Geoderma 167-168 (2011) 284–294

Contents lists available at SciVerse ScienceDirect

Geoderma

journal homepage: www.elsevier.com/locate/geoderma

Soil respiration at five sites along the Kalahari Transect: Effects of temperature, precipitation pulses and biological soil crust cover

Andrew David Thomas [a,*], Stephen Robert Hoon [a], Andrew John Dougill [b]

[a] School of Science and the Environment, Manchester Metropolitan University, Manchester, M1 5GD, UK
[b] School of Earth and Environment, University of Leeds, Leeds, LS2 9JT, UK

ARTICLE INFO

Article history:
Received 22 November 2010
Received in revised form 15 July 2011
Accepted 25 July 2011
Available online 4 November 2011

Keywords:
Soil respiration
CO_2
Kalahari Sands
Biological soil crusts
Soil organic carbon

ABSTRACT

There are increasing concerns that climatic and land use changes will enhance soil respiration rates and soil organic carbon loss, compromising agricultural productivity and further elevating atmospheric CO_2. Current understanding of dryland respiration is, however, insufficient to enable prediction of the consequences of these changes for dryland soils and CO_2 fluxes. The objectives of this paper are to present *in-situ* respiration data from five remote sites along a climatic gradient in the Kalahari of Botswana and to determine the effects of temperature, moisture and biological crust cover on soil CO_2 fluxes. Moisture was the primary limiting factor to efflux which increased with amount of simulated rainfall. On dry soils, mean CO_2 efflux was between 1.5 and 5.9 mg C m^{-2} h^{-1}. After 2 mm and 50 mm simulated wetting, mean rates increased to 4.0 to 21.8 and 8.6 to 41.5 mg C m^{-2} h^{-1} respectively. Once wet, soil CO_2 efflux increases with temperature, and sites at the hotter northern end of the transect lost more CO_2 than cooler southerly sites. Net respiration rates are, however, muted by autotrophic organisms in biological soil crusts which photosynthesise and take up CO_2. The temperature sensitivity of soil CO_2 efflux increased with moisture. Dry, 2 mm and 50 mm treated soils had a Q_{10} of 1.1, 1.5 and 1.95 respectively. Our findings indicate that higher temperatures and a loss of biological crust cover will lead to greater soil C loss through respiration.

1. Introduction

Atmospheric warming is enhancing the global flux of CO_2 respired from soils to the atmosphere leading to concerns over declining soil carbon (C) and increasing atmospheric CO_2 (Bond-Lamberty and Thomson, 2010a,b; Cox et al., 2000). Warming will also lead to more frequent droughts and precipitation changes in many locations (IPCC, 2007) affecting soil properties and processes controlling soil respiration (R_s) rates. In dryland environments, where organic matter is limited, the ecological and agricultural consequences of such changes could be particularly marked. Despite an increasing number of R_s studies in dryland areas (*e.g.* Castillo-Monroy et al., 2011; Inglima et al., 2009; Liu et al., 2009; Sheng et al., 2010; Sponseller, 2007; Thomas and Hoon, 2010) recent reviews suggest we have an incomplete understanding of C cycling in drylands (Conant, 2009; Scholes et al., 2009). *In-situ* data remain rare and our ability to predict the effects of climatic and land use change on soil CO_2 fluxes is limited. How fluxes will be affected by changing air temperatures, moisture availability and land management and the implications of changes for soil C and atmospheric composition remains an urgent interdisciplinary research priority for dryland environments.

The ability to predict R_s rates is important for improving understanding of soil processes and land-atmosphere C fluxes. Most models utilise the relationship between R_s and temperature and are based upon the Arrhenius or van't Hoff equation (Eq. (1)) using the Q_{10} exponential relationship (Davidson et al., 2006),

$$R_s(T) = R_{s0} Q_{10}^{(T-T_0)/10} \quad (1)$$

where R_s is the total soil respiration at temperature T and R_{s0} the respiration at 0 °C. Eq. (1) may not always fit R_s data from field-based studies (Czimczik et al., 2006) particularly in dryland ecosystems where precipitation is infrequent and moisture often limits primary productivity (Noy-Meir, 1973). Lloyd and Taylor (1994) and Davidson et al. (2006) have examined reasons for the complexity in the relationship between temperature and soil respiration. First is the assumption that the temperature sensitivity of enzymes responsible for respiration is linear. Whilst this may be the case over a limited range, it is unlikely at either low or high temperature extremes commonly found in drylands. Second, models do not work at extreme soil moisture conditions as R_s is limited by diffusion of soluble substrates at low moisture and by gaseous diffusion at high moisture. Third, replenishment of soil moisture after extended periods of desiccation typically results in large pulses of CO_2 efflux as microbial populations, activity and substrate availability increases (see Borken and Matzner, 2009 for a review of the processes of pulse

* Corresponding author. Tel.: +44 161 247 1568; fax: +44 161 247 6318.
E-mail address: a.d.thomas@mmu.ac.uk (A.D. Thomas).

0016-7061/$ – see front matter © 2011 Elsevier B.V. All rights reserved.
doi:10.1016/j.geoderma.2011.07.034

generation). In areas of low primary productivity, the availability of soil C may also constrain the response of respiration to temperature, particularly if soils are moist for extended periods (Sponseller, 2007).

Biological soil crusts (BSCs) are also likely to add complexity to the relationship between temperature, moisture and CO_2 efflux. Soils in dryland areas are commonly covered with a BSC which form aggregates of mineral grains with varying proportions of autotrophic and heterotrophic microorganisms (Belnap and Lange, 2003; Büdel et al., 2009). Although typically only a few millimetres thick, BSCs are often the major source of organic C in dryland soils (Elbert et al., 2009; Evans and Lange, 2003; Mager and Thomas, 2011). In most soils, R_s gases contain CO_2 derived from two principal sources: i) heterotrophic microbial respiration resulting from mineralisation of soil organic matter (R_h) and ii) gaseous plant root exudates, termed autotrophic respiration (R_a) (Eq. (2))

$$R_s = R_h + R_a \tag{2}$$

In drylands, BSC will be an important additional component of R_s (Eq. (3a))

$$R_s = R_h + R_a + R_{bsc} \tag{3a}$$

where,

$$R_{bsc} = R_{hbsc} - R_{absc} \tag{3b}$$

and R_{bsc} refers to CO_2 fluxes associated with crust organisms. The terms R_{hbsc} and R_{absc} in Eq. (3b) describe CO_2 release and photosynthetic uptake by heterotrophic and autotrophic organisms in the BSCs. There are few studies which have parameterised the conditions required for photosynthesis in BSCs (see Lange, 2003 as a rare example) or determined BSC respiration (but see Castillo-Monroy et al., 2011 and Elbert et al., 2009). Soil CO_2 fluxes in drylands will therefore reflect the balance between constantly changing rates of uptake and release in BSCs as well as R_h and R_a emissions (Thomas and Hoon, 2010). Throughout this paper we take R_s to mean the net flux of CO_2 from soils to the atmosphere which is the end product of all these processes and reactions.

We present soil CO_2 efflux and subsoil pore space CO_2 concentration data from five remote sites of contrasting mean annual rainfall, temperature regimes and BSC cover along the Kalahari Transect in Botswana. Our objectives were to: i) determine the effects of temperature on CO_2 efflux; and ii) the effects of 2 mm and 50 mm wetting treatment. The data presented in this paper are the first from *in-situ* experiments along the more arid southern end of the Kalahari Transect which show temporal trends in CO_2 efflux together with sub-soil pore space CO_2 concentrations.

2. Material and methods

2.1. Study area

The Kalahari in southern Africa is an ideal region in which to investigate the effects of temperature and moisture on soil characteristics and processes (Swap et al., 2004). Kalahari Sands are a relatively physically uniform substrate over an area greater than 2 million km^2 (Shugart et al., 2004), spanning a regional precipitation gradient from >1000 mm yr^{-1} to <200 mm yr^{-1}. The sandy, low organic matter soils are typically covered by a BSC (Dougill and Thomas, 2004) and have characteristics similar to many other dryland regions notably in Australia and Middle East (Thomas and Shaw, 1991). BSCs in the Kalahari are comprised of a heterogeneous community of bacteria and fungi but cyanobacteria are the dominant autotrophs (Büdel et al., 2009). Differences in mean annual precipitation along the transect manifest in changing net primary productivity and ultimately soil organic C. Wang et al. (2007) found soil organic C increased with mean annual precipitation, reaching a peak at locations in areas corresponding to 400–500 mm yr^{-1}. Quantifying R_s at sites along the Kalahari transect provides an opportunity to investigate the influence of different temperature, photosynthetically active radiation (PAR) regimes and soil organic C on R_s.

Field research was undertaken over the austral winter in July and August 2008 at five sites along the Kalahari Transect (Fig. 1). Mean annual precipitation ranges from 220 mm yr^{-1} at Khawa to 420 mm yr^{-1} at Ngami (Table 1). The northern end of the transect overlaps the southern portion of the International Geosphere–Biosphere Programme (IGBP) Kalahari Transect used in related studies (Shugart et al., 2004; Swap et al., 2004). Extension of the transect into drier parts of the Kalahari (Khawa and Tsabong) is important because models predict widespread desiccation across southern Africa (Hewitson and Crane, 2006; IPCC, 2007) consistent with analyses showing decreased rainfall across Botswana from 1975 to 2005 (Batisani and Yarnal, 2010).

Four of the sites (Khawa, Tsabong, Takatshwaane and Ngami) were undisturbed by domestic animals and BSC cover was correspondingly high (>80%). Tshane, however, had a much lower BSC cover (*c.* 10%) as a result of frequent grazing. At all sites, BSCs were classified as type 1 or 2 under the scheme outlined in Dougill and Thomas (2004) and were typically 2–7 mm thick. The total N and C and organic C content of the crusts was low (Table 1) with C:N ratios between 9.6 and 14.8. The absence of carbonate sources in close proximity to the sites (sites were located away from calcrete pans and on dune flanks) meant most of the soil C was organic (Table 1). Tsabong, where the crusts were best developed, had significantly more total C

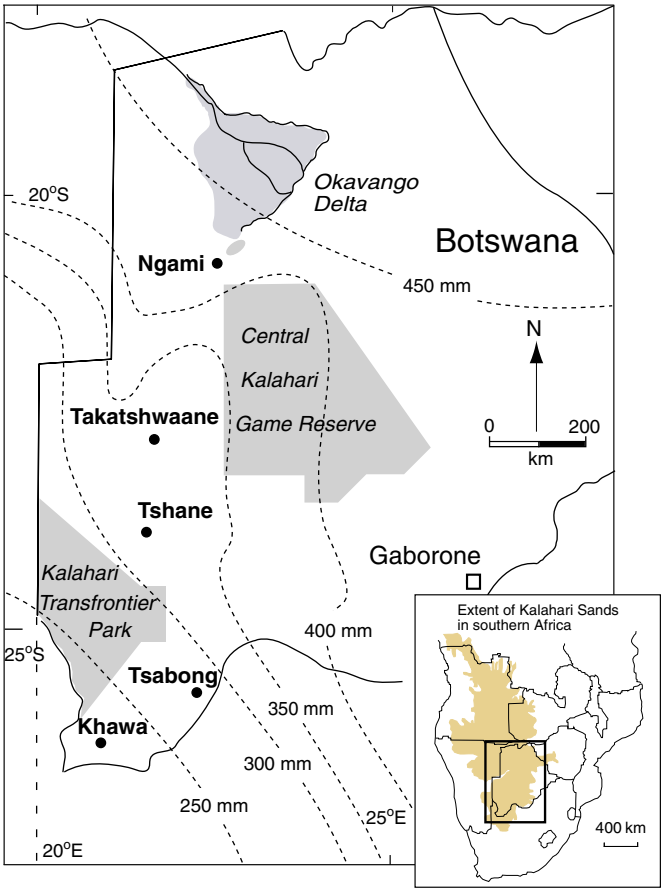

Fig. 1. Study site locations.

Table 1
Study sites and soil characteristics.

Site	Location	Mean annual precipitation	Site description
a. Site location and characteristics			
Khawa	S 26° 25′ 40.7″ E 21° 35′ 39.2″	220 mm	Ungrazed, grass dominated landscape.
Tsabong	S 25° 56′ 51″ E 22° 25′ 40″	290 mm	Experiments conducted within a bounded plot where grazing excluded.
Tshane	S 24° 11′ 49.6″ E 21° 51′ 53.7″	340 mm	Heavily grazed. Woody shrub and tree dominated landscape. No grass cover.
Takatshwaane	S 22° 47′ 11.7″ E 21° 57′ 34.3″	350 mm	Lightly grazed. Mixed shrub, tree and grass landscape.
Ngami	S 20° 43′ 57.0″ E 22° 30′ 36.1″	420 mm	Lightly grazed. Dense grass cover and mix of trees and shrubs.

Site	Cover, type and thickness	pH	Total N (%)	Total C (%)	Organic C (%)	C:N ratio
b. BSC cover, type, thickness, N and C content						
Khawa	90% type 1–2 3 mm thick	6.91 ± 0.04	–	–	0.18 ± 0.03	–
Tsabong	90% type 2 5 mm thick	5.61 ± 0.03	0.037 ± 0.01	0.547 ± 0.03	0.511 ± 0.04	14.8
Tshane	10% type 1 2 mm thick	5.58 ± 0.03	0.040 ± 0.02	0.386 ± 0.02	0.400 ± 0.08	9.65
Takatshwaane	85% type 2 3 mm thick	6.12 ± 0.07	0.045 ± 0.01	0.468 ± 0.04	0.506 ± 0.04	10.4
Ngami	60% type 1–2 3 mm thick	6.47 ± 0.06	0.041 ± 0.01	0.453 ± 0.02	0.447 ± 0.03	11.1

*n = 8 (standard error in parentheses) refers to the number of samples analysed to produce the data in part b of this table.

than other sites ($p > 0.01$). Khawa, at the arid end of the transect, had the lowest organic C. Total C was also low at Tshane where grazing disturbance was greatest and BSC cover lowest.

2.2. Field instrumentation and experiments

CO_2 flux measurements were determined over 2 days at each site using five purpose-built static respiration chambers (based on a design described in Hoon et al., 2009). Chambers were located in plant interspaces on treated and untreated soils: one un-wetted control and two replicates each for 2 mm and 50 mm wetting treatments. Prior to the first measurement, a pipette was used to carefully drop water onto the soil surface within and immediately surrounding the chambers for the 2 mm treatments. For the 50 mm treatments, a bund (0.5 m × 0.5 m) was placed around the chamber and the requisite depth of water poured carefully and slowly onto the surface. The first gas samples were taken as soon as practicable after wetting was completed and measurements made for a further 2 days. Surface and sub-soil moisture was determined using a HH2 moisture meter and a Delta-T ML2x theta probe (Delta-T Devices, Cambridge, UK) in adjacent soil pits before and during the simulated rainfall experiments.

The chambers had a volume of 510 ml and enclosed 106 cm^2 of soil. They were inserted to a depth of *c.* 35 mm to ensure a good gas seal. To prevent significant changes in CO_2 concentration altering soil–atmosphere diffusion rates the chambers were purged and vented at a flow rate of 0.75 l min^{-1} for 10 min hourly by drawing ambient air from a buffer chamber. Low pressure two-way vent valves permit pressure differences between the chamber and the atmosphere to equilibrate rapidly preventing alteration of CO_2 flux rates. The chambers incorporated a thin borosilicate glass window to permit solar illumination of the soil. PAR irradiance was measured using a QS2 Quantum Sensor (Delta-T Devices, Cambridge UK). High thermal conductivity heat sinks ensure that the internal air temperature tracks ambient air to within 1 °C throughout the full diurnal cycle. Chamber soil surface, air temperature, humidity and ambient (site) temperature and humidity was logged at 10 minute intervals by a combination of thermistors and USB 502 and 5203 loggers (Adept Science, UK). Thermistors coupled to the 5203 logger also recorded subsoil temperature at depths of 15 and 30 mm. The complete system was solar powered enabling deployment at remote sites.

2.3. Determination of C flux from CO_2 chamber data

Within each measurement cycle three samples were taken from the chambers at 15 minute intervals in order to determine the change in CO_2 concentration over time. Representative sampling of the chamber atmosphere was ensured by gentle mixing via internal electric fans for 5 min prior to sampling. Samples were extracted using a gas syringe and 16 ml injected into 12 ml pre-evacuated Exetainer® borosilicate vials (Labco, High Wycombe, UK). Over-pressurising the vials, together with an additional wax seal around the caps prevented air ingress and contamination during transport. CO_2 concentrations were determined using an Agilent gas chromatograph (GC 3000) as soon as practicable on our return to the U.K. A least squares fit was applied to the change in CO_2 over time and used to determine the average rate of change in concentration over the experimental interval prior to diffusion correction. The gradual enrichment of CO_2 in the head space of a static respiration chamber alters the natural diffusion of respired CO_2 from the soil (Pumpanen et al., 2004). This effect has been corrected for using a three-term polynomial function determined by undertaking calibration experiments. Changes in CO_2 concentration were converted to mass flux in mg m^{-2} h^{-1} corrected to the mean experimental temperature and pressure. Negative fluxes are indicative of net CO_2 uptake to the soil and positive fluxes of net release.

2.4. Spatial variability and replication

The remote locations of the field sites constrained the number of chambers it was logistically possible to support. Consequently, chamber replication is limited to duplication for the treated soils. In a subsequent experiment at Tsabong, however, we quantified CO_2 efflux within six chambers located in close proximity to each other at a range of soil moisture contents over 7 days. Variation in CO_2 efflux from each chamber was determined by the standard error of the mean which was 18% on Kalahari Sand soils. We make the assumption in this study that variations in flux between

chambers due to treatment should be greater than this value to be significant.

2.5. Subsurface CO_2 pore space concentrations

Changes in pore space CO_2 concentrations in response to the 50 mm wetting treatment were determined at each site by subsoil gas sampling at depths of 0.06 m, 0.15 m, 0.3 m and 0.6 m in a soil pit using the method of Thomas and Hoon (2010). Subsoil gas samples were collected on 8 occasions at each site, the first prior to the application of the water treatment and at 7 regular intervals thereafter. Subsoil CO_2 concentrations were determined using the GC.

2.6. Temperature sensitivity of soil efflux

Eq. (1) was used to derive estimates of the temperature sensitivity of R_s (Q_{10}) of soils across all five sites for the three moisture conditions. Because the van't Hoff model assumes the system is in steady state the first three measurements of the post-50 mm treatment efflux pulse were omitted from the analysis. These transient fluxes result from gas displacement and metabolic activity triggered by the recent arrival of the pulse of post wetting soil moisture and are consequently far from the equilibrium implicitly assumed by Eq. (1). To ensure unbiased fitting of the data, T_0 was set at 0 for all treatments and Q_{10} and R_0 changed to generate the best fit within the measured temperature range. This was determined by optimisation of the correlation coefficient and root mean squared error (RMSE). This fitting procedure avoids the need to determine or calibrate soil respiration at a particular temperature (*e.g.* 0 or 10 °C).

3. Results

3.1. R_s and water treatment

Fig. 2 shows the temporal variations in R_s and PAR over 45 h for all treatments by site. The peak and range of CO_2 flux from dry soils was low at all sites even when compared to other fluxes reported from dry

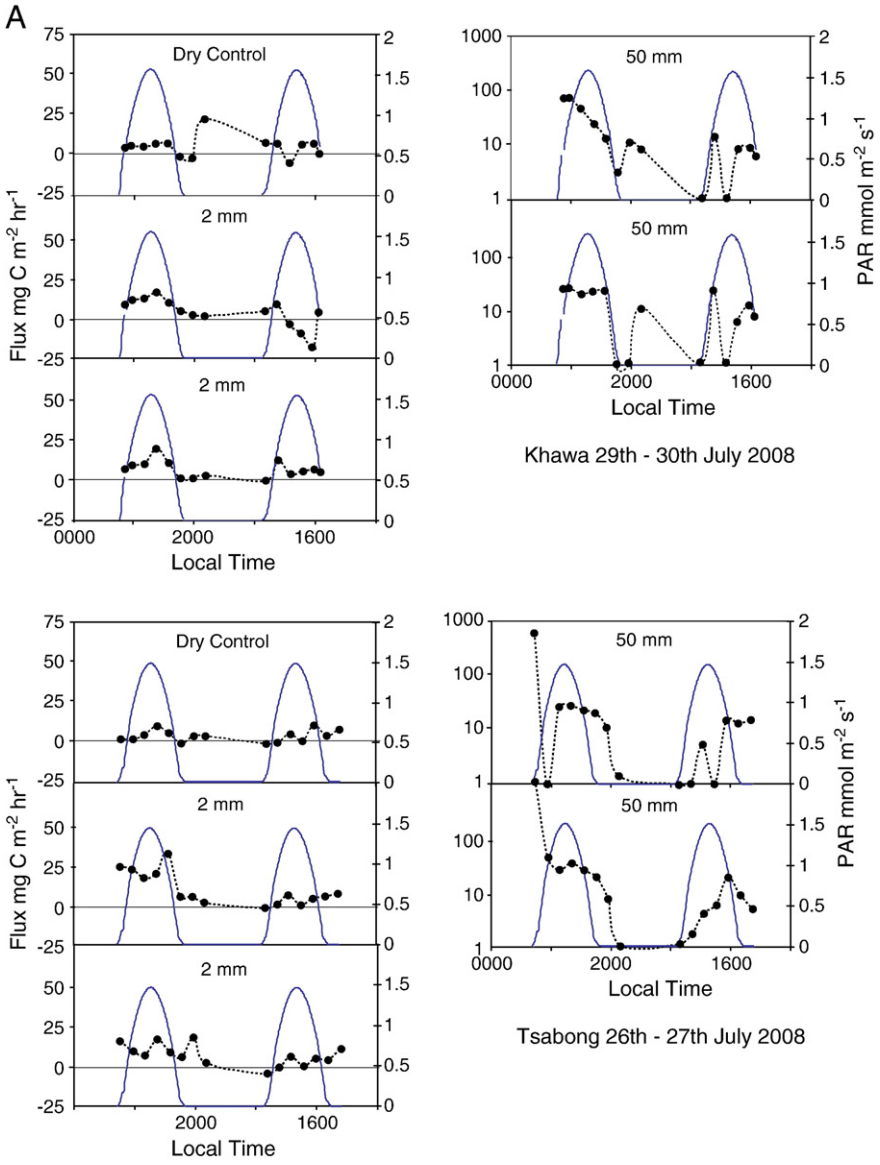

Fig. 2. Diurnal variations in soil CO_2 efflux (mg C m^{-2} h^{-1}) (black circles and dotted lines) and PAR solar irradiance (mmol m^{-2} s^{-1}) (solid line) at each site. Wetting treatment occurred immediately prior to the first measurement. Note the logarithmic scale for efflux after 50 mm wetting treatment. A) Khawa 29th–30th July 2008 and Tsabong 26th–27th July 2008. B) Tshane 2nd–3rd August 2008 and Takatshwaane 7th–8th August 2008. C) Ngami 5th–6th August 2008.

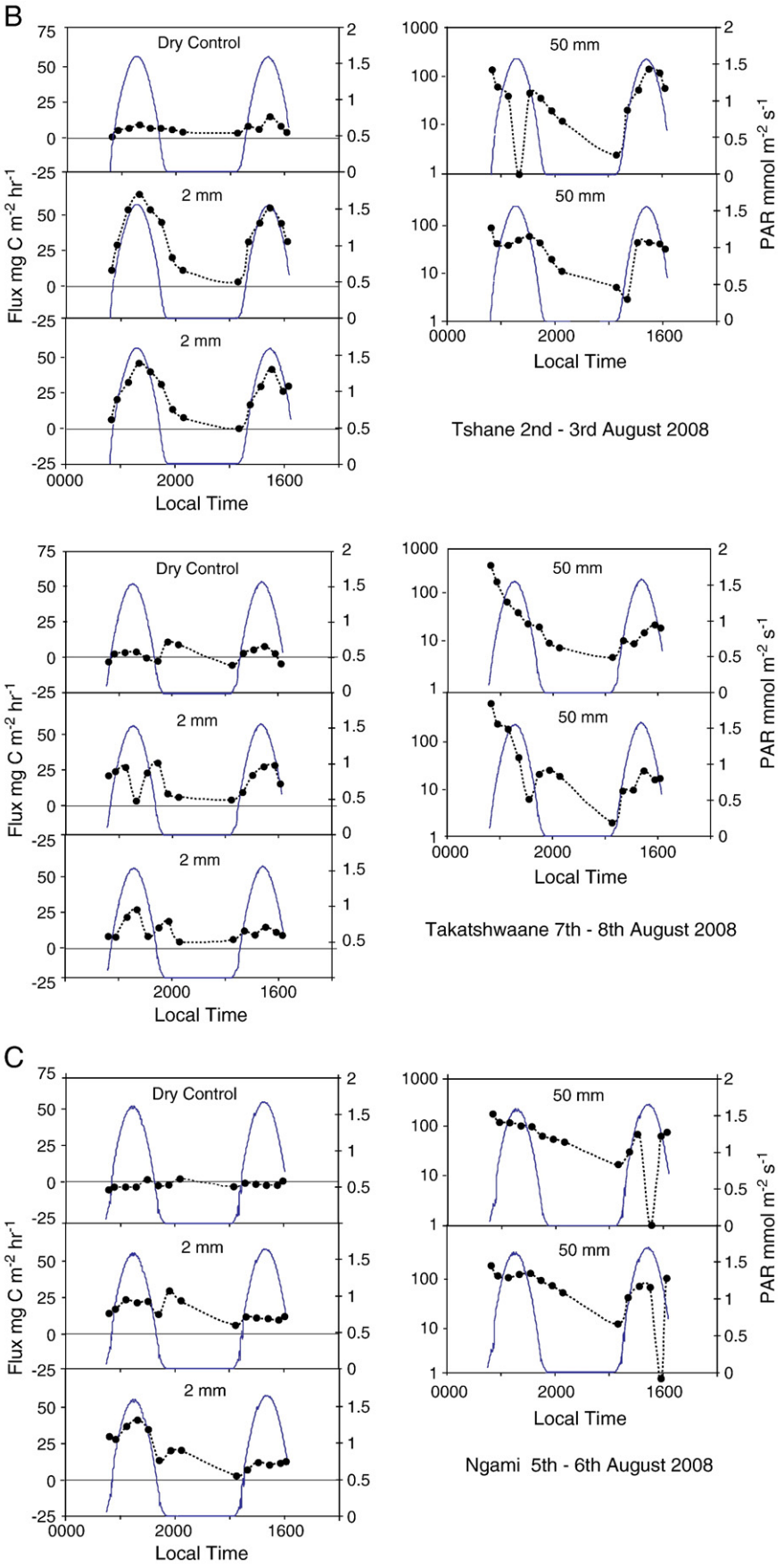

Fig. 2 (*continued*)

environments (Table 2). Highest positive R_s hourly rates varied from 22.7 mg C m^{-2} h^{-1} at Khawa to 5.6 mg C m^{-2} h^{-1} at Ngami. Lowest hourly R_s rates were all negative (net uptake to the soil) ranging from −1.3 mg C m^{-2} h^{-1} at Tsabong to −5.1 mg C m^{-2} h^{-1} at Khawa. At no time during any of the experiments were there sustained periods of C uptake to the soil. Lowest fluxes occurred in the hour after dawn when air and soil surface temperatures were coldest, increasing with temperature throughout the first day at each site. Increases in R_s in the hours after dawn were particularly marked at Khawa (Fig. 2a) and Takatshwaane (Fig. 2b). On the second day there was greater diurnal variability in R_s with notable declines in flux rates during the daytime at Khawa and Takatshwaane.

The 2 mm wetting treatment resulted in higher peak values and a greater range of R_s fluxes compared to dry soils at all sites. Lowest R_s rates typically occurred just after dawn. Periods of net C uptake occurred at all sites except Ngami but only for a short time and again usually in the early mornings. Although peak R_s usually corresponded with the highest air (and surface soil) temperatures, diurnal variations were complex and there were often double peaks during the daytime, indicative of the competing processes of uptake and release coming in and out of phase with changing light and temperature. Nevertheless, it is clear that moisture is a major limiting factor to metabolic activity and that wetting the soil surface stimulated R_s over the measurement period.

The 50 mm treatment resulted in a short-lived pulse of CO_2 immediately after wetting at all sites, although the pulse magnitude varied considerably (note the scale change in Fig. 2 for the 50 mm wetted soils). The high flux rates rarely lasted more than a few hours and the day after water treatment they were much lower but generally rising with temperature. Peak hourly CO_2 efflux rates were 73.4 mg C m^{-2} h^{-1} at Khawa but >1000 mg C m^{-2} h^{-1} in one chamber at Tsabong. Peak CO_2 fluxes at Tshane, Takatshwaane and Ngami after 50 mm wetting were 142, 559 and 193 mg C m^{-2} h^{-1} respectively.

3.2. Subsoil temperature, moisture and pore space CO_2 concentrations

The depth-moisture profiles of the soils at each site before and at two times after the 50 mm wetting treatment are shown in Fig. 3. Prior to treatment, the moisture content of the upper 0.05 m of soils at all sites was below detection limits. Moisture profiles at greater depths were initially different at each site, reflecting recent local precipitation, soil hydrological properties and evaporation rates (Fig. 3). The application of 2 mm water, initially fully wetted the top 4–7 mm of BSC and soil before rapidly draining to field capacity. The application of 50 mm water resulted in similar moisture-depth profiles at all sites with peak moisture content of *c.* 12% v/v down to *c.* 0.25 m. Initial infiltration rates were rapid as moisture moved down the soil profile (Fig. 3). Unsaturated subsoil wetting front velocities were also rapid for the first hour after treatment (*c.* 9.3 m day^{-1} at Tsabong) before slowing over the following 24 h to rates between 1.5 to 4.6 m day^{-1}. As field capacity is approached (~8% v/v) subsoil drainage rate decreases to between 0.07 and 0.1 m day^{-1}. The soil just below the surface remained moist at all sites for the duration of experiments.

Prior to wetting, subsoil pore space CO_2 concentrations ranged from 550 to 800 ppm v/v (Fig. 3). Higher CO_2 concentrations were

Table 2
Soil CO_2 efflux rates from studies in moisture-limited environments. All data have been converted to mg C m^{-2} h^{-1} to aid comparison with data from this study.

Authors	Location	MAT and MAP	Land use/vegetation	Measurement duration	Mean soil CO_2 efflux (mg C m^{-2} h^{-1})
Thomas et al. (this study)	SW Kalahari Transect	220–420 mm.	Mixed grass, shrub and acacia savanna	Days	Dry: 1.48 to 5.86 Wet (2 mm): 4.03 to 21.8 Wet (50 mm): 8.61 to 41.5
Thomas and Hoon (2010)	SW Kalahari, Botswana	20.6 °C. 297 mm	Mixed grass, shrub and acacia savanna	Days	Dry: 2.8–14.8 Wet peak (1.4 mm): 65.6 Wet peak (120 mm): 339.2
Inglima et al. (2009)	Pianosa Island, Tuscany	17.0 °C. 400 mm	Ex-agricultural land	Days	Dry: 108 Wet (40 l m^{-2}): 194
Liu et al. (2009)	Duolun County, Inner Mongolia, China	21.1 °C. 386 mm	Steppe	Bi-monthly over 2 years	Wet season peak: 97.6 Dry season minimum: 66.1
Liu et al. (2002)	Oklahoma, USA	–	Tallgrass prairie	Days	Dry: 8.64–95.0 Wet (10 and 50 mm): 346 Wet (150 mm): 173
Millard et al. (2008)	La Copita, southern Texas, USA	22.4 °C. 716 mm	Subtropical savannah grassland	Days	Dry (mid canopy): 43.2 Wet (50 mm): 307
Tang et al. (2003)	Ione, California, USA	16.3 °C. 558.7 mm	Oak-grass savanna	Daily over 2 weeks	Mean daily rate: 16.0
Maestre and Cortina (2003)	Aigües de Busot, SE Spain	16 °C. 388 mm	Mediterranean semiarid steppe	Monthly over 5 months	Bare ground: 1.8 Grass site: 13.4
Castillo-Monroy et al. (2011)	Aranjuez experimental station, central Spain	13.8 °C. 388 mm	Mediterranean semiarid grassland	Monthly over 3.5 years	Dry year: 27.4 Wet year: 36.8
Sponseller (2007)	Sonoran Desert, Arizona, USA	300 mm at 500 m 600 mm >1200 m	Velvet mesquite	Days	Dry below plants: 50 to 130 Dry under plant Interspaces: 30 to 70 Peak post-wet plants: 430 to 2200 Peak post-wet interspaces: 90 to 690
Almagro et al. (2009)	NW Murcia, SE Spain	15.5 °C. 370 mm	Aleppo pine, olive grove and ex-agricultural	Monthly over 2 years	Forest: 89.0 ± 3.02 Abandoned field: 7.40 ± 3.9 Olive grove: 48.4 ± 5.2
Jin et al. (2009)	Ordos Plateau, Inner Mongolia, China	6.7 °C. 345 mm	Grass/shrubland	Days	Dry under plants: 25.1 ± 2.95 Dry BSC : 22.0 ± 4.45 Dry bare soil: 11.4 ± 1.09 Wet (3 mm) under plants: 57.0 ± 4.58 Wet (3 mm) BSC: 47.8 ± 4.94 Wet (3 mm) bare soil: 22.87 ± 5.78
Jin et al. (2007)	Ordos Plateau, Inner Mongolia, China	6.7 °C. 345 mm	Grass/shrubland	Bi-monthly over 6 months	Dry min: 13.6 ± 4.09 Max wet: 40.9 ± 27.3
Shen et al. (2008)	Mojave Desert, Nevada US	141.2 mm	Perennial/deciduous shrubs, grasses and forbs	Monthly over 6 months	Ad Min (dry season): 5 ± 1.7 Peak (wet season): 13 ± 10

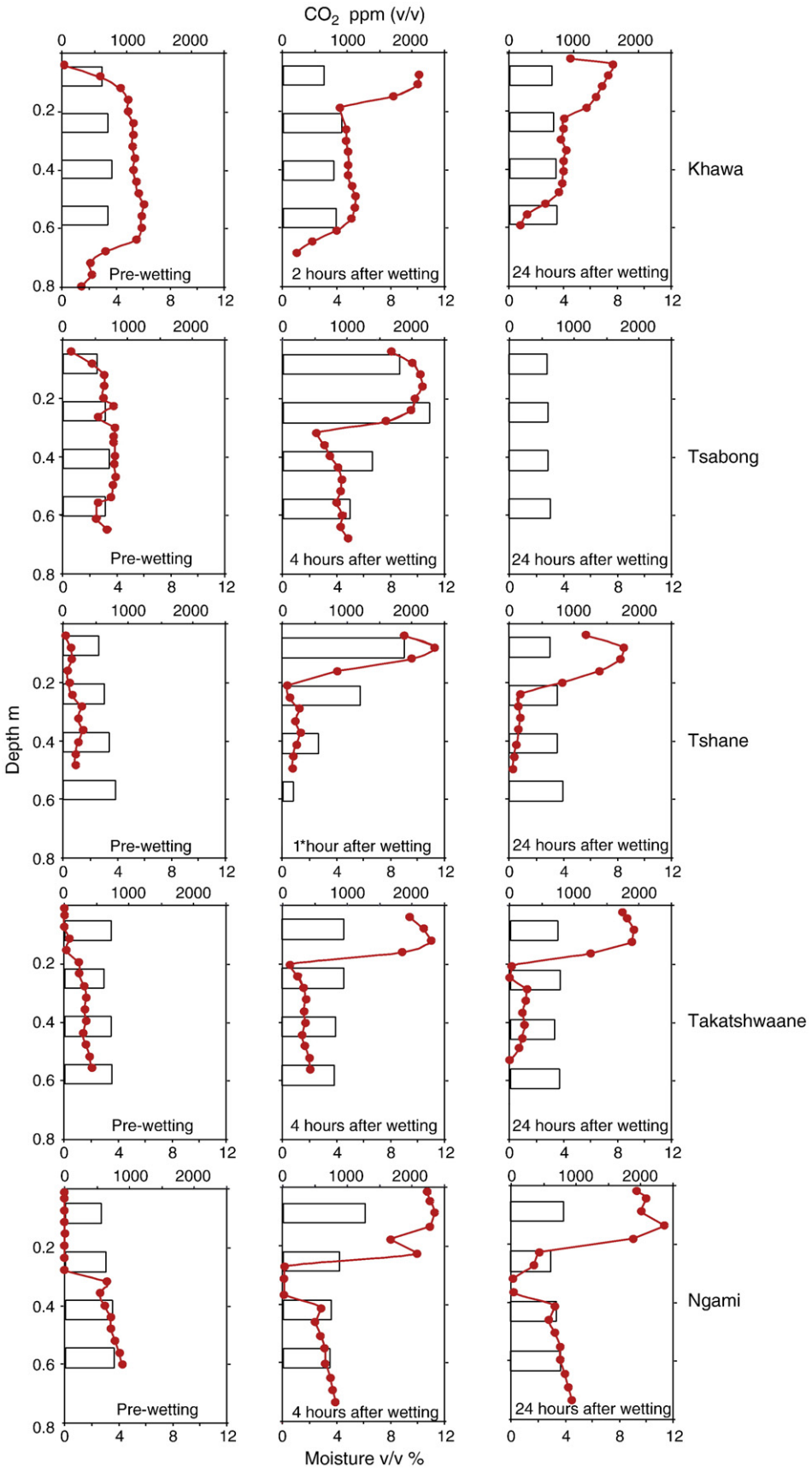

Fig. 3. Temporal changes in subsoil pore-space CO_2 concentrations (bars) and soil moisture (circles) before and after the 50 mm wetting treatment.

found at the deeper soil levels (0.35–0.5 m) where both soil moisture and transport time to the surface is greater. The CO_2 concentrations are indicative of low levels of heterotrophic soil microbial activity (R_h) as well as low photosynthetic activity by vascular plants and gaseous root exudates (R_a). In the hours immediately after wetting, pore space CO_2 concentrations increased slightly at Khawa, Takatshwaane and Ngami (Fig. 3). The greatest increases were seen at Tsabong and Tshane, were peak concentrations exceeded 2000 ppm v/v and 1400 ppm v/v respectively. All increases were short-lived, and 24 h after wetting, CO_2 concentrations returned close to pre-treatment levels.

3.3. Soil respired C losses

The integral of CO_2 flux was used to calculate net cumulative changes in C in each chamber over the duration of the experiments. The total net change was normalised to 24 h to provide an estimate of mean daily C losses in respired gases (Fig. 4). Daily net loss of C from the dry soils ranged from a low of 32.7 mg C m^{-2} day^{-1} at Ngami to a high of 140.6 mg C m^{-2} day^{-1} at Khawa where pre-treatment soil moisture content was significantly greater than the other sites (Fig. 3). Wetting treatment increased CO_2 efflux at all sites, with the exception of the 2 mm treatment at Khawa where efflux was less than the control. Daily net C losses after the 2 mm treatment ranged from 96.8 ± 31.1 to 524.8 ± 144.0 mg C m^{-2} day^{-1} and after the 50 mm treatment from 206.6 ± 45.0 to 994.8 ± 1.0 mg C m^{-2} day^{-1}. Respired C losses from the soil were greatest at the three more northerly sites where the mean daily air temperature was greatest.

3.4. Temperature sensitivity of R_s

Wetting treatment resulted in similar moisture profiles at all sites (Fig. 3). This facilitated the grouping of data from all five sites according to treatment and enhanced the ability to determine the temperature sensitivity of the efflux. When dry, R_s does not respond to temperature and the Q_{10} is 1.1 with only a poor fit to the measured data ($r^2 = 0.14$ and RMSE 0.14) (Fig. 5). However, after the 2 mm wetting treatment, the temperature sensitivity of R_s increases with a Q_{10} of 1.5 and the model is an improved fit to the measured data ($r^2 = 0.36$ and RMSE 12.2). The temperature sensitivity of R_s after 50 mm wetting is even higher with a Q_{10} of 1.95 and the model fit is also improved ($r^2 = 0.45$ and RMSE 25.9).

4. Discussion

CO_2 efflux rates are low in the Kalahari compared to other moisture-limited locations (Table 2). Our mean winter dry season rates (1.5 to 5.9 mg C m^{-2} h^{-1}) are similar to those reported by Maestre and Cortina (2003) for bare ground in central Spain and dry season rates in the Mojave (Shen et al., 2008). Responses to wetting are significant but short lived. Mean fluxes after 2 mm (4.0 to 21.8 mg C m^{-2} h^{-1}) and 50 mm (8.6 to 41.5 mg C m^{-2} h^{-1}) are comparable to wet season average rates in southern Spain (Castillo-Monroy et al., 2011), wet season rates in the Mojave (Shen et al., 2008) and rates on biologically crusted soils on the Ordos Plateaux, Inner Mongolia (Jin et al., 2007). The relatively low efflux rates most likely reflect the low soil organic C content of the soils (Table 1) and the winter temperature regime.

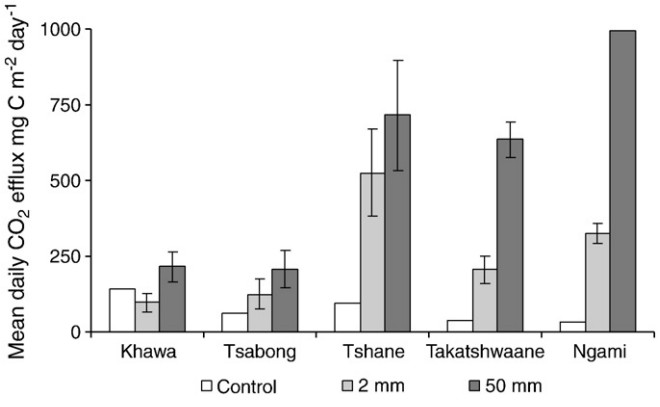

Fig. 4. Mean daily soil CO_2 efflux (mg C m^{-2} day^{-1}) at each site for each treatment type. Error bars are the standard deviation.

4.1. R_s and moisture

R_s rates increased with soil moisture confirming that microbial activity is primarily limited by moisture. Adding water to the crust (2 mm) and to crust and subsoil (50 mm) led to increases in the magnitude and range of fluxes at all sites (Fig. 2). Light rainfall events are common across the Kalahari especially at the start of the wet season and will have an important effect upon R_s and the total CO_2 respired and sequestered over a year. Large rainfall events ($\geq$50 mm) typically occur once or twice a year and are responsible for generating large, discrete pulses of CO_2 (Scholes et al., 2009). The 2 mm wetting treatment results in modest increases in flux due to the stimulation of heterotrophic activity in the BSC. There were net losses of C from soils at all sites over the duration of the experiments implying that CO_2 uptake by crust organisms due to photosynthesis was less than the CO_2 released by R_h and R_a.

The 50 mm treatment generated large, but short-lived, pulses of CO_2 efflux at most sites. Veenendaal et al. (2004) using eddy covariance to monitor ecosystem fluxes at the onset of the first rains reported large CO_2 pulses of 3–5 μmol m^{-2} s^{-1} near Maun at the northern end of our transect. They attributed these pulses to contributions from R_s. Wang et al. (2007) also reported a 10-fold increase in soil respiration after wetting at sites in Tshane, Ghanzi and Pandamatenga which is similar to the *c.* 8-fold increase we found at most sites after 50 mm wetting (Fig. 4). Previous work at the Tsabong site established that heavy wetting results in large amplitude short duration pulses of CO_2 (up to 339 mg C m^{-2} h^{-1}) from Kalahari Sand soils and that, given sufficient moisture, fluxes increase with temperature (Thomas et al., 2008). Our new data show that as the wetting front moves down the soil profile, water displaces the soil pore atmosphere and changes CO_2 concentrations with depth (Fig. 3). However, pore space gas displacement alone is insufficient to explain the large changes in CO_2 fluxes observed as the pore spaces contain only low CO_2 concentrations (<800 ppm) prior to wetting. Although there are areas of carbonate rich soils in the Kalahari (Thomas and Shaw, 1991) the soils at our sites contained little inorganic C (Table 1) and carbonates are unlikely to be a major source of CO_2 (*c.f.* Emmerich, 2003). Autotrophic respiration from plant roots is also unlikely to be a significant source of the R_s pulse as the infiltrating water did not reach the rhizosphere of trees and shrubs and it will have formed an effective gas diffusion barrier to sources from deeper in the soil. The rapidity of the response and the timing of the experiments in the dry season also suggest it was not due to greater photosynthetic activity in vascular plants. Thus the high magnitude CO_2 pulses associated with the 50 mm treatment can only be explained by an additional contribution from heterotrophic microbial respiration of C sources in the subsoil.

Fierer and Schimel (2003) suggest the source of C in newly wet soil CO_2 efflux are either microbial or soil organic matter in origin. Organic matter can be rendered accessible to microbial attack as a result of the breaking up of aggregates during wetting (Denef et al., 2001) or from a subsequent increase in zymogenous microbial populations. However, Kalahari Sands contain negligible amounts of humus with the majority of soil C labile and associated with exudates from

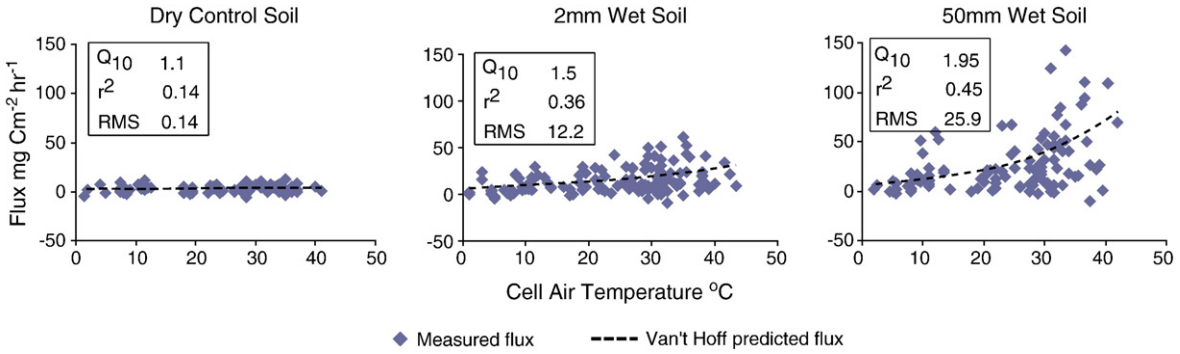

Fig. 5. The relationship between soil CO_2 efflux and chamber air temperatures. Line represents the van't Hoff/Arrhenius equation fit to dry, 2 mm and 50 mm treated soils for all five transect sites.

microbial organisms (Mager and Thomas, 2011). Some soil microorganisms will die as a result of prolonged desiccation, providing a readily available substrate for the survivors to respire (Luo and Zhou, 2006) and rapid wetting can also lead to osmotic shock and the death of some microbial cells (Borken and Matzner, 2009). The transient nature of the surface pulse and subsoil CO_2 increases after heavy wetting is indicative of soils which have a limited and rapidly exhaustible supply of available C. The most likely process producing the CO_2 pulse is therefore respiration of available C, possibly originating from the BSC, by surviving populations of heterotrophic bacteria and fungi stimulated by the increase in soil moisture and fresh substrate released by lysed cells.

After the initial pulse of CO_2 diminished, fluxes varied with temperature and for short periods resulted in negative fluxes (net uptake) at all sites except Takatshwaane. Similar short periods of net uptake were also seen in the dry control and 2 mm wetted chambers. There is some evidence that the low light and temperatures of the early morning favour uptake (Fig. 2). On dry soils this is likely to be caused by dew facilitating photosynthesis. The finite porosity of Kalahari Sand soils means that pore spaces in the upper soil profile became filled after the 50 mm wetting treatment, resulting in a temporary barrier to diffusing gases originating from deeper in the subsoil, effectively isolating the surface soil and crust as the contributors to efflux. In our study, periods of net uptake of CO_2 to the soil indicate that photosynthesis is occurring in the crust component at least for short periods once the moisture content of the BSC has decreased sufficiently.

4.2. R_s and temperature

The temperature sensitivity of R_s increases with soil moisture (Fig. 5). The Q_{10} of dry soil and after wetting with 2 mm and 50 mm water was 1.1, 1.5 and 1.95 respectively. This shows that under dry conditions temperature has little effect on flux. Once wet, increasing temperatures lead to greater R_s, particularly when both the subsoil and BSC are moist. Soil organic matter and C stored in Kalahari Sands has a number of characteristics that make R_s particularly temperature sensitive when wet. Firstly, the majority of C is associated with BSCs, either as microbial biomass or their secretions (Thomas and Dougill, 2007; Wang et al., 2007). Most C is therefore close to, or at, the soil surface and there is a very rapid decrease in soil organic matter with depth below *c.* 1 cm. Consequently, there is very little thermal buffering of the soil C store and the crust will rapidly equilibrate with air temperatures, thus coupling microbial processes with current climatic conditions. Further, most C is in a labile form and mineralisation activation energies are lower than for the heterogeneous mix of organic matter in a typical mesic soil. This helps to explain why Eq. (1) is a reasonable predictor of flux when soils are wet. That the Q_{10} values of wetted soils are toward the lower range reported for most other global soil types (Bond-Lamberty and Thomson, 2010a) suggesting that the R_s values are dampened by autotrophic microbial activity in the BSC. Increasing temperatures when soils are wet can also mean greater CO_2 uptake as well as release. Thus, when not limited by moisture, soil microbial activity does increase with temperature but the full effects are masked by autotrophic activity in the BSC.

4.3. R_s and biological soil crusts

The relative complexity of diurnal variation in efflux can be explained by differences in the relative contributions of R_a, R_h and R_{bsc} to soil efflux. There were periods of net CO_2 uptake at all sites when photosynthesis exceeded respiration of all soil organisms and roots (Fig. 2). Because BSC organisms can utilise very small amounts of moisture from dew events that will be inaccessible to plant roots and microorganism in the subsoil, the relative contribution of BSC to efflux is likely to be greatest when soils are dry. Temporal variation in metabolic behaviour of BSC organisms is, however, difficult to determine on the basis of R_s measurements alone. Our temporal data suggest that net uptake is most likely in the early morning when a window of optimal conditions for CO_2 uptake occur. These are, however, short-lived as the moisture from dew is rapidly evaporated. Consequently soil C is particularly vulnerable to changes in temporal patterns of precipitation and evapotranspiration.

Four of the sites had an extensive and well developed BSC cover (Table 1). At Tshane, however, intensive cattle grazing inhibited BSC development and cover. This, we suggest, is the reason for the high C losses at the Tshane site after the 2 mm rainfall treatment. The data suggest that inhibition of BSC development leads to a reduction in C input from autotrophic organisms and consequently greater R_s losses. It is well established that BSCs are susceptible to disturbance and degrade due to disturbance from animals and burial under wind-blown sediment. Damage and disruption to the BSC microenvironment and structure also adversely affects the composition and metabolic activity of the organisms and their ability to fix CO_2 (Belnap, 1996; Lalley and Viles, 2006). Soil crusts that were sequestering CO_2 can rapidly become a net source of CO_2 if disturbed, making dryland R_s sensitive to animal stocking densities and cultivation methods. This has important consequences for any intensification of grazing in the Kalahari which would lead to a reduction in BSC cover (Thomas and Dougill, 2006) and thus potentially could release further CO_2 into the atmosphere.

4.4. Consequences of future changes to soil CO_2 efflux

Before the consequences of soil CO_2 efflux on soil C stores and fertility can be determined, it is important to determine the proportion of efflux that originates from BSCs, heterotrophic and autotrophic respiration because of the age and type of C involved in each process. CO_2 respired from roots is recently sequestered during photosynthesis and represents 'new' soil C. Increases in CO_2 efflux driven by greater autotrophic respiration would have few, if any,

long-term consequences for soil C or atmospheric CO_2 as respiration C losses are matched and driven by greater biological productivity and C uptake. In contrast, heterotrophic soil microbes mineralise organic matter of varied composition and age and the respired CO_2 will contain C that has been resident in the soil for a longer time than C in the autotrophic component of efflux. The temperature driven increase in soil CO_2 flux reported here is a concern because it is likely occurring independently of C inputs from plants. This represents a net loss of previously stored soil C and a potential process of soil quality deterioration.

More information is also required on the soil microbial ecology of the Kalahari as this will have an important regulatory effect on soil C cycles. Dryland soils contain enzymes that can decompose proteins and recalcitrant C compounds (lignins, humic substances) at very low moisture contents (Zeglin et al., 2007). Fungi are also likely to play a significant role in the decomposition of organic matter as they can metabolise at higher temperatures and lower water potentials than either plants or bacteria (Collins et al., 2008; Crenshaw et al., 2008). Furthermore, abiotic processes, particularly photo-oxidation of surface litter (Austin and Vivanco, 2006) will continue to decompose surface organic litter even when it is too dry for net primary productivity and microbial activity (Collins et al., 2008).

5. Conclusions

This paper presents new *in-situ* R_s and subsoil pore-space CO_2 concentrations data from biologically crusted soils at five sites along the Kalahari Transect in Botswana. By manipulating soil moisture through experiments undertaken in the austral winter the effects of wetting both the surface crust and the deeper subsoil on R_s were quantified. The data were used to determine the temperature sensitivity of R_s at the different moisture conditions using a van't Hoff/Arrhenius model (Eq. (1)). Limited replication and the single season data set, however, limit the broader conclusions that we can safely draw from this study.

Soil microbial activity and CO_2 efflux was limited by moisture at all locations. Wetting the BSC led to an immediate increase in the magnitude and range of CO_2 released by respiration of organisms in both the crust and subsoil. Wetting of the crust and subsoil led to short-lived but large efflux peaks of CO_2 from soils. This was due to the stimulation of heterotrophic soil microbes utilising the limited supply of labile C. There were short periods of net CO_2 uptake on dry and lightly wetted soils, particularly in the early mornings showing that autotrophic BSC organisms can utilise the low amounts of moisture from dew events. That the autotrophic organisms in BSCs can mask respiration from crust heterotrophs suggests that photosynthetic activity is significant, at least over short periods and that without this input C losses in respired gases would be significantly higher.

Under dry conditions temperature has little effect on CO_2 flux but once wet, the temperature sensitivity of R_s increases with soil moisture to a maximum Q_{10} of 1.95 after 50 mm wetting. The temperature sensitivity of R_s is in part due to the importance of BSCs to soil organic C storage in dryland soils. Most C is in a labile form, close to the surface, and mineralisation activation energies will be relatively low. When not limited by low moisture, soil microbial activity increases with temperature but the full effects of this on CO_2 release are masked by autotrophic activity in the BSC leading to some photosynthetic uptake.

The implications of greater respired C losses depend on the source of the C. Our data suggest that during the austral winter, temperature-driven increases in respiration are a concern because increases are occurring independently of C inputs from plants and thus represent a net loss of previously stored soil C. Our experimental data suggest that increases in air temperatures in combination with an increase in the intensity or area of grazing will potentially lead to greater C losses in gases respired from dryland soils. Further research which addresses the source of C contributing to R_s from dryland soils and determines its temperature, moisture and disturbance sensitivity remains a priority for improved coupled climate-biosphere models and for assessing the future productivity of dryland agro-ecosystems.

Acknowledgements

The research was funded by a Royal Geographical Society Peter Fleming Award. We are grateful for the field and laboratory assistance provided by Sam Tucker and Helen Mairs. The continuing support of Jill Thomas of Berry Bush Farm in Tsabong is also gratefully acknowledged. The research was conducted under the Government of Botswana Research Permit EWT8/36/4 VIII(4). Thomas compiled the manuscript whilst in receipt of a Leverhulme Trust Research Fellowship. Finally, we thank two anonymous reviewers for their constructive comments which have improved the original manuscript.

References

Almagro, M., Lopez, J., Querejeta, J.I., Martnez-Mena, M., 2009. Temperature dependence of soil CO_2 efflux is strongly modulated by seasonal patterns of moisture availability in a Mediterranean ecosystem. Soil Biology and Biochemistry 41, 594–605.

Austin, A.T., Vivanco, L., 2006. Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. Nature 442 (7102), 555–558.

Batisani, N., Yarnal, B., 2010. Rainfall variability and trends in semi-arid Botswana: implications for climate change adaptation policy. Applied Geography 30, 483–489.

Belnap, J., 1996. Soil surface disturbances in cold deserts: effects on nitrogenase activity in cyanobacterial-lichen soil crusts. Biology and Fertility of Soils 23, 362–367.

Belnap, J., Lange, O.L., 2003. Structure and functioning of biological soil crusts: a synthesis. In: Lange, O.L., Belnap, J. (Eds.), Biological Soil Crusts: Structure, Function and Management. Springer-Verlag, Berlin, pp. 471–479.

Bond-Lamberty, B., Thomson, A., 2010a. Temperature-associated increases in the global soil respiration record. Nature 464 (7288), 579-583.

Bond-Lamberty, B., Thomson, A., 2010b. A global database of soil respiration data. Biogeosciences 7, 1915–1926.

Borken, W., Matzner, E., 2009. Reappraisal of drying and wetting effects on C and N mineralisation and fluxes in soils. Global Change Biology 15, 808–824.

Büdel, B., Darienko, T., Deutschewitz, K., Dojani, S., Friedl, T., Mohr, K.I., 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 Ecology 57, 229–247.

Castillo-Monroy, A.P., Maestre, F.T., Rey, A., Soliveres, S., García-Palacious, P., 2011. Biological soil crust microsites are the main contributor to soil respiration in a semiarid ecosystem. Ecosystems. doi:10.1007/s10021-011-9449-3.

Collins, S.L., Sinsabaugh, R.L., Crenshaw, C., Green, L., Porras-Alfaro, A., Stursova, M., Zeglin, L.H., 2008. Pulse dynamics and microbial processes in aridland ecosystems. Journal of Ecology 96, 413–420.

Conant, R.T., 2009. Challenges and opportunities for carbon sequestration in grassland systems: a technical report on grassland management and climate change mitigation. Prepared for the UN Food and Agriculture Organization; Crop and Grassland Service, Plant Production and Protection Division.

Cox, P.M., Betts, R.A., Jones, C.D., Spall, S.A., Totterdell, I.J., 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408, 184–187.

Crenshaw, C., Lauber, C.L., Sinsabaugh, R.L., Stavely, L.K., 2008. Fungal dominance of nitrogen transformations in semiarid grassland. Biogeochemistry 87, 17–27.

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. Global Change Biology 12 (6), 957–971.

Davidson, E.A., Janssens, I.A., Luo, Y.Q., 2006. On the variability of respiration in terrestrial ecosystems: moving beyond $Q_{(10)}$. Global Change Biology 12, 154–164.

Denef, K., Six, J., Bossuyt, H., Frey, E.T., Merckx, R., Paustian, K., 2001. Influence of dry-wet cycles on the interrelationship between aggregate, particulate organic matter, and microbial community dynamics. Soil Biology and Biochemistry 33, 1599–1611.

Dougill, A.J., Thomas, A.D., 2004. Kalahari sand soils: spatial heterogeneity and land degradation. Land Degradation and Development 15, 233–242.

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. Biogeosciences 6, 6983–7015.

Emmerich, W.E., 2003. Carbon dioxide fluxes in a semiarid environment with high carbonate soils. Agricultural and Forest Meteorology 116, 91–102.

Evans, R.D., Lange, O.L., 2003. Biological soil crusts and ecosystem N and C dynamics. In: Belnap, J., Lange, O.L. (Eds.), Biological Soil Crusts: Structure, Function & Management. Springer, pp. 155–166.

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 Science Society America Journal 67, 798–805.
Hewitson, B.C., Crane, R.G., 2006. Consensus between GCM climate change projections with empirical downscaling: precipitation downscaling over South Africa. International Journal of Climatology 26, 1315–1337.
Hoon, S.R., Thomas, A.D., Linton, P.E., 2009. The design and development of a closed chamber for the *in-situ* quantification of dryland soil carbon dioxide fluxes. Geographical Research 47 (1), 71–82.
Inglima, I., Alberti, G., Bertolini, T., Vaccari, F.P., Gioli, B., Miglietta, F., Cotrufo, M.F., Peressotti, A., 2009. Precipitation pulses enhance respiration of Mediterranean ecosystems: the balance between organic and inorganic components of increased soil CO_2 efflux. Global Change Biology 15, 1289–1301.
Inter-Governmental Panel on Climate Change (IPCC), 2007. Climate Change 2007: The Physical Science Basis. Cambridge University Press, Cambridge.
Jin, Z., QI, Y.C., Dong, Y.S., 2007. Diurnal and seasonal dynamics of soil respiration in desert shrubland of *Artemisia Ordosica* on Ordos Plateau of Inner Mongolia, China. Journal of Forestry Research 18 (3), 231–235.
Jin, Z., Dong, Y.S., QI, Y.C., Domroes, M., 2009. Precipitation pulses and soil CO_2 emission in desert shrubland of *Artemisia ordosica* on the Ordos Plateau of Inner Mongolia, China. Pedosphere 19 (6), 799–807.
Lalley, J.S., Viles, H.A., 2006. Do vehicle track disturbances affect the productivity of soil-growing lichens in a fog desert? Functional Ecology 20, 548–556.
Lange, O.L., 2003. Photosynthetic productivity of the epilithic lichen *Lecanora muralis*: long-term field monitoring of CO_2 exchange and its physiological interpretation: II. Diel and seasonal patterns of net photosynthesis and respiration. Flora 198, 55–70.
Liu, X., Wan, S., Su, B., Hui, D., Luo, Y., 2002. Response of soil CO_2 efflux to water manipulation in a tallgrass prairie ecosystem. Plant and Soil 240, 213–223.
Liu, W., Zhang, Z., Wan, S., 2009. Predominant role of water in regulating soil and microbial respiration and their responses to climate change in a semiarid grassland. Global Change Biology 15, 184–195.
Lloyd, J., Taylor, J.A., 1994. On the temperature dependence of soil respiration. Functional Ecology 8, 315–323.
Luo, Y., Zhou, X., 2006. Soil Respiration and the Environment. Academic Press, London.
Maestre, F.T., Cortina, J., 2003. Small-scale spatial variation in soil CO_2 efflux in a Mediterranean semiarid steppe. Applied Soil Ecology 23, 199–209.
Mager, D.M., Thomas, A.D., 2011. The role of extracellular polysaccharides from cyanobacterial soil crusts in dryland surface processes: a review. Journal of Arid Environments 75, 91–97.
Millard, P., Midwood, A.J., Hunt, J.E., Whitehead, D., Boutton, T.W., 2008. Partitioning soil surface CO_2 efflux into autotrophic and heterotrophic components, using natural gradients in soil $\delta^{13}C$ in an undisturbed savannah soil. Soil Biology and Biochemistry 40, 1575–1582.
Noy-Meir, I., 1973. Desert ecosystems. I. Environment and producers. Annual Reviews of Ecology and Systematics 4, 25–52.
Pumpanen, J., Kolari, P., Ilvesniemi, H., Minkkinen, K., Vesla, T., Niinistö, S., Lohila, A., Larmola, T., Morero, M., Pihlatie, M., Janssens, I., Yuste, J.C., Grünzweig, J.M., Reth, S., Subke, J.A., Savage, K., Kutsch, W., Østreng, G., Ziegler, W., Anthoni, P., Lindroth, A., Hari, P., 2004. Comparison of different chamber techniques for measuring soil CO_2 efflux. Agricultural and Forest Meteorology 123, 159–176.
Scholes, R.J., Monteiro, P.M.S., Sabine, C.L., Canadell, J.G., 2009. Systematic long-term observations of the global carbon cycle. Trends in Ecology & Evolution 24 (8), 427–430.
Shen, W., Jenerette, G.D., Hui, D., Phillips, R.P., Ren, H., 2008. Effects of changing precipitation regimes on dryland soil respiration and C pool dynamics at rainfall event, seasonal and interannual scales. Journal of Geophysical Research 113, G03024. doi:10.1029/2008JG000685.
Sheng, H., Yang, Y., Yang, Z., Chen, G., Xie, J., Guo, J., Zou, S., 2010. The dynamic response of soil respiration to land use changes in subtropical China. Global Change Biology 16, 1007–1121.
Shugart, H.H., Macko, S.A., Lesolle, P., Szuba, T.A., Mukelabai, M.M., Dowty, P., Swap, R.J., 2004. The SAFARI 2000 — Kalahari transect wet season campaign of year 2000. Global Change Biology 10, 273–280.
Sponseller, R.A., 2007. Precipitation pulses and soil CO_2 flux in a Sonoran Desert ecosystem. Global Change Biology 13, 426–436.
Swap, R.J., Aranibar, J.N., Dowty, P.R., Gilhooly III, W.P., Macko, S.A., 2004. Natural abundance of ^{13}C and ^{15}N in C_3 and C_4 vegetation of southern Africa: patterns and implications. Global Change Biology 10, 350–358.
Tang, J., Baldocchi, D.D., Qi, Y., Xu, L., 2003. Assessing soil CO_2 efflux using continuous measurements of CO_2 profiles in soils with small solid-state sensors. Agricultural and Forest Meteorology 118, 207–220.
Thomas, A.D., Dougill, A.J., 2006. Distribution and characteristics of cyanobacterial soil crusts in the Molopo Basin, southern Africa. Journal of Arid Environments 64, 270–283.
Thomas, A.D., Dougill, A.J., 2007. Spatial and temporal distribution of cyanobacterial soil crusts in the Kalahari: implications for soil surface properties. Geomorpholgy 85, 17–29.
Thomas, A.D., Hoon, S.R., 2010. Carbon dioxide fluxes from biologically-crusted Kalahari Sands after simulated wetting. Journal of Arid Environments 74, 131–139.
Thomas, D.S.G., Shaw, P.A., 1991. The Kalahari Environment. Cambridge University Press.
Thomas, A.D., Hoon, S.R., Linton, P.E., 2008. CO_2 fluxes from cyanobacteria crusted soils in the Kalahari. Applied Soil Ecology 39, 254–263.
Veenendaal, E.M., Kolle, O., Lloyd, J., 2004. Seasonal variation in energy fluxes and carbon dioxide exchange for a broad-leaved semi-arid savanna (Mopane woodland) in Southern Africa. Global Change Biology 10, 318–328.
Wang, L., D'Odorico, P., Ringrose, S., Coetzee, S., Macko, S.A., 2007. Biogeochemistry of Kalahari Sands. Journal of Arid Environments 71, 259–279.
Zeglin, L.H., Stursova, M., Sinsabaugh, R.L., Collins, S.L., 2007. Microbial responses to nitrogen addition in three contrasting grassland ecosystems. Oecologia 154, 349–359.