

Grasses continue to trump trees at soil carbon sequestration following herbivore exclusion in a semiarid African savanna

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Abstract. Although studies have shown that mammalian herbivores often limit aboveground carbon storage in savannas, their effects on belowground soil carbon storage remain unclear. Using three sets of long-term, large herbivore exclosures with paired controls, we asked how almost two decades of herbivore removal from a semiarid 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 m²/ha), and woody canopy cover (31%), translating to a ~8.5 t/ha increase in aboveground carbon over two decades. Herbivore exclusion also led to a 54% increase (20.5 t/ha) 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 semiarid system.

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

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 realized, 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 (Love-land 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; for example herbivores can prevent forests from developing (and thereby maintain savannas) in regions that have soils and climates that favor 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 and Coomes 2012, McSherry and Ritchie 2013), and above- and belowground carbon stocks. Shared effects include the direct consumption of aboveground plant biomass by herbivores, which alters soil carbon by

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changing the quantity and quality of plant litter, changing rates of soil respiration and altering rates of nutrient cycling through their waste products (Tanentzap and 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. 2002, Frank, Liebig and Hanson 1995; 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 semiarid savanna in Laikipia, Kenya affected aboveground and soil carbon storage. Previous studies at the same site (Augustine and 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 hypothesized 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 semiarid systems (e.g., Skarpe 1991, Todd and 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 (1) does belowground soil carbon increase with herbivore removal? and (2) if so, what is the major source (i.e., C₃ trees vs. C₄ grasses) of this soil carbon? Considering findings from previous work, we hypothesized that herbivore removal and the associated increase in woody cover would increase soil carbon, with the majority derived from the C₃ 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 to 2017 at the Mpala Research Centre (MRC) and Mpala Ranch, which together encompass 190 km² of semiarid savanna within the Laikipia County in central Kenya (37°53' E, 0°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 and McNaughton 2006, Pringle et al. 2016). The topography at the study sites consists of gently rolling hills interspersed with granitic inselbergs (Augustine and McNaughton 2006). Mean annual rainfall for the period 1972–2009 was 514 mm (Sankaran et al. 2013), whereas from 2003 to 2016, annual precipitation averaged 633 mm (Augustine et al. 2019). The vegetation is characterized by semiarid 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 and McNaughton 2004). The most common native ungulates include impala (*Aepyceros melampus*, about 20/km²), Günther's dik-dik (*Madoqua guentheri*, about 140/km²), and elephant (*Loxodonta africana*, about 1.7/km²); 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 2010, 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 enclosure experiment

Two paired ~0.5 ha (70 × 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 and the other was 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 aboveground level (Augustine and McNaughton 2004). The enclosures were designed to exclude all herbivores larger than 2 kg. The inner 50 × 50 m of the enclosure and paired control sites were delineated using a 10 × 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 enclosure construction in 1999, all individual trees and shrubs >0.5 m tall within the delineated 50 × 50 m area in each treatment were mapped and tagged and their basal area (at 15 cm aboveground 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 et al. (1982), where mass in kg = $[(7.49 \times \text{crown diameter in } m) - 7.76]$ (Augustine and 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 et al. 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-m² area surrounding each of the 36 iron rods) in the year the enclosures were constructed (1999), 3 yr later (2002), and 17 yr 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 Appendix S1: Table S1), both inside enclosures 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 10 of the 36 metal pegs forming the 10 × 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 to 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 10 metal pegs as before. A soil corer was used to sample soils at 0–5, 10–15, 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 enclosure site and soils were sampled at 0–5, 10–15, 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 labeled 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 ρ is bulk density (g/cm³), M_s is mass of dried soil (g), and V_s is the field-moist soil volume (cm³). During 2019, a further set of soil samples were collected at 0–5, 10–15, 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 enclosures (–herbivores) at each of the three paired enclosure 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, that is replicate soil samples sampled at metal pegs (10 replicates × 3 sites × 2 treatments × 3 depths = 180) and from bare-ground, grassy patches, and under tree canopies (5 replicates × 3 sites × 3 vegetation types × 2 treatments × 3 depths = 270) were analyzed for soil C by combustion with a LECO CHN analyzer (LECO Corp., St. Joseph, Michigan, USA).

$\delta^{13}\text{C}$ analyses

Aliquots of approximately 1.00–1.10 mg of homogenized plant samples and aliquots of approximately 30.0–40.0 mg of soil samples were weighed into tin capsules that were precleaned 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 ($\delta^{13}\text{C} = -20.26\text{‰}$, $\delta^{15}\text{N} = 7.89\text{‰}$, $\text{C}\% = 41.28$, $\text{N}\% = 15.29$) and DL-Valine ($\delta^{13}\text{C} = -10.57\text{‰}$, $\delta^{15}\text{N} = -6.15\text{‰}$, $\text{C}\% = 55.50$, $\text{N}\% = 11.86$) 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 six 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: $\delta X(\text{‰}) = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1,000$ where $X = {}^{13}\text{C}$ and R represents ${}^{13}\text{C}/{}^{12}\text{C}$, 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, and site and the peg number at which the sample was taken were treated as random effects to account for the nonindependence 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 C₄ grasses vs. C₃ woody plants we used the following mixing model adapted from Still et al. (2003):

$$\%C_{\text{grass}} = (\delta^{13}\text{C}_{\text{tree}} - \delta^{13}\text{C}_{\text{measured}}) / (\delta^{13}\text{C}_{\text{tree}} - \delta^{13}\text{C}_{\text{grass}}) \times 100$$

where $\%C_{\text{grass}}$ is the percent C₄ contribution, $\delta^{13}\text{C}_{\text{tree}}$ is the mean carbon isotopic composition of C₃ vegetation (see Appendix S1: Table S1), $\delta^{13}\text{C}_{\text{grass}}$ is the mean carbon isotopic composition of C₄ vegetation (see Appendix S1: Table S1), and $\delta^{13}\text{C}_{\text{measured}}$ 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 14 yr 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 ; Fig. 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 (Fig. 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 m² ha). However, a further 7 yr 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 m²/ha). By 2016, another 7 yr 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 ± 1.19 vs. 4.91 ± 0.6 m²/ha, Fig. 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 ($4,287 \pm 419$ vs. $3,804 \pm 219$ kg/ha). 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 ($13,480 \pm 2,734$ vs. $4,009 \pm 324$ kg/ha). 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 ($12,803 \pm 411$ vs. $3,461 \pm 87$, Fig. 1d). Seventeen years of herbivore exclusion resulted in an average increase of 8,516 kg/ha of aboveground woody carbon compared to plots with herbivores present, which showed an average decrease of 343 kg/ha of aboveground woody carbon.

At the beginning of the experiment (1999), soil carbon (0–15 cm) was similar across plots (1.14 ± 0.07 vs.

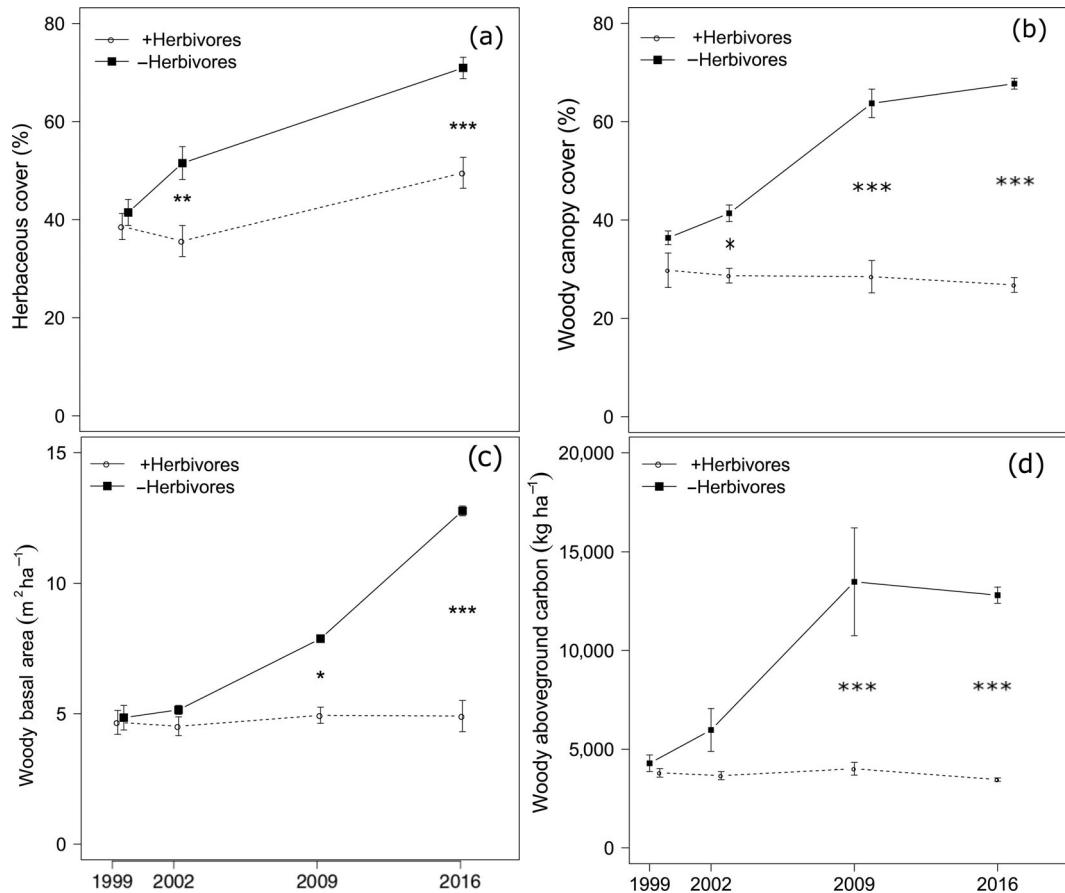


FIG. 1. Mean \pm SE of (a) total herbaceous cover (%) in 1999, 2002, and 2016; (b) total woody canopy cover (%); (c) total woody basal area (m^2/ha); and (d) aboveground woody carbon (kg/ha) in 1999, 2002, 2009, and 2016 for grazed/browsed plots (+herbivores) and ungrazed/unbrowsed plots (-herbivores). Basal area and biomass values have been scaled up from the plot level (50×50 m) and are reported on a per-hectare basis. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

0.93% \pm 0.04%). In 2016, after 17 yr of herbivore exclusion, soil total carbon (1.51 ± 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 (Fig. 2a). This effect persisted at all three measured depths (0–5, 5–10, and 25–30 cm; Fig. 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: $P < 0.001$, Fig. 2c).

Soil $\delta^{13}C$ values were significantly lower (-19.1 ± 0.28 vs. $-17.9 \pm 0.25\%$, $P < 0.05$) at 0–5 cm, marginally lower (-18.1 ± 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 (Fig. 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. $61.9 \pm 1.90\%$, $P < 0.05$). At 10–

15 cm, the h+ plots had marginally higher ($P = 0.065$) C_4 derived soil carbon (75.7 ± 1.64 vs. $69.0 \pm 1.80\%$), and at 25–30 cm there was no difference in C_4 -derived soil carbon between h+ and h- plots (78.8 ± 1.90 vs. $76.6 \pm 1.64\%$, Fig. 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 to 30-cm depth, $P < 0.001$) compared to when herbivores were present (Fig. 2d). A total of 41.6 ± 1.76 of 58.9 t/ha (71%) of soil carbon in the exclusions (h-) was derived from C_4 grasses with the remaining 17.2 ± 0.80 t/ha (29%) derived from C_3 woody biomass. In the control plots (h+) a total of 29.1 ± 1.25 of 38.4 t/ha (76%) was derived from C_4 grasses and 9.26 ± 0.40 (24%) was derived from C_3 woody biomass (Fig. 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 semiarid savanna.

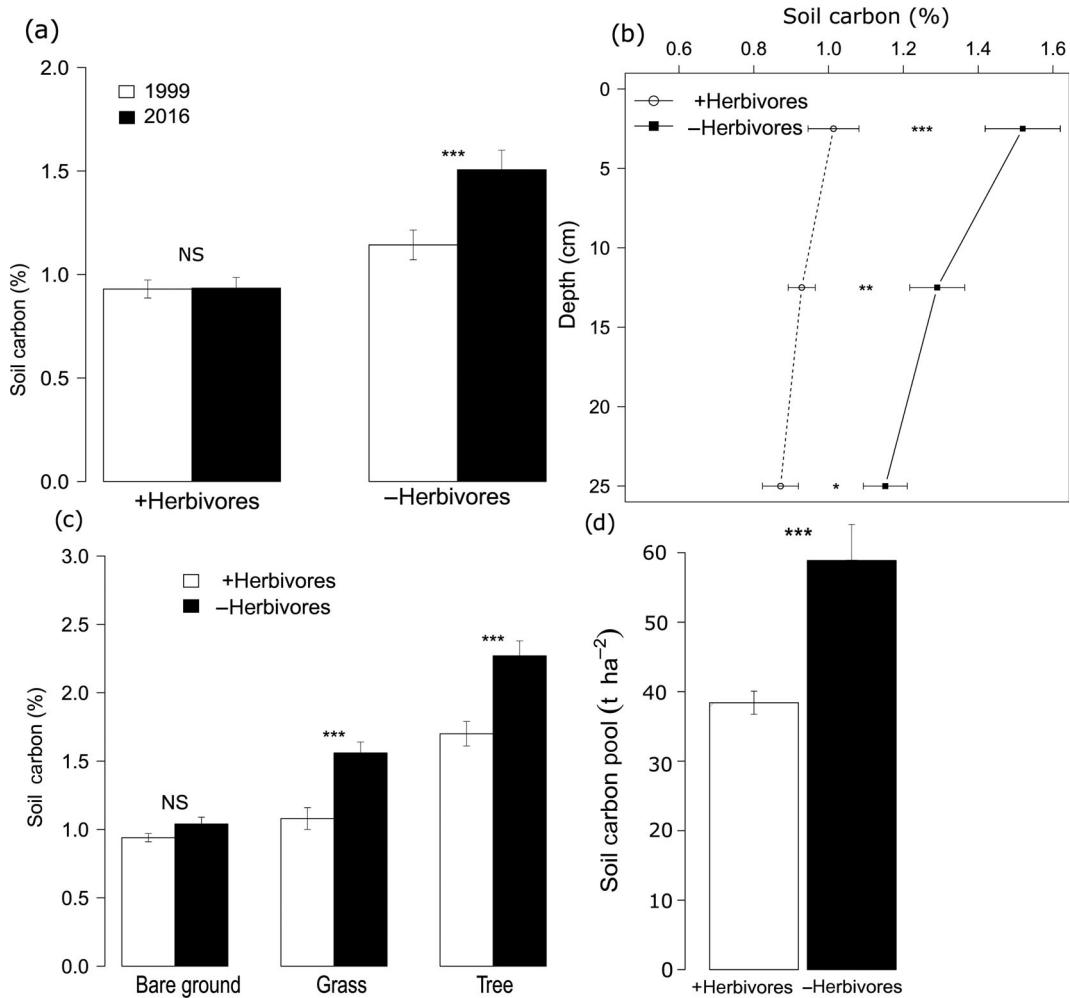


FIG. 2. Mean \pm SE in control plots (+herbivores) and enclosures (–herbivores) of (a) soil carbon sampled at 0–15-cm depth in 1999 and in 2016; (b) soil carbon sampled at 0–5-, 10–15-, and 25–30-cm depths in 2016; (c) soil carbon for soils (sampled at 0–5-, 10–15-, and 25–30 cm) in bare-ground patches, 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.

Our results show that (1) herbivore exclusion resulted in substantial increases in aboveground carbon stores in the woody layer (~ 8.5 t/ha), (2) herbivore exclusion increased soil carbon pools to at least 30 cm (~ 20 t/ha), (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 3 yr of herbivore exclusion (Augustine and McNaughton 2004), and another substantial increase after a further 7 yr of herbivore exclusion (Sankaran et al. 2013). In this study, we show that an additional 7 yr 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 10 yr 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 10 yr 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 and 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 ($\sim 70\%$ at the end of the experiment inside enclosures vs. 27% where herbivores were present). We hypothesized 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.

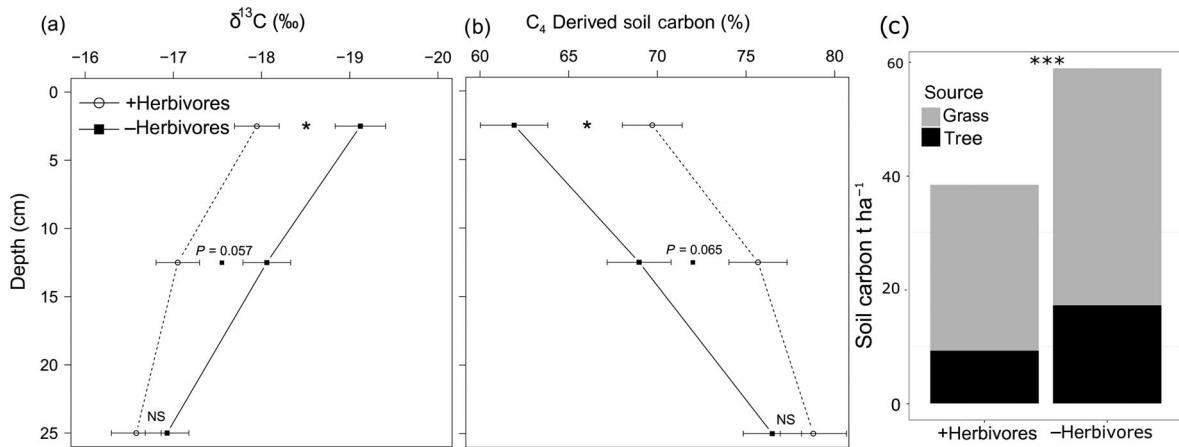


FIG. 3. Mean \pm SE of (a) soil $\delta^{13}\text{C}$ (‰); (b) C₄ (grass) derived soil carbon (%) at 0–5-, 10–15-, and 25–30-cm depths; and (c) total soil carbon pools (t/ha to a depth of 30 cm) derived from C₃ woody vegetation vs. C₄ herbaceous vegetation in control plots (+herbivores) and exclosures (–herbivores); $P < 0.1$, * $P < 0.05$, *** $P < 0.001$. C₄-derived soil carbon was calculated using an isotope mixing model adapted from Still et al. (2003).

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 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 and 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 $\delta^{13}\text{C}$ analyses have been widely used to assess the effects of vegetation change on soil carbon dynamics (Balesdent et al. 1993, Bird and Pousai 1997, Bird et al. 2002, Krull et al. 2005). Our $\delta^{13}\text{C}$ results show herbivore exclusion did increase both C₃ and C₄ 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 C₄ 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 C₄ grasses for soil C sequestration in semiarid

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 and 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 and 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 and Coughenour 1990). The importance of tree canopy density was also emphasized by Kennard and 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 semiarid 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 and McNaughton 2006).

In conclusion, we showed that despite significant increases in C₃ woody cover that occurred with herbivore exclusion in this semiarid savanna, a high proportion of soil carbon was nevertheless derived from C₄ 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 *Acacia mellifera*) that dominate this semiarid 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, semiarid savannas, which are extensive in their global extent, therefore present important opportunities for carbon sequestration via the grassy layer. Although 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 and Augustine 2004, Augustine and McNaughton 2006). Although 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 (Olf and Ritchie 1998, van Wieren and Bakker 2008, Augustine et al. 2011, Odadi et al. 2011, Lindsey et al. 2013, Katona and 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 semiarid savannas.

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