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*Research***Impact of grazing intensity on seasonal variations in soil organic carbon and soil CO₂ efflux in two semiarid grasslands in southern Botswana****Andrew D. Thomas****Institute of Geography & Earth Sciences, Aberystwyth University, Llandinam Building, Aberystwyth, SY23 3DB*

Biological soil crusts (BSCs) are an important source of organic carbon, and affect a range of ecosystem functions in arid and semiarid environments. Yet the impact of grazing disturbance on crust properties and soil CO₂ efflux remain poorly studied, particularly in African ecosystems. The effects of burial under wind-blown sand, disaggregation and removal of BSCs on seasonal variations in soil CO₂ efflux, soil organic carbon, chlorophyll *a* and scytonemin were investigated at two sites in the Kalahari of southern Botswana. Field experiments were employed to isolate CO₂ efflux originating from BSCs in order to estimate the C exchange within the crust. Organic carbon was not evenly distributed through the soil profile but concentrated in the BSC. Soil CO₂ efflux was higher in Kalahari Sand than in calcrete soils, but rates varied significantly with seasonal changes in moisture and temperature. BSCs at both sites were a small net sink of C to the soil. Soil CO₂ efflux was significantly higher in sand soils where the BSC was removed, and on calcrete where the BSC was buried under sand. The BSC removal and burial under sand also significantly reduced chlorophyll *a*, organic carbon and scytonemin. Disaggregation of the soil crust, however, led to increases in chlorophyll *a* and organic carbon. The data confirm the importance of BSCs for C cycling in drylands and indicate intensive grazing, which destroys BSCs through trampling and burial, will adversely affect C sequestration and storage. Managed grazing, where soil surfaces are only lightly disturbed, would help maintain a positive carbon balance in African drylands.

Keywords: biological soil crusts; soil CO₂ efflux; grazing; soil organic carbon**1. INTRODUCTION**

Soil organic matter (SOM) and soil organic carbon (SOC) are essential to biological productivity, and underpin numerous ecosystem functions in terrestrial environments. More reliable quantification and prediction of SOC stores, sequestration and losses are urgent research priorities because of uncertainties associated with the impacts of land use and climatic change. This is particularly important in drylands [1] because: (i) net primary productivity and SOC are low, thus small absolute changes can have a large impact on ecosystem function; (ii) drylands cover 40 per cent of the Earth's land surface and changes in soil CO₂ emissions will impact the global atmospheric concentrations; (iii) SOC is preferentially concentrated at the surface [2], making it particularly sensitive to land use change; (iv) an estimated 70 per cent of the world's poorest billion people rely on income from

pastoralism [3], and changes to SOC and its associated ecosystem functions will have an immediate effect on their livelihoods; and (v) reliable data on SOC stores and fluxes are needed to inform programmes such as REDD and REDD+ (Reducing Emissions from Deforestation and Forest Degradation in Developing Countries) that seek to incentivize land management practices which enhance C sequestration and minimize C losses; the win–win scenario described by Lal [4]. There are, however, a number of factors that add complexity to the SOC cycle in drylands which affect the ability to predict future changes, some of which are discussed in the following sections with particular reference to southern Africa.

(a) Biological crusts and soil organic C

Dryland savannas are productive areas, accounting for an estimated 13.6 per cent of global NPP and an annual C sink of 1.6 t C ha⁻¹ yr⁻¹ [5,6]. There is, however, significant variability in the distribution of SOC in the landscape. At regional scales, the amount of SOC is controlled by climate, vegetation and soil type. At smaller scales, it is affected by the heterogeneity of resources and the concentration of organic material around shrub and tree canopies, forming islands of fertility [7]. Plant

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One contribution of 10 to a Theme Issue 'Impacts of global environmental change on drylands: from ecosystem structure and functioning to poverty alleviation'.

interspaces are commonly populated by biological soil crusts (BSCs) formed from mineral grains bound with varying proportions of cyanobacteria, algae, lichens, mosses and fungi and their exudates. Although only a few millimetres thick, BSCs constitute a major pool of SOC in drylands [8–10].

Autotrophic organisms in BSCs sequester CO₂ through photosynthesis, adding to the SOC pool through the production of polysaccharides and microbial biomass [11,12]. Photosynthetic activity in BSCs can be triggered by very small amounts of moisture, including dew and fog [13,14], and can be sustained over a wide range of moisture conditions [15]. Elbert *et al.* [9] estimate the median net uptake of C by BSCs in drylands to be 16 g m⁻² yr⁻¹ with a total annual net C uptake of 1.0 Pg yr⁻¹. Büdel *et al.* [16] found BSCs to be typical of nearly all biomes from southern Angola to the Cape Peninsula and that rain frequency and duration of dry periods were key factors for BSC development and composition. They also found that the ubiquity and diversity of BSC-forming cyanobacteria is testament to the myriad of mechanisms that allow cyanobacteria to thrive in habitats characterized by extremes in temperature, moisture and solar radiation, coupled with low nutrient status and occasional disturbance.

(b) Soil respiration losses of organic carbon

The primary mechanism of SOC depletion is through microbial catabolism of organic substrates [17]. The global flux of CO₂ respired from soils to the atmosphere as a by-product of this process is 98 ± 12 Pg C yr⁻¹ [18]. Compared with mesic locations, however, soil CO₂ efflux data from drylands are rare and provide an incomplete picture of the global contribution of drylands to the land–atmosphere C flux. The *in situ* data that are available allow some generalizations to be made and demonstrate that:

- annual soil CO₂ efflux in drylands is typically much lower than in mesic systems (see for example [19–22]). This is because both heterotrophic microbial activity and autotrophic respiration from plant roots are limited by soil moisture for long periods [23];
- immediately following re-wetting, soil CO₂ efflux rates can be very high, often elevated by up to 500 per cent compared with continually moist soil [13,21,24,25]. Re-wetting pulses constitute a significant portion of the total annual CO₂ efflux from soils [24,26,27];
- communities of heterotrophic and autotrophic micro-organisms in BSCs provide an additional, subtle and often overlooked contribution to soil CO₂ efflux [28]. For example, soil respiration was significantly higher on BSC patches than on uncrusted sites in semiarid locations in Spain [19,24]. Autotrophic organisms in BSCs also led to periods of net CO₂ sequestration after light rainfall in the Kalahari [28]. Although BSCs are a vital component of the dryland soil C cycle, few studies have parameterized the conditions required for photosynthesis in BSCs ([29] is a rare example) or determined BSC respiration, but see [9,24];

- a high proportion of organic C may be lost directly from the soil surface owing to photo-degradation of plant litter [30]. This is an entirely abiotic process and reduces the potential energy supply to soil microbes as well as the passive benefits derived from organic matter within soils. Austin and Vivanco [30] hypothesized that the rapid turnover of organic material and a lack of a correlation between litter decomposition and rainfall in drylands could be explained by this process;
- soil CO₂ efflux comprises C derived from: (i) heterotrophic microbial respiration resulting from mineralization of SOM and (ii) growth and maintenance root respiration (autotrophic respiration). Autotrophic respiration is driven by photosynthesis and vascular plant activity and not SOC mineralization. CO₂ derived from the mineralization of SOM, however, is independent of photosynthesis and represents a net loss of SOC [31]. Most soil CO₂ estimates do not differentiate between these sources and it is rarely possible to infer anything about changing SOC stores from CO₂ efflux data. Although there are techniques which can be used to separate autotrophic and heterotrophic components of soil CO₂ efflux [32,33], it remains challenging and there are few examples from African drylands. Interpretation of soil CO₂ efflux data is therefore complicated by high temporal and spatial variability, autotrophic components in BSCs, multiple sources and sinks of CO₂ and potentially high C losses driven by abiotic processes.

(c) Drivers of SOC change

(i) Climate

At a global scale, atmospheric warming is enhancing soil CO₂ efflux, leading to concerns over declining SOC and increasing atmospheric CO₂ [18]. Whether this is occurring in drylands, where moisture, not temperature, is limiting to microbial activity for a large part of the year, is much less certain. Below *ca* 1% v/v soil moisture, the CO₂ efflux rates were unchanged across a temperature range of 5–40°C at sites in the Kalahari [22]. The indirect effects of warming on moisture availability and the composition of BSCs are more likely to have an impact on SOC than the direct consequences of heat. A 3 year climate manipulation experiment in central Spain has shown that warming of 2.4°C led to a decline in the richness and diversity of BSC species [34]. Büdel *et al.* [16] found that the distribution of BSCs as well as their chlorophyll and C content was greater in winter compared with summer rainfall areas across southern Africa. They conclude that the predicted changes in the frequency and duration of precipitation will have a significant effect on the distribution, composition and C sequestration potential of BSCs, and thus ecosystem functioning across the drylands of southern Africa.

(ii) Grazing and land use

Drylands are home to more than 40 per cent of the African population and as this increases, so will demands on natural resources for fuel, grazing and cropland [2]. Changes in land management (such as

tilling, grazing and biomass harvesting) affect not only organic input to the soil, but also SOC mineralization rates [35]. Impacts can be dramatic. Scholes and Hall [36] report a 50 per cent loss in SOC over 20 years resulting from conversion of tropical savannah to croplands. Land use change, largely deforestation and conversion to agricultural land, was responsible for 20 per cent of the global anthropogenic emissions of CO₂ in the 1990s [37] and is the main cause of net C release in Africa [6].

Livestock grazing is the primary livelihood activity for many dryland inhabitants. The selected removal of palatable plant species and frequent disturbance of the soil surface both affect SOC. Reliance on boreholes to provide ground water for livestock in the Kalahari means that there are predictable ecological changes along grazing gradients away from water points [38]. The most frequently disturbed areas are characterized by loose sand and largely devoid of vegetation. Further away, but where grazing is still intense, BSC cover remains sparse and unpalatable grass species and woody shrubs dominate [39,40]. Thus grazing depletes two major sources of SOC, the roots of perennial grasses and BSCs, with manure inputs unlikely to fully offset these. Although it is probable that soil respiration rates will be affected as a result of changes in BSC cover and soil temperature, moisture and microbial characteristics, few studies have quantified this effect.

(iii) *Shrub encroachment*

The increase in density or cover of indigenous woody plants into grassland savannahs affects large areas of drylands, and is driven by multiple factors including grazing, atmospheric CO₂ enrichment, N deposition, fire suppression and climate [41]. Eldridge *et al.* [41] found a positive correlation between shrub encroachment and the concentration of above and below ground C. The extent of shrub encroachment was limited by water availability in southern Africa; therefore, rainfall changes were considered more influential than grazing in driving future encroachment. The resulting changes in shading of the surface will reduce direct losses of C from surface litter via photo-degradation [30], altering soil microbial, temperature and moisture conditions, all of which will affect SOC mineralization rates.

(iv) *Fire*

Fires affect several hundred million hectares every year, combusting billions of tonnes of dry biomass [42]. Vegetation fires affect SOC directly by volatilizing C during combustion [43] and indirectly through modification of the soil temperature, moisture, C and microbial environment [31,44]. If fire results in widespread vegetation death, then organic C input to the soil as ash and part-burned vegetation will increase over the short term. Reductions in standing biomass and litter will reduce shading and insulation of soils leading to increased soil temperatures [45].

There is no consensus on how fire affects soil respiration, because impacts are dependent on site and fire conditions. Andersson *et al.* [46] report short-lived increases after rainfall on burned soils in an

southwestern Ethiopian savannah, which they attribute to the rapid decomposition of fire-liberated C. In contrast, fire had no significant effect on soil respiration in South Africa, because microbial biomass in the subsoil was unaffected by burning [47]. Post-fire changes in soil moisture are likely to be critical in determining the impact on SOC mineralization rates and respiration. Whereas fire-induced reductions in transpiration and canopy interception can lead to increased soil moisture [48], fire can also lead to lower soil moisture because of increased evaporation from warmer soils and reduced infiltration because of enhanced hydrophobicity [49]. A post-fire change in the soil microbial community will also affect SOC. Burning can lead to increases in soil microbial biomass [50], or alter bacteria–fungi ratios [51], although changes are likely to be dependent on fire intensity [46].

(d) *Future research needs*

Gaps in understanding of the dryland SOC cycle arise in part because the factors discussed in the previous section do not occur in isolation, rather a dynamic equilibrium exists between climate, fire and vegetation cover, which impacts soil properties, biomass production and stocking densities. Furthermore, there is a lack of *in situ* data on SOC form, distribution, inputs and losses. Consequently, it is unclear what the sink potential of African drylands is and whether they are currently acting as a net C source or sink [2]. There is greater uncertainty over future SOC, given the variety of drivers of change, and the associated interactions and feedback between them.

Specifically, future research should address the following as priorities:

- there is an imbalance in ecological zones for which global soil respiration data are available. Despite covering 40 per cent of the land surface, less than 5 per cent of the 439 studies reviewed by Bond-Lamberty and Thomson [18] were from drylands. Consequently, it is not known what contribution drylands make to global atmospheric CO₂;
- the effects of land use and climatic change on SOC can only be accurately predicted if future work differentiates between heterotrophic and autotrophic contributions to soil CO₂ efflux. This is particularly important given that autotrophic contributions to soil CO₂ efflux may increase owing to greater primary productivity driven by CO₂ enrichment, at least in the short term, as plants benefit from increased water use efficiency [52]. Therefore, it is possible that dryland soil CO₂ efflux rates will increase in the future; however, this may not be owing to greater SOC mineralization rates or be accompanied by a decrease in SOC;
- substantial changes can occur in the soil physical, chemical and biological environment as a result of land use change and fire. However, we currently know little about the microbial content of dryland soils. Recent advances in molecular analyses, using 454 pyro-sequencing of DNA, could greatly improve understanding of the microbial content of soils and BSCs. These data can be used to determine the functionality of different microbial groups

Table 1. Selected soil properties for the experiment sites (means and s.e.) on 23 February 2010, 3 days prior to treatment, ($n = 5$).

soil type	total N (%)	total C (%)	total organic C (%)	pH	chlorophyll <i>a</i> ($\mu\text{g g}^{-1}$)	scytonemin ($\mu\text{g g}^{-1}$)
Kalahari Sand	0.04 ± 0.02	0.390 ± 0.013	0.365 ± 0.062	5.8 ± 0.15	0.86 ± 0.06	2.25 ± 0.24
calcrete	0.02 ± 0.004	0.556 ± 0.009	0.677 ± 0.104	7.9 ± 0.04	8.16 ± 0.12	20.47 ± 1.75

and will enable a much improved process-based understanding of biogeochemical cycles;

- significant spatial and temporal variability in SOC and CO_2 efflux is typical of drylands. An improved assessment of the size of the SOC store, annual inputs and losses will come with sampling regimes that embrace this variability [19,24]. This will include greater recognition of C loss owing to photo-degradation and the range of biotic and abiotic controls over these processes;
- conventional soil sampling techniques designed to quantify the mass of SOC adopt a two-tier 0–30 and 30–100 cm stratification [53], which is not appropriate in soils where this is concentrated in a BSC. The proportion of SOC to 1 m depth that is actually contained within the BSC should be calculated;
- soil CO_2 efflux models need to allow for periods of net C sequestration owing to BSC autotrophs and for periods of quiescence during dry periods when the temperature sensitivity of efflux will be negligible;
- a field-based study was carried out to address some of these research gaps, in particular to provide new information on the impact of grazing on SOC over contrasting seasons and on different soil types. Data were collected for sand and calcrete soils in the southern Kalahari of Botswana in order to (i) determine seasonal differences in soil CO_2 efflux; (ii) quantify the effects of grazing intensity on soil CO_2 efflux, SOC, BSC C and pigment content; (iii) determine the proportion of SOC in BSCs and (iv) differentiate BSC and subsoil contributions to soil CO_2 efflux.

2. METHODS AND STUDY AREA

(a) Description of study area

The study was carried out over 15 months in south west Botswana ($25^{\circ}56'51''$ $22^{\circ}25'40''$ E) in Kalahari Sand and in calcrete soils. Both sites were open fine-leaved savanna with a mixture of perennial (*Eragrostis*) and annual (*Schmidtia*) grasses, woody shrubs (*Acacia mellifera* (Vahl) Benth and *Grewia flava* DC) and trees, predominantly *Acacia erioloba* E. Meyer. The mean annual precipitation at the study site from 1996 to 2010 was 331 mm yr^{-1} , although inter-annual and inter-seasonal variation is high. Mean daily air temperatures measured 5 cm above the soil surface under a shrub canopy ranged from 6.1°C in July to 31.5°C in November (table 2).

Sand soils are weakly acidic and calcrete soils are alkaline (table 1). Both are covered in a 3–4 mm BSC, consisting of cyanobacteria (largely species of *Microcoleus*), bacteria (mostly from the phylum Proteobacteria) and fungi (mostly from the phylum Ascomycota) [39] (appendix S1 in the electronic supplementary material). Crusts are enriched in

ammonium, total N and organic C compared with the mineral soil surface [22,39]. BSC development and cover was more than 90 per cent of the area in plant interspaces on calcrete soils. Although dominated by cyanobacteria, calcrete BSCs also contained a small number of unidentified crustose lichen (similar to the type 4 crusts described in [54]). On sand soils, there was similar BSC cover (*ca* 80%), but they were less well developed than those on calcrete, with less surface discolouration, induration and no lichen. This is reflected in the soil surface properties. Calcrete soils had significantly greater total C, organic C, chlorophyll *a* and scytonemin (a photoprotective pigment unique to cyanobacteria [55]) than sand soils (table 1). There was no horizon development in either soil, and organic matter, total N, C and organic C content were low (table 1).

BSCs at both sites contain significantly greater SOC than subsoils. In Kalahari Sand, mean SOC to 1 m was 39.4 t C ha^{-1} , and more than 10 per cent of this was contained within the upper 2 cm (5.4 t C ha^{-1}). Carbon concentrations were 0.37 per cent in the BSC compared with *ca* 0.04 per cent in soils below 50 cm. On calcrete soils, BSC C concentrations were 0.68 per cent, comprising *ca* 12 per cent (4.3 t C ha^{-1}) of the 45 t C ha^{-1} total organic C to 1 m depth.

(b) Land-use simulation experiments

In July 2009, seven months prior to the start of the experiment, a fence was erected at both sites in order to protect soils from intrusion and animal disturbance. Within the fences, experiments were undertaken in February, July and November 2010 and in April 2011 during contrasting temperature and antecedent precipitation conditions (figure 1). Grazing treatments were applied to $1 \times 1 \text{ m}$ plots within the fenced areas in February 2010. Plots were approximately 0.5 m apart. Replication was achieved using three chambers spaced 0.75–1.0 m apart within each plot. The validity of this approach, which assumes that any differences between plots are owing to treatment, depends on the spatial variability in soil properties. In June 2009, experiments were undertaken to determine the spatial variability in CO_2 efflux from sand and calcrete soils. The results demonstrate that inherent differences in soil CO_2 efflux are likely to be the same between chambers placed 1 m apart as 5 m apart, on both soil types. These data were taken as evidence that it was acceptable to assume differences between plots were owing to treatment. Full details of these experiments are given in appendix S2 in the electronic supplementary material.

In one plot, the BSC was removed to a depth of 1 cm to simulate intense grazing. In the second plot, the BSC was broken into small fragments to simulate

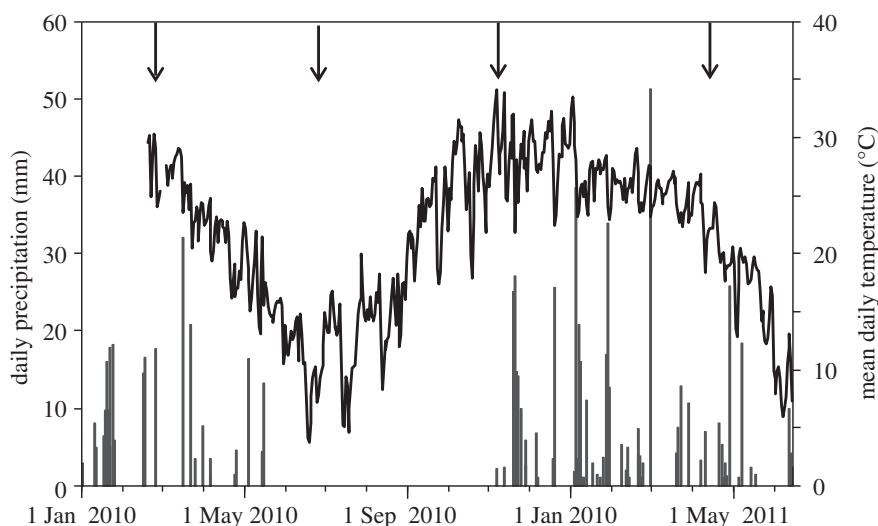


Figure 1. Daily precipitation (mm) and mean daily air temperatures ($^{\circ}\text{C}$) at the study site. Sampling periods are indicated by arrows.

light grazing. In the third plot, the surface was buried in a *ca* 1 cm layer of unconsolidated sand to simulate burial of the BSC by aeolian deposition. This is a common, albeit localized, occurrence in heavily grazed areas where the breakup of the BSC promotes sand transport. The final plot was left untreated as a control. After the initial treatment in February 2010, there was no further disturbance to the plots.

(c) *Soil and BSC CO₂ efflux measurement, field instrumentation and experiments*

CO₂ efflux was measured in each plot using static closed respiration chambers [22]. Chamber volume ranged from 510 to 580 ml and enclosed 106 cm² of soil. Two-way vent valves ensured that pressure differences between the chamber and atmosphere were minimal and rapidly equilibrated. A thin, domed, borosilicate glass window permitted solar illumination of the soil surface throughout the entire PAR spectrum. Chamber air temperatures were logged at 10 min intervals by USB502 loggers (Adept Science, UK) in one chamber in each plot. High thermal conductivity heat sinks mounted through the chamber walls ensured the internal air temperature tracks ambient air to within 1 $^{\circ}\text{C}$ throughout the diurnal cycle, minimizing disruption of natural advection within the soil.

The soil CO₂ efflux rates were determined at 6, 9 am, 12, 3, 6, 9 and 11 pm (local time) over 5 days in February, 3 days in November and 2 days in July and April. Within each measurement cycle, two 10 ml air samples were extracted from the chambers using a gas syringe at 15 min intervals and injected into 6 ml pre-evacuated glass vials. Prior to sampling, air inside the chamber was mixed by gently pumping with the syringe. CO₂ concentrations were determined using an Agilent gas chromatograph (GC 3000). Chamber design and the methodology were designed to minimize the likelihood of errors in efflux estimation associated with the use of closed chambers [56,57] particularly changes in the surface soil environment, pressure and soil-gas diffusion gradient changes owing to chamber deployment. To determine and

correct the effect of diffusion retardation on soil CO₂ efflux, replicate temporal sequences of CO₂ concentrations inside the chambers were determined over several days at 10 min intervals on sand and calcrete soils. The increasing CO₂ concentration, $C(t)$, and corresponding decreasing flux, $F(t)$, determined from the differential of $C(t)$ within the chamber headspace is described by polynomial time-dependent regression functions as in Forbrich *et al.* [58]. Equations described in [59] were used to determine mass C flux in $\text{mg m}^{-2} \text{h}^{-1}$ from the (diffusion corrected) changes in CO₂ concentration normalized to mean temperature and pressure during measurement. To ensure the mean soil CO₂ efflux rates from each plot were representative of the full range of temperature conditions and not affected by diurnal fluctuations, data from each chamber were integrated over the measurement period and the resulting cumulative change in C flux used to determine mean efflux rates.

Surface and sub-soil volumetric water content were determined using a Delta-T ML2x theta probe (Delta-T Devices, Cambridge, UK) in adjacent soil pits. Measurements were made twice daily at 0.1 m intervals to 1 m depth on freshly exposed faces. Between sample times, the pit was covered in a mylar sheet to minimize evaporative moisture loss.

(d) *Soil and BSC sampling and analysis*

During each fieldwork season, triplicate samples of the top 10 mm soil and BSC were collected from the plots using a sterile Petri dish and from 10 regular depths to 1 m from soil pits. The chlorophyll *a* content of the surface soil/BSC samples was determined within 12 h of collection by heating samples to 60 $^{\circ}\text{C}$ in the dark in HPLC-grade 100 per cent methanol. Concentrations in filtered extracts were determined from absorbance values at 652, 665.2 and 750 nm using the equations of Porra [60]. Remaining samples were air dried, bagged and returned to the UK for immediate analysis. Total C and N were determined using a Leco TruSpec total element analyser and organic C, following the Walkley–Black method. pH was

Table 2. Mean air temperature ($^{\circ}\text{C}$), soil moisture (v/v %) and soil CO_2 efflux rates ($\text{mg C m}^{-2} \text{h}^{-1}$) (with s.e.) for the untreated control and treated plots in each season

	mean air temp. ($^{\circ}\text{C}$)	mean soil moisture (% v/v)	<i>n</i> (efflux)	treatment (soil CO_2 efflux $\text{mg C m}^{-2} \text{h}^{-1}$)			
				control	removed	disagg.	buried
Kalahari Sand							
February 2010	28.9	3.7	93	38.9 ± 0.7	42.1 ± 3.9	38.2 ± 1.0	33.8 ± 0.5
July 2010	13.4	0.4	42	5.8 ± 0.14	6.2 ± 0.5	5.5 ± 0.8	5.8 ± 0.6
November 2010	31.9	0.1	66	10.8 ± 0.34	7.1 ± 0.7	8.6 ± 1.1	5.8 ± 1.2
April 2011	19.8	1.1	39	23.9 ± 1.0	27.8 ± 1.3	33.0 ± 1.6	23.0 ± 4.3
calcrete							
February 2010	25.5	4.4	87	24.1 ± 2.4	25.1 ± 2.5	22.4 ± 2.0	35.2 ± 1.4
July 2010	6.1	1.0	39	1.2 ± 0.9	2.8 ± 0.3	1.1 ± 1.4	5.4 ± 1.3
November 2010	29.4	1.1	30	6.9 ± 2.3	1.5 ± 3.0	5.8 ± 1.1	8.7 ± 1.3
April 2011	22.1	5.2	39	9.1 ± 2.0	13.6 ± 2.6	15.3 ± 5.1	15.3 ± 1.7

determined in a 1:5 soil–water concentration, after shaking for 1 h. To determine scytonemin, samples were ground in 10 ml of 100 per cent acetone, stored at 4°C for 16 h and then filtered. Concentrations were derived from absorbance values at 384, 490, 663 and 750 nm, together with an extinction coefficient of 112.6 using the equation of Fleming and Castenholz [61].

(e) BSC and subsoil contribution to soil CO_2 efflux

To isolate BSC CO_2 efflux from the underlying subsoil, two experiments were established at sites within 10 m of the respiration chambers. To measure *in situ* BSC CO_2 efflux, triplicate samples of intact crusts, *ca* 10 mm deep, were carefully removed from the soil surface and placed on sterilized subsoil contained within shallow trays (R_{BSC}). A fourth tray of sterilized sand without a BSC acted as a control (R_{control}). Trays were used to prevent mixing of subsoil CO_2 with that from the crusts. The trays were dug into the soil with the lip of the tray level with the surface. Respiration chambers were placed over the BSC in the trays and CO_2 efflux determined four times a day. BSC CO_2 efflux was calculated from $R_{\text{BSC}} - R_{\text{control}}$. Subsoil CO_2 efflux was quantified using triplicate chambers located in the centre of a broad trench where the surface 10 cm of soil and BSC had been removed. Subsoil CO_2 efflux was determined at the same time as BSC CO_2 efflux.

(f) Statistical analysis

After checking for normality, a two-way analysis of variance (ANOVA) was undertaken using SPSS (IBM, v. 19) to test the significance of differences in soil CO_2 efflux and soil properties owing to the effects of treatment and season. To test for the effects of treatment, the mean soil CO_2 efflux rates of each chamber in each season were compared. When the analysis was significant ($p < 0.05$), a post hoc comparison of means was done with the least significant difference (LSD) test to evaluate the differences. Repeated-measures ANOVA was not used as respiration chambers were removed between seasons and sampling was not conducted at regular intervals.

3. RESULTS

(a) Seasonal differences in soil CO_2 efflux and soil properties

Soil CO_2 efflux was significantly higher in Kalahari Sand than in calcrete soils in February ($F_{1,16} = 103.8$, $p < 0.01$) and April ($F_{1,16} = 40.6$, $p < 0.01$) but there were no differences in July and November.

Mean soil CO_2 efflux was also significantly different in each season in Kalahari Sands ($F_{3,32} = 535.2$, $p < 0.01$) and in calcrete ($F_{3,32} = 68.6$, $p < 0.01$). The effects of season were independent of treatment. The maximum efflux rates were measured in February 2010 and minimum rates were measured in July 2010 on both soils (table 2). Lowest rates of soil CO_2 efflux coincided with the lowest soil moisture (less than 1% v/v) and mean daily air temperatures 4°C (table 2). Soil CO_2 efflux was also very low in November, despite mean air temperatures more than 31°C but volumetric soil moisture remained less than 1 per cent. The higher CO_2 efflux rates in February 2010 and April 2011 coincided with warm mean air temperatures (more than 20°C) and soil moisture more than 4% v/v. CO_2 efflux increased with air temperature from both soils during April 2011 and February 2010 and from the calcrete soils in November 2010 (figure 2). Below *ca* 1% v/v soil moisture, CO_2 efflux was insensitive to temperature change.

In Kalahari Sands, concentrations of chlorophyll *a* ($F_{4,40} = 42.3$, $p < 0.01$), scytonemin ($F_{4,40} = 4.4$, $p = 0.005$) and organic C ($F_{4,40} = 422.6$, $p < 0.01$) varied significantly with season. In calcrete soils, the concentrations of chlorophyll *a* ($F_{4,40} = 122.0$, $p < 0.01$), scytonemin ($F_{4,40} = 369.6$, $p < 0.01$) and organic C ($F_{4,40} = 488.8$, $p < 0.01$) also varied significantly with season. Concentrations of all properties on both soil types were highest in February and April and least in July and November.

(b) The effects of grazing intensity on soil CO_2 efflux and properties

Grazing intensity had a significant effect on soil CO_2 efflux in Kalahari Sands ($F_{3,32} = 5.5$, $p = 0.004$), but post hoc test reveal these effects were only apparent in February and April and not when soils were dry in November and July. In February, soil CO_2 efflux was

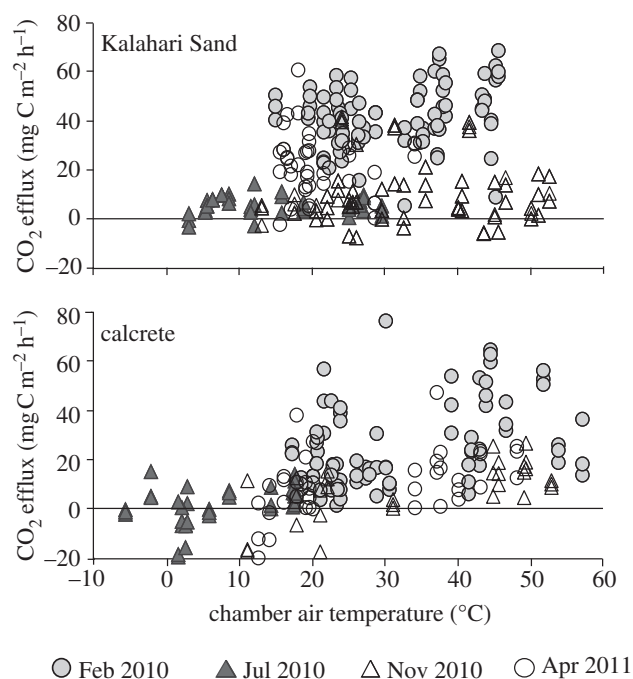


Figure 2. CO₂ efflux and air temperature inside the respiration chambers on untreated soils. Negative fluxes indicate net uptake to the soil.

significantly greater from soil where the BSC was removed than the control ($p = 0.02$) and from where the BSC was disaggregated ($p = 0.013$), and buried under sand ($p < 0.01$). In April, soil CO₂ efflux from soil where the BSC was removed was also significantly higher than from the control soil ($p = 0.02$). CO₂ efflux was also significantly higher from soil where the BSC was disaggregated than the control ($p < 0.01$) and buried under sand ($p = 0.01$). There were no significant differences between any of the other treatments.

Grazing treatment also had a significant effect on soil CO₂ efflux on calcrete soils ($F_{3,32} = 3.6$, $p = 0.02$). Post hoc tests reveal that treatment only had a significant effect on soil CO₂ efflux in February and April. In February, CO₂ efflux from the soil buried under sand was significantly greater than from all other plots ($p < 0.01$). In April, CO₂ efflux from soil where the BSC was disaggregated was significantly higher than the control ($p < 0.01$), where the BSC was removed ($p = 0.03$) and buried under sand ($p = 0.05$).

Grazing treatment in Kalahari Sand had a significant effect on chlorophyll *a* ($F_{3,40} = 20.8$, $p < 0.01$), scytonemin ($F_{3,40} = 5.7$, $p = 0.002$) and organic C ($F_{3,40} = 409.9$, $p < 0.01$). In calcrete soils, grazing treatment also had a significant effect on chlorophyll *a* ($F_{3,40} = 182.7$, $p < 0.01$), scytonemin ($F_{3,40} = 785.1$, $p < 0.01$) and organic C ($F_{3,40} = 263.4$, $p < 0.01$). Variability in soil properties between plots prior to treatment, as well as between seasons, presented a challenge for isolating the effects of individual treatments. Thus, changes in treated soil surface properties are presented as the ratio of the concentration prior to treatment to that after treatment (figure 3).

Treatment effects on soil surface properties were greatest where the BSC was removed and buried under

loose sand and least for disaggregation (figure 3). In both soils, the BSC removal resulted in significant reductions in chlorophyll *a*, scytonemin and SOC relative to control soils. In sand soils, all parameters remained less than 50 per cent of the control for the duration of the experiment. This impact was sustained for the entire measurement period in sand soils, but in calcrete soils chlorophyll *a* and SOC had recovered to control levels by April 2011.

Chlorophyll *a*, scytonemin and SOC were lower in the soil buried under sand relative to the control. The effects of burial were still evident at the end of the experiment although the extent varied according to the soil type and the property concerned. By April 2011, chlorophyll *a* and SOC were still only 20 per cent of the control on sand soils and 80 per cent in the calcrete soils.

The impact of BSC disaggregation was different to the effect of removal and burial (figure 3). In calcrete soils, chlorophyll *a*, scytonemin and SOC were all greater than the control for the duration of the experiment. In sand soils, there were reductions in chlorophyll *a* and SOC relative to the control, but these were only significant in one season and not sustained over the experiment.

(c) BSC and subsoil CO₂ efflux

BSCs were a net C sink (negative efflux values) on both soil types during all seasons with the exception of Kalahari Sands in April 2011 (table 3). The maximum mean uptake rates of -6.6 and -3 mg C m⁻² h⁻¹ occurred in November 2010 in calcrete and sand soils, respectively. The subsoil was a source of C to the atmosphere with rates ranging from 3.6 to 21.3 mg C m⁻² and 5.9 to 7.9 mg C m⁻² in sand and calcrete soils, respectively.

4. DISCUSSION AND CONCLUSIONS

The ability to accurately predict the impact of land use and climatic changes on SOC in drylands is currently affected by several knowledge gaps. As well as providing new data and insights into the effects of grazing and climate on SOC, this paper has produced a number of recommendations for research that would help focus efforts to address these gaps, and improve predictions of future C stores and fluxes.

Seasonal differences in soil CO₂ efflux were significant and demonstrate the primary controlling effect of moisture and the secondary effect of temperature on microbial and vascular plant activity (table 2). That soil CO₂ efflux becomes unresponsive to temperature changes below *ca* 1% v/v soil moisture has been established previously in the Kalahari [22]. The metabolic activity of soil organisms can be sustained even when moisture is below the wilting point for vascular plants, typically -1.9 and -2.9 MPa in the Kalahari [62]. This means that BSC organisms were still metabolically active, at least for parts of the diurnal cycle, during the dry months of July and November and were a small net sink of C (table 3).

The median net annual C uptake owing to BSCs reported in 16 studies from various drylands worldwide was 16 g m⁻² yr⁻¹ (reviewed in [9]). Lowest rates of C uptake were reported from a cyanobacteria-dominant

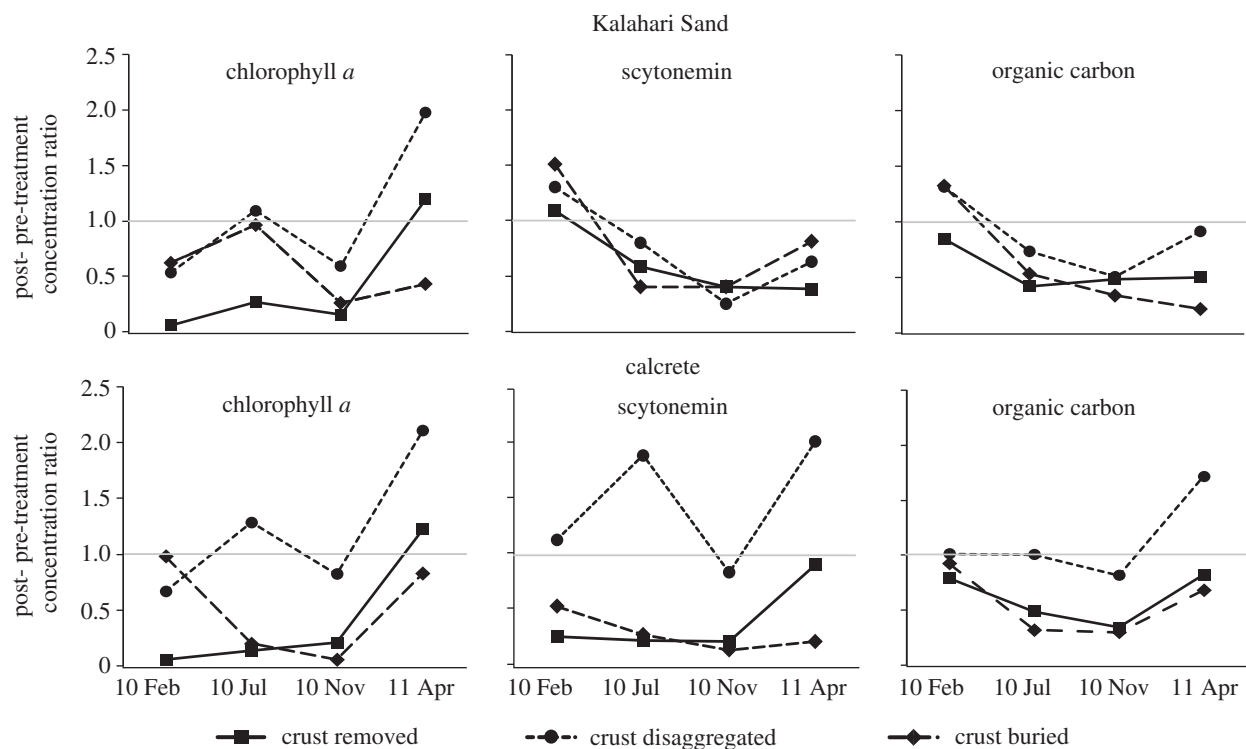


Figure 3. Post- and pre-treatment ratios of chlorophyll *a*, scytonemin and SOC in the upper 10 cm soil. A ratio more than 1 signifies an increase in concentration after treatment, less than 1 signifies a decrease.

Table 3. BSC and subsoil CO₂ efflux (mg m⁻² h⁻¹). *n* = 18, except Kalahari Sand in July where *n* = 48 and calcrete in November where *n* = 27. *n* reported as the total number of efflux measurements from the triplicate chambers used for each experiment

	July 2010	November 2010	April 2011
Kalahari Sand			
BSC	-1.02 ± 0.7	-3.01 ± 1.3	1.4 ± 1.4
subsoil	3.63 ± 0.7	4.70 ± 0.4	21.3 ± 1.8
calcrete			
BSC	—	-6.6 ± 0.65	-3.0 ± 1.1
subsoil	—	5.9 ± 1.4	7.9 ± 2.8

crust in the Kaiparowits Basin in southern Utah at 0.8 g m⁻² yr⁻¹ [63]. Highest uptake rates were reported from well-developed BSCs in the pinyon–juniper woodlands in the Utah Canyonlands of 74.9 g m⁻² yr⁻¹ [64]. Although it is not possible to fairly extrapolate the BSC CO₂ efflux data from this study to generate annual estimates, it is useful to try and make a comparison with other studies. A realistic range of net C uptake values of 1–3 mg C m⁻² h⁻¹ from this study (table 3) equates to an annual uptake of 8.8–26.3 g C m⁻² yr⁻¹. This places Kalahari BSCs towards the lower end of uptake estimates as in [9] but as BSC organisms are not exclusively autotrophic, the respiration of CO₂ within crust will mean that the actual C uptake will be larger. The assumptions and errors associated with these figures mean that C uptake estimates and comparisons with other work must be treated with caution but nevertheless it does strongly suggest BSC inputs are a significant addition to the soil C balance.

Although seasonal variations in moisture and plant activity exert a stronger influence over soil CO₂ efflux, the differences owing to grazing disturbance were significant when soils were wet (i.e. in April and February). BSC destruction and/or burial under wind-blown sand are typical of intensely grazed areas, and result in significantly increased soil CO₂ efflux on sand and calcrete soils, respectively. This is probably because autotrophic activity in BSCs is inhibited or prevented entirely. In the semiarid part of the Kalahari, these are spatially confined to areas adjacent to boreholes and other zones of intense disturbance [38,39]. This is supported by the significant reductions in phototrophic biomass (measured as chlorophyll *a*) and SOC compared with lightly grazed areas owing to the reduction in crust organism biomass and the impairment of photosynthesis in remaining organisms [8,10,29]. Recovery from this type of extreme disturbance did not occur within the 15 months of monitoring and is likely to take several years (figure 3). In contrast, disaggregation of BSCs, which typically occurs in areas of light and/or infrequent grazing, has a positive impact (or only a very short-lived reduction) on SOC, although there are differences between soil types (figure 3). This is attributed to increased micro-topography of broken crust fragments which reduces surface temperatures and evaporation and prolongs the duration of photosynthetic activity of organisms in the crust fragments.

The findings of this study are important for several reasons, including (i) understanding how dryland ecosystems will respond to changes in the future, (ii) estimating probable atmospheric CO₂ feedbacks from desert soils and (iii) for policy-makers trying to implement C payment schemes, where there are currently no data to support appropriate

decision-making. Managing land with the goal of optimizing C sequestration and SOC storage is a good idea where practicable, and one that has been explored through financial schemes such as REDD and REDD+. There is, however, a potential dilemma because accumulating SOC stores will not necessarily benefit ecosystem functioning. It is the usage of the organic C in the soil that provides the energy to microbes whose activities benefit soil processes such as nutrient mineralization [65]. A healthy dryland ecosystem therefore requires SOC to be used, and consequently depleted, but also replenished through sequestration, primarily from BSCs and perennial grasses. Although the message of 'don't overgraze' seems simple, the reality is complicated by the cultural significance of cattle ownership for farmers in the Kalahari (the Tswana in this case) and land tenure [66]. In much of rural Africa, the poor either own very small portions of land or use communal grazing areas, which may affect who could (and should) benefit from payments for conserving C [66]. As Dougill *et al.* [67] demonstrate for southern Africa, there is still much work to do in investigating how the poor can access benefits from C sequestration payments, as well as gain other ecosystem service benefits from properly managing grazing lands. However, this study clearly indicates that well-managed grazing regimes, where soils and plants have time to recover after grazing, are less likely to lead to sustained reductions in the SOC store as BSC functions are not significantly adversely affected. Intensive grazing without soil recovery periods will reduce the ability of BSCs to sequester C, and potentially lead to reductions in SOC and ultimately a deterioration in ecosystem functions.

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REFERENCES

- Conant, R. T. 2010 Challenges and opportunities for carbon sequestration in grassland systems: a technical report on grassland management and climate change mitigation. United Nations Food and Agriculture Organization (FAO). Integrated Crop Management 9, Rome.
- Ciais, P., Bombelli, A., Williams, M., Piao, S. L., Chave, J., Ryan, C. M., Henry, M., Brender, P. & Valentini, R. 2011 The carbon balance of Africa: synthesis of recent research studies. *Phil. Trans. R. Soc. A* **369**, 1–20. (doi:10.1098/rsta.2010.0328)
- Food and Agricultural Organisation (FAO). 2009 Review of evidence on drylands pastoral systems and climate change: implications and opportunities for mitigation and adaptation. In *Land and Water Discussion Paper 8* (eds C. Neely, S. Bunning, A. Wilkes), pp. 50. Rome, Italy: FAO.
- Lal, R. 2003 Carbon sequestration in dryland environments. *Environ. Manage.* **33**, 528–544.
- Grace, J., San José, J., Meir, P., Miranda, H. S. & Montes, R. A. 2006 Productivity and carbon fluxes of tropical savannas. *J. Biogeogr.* **33**, 387–400. (doi:10.1111/j.1365-2699.2005.01448.x)
- Henry, M., Valentini, R. & Benroux, M. 2009 Soil carbon stocks in ecoregions of Africa. *Biogeosciences* **6**, 797–823. (doi:10.5194/bgd-6-797-2009)
- Wang, L., Okin, G. S., Caylor, K. K. & Macko, S. A. 2009 Spatial heterogeneity and sources of soil carbon in southern African savannas. *Geoderma* **149**, 402–408. (doi:10.1016/j.geoderma.2008.12.014)
- Belnap, J. & Lange, O. L. 2003 Structure and functioning of biological soil crusts: a synthesis. In *Biological soil crusts: structure, function and management* (eds J. Belnap & O. L. Lange), pp. 471–479. Berlin, Germany: Springer.
- Elbert, W., Weber, B., Büdel, B., Andreae, M. O. & Pöschl, U. 2009 Microbiotic crusts on soil, rock and plants: neglected major players in the global cycles of carbon and nitrogen? *Biogeosci. Discussions* **6**, 6983–7015. (doi:10.5194/bgd-6-6983-2009)
- Evans, R. D. & Lange, O. L. 2003 Biological Soil Crusts and Ecosystem N and C Dynamics. In *Biological soil crusts: structure, function and management* (eds J. Belnap & O. L. Lange), pp. 263–279. Berlin, Germany: Springer.
- García-Pichel, F. & Belnap, J. 1996 Microenvironments and microscale productivity of cyanobacterial desert crusts. *J. Phycol.* **32**, 774–782. (doi: 10.1111/j.0022-3646.1996.00774.x)
- Mager, D. M. & Thomas, A. D. 2011 The role of extracellular polysaccharides from cyanobacterial soil crusts in dryland surface processes: a review. *J. Arid Environ.* **75**, 91–97. (doi:10.1016/j.jaridenv.2010.10.001)
- Cable, J. M. & Huxman, T. E. 2004 Precipitation pulse size effects on Sonoran Desert soil microbial crusts. *Oecologia* **141**, 317–324. (doi: 10.1007/s00442-003-1461-7)
- Lange, O. L., Meyer, A., Zellner, H. & Heberm, U. 1994 Photosynthesis and water relations of lichen soil crusts: field measurements in the coastal fog zone of the Namib Desert. *Funct. Ecol.* **8**, 253–264. (doi:10.2307/2389909)
- Zhao, X. M., Bi, Y. H., Chen, L., Hu, S. & Hu, Z. Y. 2008 Responses of photosynthetic activity in the drought tolerant cyanobacterium, *Nostoc flagilliforme* to rehydration at different temperature. *J. Arid Environ.* **72**, 370–377. (doi:10.1016/j.jaridenv.2007.07.002)
- Büdel, B., Darienko, T., Deuschewitz, K., Dojani, S., Friedl, T., Mohr, K. L., Salisch, M., Reisser, W. & Weber, B. 2009 Southern African biological soil crusts are ubiquitous and highly diverse in drylands, being restricted by rainfall frequency. *Microbial Ecol.* **57**, 229–247. (doi:10.1007/s00248-008-9449-9)
- Luo, Y. & Zhou, X. 2006 *Soil Respiration and the Environment*. New York, NY: Academic Press.
- Bond-Lamberty, B. & Thomson, A. 2010 Temperature-associated increases in the global soil respiration record. *Nature* **464**, 579–582. (doi:10.1038/nature08930)
- Maestre, F. T. & Cortina, J. 2003 Small-scale spatial variation in soil CO₂ efflux in a Mediterranean semiarid steppe. *Appl. Soil Ecol.* **23**, 199–209. (doi:10.1016/S0929-1393(03)00050-7)
- Shen, W., Reynolds, J. F. & Hui, D. 2009 Responses of dryland soil respiration and soil carbon pool size to abrupt vs. combined changes in soil temperature, precipitation and atmospheric CO₂: a simulation analysis. *Glob. Change Biol.* **15**, 2274–2294. (doi:10.1111/j.1365-2486.2009.01857.x)
- Thomas, A. D. & Hoon, S. R. 2010 Simulated rainfall pulses and carbon dioxide fluxes from Kalahari Sands. *J. Arid Environ.* **74**, 131–139. (doi:10.1016/j.jaridenv.2009.07.005)

- 22 Thomas, A. D., Hoon, S. R. & Dougill, A. J. 2011 Soil respiration at five sites along the Kalahari transect: effects of temperature, precipitation pulses and biological soil crust cover. *Geoderma* **167–168**, 284–294. (doi:10.1016/j.geoderma.2011.07.034)
- 23 Noy-Meir, I. 1973 Desert ecosystems: environment and producers. *Annu. Rev. Ecol. Syst.* **4**, 25–51. (doi:10.1146/annurev.es.04.110173.000325)
- 24 Castillo-Monroy, A. P., Maestre, F. T., Rey, A., Soliveres, S. & García-Palacios, P. 2011 Biological soil crust microsites are the main contributor to soil respiration in a semiarid ecosystem. *Ecosystems* **14**, 835–847. (doi:10.1007/s10021-011-9449-3)
- 25 Fierer, J. & Schimel, J. P. 2003 A proposed mechanism for the pulse in carbon dioxide production commonly observed following the rapid rewetting of a dry soil. *Soil Sci. Soc. Am. J.* **67**, 798–805. (doi:10.2136/sssaj2003.7980)
- 26 Liu, X., Wan, S., Su, B., Hui, D. & Luo, Y. 2002 Response of soil CO₂ efflux to water manipulation in a tallgrass prairie ecosystem. *Plant Soil* **240**, 213–223. (doi:10.1023/a:1015744126533)
- 27 Xu, L., Baldocchi, D. D. & Tang, J. 2004 How soil moisture, rain pulses and growth alter the response of ecosystem respiration to temperature. *Global Biogeochem. Cycles* **18**, GB4002. (doi:10.1029/2004GB002281)
- 28 Thomas, A. D., Hoon, S. R. & Linton, P. E. 2008 Carbon dioxide fluxes from cyanobacteria crusted soils in the Kalahari. *Appl. Soil Ecol.* **39**, 254–263. (doi:10.1016/j.apsoil.2007.12.015)
- 29 Lange, O. L. 2003 Photosynthesis of soil-crust biota as dependent on environmental factors. In *Biological soil crusts: structure, function and management* (eds J. Belnap & O. L. Lange), pp. 217–240. Berlin, Germany: Springer.
- 30 Austin, A. T. & Vivanco, L. 2006 Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. *Nature* **442**, 555–558. (doi:10.1038/nature05038)
- 31 Czimczik, C. I., Trumbore, S. E., Carbone, M. S. & Winston, G. C. 2006 Changing sources of soil respiration with time since fire in a boreal forest. *Glob. Change Biol.* **12**, 957–971. (doi:10.1111/j.1365-2486.2006.01107.x)
- 32 Hanson, P. J., Edwards, N. T., Garten Jr, C. T. & Andrews, J. A. 2000 Separating root and soil microbial contributions to soil respiration: a review of methods and observations. *Biogeochemistry* **48**, 115–146. (doi:10.1023/a:1006244819642)
- 33 Trumbore, S. 2006 Carbon respired by terrestrial ecosystems—recent progress and challenges. *Glob. Change Biol.* **12**, 141–153. (doi:10.1111/j.1365-2486.2005.01067.x)
- 34 Cao, G., Tang, Y., Mo, W., Wang, Y., Li, Y. & Zhao, X. 2004 Grazing intensity alters soil respiration in an alpine meadow on the Tibetan plateau. *Soil Biol. Biochem.* **36**, 237–243. (doi:10.1016/j.soilbio.2003.09.010)
- 35 Escolar, C., Martínez, I., Bowker, M. A. & Maestre, F. T. 2012 Warming reduces the growth and diversity of biological soil crusts in a semi-arid environment: implications for ecosystem structure and functioning. *Phil. Trans. R. Soc. B* **367**, 3087–3099. (doi:10.1098/rstb.2011.0344)
- 36 Scholes, R. J. & Hall, D. O. 1996 The carbon budget of tropical savannas, woodlands and grasslands. In *Global change: effects on coniferous forests and grasslands* (eds A. Breymeyer *et al.*), 69–100. SCOPE 56. Chichester, UK: Wiley.
- 37 Inter-Governmental Panel on Climate Change (IPCC) 2007 *Climate change 2007: the physical science basis*. Cambridge, UK: Cambridge University Press.
- 38 Perkins, J. S. & Thomas, D. S. G. 1993 Spreading deserts or spatially confined environmental impacts? Land degradation and cattle ranching in the Kalahari desert of Botswana. *Land Degrad. Rehabil.* **4**, 179–194. (doi:10.1002/ldr.3400040307)
- 39 Thomas, A. D. & Dougill, A. J. 2007 Spatial and temporal distribution of cyanobacterial soil crusts in the Kalahari: implications for soil surface properties. *Geomorphology* **85**, 17–29. (doi:10.1016/j.geomorph.2006.03.029)
- 40 Dougill, A. J., Thomas, D. S. G. & Heathwaite, A. L. 1999 Environmental change in the Kalahari: integrated land degradation studies for non equilibrium dryland environments. *Ann. Assoc. Am. Geogr.* **89**, 420–442. (doi:10.1111/0004-5608.00156)
- 41 Eldridge, D. J., Bowker, M. A., Maestre, F. T., Roger, E., Reynolds, J. F. & Whitford, W. G. 2011 Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecol. Lett.* **14**, 709–722. (doi:10.1111/j.1461-0248.2011.01630.x)
- 42 Shakesby, R. A. & Doerr, S. H. 2006 Wildfire as a hydrological and geomorphological agent. *Earth-Sci. Rev.* **74**, 269–307. (doi:10.1016/j.earscirev.2005.10.006)
- 43 Flannigan, M. D., Krawchuck, M. A., de Groot, W. J., Wotton, B. M. & Gowman, L. M. 2009 Implications of changing climate for global wildland fire. *Int. J. Wildland Fire* **18**, 483–507. (doi.org/10.1071/WF08187)
- 44 Hamman, S. T., Burke, I. C. & Stromberger, M. E. 2007 Relationships between microbial community structure and soil environmental conditions in a recently burned system. *Soil Biol. Biochem.* **39**, 1703–1711. (doi:10.1016/j.soilbio.2007.01.018)
- 45 Wolfson, B. A. S., Kolb, T. E., Sieg, C. H. & Clancy, K. M. 2005 Effects of post-fire conditions on germination and seedling success of diffuse knapweed in northern Arizona. *Forest Ecol. Manag.* **216**, 342–358. (doi:10.1016/j.foreco.2005.05.047)
- 46 Andersson, M., Michelsen, A., Jensen, M. & Kjølner, A. 2004 Tropical savannah woodland: effects of experimental fire on soil microorganisms and soil emissions of carbon dioxide. *Soil Biol. Biochem.* **36**, 849–858. (doi:10.1016/j.soilbio.2004.01.015)
- 47 Zepp, R. G., Miller, W. L., Burke, R. A., Dirk, A., Parsons, B. & Scholes, M. C. 1996 Effects of moisture and burning on soil atmosphere exchange of trace carbon gases in a southern African savanna. *J. Geophys. Res.* **101**, 23 699–23 706. (doi:10.1029/95JD01371)
- 48 Grady, K. C. & Hart, S. C. 2006 Influences of thinning, prescribed burning, and wildfire on soil processes and properties in southwestern ponderosa pine forests: a retrospective study. *Forest Ecol. Manag.* **234**, 123–135. (doi:10.1016/j.foreco.2006.06.031)
- 49 Doerr, S. H. & Moody, J. 2004 Hydrological impacts of soil water repellency: on spatial and temporal uncertainties. *Hydrol. Process.* **18**, 829–832. (doi:10.1002/hyp.5518)
- 50 Singh, R. S. 1994 Changes in soil nutrients following burning of dry tropical savanna. *Int. J. Wildland Fire* **4**, 187–194. (doi:10.1071/WF9940187)
- 51 D’Ascoli, R., Rutigliano, F. A., De Pascale, R. A., Gentile, A. & Virzo DeSanto, A. 2005 Functional diversity of the microbial community in Mediterranean maquis soils as affected by fires. *Int. J. Wildland Fire* **14**, 355–363. (doi:10.1071/WF05032)
- 52 Smith, S. D., Huxman, T. E., Zitzer, S. F., Charlet, T. N., Housman, D. C., Coleman, J. S., Fenstermaker, L. K., Seemann, J. R. & Nowak, R. S. 2000 Elevated CO₂ increases productivity and invasive species success in an arid ecosystem. *Nature* **408**, 79–82. (doi:10.1038/35040544)
- 53 Inter-Governmental Panel on Climate Change (IPCC) 2003 *Good practice guidance for land use, land-use change and forestry*. Kanagawa, Japan: IPCC National Greenhouse Gas Inventories Programme.

- 54 Dougill, A. J. & Thomas, A. D. 2004 Kalahari Sand soils: spatial heterogeneity and land degradation. *Land Degrad. Dev.* **15**, 233–242. (doi:10.1002/ldr.611)
- 55 Garcia-Pichel, F. & Castenholz, R. W. 1991 Characterisation and biological implications of scytonemin, a cyanobacterial sheath pigment. *J. Phycol.* **27**, 395–409. (doi:10.1111/j.0022-3646.1991.00395.x)
- 56 Davidson, E. A., Savage, K., Verchot, L. V. & Navarro, R. 2002 Minimizing artefacts and biases in chamber-based measurements of soil respiration. *Agr. Forest Meteorol.* **113**, 21–37. (doi:org/10.1016/S0168-1923(02)00100-4)
- 57 Pumpanen, J. *et al.* 2004 Comparison of different chamber techniques for measuring soil CO₂ efflux. *Agr. Forest Meteorol.* **124**, 159–176. (doi:10.1016/j.agrfor.met.2003.12.001)
- 58 Forbrich, I., Kutzbach, L., Hormann, A. & Wilmking, M. 2010 A comparison of linear and exponential regression for estimating diffusive CH₄ fluxes by closed-chambers in peatlands. *Soil Biol. Biochem.* **42**, 507–515. (doi:10.1016/j.soilbio.2009.12.004)
- 59 Kutzbach, L., Schneider, J., Sachs, T., Giebels, M., Nykänen, H., Shurpali, N. J., Martikainen, P. J., Alm, J. & Wilmking, M. 2007 CO₂ flux determination by closed-chamber methods can be seriously biased by inappropriate application of linear regression. *Biogeosciences* **4**, 1005–1025. (doi:10.5194/bg-4-1005-2007)
- 60 Porra, R. J. 2006 Spectrometric assays for plant, algal and bacterial chlorophylls. In *Advances in photosynthesis and respiration. Chlorophylls and bacteriochlorophylls: biochemistry, biophysics, function and application* (eds B. Grimm, R. J. Porra, W. Rüdiger & H. Scheer). New York, NY: Springer.
- 61 Fleming, E. D. & Castenholz, R. W. 2007 Effects of periodic desiccation on the synthesis of the UV-screening compound, scytonemin, in cyanobacteria. *Environ. Microbiol.* **9**, 1448–1455. (doi:10.1111/j.1462-2920.2007.01261.x)
- 62 Scholes, R. J. & Walker, B. H. 1993 *An African savanna*. Cambridge, UK: Cambridge University Press.
- 63 Jeffries, D. L., Link, S. O. & Klopatek, J. M. 1993 CO₂ fluxes of cryptogamic crusts. I. Response to resaturation. *New Phytol.* **125**, 163–173. (doi:10.1111/j.1469-8137.1993.tb03874.x)
- 64 Housman, D. C., Powers, H. H., Collins, A. D. & Belnap, J. 2006 Carbon and nitrogen fixation differ between successional stages of biological soil crusts in the Colorado Plateau and Chihuahuan Desert. *J. Arid Environ.* **66**, 620–634. (doi:org/10.1016/j.jaridenv.2005.11.014)
- 65 Janzen, H. H. 2006 The soil carbon dilemma: shall we hoard it or use it? *Soil Biol. Biochem.* **38**, 419–424. (doi:10.1016/j.soilbio.2005.10.008)
- 66 Stringer, L. *et al.* 2012 Challenges and opportunities in linking carbon sequestration, livelihoods and ecosystem service provision in drylands. *Environ. Sci. Policy.* **19–20**, 121–135. (doi:org/10.1016/j.envsci.2012.02.004)
- 67 Dougill, A. J., Stringer, L. C., Leventon, J., Riddell, M., Rueff, H., Spracklen, D. V. & Butt, E. 2012 Lessons from community-based payment for ecosystem service schemes: from forests to rangelands. *Phil. Trans. R. Soc. B* **367**, 3178–3190. (doi:10.1098/rstb.2011.0418)