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Carbon dioxide fluxes from biologically-crusted Kalahari Sands after simulated wetting

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ABSTRACT

We report surface CO_2 efflux and subsoil CO_2 concentrations in biologically-crusted soils from the Kalahari. Fluxes were determined in-situ using a closed chamber coupled to a portable gas chromatograph on dry soils and on soils subject to simulated light and heavy rainfall. Surface efflux was measured in an artificially darkened environment in order to determine by difference, whether photosynthesis was occurring. Dry soil efflux rates were 2.8–14.8 mg C m^2 h^{-1} throughout a diurnal cycle. Light rainfall led to an immediate increase in efflux to a peak of 65.6 mg C m^2 h^{-1}. Heavy rainfall resulted in a large pulse of CO_2 with efflux rates of 339.2 mg C m^2 h^{-1} over the first hour after wetting. Peak rates remained high over the following 2 days (87.8 and 87.0 mg C m^2 h^{-1}). Given sufficient moisture, fluxes increased with temperature. We believe hydration of the subsoil stimulates microorganisms which repsire available C either from extracellular polysaccharide sheaths (EPS) or released into the soil through lysis of microbial cells. Higher fluxes from the soil kept in the dark suggests photosynthesis occurs in wetted crusts during the daytime but net C uptake is masked by respiration from other microorganisms.

1. Introduction

Soil respiration resulting from microbial catabolism of organic C is one of the most important contributors of CO_2 to the atmosphere, releasing one order of magnitude more C per annum than current global anthropogenic emissions (Luo and Zhou, 2006; Raich and Schlesinger, 1992). Any increase in soil respiration could deplete soil C and adversely affect fertility as well as elevate atmospheric CO_2 concentrations (Cox et al., 2000). Despite wide ranging environmental significance our understanding of controls on soil respiration remains incomplete (Luo, and Zhou, 2006). This is particularly acute in drylands where although respiration is a major process of soil C loss (Conant et al., 2000) there have been few field studies (Raich and Schlesinger, 1992) and processes affecting rates and the magnitude of CO_2 fluxes remain an active area of debate (Schlesinger et al., 2009; Wohlfahrt et al., 2008; Xie et al., 2008). Improving prediction of soil CO_2 efflux in drylands depends to a large extent on better understanding the responsiveness of microbial populations in the soil surface and subsurface to variations in moisture and temperature (Huxman et al., 2004).

Conceptually, many dryland sandy soils can be thought of as comprising a surface layer relatively rich in organic matter and microbial biomass (often in the form of a biological crust) overlying a subsoil of limited organic matter and humic substances. Whilst surface microorganisms will be highly responsive to diurnal changes in temperature and precipitation, subsoil microorganisms are buffered from temperature extremes and will experience extended periods of desiccation, punctuated by periods of moisture availability resulting from only high magnitude rainfall events. After rewetting, CO_2 respiration rates in soils are often elevated by up to 500% compared to soil kept continually moist (Fierer and Schimel, 2003). Thus rewetting pulses may constitute a significant portion of the total annual CO_2 efflux from soils (Liu et al., 2002; Thomas et al., 2008; Xu et al., 2004).

The source of the C respired during these events remains uncertain. Fierer and Schimel (2003) suggest the sources are likely 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 (e.g., Appel, 1998; Denef et al., 2001) or from a subsequent increase in zymogenous microbial populations. Many soil microorganisms will have died as a result of desiccation (van Gestel et al., 1991), providing available substrate for the survivors which will respire C from the dead cells (Luo and Zhou, 2006). If the rate of change of soil water potential is rapid, physiological stresses associated with hydration can lead to

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cell death (Harris, 1981; Kieft et al., 1987) and the release of fresh substrate into the soil. During large precipitation events, C from extracellular polymeric substances (EPS) could also provide a source of readily available energy to heterotrophic microbial communities in the subsoil (Mager, 2009).

At steady state, CO_2 efflux rates measured at the soil surface will normally be expected to equal the rate of CO_2 production in the soil or crust (Luo and Zhou, 2006). There are, however, a number of complicating factors which can invalidate this assumption. In the Kalahari, surface crusts are predominantly comprised of cyanobacteria (Dougill and Thomas, 2004; Thomas and Dougill, 2007) which have the ability to obtain C (and energy) from CO_2 in the light or through catabolism of organic C in the dark (Tandeau de Marsac et al., 2001). It is possible that there are occasions when some crust organisms in the upper photic zone of the crust are obtaining energy from photosynthesis whilst other species below the zone of light penetration are utilising organic C. Free-living species of cyanobacteria, however, are not likely to be able to successfully compete with heterotrophic bacteria in the absence of light for long (Stal, 1995). CO_2 efflux from the surface layer can therefore be either positive or negative depending on the environmental conditions and the dominant metabolic strategy of the ensemble of organisms. Optimal conditions for cyanobacterial photosynthesis and respiration may or may not coincide temporally. Thus simple relationships between environmental variables and soil respiration rates should not be expected; rather surface fluxes will reflect interactions between constantly changing rates of uptake and release of CO_2.

Subsoils are less affected by diurnal changes in temperature and much less frequently wetted, contributing little CO_2 to surface efflux for long periods. After heavy rainfall, however, water percolating into pore spaces will initially displace resident air enriched in CO_2 due to the actions of bacteria, roots and mycorrhiza. Resident and dormant populations of heterotrophic bacteria are then activated by the moisture pulse, rapidly multiplying as they consume the available C. During this process CO_2 will be respired and contribute to the measured efflux at the surface. In this state, surface efflux rates will also be affected by the transport rate of CO_2 through the soil profile and from the surface (Luo and Zhou, 2006) which may also be physically impeded by the crust (Belnap et al., 2003). The intermittent contribution of the subsoil to surface efflux further complicates the interpretation of respiration measurements (Humxan et al., 2004). Studies on dryland soils which combine simultaneous measurement of surface CO_2 efflux with subsoil pore space concentrations have, to our knowledge, not yet been published.

The objectives of this research were to simultaneously quantify surface and subsoil CO_2 fluxes under dry conditions and in response to simulated pulses of light and heavy rainfall. Integral to our hypothesis is the implicit assumption that fluxes after light rainfall originate solely from the soil surface whilst heavy rainfall pulses will also stimulate heterotrophic respiration from the deeper soil. Surface efflux was also measured in a dark chamber in order to determine by difference, whether photosynthesis was occurring in chambers exposed to daylight. In order to understand controls on surface CO_2 efflux rates under varying moisture conditions, air temperature and photosynthetically active radiation were also continuously recorded.

2. Materials and methods

2.1. Study area

Fieldwork was undertaken between July 26th and August 4th 2007 on undisturbed plots sited within the boundary of lightly grazed farmland near Tsabong in the south west of Botswana (25°56′51″S 22°25′40″E). Vegetation cover is a mix of grass (*Eragrostis*, *Stipagrostis* and *Schmidtia* species), woody shrubs (*Acacia mellifera* (Vahl) Benth and *Grewia flava* DC) and trees (mainly *Acacia* species).

All measurements were conducted on Kalahari Sand soils characterised by a strongly uni-modal (>97%) grain size of fine sand (Dougill and Thomas, 2004) and a pH of 5.9 +/− 0.4 (Thomas and Dougill, 2007). The soil surface is commonly covered in cyanobacterial soil crust (Dougill and Thomas, 2004; Thomas and Dougill, 2007) or wind-blown sand (Berkeley et al., 2005). The loose cover of wind-blown sand had a bulk density of 1.85 +/− 0.03 g cm^3 and a porosity of 0.23 +/−0.01 v/v (Table 1). The cyanobacterial crust has a lower bulk density of 1.33 +/− 0.03 g cm^3 and a (non-sand grain volume fraction) porosity of 0.34 +/−0.01 v/v reflecting the microbial and EPS constituents of the crust which provides additional organic material as well as altering the pore space of the surface soil structure. Crusts are typically 3–4 mm thick and of three broad morphological types: a weakly consolidated crust with no surface discolouration (type 1); a more consolidated crust with a black or brown speckled surface (type 2); and a crust with a bumpy surface and intensely coloured black/brown surface (type 3). Across the study sites, intact biological crust covers an average of 26% of the ground surface area (Dougill and Thomas, 2004).

Precipitation data for Tsabong are typical of a semi-arid region with low annual rainfall and high inter-annual variability. They describe a pulse-driven system where ecosystem components experience long periods of desiccation punctuated by often high intensity short duration rainfall. Mean annual precipitation at Tsabong between 1934 and 1988 was 296.9 mm yr^{-1} (the 1996–2007 average 7 km north east of Tsabong at the field site was 323.6 mm yr^{-1}) although inter-annual variation is high (Table 2). Between 1996 and 2007 the modal rainfall event was 5–10 mm (occurring on 90 occasions) whilst 2 events of between 50 and 60 mm and 7 events >60 mm also occurred. Estimated potential evapotranspiration at Gaborone 400 km to the east, at the end of July / beginning of August is 2 mm day (Persaud et al., 2006). Thus the most frequent rainfall events will only wet the upper surface of the soil and crust for a short period of time.

Four Measurement Science USB502 (Adept Science, UK) data logging probes were used to obtain continual air temperature and relative humidity data at 5 min intervals at the field site for the duration of the experiment. A composite data set was compiled and is shown in Fig. 1. Photosynthetically active radiation (PAR) irradiance at the plots was also recorded using a QS2 Quantum Sensor (Delta-T Devices, Cambridge UK). At solar zenith, 12:38 h (local time), PAR was typically 1.51 mmole m^2 s^{-1}. Peak air temperatures occurred just before 15:00 h (local time) on each day with the highest temperatures recorded towards the end of the experiment on the 30th and 31st July and 1st August (32 to 34 °C). Minimum temperatures occurred immediately prior to sunrise and were as low as −7 °C. Relative humidity declined rapidly with climbing temperatures during the mornings (Fig. 1) and then rose throughout the night time to peaks of >90% on 28th July but were

Table 1
Surface crust, subsoil and wind-blown sand porosity, bulk and particle density.

	Surface crust[a] $n=2$	Wind-blown sand $n=3$	Subsoil $n=5$
Bulk density (g cm^3)	1.33	1.85 ± 0.03	1.52 ± 0.03
Particle density (g cm^3)	–	2.41 ± 0.01	2.48 ± 0.11
Porosity[b] (v/v)	0.34	0.23 ± 0.01	0.39 ± 0.03

[a] Pore spaces partially filled with extracellular polysaccharide sheath (EPS) thus low bulk density but still a fairly low porosity.
[b] Porosity was determined by total water penetration volume and thus includes the volume of solution of soluble EPS for example, thus slightly over estimates the air volume as distinct to the non-sand grain porosity.

Table 2
Precipitation data for Berry Bush Farm, Tsabong 1996–2007.

Year Sept – Aug	Rainfall (mm)	Rain days	Days of ≥20 mm rain	Total rain in events >20 mm	% of annual rain falling in events >20 mm
1996–1997	436	28	5	166	38
1997–1998	359.5	30	8	216	61
1998–1999	243.4	36	2	50.5	21
1999–2000	430.2	40	5	159.4	37
2000–2001	319.3	34	4	130.2	41
2001–2002	545.3	45	7	273.6	50
2002–2003	130.2	14	1	28	22
2003–2004	229	15	6	188.6	82
2004–2005	259.9	26	4	134.8	52
2005–2006	492	37	8	289.8	59
2006–2007	114.4	19	1	34.7	30
Mean	**323.6**	**29**	**4.6**	**152**	**45**

never higher than 50% for the last two days of the experiments. Delta-T (Delta-T Devices, Cambridge, UK) ML2 and PR2 surface and profile probes were used to quantify soil moisture levels during the simulated pulse rainfall experiments.

2.2. CO_2 efflux instrumentation and analysis

Surface soil efflux was determined from the changes in CO_2 concentration over time inside a fully automated, *in-situ* closed chamber (ISCC). The instrumentation was used to monitor and control temperature, ambient light, relative humidity and pressure so that diurnal variations in soil CO_2 fluxes could be determined under ambient conditions (Hoon et al., 2009 and Thomas et al., 2008). The ISCC chamber has a headspace of 722 ml and encloses a soil area of 84 cm^2. CO_2 concentrations inside the ISCC were determined every 10 min using a high sensitivity (~50ppb) Agilent portable gas chromatograph (GC 3000) employing a silicon microchannel time of flight and thermal conductivity detector (TOF/TCD) and high purity helium (99.999%) carrier gas. Sample injection volumes were 10 µl. The temperature, pressure and light inside the ISCC were recorded every 5 min. Purging and venting of the ISCC was undertaken hourly, allowing the rate of change in CO_2 concentration for a given set of conditions to be determined before significant changes in CO_2 affected diffusion rates from the soil. Hourly chamber venting was close to that which Ohlsson et al. (2005) determined, by a sensitivity analysis, as being optimum when using static gas chambers on soils. Gas fluxes were calculated using the change in CO_2 concentration within the chamber head space over the central 50 min of each cycle, normalised to the soil area and gas volume within the chamber. To convert CO_2 as a concentration to that of mass in mg per m^{-3} changes in concentration were multiplied by the ratio of the gram molecular weight of a standard atmosphere of air (78% N_2, 21% O_2, 0.93% Ar, 0.037% CO_2), i.e. 28.958 grams, and the gram molar volume of a gas at normal temperature and pressure (22,414 cm^3) corrected to the mean experimental temperature and pressure. Subsoil pore space gas concentrations were determined on the same GC but from samples manually extracted by syringe and stored in pre-evacuated Exetainer® vials (Labco, High Wycombe, UK).

Description of thermally-driven biological and soil microbial processes such as respiration, $R(T)$, is often based upon an Arrhenius model using the Q_{10} exponential relationship (Tjoelker et al., 2001):

$$R(T) = R_0 Q_{10}^{T-T_0/10} \quad (1)$$

where R_0 is the respiration at reference temperature T_0 . Thus for $Q_{10} = 2$ the respiration rate doubles every 10 °C. Here surface respiration data have been used to determine soil Q_{10} values as a function of temperature by plotting hourly respiration (R) against hourly average cell temperature (T) for each soil treatment condition. A standard exponential Q_{10} model was fitted to the soil CO_2 surface gas efflux data and the fitting algorithm maximised the correlation coefficient $r^2(Q_{10})$ with the initial conditions $R_0 = R(0)$ and $T_0 = 0$ enabling the assessment of the sensitivity of respiration to temperature and moisture.

2.3. Experimental design and sampling

Because crust behaviour is affected by disturbance (Belnap, 1996) and the crust forms an integral boundary between the surface, atmosphere and subsoil (Belnap et al., 2003) a key rationale of our research design was to preserve crust integrity and undertake *in-situ* experiments. This non destructive *in-situ* approach also avoids the convolution of experimental cycles and natural circadian rhythms which have been shown to exist in cyanobacterial communities (Yen et al., 2004). Experiments were undertaken on undisturbed ground in areas away from plants to minimise the likelihood of contributions to CO_2 efflux from roots and mycorrhiza. A permanent fenced plot (5 m × 5 m) erected in 2004, provided the location for the surface experiments. An adjacent plot was used for the subsoil experiments.

In-situ soil CO_2 fluxes were quantified during 4 sequential experiments lasting between 12½ and 52 h on dry (D), lightly wetted (LW), lightly wetted and kept dark (LWD) and heavily wetted (HW) soil. The ISCC was not re-located during the fieldwork and the same soil was used for all surface efflux experiments. Although the experiments were sequential on the same area of soil, the incremental nature of the simulated rainfall treatments effectively means previous experimental conditions were overwritten. This had the advantage of providing high resolution efflux and environmental data on an undisturbed crusted surface in the field but at the cost of replication. The lack of replication together with the single sampling location and season are limitations of this study and we are mindful not to extrapolate the findings too widely. Nevertheless, our primary purpose was to improve understanding of soil processes and obtain new data on respiration responses to rainfall and for this the approach was successful.

Efflux was initially calculated for dry (ambient) conditions, then after the application of 10 ml distilled water over the chamber soil

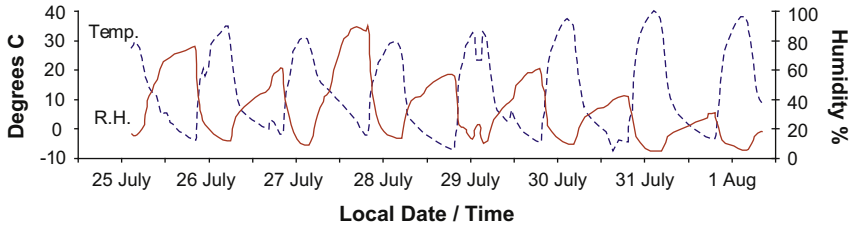

Fig. 1. Continuous temperature (°C) and Relative Humidity (%) at Berry Bush farm, Tsabong for the duration of the experiments (25th July to 1st August 2007).

surface area (equivalent to 1.4 mm rainfall) on both the second and third days of the experiment in order to maintain moist conditions in the surface crust in the presence of evaporative losses (Table 3). On the fourth day a further 10 ml of distilled water was applied and the window of the ISCC covered in order to prevent light reaching the surface (LWD). For the final experiment the ISCC was temporarily detached from the uPVC stub and a bund (0.16 m^2) placed around the area. To simulate heavy rainfall (HW), 20 litres of water (equivalent to 120 mm of rainfall) was carefully poured into the bund, periodically allowing the water to infiltrate after ponding (Table 3). This volume was chosen to ensure moisture penetrated the subsoil to a depth of at least 60 cm (the depth of the deepest subsoil pore space gas sampling device). Although this procedure led to some disruption to the surface crust, this reflects what would happen naturally during the high intensity rainfall events recorded for the field site. The ISCC was reattached and gas fluxes quantified over the following 52 h.

An adjacent plot was used to determine changes in pore space CO_2 concentrations in response to a heavy wetting pulse. A soil pit, approximately 1.5 meters deep by 2 m by 1.5 m was dug and gas sampling tubes inserted into a face of the pit at 6 cm, 15 cm, 30 cm and 60 cm. These were constructed from hollow resin tubing of ~7 mm O.D. fitted with internal sliding screw-threaded stainless steel rods. A small air passage was formed by grinding the rods along their length to form a D-shaped cross section. At each end of the steel rods were nuts which allowed the gas tubes to be either sealed or open to the internal soil air environment. Onto the external end of the cylinder a copper tubular stub was glued to enable mounting of a gas tight Suba Seal® through which a gas syringe could be inserted to withdraw soil air samples. The gas tubes were inserted into pre-drilled holes excavated into the case-hardened soils using a hollow drill bit to permit extraction of the tailings without enlarging the bore of the hole. To ensure a tight seal between the soil and gas tubes PTFE and eurothane foam sheeting was wrapped around the soil tubes and silicone sealant applied around the tubes at the soil surface. The tubes were left *in-situ* for 24 h prior to use and initially flushed by drawing out 25 ml of subsoil pore air. 16 ml of gas was drawn out each time using the syringe and stored, slightly over-pressured, in a pre-evacuated 12 ml Exetainer vial. To prevent the unlikely event of gas diffusion through the Exetainer seal during storage and transport, each vial was dipped in hot candle wax. Samples were collected on 8 occasions, the first prior to the application of the water and the subsequent 7 at regular intervals thereafter. When not in use, corrugated galvanised iron sheeting was used to cover the pit in order to prevent excessive evaporation from the exposed soil surfaces.

3. Results

3.1. The effects of light wetting on C efflux

Changes in the concentration of CO_2 inside the ISCC headspace are shown in Appendix 1 (electronic version only). The raw data have a "saw tooth" appearance as the CO_2 concentration increases inside the ISCC during each cycle and is then vented from the buffer chamber and reset each hour. The gap in the data from 05:00 h on the 27th July was due to generator failure. These data were used to determine efflux rates for each of the hourly cycles (Fig. 2). The base line variation in initial CO_2 concentration at the start of each cycle (i.e. after purging) reflects the CO_2 concentration in the soil free buffer chamber from which the ambient atmospheric purge gas is withdrawn. Daily changes in air temperatures within the ISCC are broadly similar with temperatures falling to close to or below freezing by 03:00 h. The temperature synchronicity between the ISCC and ambient is due to the active temperature control employed (Hoon et al., 2009). Temperatures climb rapidly after sunrise and peak between 15:00 and 16:00 h.

Carbon efflux from dry soil varied between 2.8 and 14.8 mg C m^2 h^{-1} with highest rates occurring at the beginning of the experiment and in the early afternoon (Fig. 2). The timing of peak efflux from dry soils is likely to be related to temperature and relative humidity (RH) and dew formation which provided the only moisture source during this experiment. RH is greatest at dawn (Fig. 1) but low temperatures will be a limiting factor to crust organism metabolic activity. Conversely when temperatures peak in the mid afternoon RH is at its lowest (Fig. 1) and moisture availability is likely to be limiting. Thus mid morning to early afternoon is the optimal time for activity and C efflux, in the absence of soil moisture from rainfall. There were no obvious effects of night time freezing on morning fluxes in any experiment.

The application of the equivalent of 1.4 mm of rainfall had an immediate and significant effect on efflux, with peaks of 65.6 and 64.0 mg C m^2 h^{-1} (Fig. 2). Efflux was also temperature sensitive with the highest rates occurring at peak temperatures and declining with temperature through the late afternoon and evening. Fluxes in both experiments were between 5 and 8 mg C m^2 h^{-1} through the night time when temperatures were lowest. C fluxes were even higher during a further light wetting experiment when the soil surface was kept dark to exclude the possibility of photosynthesis, fluxes increasing rapidly to a peak of 90.5 mg C m^2 h^{-1} (Fig. 2). Again fluxes appeared to correlate with temperatures and declined to a low of 3.1 mg C m^2 h^{-1} at 18:00 h local time. Intriguingly, in all experiments efflux rates climb rapidly to a peak in mid to late morning before falling slightly and then rising to a second peak in the early afternoon. Given the consistency of the pattern across all experiments (there is also some suggestion it occurs on the 2nd and 3rd day of the heavy wetting experiment) it seems to be a real phenomena. It also occurred during the dark experiment, and is therefore unlikely to be related to an increase in photosynthesis unless metabolic activity in the dark chamber is affected by a circadian rhythm.

3.2. The effects of heavy wetting on C efflux

In the first hour after the application of the equivalent of 120 mm of rain C fluxes increased significantly, peaking at 339.2 mg C m^2 h^{-1}. Thereafter there was a decline in efflux to a low

Table 3
Details of the water applied to simulate rainfall events during the experiments.

	Heavy rain simulation			Light rain simulation		
	Volume (litres)	Rain equiv (mm)	Saturation depth (m)	Volume (litres)	Rain equiv (mm)	Saturation depth (m)
Surface efflux plot	20	119.0	0.31	0.0001	1.4	0.004
Subsoil plot	65	120.5	0.31	–	–	–

*Heavy wetting: subsoil plot 0.54 m^2 and Surface efflux plot 0.16 m^2. Subsoil porosity 0.39.
Light wetting: wetted area 0.029 m^2. Crust porosity 0.34.
N.B. Light rain simulation only used a small amount of water but because of the limited evaporation from the surface it will be sufficient to wet the crust over a relatively short period of <24 h.

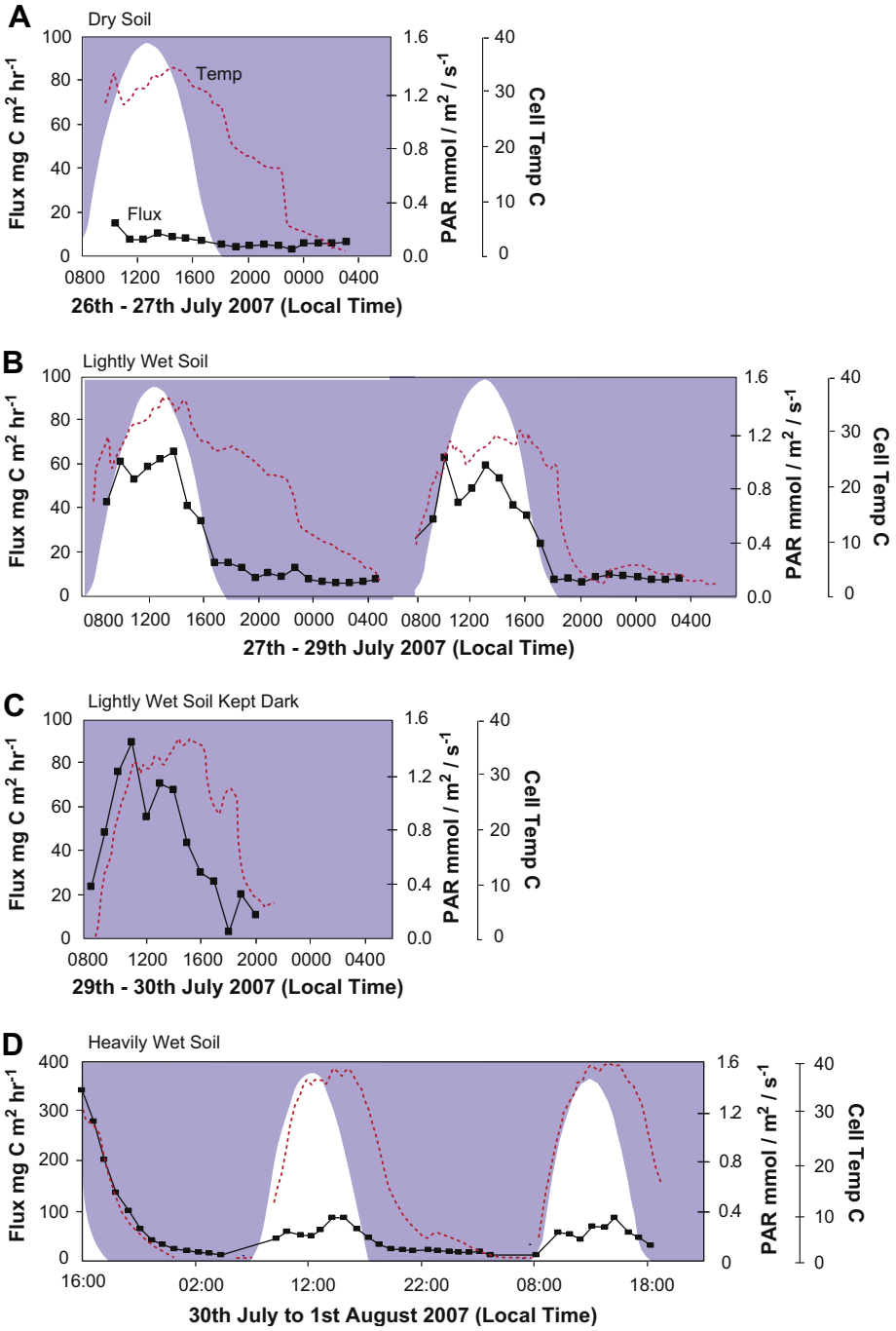

Fig. 2. Carbon flux, solar irradiance and air temperature inside the respiration cell on A) dry soil, B) lightly wet soil, C) lightly wet soil kept dark and D) heavily wet soil.

of 13.8 mg C m^2 h^{-1} at 04:00 h. The decline in efflux rates over the first evening is closely related to the decline in temperature (Fig. 2). On the second day after wetting, C efflux rose again in the pre-dawn hours to a peak of 87.8 mg C m^2 h^{-1} at 18:00 h. There was a similar trend on the third and final day of the experiment with low efflux values throughout the night (13.7 to 21.4 mg C m^2 h^{-1}) rising through the day to a peak of 87.0 mg C m^2 h^{-1} at 15:00 h.

3.3. *Subsoil CO_2 concentrations*

CO_2 concentrations in the dry subsoil pore spaces were just above ambient air concentrations at all depths (Fig. 3). Unsurprisingly, the application of 120 mm rainfall led to an immediate and marked increase in subsoil moisture which slowly declined over time. Moisture content ranged from 10% at the surface to 19.6% at 59 cm immediately after wetting to 7% at the surface to 8.5 % at 59 cm at the end of the experiment. The effect of wetting on the CO_2 concentrations in the subsoil pores spaces was marked but short-lived with increases at all four depths where samples were collected. The biggest increase was observed at 15 cm where then CO_2 concentration increased to nearly 1200 ppm. Concentrations at the top three depths returned close to ambient 21 h after wetting. The concentration at 60 cm increased to 550 ppm. Thereafter for the duration of the experiment concentrations at all depths were close to ambient (Fig. 3).

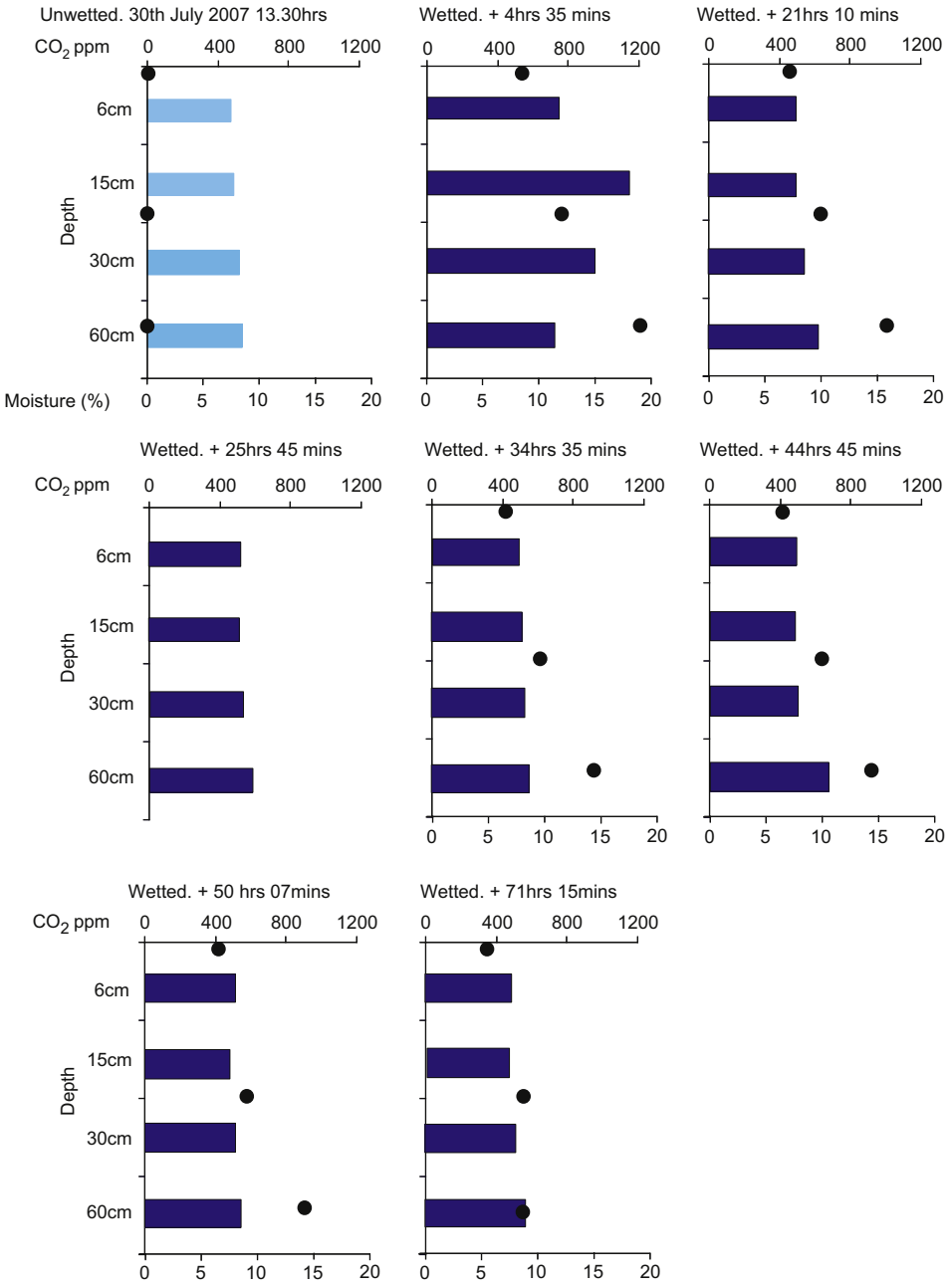

Fig. 3. Subsoil pore space CO_2 concentrations and moisture content (%v/v filled circles) before and after the application of simulated heavy rainfall. Initial moisture levels for the case-hardened dry soil were < 2%v/v (unplotted).

3.4. Temperature sensitivity of efflux

Where both morning and afternoon fluxes were measured, hysteresis in soil efflux was observed (Fig. 4). Comparing equivalent temperatures in the morning and afternoon, net respiration is higher for light wetting treatments in the morning with net respiration in the late afternoon almost identical to that of dry soil. The reduced hysteresis observed for heavy wetting experiment is consistent with net respiration not being moisture limited.

Table 4 displays the Q_{10} and R_0 values determined using Eq. (1) to model the respiration data. A single fit was applied to each day to average out the thermal hysteresis observed in all treatments with the exception of the first day after heavy wetting for which only decreasing temperature data were available. Model outputs are omitted from Fig. 4 for clarity but correlation coefficients are given in Table 4 together with base respiration rate, Q_{10} and T_0. The largest thermal hysteresis is observed for days when soils were lightly wet, hence the lower values of r^2 and greater uncertainty in Q_{10} (1.70 ± 0.05).

Efflux during the first day after heavy wetting was large and the relationship with temperature is as a consequence particularly noise free. There appear to be two stages in the process of respiration after heavy wetting above and below a transition region between 8 and 10 °C (annotated on Fig. 4b). Below 9 °C a rapid decrease in respiration is observed and Q_{10} is large (12.6) whilst above 9 °C respiration increases and Q_{10} is significantly smaller (1.64). This is a clear indication that the dominant respiration process or processes differ above and below 8 °C.

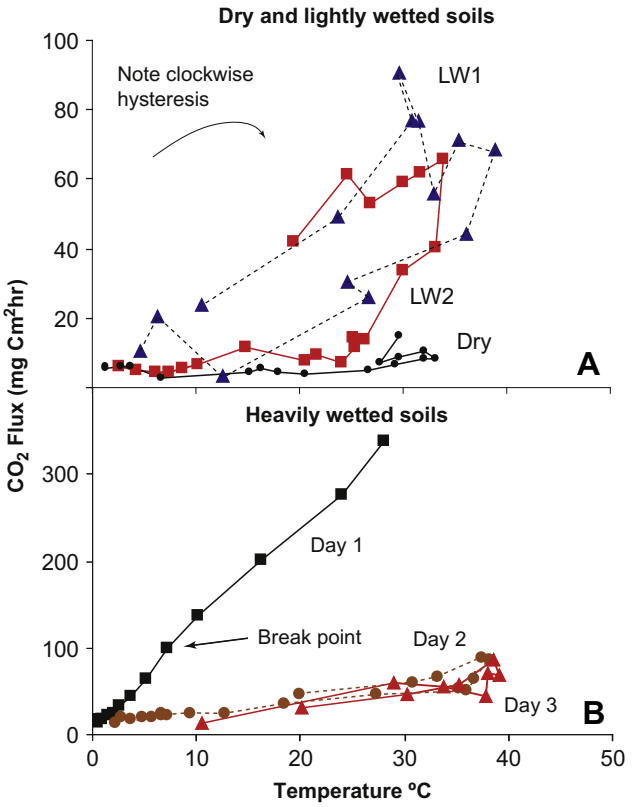

Fig. 4. A) Soil respiration *R* expressed as the soil CO_2 efflux in mg C m^{-2} h^{-1} for dry soil (circles), light wet 1 (squares), light wet 3 dark (triangles). Data for light wet 2 and 3 have been omitted for clarity. B) Soil respiration *R* expressed as the soil CO_2 efflux in mg C m^{-2} h^{-1} for heavy wet 1 (squares), 2 (circles) and 3 (triangles).

4. Discussion and conclusions

The methodology and instrumentation employed in this study facilitated the gathering of high quality estimates of surface efflux data from crusted soils in the south west Kalahari (see Hoon et al., 2009 for more details). In order to produce realistic estimates of efflux, a number of conditions had to be satisfied: Crusts had to remain intact; the temperature of the air above the crust and incoming solar radiation remain close to ambient; and diurnal variations in efflux accounted for. In their review of measurement methods of soil respiration Luo and Zhou (2006) stress the importance of not disturbing the CO_2 concentration gradient that exists between the subsoil and surface and minimising perturbation of surface conditions for producing accurate data. Perturbation was minimised in the field by ensuring that the internal cell and external ambient atmospheric conditions tracked one another as best as possible using regular venting and active temperature control (Hoon et al., 2009). Further, a key finding from the modelling work of D'Odorico et al. (2004) was that in order to improve understanding of the impact of soil moisture on dryland soil C (and *N*) dynamics there is a need for high temporal resolution data that coincide with wetting and drying events. Our approach satisfies these criteria, although data were taken from a small area of soil and spatial variability in efflux rates remains uncertain. The timing of the research (in the dry season) meant that soils were artificially wetted when under natural conditions rain would be unlikely. It is probable that efflux rates would be greater if the experiment was conducted in the wet summer season when air and soil temperatures are higher. Wang et al. (2007) quantified short-term soil respiration rates on dry soils and immediately after wetting at four locations across the Kalahari in January when soil moisture and air temperatures would have been far greater than during this study. Dry soil CO_2 fluxes were higher than in this study, ranging from 0.23 to 0.74 g CO_2 m^2 h^{-1} (equivalent to 83–267 mg C m^2 h^{-1} for direct comparison) increasing with the mean annual precipitation of the site.

Our experiments demonstrate that CO_2 fluxes from Kalahari Sands will be limited by moisture availability for most of the year. Provided there is sufficient moisture, fluxes are highly temperature sensitive and increase with temperature (Fig. 2). Carbon dioxide fluxes from the dry soil (when moisture content was below detection limits) ranged from 2.8 to 14.8 mg C m^2 h^{-1} throughout a diurnal cycle suggesting crust organisms can utilise very low moisture, most likely supplied in the form of dew. A window of opportunity presents itself in mid morning when the high pre-dawn relative humidity provides moisture and rising air temperatures warm the soil surface enough to provide energy for metabolic activity but not to completely evaporate the moisture. Veste et al. (2008) report similar patterns of metabolic activity from their investigation into the role of dew in the activity of lichenous soil crusts in the Haluza dunes of the Negev Desert. Simulated light rainfall (1.4 mm), enough to hydrate the surface crust, led to a large and immediate increase in efflux with peak rates of 65.6 mg C m^2 h^{-1}. Rainfall of 5 mm or less occurred on average 21 times a year between 1996 and 2007 in Tsabong. The frequency of these events will therefore have a large effect on the total amount of respired CO_2 over a year.

Conant et al. (2004) investigated the effects of temperature, moisture, microbial community structure and soil C on respiration from dryland soils. As in this study, they found soil respiration responded positively with temperature but that the response is ameliorated at low soil moisture contents. They attributed soil respiration responses to changes in temperature to the impact on the activity of the soil microbial community. Wang et al. (2007) also report increases in soil respiration rates of up to 10 times after simulated rainfall at sites across the Kalahari. Similar findings are reported by Lange et al. (1998) and Zaady et al. (2000) from the Negev where the extensive but thin layer of photosynthetically active crust organisms form an important component of the C cycle (Lange et al., 1992). At no time during any of the experiments were there sustained periods of significant C uptake to the soil. This is in contrast to Wohlfahrt et al. (2008) who believe biological soil crusts to be, at least partly, responsible for the large net gains of the C to the ecosystem in the Mojave.

The hysteresis seen in diurnal changes in efflux against temperature is consistent with crust microorganisms utilising the

Table 4
Base respiration rate R_0 at T_0, Q_{10} and correlation coefficient r^2.

	Dry	LW Day 1	LW Day 2	LWD	HW Day 1 (T>9C)	HW Day 1 (T<9C)	HW Day 2	HW Day 3
R_0 mgC/m^2/h	3.79	8.16	10.68	10.22	85.23	16.58	16.74	14.36
Q_{10}	1.30	1.70 ± 0.05	1.70 ± 0.05	1.70 ± 0.05	1.64	12.60	1.48	1.50
To	0	0	0	0	6	0	0	0
r^2	0.338	0.519	0.845	0.558	0.994	0.992	0.899	0.726

R_0 (CO_2) calculated for the mean cell temperature corrected to standard pressure taking the molecular weight of the composition of a standard atmosphere of dry air to be 28.958.

short period of elevated moisture availability (Fig. 4). The slightly greater efflux seen for lightly wetted soil kept in the dark, in comparison to in the light, is consistent with masking of photosynthesis by respiration from autotrophic bacteria. If this hysteresis were due to thermal effects alone we would expect efflux to lag uniformly behind both the increasing air temperature during the morning and decreasing afternoon air temperatures due to the marked differences between the low heat capacity and high thermal conductivity of air and the high thermal capacity and low diffusivity sand soil. Likewise the heat capacity of the soil buffers microorganisms from the rapidly changing cool night air temperatures resulting in the observed gradual decrease in efflux between sunset and dawn. Combined, these observations also suggest that it is predominantly microorganisms in the soil surface that are responsible for net respiration following light wetting.

Rainfall events of sufficient size to hydrate the subsoil are less common but remain a characteristic feature of the Kalahari environment. A high proportion (21 to 82%) of annual rainfall occurred in events of more than 20 mm between 1996 and 2007 at Tsabong (Table 2). For the purposes of this experiment an extreme rainfall event of 120 mm was simulated to ensure the dry subsoils were hydrated to a depth of at least 60 cm. The application of the water led to an immediate and large pulse of CO_2 from the soils. Efflux averaged 339.2 mg C m^2 h^{-1} over the first hour after the water was applied (Fig. 2). Peak efflux rates were also high over the following 2 days (87.8 and 87.0 mg C m^2 h^{-1}). The reduced hysteresis observed in the efflux data for these events (Fig. 4) is consistent with net respiration not being moisture limited. The large wetting pulse initially provides sufficient moisture in both the surface and at depth to guarantee strong heterotrophic respiration as labile C is metabolised. Measurement of the soil moisture profile indicates that moisture in excess of the soil field capacity drains rapidly through initially dry soil. Two hours after heavy wetting moisture levels of ~8% v/v were observed in the top 10cms and ~18% at 60 cm depth.

Our data show that when dry, the subsoil pore space CO_2 concentration was just above ambient but increased significantly upon wetting (Fig. 3). Elevated subsoil CO_2 concentrations were, however, short-lived and by 25 h after the experiment levels were close to pre-hydrated values. Humxan et al. (2004) attributed short-lived pulses of CO_2 from dryland subsoils following rainfall to the physical displacement of higher concentrations of CO_2 that will have accumulated in pore spaces between rainfall pulses. Physical displacement of pore space air occurred in this study (bubbles were observed rising through the ponding water when it was applied to the surface), but this was not sampled as the first subsoil gas data were collected 4 h after the application of the water. However, the CO_2 concentration of the pore space air when dry was only just above atmospheric concentration, and thus not sufficient to explain the high post wetting pulse. Although the exact source of C respired during large wetting events is unsure we hypothesize that a significant proportion of it is likely derived from C leached from the surface crust or released by lysed cells. The rapid decline of $R(T)_{HW\ day1}$ and the similarity of $R(T)_{HW\ days2-3}$ to $R(T)_{LW}$ and $Q_{10\ HW\ days2-3}$ to $Q_{10\ LW}$ indicates that the labile C is rapidly depleted in the soil column. This conclusion is also consistent with the transient nature of the subsoil CO_2 pulse that occurs in response to heavy wetting.

Although conditions might have been expected to be optimal for photosynthesis after light wetting, in this study net efflux was always positive to the atmosphere. However, higher peak fluxes occurred after light rainfall when the soil enclosed within the ISCC was kept in the dark (90.5 mg C m^2 h^{-1} compared to 65.6 mg C m^2 h^{-1} in the light). These data support the hypothesis that photosynthesis is occurring in lightly wetted crusts during the daytime but that net C uptake is masked by respiration from other crust microorganisms adopting a heterotrophic metabolic pathway. As yet, we do not yet fully understand the conditions necessary for net photosynthesis and C uptake to the soil to occur and further field and laboratory experiments are needed in order to better isolate interdependent biological and physical variables affecting the efflux of C in dryland soil crusts.

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Appendix. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi 10.1016/j.jaridenv.2009.07.005.

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