**Article:**

Wigley, BJ, Augustine, DJ, Coetsee, C et al. (2 more authors) (2020) Grasses continue to trump trees at soil carbon sequestration following herbivore exclusion in a semiarid African savanna. Ecology, 101 (5). e03008. ISSN 0012-9658

https://doi.org/10.1002/ecy.3008

**Grasses continue to trump trees at soil carbon sequestration following herbivore exclusion in a semi-arid African savanna**

BENJAMIN J. WIGLEY,[1,2*] DAVID J. AUGUSTINE,[3] CORLI COETSEE,[2,4] JAYASHREE RATNAM,[1] AND MAHESH SANKARAN[1,6]

[1]National Centre for Biological Sciences, Tata Institute of Fundamental Research, Bangalore, India.

[2]School of Natural Resource Management, Nelson Mandela University, George, South Africa.

[3]Rangeland Resources Research Unit, USDA, Agricultural Research Service, Fort Collins, Colorado.

[4]Scientific Services, South African National Parks, Skukuza, South Africa.

[5]Faculty of Biological Sciences, School of Biology, University of Leeds, Leeds, UK

[*]Corresponding author: Benjamin J Wigley; email: benwigley@gmail.com

Running Head: Grasses boost soil C storage in savanna

Key words: aboveground biomass; browsers; $C^{13}$ isotopes; grazers; herbivore exclosures; isotopic mixing models

Abstract

While studies have shown that mammalian herbivores often limit aboveground carbon storage in savannas, their effects on belowground soil carbon storage remains unclear. Using three sets of long-term, large herbivore exclosures with paired controls, we asked how almost two decades of herbivore removal from a semi-arid savanna in Laikipia, Kenya affected aboveground (woody and grass) and belowground soil carbon sequestration, and determined the major source ($C_3$ *vs*. $C_4$) of belowground carbon sequestered in soils with and without herbivores present. Large herbivore exclusion, which included a diverse community of grazers, browsers, and mixed-feeding ungulates, resulted in significant increases in grass cover (~22%), woody basal area (~8 $m^2$ $ha^{-1}$) and woody canopy cover (31%), translating to a ~8.5 t $ha^{-1}$ increase in aboveground carbon over two decades. Herbivore exclusion also led to a 54% increase (20.5 t $ha^{-1}$) in total soil carbon to 30 cm depth, with ~71% of this derived from $C_4$ grasses (*vs*. ~76% with herbivores present) despite substantial increases in woody cover. We attribute this continued high contribution of $C_4$ grasses to soil C sequestration to the reduced offtake of grass biomass with herbivore exclusion together with the facilitative influence of open sparse woody canopies (e.g. *Acacia* spp.) on grass cover and productivity in this semi-arid system.

## INTRODUCTION

Soils comprise the world's largest terrestrial reservoir of carbon, storing more than twice the amount of carbon stored in the atmosphere (Eswaran et al. 1993, Batjes and Sombroek 1997, Percival et al. 2000) as decomposed plant litter and residue (Melillo et al. 1989, Cole et al. 1993, Batjes and Sombroek 1997). Savannas – vegetation where both trees and grasses co-exist – have a high potential for belowground carbon storage in soils (Reid et al. 2004). However, this potential is often not realised as many savanna rangelands show a decreased capacity to store carbon as a result of improper grazing management, soil erosion, biomass burning, and land conversion to cropland (Watson et al. 2000, Reid et al. 2004). This is particularly relevant in Africa, where savannas cover >27% of the land surface (Loveland et al. 2000).

African savannas are unique in that they often contain a diverse suite of large mammalian herbivores ranging in size from a few kilograms to over six tonnes. This rich mix of large herbivores, which includes grazers, browsers and mixed feeders, exert strong top-down control on vegetation at the landscape level, e.g., herbivores can prevent forests from developing (and thereby maintain savannas) in regions which have soils and climates that favour closed canopy vegetation (Bond 2005, Tanentzap and Coomes 2012, Stevens et al. 2016). How large herbivores directly and indirectly affect aboveground and belowground carbon sequestration in savannas however remains poorly understood.

Differences in dominant herbivore guilds (e.g. grazers *vs*. browsers) further complicate the expected patterns of carbon storage in savannas as they have similar as well as disparate (and sometimes opposing) direct and indirect effects on both vegetation (reviewed by Tanentzap & Coomes 2012, McSherry & Ritchie 2013), and above- and below-ground carbon stocks. Shared effects include the direct consumption of aboveground plant biomass by herbivores which alters soil carbon by changing the quantity and quality of plant litter, changing rates of soil respiration and altering rates of nutrient cycling through their waste products (Tanentzap & Coomes 2012). Grazers may have both negative and positive effects on soil C. Negative effects include a decrease in herbaceous vegetation and associated increase in bare ground with heavy grazing on arid, sandy grasslands which accelerates soil drying and erosion, culminating in decreased soil carbon (Li et al. 2008, Steffens et al. 2008). On the other hand, grazing may stimulate fine, shallow roots of grasses which can compensate for the reduced aboveground carbon inputs to soils as a result of herbivore consumption, thereby resulting in a lack of any long-term effects on soil carbon (Derner et al. 2019), or alternately lead to increased soil carbon where belowground production offsets aboveground consumption (Frank et al. 1995, Frank et al. 2002; Derner et al. 2006). The effects of browsers on ecosystem C are often indirect and come about as a result of changes in woody cover (Mekuria et al. 2011, Sankaran et al. 2013, Wigley et al. 2014, Bakker et al. 2016, Bikila et al. 2016). Changes in tree and shrub densities have been shown to affect the spatial distribution and cycling of nutrients and carbon by altering soil structure, microbial biomass, soil moisture and microclimate. Trees may also result in increased turnover of standing root biomass which results in an accumulation of organic matter under their canopies (Binkley and Giardina 1998, Schlesinger and Pilmanis 1998, Hibbard et al. 2001).

Woody encroachment in savannas – an increase in the woody layer at the expense of grasses – has often been shown to result in an increase in both aboveground and soil carbon storage (Boutton et al. 1998, Archer et al. 2001, Hibbard et al. 2001, Hughes et al. 2006, Blaser et al. 2014). Other studies, however, have found no evidence for increased soil carbon with woody encroachment (Jackson et al. 2002, Hughes et al. 2006), or a nonlinear response of carbon storage with woody thickening (Coetsee et al. 2013). In some cases where soil carbon (and more importantly, total ecosystem carbon) did not increase with woody thickening, studies found that aboveground gains were offset by high losses of belowground soil organic matter via the loss of grasses (particularly grass roots) which occurs at high woody densities (Jackson et al. 2002, Hudak et al. 2003). Hence, although studies have shown that herbivores often limit aboveground carbon storage in savanna ecosystems (i.e. increased woody cover with herbivore removal), it is still not clear how this translates to belowground soil carbon storage.

In this study we asked how nearly two decades of herbivore removal from a semi-arid savanna in Laikipia, Kenya affected aboveground and soil carbon storage. Previous studies at the same site (Augustine & McNaughton 2004, Sankaran et al. 2013, Wigley et al. 2019) have documented substantial increases in woody cover, biomass and growth rates with herbivore exclusion. Our first objective was to determine how herbivore removal influenced aboveground carbon storage in both the woody and grass layers. We hypothesised that increased woody cover following herbivore removal would culminate in reduced grass cover (e.g., see Scholes and Archer 1997, Jackson et al. 2002, Hudak et al. 2003), but that any decrease in herbaceous cover, which is strongly related to aboveground biomass in semi-arid systems (e.g., Skarpe 1991, Todd & Hoffman 1999), would be more than offset by increases in aboveground carbon stored in woody vegetation. In our second objective, we investigated if and how herbivore-driven changes in aboveground vegetation cover affected soil carbon. We specifically asked: i) does belowground soil carbon increase with herbivore removal? and ii) if so, what is the major source (i.e. $C_3$ trees vs. $C_4$ grasses) of this soil carbon? Considering findings from previous work, we hypothesised that herbivore removal and the associated increase in woody cover would increase soil carbon, with the majority derived from the $C_3$ woody layer (e.g. see Archer et al. 2001, Hibbard et al. 2001, Asner et al. 2003, Hughes et al. 2006, Blaser et al. 2014).

## METHODS

### Study location

This study was conducted from 1999-2017 at the Mpala Research Centre (MRC) and Mpala Ranch which together encompass 190 $km^2$ of semiarid savanna within the Laikipia County in central Kenya (37°53' E, O°17' N). The study sites occur on sandy red loam soils (74.3% sand, 14.8% clay) originating from basement metamorphic parent materials (Augustine 2003, Augustine & McNaughton 2006, Pringle et al. 2016). The topography at the study sites consists of gently rolling hills interspersed with granitic inselbergs (Augustine & McNaughton 2006). Mean annual rainfall for the period 1972–2009 was 514 mm (Sankaran et al. 2013), while from 2003 to 2016, annual precipitation averaged 633 mm (Augustine et al. 2019). The vegetation is characterized by semi-arid savannas with an Acacia-dominated tree and shrub community and a discontinuous layer of perennial grasses (Augustine 2003). Since the mid-1990s MRC has been managed for cattle production (*c*. 12.2 $km^{-2}$) using traditional Maasai herding methods, and the borders of the property have remained unfenced (Augustine 2003, Augustine & McNaughton 2004). The most common native ungulates include impala (*Aepyceros melampus,* c. 20 $km^{-2}$), Günther's dik-dik (*Madoqua guentheri* c. 140 $km^{-2}$) and elephant (*Loxodonta africana* c. 1.7 $km^{-2}$), while giraffe (*Giraffa camelopardalis)*, greater kudu (*Tragelaphus strepsiceros)*, zebra (*Equus burchellii*), waterbuck (*Kobus ellipsiprymnus*), buffalo (*Syncerus caffer*) and eland (*Taurotragus oryx*) occur at lower densities (Augustine 2010b, Sankaran et al. 2013). Native predators include spotted hyaena (*Crocuta crocuta*), wild dog (*Lycaon pictus*), lion (*Panthera leo*), and leopard (*Panthera pardus*).

Long-term herbivore exclosure experiment

Two paired ~0.5 ha (70 x 70 m) plots were demarcated at three sites located on red sandy soils in central and southern MRC in 1999. For each pair of these plots, one was retained as a control while the other fenced to exclude herbivores. These were protected using a 3 m tall electrified fence, consisting of 11 wire strands with additional mesh and electrified wires from ground level to half a meter above ground level (Augustine and McNaughton 2004). The exclosures were designed to exclude all herbivores larger than 2 kg. The inner 50 x 50 meters of each exclosure and paired control sites were delineated using a 10 x 10 m grid marked with round iron metal pegs knocked into the ground, with the upper 10 cm protruding above the ground and painted white. These pegs were numbered from 1 to 36 in a standard fashion across all plots.

Field sampling

At the time of exclosure construction in 1999, all individual trees and shrubs >0.5 m tall within the delineated 50 x 50 m area in each treatment were mapped, tagged and their basal area (at 15 cm above-ground level, including all stems on multi-stemmed individuals), canopy dimensions (maximum length and width in the cardinal directions) and height measured. All plots were fully censused again in 2002, 2009 and 2016. During each census, the height, basal area and canopy dimensions of all previously tagged plants that were alive were remeasured, any mortality noted, and all new recruits (>0.5 m tall) mapped and measured. Total aboveground woody biomass was calculated for each of the sampled years according to the relationship derived by Epp, Herlocker & Peden (1982) where mass in kg = [(7.49 x crown diameter in m) - 7.76] (Augustine & McNaughton 2004, Sankaran et al. 2013). We then converted aboveground biomass to aboveground carbon by multiplying total biomass by 49% based on estimates from other savanna ecosystems (Chen, Hutley & Eamus 2003, Hughes et al. 2006).

At the beginning of our experiment, the herbaceous layer consisted of a two-phase mosaic of bare soil patches interspersed with vegetated patches. Herbaceous patches were dominated by a diverse community of perennial grasses found both under woody canopies or in open patches away from trees; bare soil patches were typically 5-15 m in diameter, and in some cases had become sufficiently large and interconnected that they formed a background matrix within which the vegetated patches were embedded (Augustine 2003). We estimated herbaceous cover in subplots surrounding each permanent monitoring point (i.e. a 1 m radius or 3.14 $m^2$ area surrounding each of the 36 iron rods) in the year the exclosures were constructed (1999), 3 years later (2002), and 17 years later (2016).

We collected fully expanded, sun-exposed leaf material from trees and grasses during the peak of the 2017 growing season for nutrient and isotope analyses. We randomly selected five individuals of each of the dominant woody and grass species at each site (see Table S1), both inside exclosures and in adjacent control plots with herbivores present. All leaf material was air-dried at Mpala Research Station until samples reached constant weight. Samples were then milled using a MF10 basic IKA grinder fitted with a 1 mm sieve.

Soil sampling

In 1999, we randomly selected ten of the 36 metal pegs forming the 10 x 10 m grid in each paired plot. Soils were then sampled 10 cm to the north of each of the selected pegs using a soil corer. Soils were sampled from 0-15 cm, sieved, air dried and taken to the laboratory for carbon (C) and nitrogen (N) analyses. In 2016, soils were resampled at the same ten metal pegs as before. A soil corer was used to sample soils at 0-5 cm, 10-15 cm and 25-30 cm. All soil samples were air-dried until constant weight, then sieved using a 2 mm soil sieve and subsampled for nutrient and isotope analyses. In addition, a soil pit was excavated to a depth of 30 cm at each paired exclosure site and soils were sampled at 0-5 cm, 10-15 cm and 25-30 cm for the determination of soil bulk density. Bulk density samples were collected by vertically knocking a sharpened 50 mm diameter steel pipe 5 cm into the soil, on each of the four sides of the soil pit, at each of the above depths. We used a spade to dig out the side of the pit until the pipe was exposed, and then placed the spade underneath the rim of the pipe to ensure that no soil was lost while the core was retrieved. The soil cores were then emptied into labelled brown paper bags and air dried to constant weight. Soil bulk density was calculated as $\rho = M_s / V_s$ (Boone et al. 1999), where $\rho$ is bulk density (g $cm^{-3}$), $M_s$ is mass of dried soil (g), and $V_s$ is the field-moist soil volume ($cm^3$). During 2019, a further set of soil samples were collected at 0-5 cm, 10-15 cm and 25-30 cm in five bare ground patches, five patches of grass and under the canopy of five large trees (which in most cases also had an herbaceous layer) in control plots (+ herbivores) and in exclosures (- herbivores) at each of the three paired exclosures sites. These samples were also air dried to constant weight, sieved using a 2 mm soil sieve, then subsampled for carbon analyses.

Laboratory analyses

All soil samples, i.e. replicate soil samples sampled at metal pegs (10 replicates x 3 sites x 2 treatments x 3 depths = 180) and from bare ground, grassy patches and under tree canopies (5 replicates x 3 sites x 3 vegetation types x 2 treatments x 3 depths = 270) were analysed for soil C by combustion with a LECO CHN analyser (LECO Corp, St. Joseph, MI, USA).

$\delta^{13}C$ analyses

Aliquots of approximately 1.00 to 1.10 mg of homogenized plant samples and aliquots of approximately 30.0 to 40.0 mg of soil samples were weighed into tin capsules that were pre-cleaned in toluene. Isotopic analysis was done on a Flash EA 1112 Series coupled to a Delta V Plus stable light isotope ratio mass spectrometer via a ConFlo IV system (all equipment supplied by Thermo Fischer, Bremen, Germany), housed at the UP Stable Isotope Laboratory, Mammal Research Institute, University of Pretoria. Two laboratory running standards Merck Gel ($\delta^{13}C$ = -

20.26‰, $\delta^{15}N$=7.89‰, C%=41.28, N%=15.29) and DL-Valine ($\delta^{13}C$ = -10.57‰, $\delta^{15}N$=-6.15‰, C%=55.50, N%=11.86) and a blank sample were run after every 11 unknown samples for plant samples (96 plant samples per run). Soil samples were run in batches of 18 with a blank and standards run after every 6 samples. All results are referenced to Vienna Pee-Dee Belemnite for C isotope values. Results are expressed in delta notation using a per mille scale using the standard equation: $\delta X(‰) = [(R_{sample}/R_{standard})-1]x1000$ where X = $^{13}C$ and R represents $^{13}C/^{12}C$ respectively. For the isotope analyses, 56 of 142 plant samples were run in triplicate and 35 of 180 soil samples were run in duplicate to test for variability.

Data analyses

All analyses were performed using R version 3.4.2 (R Development Core Team 2017). We used the Fligner-Killeen test of homogeneity of variance (fligner.test in the *stats* package for R) to determine if data used for treatment comparisons (herbivores absent (h-) *vs*. herbivores present (h+)) had equal variance. Several measured variables were approximately log-normally distributed and were therefore log-transformed to attain approximate normality and homogeneity of residuals prior to analyses. When the assumption of normality was met, we used ANOVA and paired t-tests to evaluate effects of browser exclusion on plant and soil C, and isotopic values. When the assumption of normality was violated, we used the nonparametric Kruskal-Wallis test to test for differences between h- and h+ treatments. We used linear mixed effects models to test for the effect of treatment and depth on soil carbon, and soil isotopes using the *lme* function available in the *nlme* (V. 3.1-137, Pinheiro et al. 2018) package in R. Treatment, depth and their interactions were treated as fixed effects while site and the peg number at which the sample was taken were treated as random effects to account for the non-independence of soil measurements at each site and peg. We used the function *lsmeans* in the *lsmeans* package (V. 2.30-0, Lenth and Lenth 2018) to perform post-hoc comparisons of the mixed effects models using the Tukey adjustment for multiple comparisons.

To calculate the proportion of soil carbon derived from $C_4$ grasses *vs*. $C_3$ woody plants we used the following mixing model adapted from Still et al. (2003):

$\% C_{grass} = (\delta^{13}C_{tree} - \delta^{13}C_{measured})/(\delta^{13}C_{tree} - \delta^{13}C_{grass}) \times 100$, where $\% C_{grass}$ is the percent $C_4$ contribution, $\delta^{13}C_{tree}$ is the mean carbon isotopic composition of $C_3$ vegetation (see Appendix S1: Table S1), $\delta^{13}C_{grass}$ is the mean carbon isotopic composition of $C_4$ vegetation (see Appendix S1: Table S1), and $^{13}C_{measured}$ is the isotopic composition of the measured sample.

## RESULTS

Herbaceous cover was similar between h+ and h- treatments in 1999 (~39-42 %). Three years of herbivore exclusion resulted in significantly higher ($p < 0.01$) herbaceous cover in the h- plots compared to h+ plots (52.2 ± 3.4 *vs*. 36.1 ± 3.2), and another fourteen years of herbivore exclusion resulted in a further significant increase ($p < 0.001$) in herbaceous cover in the h- plots compared to the h+ plots (71.9 ± 2.2 *vs*. 50.2 ± 3.2, Figure 1a). Initial woody canopy cover was similar between h+ and h-treatments (30-37%). By 2002, canopy cover was significantly higher in the herbivore exclusion plots and continued to increase in these plots, reaching ~70% by 2016 compared to 27% in plots open to herbivores (Figure 1b). Woody stem basal area initially increased slowly; total woody basal area did not differ between h- and h+ plots in 1999 and 2002 (~4.5-5.2 $m^2$ $ha^{-1}$). However, a further seven years of herbivore exclusion resulted in significantly higher ($p < 0.05$) total basal area compared to the h+ plots in 2009 (7.88 ± 0.14 vs. 4.94 ± 0.31 $m^2$ $ha^{-1}$). By 2016, another seven years of herbivore exclusion had resulted in a further highly significant ($p < 0.001$) increase in total basal area in h- plots compared to h+ plots ($12.78 \pm 1.19$ vs. $4.91 \pm 0.6$ $m^2$ $ha^{-1}$, Figure 1c). Woody stem basal area outside exclosures did not change for the entire study period. Total aboveground carbon was similar between h- and h+ plots in 1999 ($4287 \pm 419$ vs. $3804 \pm 219$ kg $ha^{-1}$). The removal of herbivores led to a slight increase in aboveground woody biomass by 2002, and by 2009, aboveground woody carbon storage more than doubled inside relative to outside exclosures ($13480 \pm 2734$ vs. $4009 \pm 324$ kg $ha^{-1}$). Aboveground woody carbon decreased slightly between 2009 and 2016 in both treatments; however, the difference between h- and h+ plots was still highly significant ($p < 0.001$) in 2016 ($12803 \pm 411$ vs. $3461 \pm 87$, Figure 1d). Seventeen years of herbivore exclusion resulted in an average increase of 8516 kg $ha^{-1}$ of aboveground woody carbon compared to plots with herbivores present, which showed an average decrease of 343 kg $ha^{-1}$ of aboveground woody carbon.

At the beginning of the experiment (1999), soil carbon (0-15 cm) was similar across plots ($1.14 \pm 0.07$ *vs*. $0.93 \pm 0.04$ %). In 2016, after seventeen years of herbivore exclusion, soil total carbon ($1.51 \pm 0.09$ vs. $0.93 \pm 0.05$ %, Tukey post hoc test: $p < 0.001$) was significantly higher in the h- plots, but remained unchanged where herbivores were present (Figure 2a). This effect persisted at all three measured depths (0-5 cm, 5-10 cm and 25-30 cm) (Figure 2b, Appendix S1:Table S2). Herbivore removal had no effect on soil carbon in bare soil patches but resulted in significantly higher soil carbon (to 30 cm depth) in soils under grass patches ($F_{5,263} = 46.6$, $p < 0.001$) and under tree canopies (Tukey post hoc test: $p < 0.001$, Figure 2c).

Soil $\delta^{13}C$ values were significantly lower ($-19.1 \pm 0.28$ *vs*. $-17.9 \pm 0.25$ ‰, $p < 0.05$) at 0-5 cm, marginally lower ($-18.1 \pm 0.27$ *vs*. $-17.0 \pm 0.25$ ‰, $p = 0.057$) at 10-15 cm in control (h+) plots and did not differ between treatments at 25-30 cm (Figure 3a, Appendix S1:Table S2). Our

$\delta^{13}C$ mixing models showed that when herbivores were present, soils had a significantly higher proportion of carbon derived from $C_4$ grasses at 0-5 cm than when they were excluded (69.7 ± 1.68 *vs*. 61.9 ± 1.90 %, $p < 0.05$). At 10-15 cm, the h+ plots had marginally higher ($p = 0.065$) $C_4$ derived soil carbon (75.7 ± 1.64 *vs*. 69.0 ± 1.80 %), while at 25-30 cm there was no difference in $C_4$ derived soil carbon between h+ and h- plots (78.8 ± 1.90 *vs*. 76.6 ± 1.64 %, Figure 3b, Appendix S1:Table S2).

The removal of herbivores culminated in significantly higher soil carbon pools (58.9 ± 2.53 *vs*. 38.4 ± 1.60 t $ha^{-1}$ to 30 cm depth, $p < 0.001$) compared to when herbivores were present (Figure 2d). A total of 41.6 ± 1.76 of 58.9 t $ha^{-1}$ (71%) of soil carbon in the exclosures (h-) was derived from $C_4$ grasses with the remaining 17.2 ± 0.80 t $ha^{-1}$ (29%) derived from $C_3$ woody biomass. In the control plots (h+) a total of 29.1 ± 1.25 of 38.4 t $ha^{-1}$ (76%) was derived from $C_4$ grasses and 9.26 ± 0.40 (24%) was derived from $C_3$ woody biomass (Figure 3c).

## Discussion

Nearly two decades of herbivore exclusion provided a unique opportunity to test the importance of large, mammalian herbivores in driving both aboveground and belowground soil carbon storage in a semi-arid savanna. Our results show that 1) herbivore exclusion resulted in substantial increases in aboveground carbon stores in the woody layer (~8.5 t $ha^{-1}$), 2) herbivore exclusion increased soil carbon pools to at least 30 cm (~20 t $ha^{-1}$), 3) these belowground soil carbon gains were primarily driven by $C_4$ grasses, which 4) we attribute to increases in both grass cover and productivity, despite the significant increases in woody canopy cover.

Previous studies at the same sites documented significant increases in woody biomass after just three years of herbivore exclusion (Augustine & McNaughton 2004), and another substantial increase after a further seven years of herbivore exclusion (Sankaran et al. 2013). In this study, we show that an additional seven years of herbivore exclusion resulted in a further increase in basal area but did not translate to higher total woody biomass (see Fig. 1). The most likely explanation is that the first ten years of herbivore exclusion resulted in rapid increases in recruitment rates overall, particularly of seedlings/saplings into larger size classes with associated substantial increases in canopy cover. After ten years of herbivore removal, however, competition appears to have come into play (e.g., theory of self-thinning) (Wiegand et al. 2006, Belay and Moe 2012, Sea & Hanan 2012, Dohn et al. 2017), resulting in a decrease in tree density and a slight increase in average canopy size (see Appendix S1: Fig. S1) and basal diameters (Fig. 1C).

Regardless of an evident slowing in aboveground woody biomass accumulation over time, herbivore exclusion resulted in much higher woody canopy cover compared to where herbivores were present (~70% at the end of the experiment inside exclosures *vs*. 27% where herbivores were present). We hypothesised that the marked increase in woody cover would result in higher rates of soil carbon sequestration and that soil carbon would be derived predominantly from $C_3$ trees and shrubs. Herbivore exclusion led to a 54% increase in total soil carbon in the 0 – 30 cm layer, which was equivalent to an increase of 20.5 t $ha^{-1}$ in belowground C, or more than double the increase in aboveground carbon storage in the woody layer. The effects of herbivore removal on soil C appear to be strongly related to altered vegetation patterns and increased aboveground biomass, resulting in higher C inputs from plants in the shallower layers of soil. Slower decomposition rates below woody canopies (Throop & Archer 2008), changes in rates of soil organic matter turnover (Guillaume et al. 2015), greater root biomass below woody canopies (Hibbard et al. 2001) and a deeper distribution of woody roots compared to herbaceous roots

(Jackson et al. 1996) are also likely to have contributed to higher soil C with herbivore exclusion. Furthermore, we found herbivore exclusion to have no effect on soil carbon under bare soil patches. If the direct effects of herbivores (e.g., trampling, addition of carbon in dung) were strong, we would have expected these differences to be evident (i.e. higher soil C) in the bare patches where herbivores were present.

Soil $\delta^{13}C$ analyses have been widely used to assess the effects of vegetation change on soil carbon dynamics (Balesdent et al. 1993, Bird & Pousai 1997, Bird et al. 2002, Krull et al. 2005). Our $\delta^{13}C$ results show herbivore exclusion did increase both $C_3$ and $C_4$ contributions to soil carbon. However, despite the dramatic increases in woody cover and aboveground biomass with herbivore exclusion, the majority of soil carbon (> 70% for upper 30 cm of soil) in the herbivore exclusion plots was derived from $C_4$ grasses (Fig 3). As grass cover significantly increased with herbivore exclusion, even below tree canopies, both soil carbon originating from grass litter as well as soil carbon inputs from grass roots likely increased with herbivore removal (Jackson et al. 2002, Hudak et al. 2003). These results underscore the importance of $C_4$ grasses for soil C sequestration in semi-arid savannas (Jackson et al. 2002, Hudak et al. 2003), even in systems with relatively high and increasing woody cover.

A negative relationship between woody cover and herbaceous biomass has been widely reported (reviewed by Scholes & Archer 1997, Archer et al. 2001, Hibbard et al. 2001, Hudak et al. 2003, Hughes et al. 2006, Riginos et al. 2009, Van Auken 2009), with many studies showing that grass productivity decreases with increased woody cover (e.g., no grass cover above leaf area index of three; Hoffmann et al. 2012). Trees, however, may facilitate the productivity of grasses in certain situations (Belsky et al. 1989, 1993, Georgiadis 1989, Weltzin & Coughenour 1990, Riginos et al. 2009, Dohn et al. 2013, Moustakas et al. 2013). For instance, grass productivity has been found to be higher under Acacia and *Adansonia digitata* (baobab) trees, which are known to have sparse foliage with lower levels of light interception and limited effects on photosynthesis (Belsky et al. 1989, Weltzin & Coughenour 1990). The importance of tree canopy density was also emphasized by Kennard & Walker (1973) and Riginos et al. (2009), who found grass biomass in savannas to be highest under open sparse canopies and lowest under dense closed canopies with intermediate values in open areas away from tree canopies. Our results also suggest a facilitative role of trees on grasses in this fine-leaved semi-arid savanna, and that woody plants have not yet imposed a negative, stand-level effect on grass production and inputs to the soil (*sensu* Riginos et al. 2009). Despite significant increases in woody cover, total grass cover also increased substantially between 1999 and 2016 and was significantly higher in the absence of herbivores by the end of the study period (~72% cover in exclosures *vs*. 50% outside, see Fig. 1a). Although we did not measure grass biomass directly during this study, earlier work at the site has established a positive correlation between grass cover and biomass as well as enhanced aboveground net primary productivity by grasses following herbivore exclusion (Augustine & McNaughton 2006).

In conclusion, we showed that despite significant increases in $C_3$ woody cover that occurred with herbivore exclusion in this semi-arid savanna, a high proportion of soil carbon was nevertheless derived from $C_4$ grasses which also increased with herbivore exclusion. We suggest this is possible because the fine-leaved woody species with 'sparse open' canopies (e.g. *Acacia etbaica* and *A. mellifera)* that dominate this semi-arid savanna did not suppress grass cover. Similar responses may not be expected in more dense, broad-leaved savannas where high woody canopy cover can result in canopy closure and the exclusion of grasses. Fine-leaved, semi-arid savannas, which are extensive in their global extent, therefore present important opportunities for carbon sequestration via the grassy layer. While we see an overall decrease in soil and aboveground carbon with herbivory, this result may be specific to the combination of herbivore species, densities and soil nutrient status at our study site. We know from a range of other systems that herbivores can sometimes increase soil carbon because they stimulate grasses (and grass roots) to grow faster and therefore result in greater carbon sequestration (Frank et al. 1995, Derner et al. 2006). However, in this system, herbivore offtake of carbon appears to exceed any enhancement through increased herbaceous production (Sankaran & Augustine 2004; Augustine & McNaughton 2006). While our results suggest that herbivores reduce both above- and belowground carbon in this ecosystem, these carbon losses must be evaluated against the biodiversity and livelihood benefits (Olff & Ritchie 1998, van Wieren & Bakker 2008, Augustine et al. 2011, Odadi et al. 2011, Lindsey et al. 2013, Katona & Coetsee 2019) provided by these herbivore-rich ecosystems where both wild and domestic herbivores are supported. Given the global declines in large herbivore populations (Ripple et al. 2015), restoring and maintaining grassy cover can serve as an important management tool and provide co-benefits by reducing carbon losses while also maintaining the suite of services provided by such semi-arid savannas.

ACKNOWLEDGEMENTS

This work was funded by the National Centre for Biological Sciences, TIFR, India, National Geographic (Grant Number 982815) and NERC (Grant NE- E017436- 1). We are grateful to Mpala Research Centre for logistical support and the Office of the President of the Republic of Kenya for permission to conduct the research. We are also grateful to Junior Parsare for his assistance with fieldwork and Chengappa S.K. and Balavignesh B. for their assistance with laboratory analyses.

LITERATURE CITED

Archer, S., T. W. Boutton, and K. A. Hibbard. 2001. Trees in grasslands: biogeochemical consequences of woody plant expansion. Global biogeochemical cycles in the climate system:115–138.

Asner, G. P., S. Archer, R. F. Hughes, R. J. Ansley, and C. A. Wessman. 2003. Net changes in regional woody vegetation cover and carbon storage in Texas drylands, 1937–1999. Global Change Biology 9:316–335.

Augustine, D. J. 2003. Long-term, livestock-mediated redistribution of nitrogen and phosphorus in an East African savanna. Journal of Applied Ecology 40:137–149.

Augustine, D. J. 2010a. Response of native ungulates to drought in semi-arid Kenyan rangeland. African Journal of Ecology 48:1009–1020.

Augustine, D. J. 2010b. Response of native ungulates to drought in semi-arid Kenyan rangeland. African Journal of Ecology 48:1009–1020.

Augustine, D. J., and S. J. McNaughton. 2004. Regulation of shrub dynamics by native browsing ungulates on East African rangeland. Journal of Applied Ecology 41:45–58.

Augustine, D. J., and S. J. McNaughton. 2006. Interactive effects of ungulate herbivores, soil fertility, and variable rainfall on ecosystem processes in a semi-arid savanna. Ecosystems 9:1242–1256.

Augustine, D. J., K. E. Veblen, J. R. Goheen, C. Riginos, and T. P. Young. 2011. Pathways for positive cattle–wildlife interactions in semiarid rangelands. Smithsonian Contributions to Zoology 632:55–71.

Augustine, D.J., B.J. Wigley, J. Ratnam, S. Kibet, M. Nyangito, and M. Sankaran. 2019. Large herbivores maintain a two-phase herbaceous vegetation mosaic in a semi-arid savanna. Ecology and Evolution 9:12779–12788.

Bakker, E. S., J. L. Gill, C. N. Johnson, F. W. Vera, C. J. Sandom, G. P. Asner, and J.-C. Svenning. 2016. Combining paleo-data and modern exclosure experiments to assess the impact of megafauna extinctions on woody vegetation. Proceedings of the National Academy of Sciences 113:847–855.

Balesdent, J., C. Girardin, and A. Mariotti. 1993. Site-Related^(13) C of Tree Leaves and Soil Organic Matter in a Temperate Forest. Ecology 74:1713–1721.

Batjes, N. H., and W. G. Sombroek. 1997. Possibilities for carbon sequestration in tropical and subtropical soils. Global Change Biology 3:161–173.

Belay, T. A., and S. R. Moe. 2012. Woody dominance in a semi-arid savanna rangeland–Evidence for competitive self-thinning. Acta oecologica 45:98–105.

Belsky, A. J., R. G. Amundson, J. M. Duxbury, S. J. Riha, A. R. Ali, and S. M. Mwonga. 1989. The effects of trees on their physical, chemical and biological environments in a semi-arid savanna in Kenya. Journal of applied ecology:1005–1024.

Belsky, A. J., S. M. Mwonga, R. G. Amundson, J. M. Duxbury, and A. R. Ali. 1993. Comparative effects of isolated trees on their undercanopy environments in high-and low-rainfall savannas. Journal of Applied Ecology:143–155.

Bikila, N. G., Z. K. Tessema, and E. G. Abule. 2016. Carbon sequestration potentials of semi-arid rangelands under traditional management practices in Borana, Southern Ethiopia. Agriculture, Ecosystems & Environment 223:108–114.

Binkley, D. A. N., and C. Giardina. 1998. Why do tree species affect soils? The warp and woof of tree-soil interactions. Biogeochemistry 42:89–106.

Bird, M. I., and P. Pousai. 1997. Variations of δ13C in the surface soil organic carbon pool. Global Biogeochemical Cycles 11:313–322.

Bird, M. I., H. Santruckova, A. Arneth, S. Grigoriev, G. Gleixner, Y. N. Kalaschnikov, J. Lloyd, and E.-D. Schulze. 2002. Soil carbon inventories and carbon-13 on a latitude transect in Siberia. Tellus B 54:631–641.

Blaser, W. J., G. K. Shanungu, P. J. Edwards, and H. Olde Venterink. 2014. Woody encroachment reduces nutrient limitation and promotes soil carbon sequestration. Ecology and evolution 4:1423–1438.

Bond, W. J. 2005. Large parts of the world are brown or black: a different view on the 'Green World'hypothesis. Journal of Vegetation Science 16:261–266.

Boone, R. B., D. F. Grigal, P. Sollins, R. N. Ahrens, and D. E. Armstrong. 1999. Soil sampling, preparation, archiving and quality control. Page *in* G. P. Robertson, D. C. Coleman, C. S. Bledsoe, and P. Sollins, editors. Standard Soil Methods for Long-term Ecological Research. Oxford University Press, Oxford, USA.

Boutton, T. W., S. R. Archer, A. J. Midwood, S. F. Zitzer, and R. Bol. 1998. δ 13 C values of soil organic carbon and their use in documenting vegetation change in a subtropical savanna ecosystem. Geoderma 82:5–41.

Chen, X., L. B. Hutley, and D. Eamus. 2003. Carbon balance of a tropical savanna of northern Australia. Oecologia 137:405–416.

Coetsee, C., E. F. Gray, J. Wakeling, B. J. Wigley, and W. J. Bond. 2013. Low gains in ecosystem carbon with woody plant encroachment in a South African savanna. Journal of Tropical Ecology 29:49–60.

Cole, C. V., K. Paustian, E. T. Elliott, A. K. Metherell, D. S. Ojima, and W. J. Parton. 1993. Analysis of agroecosystem carbon pools. Water, Air, and Soil Pollution 70:357–371.

Derner, J. D., T. W. Boutton, and D. D. Briske. 2006. Grazing and ecosystem carbon storage in the North American Great Plains. Plant and Soil 280:77–90.

Derner, J.D., Augustine, D.J. and Frank, D.A., 2019. Does Grazing Matter for Soil Organic Carbon Sequestration in the Western North American Great Plains?. Ecosystems 22:1088-1094.

Dohn, J., Dembélé, F., Karembé, M., Moustakas, A., Amévor, K.A. and Hanan, N.P., 2013. Tree effects on grass growth in savannas: competition, facilitation and the stress-gradient hypothesis. Journal of Ecology 101:202-209.

Dohn, J., D. J. Augustine, N. P. Hanan, J. Ratnam, and M. Sankaran. 2017. Spatial vegetation patterns and neighborhood competition among woody plants in an East African savanna. Ecology 98:478–488.

Epp, H., D. Herlocker. and D. Peden. 1982. The use of large-scale aerial photography to determine wood biomass in the arid and semi-arid areas of Kenya. Kenya Rangeland Ecological Monitoring Unit. Technical Report Series No. 51, Kenya Rangeland Ecological Monitoring Unit, Nairobi, Kenya.

Eswaran, H., E. Van Den Berg, and P. Reich. 1993. Organic carbon in soils of the world. Soil science society of America journal 57:192–194.

Frank, A. B., D. L. Tanaka, L. Hofmann, and R. F. Follett. 1995. Soil carbon and nitrogen of Northern Great Plains grasslands as influenced by long-term grazing. Journal of Range Management:470–474.

Georgiadis, N. J. 1989. Microhabitat variation in an African savanna: effects of woody cover and herbivores in Kenya. Journal of Tropical Ecology 5:93–108.

Guillaume, T., M. Damris, and Y. Kuzyakov. 2015. Losses of soil carbon by converting tropical forest to plantations: erosion and decomposition estimated by δ13C. Global change biology 21:3548–3560.

Hibbard, K. A., S. Archer, D. S. Schimel, and D. W. Valentine. 2001. Biogeochemical changes accompanying woody plant encroachment in a subtropical savanna. Ecology 82:1999–2011.

Hoffmann, W. A., E. L. Geiger, S. G. Gotsch, D. R. Rossatto, L. C. Silva, O. L. Lau, M. Haridasan, and A. C. Franco. 2012. Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. Ecology letters 15:759–768.

Hudak, A. T., C. A. Wessman, and T. R. Seastedt. 2003. Woody overstorey effects on soil carbon and nitrogen pools in South African savanna. Austral Ecology 28:173–181.

Hughes, R. F., S. R. Archer, G. P. Asner, C. A. Wessman, C. McMurtry, J. I. M. Nelson, and R. J. Ansley. 2006. Changes in aboveground primary production and carbon and nitrogen pools accompanying woody plant encroachment in a temperate savanna. Global Change Biology 12:1733–1747.

Jackson, R. B., J. L. Banner, E. G. Jobbágy, W. T. Pockman, and D. H. Wall. 2002. Ecosystem carbon loss with woody plant invasion of grasslands. Nature 418:623–626.

Jackson, R. B., J. Canadell, J. R. Ehleringer, H. A. Mooney, O. E. Sala, and E. D. Schulze. 1996. A global analysis of root distributions for terrestrial biomes. Oecologia 108:389–411.

Katona, K. and C. Coetsee. 2019. Impacts of Browsing and Grazing Ungulates on Faunal Biodiversity. In: Gordon I., Prins H. (eds) *The Ecology of Browsing and Grazing II* (pp. 277-300). Springer, Cham.

Kennard, D. G., and B. H. Walker. 1973. Relationships between tree canopy cover and Panicum maximum in the vicinity of Fort Victoria. Rhodesia, Zambia and Malawi journal of agricultural research.

Krull, E. S., J. O. Skjemstad, W. H. Burrows, S. G. Bray, J. G. Wynn, R. Bol, L. Spouncer, and B. Harms. 2005. Recent vegetation changes in central Queensland, Australia: evidence from δ13C and 14C analyses of soil organic matter. Geoderma 126:241–259.

Lenth, R., and M. R. Lenth. 2018. Package ‘lsmeans.’ The American Statistician 34:216–221.

Li, C., X. Hao, M. Zhao, G. Han, and W. D. Willms. 2008. Influence of historic sheep grazing on vegetation and soil properties of a Desert Steppe in Inner Mongolia. Agriculture, Ecosystems & Environment 128:109–116.

Lindsey, P. A., C. P. Havemann, R. M. Lines, A. E. Price, T. A. Retief, T. Rhebergen, C. Van der Waal, and S. S. Romañach. 2013. Benefits of wildlife-based land uses on private lands in Namibia and limitations affecting their development. Oryx 47:41–53.

Loveland, T. R., B. C. Reed, J. F. Brown, D. O. Ohlen, Z. Zhu, L. Yang, and J. W. Merchant. 2000. Development of a global land cover characteristics database and IGBP DISCover from 1 km AVHRR data. International Journal of Remote Sensing 21:1303–1330.

Ludwig, F., T. E. Dawson, H. de Kroon, F. Berendse, and H. H. Prins. 2003. Hydraulic lift in Acacia tortilis trees on an East African savanna. Oecologia 134:293–300.

McSherry, M. E., and M. E. Ritchie. 2013. Effects of grazing on grassland soil carbon: a global review. Global Change Biology 19:1347–1357.

Mekuria, W., E. Veldkamp, M. D. Corre, and M. Haile. 2011. Restoration of ecosystem carbon stocks following exclosure establishment in communal grazing lands in Tigray, Ethiopia. Soil Science Society of America Journal 75:246–256.

Melillo, J. M., J. D. Aber, A. E. Linkins, A. Ricca, B. Fry, and K. J. Nadelhoffer. 1989. Carbon and nitrogen dynamics along the decay continuum: plant litter to soil organic matter. Plant and soil 115:189–198.

Moustakas, A., Kunin, W.E., Cameron, T.C. and Sankaran, M., 2013. Facilitation or competition? Tree effects on grass biomass across a precipitation gradient. PLoS One 8:p.e57025.

Odadi, W. O., M. K. Karachi, S. A. Abdulrazak, and T. P. Young. 2011. African wild ungulates compete with or facilitate cattle depending on season. science 333:1753–1755.

Olff, H., and M. E. Ritchie. 1998. Effects of herbivores on grassland plant diversity. Trends in ecology & evolution 13:261–265.

Percival, H. J., R. L. Parfitt, and N. A. Scott. 2000. Factors controlling soil carbon levels in New Zealand grasslands is clay content important? Soil Science Society of America Journal 64:1623–1630.

Pinheiro, J., D. Bates, S. DebRoy, and D. Sarkar. 2018. nlme: linear and nonlinear mixed effects models. R package version 3.1-137.

Pringle, R. M., K. M. Prior, T. M. Palmer, T. P. Young, and J. R. Goheen. 2016. Large herbivores promote habitat specialization and beta diversity of African savanna trees. Ecology 97:2640–2657.

R Development Core Team. 2017. R: A language and environment for statistical computing [Computer software]. Vienna: R Foundation for Statistical Computing.

Reid, R. S., P. K. Thornton, G. J. McCrabb, R. L. Kruska, F. Atieno, and P. G. Jones. 2004. Is it possible to mitigate greenhouse gas emissions in pastoral ecosystems of the tropics? Pages 91–109 Tropical Agriculture in Transition—Opportunities for Mitigating Greenhouse Gas Emissions? Springer.

Riginos, C., J.B. Grace, D.J. Augustine, and T.P. Young. 2009. Local versus landscape-scale effects of savanna trees on grasses. Journal of Ecology 97: 1337-1345.

Ripple, W. J., T. M. Newsome, C. Wolf, R. Dirzo, K. T. Everatt, M. Galetti, M. W. Hayward, G. I. Kerley, T. Levi, and P. A. Lindsey. 2015. Collapse of the world's largest herbivores. Science advances 1:e1400103.

Sankaran, M., D. J. Augustine, and J. Ratnam. 2013. Native ungulates of diverse body sizes collectively regulate long-term woody plant demography and structure of a semi-arid savanna. Journal of Ecology 101:1389–1399.

Schlesinger, W. H., and A. M. Pilmanis. 1998. Plant-soil interactions in deserts. Biogeochemistry 42:169–187.

Scholes, R. J., and S. R. Archer. 1997. Tree-grass interactions in savannas. Annual review of Ecology and Systematics 28:517–544.

Sea, W. B., and N. P. Hanan. 2012. Self-thinning and tree competition in savannas. Biotropica 44:189–196.

Skarpe, C., 1991. Impact of grazing in savanna ecosystems. Forestry and the Environment 20: 351-356.

Steffens, M., A. Kölbl, K. U. Totsche, and I. Kögel-Knabner. 2008. Grazing effects on soil chemical and physical properties in a semiarid steppe of Inner Mongolia (PR China). Geoderma 143:63–72.

Stevens, N., B. F. N. Erasmus, S. Archibald, and W. J. Bond. 2016. Woody encroachment over 70 years in South African savannahs: overgrazing, global change or extinction aftershock? Phil. Trans. R. Soc. B 371:20150437.

Still, C. J., J. A. Berry, M. Ribas-Carbo, and B. R. Helliker. 2003. The contribution of C3 and C4 plants to the carbon cycle of a tallgrass prairie: an isotopic approach. Oecologia 136:347–359.

Tanentzap, A. J., and D. A. Coomes. 2012. Carbon storage in terrestrial ecosystems: do browsing and grazing herbivores matter? Biological Reviews 87:72–94.

Throop, H. L., and S. R. Archer. 2008. Shrub (Prosopis velutina) encroachment in a semidesert grassland: spatial–temporal changes in soil organic carbon and nitrogen pools. Global Change Biology 14:2420–2431.

Todd, S.W., and M.T. Hoffman. 1999. A fence- line contrast reveals effects of heavy grazing on plant diversity and community composition in Namaqualand, South Africa. Plant Ecology 142: 169-178.

Van Auken, O. W. 2009. Causes and consequences of woody plant encroachment into western North American grasslands. Journal of environmental management 90:2931–2942.

Watson, R. T., I. R. Noble, B. Bolin, N. H. Ravindranath, D. J. Verardo, and D. J. Dokken. 2000. Land use, land-use change and forestry: a special report of the Intergovernmental Panel on Climate Change. Cambridge University Press.

Weltzin, J. F., and M. B. Coughenour. 1990. Savanna tree influence on understory vegetation and soil nutrients in northwestern Kenya. Journal of vegetation science 1:325–334.

Wiegand, K., D. Saltz, and D. Ward. 2006. A patch-dynamics approach to savanna dynamics and woody plant encroachment–insights from an arid savanna. Perspectives in Plant Ecology, Evolution and Systematics 7:229–242.

van Wieren, S. E., and J. P. Bakker. 2008. The impact of browsing and grazing herbivores on biodiversity. Pages 263–292 The ecology of browsing and grazing. Springer.

Wigley, B. J., H. Fritz, C. Coetsee, and W. J. Bond. 2014. Herbivores shape woody plant communities in the Kruger National Park: Lessons from three long-term exclosures. Koedoe 56:1–12.

Wigley, B. J., C. Coetsee, D. J. Augustine, J. Ratnam, D. Hattas, and M. Sankaran. 2019. A thorny issue: Woody plant defence and growth in an East African savanna. Journal of Ecology 107: 1839–1851.

FIGURES

Figure legends

Figure 1 Mean ± se of a) total herbaceous cover (%) in 1999, 2002 and 2016, b) total woody canopy cover (%), c) total woody basal area ($m^2$ $ha^{-1}$) and d) above-ground woody carbon (kg $ha^{-1}$) in 1999, 2002, 2009 and 2016 for grazed/browsed plots (h+) and ungrazed/unbrowsed plots (h-). Basal area and biomass values have been scaled up from the plot level (50 x 50 m) and are reported on a per hectare basis. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Figure 2 Mean ± se in control plots (+ herbivores) and exclosures (- herbivores) of a) soil carbon sampled at 0 -15 cm depth in 1999 and in 2016, b) soil carbon sampled at 0-5, 10-15 and 25-30 cm depths in 2016, c) soil carbon for soils (sampled at 0-5, 10-15 and 25-30 cm) in bare ground patches, in patches of grass and under the canopy of large trees and d) soil total carbon pools to a depth of 30 cm. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$ for all comparisons.

Figure 3 Mean ± se of a) soil $\delta^{13}C$ (‰) and b) $C_4$ (grass) derived soil carbon (%) at 0-5, 10-15 and 25-30 cm depths and c) total soil carbon pools (t $ha^{-1}$ to a depth of 30 cm) derived from $C_3$ woody vegetation *vs*. $C_4$ herbaceous vegetation in control plots (+ herbivores) and exclosures (- herbivores), · $p < 0.1$, * $p < 0.05$, *** $p < 0.001$. $C_4$ derived soil carbon was calculated using an isotope mixing model adapted from Still et al. (2003).

FIG 1

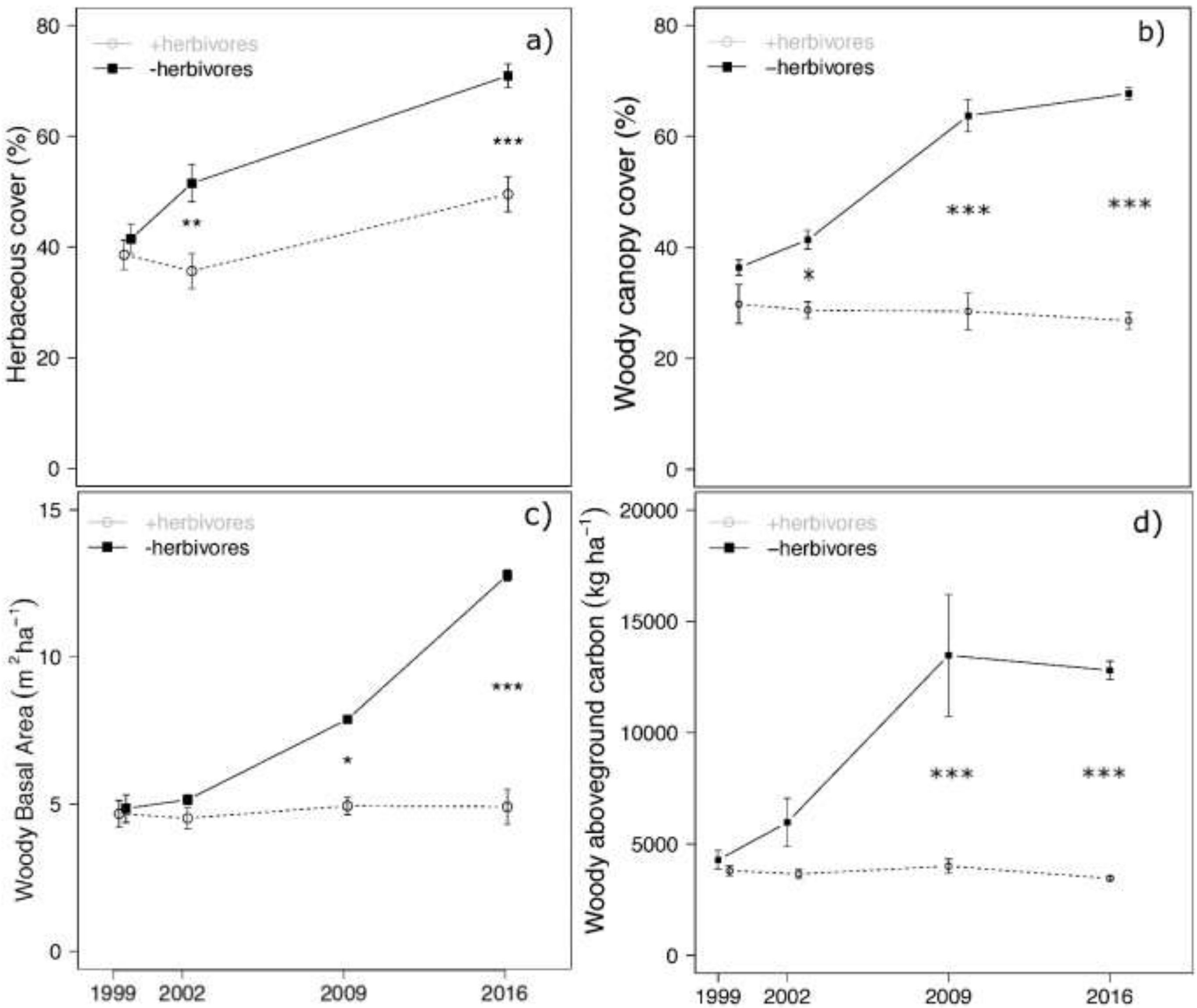


Figure 1 Mean ± se of a) total herbaceous cover (%) in 1999, 2002 and 2016, b) total woody canopy cover (%), c) total woody basal area ($m^2$ $ha^{-1}$) and d) above-ground woody carbon (kg $ha^{-1}$) in 1999, 2002, 2009 and 2016 for grazed/browsed plots (h+) and ungrazed/unbrowsed plots (h-). Basal area and biomass values have been scaled up from the plot level (50 x 50 m) and are reported on a per hectare basis. * $p < 0.05$, **$p < 0.01$, *** $p < 0.001$.

FIG 2

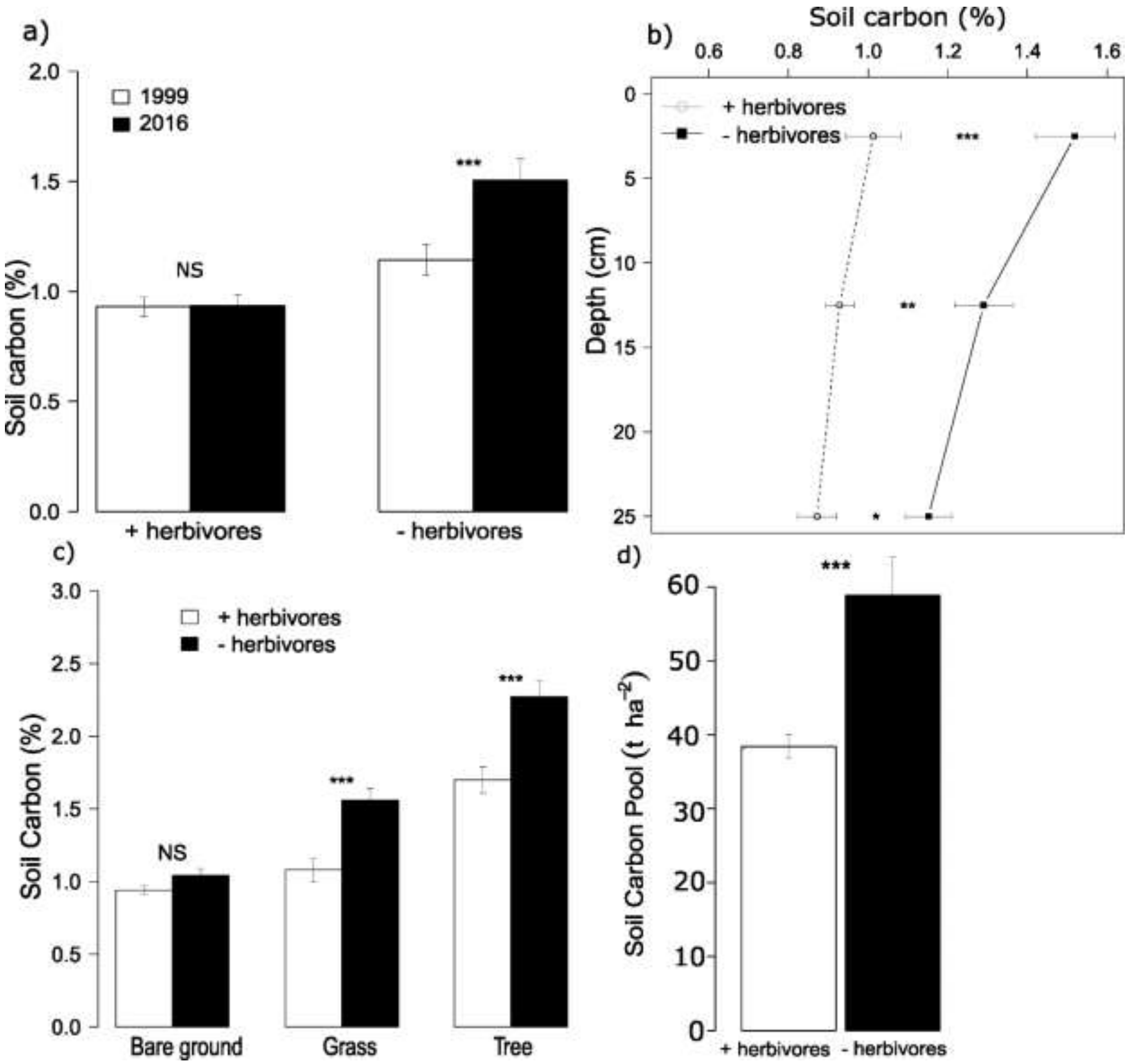


Figure 2 Mean ± se in control plots (+ herbivores) and exclosures (- herbivores) of a) soil carbon sampled at 0 -15 cm depth in 1999 and in 2016, b) soil carbon sampled at 0-5, 10-15 and 25-30 cm depths in 2016, c) soil carbon for soils (sampled at 0-5, 10-15 and 25-30 cm) in bare ground patches, in patches of grass and under the canopy of large trees and d) soil total carbon pools to a depth of 30 cm. * $p < 0.05$, **$p < 0.01$, *** $p < 0.001$ for all comparisons.

FIG 3

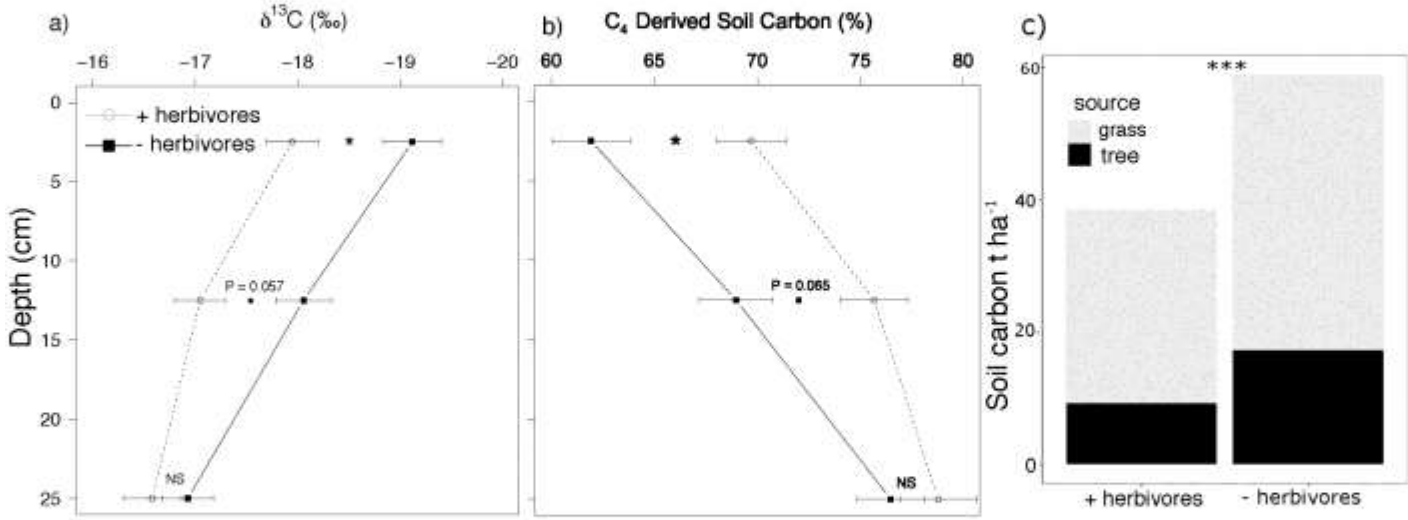


Figure 3 Mean ± se of a) soil $\delta^{13}C$ (‰) and b) $C_4$ (grass) derived soil carbon (%) at 0-5, 10-15 and 25-30 cm depths and c) total soil carbon pools (t $ha^{-1}$ to a depth of 30 cm) derived from $C_3$ woody vegetation *vs*. $C_4$ herbaceous vegetation in control plots (+ herbivores) and exclosures (- herbivores), · $p < 0.1$, * $p < 0.05$, *** $p < 0.001$. $C_4$ derived soil carbon was calculated using an isotope mixing model adapted from Still et al. (2003).