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Long-term frequent fires do not decrease topsoil carbon and nitrogen in an Afromontane grassland

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Fire has been an integral evolutionary force shaping and maintaining grassy biomes, such as the Afromontane grasslands of South Africa. Afromontane grasslands represent a large carbon reservoir, but it is uncertain how fire affects their long-term C storage. We investigated the effect of fire regime on soil organic C and N (SOC; SON) in a long-term (39-year) burning experiment in the Maloti-Drakensberg Park, South Africa. We compared SOC and SON sampled in 2004 and 2019 from six treatments differing in fire frequency (annual, biennial, five-year, infrequent) and season (spring, autumn). Average SOC increased significantly between 2004 and 2019. Average SON increased slightly, resulting in a significant increase in C:N ratio, indicating that soil organic matter is becoming less N-eutrophic. Importantly, burning annually in spring increased SOC and SON. This unexpected response is attributed to the aluandic (acidic, high organic matter) properties of Drakensberg soils. Burning in autumn did not increase SOC and SON. The lowest C stocks were observed in infrequently burnt plots. Average C sequestration across all fire treatments was 0.30 Mg ha⁻¹ y⁻¹. The observed increase in SOC under frequent fires is contrary to many findings from other studies in grassy ecosystems and notably driven by fire season.

Keywords: fire regime, montane grassland, soil

Supplementary material: available at <https://doi.org/10.2989/10220119.2021.2016966>

Introduction

Climate and land-use changes are altering fire regimes across the globe, with consequences for the carbon cycle (Bowman et al. 2009; Pellegrini et al. 2018). Global fire emissions have been well-quantified (van der Werf et al. 2010), but we know much less about how fire affects carbon storage of ecosystems, especially how changes in fire frequency and/or fire season affect long-term soil carbon storage (Pellegrini et al. 2018). In grassy biomes, such as the temperate, C₄-dominated Afromontane grasslands of South Africa, fire has been an integral evolutionary force, shaping and maintaining these biodiverse systems.

Fire is a principal management tool in Afromontane grasslands (Everson and Everson 2016). Although fire is key to maintaining grassland ecological functioning and biodiversity (Everson and Tainton 1984; Bijker et al. 2001; Uys and Lechmere-Oertel 2006), there continues to be vigorous debate regarding the use of prescribed fire. Globally there is a negative perception of grassland fire that is reflected in a history of fire

suppression and international afforestation programmes (Parr et al. 2014; Eloy et al. 2019). This has been driven by a research bias focusing on the damaging effects of wildfires (Hiers et al. 2020) and the view that grasslands existing in areas climatically capable of sustaining forests have been anthropogenically engineered through the use of fire (Meadows and Linder 1993; Sala et al. 2001; Finch et al. 2021). That trees are largely absent from Afromontane grasslands is incongruous with Whittaker's (1975) temperature/precipitation plane and Clementsian successional theory, accordingly appearing to support the view that anthropogenic fire reduced the widespread forested areas that previously existed. However, recent research supports continuous grass dominance throughout the late Pleistocene (Stewart et al. 2016), despite the more recent introduction of human-altered fire regimes (Archibald et al. 2012; Finch et al. 2021). Hence, the biodiversity and ecosystem processes that exist in the Afromontane grasslands present an ancient and unique ecology; their evolution and persistence is a result of

complex interactions between a suite of factors, which include climate, soil resources and fire.

This study was conducted in the Maloti-Drakensberg Transfrontier Park, which is part of the eastern Main Escarpment of southern Africa, a plateau-edge that lies as a margin around the subcontinent (Nel and Sumner 2006; Clark et al. 2011) and forms the southern reaches of the Afromontane archipelago (White 1983). Grasslands form a major component of the vegetation of the Maloti-Drakensberg (Mucina and Rutherford 2006). They are represented by a rich and diverse flora and fauna with a high level of endemism (van Wyk and Smith 2001; Carbutt and Edwards 2006; Clark et al. 2011). In addition to their biodiversity value, the grasslands provide ecosystem services of natural and economic importance: the Maloti-Drakensberg is the primary water catchment area of KwaZulu-Natal and Gauteng (Tyson et al. 1976; Le Maitre et al. 2018), and the highly productive grasses are vital for soil formation, erosion control (Muller et al. 2021) and greenhouse gas mitigation (Everson and Everson 2016).

There has been a strong research interest in the response of these grasslands to fire, where multiple studies have focused on the effect of prescribed fire on vegetation productivity and species composition (e.g. Everson and Tainton 1984; Everson 1985; Uys 2000; Bijker et al. 2001; O'Connor et al. 2004; Everson and Everson 2016; Gordijn et al. 2018; Morris et al. 2020; te Beest et al. 2021). However, comparatively few studies have examined the effect of fire regime on soil organic matter (SOM; this includes soil organic carbon (SOC) and soil organic nitrogen (SON) (Pineiro et al. 2010)) in the Maloti-Drakensberg, and in Afromontane grasslands in general. This reflects a knowledge gap, particularly because, like other montane grasslands, the acidic Andosols of these grasslands are a large carbon reservoir (Oliver et al. 2017), and significant amounts of C and N are volatilised from burning vegetation (Fynn et al. 2003). This is of concern because of the implications regarding climate change and the long-term soil health and productivity of grasslands.

The effect of fire on SOM depends on many factors, including vegetation type and fuel load, soil properties, soil biology and fire severity (González-Pérez et al. 2004; Knicker 2007). Regular burning is reported to result in a decline in soil organic matter over time (Mills and Fey 2004; Knicker 2007; Jones et al. 2014; Ojima et al. 2017). Significant effects of fire on SOM are often difficult to detect (Fynn et al. 2003; Manson et al. 2007; Oliver et al. 2017) and it can take decades for significant differences in SOM response to fire frequency to be observed (Pellegrini et al. 2018). In their study in tropical montane grasslands in Peru, Oliver et al. (2017) observed consistently higher soil C stocks in burnt vs unburnt treatments, although the difference was not significant. Fynn et al. (2003) reported significant declines of SOC in the top 0–20 mm of a tropical grassland soil with annual and biennial dormant-season (autumn, winter) fires, whereas in spring burns no significant effect of fire on SOC was observed. Therefore, timing of burning may also have a large effect on SOM. Studies on the effect of burning on soil N also report variable results, indicating a context-dependent response that is partly influenced by fire intensity and frequency (Jones et al. 2014;

Reinhart et al. 2016). Cook (1994) reported a net loss of N from savanna soils in Australia after annual burning, leading to a depletion of soil N over time. In contrast, Stock and Lewis (1986) observed a post-fire increase in total soil N and nitrate-N in South African coastal fynbos soils, which lasted for nine months after the fire.

Many studies are geographically- or biome-biased, occurring in the northern hemisphere and in forest, wooded or agricultural landscapes and we do not know whether findings in other systems are valid for Afromontane grasslands; apart from climate and vegetation differences, the soils in the Maloti-Drakensberg grasslands classify as acidic Aluandic Andosols (FAO 2014), which are high organic matter soils that have distinctive chemical properties not found in most other soil types (Kögel-Knabner and Amelung 2014). This study aimed to improve our understanding of how fire regimes might influence C stocks and total N over the long term and increase our understanding of the mechanisms of the effects of fire.

We investigated how 39 years of maintained fire treatments have affected the soil organic C and N content in Afromontane grasslands of the Drakensberg. We hypothesised that long-term fire would decrease soil organic C and N when compared with unburned treatments. We expected the effects of fire to increase with fire frequency, but we were unclear how season of burning would affect SOC and SON. To test these hypotheses, we quantified decadal changes in soil organic C and N independent of fire regime by repeating a survey conducted in 2004. We also quantified and compared the effects of long-term fire treatment on SOC and SON. Possible mechanisms for directional changes in soil C and N in response to fire treatment are discussed.

Materials and methods

Site location and climate

The study was undertaken at the Brotherton burning trial (see Supplementary material, Figure S1 for trial location and plot plan), located on the flat to gently rolling Brotherton plateau in the mesic montane grasslands of the Cathedral Peak area in the northern Maloti-Drakensberg Park, South Africa (28°58.2' S, 29°15.7' E; 1 900 m asl).

This area has a temperate humid climate, with a mean annual temperature of 13.8 °C (Everson and Everson 2016). Mean monthly temperatures range from 10.0 °C in the coldest month (June) to 17.1 °C during January (Manson et al. 2007). Mean annual precipitation is approximately 1 380 mm (Gordijn et al. 2018), 84% of which falls in summer between October and March, with occasional snowfalls during winter (May to August) (Tyson et al. 1976).

Geology, soils and vegetation of the site

At altitudes of 1 700 to 3 000 m asl within KwaZulu-Natal, the steep Drakensberg escarpment is visually dominated by near-vertical basalt and sandstone outcrops. There are, however, extensive areas of grassland on largely shallow soils, but they may be over a metre deep in valleys and on plateaux. Above altitudes of 1 850 m asl, the soils are derived almost exclusively from highly weathered basalt. The geology underlying the Brotherton plateau consists

of layers of basalt (about 140 m thick) on top of Elliot and Clarens Sandstone Formations (King 1944). Soils over the experimental area are generally shallow (<0.5 m) and predominantly Aluandic Andosols of the Inanda and Nomanci forms (Soil Classification Working Group 1991). They are generally acidic (pH_{KCl} 3.8 to 4.5), highly leached and highly weathered, as a result of the high annual rainfall and long exposure to weathering (Manson et al. 2007). Whether shallow or deep, these are humic soils (Fey et al. 2010); the topsoils generally have a carbon content of more than 60 g kg^{-1} through a depth of 50 to 200 mm. The sand content seldom exceeds 40% (Turner 2000) and clay mineralogy is dominated by kaolin (halloysite and kaolinite), iron oxides (goethite and hematite) and aluminium hydroxide (gibbsite) (Fey 1974; Fey et al. 2010). Subsoils are predominantly well drained, but small wetlands feed the headwaters of streams and also occur where there are gently sloping toe-slopes in valley bottoms.

Mucina and Rutherford (2006) classify the vegetation as uKhahlamba Basalt Grassland, dominated by *Themeda triandra*. This vegetation type is part of the Afromontane grassland biome, which is widespread across Africa (Meadows and Linder 1993), although critically endangered in southern Africa (Olson and Dinerstein 1998; Carbutt et al. 2011). Afromontane grasslands are an ancient grassland type, which developed from 5.3 to 2.5 MYA, during the late Miocene to early Pleistocene (Fox et al. 2012; Stewart et al. 2016) during periods of low and variable atmospheric CO_2 , increasing temperatures and aridity (Fox et al. 2018) and recurrent natural fires (Morris et al. 2020). The Maloti-Drakensberg Afromontane grasslands host a diverse and unique community of plant species, including 188 angiosperm species that are endemic to the montane belt and reflect its inclusion in the Drakensberg Mountain Centre of plant endemism (Carbutt 2019).

Fire management

Fire has played a key role in the development of the Maloti-Drakensberg grasslands (Morris et al. 2020) and many of the plant species have evolved with, and are adapted to, frequent fires (Linder 2014). Across the Maloti-Drakensberg grasslands the historical fire occurrence patterns are linked to the phases of human occupation in the area, ranging from prehuman natural fire events (lightning-ignition) to hunter-gatherer, agropastoralist, colonial and contemporary fire management (Morris et al. 2020; Finch et al. 2021). The fire regime across the Ezemvelo KZN Wildlife-managed regions of the Drakensberg is the implementation of a prescribed burning regime, directed by current understanding of the effects of fire on grassland ecosystems, and the management objective of maintaining biodiversity and ecosystem services (Lodder et al. 2018). Currently this entails a biennial burn between the first frosts to soon after the onset of spring growth in a pattern of non-contiguous blocks, which promotes structural heterogeneity across the grassland (Everson et al. 1985; Morris et al. 2020).

Experimental design

The Brotherton trial is a long-term fire-manipulation experiment that was established in 1980 to examine the effects of fire frequency and burning season on plant

community dynamics in Afromontane grasslands (Uys et al. 2004). It now forms part of the Cathedral Peak ILTER site, which is under the management of Ezemvelo KwaZulu-Natal Wildlife and the South African Environmental Observation Network (SAEON). The site is fenced to protect the trial from concentrated grazing by large herbivores. Herbivore density on the Brotherton plateau is extremely low, and no signs of grazing (grazed tips of regrowth after burning or dung) were observed on the trial site.

The Brotherton burning trial comprises 45 plots laid out in a randomised block design (see Supplementary material, Figure S1 for plot plan). In this study, six fire treatments that were maintained since 1980 were sampled: annual/biennial autumn burns; annual/biennial spring burns; five-year rotation alternating between autumn and spring, and the fire exclusion treatment. Treatments were replicated a total of three times, that is, one replicate per each of the three trial blocks in $25 \times 25 \text{ m}^2$ plots. Autumn burns were applied after the first frost and spring burns after the first significant rainfall. Even though fires were attempted to be fully excluded in the fire exclusion treatment, it nevertheless burned three times during the history of the trial (see Supplementary Material Table S1, for the burn history of the trial). During the winters of 2000, 2007 and 2016 (June/July) unplanned (accidental or arson) fires burned through the whole experiment, including the infrequent burn. In addition, a smaller section of the trial was burnt in an arson fire during the winter of 2017, affecting a biennial burn treatment (te Beest et al. 2021). The fire exclusion treatment is therefore referred to hereafter as an infrequent burn.

Data collection

Identical sampling methods, sample preparation and analytical techniques were used in 2019 as in the 2004 study by Manson et al. (2007) to ensure that a direct comparison between years could be made. Soil samples were taken in March 2019 from the allowed sampling areas (within the 2 m wide low intensity soil sampling buffer) in each plot using a Beater auger. Each composite sample comprised 20 subsamples. Samples collected in 2004 were taken from 0 to 200 mm at 50 mm depth increments, whereas those collected in 2019 were only taken from depths of 0–50 and 50–150 mm. To allow a fair comparison between 2004 and 2019 depths subsamples from the 2004 data had to be aggregated. For the aggregation of 2004 samples weighted averages were applied to SOC and SON in 50–100 mm and 100–150 mm sub samples based on their densities. This aggregation allowed comparison of two equal depth samples of 0–50 and 50–150 mm.

The analytical work for both the 2004 and 2019 studies was done in the KwaZulu-Natal Department of Agriculture and Rural Development Analytical Services soil laboratory at Cedara Research Station, using identical protocols. Composite samples were air-dried at room temperature for seven days, after which they were gently comminuted between spring-loaded, rubber conveyer belts to pass through a 1 mm mesh. This is a highly weathered and organic soil, and samples were devoid of rock fragments and gravel. Sample density was determined using a scooped volume weight of soil and the samples were then analysed for total C and N (automated Dumas dry

combustion as described in Manson et al. 2020) using a LECO CNS analyser. Bulk density was estimated using the relationship between measured sample densities and bulk densities on a smaller dataset. In these soils, total C is essentially equivalent to SOC, because the soils are highly weathered and acid and therefore have no carbonate-containing minerals (Nelson and Sommers 1983). Inorganic N (nitrate-N and ammonium-N) concentrations are less than 5 ppm in these soils, making total N and SON essentially equivalent.

Data analysis

To determine whether there were differences in SOC, SON amounts and C:N ratios between samples collected in 2004 and 2019, these were tested with a one-way ANOVA with year as fixed effect. To analyse the effect of fire frequency and season of burn on SOC, SON and C:N ratio we used a one-way ANOVA with fire treatment as fixed effect. We excluded the five-year rotation treatment from the analyses that examined the effect of season of burn on the response variables as the prescribed burns alternated between autumn and spring. Separate models were run for each sampling depth.

The influence of fire treatments on carbon stocks were evaluated using a one-way ANOVA with Fisher's protected LSD *post hoc* contrasts. The rates of change in C stocks were also calculated from SOC and bulk density for each treatment per sampling depth following Pearson et al. (2005). The stocks for the two sample depths were summed for each treatment plot to give C stocks (Mg) per hectare to a depth of 150 mm. We tested whether fire treatment affects C stocks using a one-way ANOVA with fire treatment as a fixed effect. The effect of treatment on annual change in C stocks was tested using a one-way ANOVA.

Statistical analyses were performed using GENSTAT 18 (VSN International 2015). Prior to analysis, data were checked for normality and homogeneity of variance using the Shapiro-Wilk test. Data were excluded from one infrequently burnt plot that has been invaded with non-native bramble (*Rubus cuneifolius*) and from an annual spring burn plot that is characterised by extremely shallow soils, often with bedrock within 150 mm of the surface. When included in the ANOVA, they were identified as having large residuals.

Results

Decadal changes in soil carbon and nitrogen

There was a significant increase in SOM over the 15-year period between 2004 and 2019, which was largely independent of fire treatment (Figure 1, Table 1; see Supplementary Material Table S2, for the full set of ANOVA results). Average SOC levels increased by almost a tenth that is, by 9.43 g kg⁻¹ (8.2%) and 7.67 g kg⁻¹ (8.1%) in the 0–50 mm and 50–150 mm depth increments, respectively, (0–50 mm: $F_{(1,17)} = 44.32$, $p < 0.001$; 50–150 mm: $F_{(1,17)} = 30.18$, $p < 0.001$) (Figure 1a). A small, but statistically significant increase in SON of 0.3 g N kg⁻¹ was observed in the 0–50 mm sampling depth between 2004 and 2019 ($F_{(1,17)} = 8.62$, $p = 0.009$), but there was no change in the 50–150 mm depth increment ($F_{(1,17)} = 0.32$, $p = 0.576$; Figure

1b). The associated increase in C:N ratios were significant at both depths (0–50 mm: $F_{(1,17)} = 38.38$, $p < 0.001$; 50–150 mm: $F_{(1,17)} = 109.69$, $p < 0.001$) (Figure 1c). The change in C:N ratio between sampling events was greater in the 50–150 mm depth increment (1.08 or 7.57% increase) than in the 0–50 mm soil sample (0.66 or 4.35% increase).

Fire regime and soil organic matter

Soil organic C was significantly higher for both sampling depths in the annual spring burn treatment compared with the other fire treatments in 2019 (0–50 mm: $F_{(4,8)} = 8.99$, $p = 0.005$; 50–150 mm: $F_{(4,8)} = 18.34$, $p < 0.001$) (Figure 2a). There were no differences in SOC between the remaining fire treatments in the 0–50 mm depth increment. However, SOC was significantly lower in the infrequent burn treatment than the biennial autumn and spring burns in the 50–150 mm depth increment. Soil organic C in the annual spring burn was significantly higher than in the biennial spring burn. There was no difference in SOC between the annual and biennial autumn burn treatments. Soil organic N was highest in the annual spring burn (Figure 2b). This response was evident in both depth increments (0–50 mm: $F_{(4,8)} = 11.47$, $p = 0.002$; 50–150 mm: $F_{(4,8)} = 20.56$, $p < 0.001$). There was a significant difference between SON content in the annual and biennial spring burns, but SON did not differ between the annual and biennial autumn burns. The C:N ratio was significantly lower in the infrequently burnt plots (Figure 2c) in both depth increments (0–50 mm: $F_{(4,8)} = 5.43$, $p = 0.021$; 50–150 mm: $F_{(4,8)} = 5.61$, $p = 0.019$). This reflects an increase in SOC with fire frequency, rather than a decrease in SON (see Supplementary Material Table S3 for the full set of ANOVA results).

The effect of fire regime on C stocks

Carbon stocks measured in 2019 in the top 150 mm of soil ranged from 90.15 to 111.43 Mg C ha⁻¹. Fire treatment had a significant effect on C stocks ($F_{(4,6)} = 10.83$, $p = 0.007$) (Figure 3). Stocks in the infrequently burnt treatment were significantly lower than the other treatments. Carbon stocks in the spring-burn fire treatments increased with increasing fire frequency (from annual to biennial burns), but there was no change in C stocks with fire frequency in the autumn burn treatments (see Supplementary Material Table S4 for the full set of ANOVA results). Average C stocks increased from 97.21 to 101.65 between 2004 and 2019, with an average change of 0.30 Mg C ha⁻¹ y⁻¹. Fire treatment did not influence the change in C stocks, which is likely because of high within-treatment variation (CV = 194.7%).

Discussion

We studied the effects of fire frequency and season on SOC, SON and C:N ratio in a long-term fire experiment in an Afromontane grassland. Soil organic C increased significantly between 2004 and 2019, with a carbon sequestration rate across all fire treatments of 0.30 Mg ha⁻¹ y⁻¹, which disproves our hypothesis that long-term, frequent fires reduce soil C. Although there was a slight increase in SON in the 0–50 mm sampling depth, the significant increase in C:N ratio indicates that the system is becoming more N-limited. Change in SOC, SON

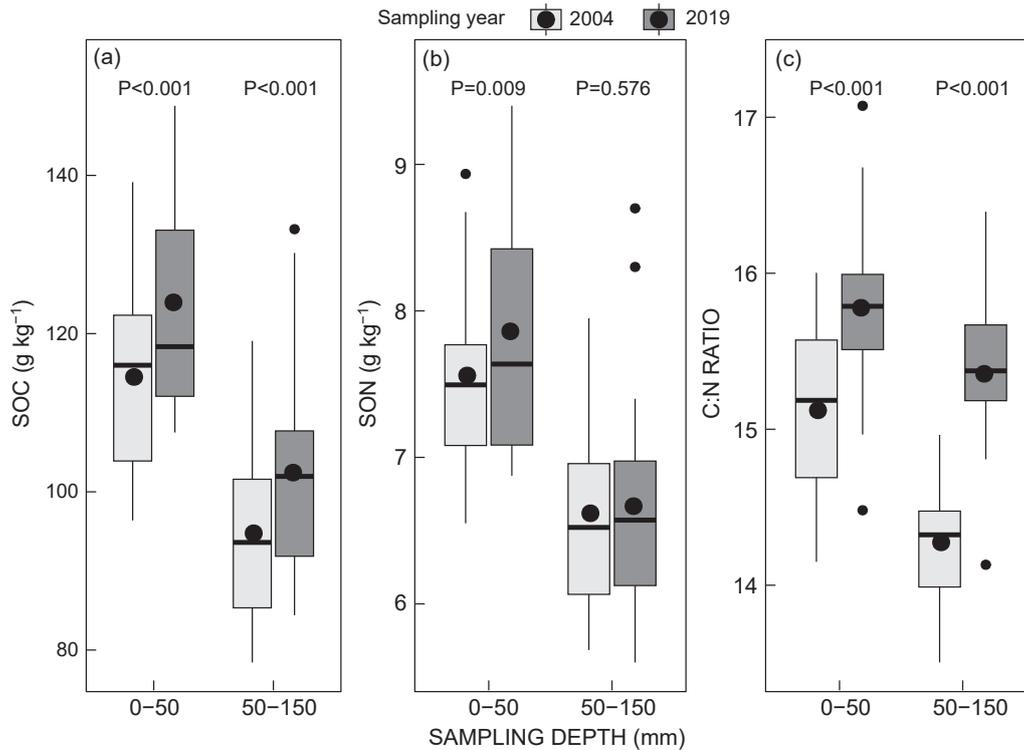


Figure 1: Change in average a) SOC, b) SON and c) C:N ratio, at two sampling depths, between 2004 and 2019 ($n = 36$ per sampling depth). Lower and upper box boundaries represent 25th and 75th percentiles, respectively; the line inside box the median; the dot inside the box the mean; lower and upper whiskers the 10th and 90th percentiles, respectively. Points above the whiskers indicate datapoints falling outside the 90th percentile. A one-way ANOVA (Supplementary Material Table S1) indicates a significant difference in SOC and C:N ratio at both depth increments between 2004 and 2019. A small, but significant change in average SON in the 0–50 mm depth increment was observed

Table 1: Mean values (\pm SE) of SOC, SON and C:N ratio measured in 2004 and in 2019 at two depth increments in the Brotherton burning trial ($n = 36$ per sampling depth). Different superscript letters denote significant differences in SOC and SON content and C:N ratio between sampling years after *post hoc* testing. Upper case superscripts distinguish sampling depths; lower case superscripts refer to differences between the two years. SOC (0–50 mm: $p < 0.001$, $LSD_{0.05} = 2.989$; 50–150 mm: $p < 0.001$, $LSD_{0.05} = 2.944$) and C:N ratio (0–50 mm: $p < 0.001$, $LSD_{0.05} = 0.2239$; 50–150 mm: $p < 0.001$, $LSD_{0.05} = 0.2177$) increased significantly at both sampling depths between sampling years. A small, but significant increase in SON was observed in the top 50 mm soil sample only ($p = 0.009$, $LSD_{0.05} = 0.2163$)

	0–50 mm		50–150 mm	
	2004	2019	2004	2019
SOC ($g\ kg^{-1}$)	114.52 ^{Aa} \pm 3.069	123.95 ^{Ab} \pm 3.332	94.76 ^{Ba} \pm 2.796	102.43 ^{Bb} \pm 3.221
SON ($g\ kg^{-1}$)	7.56 ^{Aa} \pm 0.159	7.86 ^{Ab} \pm 0.210	6.62 ^{NS} \pm 0.159	6.67 ^{NS} \pm 0.198
C:N	15.12 ^{Aa} \pm 0.130	15.78 ^{Ab} \pm 0.142	14.27 ^{Ba} \pm 0.096	15.36 ^{Bb} \pm 0.114

and C:N ratio between 2004 and 2019 was not affected by fire frequency or season of burn (Figure 1, Table 1). We expected frequent fire to significantly decrease soil organic C and N, however SOC and SON were significantly higher in the annual spring burn treatment than the other fire treatments. We also found that soils in annual spring burn treatments had higher SOC and SON values than those in the annual autumn burn, suggesting an important effect of fire season. However, this seasonal effect was not found for the biennial burns. There was also no significant difference in SOC and SON between the annual and biennial autumn burns. Because C stocks were calculated from soil C

content, we expected the effect of fire treatment on C stocks to echo the response observed with SOC. Indeed, C stocks in spring-burnt plots increased with increasing fire frequency (from biennial to annual burns). We found no change in C stocks with fire frequency in the autumn burn treatments. The lowest C stocks were observed in the infrequently burnt plots.

Decadal changes in soil carbon and nitrogen

Despite many studies examining the effects of long-term restorative land management on grassland SOC (e.g. Ghimire et al. 2019), there is limited information on

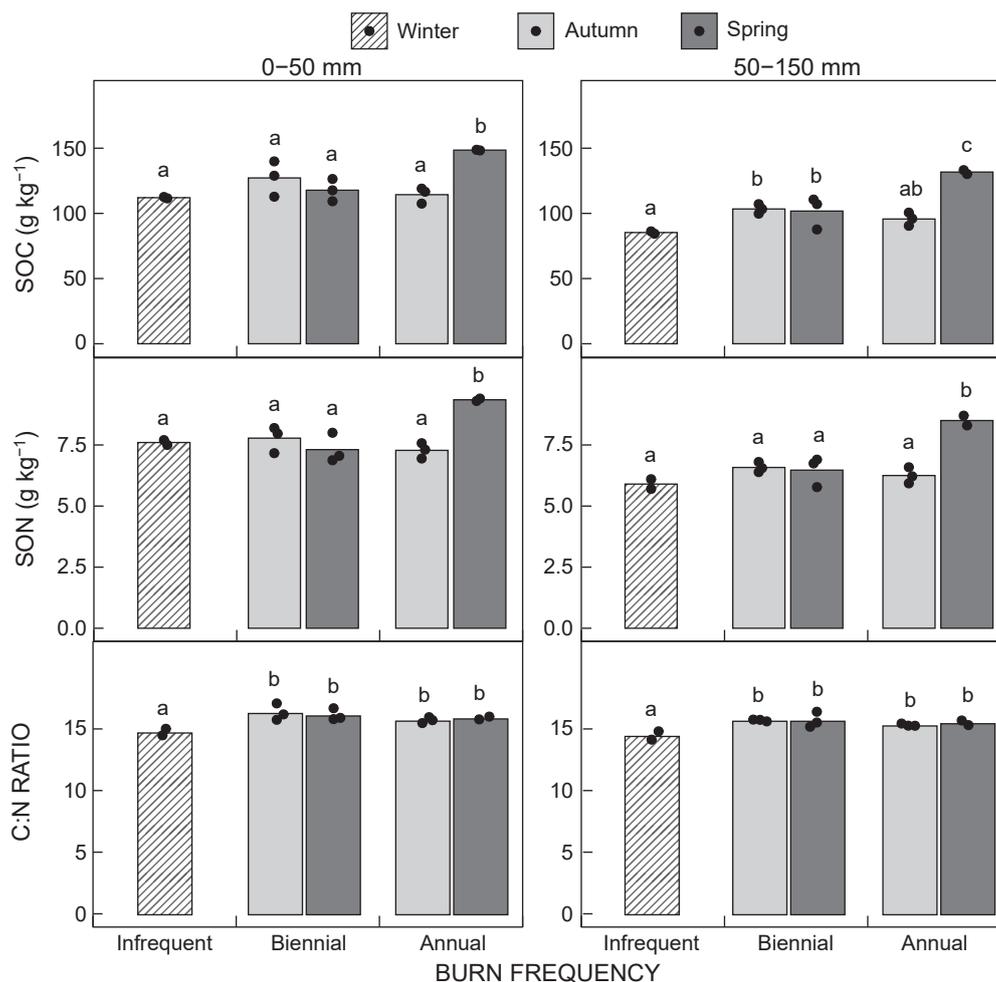


Figure 2: Soil organic C, SON and C:N ratio in the top 0–50 mm and 50–150 mm of soil, grouped according to five fire treatments: infrequent (infrequently-burned fire-exclusion plots - winter burn), biennial (autumn and spring burns) and annual (autumn and spring burns) for the 2019 data only. ANOVA models indicate a significant treatment effect at both depths on a) SOC (0–50 mm: $p = 0.005$, $LSD_{0.05} = 16.2$; 50–150 mm: $p < 0.001$, $LSD_{0.05} = 13.14$); b) SON (0–50 mm: $p = 0.002$, $LSD_{0.05} = 0.825$; 50–150 mm: $p < 0.001$, $LSD_{0.05} = 0.732$) and c) C:N ratio (0–50 mm: $p = 0.021$, $LSD_{0.05} = 0.859$; 50–150 mm: $p = 0.019$, $LSD_{0.05} = 0.704$). Dots indicate the individual treatment plots. Different letters denote significant differences in SOC and SON content and C:N ratio determined by *post hoc* testing (Fisher's protected LSD). See Supplementary Material Table S3 for full ANOVA

long-term SOC fluxes in undisturbed soils. Studies suggest that SOC in restored soils may continue to accumulate over multidecadal timescales (Schlesinger and Amundson 2019; Yang et al. 2019), but it is generally accepted that C accumulation only occurs over a finite period, up to a point where a new equilibrium is reached and soil C efflux is balanced by total C input (Sommer and Bossio 2014; Ghimire et al. 2019; Guillaume et al. 2021). Hence undisturbed soils are believed to have a low potential for added C storage and can only change slowly (Schlesinger 1990; Smith 2014). On the contrary, we found a significant increase in SOC content in both 0–50 mm and 50–150 mm depth increments in grassland soils that have never been tilled and have been protected from concentrated grazing since the early 1940s (Morris et al. 2020). The increase in C stocks between 2004 and 2019 was unexpected, given the highly weathered nature of the soil, the already high SOC content of the soil and the assumption that, under

steady-state conditions, the rate of soil C accumulation slows over time. This suggests that a shift in environmental conditions has allowed for continued localised increase in SOC with a rate of $0.30 \text{ Mg ha}^{-1} \text{ y}^{-1}$.

Because the increase in SOC between 2004 and 2019 occurred across all fire treatments, it is likely independent of the fire regime, which was kept constant since 1980. The increase is also unlikely to be a methodological effect, because the same sampling and analytical methods were employed in both 2004 and 2019. It is more likely that the cause for the increase is one or more of: CO_2 fertilisation; increased N deposition; higher temperature; and the change in management in the 1940s when livestock grazing was stopped.

The known increase in atmospheric CO_2 since the start of industrialisation, over the duration of the trial alone atmospheric C has increased by 8.8% (Dlugokencky and Tans 2021), is likely to have resulted in CO_2 fertilisation

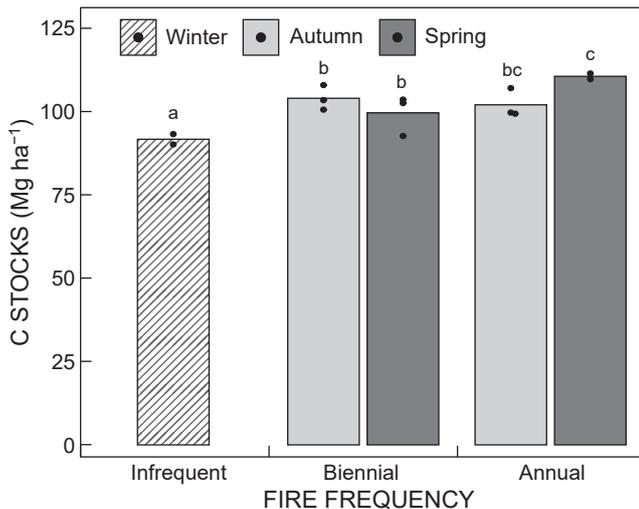


Figure 3: Carbon stocks in the top 150 mm of soil (Mg C ha^{-1}) measured in 2019 and grouped according to fire frequency and season of burn ($p = 0.007$, $\text{LSD}_{0.05} = 5.933$). Bars indicate the treatment averages; dots indicate the individual treatment plots. The winter fire events were unplanned arson fires in the fire-exclusion treatment, which occurred in three of the 39 years since trial inception. Carbon stocks were significantly lower in infrequently burnt plots. Different letters denote significant differences in C stocks determined by *post hoc* testing (Fisher's protected LSD). See Supplementary Material Table S4 for full ANOVA

(Ainsworth et al. 2020). In addition, SOC accumulation can be promoted by N deposition in N-limited environments by the resulting increase in net primary productivity (LeBauer and Treseder 2008). It is likely that N inputs have increased across the Drakensberg: Mompoti (2019) showed that total annual (2015 to 2016) N deposition at Cathedral Peak was $5.61 \text{ kg ha}^{-1} \text{ y}^{-1}$, more than half of which was anthropogenic. However, as predicted by the Century model (Schimel et al. 1997), N availability and plant N demand are strongly correlated to temperature. Global surface temperatures have increased by approximately $0.8 \text{ }^\circ\text{C}$ in the past century (IPCC 2013). Higher temperatures promote both plant growth and microbial respiration-mineralisation, which may either result in a net increase or decrease on SOC. Because this is a functionally N-limited grassland (Manson et al. 2007), accelerated N mineralisation (Carbutt et al. 2013) may already be supplementing deposition of N from the atmosphere. Average annual maximum and minimum temperatures in the Maloti-Drakensburg increased by 0.03 and $0.01 \text{ }^\circ\text{C}$, respectively, between 1960 and 2016 (Mohamed and Mukwada 2019). Although there is strong evidence for warming, particularly since 2000, current anthropogenic increases in available N may not be sufficient to drive a significant increase in net primary productivity (NPP) without a corresponding increase in annual temperature and hence plant N demand. This is supported by the significant increase in C:N ratio, which suggests that the increase in atmospheric C and resulting CO_2 fertilisation predominates over N deposition as a driver of C accumulation (Wang et al. 2021).

Moreover, it is possible that livestock grazing on the Brotherton plateau before the 1940s decreased SOC concentrations (Alvarez et al. 2021) and the measured increase in SOC has been promoted by a continued response to the withdrawal of the intensive grazing.

Although the C:N ratio has changed over time, the trend in SON often mirrors that of SOC. This is because the major processes driving trends in both SON and SOC are those that drive grassland productivity (mainly inputs from root death) and those that drive organic matter mineralisation (microbial degradation of SOM).

Fire regime effects on soil organic C and N

Studies in grasslands and savannas report that frequent fire often decreases SOC concentrations (O'Connor et al. 2004; Manson et al. 2007; Pellegrini et al. 2018). Although fire treatment effects in this trial were small, SOC in the annual spring burn was higher than in other treatments, including the annual autumn burn (Figure 2). Similar seasonal trends in response to timing of burning have been reported (Fynn et al. 2003; Hatten et al. 2008; Zhao et al. 2012; Pastore et al. 2021). In the moist tall grassveld of KwaZulu-Natal, Fynn et al. (2003) measured a reduction in SOC in the surface 2 cm with annual, biennial and triennial autumn burning, but annual and biennial spring burning did not result in a decrease in SOC. Pastore et al. (2021) report a rapid accumulation of soil C in the first 15 years after grassland establishment on previously cultivated lands in Minnesota. Over the following four years they found large decreases in soil C, to almost pretreatment levels. Although they were unable to determine the cause of the reversal in soil C accumulation, it coincided with a change in the timing of prescribed burns from early spring to late autumn, suggesting an important effect of timing of burning on SOC accumulation.

Change in SOC represents the net effect of short-term biogeochemical processes in an ecosystem, affecting C inputs and losses (Schmidt et al. 2011). The seasonal difference in SOC response to burning may be a consequence of several factors that interact. In the presence of sufficient rainfall, annual burns promote greater aboveground net primary productivity compared with infrequent fire (Ojima et al. 1994; Briggs and Knapp 1995). Several studies report that less severe fires have insignificant (Jones et al. 2014; Reinhart et al. 2016) or short-lived (Bond and Keane 2017) effects on biomass and ecosystem nutrients. Autumn (late-May) burns in the Cathedral Peak catchments are more severe, because of late-season, drier conditions. Removal of aboveground material is complete (Everson et al. 1985), with between 90% and 100% of the grass material being available as fuel, because of the low moisture content. The topsoil remains exposed throughout winter, which may result in soil C losses by wind or water erosion (Asmal 1995; Fynn et al. 2003; Vermeire et al. 2005; Knicker 2007). Wind is a dominant feature in the Drakensberg, and katabatic winds during late winter and early spring can exceed 75 km h^{-1} (Brown and Piper 1988). These August/September winds come before the spring rains, moving surface organic material and accelerating drying of the topsoil, which has shown to be warmer and drier in burned than unburned sites (Ojima et al.

1994). Autumn burns are likely to increase soil temperatures in late winter and early spring (Vermeire et al. 2005), which would promote microbial decomposition of SOM at a time when covered soils are still too cool for significant microbial activity to occur. In contrast, spring burns occur after the first significant rainfall, when there is already spring greening and more moisture in the sward. An incomplete burn results (Schmidt et al. 2017) and there is less loss of C and N during a spring burn than occurs under autumn burning. Because it is in an active growth period, the sward recovers quickly, thus protecting the soil and remaining litter from erosion. In addition, spring burning affords an opportunity for litter accumulated during the previous growing season to begin to decompose or to be incorporated into the topsoil (Fynn et al. 2003).

Fire plays a dominant role in recycling organic matter in regions where decomposition of organic matter is restricted by either dry or cold climates, or saturated conditions (DeBano et al. 1998; Carbutt et al. 2013). A temporary increase in soil N after fire has been reported due to the mineralisation of N in organic matter and deposition of ash (Dijkstra et al. 2017). Thereafter, most studies agree that, in the long term, frequent fire results in a reduction in topsoil SON (Pellegrini et al. 2020). There is still, however, considerable disagreement about the effect of fire on soil N. In their analysis of decadal effects of fire on savanna grasslands, broadleaf forests and needleleaf forests, Pellegrini et al. (2018) found N depletion in 67% of sites. They also report N enrichment in needleleaf forest soils, which are burnt frequently in low-intensity, prescribed fires. They suggest the N increase could be ascribed to colonisation by N-fixing plant species or redistribution of mobilised N from the smouldering litter on the forest floor. However, the Maloti-Drakensberg grasslands are intrinsically N-rich (Carbutt and Edwards 2015): the low concentration of plant-available N is driven by the effect of cooler temperatures on N mineralisation (Carbutt et al. 2013). Nitrogen mineralisation is stimulated following fire (Knicker 2007; Dijkstra et al. 2017) and soils in annually burnt plots may benefit from pyromineralisation (Hartshorn et al. 2009). Chen et al. (2021) report that low levels of N addition results in increases in labile-fraction soil organic matter, which may promote root autotrophic activity in a N-limited system (Geng et al. 2017). Uptake of N from the soil by microbes results in N immobilisation (Fynn et al. 2003), which is unavailable for plant uptake and constitutes part of the SON measured during analysis. Accordingly, in the Brotherton burning trial, annual spring burns increase N-cycling in the topsoil, contributing to the plant-available N pool by pyromineralisation and promoting aboveground growth. In contrast, unburnt grasslands experience a decrease in both aboveground NPP and belowground plant biomass, whereas moribund material remains as a dense mat on the soil surface.

The increased C:N ratio in annually and biennially burnt plots compared with infrequently burnt plots is indicative of the greater N losses, because of the combustion of above-ground biomass (which would otherwise have contributed the return of N to the soil in plant litter). This effect is probably more evident in Aluandic Andosols (soils with high SOM and $\text{pH}_{\text{water}} 3.8\text{--}5.0$) because the long-term

storage of SOM in these soils has a high proportion of plant-derived compounds (aliphatic compounds and lignin-derived polymers) that are stabilised by Al^{3+} complexation (Matus et al. 2014), and C:N ratios mostly fall within the range 14–22 (Caner et al. 2000; Tonneijck et al. 2010; Dos Santos Junior and de Almeida 2021). In most soils ($\text{pH} > 5.0$), recalcitrant SOM is dominated by microbial remains, and only a small proportion of plant-derived compounds are stabilised for more than a decade; hence in most grasslands C:N ratios fall within the range 12.9 to 13.8, closer to that of the microbial biomass (6.2–6.9) (Xu et al. 2013).

C stocks in grasslands with acid soils

Fire affects C stocks indirectly through its effects on vegetation (Novara et al. 2013) and C inputs. Hence the effect of fire treatment on soil C stocks relates to the previous discussion on SOC inputs and losses. The increase in C stocks observed between 2004 and 2019 ($0.30 \text{ Mg ha}^{-1} \text{ y}^{-1}$ independent of fire treatment) was unexpected, because of the multidecadal timescale of the Brotherton burning trial: rates of SOC accumulation are generally negatively related to SOC content in a particular soil (Capriel 2013; Gubler et al. 2019; Keel et al. 2019), this being evident as a diminishing return for practices designed to increase SOC as that SOC increases with time. The amount of C that can be stabilised in each soil layer is often viewed as being limited by the potential sorption of organic compounds on the surfaces of clay and silt minerals (Six et al. 2002; Feng et al. 2013; Powlson et al. 2014). However, in Aluandic Andosols, the mechanism of C stabilisation is complexation of SOM by soil aluminium (Al^{3+}) rather than adsorption on clay and silt particles (Scheel et al. 2008; Takahashi and Dahlgren 2016; Rasmussen et al. 2018). In the Drakensberg Afromontane grassland soils, therefore, the key limitations to C sequestration are the rate of organic inputs and the availability of Al^{3+} from the dissolution of aluminous clay minerals at $\text{pH} < 5$. These conditions can exist even on highly weathered soils (as in Caner et al. 2000); in fact, weathering in these soils is driven by soil solution equilibria between CO_2 and kaolinite that generate sufficient acidity to dissolve clay minerals (Van Breemen and Wielemaker 1974). This can sustain the concentrations of Al^{3+} required for complexation of carboxylate groups in SOM (Cronan et al. 1986; Thomas et al. 1991), protecting it from microbial decomposition. Consequently, complexation of SOM by Al^{3+} is the probable reason for the low rates of microbial degradation that allow the persistence of SOM in these soils. This mechanism also calls into question the applicability of a C-saturation model, based on the sorption of organic compounds on mineral surfaces (Hassink 1997).

The increase in C stocks in this study is comparable with annual increases in grasslands reported in the synthesis of Conant et al. (2017). They found that average increases associated with different pasture management interventions ranged between 0.02 and 0.87. The largest increases in C stocks occurred under land use conversion from intensive agriculture to pasture; the conversion from native grasslands to pasture returned the smallest increases in annual C stocks.

The increases at the Brotherton burning trial are important if similar changes are occurring more widely in the Drakensberg, and call for more intensive monitoring of

soil-C trends in this ecosystem and other cool, high-rainfall grasslands worldwide. This study indicated that the topsoil is more susceptible to changes, because of management practices, than the subsoil and that C sequestration occurs principally in upper horizons (Franzluubbers 2005). However, the surface horizon is not the layer with the highest potential for SOC sequestration because the SOC at depth occurs in stable forms and it is highly recalcitrant to biodegradation processes (Lorenz and Lal 2005). It is important to confirm that whole-soil C sequestration is real, requiring a more complete picture of C stocks at depths of greater than 150 mm (baseline soil C measurements to a depth of a metre; CO₂ flux measurements), to ascertain whether the effects of fire on SOM are restricted to topsoil nutrient cycling, or if they translate to long-term C storage deeper in the soil profile.

Conclusion

Fire is an essential ecological driver of grassland and savanna ecosystems (He and Lamont 2018). This includes ancient Afromontane grasslands (Linder 2014), which contain a biodiverse suite of floral and faunal species that have evolved with fire, and are unique ecosystems that require fire to maintain their biodiversity and function. The critical role of fire in the continued existence of these ecosystems is easily overlooked in light of the negative effects of fire on global climate change. Globally, an estimated 1 833 Tg C was lost to the atmosphere in 2018, as a result of fire, 34% of which is attributed to fires in savannas and grasslands (Randerson et al. 2018). Global projects, such as the '4 per 1 000' initiative, drive pressure to limit the use of fire, supported by current literature showing that soil C and N decline in landscapes that are regularly burnt (e.g. Mills and Fey 2004; Pellegrini et al. 2018). The potentially devastating implications for fire-dependent grassy biomes demands focussed research attention that contributes to current understanding of the net effects of fire on the C and N balance in these ecosystems.

Contrary to our expectations, the ancient Afromontane grassland soils on the Brotherton plateau have continued to sequester C more than 40 years after the implementation of a prescribed fire regime to maintain valuable biodiversity and ecosystem processes (especially water production), with an average increase in soil C of 0.30 Mg C ha⁻¹ y⁻¹ between 2004 and 2019. Importantly, our data show that this increase is most pronounced in spring burns and absent in autumn burns. This significant effect of season of prescribed burn on soil C and N is an indication of a dynamic response to fire, which reinforces the requirement for ongoing evaluation of fire policies and management plans, particularly as growing seasons shift in response to climate change. Our study indicates a need for review of the effects of fire in other mesic, high-altitude grasslands globally. Study of the C fractions in these soils is also likely to improve our understanding of the impacts of fire regime on C dynamics and stocks.

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