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INCREASED TREE DENSITIES IN SOUTH AFRICAN SAVANNAS: > 50 YEARS OF DATA SUGGESTS CO₂ AS A DRIVER

Running title: CO₂ and woody encroachment in savannas

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ABSTRACT

For the past century woody plants have increased in grasslands and savannas worldwide. Woody encroachment may significantly alter ecosystem functioning including fire regimes, herbivore carrying capacity, biodiversity, and carbon storage capacity. Traditionally, increases in woody cover and density have been ascribed to changes in the disturbance regime (fire and herbivores) or rainfall. Increased atmospheric CO₂ concentrations may also contribute, by increasing growth rates of trees relative to grasses. This hypothesis is still heavily debated. This is an Accepted Article that has been peer-reviewed and approved for publication in the *Global Change Biology*, but has yet to undergo copy-editing and proof correction. Please cite this article as an “Accepted Article”; doi: 10.1111/j.1365-2486.2011.02561.x

because usually potential CO₂ effects are confounded by changes in land use (disturbance regime). Here we analyse changes in woody density in fire experiments at three sites in South African savannas where the disturbance regime (fire and herbivores) was kept constant for 30 and 50 years. If global drivers had significant effects on woody plants, we would expect significant increases in tree densities and biomass over time under the constant disturbance regime. Woody density remained constant in a semi-arid savanna but tripled in a mesic savanna between the 1970s and 1990s. At the third site, a semi-arid savanna near the southern limits of the biome, tree density doubled from the mid 1990s to 2010. Interpretation of the causes is confounded by population recovery after clearing, but aerial photograph analysis on adjacent non-cleared areas showed an accompanying 48% increase in woody cover. Increased CO₂ concentrations are consistent with increased woody density while other global drivers (rainfall) remained constant over the duration of the experiments. The absence of a response in one semi-arid savanna could be explained by a smaller carbon sink capacity of the dominant species, which would therefore benefit less from increased CO₂. Understanding how savannas and grassland respond to increased CO₂ and identifying the causes of woody encroachment are essential for the successful management of these systems.

INTRODUCTION

There are many reports of woody plant increase in grasslands and savannas worldwide over the past century. The increases may cause biome shifts from grassland to scrub forest (Briggs *et al.* 2005; Brook, Bowman 2006; Bowman *et al.* 2010; Wigley *et al.* 2010), or may be gradual and reversible increases of trees within savannas (Hoffman, O'Connor 1999; O'Connor, Crow 1999; Archer *et al.* 2001; Roques *et al.* 2001; Goslee *et al.* 2003; Asner *et al.* 2004; Walker, Meyers 2004; Van Auken 2009; Jordaan 2010). Large increases in tree density in grass dominated or mixed tree-grass systems will significantly alter their functioning and

biodiversity (Blaum *et al.* 2009; Sirami *et al.* 2009), and will reduce the yield and economic profit from rangelands (Scholes 2003). It is therefore essential to identify the drivers of increased woody cover and their interactions.

Woody cover in savannas may be regulated by many variables including climate (Sankaran *et al.* 2005), fire regimes (Trollope 1984; Higgins *et al.* 2000), herbivory (O'Connor 1985; Prins, van der Jeugd 1993), and scale-dependent interactions between these variables (Scholes, Archer 1997; Bond 2008; Sankaran *et al.* 2008; Staver *et al.* 2011). Woody plant thickening is generally attributed to changes in land use practise, particularly grazing and fire use (Scholes & Archer 1997), and to episodes of high or low rainfall (Sankaran *et al.* 2005). The phenomenon may also have been influenced by increasing atmospheric CO₂ (Idso 1992; Polley 1997; Bond, Midgley 2000). For African savannas, simulations of tree populations subjected to frequent fires predict high sensitivity to changing CO₂ (Bond *et al.* 2003; Scheiter, Higgins 2009). Glasshouse experiments in which seedlings of common South African tree species were grown across a gradient of CO₂ from very low (glacial, 180 ppm) to ambient (360 ppm) and elevated levels (550, 700 and 1000 ppm), supported the simulations in showing large responses in stem growth and resprouting response to simulated fire (Kgope *et al.* 2010). Field experiments that quantify interactive effects between elevated CO₂ and other drivers of vegetation such as Free Air CO₂ Enrichment (FACE) have not been established in savannas. FACE experiments are also unable to address historic changes in CO₂ that might have caused the patterns observed today.

In the absence of field studies, there is still considerable debate over whether CO₂ has been a significant driver of woody thickening (Archer *et al.* 1995; Van Auken 2009; Bowman *et al.* 2010; Ward 2010) and in which kinds of savannas. A key difficulty in attributing causes of

woody thickening is partitioning effects of land use (grazing, fire) from effects of global drivers such as CO₂ or rainfall (see e.g. Bowman *et al.* 2009; vs. Petty, Werner 2009; Wigley *et al.* 2010). Measuring effects of CO₂ on woody cover requires long periods during which other major drivers such as fire and grazing need to be held constant. There are very few documented examples for savanna ecosystems in which fire or grazing has been constant for long enough to differentiate effects of increasing CO₂ on woody vegetation.

Here we analyse datasets from three savannas in two independent fire experiments in South African savannas, where the disturbance regime was kept constant over the past 30-50 years. The first experiment was established in the Kruger National Park (KNP) in 1954 (Biggs *et al.* 2003) with treatments applied in both a mesic and a semi-arid savanna. The second experiment was set up in the Eastern Cape (EC) province in 1980 near the southern limits of African savannas at 32.5° S (Trollope, Tainton 1986). While both experiments have inevitable complications concerning experimental setup and data collection, the information from both experiments is highly complementary and permits us to track woody density over time. We evaluated possible global change impacts on woody cover by assessing temporal change in treatment responses over the duration of the experiments. If global drivers had significant effects on woody plants, we would expect significant increases in tree densities and biomass over time. Conversely, the absence of significant temporal changes in tree response would suggest that global drivers are a minor contributor to woody thickening in the experimental system.

METHODS

Kruger National Park experiment

Experimental setup

Biggs *et al.* (2003) give a very useful overview and history of the fire experiment in KNP.

The trial was established between 1954 and 1956 to study the effects of fire on flora and fauna at bio-geographically distinct regions, referred to as landscapes (Gertenbach 1983), within KNP. Each landscape block contains four replicate sub-blocks, referred to as "strings". Each string consists of 12-14 contiguous plots of approximately 7 ha, each of which is burned at a unique combination of fire frequency and season. Every fire treatment is thus replicated four times (once in each of four strings) for each of the four landscapes. The experimental plots are not fenced and KNP contains all large mammals native to the region.

Here we analyse data from two landscapes spaced ~100 km apart with contrasting climate and soils. The northern site (Satara, Lat: -24.39 – -24.66, Lon: 31.72 – 31.96) is semi-arid (MAP 537 mm y⁻¹) on basaltic clay soils, with the woody vegetation being dominated by *Acacia nigrescens* and *Dichrostachys cinerea*, while the southern site (Pretoriuskop, Lat: -25.10 – -25.21, Lon: 31.21 – 31.29) is more mesic (MAP 737 mm y⁻¹) on sandy granitic soils, with the woody vegetation dominated by *Terminalia sericea* and *Dichrostachys cinerea*. The original burn experiment included two additional landscapes, however data for more recent years was not available for these plots and they were therefore excluded from the analysis. Within each replicate string of these landscapes we analyse four distinct fire treatments: annual dry season (August), triennial wet season (February), and triennial dry season (August) burns. These fire treatments were selected for analysis because they are broadly representative of fire management strategies in African savannas, both inside and outside protected areas. Fire exclusion treatments were not analysed as they are highly unnatural in these savannas and

recent data on other fire treatments was not available. The two landscapes represent a semi-arid *versus* a mesic savanna.

Field methods

The woody vegetation in the experimental plots was surveyed four times between 1954 and 2004; at establishment between 1954 and 1957, between 1971 and 1973, between 1996 and 1999 and between 2002 and 2004. We will henceforth label these surveys by the decade in which they were done i.e. 1950s, 1970s, 1990s and 2000s. In the 1950s and 1990s vegetation within each plot was surveyed on two diagonal belt transects, while in the 1970s and 2000s permanent sub-plots were surveyed.

The diagonal belt transects measured 305 x 1.52 m in the 1950s, while in the 1990s transect width was increased to 2 m and transect length varied between 123 and 691 m. Within transects, each woody individual was identified to species level. In the 1950s basal stem diameter was recorded in classes while in the 1990s actual basal stem diameter and tree height were measured.

In the 1970s each woody individual in a 50 x 100 m grid of 1x1 m quadrats (5000 grid squares covering 0.5 ha) within each fire treatment plot was identified to species level. Tree height and stem diameter were also recorded. Grid corners were marked with metal stakes in the 1970s. In the 2000s all plots which still had sufficient markers in place to map out the grid were re-sampled. In the mesic Pretoriuskop plots an area of 750 m² was re-sampled (instead of the full 0.5 ha) and tree densities compared with exactly the same 750 m² area sampled in the 1970s.

Eastern Cape experiment

Experimental setup

This experiment was established in 1980 on the Fort Hare University experimental farm near Alice in the Eastern Cape province of South Africa (Lat: -32.800, Lon: 26.874). Mean annual rainfall is 614 mm. The vegetation in this area is classified as Bisho Thornveld (Mucina, Rutherford 2006), and is characterised by a grass layer with varying densities of *Acacia karroo*, dotted with clumps of broad-leaved woody species ('Albany thicket'). The experiment was initiated to study the effects of fire frequency and intensity on woody plant density and rangeland condition. Presumably to eliminate inter-plot differences in initial tree densities, all woody individuals were cleared at the start of the experiment by cutting stems at ground level and subsequent treatment with an herbicide. Six experimental burn regimes were applied since 1980: 1, 2, 3, 4 and 6 year burns in late winter (July/August). The experimental layout followed a randomised block design with 10 contiguous plots (0.4-0.6 ha) with each fire treatment replicated twice.

Field methods

In permanent vegetation plots (1280-1546 m²), within the centre of each of the 10 experimental plots, all woody individuals were identified to species level and tree height was measured. Notably, the same observer collected these data over the entire course of the experiment, reducing observer bias. Here we analyse data over a 30 year period for survey intervals of 3-6 years: 1981, 1985, 1989, 1993, 1997, 2001, 2004, and 2010.

Aerial photos

Tree density in the experimental plots was not measured before clearing at the start of the experiment. To examine how recent tree density compares to pre-clearing density we quantified tree cover in the plots from aerial photographs in 1973 (scale 1:50000), which were nearest in time to the start of the experiment in 1980, and compared this to tree cover on the most recent photographs taken in 2007 (scale 1:20000). To get an impression of changes in the surrounding landscape we also compared areas (10.7 ha) neighbouring the experimental plots. Aerial photographs from 2007 were obtained as digital ortho-rectified and geo-referenced images, while 1973 photographs were scanned at 800 dpi and geo-referenced manually in ArcGIS 9.3 (ESRI 2008). We used the object-based image analysis software eCognition 5 (Definiens Imaging 2006) to classify trees from the images. Multi-resolutional segmentation and classification were applied to the images. The image was segmented at both a fine scale (parameters: scale = 3, shape = 0.2, smoothness = 0.8), and a larger scale (parameters: scale = 100, shape = 0.5, smoothness = 0.5). A scale of 3 for segmentation was chosen to ensure that image objects were small enough to represent individual trees. Trees were classified by a combination of two methods: difference in brightness between trees and the background using the fine level of segmentation and the ratio between the mean size of fine scale segmented objects (trees) and larger scale segmented objects (Levick 2008). To assess the accuracy of the automated classification, we compared it to a visual classification using an accuracy error matrix. The matrix shows what proportion of pixels was assigned the same classification between the two methods, giving the overall accuracy in percentages.

To establish if tree density has exceeded pre-clearing densities we examined the relationship between tree cover from recent (2007) aerial photographs and measured tree density with a simple linear regression. We then applied this function to the pre-clearing cover estimates to estimate pre-clearing tree density.

Analyses

The density of woody individuals was calculated from survey data of both experiments and was the primary response variable in this study. Data from both experiments was analysed with linear mixed-effects models in the nlme package (Pinheiro *et al.* 2011) for R (R Development Core Team 2010), which allow inclusion of both fixed (landscape, year, fire treatment, rainfall) and random (string, plot) variables and are robust to missing data (Pinheiro, Bates 2000). The inclusion of plot as a random variable allows for correlated error terms caused by repeated measurements on the same plots. The random model structure was assessed with log-Likelihood tests between competing models and the Akaike Information Criterion (AIC) which decreases as model fit improves. Tree density of both experiments was log-transformed to meet model assumptions of normality.

The survey frequency in the EC experiment allowed the inclusion of rainfall as a predictor variable in the initial model. We used annual (July to June) rainfall of the previous year.

Tree height distributions are shown for the most common species in each experimental site where available. For KNP we used only 1970s and 2000s data that were collected at exactly the same location from permanent grids and which therefore allow a very precise assessment of changes in tree height.

Climate data were recorded by KNP and University of Fort Hare staff and were analysed for time trends with linear regressions. Eastern Cape data was collected on site, while KNP data were collected between 1 and 30 km from the experimental sites. Test results are only displayed when results were significant.

RESULTS

KNP experiment

Tree density

Tree density increased almost threefold between the 1970s and 1990s in the mesic site, while no significant changes occurred in the semi-arid site (Fig. 1). This interaction between landscape and year was highly significant ($F_{3,56} = 25.4$, $P < 0.0001$) and explained 46% of the variance. While the main effects of both landscape ($F_{1,6} = 25.2$, $P < 0.01$, 5% of variance) and year ($F_{3,56} = 20.6$, $P < 0.0001$, 32% of variance) were also highly significant. Fire treatment surprisingly had no significant effect on tree density ($F_{2,14} = 0.1$, $P = 0.95$) and explained less than 0.1% of the variance.

The inclusion of both string (4% of variance) and plot nested within string (4% of variance) as random variables produced the best model fit. The remaining 9% of variance was due to unmeasured within plot differences.

Vegetation structure

Measurements of tree height in the 1970s and 2000s allow an examination of trends in the physical structure of these species and, to some extent, of their demographic structure. The two most dominant species in the semi-arid KNP site, *Dichrostachys cinerea* and *Acacia nigrescens*, showed no clear trends in demographic and physical structure over time (Fig. 2).

However, the dominant species at the mesic site, *Dichrostachys cinerea* and *Terminalia sericea*, show significant increases in the abundance of all height classes, including adult trees. Both species show similar trends in tree height distribution over time (Fig. 3). In the 1970s trees in height classes below 2 m were most common, while taller trees were less common. In the 2000s height distribution follows a distribution with a large peak for the smallest height classes, and ostensibly a small peak for trees >3 m, while trees between 2 and 3 m are the least common. The density of smaller trees increased markedly since the previous survey, while tall trees increased primarily for *T. sericea*.

Climate

Rainfall data obtained from the KNP showed no significant trends in rainfall between 1932 and 2006 in either site.

EC experiment

Tree density

Tree density increased significantly over time ($F_{1,68} = 164.6$, $P < 0.0001$) but decreased with rainfall of the previous year ($F_{1,68} = 7.0$, $P < 0.05$). The interaction between time and rainfall was not significant, indicating that the relationship between tree density and rainfall did not change over time. As in the KNP study, fire frequency had no significant effects on tree density ($F_{1,8} = 1.8$, $P = 0.2$). The fixed variables in the model explained very little variance, and most variance was due to random differences between plots (26%), and within plot variation (72%). This suggests that while tree density increased significantly over time, there were other unmeasured sources of variation.

To test if the negative effect of rainfall on tree density did not just result from increased seedling emergence in response to low rainfall, we re-analysed the data without seedlings (trees < 0.5 m). The significant increase in tree density over time ($F_{1,58} = 51.7$, $P < 0.0001$) was retained (Fig. 4), while the effect of rainfall also remained significant ($F_{1,58} = 10.9$, $P < 0.01$), suggesting that rainfall variability has an effect on both seedling emergence as well as on growth and establishment of older trees.

Vegetation structure

Increased tree densities in the Eastern Cape experiment were primarily caused by *Acacia karroo*. Despite the fire treatments, trees increased in size over the duration of the experiment. Trees taller than 3m, where they escape topkill by fire, only appeared in the second half of the experiment (Fig. 5).

Aerial photography

Detectable tree cover in the experimental plots ranged between 2.8 and 14.2 percent in 1973 and between 0.5 and 18.7 percent in 2007. We found that tree cover on aerial photographs correlated well with the density of trees taller than 2 m ($R^2 = 0.73$), but this relationship broke down when smaller trees were included in the analysis. In this type of vegetation aerial photographs with scale 1:20000 can therefore be used to estimate the density of adult trees (> 2 m), but did not allow us to estimate total stem density from before clearing at the start of the experiment.

In areas outside the experimental plots tree cover increased dramatically from 1% in 1973 to 50% in 2007, suggesting that taller trees have become much more abundant (Fig. 6). The software classification accuracy for visible trees was 86% for the 1973 images and 84% for the 2007 images.

Climate

Inter-annual variation in annual rainfall was high (coefficient of variation is 21%) as is common over much of southern Africa however no precipitation trends could be detected from locally collected monthly rainfall data between 1970 and 2010.

There were no significant temperature trends in locally collected data between 1980 and 2009. A significant change over time in class A pan evaporation was detected, which was best modelled by a polynomial function with the year 1980 set to zero (evaporation = $0.95 \cdot \text{year}^2 - 37.6 \cdot \text{year} + 1935.8$, $F_{2,23} = 12.2$, $P < 0.001$, $R^2 = 0.52$). Evaporation decreased by 19.2% from 1935.8 mm y^{-1} in 1980 to 1564.6 mm y^{-1} in 2000, after which it increased slightly by 5% to 1645.9 mm y^{-1} in 2009. The decrease in evaporation is consistent with a global trend that appears to stem from reduced wind speed and solar irradiance (Roderick, Farquhar 2002; Roderick *et al.* 2007).

DISCUSSION

We set out to test whether global drivers had influenced woody thickening by assessing trends in field experiments in which the same fire regime had been applied for thirty years or more. If global drivers, such as increasing atmospheric CO_2 , had altered the ecology of trees, we expected to see increasing woody biomass over the duration of the experiment. For the longest running experiments, in the Kruger National Park, there was very little change in tree

densities in the first 20 years from the 1950s to the 1970s. In the semi-arid savannas, tree populations also remained very similar over the next 20+ years into the 1990s and 2000s. Thus, for the more arid savannas, there was no indication of global drivers promoting woody increase over this period. The trends for the mesic savanna were quite different with tree densities tripling in the 20+ years from the 1970s to the 1990s and 2000s. More trees escaped the fire trap in the second period so that woody density increased by 194% from the 1970s to the 2000s in the mesic savanna but 3% in the semiarid savanna. In the EC experiment, *Acacia karroo* densities increased from the start of the experiment with the first trees emerging above the flame zone (> 3m) from the mid 1990s, halfway through this 30 year long experiment. Large increases in adult *A. karroo* were observed in aerial photos of areas adjacent to the experiment and from repeat photos elsewhere in the Eastern Cape since the 1990s (M.T. Hoffmann, pers. comm.).

The value of these experiments for exploring causes of woody thickening lies in the constant disturbance regime that has been implemented for over 50 years at KNP and 30 years at EC. Because fire frequency and burn season were constant, the increase in tree density over time cannot be explained by temporal changes in the fire regime. Moreover, tree density did not differ between fire treatments, suggesting that fire frequency and burn season did not control tree density for the range of treatments applied. Higgins *et al.* (2007) reached the same conclusion from spatially more extensive, but temporally more restricted data at KNP, and suggested that fire may affect vegetation structure by inducing above-ground stem dieback but rarely kills individuals.

Both experimental set-ups have complications for wider interpretation. KNP is a national park containing an African mega-fauna, an unusual ecological setting relative to most savannas. An often stated complication of the KNP fire experiment is that, because the plots were not fenced, the different fire treatments might have affected herbivore impact on the plots divergently. We feel however that this does not affect the observed patterns, firstly because we found no differences in tree density between the different fire treatments and secondly because a potential herbivore effect on tree density would also be expected to show up in the semi-arid site, where tree density did not change over time. The EC experimental set up included clearing of trees prior to the experiment so that global change effects are confounded with population recovery. However, the trends observed in this experiment were matched by large tree increases in areas adjacent to the experimental plots as revealed by aerial photo analysis, and more widely in the region as revealed by fixed-point photos taken at different intervals over the last few decades (O'Connor, Crow 1999; Puttick *et al.* 2011).

With fire and herbivores ruled out as explanations for the observed increase in tree density, global drivers of woody thickening need to be considered. We found no evidence for climate trends that could account for woody increase over the experimental period either in KNP or EC. Inter-annual rainfall is highly variable in these (and most) savannas. Other analyses of climate trends from 1950 to 1999 also showed no trends in annual rainfall at KNP, minor changes in monthly and seasonal rainfall distribution and a very slight warming trend of 0.05 °C per decade (Scholes *et al.* 2001; Kruger *et al.* 2002; Hewitson *et al.* 2005; Warburton, Schulze 2005). The EC site has a similar record of variable rainfall with no trends in mean annual precipitation and only very minor trends in monthly and seasonal precipitation variables in the study area (Hewitson *et al.* 2005; Warburton, Schulze 2005). There were no significant temperature trends over the experimental period (Warburton *et al.* 2005).

The most likely global driver of woody increase over the last half century in the region is increasing atmospheric CO₂. Pre-industrial levels of ~280 parts per million (ppm) increased to ~315 in 1959 just after the start of the KNP experiment and ~390 ppm by 2010. This means that approximately two thirds of the anthropogenically driven increase in atmospheric CO₂ took place during the lifespan of the experiment. Plants have not had to deal with such high atmospheric CO₂ for at least the past 650 thousand yrs but probably not for the past 3 million yrs or longer (Pearson, Palmer 2000). There are many studies on the effects of elevated CO₂ on the physiological performance of individual plants in glass houses, open top chambers and FACE experiments (Drake *et al.* 1997; Poorter, Navas 2003; Ainsworth, Long 2005) and some on plant responses to below-ambient CO₂ (reviewed in Gerhart, Ward 2010). A few of these studies are on savanna trees (Polley *et al.* 1997a; Polley *et al.* 1999; Hoffmann *et al.* 2000; Eamus, Palmer 2007) including South Africa species in the burn experiments (Kgope *et al.* 2010). *Acacia karroo*, the dominant species in the EC site, was very responsive to increasing CO₂ with a three-fold increase in both stem biomass and below ground starch reserves from 270 to 380 ppm CO₂ treatments (Fig. 7). *Terminalia sericea*, the dominant tree in the mesic KNP savanna, also showed a three-fold increase in total biomass across the same range of CO₂ treatments (Midgley, Kgope, Bond in prep). In both cases, plants were grown for a year, cut to simulate fire, and then harvested after a second growing season. Both these species would be predicted to show a population increase in the field based on these experimental results. *Acacia nigrescens*, the dominant tree in the semi-arid savanna has not been grown under varying CO₂. It has a slow relative growth rate compared to other South African acacias and might therefore be expected to have low CO₂ responsiveness (Poorter, Navas 2003).

The evidence for increased tree densities and sizes for two of the three experiments is consistent with CO₂ as a major global driver of woody increase, but it does not explain why tree density did not change in the semi-arid KNP site (see also Higgins *et al.* 2007). The lack of response in the semi-arid savanna is surprising since field CO₂ fertilisation of grasslands has consistently shown increases in soil water (Morgan *et al.* 2004) which would be expected to promote tree recruitment (Polley *et al.* 1997b; Kraaij, Ward 2006). CO₂ responses can be sensitive to soil nutrients but all the sites have relatively nutrient rich soils and the site with the richest soil (KNP semi-arid) showed the least temporal response. The growth response of plants to CO₂ varies among functional types, among species within the same functional type, and among phylogenetically related species (Atkin *et al.* 1999; Poorter, Navas 2003). The basis for this variation is an active area of research. One hypothesis, of particular relevance to savanna species, is that plants with large carbon sinks will benefit most from increasing CO₂. The ability to store carbon as root starch is a common trait in mesic savanna trees, as it enables resprouting following frequent fires and herbivory (Hoffmann *et al.* 2003; Schutz *et al.* 2009; Wigley *et al.* 2009). Experimental CO₂ fertilisation indeed results in increased root starch storage in savanna trees (Hoffmann *et al.* 2000; Kgope *et al.* 2010) and would be expected to promote post-burn recovery in species such as *Acacia karroo* (Schutz *et al.* 2009).

Besides the capacity for storage, other carbon sinks such as root elongation can significantly increase plant growth in response to elevated CO₂ (Lambers *et al.* 2008). Species with extensive root elongation, such as those that spread clonally by root-suckering, are therefore expected to sustain higher rates of carbon assimilation without having to down-regulate photosynthesis. The highly variable *Dichrostachys cinerea*, a common shrub species in the KNP sites, spreads by root suckers in frequently burnt mesic savannas dominated by the variety *nyassana* (Neke *et al.* 2006; Munkert 2009; Wakeling, Bond 2009). In semi-arid areas,

the *africana* form is common and populations in Hluhluwe-iMfolozi Park, South Africa, do not form root suckers (W.J. Bond unpublished). The divergent ecological responses of this shrub species in the two KNP savannas may therefore have a physiological basis in different rooting strategies of the different forms resulting in different sink strengths.

Our analysis has shown significant increase in tree densities and stature that are consistent with global drivers promoting woody thickening. The only plausible candidate in the experimental areas is increasing CO₂ since there were no significant temperature or rainfall trends over the last fifty years. There are a number of similar long-term burning experiments in Africa and elsewhere. Where treatments have been maintained and sufficient censuses are available, these would be worth exploring for temporal trends driven by factors other than land use change. For example, Briggs *et al.* (2002), reported on a 15 year study in tall grass prairies with different burning and grazing treatments. As in our study, some woody species showed marked increases in density, despite being exposed to the same disturbance regime. Although Briggs *et al.* (2002) noted that the largest responses were from disturbance regimes thought to match those of past centuries, when the grasslands were reported to be tree-less, they did not discuss CO₂ or other possible global drivers as causes of the woody increase.

We suggest that CO₂-fuelled increases in woody plant growth have altered the rules for tree-grass ecology in South Africa. The implication is that land managers in the mesic savannas will have to work much harder to prevent loss of open grassy ecosystems to trees. The practises of the past will no longer be as effective in controlling tree densities. On the limited available evidence, however, the impact of global drivers on woody increase in arid savannas in the region is negligible relative to the effects of herbivores and fire suppression (Trollope,

Dondofema 2003; Higgins *et al.* 2007). This is similar to the conclusion reached by Van Auken (2009) for the arid grasslands of the south-western USA.

While CO₂ may have contributed to the large tree increases in more humid savannas in the 20th century, this does not mean that it will continue to do so in the future. CO₂ stimulation of growth levels off at high CO₂ while future increases in temperature and changes in precipitation patterns may produce unexpected results. To address these uncertainties and generate predictive ability that may inform potential management strategies, field scale CO₂ manipulation experiments in African savannas are essential.

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FIGURE LEGENDS

Figure 1. Boxplots of tree density over time in different fire treatments (fire frequency and season), in a semi-arid and mesic savanna. The data are from a long-term fire experiment in the Kruger National Park, South Africa, where the fire regime was kept constant for over 50 years. The horizontal bar displays the median and the box contains 75% of data points.

Whiskers contain $Q1 - 1.5 * IQR$ to $Q3 + 1.5 * IQR$ of data points (Q = quartile, IQR = inter quartile range) and outliers are displayed by dots.

Figure 2. Changes in density and size structure of the two dominant woody species in a semi-arid savanna subjected to the same fire treatments for 20 years (1970s) and 20+ years later (2000s) in the Kruger National Park. Error bars display standard errors.

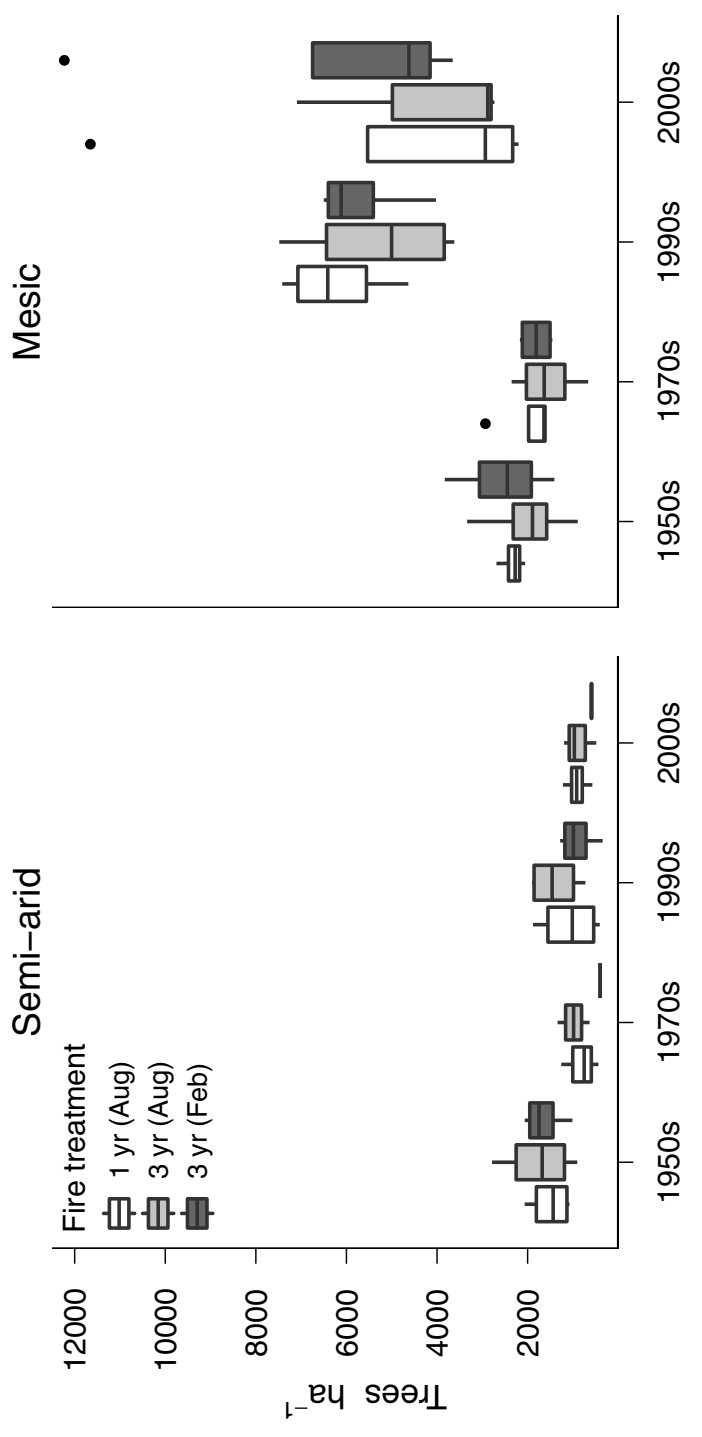
Figure 3. Changes in density and size structure of the two dominant woody species in a mesic savanna subjected to the same fire treatments for 20 years (1970s) and 20+ years later (2000s) in the Kruger National Park. Error bars display standard errors.

Figure 4. Boxplot of tree (>0.5 m) density over time in the Eastern Cape fire experiment. The horizontal bar displays the median and the box contains 75% of data points. Whiskers contain $Q1 - 1.5 * IQR$ to $Q3 + 1.5 * IQR$ of data points (Q = quartile, IQR = inter quartile range) and outliers are displayed by dots.

Figure 5. Changes over time in density and size structure of the dominant woody species in a semi-arid savanna subjected to the same fire treatments for 30 years.

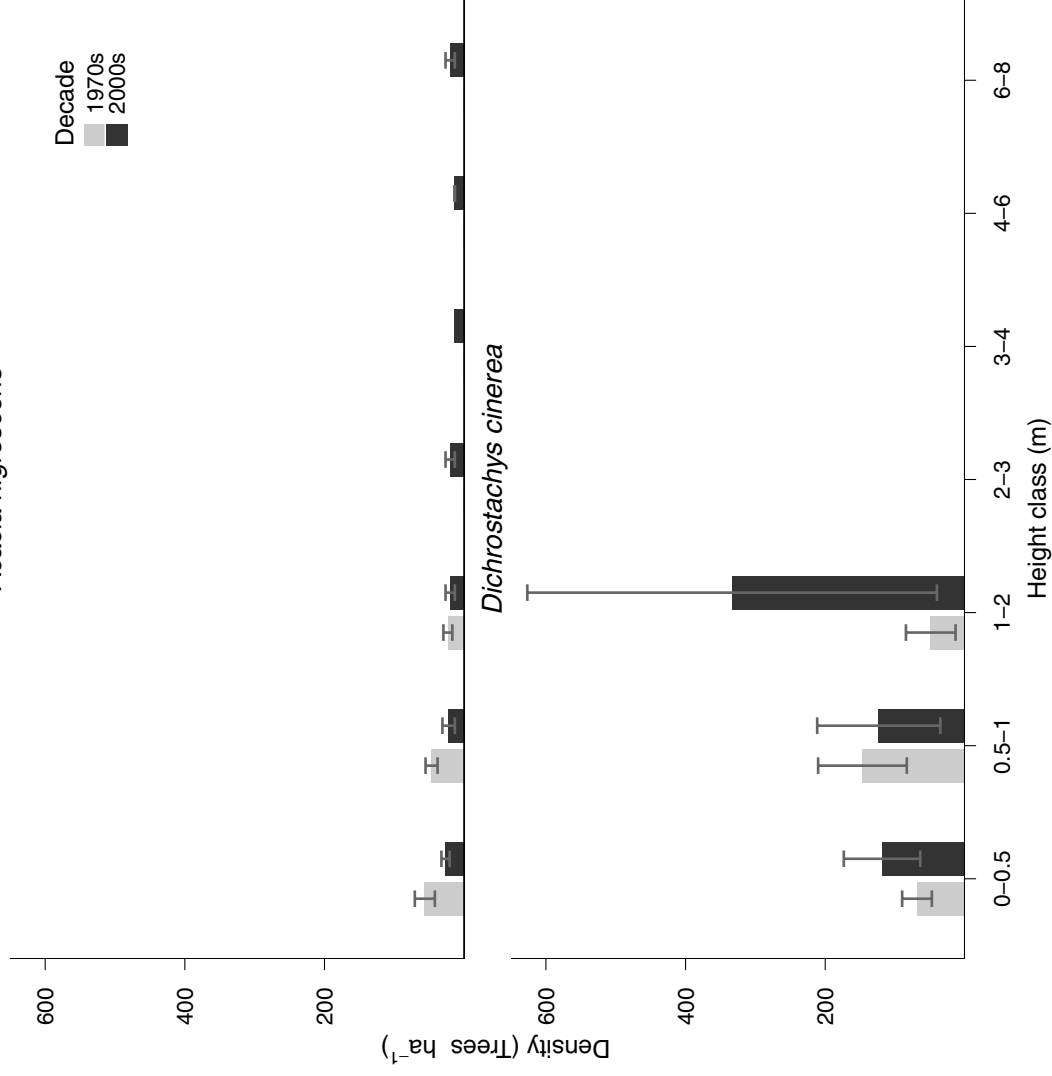
Figure 6. a) An aerial photograph of the area around the experimental plots in the Eastern Cape in 1973. b) The same area in 2007, showing large increases in woody cover.

Figure 7. Below-ground response of *Acacia karroo* to a CO₂ gradient. Plants were grown in open-top chambers in a glasshouse for a year at each treatment, cut to simulate fire, and harvested after a second growing season. See Kgope *et al.* (2010) and Midgley, Kgope, Bond (in prep.). LGM = Last Glacial Maximum, ppm = parts per million.

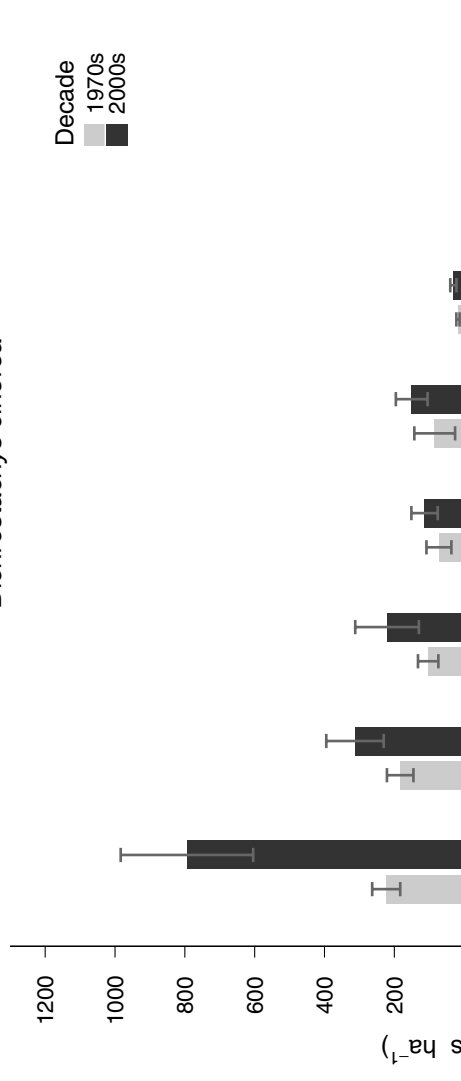


Acacia nigrescens

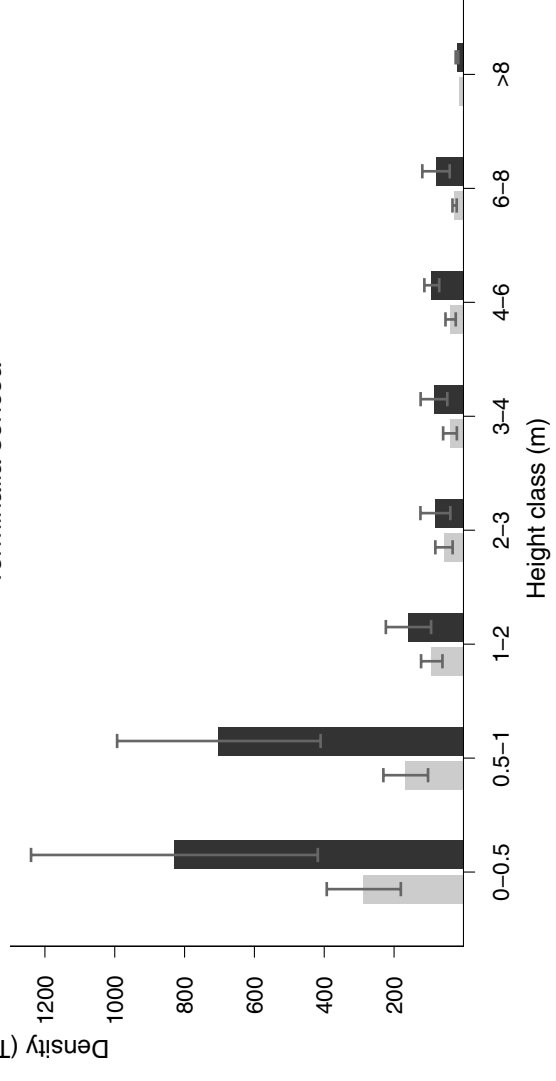
Decade
1970s
2000s



Dichrostachys cinerea

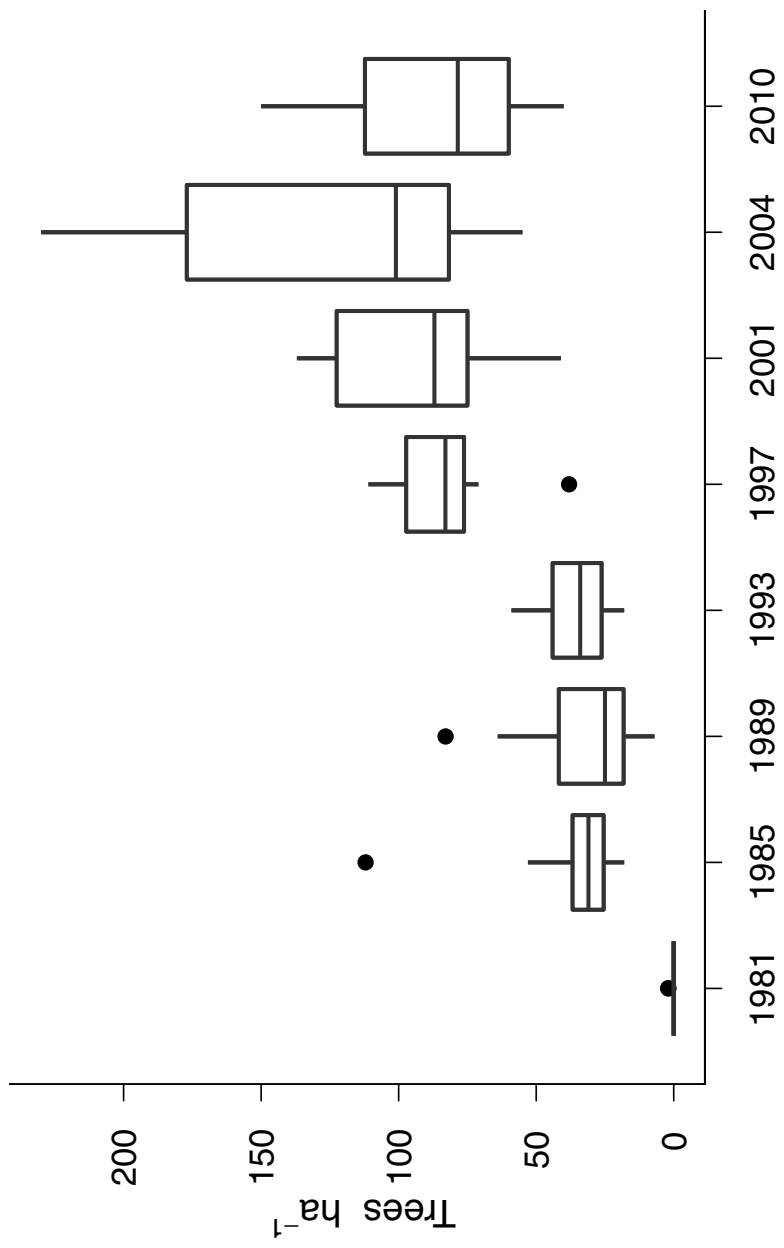


Terminalia sericea

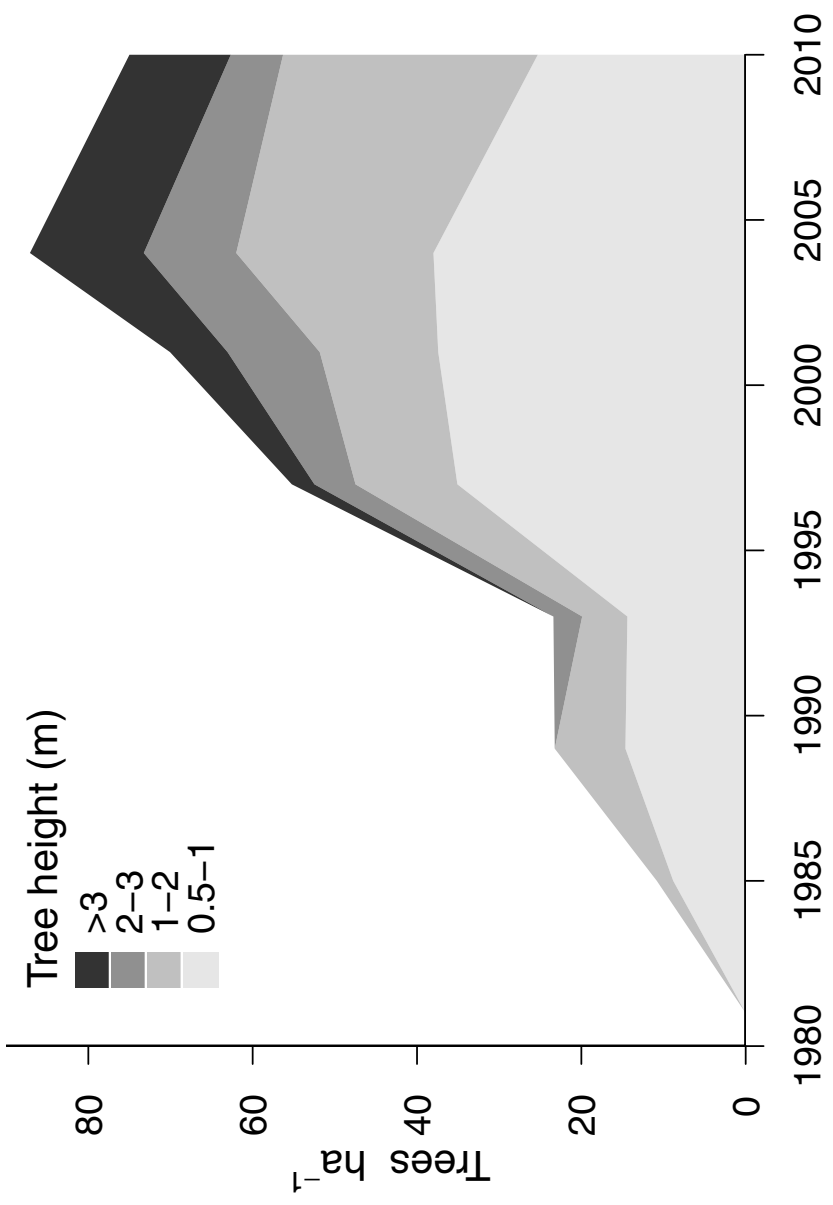


Decade
1970s
2000s

EC Semi-arid



Acacia karroo



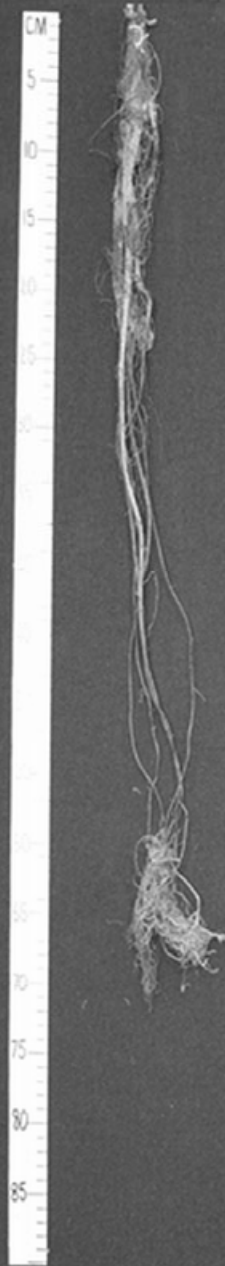




LGM
180 ppm



Pre-industrial
260 ppm



Ambient
375 ppm

