas with growth of grass and trees modified from estimates of current conditions according to DGVM simulations at different CO_2 levels.**

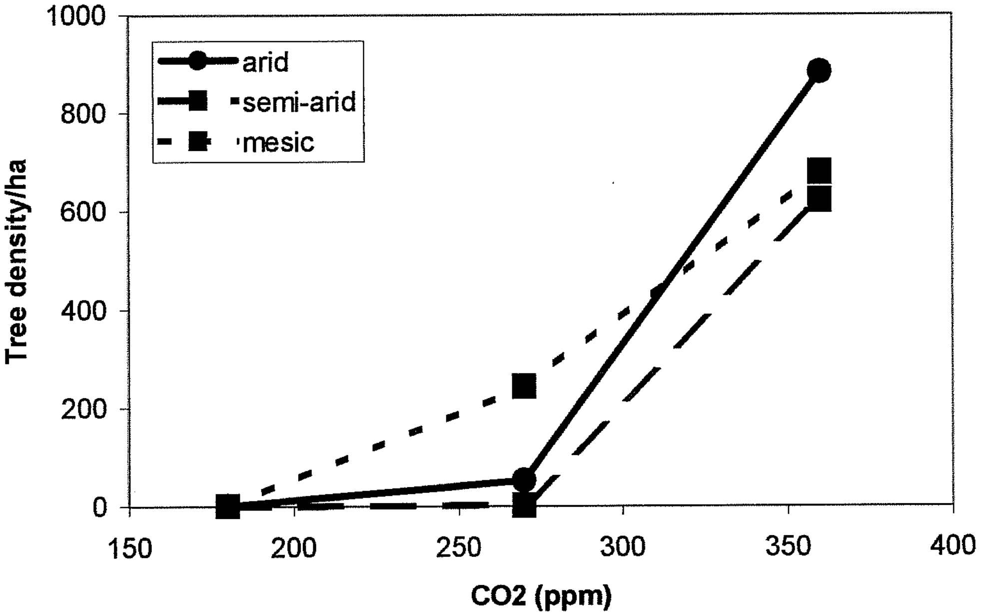


Figure 2. **Median tree densities in relation to atmospheric CO_2 for an arid, semi-arid and mesic savanna. Medians are calculated for a 5000 year simulation run (Figure 1).**

5. Discussion

How well do these simulated changes fit with what we know of tree/grass changes through time?

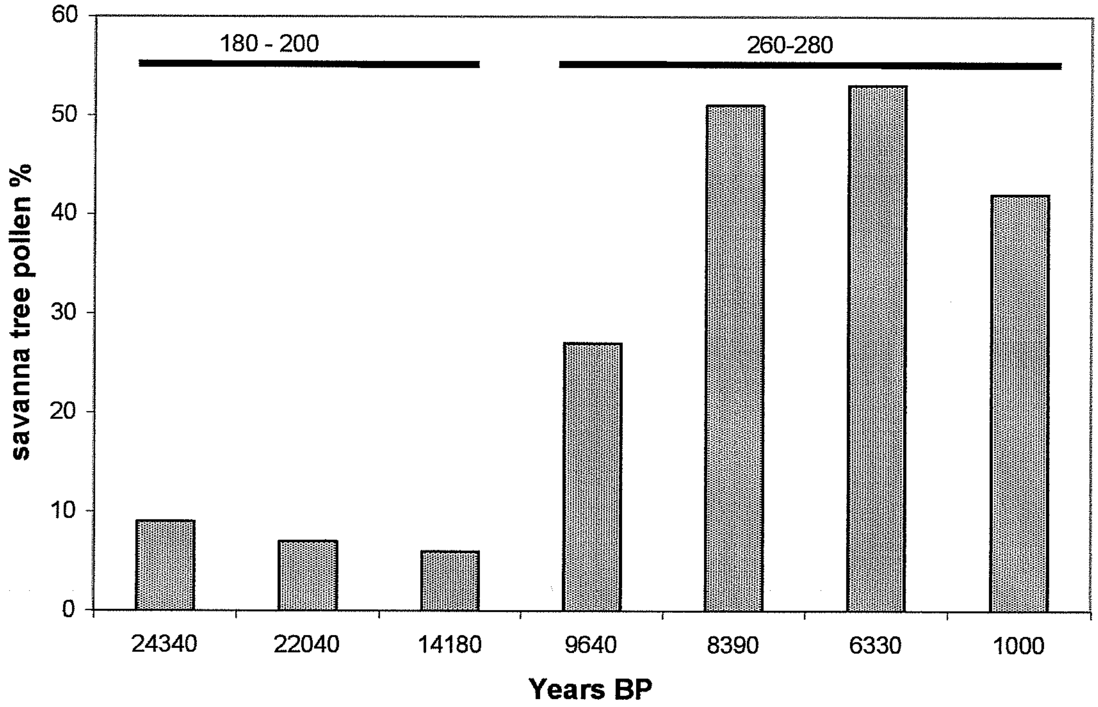


Figure 3. Pollen (%) of savanna trees from dated cores covering the last glacial through to the current inter-glacial, Wonderkrater, South Africa (from Scott, 1999). Bars represent summed pollen % for pollen from the following savanna tree taxa: *Acacia*, *Burkea*, Capparaceae, Combretaceae, *Euclea*, Oleaceae, *Peltophorum*, *Spirostachys*, *Tarconanthus*. The horizontal bars indicate glacial (180-200) and interglacial (260-280) CO_2 levels for the samples.

Figure 3 shows changes in savanna tree densities, as reflected in pollen, at Wonderkrater in north-eastern South Africa (Scott, 1999). This area is currently surrounded by mesic savannas. But the pollen evidence is consistent with our model results in showing virtual absence of savanna trees in the last glacial. Charcoal records indicate that grasslands continued to burn throughout the period, a key assumption of our model (Scott, 2002). The pollen data has yet to be assimilated by ecologists. It is remarkable that our savannas are so young, with trees only appearing in the last 10 000 years. What happened to the large mammal browsers during the glacial period? Are our savannas still equilibrating with some species not present because of slow migration of trees from warmer areas to the north? Is the puzzling scarcity of miombo species in South Africa (e.g. *Brachystegia* and *Julbernardia*) a dispersal problem or are growing conditions in South Africa unsuitable? In any event, the palaeoecological evidence seems consistent with our simulations in which CO_2 alone can cause the demise of trees without any change in climate.

The second prediction is that tree densities should have increased as CO_2 levels increased in the atmosphere over the last century. There are a number of studies documenting just such an increase in many parts of South Africa using a variety of different approaches, including paired photographs (Hoffmann and O'Connor, 2001) and aerial photographs (O'Connor and Crow, 1999, Roques *et al.*, 2001). In short, the phenomenon of bush encroachment may partly be explained by increasing CO_2 levels over the last century. We do not wish to imply that this is the "answer" to bush encroachment. Changes in fire regime, variation in grazing pressure, changes in wood use by people will undoubtedly have affected the process locally. However we do suggest that increased CO_2 in the atmosphere, a global phenomenon, has tipped the balance towards trees in many ecosystems. Because the increases are global, we would expect bush encroachment to also occur in savanna ecosystems elsewhere in the world if they experience similar tree/grass dynamics. As we stated in the introduction, the problem is, indeed, a global one.

Our study is based entirely on simulation models. Clearly we need experiments to test the validity of the models and gain greater confidence in their predictions. A glasshouse experiment is currently in progress at Kirstenbosch in which grasses and three savanna woody species (*Acacia karroo, A. nilotica* and *Dichrostachys cinerea*) are being grown at CO_2 concentrations fo 180, 270, 360, 500, 700 and 1000 ppm. Preliminary results (B. Kgope, pers comm, 2002) show a close fit to model predictions for 180 and 270 ppm relative to current atmospheres but lower growth than that predicted by the simulation for above-ambient CO_2. The DBM model for tree demography is also being tested in the Kruger National Park using the 50 years burning experiments there. We still lack information on the response of tree growth to variable rainfall and the response of fire regimes to global warming, both of which might also influence the tree/grass balance. Ideally we would like to manipulate CO_2 levels in field grown plants but this is an expensive and difficult undertaking. It is also important to note that we have simulated the release bottleneck and not recruitment bottlenecks. We do not understand the processes involved in bush encroachment by shrubby savanna species such as *Dichrostachys cinerea* to model CO_2 effects.

6. Conclusions

If increased CO_2 is partly responsible for bush encroachment in some savannas, there are a number of implications for savanna management, whether for conservation or livestock farming. A laissez faire policy of "letting nature do its thing" could be dangerous threatening large areas of mesic savanna with conversion to closed woodland and scrub forest. "Nature" is no longer the same. By releasing vast quantities of carbon from the burning of fossil fuels, we have created conditions that are unprecedented for our plants. Trollope has shown that tree densities can be controlled by skilled management under current climate conditions. We may need much more active intervention, especially in the use of fire, to prevent large areas of open grassy country turning to "bush" in the coming decades.

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Bush encroachment in savannas

In savannas, the natural balance between the ratio of trees to grasses can be upset by cattle and sheep which eat grass but seldom browse trees. Conventionally, it is considered that grasses, being fast-growing plants with roots in the upper layers of the soil, outcompete trees (which are slow-growing and have deeper root systems) for water and soil nutrients. When heavy grazing (also called 'overgrazing') occurs, the grasses are removed, freeing up water and soil resources for the trees to exploit. Tree seeds are then able to germinate *en masse* , creating an impenetrable thicket. This phenomenon is known as bush encroachment.

Bush encroachment by Acacia mellifera

In Africa, the main encroaching species are thorn trees (e.g. *Acacia mellifera* (the encroaching species at Pniel), *A. karroo* , *A. reficiens* , *A. tortilis* and *Dichrostachys cinerea*). These species also tend to have very high levels of phenolic compounds (e.g. tannins) in their leaves, which reduces their digestibility to livestock (Rohner and Ward 1997). The combination of thorniness and low digestibility of *Acacia* trees reduces their accessibility and nutritional value to livestock, thereby reducing the ability of the land to sustain people and their livestock. It is estimated that some 20 million hectares of South Africa are currently affected by bush encroachment. Thus, bush encroachment can lead to serious reductions in livestock, ultimately causing famine, which is often exacerbated by drought.

Bush encroachment is an example of an agricultural problem that is also a biodiversity problem: reduced agricultural productivity occurs because of the low value of thorn trees to livestock; reduced biodiversity occurs because a multi-species grass sward is replaced with a single tree species. Finding a solution to the problem of bush encroachment is therefore of mutual benefit to agriculture and conservation. Furthermore, when bush encroachment occurs, many indigenous plants that are traditionally used by people for nutritional and health purposes are outcompeted or shaded out by trees. This leads to a serious decline in the quality of life for the people who use these plants.

The problem of bush encroachment is particularly acute in the communal rangelands of South Africa where human and livestock population densities are very high and, consequently, heavy grazing (which may often lead to bush encroachment) is common. Various attempts have been made to solve the problem of bush encroachment, but the vast majority of these have been unsuccessful. It has become clear that our understanding of the ecological mechanism that causes bush encroachment is very poor and hampers our ability to find a solution to the problem. The conventional model of bush encroachment (called the "two-layer model") outlined above, which claims that heavy grazing removes dominant grasses from competing with trees in the upper soil layer, has been found to be inappropriate or even wrong in many situations. For example, there are large areas of southern Africa where there is only a shallow soil layer with insufficient depth for the stratification of grass and tree roots into different layers, yet bush encroachment still occurs there. It is suspected, although not convincingly demonstrated, that rainfall amount and frequency may play a key role in the occurrence of bush encroachment because trees require more rain to germinate than do grasses and may germinate *en masse* with or without grazing in rare, high rainfall years. In some cases, the presence of fire can increase the likelihood that bush encroachment will occur, while other areas are bush encroached in spite of insufficient fuel loads for fires. Furthermore, tree species may encroach in some areas and not in others in spite of similar levels of grazing, rainfall and fire.

For an excellent introduction to the problem of bush encroachment, see Steve Archer's web page.

For more information see Tineke Kraaij's masters thesis topic "Factors causing bush encroachment in the semi-arid savanna of southern Africa ", supervised by Prof. David Ward.