

RESEARCH ARTICLE

Soil organic carbon is buffered by grass inputs regardless of woody cover or fire frequency in an African savanna

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Abstract

1. Woody plant encroachment (WPE) is a global trend that occurs in many biomes, including savannas, and accelerates with fire suppression. Since WPE can result in increased storage of soil organic carbon (SOC), fire management, which may include fire suppression, can improve ecosystem carbon (C) sequestration in savannas.
2. At our study site in Kruger National Park, South Africa, we used a long-term (~70 year) fire experiment to study the drivers and consequences of changes in woody cover (trees and shrubs) on SOC sequestration. We surveyed four fire manipulation treatments, replicated at eight locations within the park: annual high-intensity burns, triennial high (dry season) and low-intensity (wet season) burns, and fire exclusion, to capture the range of fire management scenarios under consideration. The changes in woody cover were calculated over a period similar to the experiment's duration (~80 years) using aerial photographs (1944–2018). Soils were analysed to 30 cm depth for SOC and $\delta^{13}\text{C}$, under and away from the tree canopy to isolate local- and landscape-level effects of WPE on SOC.
3. The largest increases in woody cover occurred with fire exclusion. We found that plots with higher increases in woody cover also had higher SOC. However, trees were not the only contributor to SOC gains, sustained high inputs of C_4 -derived C (grasses), even under canopies in fire suppression plots, contributed significantly to SOC. We observed little difference in SOC sequestration between cooler triennial (wet season) burns and fire suppression.
4. *Synthesis*. Grass input to soil organic carbon (SOC) remained high across the full range of woody cover created by varying burning regimes. The total SOC stocks stored from tree input only matched grass-derived SOC stocks after almost 70 years of fire exclusion. Our results point to C_4 grasses as a resilient contributor

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to SOC under altered fire regimes and further challenge the assumption that increasing tree cover, either through afforestation schemes or fire suppression, will result in large gains in C sequestration in savanna soils, even after 70 years.

KEYWORDS

fire manipulation, grass biomass inputs, historic aerial photos, savanna fires, soil organic carbon sequestration, woody cover changes

1 | INTRODUCTION

Woody plant encroachment (WPE) has increased globally across a diversity of biomes, including savannas, over the last century (Archer et al., 2017; García Criado et al., 2020; Saintilan & Rogers, 2015 and references therein; Sala & Maestre, 2014 and other papers in this special issue; Stevens et al., 2017). The drivers suggested for this trend are numerous and include local and global causes such as overgrazing and elevated atmospheric CO₂ (Buitenwerf et al., 2012; Moncrieff et al., 2014; Venter et al., 2018; Wigley et al., 2010). There is also ample evidence that fire suppression results in increased woody biomass (Abreu et al., 2017; Durigan & Ratter, 2016; Higgins et al., 2000, 2007; Staver et al., 2009, 2011; Staver & Bond, 2014). This increase in WPE has resulted in considerable biodiversity and economic losses (Gray & Bond, 2013; Parr et al., 2012; Ratajczak et al., 2012), sometimes justified by the putative gains in the storage of carbon (C) in ecosystems.

WPE can be a significant pathway for increased ecosystem C sequestration (Bastin et al., 2019; Blaser et al., 2014; Cook-Patton et al., 2021; Geesing et al., 2000; Griscom et al., 2017; Hibbard et al., 2001; Hudak et al., 2003); however, these effects depend on climatic conditions and plant rooting profiles (Jackson et al., 2002). Given that savannas contain up to 30% of the global soil organic C (SOC) pool (Dintwe & Okin, 2018; Grace et al., 2006), it is important to develop a mechanistic understanding of the relationship between changes in tree cover and changes in ecosystem C stores. An increase in soil C can be the result of fire suppression; for example, frequent fires can volatilize C and in this way result in losses of C to the atmosphere (Bustamante et al., 2006; Kauffman et al., 1994; Seiler & Crutzen, 1980). However, in drier ecosystems, including savannas and grasslands, most SOC is in the mineral horizon where little direct combustion of C occurs (Ansley et al., 2006; Pellegrini & Jackson, 2020). In savannas, changes in soil C after fire suppression are often correlated with increases in woody biomass and changes in the ratio of trees to grasses (Coetsee et al., 2010; Holdo et al., 2012; Pellegrini et al., 2015, 2018, 2020).

Increases in woody cover resulting from fire suppression are often accompanied by increases in above-ground C. For example, long-term (58–64 years) fire exclusion in African savannas results in up to 2 Mgha⁻¹ increases in above-ground woody C when compared to annual burning (Pellegrini et al., 2017; Singh et al., 2018) and frequent, severe fire in mesic Australian savannas result in

above-ground woody losses of up to 0.5 Mgha⁻¹ year⁻¹ (Murphy et al., 2010). The patterns below-ground, however, are more complex and may respond in different ways. In some cases, WPE can reduce grass biomass above- and below-ground to such an extent that net inputs to SOC decline and there is a net loss of SOC (Hudak et al., 2003; Jackson et al., 2002). In other studies, soil C has been found to increase with increased WPE; either because the amount and stability of inputs from woody vegetation outweighed the inputs contributed by grasses (Eldridge et al., 2011) or grass productivity increased with woody cover, so that the combined effect of C inputs was substantial (Dohn et al., 2013; Wigley et al., 2020).

Once C has been added to the soils, the ultimate long-term accumulation of SOC also depends on the stability of SOC in the soil, which can in turn depend on the physicochemical properties of the soil that affect the loss of organic matter in the soil to oxidation and microbial respiration, as well as leaching and erosion (Georgiou et al., 2022; Pellegrini et al., 2022). Organo-mineral interactions slow the ability of microbes to decompose SOM because minerals occlude SOM and create physicochemical barriers for microbes to access C (Cotrufo et al., 2019; Doetterl et al., 2015; Sollins et al., 1996). The potential for organo-mineral interactions depends on edaphic characteristics, such as the amount of silt and clay and the types of clay minerals, that can govern the quantity and turnover of the stored C (Six et al., 2002; Torn et al., 1997). However, with low-intensity fires, fire can interact with these soil characteristics, potentially increasing soil C storage by increasing the portion of C associated with minerals and reducing losses resulting from decomposition (Pellegrini, Caprio, et al., 2021).

Several studies have documented increases in woody biomass with fire suppression at our study site (Higgins et al., 2007; Pellegrini et al., 2015, 2017; Zhou et al., 2022). We hypothesize that the increase in above-ground biomass of trees with lower intensity fires will result in an increased relative contribution of C₃ (tree)-derived C to SOC compared to C₄ (grass)-derived C. However, with more frequent fires, C₄ (grass)-derived C is expected to dominate SOC stocks. The net change in SOC with increases in woody biomass remains uncertain at our study site. Possibilities include (i) woody inputs increase and grass inputs remain similar or decrease slightly with a net effect of increased C, (ii) grass inputs decrease to such an extent that SOC decreases or (iii) grass biomass increases with woody increases and SOC rises because of gains in total leaf and root litter inputs. Given the patchy nature of trees in savannas, trends at the landscape scale may arise from changes in local-scale

differences in SOC underneath tree canopies. Pellegrini et al. (2015) proposed that with frequent fire, input from trees will be diminished to such an extent that there will be no differences when comparing under canopies and away from canopies. However, with fire exclusion, the differences under and away from the canopies should be much more pronounced because tree litter can decompose in the soil. Given the potential for stabilization of SOC inputs, we also anticipated a higher accumulation (and retention) of C over time on soils that were higher in clay.

We analysed soils for SOC and $\delta^{13}\text{C}$ at four depths down to 30 cm, under and away from tree canopies, on four different treatments of Experimental Burn Plots (EBPs) in the Kruger National Park (KNP; Biggs et al., 2003; Higgins et al., 2007; Van Wilgen et al., 2007). In addition to this, we analysed the change in woody cover over the past ~80 years on the same treatments using historical aerial photography. To test whether the woody cover increased to such an extent with fire suppression as to suppress the herbaceous layer, we asked (i) what were the effects of different fire regimes on woody cover and herbaceous biomass? To test the importance of direct fire effects on soil C versus indirect fire effects on C through changes in woody canopy, we asked (ii) how did soil C vary under and away from woody canopies with varying fire regimes? To test how different fire regimes affected contributions of woody versus grass-derived C to soil C, we asked (iii) what were the contributions of C_3 - versus C_4 -derived C under and away from woody canopies with different fire regimes? Lastly, to ascertain drivers of soil C, we asked (iv) how important was soil texture (clay: sand), woody cover change and fire return in determining soil C?

2 | MATERIALS AND METHODS

2.1 | Study design

Long-term experimental burn plots in KNP are extensively described elsewhere (Biggs et al., 2003; Van Wilgen et al., 2007). Here, we do so very briefly, only as it pertains to this study. Established in 1954 the experiment aims to ascertain the extent to which fire frequency and season of burn determine vegetation structure. The experiment is replicated 16 times, with four replicates each in four of the major vegetation types in the KNP in an area open to herbivores. Each replicate, called 'string', consists of 12–14 fire treatments (see Figure S1 for the experimental layout). Our study uses the four strings on two types of vegetation, Pretoriuskop (22°20' to 25°30' S) and Skukuza (31°10' to 32°00' E) in the southern section of the KNP. The experiment includes annual dry season fires in August and triennial fires in August, October, December, February and April. We use four of the treatments on each string; an annual late dry season burn (Aug 1yr), a triennial late dry season burn (Aug 3yr), a triennial wet season burn (Feb 3yr) and fire exclusion (NB). Triennial burns in the growing season (February) are typically of lower intensity than late dry season burns (in August) as fuel is much greener (Govender et al., 2006).

Only one annual treatment is part of the EBPs because the late dry season is the only time during the year that the fuel is dry enough to carry a fire after 1 year of accumulation of herbaceous biomass.

2.2 | Study site

The mean annual rainfall in Skukuza is 588 mm and in Pretoriuskop 707 mm (SANParks Scientific Services). Rainfall is distinctly seasonal with a warm wet season between October and April followed by a cool dry season. The soils are derived from the underlying Nelspruit granite suite consisting of migmatite, gneiss and granite and are moderately deep (~100 cm), nutrient-poor, red loamy sands (Barton et al., 1986; Venter et al., 2003). The vegetation at Pretoriuskop is classified as Pretoriuskop Sour Bushveld with *Terminalia sericea* and *Dichrostachys cinerea* being the common woody species and *Hyperthelia dissoluta* and *Setaria sphacelata* the common grasses (Rutherford et al., 2006). Vegetation at Skukuza is classified as Granite Lowveld and *T. sericea*, *Combretum zeyheri* and *C. apiculatum* are common tree species with *Pogonarthria squarrosa* and *Eragrostis rigidior* common grasses (Rutherford et al., 2006). The average long-term fire return interval for Kruger is about 4 years, but fire regimes vary spatially across the park, ranging from one fire per year to one every 34 years (Van Wilgen et al., 2000). The Aug 3yr treatment can be considered to be the closest to the baseline or background natural burning regime. The fieldwork was conducted under SANParks permit number COEC1504.

2.3 | Woody cover and grass biomass

To estimate above-ground woody biomass, we used two surveys; the first took place during 1956 and 1957 and the second during 2016. The first survey used two transects (305 m long \times 1.52 m wide) placed diagonally across the plots and all individuals were counted, identified to species and placed in size classes. Size classes were converted to height by Higgins et al. (2007). In the second survey, all individuals less than 5 m tall were identified according to species and diameter and heights taken in eight circles (each with 5 m diameter). Trees taller than 5 m tall were measured in an additional 7540 m² per burn plot. We then used height (m) to estimate biomass (Mgha⁻¹) using the methods of Davies and Asner (2019) and Nickless et al. (2011).

To document changes in woody cover for the 74-year period, we used historical aerial photography from 1944 to 2018. For the 1944 imagery, high-resolution scans of the black-and-white aerial photographs covering the study area were acquired from the National Geospatial Information (NGI), Department of Rural Development and Land Reform, Mowbray, Cape Town. These scans were then georeferenced and ortho-mosaiced by AAM, an international geosolutions company (AAMgroup.com). The 2018 imagery covering the same areas was acquired from NGI as RGB images that were already mosaiced and orthorectified. We used ArcGIS Pro (v.2.5.1) for

all analyses and image preparation. Prior to classification, the 2018 RGB imagery was converted to black and white and the resolution was resampled to equal that of the 1944 imagery (0.75 m). The images were then clipped to extract images (approximately 7 ha) for each of the four treatments in each of the four strings of the EBPs in the Skukuza and Pretoriuskop landscapes. Classifications of 1944 and 2018 images were performed using the Image Classification Wizard in ArcGIS Pro. We performed supervised pixel-based classifications using training data to define two groups (tree cover and grass cover) for each of the images. For the 2018 imagery we were able to overlay the original higher resolution (0.25 m) RGB images to assess the classifications. The results of the supervised classification of the 0.75-m resolution black-and-white 1940 and true colour resampled 0.25 m 2018 aerial photographs were validated (see Figure S2) using visual interpretation, because of the lack of field sampling for the historical images, following the methods of Congalton (1991) and Landis and Koch (1977). Stratified random sample points were derived using the QGIS Semi-Automatic Classification Plugin. A total of 200 points over the 16 plots of the Skukuza string were visually classified as 'tree' or 'not a tree' and the accuracy assessment for each set was calculated using a confusion matrix. The method was repeated for the 16 plots of the Pretoriuskop string for each of the 2 years, giving a total of 800 points. After classification, the total number of pixels of each class was determined and the total area covered by each class (tree and grass) was calculated for 1944 and 2018. To quantify the change in woody cover per plot over time, we subtracted the earlier values from the latter ones.

In each plot, herbaceous biomass (5%–10% of individuals are non-woody forbs) was estimated using a disc pasture meter (DPM; Zambatis et al., 2006); 50 DPM readings were taken along a U-shaped transect across the plot. These measurements were taken shortly before the management burns were applied. The average height of the grass sward was then converted to a biomass estimate in kg ha^{-1} (and converted to Mg ha^{-1} to be similar to tree biomass) using the correction in Zambatis et al. (2006). As measurements are only taken before a burn treatment is applied (starting in 1982), annual values are available for annual burns, triennial values for triennial burns and no values for no burn treatments. However, in KNP, herbaceous biomass tends to asymptote after 3 years following fire (Pellegrini et al., 2015), so we assumed that no burn biomass was similar to low-intensity triennial burns. Values of triennial burns were divided by three to estimate annual herbaceous productivity.

2.4 | Isotope composition of soil carbon

Soil samples were obtained under and away from the canopy of five large trees (>6 m) of *Sclerocarya birrea* in each plot in 2016. Under the canopy, samples were taken halfway between the tree trunk and the edge of the canopy. Away from the canopy, the samples were taken at least 5 m away from the edge of the canopy of the nearest tree. After the litter was removed, a trowel was used to sample 5 cm and, below this depth, a 4 cm diameter soil auger was used to sample 5–30 cm (in

increments of 5–10, 10–20 and 20–30 cm) and soils kept separate for each depth. The soil was dried and sieved through a 2 mm sieve to remove all roots, after which a bulk sample was taken to make one sample per canopy and one away from the canopy per plot per depth [two vegetation types \times 4 replicates (strings) \times 4 fire treatments \times canopy type (tree canopy/away from canopy) \times 4 depths = 256 samples]. After soil sampling, soil texture (proportions of sand, clay and silt) was analysed at Elsenburg Laboratory following the hydrometer method for soil particle analysis (Committee, 1990).

Soil C and $^{13}\text{C}/^{12}\text{C}$ ratios of the soil C were determined using a Thermo Finnigan Delta plus XP mass spectrometer coupled with a conflo III device to a Thermo Finnigan Flash EA1112 Elemental Analyser with automatic sampler (Thermo Electron). Although we did not expect to find carbonates in our study soils based on the pH values of the soils, we treated a subset (about 25%) of soil samples with HCl to remove carbonates and reran them for variation in C content, which confirmed the absence of inorganic C. These results were calibrated relative to Pee-Dee Belemnite, as well as to correct for drift in the reference gas. The results are expressed as parts per thousand (‰) and relative to the Pee-Dee Belemnite standard are denoted by the term δ , with a precision of duplicate analysis 0.1‰ (February et al., 2011). Based on the $\delta^{13}\text{C}$ values of the soil and end-member (mean) $\delta^{13}\text{C}$ values of the grasses (−13.17‰) and trees (−27.61‰) at our study site (February & Higgins, 2010), a standard end-member mixing model was used to determine the relative proportion of C derived from C_3 (trees) and C_4 (grass) in the soil. This mixing model was only applied to the top 30 cm of soils (surface soils) because of unrelated fractionation processes at deeper depths causing enrichment of soil $\delta^{13}\text{C}$ unrelated to the inputs from C_3 - or C_4 -derived C (Balesdent & Mariotti, 1996; Nel et al., 2018).

We calculated the bulk density of the soil (Wigley et al., 2013) for each depth category and used this value to convert C concentrations to total C per volume of soil (i.e. stocks). Stocks of C per m^2 for each depth was calculated before summing these values and converting to total soil C per ha for soils from 0 to 30 cm deep (Mg ha^{-1}). We then incorporated the impact of localized enrichment of tree canopies on SOC by weighting our calculation of C stocks by the relative tree cover using the following equation:

$$\text{plot total C (Mg ha}^{-1}\text{)} = ((\text{proportion woody cover} \times \text{soil C}_{\text{tree}}) + (\text{proportion grass cover} \times \text{soil C}_{\text{grass}})),$$

where grass cover equals 1 – woody cover.

2.5 | Statistical analyses

All analyses were performed using R version 3.4.2 (R Core Team, 2021). We used the Fligner-Killeen test of homogeneity of variance (fligner.test in the stats package for R) to determine if the data used for treatment comparisons had equal variance. For unequal variance, such as was the case when comparing woody cover change across fire treatment (Figure 1c) and soil C across fire treatments

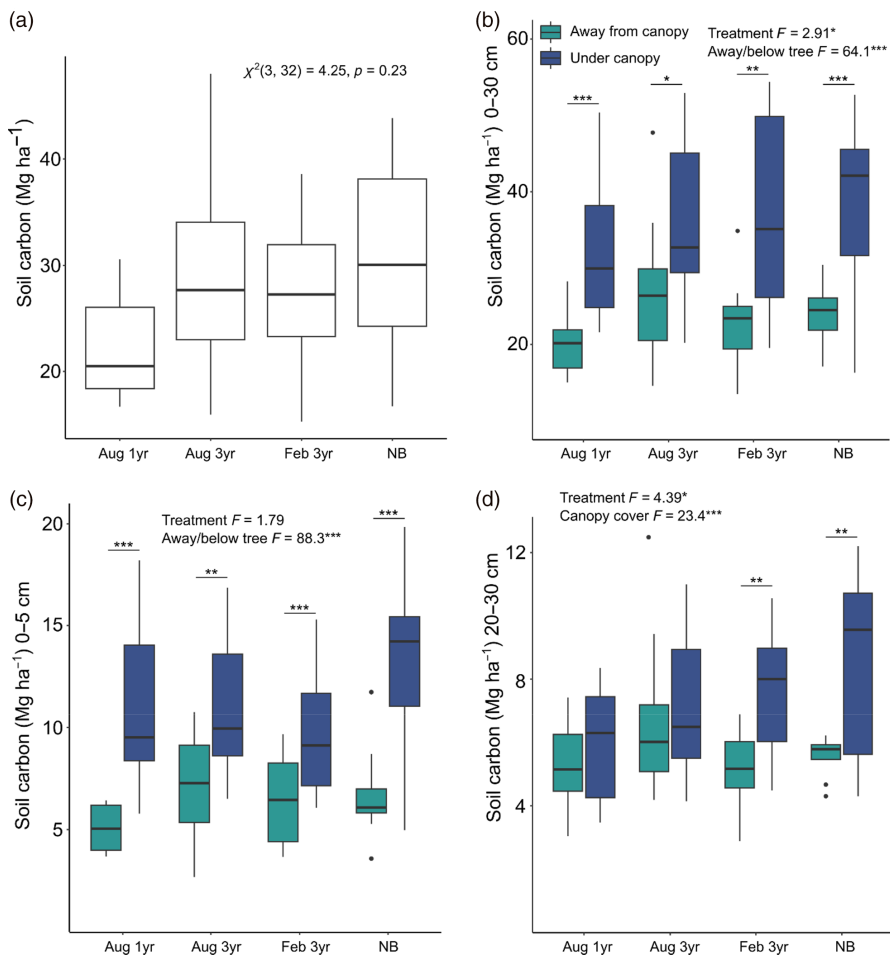


FIGURE 2 (a) Total soil carbon (Mg ha^{-1}) corrected for tree canopy presence were compared among fire treatments. (b) Soil C (Mg ha^{-1}) below and away from canopies for the entire depth to 30 cm. (c) Soil C (Mg ha^{-1}) below and away from canopies for 0–5 cm and (d) 20–30 cm soil. For (b)–(d), values are not corrected for tree canopies because soil C under tree canopies versus away from canopies were compared. p -Values marked with an * significant at a level of $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

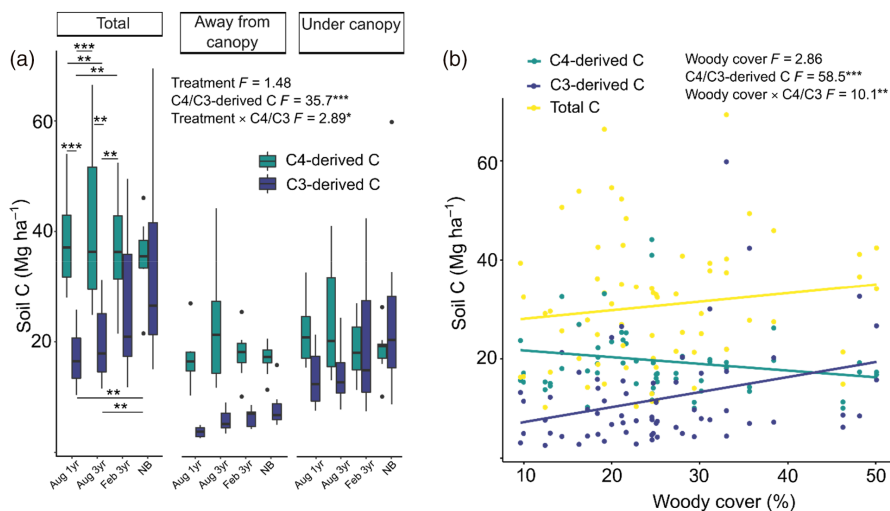


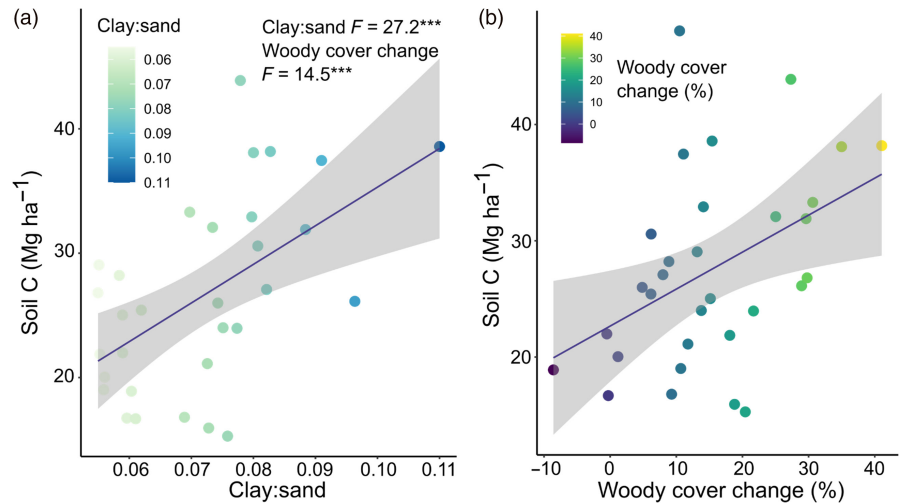
FIGURE 3 (a) Soil carbon (Mg ha^{-1}) derived from C_4 as opposed to C_3 , away from canopies and under canopies to 30 cm, with the total amounts in the first set (all the tree- vs. grass-derived carbon, summed from under trees and grass). (b) Relationship between soil C and woody cover; there were no significant correlations between woody cover (%) and soil C, we show trends of patterns for C_3 -derived C, C_4 (grass)-derived C and total C separately. p -Values marked with an * significant at a level of $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

(Figure 1b, $p > 0.05$). By 2018, relative to the 1940s, woody cover had increased on all treatments except Aug 1yr (2018 mean of 17.0% cover in Aug 1yr, 21.4% cover in Aug 3yr, 25.9% cover in Feb 3yr and 38.2% cover on no burn plots; Figure 1b). These increases resulted in the no and low-intensity burns gaining most woody cover (Figure 1c).

We tested whether increases in woody biomass resulting from less frequent fires resulted in a concurrent decrease in herbaceous

productivity. Herbaceous productivity was the highest in Aug 1yr plots (Figure 1d). For earlier dates (1982–1990), productivity in the Aug 1yr ($2.79 \text{ Mg ha}^{-1} \text{ year}^{-1}$) was 1.82 times that of Aug 3yr burns ($1.52 \text{ Mg ha}^{-1} \text{ year}^{-1}$, $p = 0.0002$) and although 1.73 times that of Feb 3yr burns, not statistically different ($1.62 \text{ Mg ha}^{-1} \text{ year}^{-1}$, $p > 0.05$). Triennial herbaceous biomass values were divided by three to obtain annual production. More recently (2015–2019), annual herbaceous production (1.70 Mg ha^{-1}) was 2.44 times that of high-intensity

FIGURE 4 (a) Relationships between soil carbon (Mg ha^{-1}) to 30 cm and clay:sand and (b) between soil carbon (Mg ha^{-1}) to 30 cm and woody cover change (%). p -Values marked with an * significant at a level of $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.



triennial burns ($0.70 \text{ Mg ha}^{-1} \text{ year}^{-1}$, $p = 0.0001$) and the triennial February biomass per annum (1.55 Mg ha^{-1}) was 2.21 times that of the triennial August burn annual biomass ($p = 0.007$). Consequently, herbaceous biomass productivity was highest in the most frequently burned plots overall but tended to be similar to the low-intensity Feb 3yr burns, and greater than the higher intensity Aug 3yr burns.

3.2 | Soil carbon changes determined by clay content and fire-driven shifts in woody cover

Treatments with lower fire frequencies or less intense fires tended to have higher soil C stocks in the upper 30 cm, but these differences were not statistically significant when compared between fire treatments ($p > 0.05$, Figure 2a). Trees played an important role in determining shifts in total plot SOC because SOC was enriched directly under tree canopies, and fire changed the cover of trees, and thus the cover of the associated SOC enrichment. We tested whether there was an interaction between fire treatment and canopy type, that is, did soil SOC under/away from tree canopies differ across fire treatments versus the effects of canopies within a fire treatment (Figure 2b–d). Under tree canopies to 30 cm (Figure 2b), Aug 1yr had 1.62 times the soil C than away from canopies (32.6 vs. 20.1 Mg ha^{-1} , $p = 0.003$), Feb 3yr canopies had 1.6 times the SOC than away from canopies (37.0 vs. 23.1 Mg ha^{-1} , $p = 0.005$), no burn canopies 1.8 more SOC than away from canopies (43.0 vs. 23.8 Mg ha^{-1} , $p = 0.0004$) and although Aug 3yr canopies had higher mean soil C than away from canopies, this was not statistically significant ($p > 0.05$). For 0–5 cm (Figure 2c), the soils under the tree canopies on the Aug 1yr had more than double the soil C than soil away from canopies (11.1 vs. 5.06 Mg ha^{-1} , $p < 0.0001$), Aug 3yr canopies had 1.5-fold more C (10.8 vs. 7.06 Mg ha^{-1} , $p = 0.001$), Feb 3yr canopies (12.4 vs. 6.42 Mg ha^{-1} , $p < 0.0001$) as well as no burn canopies had almost double the C (13.2 vs. 6.73 Mg ha^{-1} , $p < 0.0001$). For the deepest soils (20–30 cm, Figure 2d), a canopy effect on soil C remained conspicuous in the Feb 3yr and no burn plots (8.50 vs. 5.54 Mg ha^{-1} , $p = 0.001$ for no burn and 7.69 vs. 5.15 Mg ha^{-1} , $p = 0.0004$

for Feb 3yr) but soil C did not differ under versus away from a tree canopy in the Aug 1yr (5.93 vs. 5.27 Mg ha^{-1} , under vs. away, respectively, $p > 0.05$) and Aug 3yr (7.94 vs. 6.78 Mg ha^{-1} , under vs. away, respectively, $p > 0.05$) treatments. In summary, gains in tree cover increase soil C in the landscape through localized enrichment of the topsoil, which is robust to more intense burns (August) in the topsoil but becomes minimal at greater soil depths.

Any losses in soil C with frequent fire were likely partly offset via the sustained inputs by grasses (e.g. Aug 1yr plots had the highest annual herbaceous net primary productivity). Using C isotopes to quantify the contribution of C_4 grasses, we found that absolute grass-derived SOC remained high regardless of fire treatment (Figure 3a). Soil C_4 -derived stocks down to 30 cm depths ranged from $35.3 \pm 2.51 \text{ Mg ha}^{-1}$ in the no burn to $40.4 \pm 5.15 \text{ Mg ha}^{-1}$ in the August 3yr (these are C_4 -derived C from both under canopies and away, Figure 3a, first panel). However, the relative contribution of C_3 versus C_4 plants changed with burning and tree canopy presence, with higher C_4 -derived C than C_3 -derived C in the two August burns ($p < 0.0001$ and $p < 0.01$ respectively for Aug 1yr and Aug 3yr burns). Away from canopies, C_4 -derived C contributed between 68% (for no burn) and 81% (annual burn) of total SOC. Under canopies, C_4 -derived C contributed between 45% (for the no burn) and 63% (in annual burn). On the contrary, C_3 -derived C from tree (and a small proportion of forb) inputs were clearly concentrated under tree canopies, with almost twice (1.94) higher C_3 -derived soil C in the no burn compared to the annual burns, with most of this C found below canopies (78% in the annual burns to 76% in the no burn, Figure 3a). The total C_3 -derived C means varied between $16.9 \pm 5.42 \text{ Mg ha}^{-1}$ in the annual burns and $32.8 \pm 2.51 \text{ Mg ha}^{-1}$ in the no burns (no significant differences between treatments).

Figure 3b shows the total C_4 - versus C_3 -derived C in the soil along a woody cover gradient (woody cover obtained from aerial photography). The main effect of woody cover was not statistically significant ($F_{1,124} = 2.86$, $p = 0.09$) in the prediction of soil C, while there was a statistically significant ($F_{1,124} = 58.46$, $p < 0.001$) difference between total C_4 - versus C_3 -derived C, and the interaction between woody cover (%) and C type was statistically significant

($F_{1,124} = 10.1$, $p = 0.002$). Tree-derived (C_3) C surpassed grass-derived (C_4) C around 45% woody cover (Figure 3b). Taken together, grass biomass inputs are an important source of total SOC across fire regimes, but gains and losses in total SOC were driven by shifts in C_3 biomass inputs.

Soil clay content also influenced the changes in soil C stocks in combination with changes in tree cover (a model with clay:sand ratio and change in woody cover as factors and string as random factor had a high total explanatory power with $R^2 = 0.78$ and the part related to fixed effects alone had marginal $R^2 = 0.54$). Clay:sand ratio ($p < 0.0001$, Figure 4a) and change in woody cover from 1940 to 2016 ($p = 0.0008$, Figure 4b) were significant in the combined model. The higher clay:sand content and the gains in woody cover were positively related to increases in SOC. There was no significant interaction between the change in woody cover and soil clay:sand in predicting the effects on SOC.

4 | DISCUSSION

World-wide, savanna covers 22% of the land area (Ramankutty & Foley, 1999) and with an increase in WPE combined with a suppression of fire, previous work suggests that the potential for above- and below-ground C storage is significant (Scurlock & Hall, 1998). Fire exclusion experiments demonstrate that fire exclusion often results in an increase in woody biomass (Higgins et al., 2007; Murphy et al., 2010; Singh et al., 2018) and canopy cover (Bird et al., 2000; Devine et al., 2015; Pinheiro et al., 2021; Singh et al., 2018; Smit et al., 2010). However, the rates are not similar, with the fastest woody invasion rates in the savannas of South America and the lowest rates in Australia (Murphy et al., 2014; Stevens et al., 2017). Woody encroachment rates have been shown to increase with wetter wet seasons and milder dry seasons (Pellegrini, Refsland, et al., 2021). Using aerial photography, we go back to the 1940s, where we showed that tree canopy covered about 10% of the area at our study sites and subsequently increased dramatically regardless of fire treatment, so that woody cover increased 1.70 times in annual dry season burn (Aug 1yr) and 4.75 times on the no burn treatment by 2018.

With the increases in woody cover that accompanied less frequent fire over almost 70 years, we expected below-ground C storage to increase (Bird et al., 2000; Boutton et al., 1998; Pellegrini et al., 2020; Zhou et al., 2022). However, changes in total soil C to 30cm did not scale with changes in total tree cover, ranging from 22.0 Mg ha^{-1} in annual burns to 30.5 Mg ha^{-1} in the fire exclusion. Several mechanisms can account for the nonproportional increases in soil C with woody cover, such as disproportionately smaller gains in below-ground biomass inputs, large gains in decomposition and turnover of SOC and/or saturation in SOC storage capacity. Although we could not measure grass productivity over time in fire suppression plots, our results show that grasses still contributed significant amounts of C (45% under tree canopies to 68% away from canopies) to soils in these plots. This

study supports results from previous studies that included deeper soil layers and higher woody cover (to 80%) in demonstrating that grasses dominate inputs of C in savanna soils (Dohn et al., 2013; Wigley et al., 2020; Zhou et al., 2022).

In more mesic savannas, there may be a tipping point of woody cover (Hoffmann et al., 2012) where grasses and fire are excluded, and depending on soil type, this may result in increased SOC (Pellegrini et al., 2014; Zhou et al., 2017). The variability in the effects of loss of grass inputs on SOC between sites is believed to be driven by the productivity of below-ground biomass in grasses relative to woody plants in a site (Jackson et al., 2002; Yusuf et al., 2015). Some previous work has suggested that increased soil C with woody encroachment is more prevalent in arid ecosystems, possibly due to deeper rooted woody plants (Geesing et al., 2000; Jackson et al., 2002; Mureva et al., 2018; Wheeler et al., 2007). Given the persistence of grass-derived SOC in our system, we infer that there are either sustained inputs of grass biomass and/or high stability of residual SOC derived from grasses.

We assumed changes in SOC $\delta^{13}\text{C}$ arose primarily from differences in plant inputs, both above-ground and below-ground. Although isotope fractionation during decomposition and humification can also influence $\delta^{13}\text{C}$ (Boström et al., 2007; Natelhoffer & Fry, 1988; Nel et al., 2018), these changes are on a much smaller magnitude than the ^{13}C differences between C_3 and C_4 photosynthetic tissues. Depth can also play a role as well because SOM becomes ^{13}C -enriched, when compared to litter, with increasing depth in the soil profile, this enrichment is usually 1‰–2‰ in the upper 20–30cm of soil (Balesdent et al., 1993; Natelhoffer & Fry, 1988). If ^{13}C became enriched with depth due to processes that occurred during decomposition, then we may have overestimated the contribution of grass-derived C to soil C. Physiological differences between grasses and trees, such as root traits, also impact the C inputs to soils and the recalcitrance and stability of these inputs (Poirier et al., 2018; Rossi et al., 2020). There is evidence that indicates that the inputs of C_4 vegetation decompose more rapidly than those from C_3 vegetation (Saiz et al., 2018; Wynn & Bird, 2007), which would result in an underestimate in the proportion of C derived from C_4 . However, Rossi et al. (2020) have shown that although grasses produce roots rich in lignin and cellulose with a high C:N ratio that slows microbial activity and therefore root decomposition rates, there was a higher accumulation of particulate organic matter, a form that is more accessible to decomposers and thus less persistent in the soil.

Other mechanisms for nonproportional increases (i.e. smaller below-ground changes when compared to above-ground woody increases) in soil C with woody cover could be the delayed incorporation of greater woody biomass inputs into SOC stocks (soils generally lag plant biomass changes following a change in disturbance), leading to a decoupling between changes in plant biomass and SOC. Furthermore, woody cover is not linearly proportionate to biomass inputs since, as trees grow larger, a greater proportion of their biomass is invested in wood, which turns over slowly, relative to leaves and fine roots. Thus, there may be diminishing

returns between the gains in tree cover and the potential inputs into the soil pools. Finally, Pellegrini et al. (2020) showed that less frequent burning increased the decomposition of particular types of organic matter (i.e. cellulose, hemicellulose and starch), and tree canopies tended to have even higher decomposition rates of some types of organic matter (aromatic compounds) when fire was excluded. Thus, higher rates of SOC turnover may offset increases in inputs to some extent.

Consistent with possible C saturation in more sandy soils, soil texture was an important predictor of SOC in this study, with a greater potential for soil C sequestration when soils had higher clay:sand ratios. When soil mineral surfaces are free, there is a high potential to absorb organic matter formed from the decomposition of new biomass inputs (Franzuebbers et al., 1996; Georgiou et al., 2022; Hassink et al., 1993). Soils with a higher clay content accumulate SOC more than sandy soils (Georgiou et al., 2022; McClelland et al., 2021), in line with our findings that the gains in SOC after a reduction in fire frequency were greater in soils with a higher clay content. However, the mineral sorption capacity is hypothesized to be limited and thus the SOC accumulation is likely to saturate at some point, with lower saturation capacities in sandier soils. The mechanism is likely that organo-mineral interactions create physicochemical barriers for microorganisms to access SOC sources (Cotrufo et al., 2019; Doetterl et al., 2015; Sollins et al., 1996). As a result, mineral-associated C has much lower turnover rates with increased efficacy of longer-term C sequestration (Cotrufo et al., 2013; Georgiou et al., 2022; Trumbore, 2000). The interaction between fire-driven C losses and stabilization of C through interactions with minerals probably explains in part the varying trend of SOC responses to fire across the EBPs and other fire manipulation experiments (Pellegrini et al., 2022; Pellegrini, Caprio, et al., 2021), and deserves further study.

The increase in bush encroachment in savannas globally (Archer et al., 2017) will have an enormous impact on biodiversity (Costello et al., 2000; Veldman et al., 2015a). The evolution of savanna ecosystems began in the Miocene or early Pliocene some 8–5 Mya (Cerling et al., 1998). This long evolutionary history of grassy ecosystems has resulted in high levels of plant diversity in savannas and grasslands (Bond & Parr, 2010; Veldman, 2016). These open ecosystem plants need direct sunlight, and with the low light conditions that occur as tree biomass increases, plant diversity will decrease. Additionally, animal diversity can be negatively affected by increased woodiness in savanna (McCleery et al., 2018; Stanton Jr. et al., 2018). Several studies demonstrate that maintaining biodiversity can be at odds with actions that result in C storage in savannas, including fire suppression to encourage woody encroachment (Pellegrini et al., 2016; Peterson & Reich, 2008). In addition to the effects on biodiversity, increased woodiness also leads to environmental costs, including reduced water availability and altered nutrient cycling (Veldman et al., 2015b). Set against these potential high costs of increased woody cover, there are the very long periods without fire needed to increase soil C. A realignment of our focus on fire suppression

to using fire wisely to promote C sequestration is needed if we are to avoid significant consequences for biodiversity and ecosystem functioning (Adams, 2013; Hermoso et al., 2021).

Our results show that less frequent, low-intensity fires had little effect on woody cover or SOC. Previous work in various ecosystems has shown that low-intensity fires can increase soil C storage. For instance, Pellegrini, Refsland, et al. (2021); Pellegrini, Caprio, et al. (2021) showed that in coniferous forests, low-intensity and frequent fire decreased decomposition and increased the proportion of mineral-associated C which resulted in stabilization of C. Similarly in tropical Australian savannas, Richards et al. (2011) showed through using the CENTURY Soil Organic Matter Model, that the greatest soil C storage was achieved with a low-intensity fire every 5 years. Much other work reinforces the advantages that frequent, low-intensity fire may have for ecosystem C (and nutrient) dynamics (Nave et al., 2011; Page-Dumroese et al., 2002; Sawyer et al., 2018; Verma & Jayakumar, 2012).

In summary, we found that fire indirectly changed the organic C of the soil by shifting the inputs of trees, rather than through direct C losses related to fires. However, because grasses were the dominant contributors to SOC, the relative net changes were minor and only existed under the most extreme comparisons (i.e. complete fire suppression over many decades). Grass productivity remained high under frequent burning, likely explaining the lack of change in absolute C₄-derived C across the different fire regimes. Maintaining a vigorous grass layer, which is critical for C sequestration in open systems (Wigley et al., 2020; Zhou et al., 2022), is likely to be increasingly important in the face of increasing disturbance regimes. For open systems such as savannas, there is a pressing need to investigate alternative nature-based solutions, which do not involve tree planting and fire suppression, which may result in a loss of biodiversity, and which should include appropriate fire and grazing management (Seddon, 2022). One of the ways in which fire can be better managed may be the application of frequent, low-intensity fires.

AUTHOR CONTRIBUTIONS

C. Coetsee, B. J. Wigley, L. O. Hedin and A. Pellegrini conceived the ideas and designed the methodology; C. Coetsee, B. J. Wigley and E. C. February collected the data; C. Coetsee, B. J. Wigley, L. Kleyn and A. Pellegrini analysed the data; C. Coetsee, E. C. February and A. Pellegrini led the writing of the manuscript. All authors critically contributed to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest.

PEER REVIEW

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: A map showing the four strings of Pretoriuskop (Numbi, Shabeni, Kambeni and Fayi) and Skukuza (Skukuza, Napi, Nwaswitshaka and Biyamiti). Numbi has been used as an example to show the location of the fire treatments.

Figure S2: Examples of woody classifications for the 1940s and later aerial photographs. For each set, estimated woody cover is shown in the first line with classification accuracy and kappa values in the second line. The overall accuracy of the tree/no-tree classification for the Skukuza string for 1940 was 85% with a kappa coefficient (K-hat) of 0.52 and for 2018, overall accuracy was 83% and kappa coefficient of 0.54. The Pretoriuskop string overall accuracy is 89% (kappa coefficient of 0.49) for 1940 and 73% (kappa coefficient of 0.38) for 2018.

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