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RESEARCH ARTICLE

The influence of trees, shrubs, and grasses on microclimate, soil carbon, nitrogen, and CO₂ efflux: Potential implications of shrub encroachment for Kalahari rangelands

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Abstract

Shrub encroachment is a well-documented phenomenon affecting many of the world's drylands. The alteration of vegetation structure and species composition can lead to changes in local microclimate and soil properties which in turn affect carbon cycling. The objectives of this paper were to quantify differences in air temperatures, soil carbon, nitrogen, and CO₂ efflux under trees (*Vachellia erioloba*), shrubs (*Grewia flava*), and annual and perennial grasses (*Schmidtia kalahariensis* and *Eragrostis lehmanniana*) collected over three seasons at a site in Kgalagadi District, Botswana, in order to determine the vegetation-soil feedback mechanism affecting the carbon cycle. Air temperatures were logged continuously, and soil CO₂ efflux was determined throughout the day and evening using closed respiration chambers and an infrared gas analyser. There were significant differences in soil carbon, total nitrogen, CO₂ efflux, light, and temperatures beneath the canopies of trees, shrubs, and grasses. Daytime air temperatures beneath shrubs and trees were cooler compared with grass sites, particularly in summer months. Night-time air temperatures under shrubs and trees were, however, warmer than at the grass sites. There was also significantly more soil carbon, nitrogen, and CO₂ efflux under shrubs and trees compared with grasses. Although the differences observed in soils and microclimate may reinforce the competitive dominance of shrubs and present challenges to strategies designed to manage encroachment, they should not be viewed as entirely negative. Our findings highlight some of the dichotomies and challenges to be addressed before interventions aiming to bring about more sustainable land management can be implemented.

KEYWORDS

dryland carbon cycles, microclimate, shrub encroachment, soil-vegetation feedbacks, vegetation change

1 | INTRODUCTION

The impact of livestock on soils and vegetation has been well documented in the Kalahari (e.g., Bhattachan, D'Odorico, Dintwe, Okin, & Collins, 2014) and elsewhere (e.g., Linstädter et al., 2014). With limited animal disturbance, Kalahari soils are typically covered in a cyanobacterial biocrust (Büdel et al., 2009) which provides numerous ecosystem benefits (Belnap & Lange, 2003). Biocrust microorganisms

have been identified as common rhizosphere and endophyte species in overlying grasses and shrubs (Elliott, Thomas, Hoon, & Sen, 2014; Steven, Gallegos-Graves, & Kuske, 2014) suggesting functional interdependence and an important beneficial microbial refugia role for biocrusts. They are, however, easily damaged by livestock trampling, and a reduction in the area covered by biocrusts is an immediate consequence of grazing disturbance (Dougill & Thomas, 2004). Diminished biocrust cover is synonymous with increased soil erodibility (Ravi et al., 2011) and a

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reduction in soil nitrogen (Belnap & Lange, 2003) and carbon (Thomas, Hoon, Dougill, & Mairs, 2012). However, the negative impacts of short periods of intense grazing are temporary, and damaged biocrusts can recover after a period of respite (Thomas, Elliott, Griffith, & Mairs, 2015).

Over longer time scales, unsustainable grazing can affect competition between plant species, initially reducing perennial grass cover in favour of less palatable annual grasses and ultimately replacing grasses with shrubs (Eldridge et al., 2011; Van Auken, 2000). Shrub encroachment has long been a feature of the Kalahari, with reports that >1 million ha of Kalahari rangeland was affected by *Senegalia mellifera* expansion as long ago as the 1950s (Ebersohn, Roberts, & Vorster, 1960, cited in Hagos & Smit, 2005). In southern Africa, numerous studies have attributed shrub encroachment to long-term grazing (e.g., Joubert, Smit, & Hoffman, 2013; O'Connor, Puttick, & Hoffman, 2014). The universal occurrence of shrub encroachment across the world's drylands is, however, suggestive of global drivers of change (Stevens, Lehmann, Murphy, & Durigan, 2017; Van Auken, 2000). The increase in atmospheric CO₂ favours C₃ photosynthetic shrubs because it leads to improved water and N use efficiencies over lower CO₂ adapted C₄ grasses (Leakey et al., 2009). Warming could also enhance the survival and growth rates of cold intolerant woody shrubs (D'Odorico et al., 2013). In southwestern Ethiopia, pollen records suggest that the savannah has been affected by multiple phases of shrub encroachment over the last two millennia, the primary drivers of which were changes in rainfall and fire occurrence (Gil-Romera, Lamb, Turton, Sevilla-Callejo, & Umer, 2010). Nevertheless, although global and regional factors may be a driver of vegetation change in drylands, they cannot alone explain local differences (Bond & Midgley, 2012; D'Odorico, Okin, & Bestelmeyer, 2012). Ultimately, the vulnerability of an area to shrub encroachment will depend on land use and the functional traits of plants that govern their responsiveness to all drivers, human, and climatic (Bond, 2008; Stevens et al., 2017; Van Auken, 2000).

The decline in grazing value associated with shrub encroachment is the primary reason why it is considered both a cause and symptom of land degradation in drylands. Changing vegetation composition will, however, have a range of impacts, including the development of islands of fertility resulting from the unequal distribution of resources (Schlesinger et al., 1990). Localised nutrient enrichment occurs as plants (primarily shrubs and trees) obstruct sediment and water movement (Tongway & Ludwig, 1994) and through dung enrichment from animals attracted by the shade (Dean, Milton, & Jeltsch, 1999). Shading also reduces direct losses of C from surface litter via photo-degradation (Austin & Vivanco, 2006), altering soil microbial, temperature, and moisture conditions, all of which will affect organic matter mineralisation rates and soil C stores. This partly explains why Eldridge and Soliveres (2014) found a positive correlation between shrub density and a range of ecosystem characteristics such as biodiversity, C sequestration, soil fertility, and rainfall capture. The positive impact of shrubs on a range of ecosystem characteristics is, however, density dependent. Where canopy cover exceeds 40–60%, they found that impacts across a range of parameters became negative (Eldridge & Soliveres, 2014) as the ability of individual shrubs to capture runoff and sediment declines (Breshears, 2006).

Despite widespread vegetation changes, the species specific impact of trees, shrubs, and grasses on microclimate and C cycling is poorly documented in the sandy soils of the Kalahari. Quantifying

these changes for different plant species and understanding their implications are vital if we are to improve our understanding of terrestrial C stores and cycles and a prerequisite to inform sustainable land management in drylands. This paper presents soil and climatic data collected during three contrasting seasons in the Kgalagadi District, Botswana, relevant to the C cycle and soil-vegetation feedback processes in shrub encroached rangelands. The objectives were to determine how tree, shrub, and grass cover affect (a) microclimate (light and air temperature) and (b) soil C, N, CO₂ efflux, and the δ¹³C of respired gases. The results are discussed in the context of terrestrial C cycles, land degradation, and management options that could be employed in order to facilitate more sustainable land management in the Kalahari rangelands.

2 | MATERIALS AND METHODS

2.1 | Study site and data collection

Field work was undertaken in 2011–2012, approximately 15 km north of Tsabong (25°56'51'S, 22°25'40"E) in the Kgalagadi District of Botswana (Figure 1). The site is 980 m above sea level and situated on level ground on the periphery of the Kalahari dunefield. Soils are Arenosols (Food and Agriculture Organisation, 2014) and are acidic (pH 5.8 ± 0.2), fine-grained sands, with little horizon development and low concentrations of soil N and C (Wang, Okin, Caylor, & Macko, 2009). Mean annual precipitation is 334 mm. At the time of sampling, a 3–4-mm deep biocrust, composed of bacteria, cyanobacteria, and fungi (Elliott et al., 2014), covered approximately 30% of the soil surface.

Data were collected within a fenced area enclosing several hectares typical of the rangelands in the region, although for the duration of the study, livestock was excluded to allow installation of monitoring equipment. Three replicate microsites characterised by trees (*Vachellia erioloba* E. Mayer), shrubs (*Grewia flava* DC), and

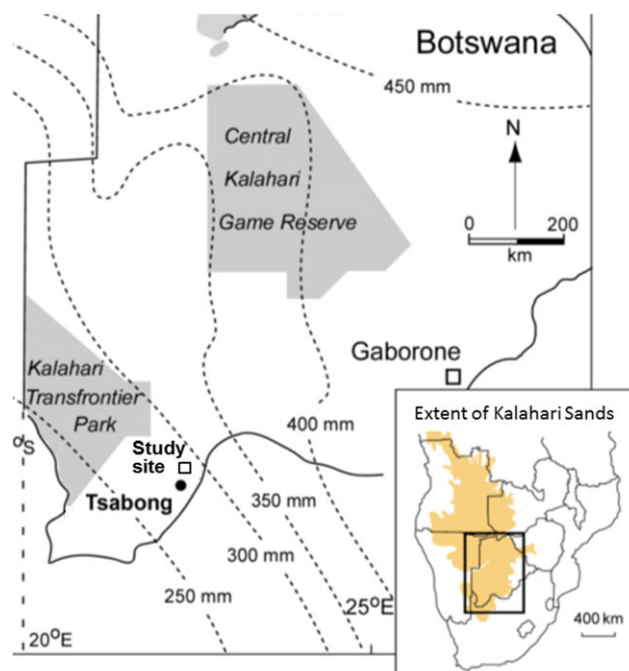


FIGURE 1 Location of study site [Colour figure can be viewed at wileyonlinelibrary.com]

perennial and C₄ annual grasses (*Eragrostis lehmanniana* [Nees] and *Schmidtia kalahariensis* [Stent]) were sampled over 4 days in November 2011, 6 days in February 2012, and 6 days in July 2012 ensuring a range of weather and soil conditions (Figure 2). To avoid pseudoreplication, the microsites were distributed across the entire enclosure a minimum of 20 m apart.

2.2 | Temperature, precipitation, and soil moisture

Air temperatures were logged continuously at 1-min intervals approximately 10 cm from the ground surface by USB502 loggers (Adept Science, UK) at each of the microsites. The sensors were shaded from direct sunlight and protected from rain ingress. For the purpose of the analyses, data were categorised as either daytime or night-time with 7 p.m.–5 a.m. in March and November and 6 p.m.–6 a.m. in June classified as night-time. For the duration of the experiment, soil volumetric water content and temperature were determined every 2 hr using a Decagon EM4 logger and 5TM moisture/temperature sensors installed in the preceding year to permit soil recovery in the centre of the fenced area. Sensors were inserted laterally into a backfilled soil pit at 0.1, 0.3, and 1.0 m.

2.3 | Soil CO₂ efflux and $\delta^{13}\text{C}$

Soil CO₂ efflux was determined using closed respiration chambers and an infrared gas analyser (PP Systems, Amesbury, USA) which facilitated multiple replication and near simultaneous determination of efflux. Details of the chambers, field methods, and quality control procedures are supplied in the Supporting Information. CO₂ efflux measurements were undertaken in the early morning, at noon, in the mid-afternoon, and evening on each day to encompass a range of temperature, humidity, and light conditions representative of diurnal cycles. For the shrub and tree microsites, measurements were taken on both east and west sides of the canopies and the mean used as a single value for the analyses. In total, there were 144 CO₂ flux measurements from soil under each grass type and 288 measurements from soils beneath both the shrub and tree canopies. The short-duration but high intensity measurement protocol repeated over contrasting seasons allows for more reliable quantification of efflux than periodic daily or weekly measurement for identifying differences between soils under different vegetation types and under different weather conditions. This protocol was adopted on the basis of experience in soil efflux measurement in this environment (e.g., Thomas, 2012).

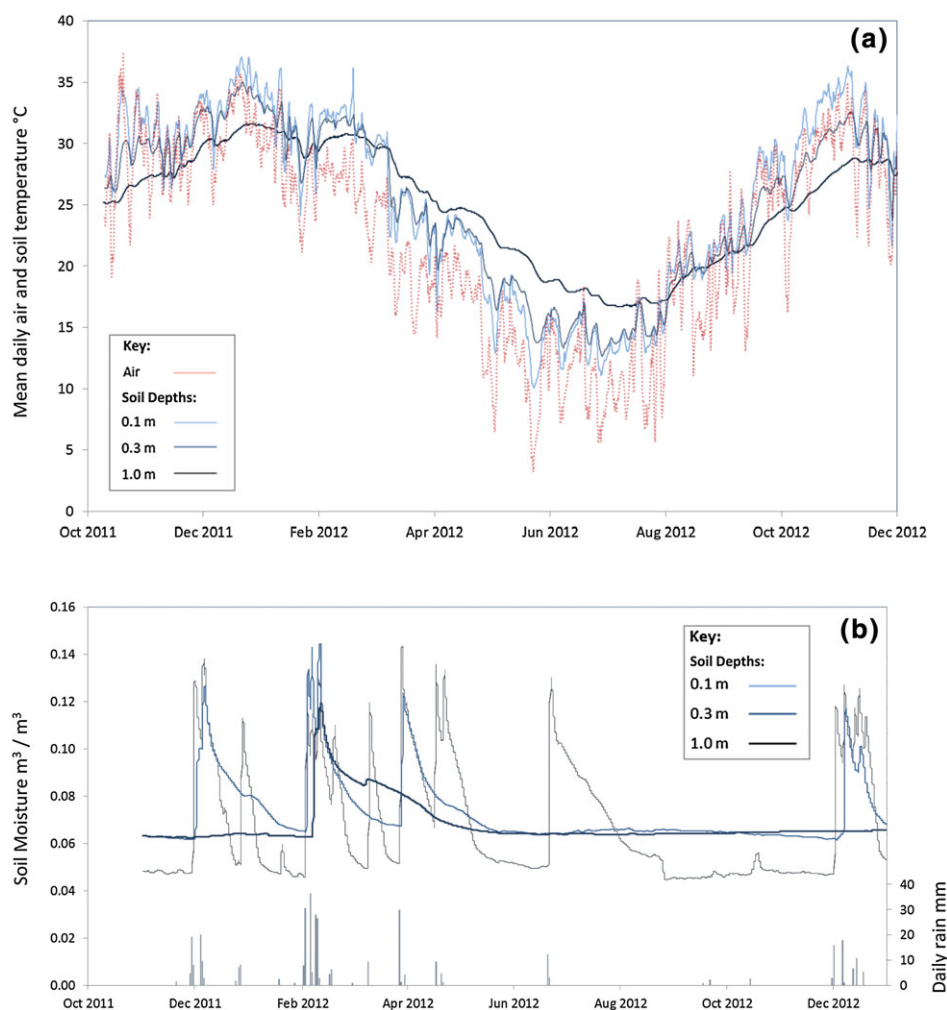


FIGURE 2 (a) Daily air and soil temperatures at 0.1-, 0.3-, and 1.0-m depths (daily mean of 48 bihourly measurements) from a grass covered area. (b) Daily precipitation and mean daily soil moisture at 1.0-, 0.3-, and 0.1-m depths (mean of 48 bihourly measurements). Sampling periods marked with arrows [Colour figure can be viewed at wileyonlinelibrary.com]

Biological respiratory systems discriminate to a greater or lesser extent between the two stable C isotopes, ^{12}C and ^{13}C . This fractionation can be used to identify biological sources and pathways in soils and their interaction with the atmosphere (Amundson, Stern, Raisden, & Wang, 1998). On March 8, 2012, the 6 p.m. cycle was used to collect gas samples for determination of their ^{12}C and ^{13}C isotopic compositions. Three gas samples were collected from the chambers and injected into pre-evacuated 12 mL borosilicate Exetainer® vials. To prevent contamination, the vials were over-pressurized, and lids were dipped in hot wax before transportation to a stable isotope facility (CEH, Lancaster, UK). Samples of leaf litter from beneath *G. flava* and *E. lehmanniana* were collected, and their ^{12}C and ^{13}C isotopic compositions determined. Stable $^{13}\text{C}/^{14}\text{C}$ isotopic ratios for each sample, $R_{\text{sample}} = \delta^{13}\text{C}$ are reported in parts per thousand (per mil, ‰) variation from the ratio in the Pee Dee Belemnite (PDB) international standard (Equation 1).

$$\delta^{13}\text{C}_{\text{PDB}} = \left(\frac{R_{\text{sample}} - R_{\text{PDB}}}{R_{\text{PDB}}} \right) \times 10^3. \quad (1)$$

2.4 | Soil total C, N, and bulk density

Soil samples were collected from five depths (0–1, which included biocrust where present, 1–2, 2–5, 5–10, and 10–20 cm). Three replicate pits were sampled from soils under each of the microsites (tree, shrub, and annual and perennial grass) during each field season. Soils were sieved to remove particles >2 mm, air-dried, bagged, and stored prior to analysis. Total C and N were determined using a Leco TruSpec CN element analyser (Matejovic, 1997). Soil bulk density was determined on samples collected from 5-cm depth using a metal cylinder with internal dimensions of 10 cm × 4.8 cm. Sample mass was determined after sieving and oven drying at 105 °C.

2.5 | Photosynthetically active radiation

Incoming solar radiation in the photosynthetically active wavelengths (400–700 nm) was measured continuously and simultaneously 2 m above the ground surface in an open area and beneath a *G. flava* shrub canopy using photosynthetically active radiation quantum sensors (Skye Instruments Ltd., UK) connected to data loggers.

2.6 | Statistical analyses

All statistical analyses were performed using SPSS (IBM v. 24). To test the hypothesis that mean values of the dependent factors (soil C, soil N, soil CO_2 efflux, and daytime and night-time air temperatures) were significantly different at each vegetation microsite, one-way analysis of variance (ANOVA) was used. The analyses were run independently for each of the three sampling periods for all variables except soil C and N which were amalgamated into one dataset (as in comparison with the other variables sample numbers were low and relatively unresponsive to changes in season). Data were first checked for normality using the Shapiro–Wilk test. Soil C and N data were grouped for all depths and were found to be normally distributed and required no transformation. However, CO_2 efflux and daytime and night-time air temperatures were not normally distributed and required a log₁₀ transformation. The Levene's *F* statistic was then used to test equality

of variance, and although ANOVA can tolerate inhomogeneous variance, where these conditions were not met, the more robust Welch and Brown Forsythe tests of significance were used. Tukey's honest significant difference post hoc test was undertaken to further evaluate significant ($p < .05$) differences along with Cohen's *d* to evaluate the size of the effect calculated using (Equation 2).

$$d = \frac{\bar{X}_1 - \bar{X}_2}{(SD_1 - SD_2)/2}. \quad (2)$$

Cohen's *d* values of <0.2 were attributed to small effect sizes; up to 0.5 medium effect sizes and >0.8 were considered large effect sizes. To test the effects of temperature and moisture on CO_2 efflux, linear and multiple linear regression tests were performed. The temperature sensitivity of CO_2 efflux at each site within each season was described with a Q_{10} exponential model. We used a fitting algorithm to maximise the correlation coefficient r^2 (Q_{10}) with the initial conditions $R_0 = R(0)$ and $T_0 = 0$, where R_0 is efflux at reference temperature T_0 (Thomas & Hoon, 2010).

3 | RESULTS

3.1 | Soil moisture and precipitation

Soils contained least moisture (<0.06 $\text{m}^3 \text{m}^{-3}$) at the end of the dry season in November 2011 (Figure 2). Thereafter, a series of large (>30 mm) precipitation events during March 2012 led to moisture recharge in the deep subsoil (>1 m). Mean daily air temperatures in June were typical for winter, ranging from 6 to 12 °C, but unseasonal rainfall led to increases in soil moisture at 0.1 m. By June 2012, moisture below 0.3 m was depleted by a combination of drainage and transpiration and was decoupled once more from surface diurnal moisture variations. The interaction between soil temperature and moisture at different depths can be seen in Figure 2, where, as is to be expected, annual and diurnal variations in soil temperature decrease in amplitude with depth.

3.2 | Air temperature and solar radiation

There were significant differences in mean daytime and night-time air temperatures between vegetation microsites in all months (Figure 3a, b). The one-way ANOVA yielded a statistically significant effect for daytime temperatures in November ($F = 20.3$, $p \leq .01$, $df = 3$), March ($F = 234.7$, $p \leq .01$, $df = 3$), and June ($F = 88.9$, $p \leq .01$, $df = 3$). There was a similarly statistically significant difference in night-time temperatures between vegetation microsites in November ($F = 365.1$, $p \leq .01$, $df = 3$), March ($F = 4520$, $p \leq .01$, $df = 3$), and June ($F = 24.9$, $p \leq .01$, $df = 3$). The results of the post hoc analyses (Table 1a,b) show that in most cases (30 out of 36 comparisons), the daytime and night-time temperatures at all vegetation microsites were significantly different to each other in all months ($p \leq .01$) although the effect size was generally small to medium. In general, summer daytime temperatures under shrubs and trees were cooler than at the grass sites (Figure 3a) and warmer during the winter and summer nights, although this latter effect was much smaller (Figure 3b).

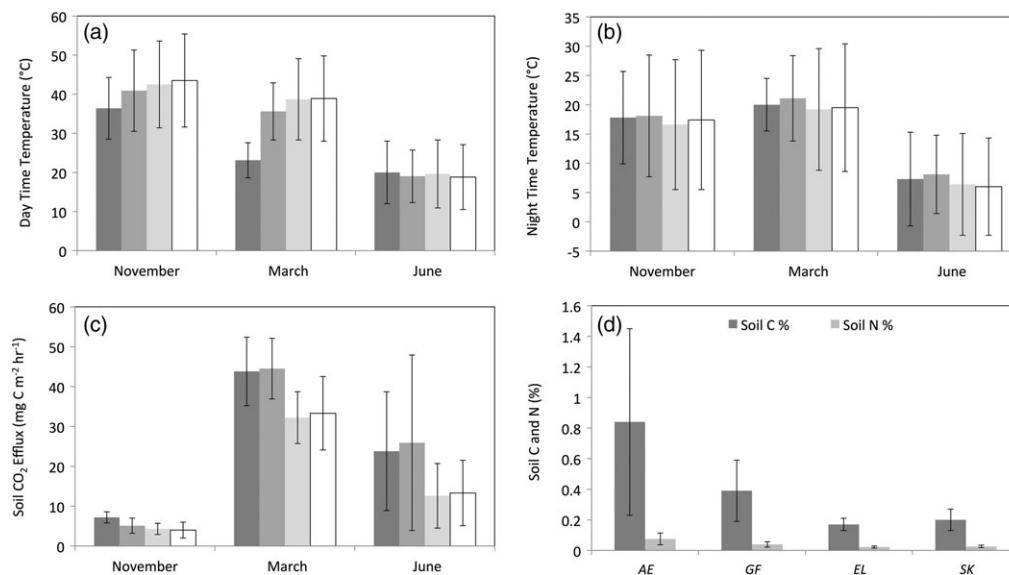


FIGURE 3 (a) Daytime temperatures (°C); (b) night-time temperatures (°C); and (c) soil CO₂ efflux (mg C m⁻² hr⁻¹) at each vegetation microsite in each sampling month. *Vachellia erioloba* is dark grey, *Grewia flava* light grey, *Eragrostis lehmanniana* lighter grey, and *Schmidtia kalahariensis* is unshaded. (d) Mean soil total C and N (%) over all three sampling months at each vegetation microsite. Means with standard deviations

Lower amounts of solar radiation reached the soil surface under *G. flava* canopies compared with soils at the grass site (Figure 4). This was particularly noticeable in June, when despite the lack of leaf cover, the woody branches and lower sun angle meant that less light penetrated through shrub canopies to the soil surface.

3.3 | Soil total C and total N

There were significant differences in mean soil C and N between vegetation microsites (Figure 3d). The one-way ANOVA yielded a statistically significant effect for total C ($F = 13.8, p \leq .01, df = 3$) and N ($F = 17.7, p \leq .01, df = 3$). Post hoc analyses show the significant differences to be associated with soil beneath *V. erioloba* trees which was significantly enriched in both soil C and N compared with soil beneath all other vegetation microsites (Table 1c). The effect size of these differences was large in all cases. Differences in soil C and N concentrations beneath *G. flava* and beneath grasses were not significant (Table 1c, Figure 3d).

Total C and N concentrations declined with depth at all sites (Figure 5) but remained higher at depth beneath shrubs and trees compared with grasses. Incorporation of leaf litter into the surface soils reduced bulk densities from $1.51 \pm 0.05 \text{ g cm}^{-3}$ under shrubs to $1.28 \pm 0.05 \text{ g cm}^{-3}$ in soils under grass, but soils still contained significantly greater C stores than the surrounding grass covered areas. C:N ratios at the surface of soils under grasses were 8.4–8.6 declining with soil depth to 6.4–6.9. C:N ratios in surface soils under shrubs and trees were higher (10.6 and 12.1, respectively) declining to 9.5 and 6.2, respectively, at 10–20 cm.

3.4 | Soil CO₂ efflux

There were significant differences in mean soil CO₂ efflux between vegetation microsites in all months (Figure 3c). The one-way ANOVA yielded a statistically significant effect in November ($F = 24.7,$

$p \leq .01, df = 3$), March ($F = 47.7, p \leq .01, df = 3$), and June ($F = 11.81, p \leq .01, df = 3$). The post hoc analyses (Table 1d) show that CO₂ efflux from soils beneath *V. erioloba* trees was significantly greater than from soils beneath grasses in all months ($p \leq .01$). Furthermore, there was significantly greater soil CO₂ efflux beneath *G. flava* shrubs in March and June compared with soils beneath grasses ($p \leq .01$; Table 1d).

The temperature sensitivity of soil CO₂ efflux is strongly affected by soil moisture conditions (Figures 2 and 6). In November 2011, when soils were dry, CO₂ efflux from soil under all vegetation types was uniformly low and unresponsive to soil temperature, with Q_{10} ranging from 1.20 to 1.25. However, with elevated soil moisture in both cool winter and warm autumn conditions, soil CO₂ efflux increased with temperature at all sites, and the Q_{10} was between 1.35 and 1.40.

The $\delta^{13}\text{C}$ of efflux gases in March 2012 shows different signatures between soil CO₂ efflux originating from soil beneath C₄ grasses and C₃ shrubs and trees (Figure 7). There was, however, no significant difference in the isotopic signatures of gas respired from annual and perennial grass sites. The y axis intercepts of Keeling plots (Figure 7) are unique and identify the source gas (or proportions of contributory gases) of the soil CO₂ efflux at each location. Under *G. flava* shrubs, it was $-14\text{‰ } \delta^{13}\text{C}$, under both grasses, it was $-10.5\text{‰ } \delta^{13}\text{C}$, and under *V. erioloba* trees, it was $-12\text{‰ } \delta^{13}\text{C}$.

4 | DISCUSSION

This study has demonstrated how soil properties and microclimates differ significantly between vegetation microsites at a grazed rangeland site in the Kalahari. Soils beneath trees and shrubs were enriched in C and N and were hotspots of microbial activity compared with soils in grass covered areas. Furthermore, air temperatures were less extreme, with cooler summer daytime and warmer night-time temperatures beneath the canopies of trees and shrubs compared with grass

TABLE 1 Tukey's honest significant difference multiple comparisons of air temperatures at each vegetation microsite (a) daytime; (b) mean night-time temperatures; (c) soil C and N; (d) soil CO₂ efflux

		November		March		June	
(a) Daytime comparisons		<i>p</i>	<i>d</i>	<i>p</i>	<i>d</i>	<i>p</i>	<i>d</i>
VE	GF	.34	-0.05	<.01	-0.32	<.01	-0.21
VE	EL	<.01	0.16	<.01	0.21	<.01	0.09
VE	SK	.13	0.06	<.01	0.15	<.01	0.11
GF	EL	<.01	0.21	<.01	0.53	<.01	0.31
GF	SK	<.01	0.11	<.01	0.47	<.01	0.33
EL	SK	<.01	-0.10	.01	-0.06	.77	0.02
		November		March		June	
(b) Night-time comparisons		<i>p</i>	<i>d</i>	<i>p</i>	<i>d</i>	<i>p</i>	<i>d</i>
VE	GF	<.01	-0.50	<.01	-0.87	<.01	0.14
VE	EL	<.01	-0.65	<.01	-1.05	.127	0.04
VE	SK	<.01	-0.72	<.01	-1.04	<.01	0.15
GF	EL	<.01	-0.15	<.01	-0.35	<.01	-0.08
GF	SK	<.01	-0.23	<.01	-0.36	.484	0.03
EL	SK	<.01	-0.08	.60	-0.02	<.01	0.00
		Soil C		Soil N			
(c) Soil C and N comparisons		<i>p</i>	<i>d</i>	<i>p</i>	<i>d</i>		
VE	GF	<.01	1.11	<.01	1.26		
VE	EL	<.01	2.06	<.01	2.30		
VE	SK	<.01	1.88	<.01	2.09		
GF	EL	.27	1.83	.20	1.36		
GF	SK	.40	1.41	.41	1.00		
EL	SK	.99	-0.55	.97	-0.53		
		November		March		June	
(d) Soil CO ₂ efflux comparisons		<i>p</i>	<i>d</i>	<i>p</i>	<i>d</i>	<i>p</i>	<i>d</i>
AE	GF	<.01	1.27	.94	-0.09	.87	-0.12
AE	EL	<.01	2.11	<.01	1.54	<.01	0.97
AE	SK	<.01	2.15	<.01	1.41	<.01	0.91
GF	EL	.21	0.50	<.01	1.75	<.01	0.88
GF	SK	.03	0.66	<.01	1.62	<.01	0.83
EL	SK	.84	0.23	.85	-0.17	.99	-0.08

Note. Effect size is given by Cohen's *d* where values of <0.2 are attributed to small effect sizes; up to 0.5 medium effect sizes, and >0.8 large effect sizes. VE = *Vachellia erioloba*; GF = *Grewia flava*; EL = *Eragrostis lehmanniana*; SK = *Schmidtia kalahariensis*.

areas (see also D'Odorico et al., 2010). The data are useful in understanding how vegetation change, particularly shrub encroachment, will impact the C cycle and other ecosystem characteristics in the future. This is important for several reasons. First, changes in dryland net primary productivity, soil C storage, and fluxes will have global impacts (Ahlström et al., 2015; Le Quéré et al., 2013). Second, vegetation change will alter the fire regime, and an increase in shrubs at the expense of grasses will reduce fuel loads and likely reduce the frequency and severity of fires (Bond, 2008; Mouillot & Field, 2005). Third, different plants affect ecosystem properties in different ways, and these impacts will themselves be dependent on plant density, making for a complex and dynamic ecosystem response to vegetation change that is scale dependent. Finally, feedbacks between vegetation, soil, and microclimate are likely to affect the persistence of shrub

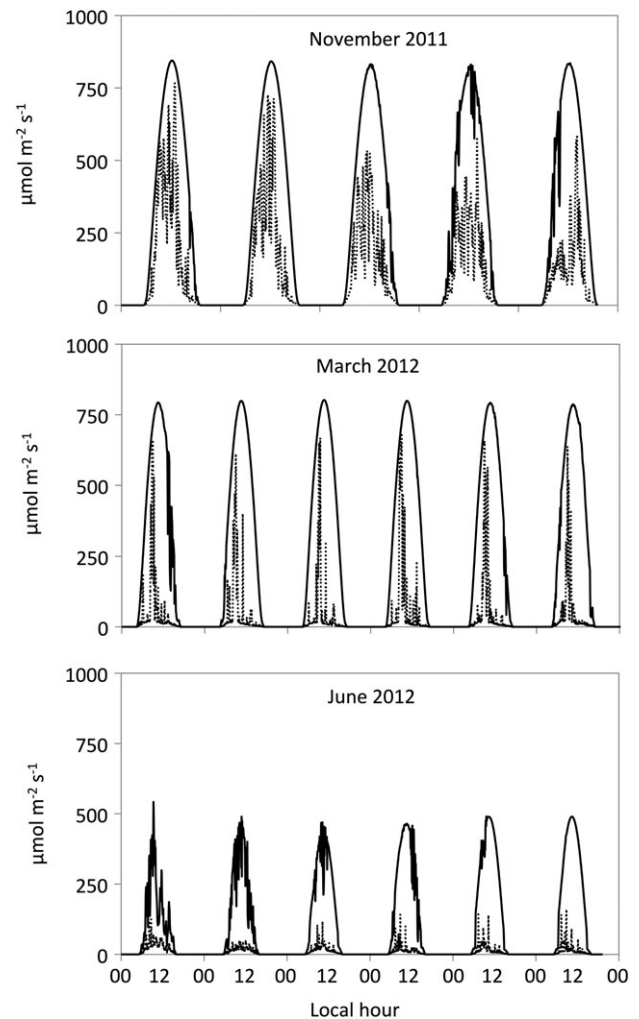


FIGURE 4 Diurnal variation in open-grass site (solid line) and below *Grewia flava* canopy (dashed line) incoming solar radiation (630 nm) in November 2011 and March, June 2012

encroached systems and ultimately the success of rangeland management policy seeking to increase grass cover (D'Odorico et al., 2012).

4.1 | Microclimates beneath tree, shrubs, and grasses

Seasonal weather was the dominant driver of near soil surface air temperature (Figure 2), and in comparison, the mitigating effects of vegetation on microclimate were subtle (Figure 3a,b). Nevertheless, the mosaic of trees, shrubs, and grasses typical of the field site and the wider Kalahari result in significant differences in near ground air temperatures. The air beneath tree (and to a lesser extent shrub) canopies was cooler than the soil boundary layer under grasses during the daytime, particularly in the hotter months. The closed canopy of *G. flava* shrubs also had a significant impact in reducing cooling and keeping the air beneath shrubs warmer than in grass areas during cold winter nights. If this leads to fewer winter ground frosts, it may contribute to shrub survival and provide a further competitive advantage to shrubs over grasses (D'Odorico et al., 2012; He, D'Odorico, De Wekker, Fuentes, & Litvak, 2010). A number of factors are leading to the observed differences. Shading from tree and shrub canopies (Figure 4) will reduce the energy reaching the surface, leading to

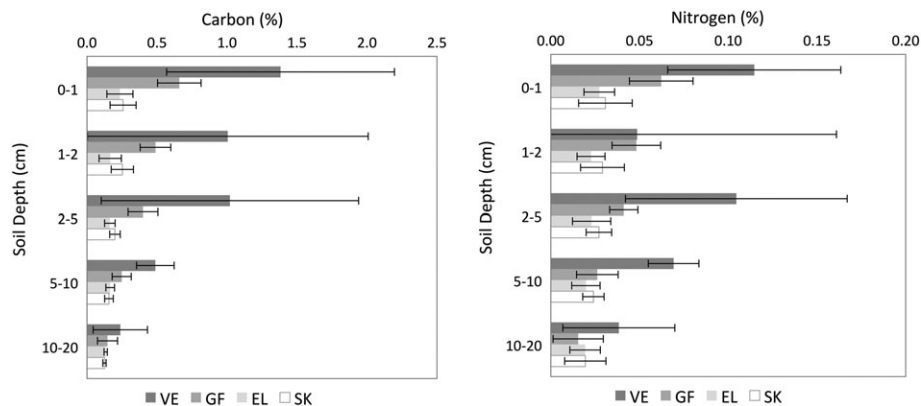


FIGURE 5 Total N and total C concentrations at five soil depths at each microsite. VE = *Vachellia erioloba*; GF = *Grewia flava*; EL = *Eragrostis lehmanniana*; and SK = *Schmidtia kalahariensis*. Means with standard deviation, $n = 15$ in each case (five replicates sampled in each season)

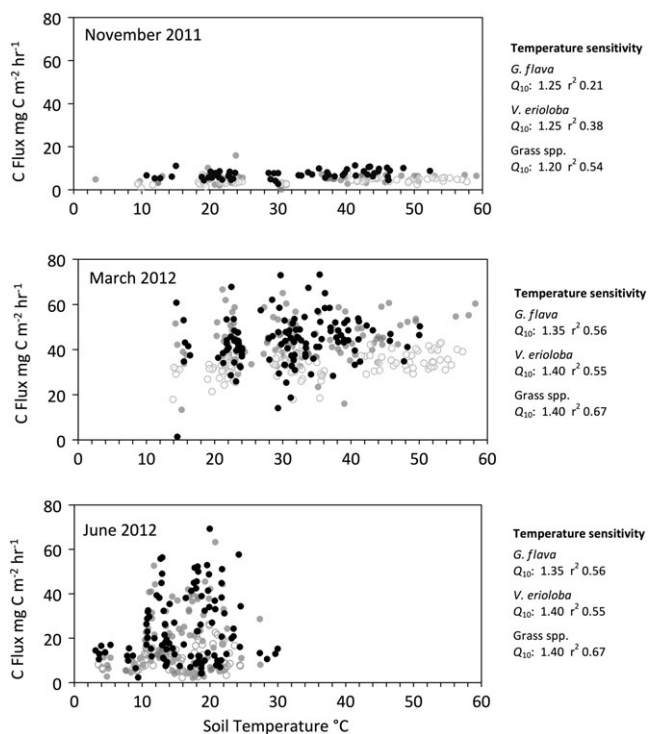


FIGURE 6 Soil CO_2 efflux and air temperature under *Vachellia erioloba* (black), *Grewia flava* (grey), and *Eragrostis lehmanniana* with *Schmidtia kalahariensis* plotted together as grasses (no shading) in November 2011, March 2012, and June 2012. $n = 57$ in November, 106 in June, and 119 in March

cooling and reducing soil moisture evaporation. Wind permeability, air movement, and convection will also be reduced in shrub canopies compared with more open grass covered sites. There is likely to be a vertical shifting of the wind velocity profile around taller vegetation. Shrubs and trees typically have a lower albedo than grasses, particularly in the dry season when grass foliage is dead (Hayden, 1998), and this is likely to have an impact on regional heat balances. From a mesoclimatic perspective, because woody plants reduce temperature extremes experienced at the soil surface, an increase in their cover will homogenise temperatures across the landscape compared with areas with both grasses and woody plants. Whether or not this is favourable to the ecosystem remains questionable.

The microclimatic (and edaphic) changes associated with higher shrub densities may tip the competitive balance in favour of shrubs, thus contributing to their persistence once established. Future climatic changes affecting air temperatures and the distribution and timing of rainfall could also affect the shrub–grass–tree balance in the Kalahari (Intergovernmental Panel on Climate Change, 2013) although impacts on nutrient cycling are less clear. Wang, D'Odorico, Manzoni, Porporato, and Macko (2009) modelled the effects of a 10% reduction in rainfall across the Kalahari transect and concluded that there would be minimal impacts on N and C pool sizes and fluxes. The Walter (1971) hypothesis of grass and tree root niche separation has been used to explain coexistence and competition in mixed tree, shrub, and grass savannahs, although this has been the source of some contention in southern Africa. For example, Scholes and Archer (1997) and Hipondoka, Aranibar, Chirara, Lihavha, and Macko (2003) considered it unlikely because of interspecies root interaction at all soil depths, likely mediated by arbuscular mycorrhizal networks. More recently, however, Ward, Wiegand, and Getzin (2013) provide a convincing case for support in dry savannahs such as the Kalahari. Warmer air temperatures will generate higher evaporation pressures in the soil profile, and percolating rain water will have to penetrate deeper before it is below evaporation depths. Currently, the most frequently occurring rainfall event at the study site is <5 mm, and this infiltrates to relatively shallow depths of approximately 0.1 m. Deep soil moisture recharge was only observed after successive, large (> 20 mm) rainfall events, and this is a much less frequent occurrence (Figure 2). A shift to more intense rainfall events would lead to greater soil moisture recharge accompanied by increased microbial activity, and potentially, the ability of plant roots currently only extending into dry subsoil zones to access new sources of moisture. Conversely, more rain days, with fewer large events, could favour grasses (and biocrusts), delivering water to only shallow depths.

4.2 | Vegetation types and C stores and fluxes

Shrubs and trees are hotspots of biological activity, C and N cycling (see, e.g., Tews et al., 2004). Stores and concentrations of soil C and N (Figures 3d and 5), microbial activity, and CO_2 efflux (Figure 3c) were significantly higher under shrubs and trees compared with grasses.

Site	Mean respired gas $\delta^{13}\text{C} \text{ ‰}$	CO_2 efflux ($\text{mg C m}^{-2} \text{ hr}^{-1}$)	Litter $\delta^{13}\text{C} \text{ ‰}$
<i>G. flava</i>	-10.73 ± 1.26	33.7 ± 6.5	-26.08 ± 0.37
<i>S. kalahariensis</i>	-9.02 ± 0.48	28.7 ± 2.3	-
<i>E. lehmanniana</i>	-9.05 ± 0.53	27.1 ± 8.0	-14.30 ± 0.33
<i>V. erioloba</i>	-9.75 ± 0.55	35.9 ± 5.4	-
Air	-7.92 ± 0.18	n/a	

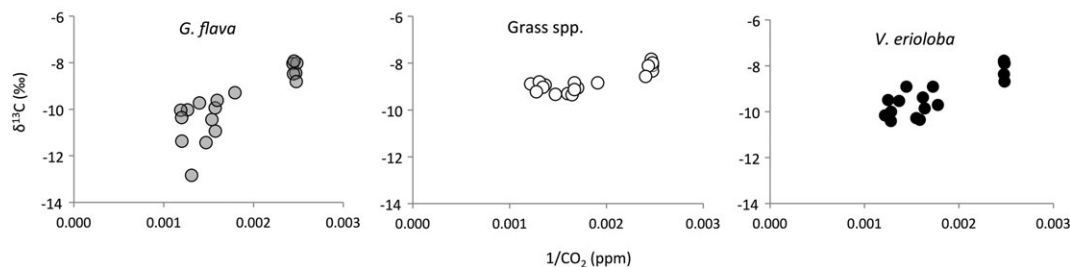


FIGURE 7 $\delta^{13}\text{C}$ of leaf litter and soil respired gases and air collected during the 6 p.m. cycle on March 2012. Keeling plots of $\delta^{13}\text{C}$ and the reciprocal of CO_2 concentrations of soil efflux gas for *Grewia flava*, *Vachellia erioloba*, and *Eragrostis lehmanniana* with *Schmidtia kalahariensis* (plotted together as grass species)

There are numerous pathways in which the soil is enriched under vegetation including hydrological (stemflow and throughfall), rhizospheric (root exudates and N-fixation by leguminous species such as *S. mellifera*), vegetation (primarily leaf litter), and animals (dung and urine). Shrub and tree productivity is underpinned by moisture made available by deep roots, and consequently, they generate more leaf litter, soil organic matter, and C and N than grasses (Su, Li, Liu, Xu, & Sun, 2014). Wang, D'Odorico, et al. (2009) found well-developed islands of fertility under plant canopies at Tshane, a site approximately 200 km to the north of our study site. Soils under plant canopies had consistently higher moisture and significantly larger C pools compared with open areas. Their work concluded that over regional scales, the availability of moisture controls nutrient cycling rates, whereas at a local scale, vegetation patchiness is the key control.

Findings from a parallel study at the same microsites demonstrated that vegetation cover was also related to soil microbial community structure (Elliott et al., 2014). Of particular significance were cyanobacteria, capable of sequestering CO_2 and fixing N_2 (Flores, López-Lozano, & Herrero, 2015). Cyanobacteria were abundant in soil surfaces at grass sites but were present in only very low levels in soils beneath trees and shrubs. This is likely explained by competition from plants, including significantly reduced light levels and changes to the temperature and moisture regime at the soil surface (Figures 2 and 3). Litter inputs from plants and animals will provide resources for heterotrophic microbial competitors and further constrain cyanobacterial populations. Recovery of biocrusts may be affected by a loss of microbial inoculum, particularly cyanobacteria, associated with an increase in shrubs and trees. The protection of small refuge areas could, however, provide natural inoculum to surrounding degraded areas, facilitating crust regeneration when grazing pressure eases.

Higher CO_2 efflux associated with soils under trees and shrubs was most likely due to a combination of factors including greater heterotrophic microbial and plant root respiration, higher concentrations of C, and more favourable conditions for microbial respiration (Tang & Baldocchi, 2005). Soil microbial populations, respired CO_2 , and gas diffusion will all be affected by changes to soil properties associated

with vegetation change. The soil surface under shrubs and trees has a lower bulk density than beneath grasses, and this will facilitate water and gas movement through the soil profile. Soil CO_2 efflux of biotic origin is moisture limited for most of the year in the Kalahari, and in dry soils, the sensitivity of CO_2 emissions to changes in temperature is almost zero (Figure 6). In dry soils, heterotrophic respiration will be mainly due to fungal and, to a lesser extent, fungal associated bacteria, due to their ability to translocate water directly or via mycorrhizal associations from host plant sources. The approximately 10% increase in Q_{10} during moist soil conditions is likely due to enhanced bacterial activity. The soil moisture regime is thus vital to soil microbial activity, decomposition processes, respiration, and soil CO_2 efflux (see also Wang, D'Odorico, et al., 2009). There are complex temporal variations in soil moisture profiles, associated with rainfall, infiltration, and evaporative pressure (Figure 2), all of which will be affected by vegetation. Across the continent, land use changes, particularly conversion of natural land to agriculture and agricultural intensification, have been identified as accelerating CO_2 efflux from African soils (Kim et al., 2016). Our results demonstrate that shrub encroachment is another driver that will lead to significantly greater CO_2 efflux from dryland sand soils.

Whether or not the increased CO_2 efflux from soil beneath trees and shrubs represents a long-term decline in the soil, C store depends on the provenance of the C. The majority is likely to be associated with autotrophic (root) respiration and does not necessarily mean a net loss of soil C to the atmosphere. CO_2 efflux will also depend on the nature of the soil organic C which will reflect the form of the litter inputs from grasses, trees, and shrubs, all of which have unique C:N and $^{12}\text{C}:^{13}\text{C}$ ratios. The distinctive $\delta^{13}\text{C}$ signatures of CO_2 efflux from soils under grasses, shrubs, and trees demonstrated the different C fractionation processes and C origins (Thompson, Zaady, Huancheng, Wilson, & Martens, 2006; Figure 7). The high standard deviation associated with the mean $\delta^{13}\text{C}$ of gas from soil underneath *G. flava* suggests that there are two distinct contributory sources with unique isotopic signatures. The y intercept of the grass Keeling plot is clear and suggests a typical C source that has been fractionated by a C_4 photosynthetic pathway.

Vegetation changes will alter the type of organic compounds stored in the soil and the ease with which they are respired and ultimately their residence times. Further work is needed to determine the implications of these differences for the soil C store.

4.3 | Challenges to sustainable pastoral management in the Kalahari

Findings from our biophysical measurements have important implications for the management of grazing systems in the Kalahari. Our study shows that relationships between grazing management and C storage are not simple in the Kalahari rangelands, where there are complex links and feedbacks between vegetation, soils, and microclimate. From a pastoral perspective, shrub encroached rangelands are frequently classified as degraded (van Rooyen, 1998) because of the reduction of palatable grasses, the activation of dune crests, and the development of shrub thickets. However, it is too simplistic to view shrub encroachment as entirely negative (Eldridge & Soliveres, 2014) because it also forms new habitats for a variety of species (Smit & Swart, 1994), enriches the C and N of soils, provides a more favourable microclimate, and encourages a greater soil microbial diversity across the landscape. The challenge for sustainable grazing in the Kalahari is to adopt management strategies that avoid driving significant longer term shifts in vegetation structure but that also accommodate a degree of vegetation change. Nevertheless, an ever-increasing number of livestock on a decreasing amount of communal grazing land resulting in widespread, dense thickets of shrubs is not advisable, particularly when it could compromise other rangeland uses (e.g., collection of medicinal herbs or thatching grasses [Sallu, Twyman, & Stringer, 2010]).

Labour intensive intervention programmes involving removal of shrubs have been recommended (Reed et al., 2015). However, clearance of encroaching shrubs would result in a significant loss of soil nutrients from an already nutrient poor system and more extreme air temperatures, and selective thinning of dense thickets might be a more appropriate intervention (Hagos & Smit, 2005). Strategies that prevent land falling into the later stages of grazing-induced degradation will have numerous benefits for ecosystem services as natural recovery from shrub-encroached, or bare dune states are unlikely without significant intervention. Consequently, management practices that prevent shrub encroachment from occurring in the first place, such as through destocking in times of drought and manual bush removal or stem burning, will be more cost-effective over the long term.

5 | CONCLUSION

This study clearly demonstrates that there were significant differences in soil C, N, CO₂ efflux, and microclimate beneath the canopies of trees, shrubs, and grasses at a rangeland site in the Kalahari. The soil surface beneath shrubs and trees was cooler during the summer daytime, warmer during winter nights, and experienced less intense solar radiation than grass sites. Soils beneath trees and shrubs contain greater total C and N and contribute to greater soil microbial diversity in the landscape. Consequently, microbial activity was also higher resulting in more rapid nutrient cycling. Although associated with a loss

of palatable grasses, an increase in shrubs will also be associated with higher soil C stores and less extreme ground air temperatures. This has important implications for grazing land management which our findings show should not seek to remove low density shrub thickets but rather seek to exploit the wider benefits from a mosaic of dryland vegetation types.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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