

Rapid soil respiration responses to simulated rainfall along the Namib Desert climate gradient

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Abstract

Increasing carbon dioxide (CO₂) concentration in the atmosphere is rapidly altering the earth's climate. While human activities are driving this increase in atmospheric CO₂, these human activities account for a small portion of the exchange of carbon (C) between the earth's surface and the atmosphere. Soil respiration, the release of CO₂ from soils through metabolic activity of soil organisms and roots, is the largest annual transfer of CO₂ from land surfaces to the atmosphere. Although soil respiration is generally well balanced by plant uptake of CO₂ through photosynthesis, small differences in these processes influence atmospheric CO₂. Improving understanding of the controls over terrestrial C cycling is needed for accurate global C cycle models that inform climate models. Dryland (arid and semi-arid) ecosystems appear to play an important role in both total C exchange and in the year-to-year variability of C cycling. There is particular uncertainty in how dryland

C cycling might change under shifting climate conditions, given lack of climate change research to date in these systems. The opposing rainfall and fog gradients in the central Namib Desert presents an excellent opportunity to address this critical research need, as the natural variability in climate, soil surfaces, and vegetation cover can be used to explore factors controlling carbon cycle processes such as soil respiration. Working at six sites across this natural gradient, we quantified rates of soil respiration and their variability in response to soil surfaces (dunes or gravel plains) and vegetation patch types (bare areas and hummocks on dunes, uplands and watercourses on gravel plains). We simulated rainfall and measured soil respiration responses for 48 hours after the rain event. There was considerable variation in respiration rates, reflecting the influences of topography, soil properties, and ambient climate conditions. Soil respiration differed dramatically, with rates generally reflecting apparent patterns of plant production and/or soil organic material accumulation (e.g., high annual rainfall > low annual rainfall, gravel plains > dunes, vegetated > unvegetated patches). Soil respiration was enhanced by simulated rainfall at most sites, although sites with very low plant production (e.g., bare patches in dunes at the low end of the rainfall gradient) had little response to rainfall. Rainfall responses were inconsistent at the middle, driest portion of the climate gradient where production may be limited by infrequent rainfall and fog. Research results suggest that characterizing soil respiration in drylands will be most successful if variability in soil surface, vegetation patch type, and topography are considered. The natural climate gradient in the central Namib Desert provides a unique opportunity to improve understanding of carbon cycling processes; doing so will help advance predictions of global carbon cycling and climate change.

Introduction

Humans are rapidly changing the earth's climate through additions of heat-trapping gases into atmosphere (IPCC 2013). Carbon dioxide (CO₂) is the most important heat-trapping gas in influencing climate change due to the magnitude of anthropogenic inputs (largely from fossil fuel combustion, concrete manufacture, and land use change) coupled with the strong radiative impact of CO₂ in the atmosphere. Predicting future changes in the earth's climate requires reliable estimates of future atmospheric CO₂. However, estimates of future CO₂ concentrations are complicated as they require forecasting both human CO₂ emissions and the balance of CO₂ uptake and release from the biosphere as a whole. While human activities have dramatically increased atmospheric CO₂ concentrations (from 270 parts per million before the industrial revolution to >400 parts per million in 2016), the carbon (C) residing in the atmosphere as CO₂ is a small fraction of total C in the biosphere (Schlesinger & Bernhardt 2013). As a result, atmospheric CO₂ can be influenced by relatively small changes in the amount of C stored in terrestrial pools (e.g., plants, soils, fossil fuels). The biggest pathway of transfer of C from the earth to the atmo-

sphere is soil respiration, the release of CO₂ from soil as a result of metabolic activity of either soil organisms (in particular, microorganisms such as bacteria and fungi) or roots ('root respiration'). Soil respiration releases about ten times more CO₂ into the atmosphere annually than human activities (Schlesinger & Bernhardt 2013). However, unlike human activities, the vast majority of CO₂ released by soil respiration is effectively balanced out by CO₂ uptake by plants in natural systems through the process of photosynthesis. Small imbalances between uptake through photosynthesis and release by soil respiration have the potential to alter atmospheric CO₂ concentrations. Scientific understanding of the controls over soil respiration, the major release of terrestrial release of CO₂, lags[^] that of anthropogenic releases or CO₂ uptake by photosynthesis. Understanding of controls over soil respiration is particularly limited in dryland (arid and semi-arid) systems relative to wetter ecosystems (de Graaff et al. 2014). Further, the biological processes that control transfer of C among storage pools may be influenced by climate change and very few studies to date assess how C cycling processes could be influenced by climate change (de Graaff et al. 2014).

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Improved understanding of C cycling processes in drylands is critical to developing accurate global C cycling models that are needed for refining global climate models. Although drylands typically have lower overall C storage and rates of C exchange than mesic systems, drylands are important global players for several reasons. First, drylands cover approximately 40% of the global land surface, contributing roughly one third of terrestrial net C uptake through photosynthesis and account for nearly 20% of the global soil C pool (Field et al. 1998, Lal 2004). Changes in the relative uptake, release, and net storage in of C in these dryland pools thus have the potential to influence atmospheric CO₂ concentrations and hence climate. Second, many drylands have undergone major land cover change in the past 150 years, with increased woody plant growth and an increase in total C storage (Barger et al. 2011, King et al. 2012). Third, drylands appear to have particularly high year-to-year fluctuations in C cycling in response to changes in rainfall; these fluctuations account for a sizeable portion of global inter-annual variability in C cycling (Ahlström et al. 2015, Poulter et al. 2014). Finally, drylands are socioeconomically important systems, accounting for a large and rapidly growing human population, the majority of the world's livestock, and frequently intensive land disturbance (Reynolds et al. 2007, Wang et al. 2012).

The need to gain a mechanistic understanding of C cycling controls in drylands is magnified by current predictions that suggest that drylands may be particularly strongly impacted by climate change (Overpeck & Udall 2010). Most drylands are predicted to become hotter and drier with greater length and intensity of drought conditions and an overall decrease in water availability (IPCC 2013, Milly et al. 2005). However, regional climate change predictions lag behind global-scale predictions with recent improvement in drought modelling suggesting that global climate models may substantially underestimate the probability of severe drought in drylands (Ault et al. 2014). In addition, regional climate anomalies that may have significant ecological impacts, such as fog in the Namib

Desert, are not currently well predicted by global climate models (Wang et al. 2015). Very little work to date has assessed the impact of climate change on dryland systems; perspectives currently conflict as to whether dryland biological processes should be robust to climate change due to dryland organisms being adapted to extreme conditions or whether drylands should be particularly vulnerable to climate change as dryland organisms are already frequently operating near physiological thresholds (de Graaff et al 2015). Of the work on dryland responses to climate change, most is focused on semi-arid systems with virtually no work on hyper-arid systems. Improved understanding of how environmental conditions affect C cycling processes in drylands is therefore critical for understanding both how these systems may respond to changing climate and for understanding potential feed backs to climate that may occur under changing conditions.

Soil respiration is the major pathway by which C gets released from the biosphere into the atmosphere. In most systems, the majority of soil respiration is attributed to metabolic activity of heterotrophic soil organisms (in particular bacteria and fungi) catabolizing dead organic matter (e.g., dead plant leaves and roots) with a smaller component from respiration of live roots (Del Grosso et al. 2005). Environmental conditions, including soil moisture, temperature, and carbon substrate availability can strongly influence activity of organisms responsible for soil respiration; quantitative understanding how these factors control rates of soil respiration is critical for developing improved models of C cycling (Del Grosso et al. 2005). Temperature is a key controlling variable in many temperate systems, with greater soil respiration under warmer temperatures as a result of greater microbial activity (Sulzman et al. 2005). However, temperature may play a secondary role to moisture in drylands where water frequently leads to long-term periods with little or no biological activity (Austin et al. 2004). Soil organisms in drylands typically increase metabolic activity, and hence soil respiration increases, following rainfall pulses (Fernandez et al. 2006, Sponseller 2007).

While environmental conditions such as rainfall and temperature influence the opportunity for biological activity, these operate across the context of a heterogeneous environment. Drylands are inherently heterogeneous systems, land cover typically composed of a matrix of bare ground and vegetation patches, in contrast to the more continuous canopy cover of mesic systems. Soil respiration, like other ecological processes, would be expected to be very different in these patch types (Barron-Gafford et al. 2011). Differences in topography or soil properties can also potentially cause profound influences in soil respiration rates by influencing soil moisture accumulation, availability, or retention and subsequently influencing what plants are present (Cable et al. 2008, Fernandez et al. 2006, Sponseller 2007).

The majority of soil respiration in drylands is in response to rainfall pulses, with biological activity potentially lasting for only a short time, ~~require~~ rapid up-regulation of metabolic activity to take advantages of these moisture pulses. Thus, the timing and size of precipitation events is thought to be a key regulator of dryland C cycling (Austin et al. 2004). However, the rate and dynamics by which soil organisms respond to moisture requiring

pulses will be a function not only of the pulse itself but also a function of long-term climate patterns that influence the patterns of vegetation, litter accumulation, microorganism productivity in combination with site-specific features such as soil properties and topography.

We took advantage of the unique physical environment of the Namib Desert to explore short- and long-term controls of environmental condition over soil respiration in a hyper-arid desert. We embraced the variation in surface cover, topography, soil properties, and climate patterns to gain an understanding of how this inherent site-specific variability influences soil respiration rates. By comparing respiration rates on different soil surfaces, we quantified how dominant soil surfaces differ in respiration rates. Within each soil surface we measured soil respiration across two dominant patch types, allowing us to assess how patch types differ in respiration. We manipulated rainfall and followed short-term (48 h) responses in soil respiration, allowing us to assess how soil surface x patch types differ in response to summer PPT. Finally, we conducted the manipulative study across the Namib precipitation gradient, allowing us to quantify the impact of short-term rainfall treatments on soil respiration.

Methods

Study Locations

The study was conducted in the Namib-Naukluft Park, within the central Namib Desert of Namibia. Six study sites were selected at three climate zones along the east-west climate gradient of the Namib, with one dune study site and one gravel/gypsum plains site at each climate zone (Figure 1). There is a strong climate gradient in this region (Lancaster et al. 1984). The west climate zone is characterized by high precipitation inputs from fog and low precipitation inputs from rain, the middle, driest climate zone is near the edge of regular fog inputs with low rainfall, and the east climate zone receives relatively high rainfall but almost no fog (Table 1).

The gravel plains sites are all north of the Kuiseb River. The gravel plains soils are rich in gypsum to the west, transitioning to calcium carbonate dominance in the east (Eckardt et al. 2013). The uplands of the gravel plains are intersected by lower-lying, shallow ‘watercourses’ that typically have loose, sandy soils. Movement of water through these watercourses occurs infrequently when there is adequate rainfall for surface run-off. The uplands are sparsely vegetated with perennial grasses (e.g., *Stipagrostis ciliata* at Kleinberg, *Stipagrostis gonatostachys* at Gobabeb Plains, and *Stipagrostis uniplumis* at Ganab), although at the time of sampling all grass clumps were quiescent with nearly all aboveground tissue removed by native grazers. Hypoliths and evidence of biological soil crusts are present in uplands at all three gravel plains sites. At Kleinberg, crustose and foliose lichens are abundant in the uplands but absent in watercourses. The watercourses are typically free of grasses, although the small shrub *Arthroa leubnitziae* is present in

watercourses at Kleinberg and camelthorn acacia trees (*Vachellia erioloba*) grow along the watercourses at Ganab. There is visible litter accumulation in the watercourse at Ganab.



Figure 1. Location of soil respiration study sites in the central Namib Desert. The Kuiseb River separates the gravel plains (north) from the sand dunes of the Namib Sand Sea (south). The study locations are notated by letters as follows: K – Kleinberg, P – Gobabeb Plains, G – Ganab, S – Swartbank, D – Gobabeb Dunes, F – Far East. Map data are from Landsat and Google Earth.

The dune sites lie south of the Kuiseb River at the northern edge of the Namib Sand Sea, where gravel plains have been covered over by alluvium transported down the Orange River drainage (Eckardt et al. 2013). The high sand dunes typically have little vegetation, with plants present primarily in ‘hummocks’ where sand accumulates around the base of perennial plants. These are most typically found near the base of dunes. These hummocks are typically distinct patches surrounded by unvegetated ‘bare’ areas characterized by relatively flat, shifting sands. The dune grass *Stipagrostis sabulicola* is the dominant hummock-forming grass at all dune sites across the climate gradient. The grass *Cladoraphis spinosa* is also present at all sites, with *Acanthosicyos horridus* forming hummocks at Gobabeb Dunes and the shrub *Trianthema hereroensis* abundant at Swartbank.

Table 1. Mean annual climate conditions and location of the six study sites in the Namib-Naukluft Park. Values are presented for mean annual rainfall in mm (MAP), mean annual temperature in °C (MAT), mean annual fog precipitation in mm (MAF), and minimum and maximum annual temperatures in °C (Temperature Range). Data are from Lancaster et al. (1984).

	Gravel Plains			Dunes		
	Kleinberg ^a	Gobabeb Plains	Ganab	Swartbank	Gobabeb Dunes	Far East ^b
MAP (mm)	18.8	27.2	87.0	18.8	27.2	87.0
MAF (mm)	183.6	30.8	2.7	183.6	30.8	2.7
MAT (°C)	19.3	21.1	21.5	19.3	21.1	21.5
Temperature Range (°C)	11.2 - 27.5	12.8 - 29.5	14.6 - 28.5	11.2 - 27.5	12.8 - 29.5	14.6 - 28.5
Coordinates	22°59'16.9"S 14°43'51.9"E	23°31'30.20"S 15°2'28.82"E	23°5'43.35"S 15°30'45.47"	23°21'17.4"S 14°48'10.8"E	23°34'13.6"S 15°02'28.1"E	23°47'34.94"S 15°47'2.10"E

^a Climate data presented are from Swartbank; the two sites are roughly the same location along the Namib climate gradient.

^b Climate data presented are from Ganab; the two sites are roughly the same location along the Namib climate gradient.



Figure 2. The six locations where the study was carried out. The three gravel plains sites are shown in the top row (a, b, c) and the three dunes sites are shown in the bottom row (d, e, f). The study sites are arrayed along the climate gradient with high fog (coastal) sites to left and high rainfall (inland) sites to right. Examples of patch types are annotated as ‘W’ for watercourses and ‘U’ for uplands in gravel plains and ‘B’ for bare and ‘H’ for hummocks in dunes.

Field Methods

We selected representative patches for soil respiration measurements at each of the study sites. For dunes sites, we selected representative ‘hummock’ and ‘bare’ patches. Hummocks were centred around *Stipagrostis sabulicola* plants. Hummocks were selected for uniformity by measuring length, width, height of soil mound, height of grasses, and distance to nearest neighbouring hummock and characterizing the amount of litter and bare ground in each hummock. Bare patches were selected to be the centre of the largest bare area adjacent to each of the selected hummocks. For the gravel plains sites, we selected representative patches within ‘uplands’ and ‘watercourse’. For both patch types, we selected locations based on uniformity. At each of the six sites, we selected five replicates for each of the two patch types.

Within each of the 10 selected patches at each of the six study sites, we designated three 50 cm diameter sub-plots for rainfall treatments. One sub-plot in each patch was designated for each of the three rainfall treatments: 0, 5, and 10 mm rain events. The appropriate volume of deionized water to simulate the rainfall depth (0, 0.98, and 1.96 L for 0, 5, and 10 mm events, respectively) was evenly distributed within the sub-plot using a garden watering can. Following the rainfall treatment, a PVC collar (10 cm diameter, 4.4 cm height) for measuring soil respiration was inserted 1 cm into the soil in the centre of each sub-plot.

Soil respiration measurements commenced approximately 30 minutes after watering. Soil respiration was measured with a LiCor 6400-09XT portable gas exchange system fitted with a 6400-09 soil respiration chamber (Licor, Lincoln, NE, USA). Soil respiration was measured as the mean CO₂ efflux rate at ambient CO₂ (390 ppm) from 3-6 drawdown cycles where CO₂ efflux was measured from 385-395 ppm. Soil temperature, chamber temperature, and chamber relative humidity were recorded concurrently with respiration. Respiration measurements were made sequentially through all 30 soil collars at each site, with continuous measurements for a 48 hour period following the watering treatment (with the exception of Gobabeb Dunes, where respiration measurements were halted after ~31 h). Speed of measurement varied with flux rates and ambient weather conditions, but there were on average 1765 measurements made at each site. Field measurements took place from 29 November to 17 December 2015, with separate 48 h field campaigns at each site. There was no measureable rainfall at any of the sites during the measurement period.

Data Analysis

A mean value for each measured variable (soil respiration, soil temperature, chamber temperature, and chamber relative humidity) was calculated from all replicate drawdown cycles each time measurements were made on a soil collar. Values from the entire measurement period were pooled for statistical analyses.

One- and two-way analysis of variance (ANOVA) procedures were used to assess soil respiration differences among soil surfaces and patch types and in response to precipitation manipulations. *Post-hoc* pairwise comparisons were performed with Student's *t* tests.

Results

Soil Surface and Patch Type Comparisons

When data were pooled across all precipitation treatments and patch types, there was considerably greater soil respiration in the gravel plains than the dunes (Fig. 3; $F_{1,3527} = 64.66$, $P < 0.0001$). When data were pooled for all gravel plains measurements, there was a significant site effect on soil respiration, with greatest respiration at Ganab, lowest respiration at Gobabeb Plains, and intermediate respiration at Kleinberg (Fig. 4a; $F_{2,2318} = 80.01$, $P < 0.0001$). Soil respiration was greater in the watercourses than the uplands ($F_{1,2318} = 71.16$, $P < 0.0001$). However, there was a significant site*patch interaction ($F_{2,2318} = 64.11$, $P < 0.0001$) where soil respiration was more than twice as high in the watercourse as in the upland at Ganab, slightly but significantly higher in the watercourse than upland at Kleinberg, and not significantly different among patch types at Gobabeb Plains. In the dunes, respiration differed among study sites (Fig. 4b; $F_{2,1208} = 13.55$, $P < 0.0001$), with greater respiration at Far East than Gobabeb or Swartbank. There was greater respiration in the

hummocks than bare patches ($F_{1,1208} = 102.43, P < 0.0001$). However, the relative increase in respiration from bare patches to hummocks was similar across study sites, with no significant site*patch interaction ($F_{2,1208} = 1.64, P < 0.19$).

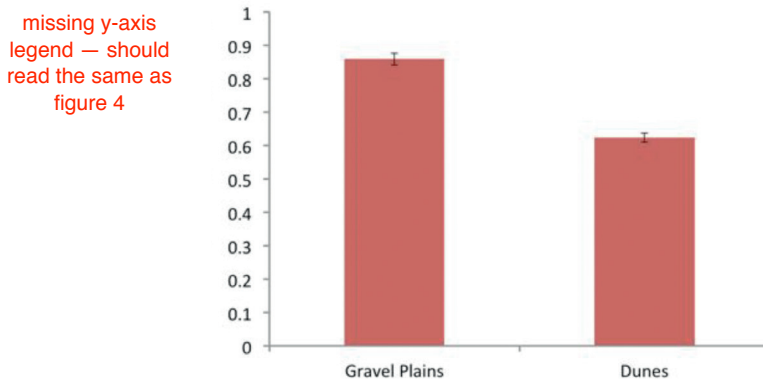


Figure 3. Soil respiration rates from the two contrasting soil surfaces. Soil respiration values are means (\pm SE) for all rainfall treatments and all vegetation patch types in each of the soil surfaces.

Soil Respiration Responses to Rainfall

In the gravel plains, soil respiration generally increased with increasing simulated rainfall treatments. At Kleinberg and Ganab, both uplands and watercourse patches responded positively to increases in precipitation (10 mm > 5 mm > 0 mm), although respiration was overall greater in watercourses than uplands (Figs. 5a & 5c; for Kleinberg: patch type $F_{1,686} = 5.12, P = 0.02$; rainfall $F_{2,686} = 28.52, P < 0.0001$; patch*rainfall $F_{2,686} = 1.17, P = 0.31$; for Ganab: patch type $F_{1,916} = 174.57, P < 0.0001$; rainfall $F_{2,916} = 31.80, P < 0.0001$; patch*rainfall $F_{2,686} = 3.84, P = 0.02$). In contrast to the other gravel plains sites, soil respiration at Gobabeb Plains increased with the 5 mm treatment but did not increase further with the 10 mm treatment and respiration was overall greater in the uplands than the watercourse (Fig. 5b; patch type $F_{1,704} = 7.45, P = 0.006$; rainfall $F_{2,704} = 29.30, P < 0.0001$; patch*rainfall $F_{2,704} = 3.39, P = 0.03$).

Similar to the gravel plains, simulated rainfall generally increased in soil respiration in the dunes in hummock patches. There were inconsistent responses to rainfall in the bare patches, however. At Swartbank, simulated rainfall increased soil respiration on hummocks while it caused no change in respiration on bare patches (Fig. 5d; patch type $F_{1,690} =$

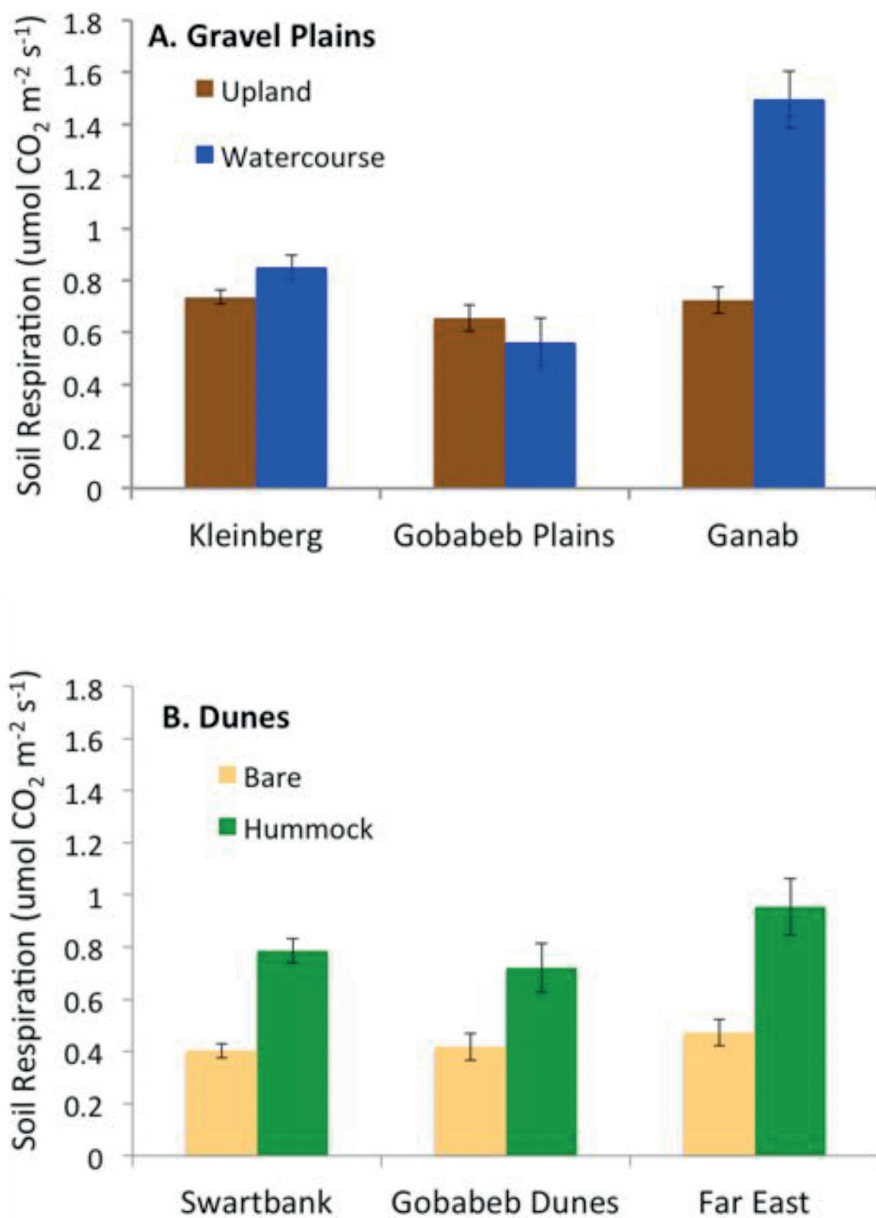


Figure 4. Soil respiration rates in the two vegetation patch types in a) gravel plains and b) dunes. Soil respiration values are mean (\pm SE) for all rainfall treatments in each of the soil surface \times vegetation patch type combinations. Study sites are arrayed along the climate gradient with high fog (coastal) sites to left and high rainfall (inland) sites to right. Note differences in y-axis scale.

434.00, $P < 0.0001$; rainfall $F_{2,690} = 58.84$, $P < 0.0001$; patch*rainfall $F_{2,690} = 9.32$, $P < 0.0001$). At Far East, both hummocks and bare patches responded positively to simulated rainfall, although the response was stronger in hummocks than bare patches (Fig. 5f; patch type $F_{1,323} = 19.62$, $P < 0.0001$; rainfall $F_{2,323} = 16.23$, $P < 0.0001$; patch*rainfall $F_{2,323} = 7.41$, $P < 0.001$). Soil respiration at Gobabeb Dunes was markedly different from the other sites. Although respiration was greater in hummocks than bare patches, soil respiration was depressed by simulated rainfall, particularly in the bare patches (Fig. 5e; patch type $F_{1,183} = 56.13$, $P < 0.0001$; rainfall $F_{2,183} = 5.45$, $P < 0.001$; patch*rainfall $F_{2,183} = 5.75$, $P < 0.01$).

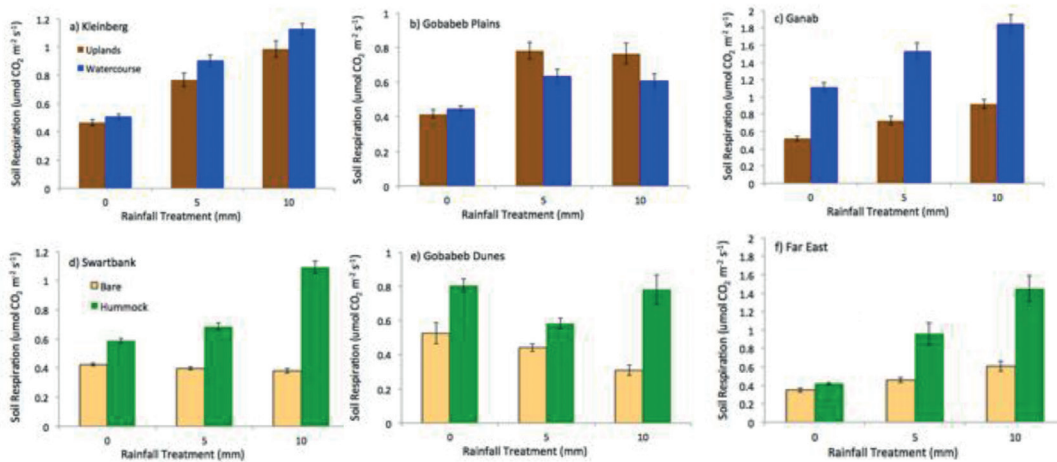


Figure 5. Soil respiration rates in response to rainfall manipulations (0, 5, and 10 mm one-time rainfall pulse additions) in the two vegetation patch types in gravel plains (a, b, c) and dunes (d, e, f). Soil respiration values are mean (\pm SE) for each rainfall treatment in each of the soil surface \times vegetation patch type combinations. Figures are arrayed along the climate gradient with high fog (coastal) sites to left and high rainfall (inland) sites to right. Note differences in y-axis scales at different locations along the climate gradient.

Discussion

Soil respiration rates varied strongly, but generally consistently, among the different patch types, study sites, and rainfall treatments, underscoring the importance of considering spatial patterns of variability when assessing C cycling patterns and dynamics. Nearly all measurement locations responded positively to short-term simulated rainfall, although the magnitude of response varied among patch types and study sites.

Soil Respiration Responses to Soil Surface

Soil respiration rates in the gravel plains were consistently higher overall than in the dunes. Differences between the two surfaces in both soil texture and topography could be responsible for differences in respiration. Soils on the dunes are coarse and composed of coarse sand grains relative to the finer-grained soils of the gravel plains. Coarse sands typically have higher water infiltration and lower moisture retention than finer-textured soils, leading to lower productivity and soil respiration on coarse-textured soils (Cable et al. 2008). However, high productivity and respiration has been observed in some coarse dryland soils. This has been attributed to reduced evaporative losses from surface layers and rapid infiltration of moisture to deep soil layers where deep-rooted plants can access moisture (the “inverse texture hypothesis”; Fernandez et al. 2006, Noy-Meir 1973). Our results provide support for the idea that productivity and soil respiration are enhanced by finer texture soils in the Namib (in contrast to the inverse texture hypothesis). However, another possible factor is topographic difference between the soil surfaces. Depth to bedrock is generally quite shallow in the gravel plains (Eckardt et al. 2013), suggesting water may be retained in the system more readily than the deep soils of the dunes.

Soil Respiration Responses to Patch Types and Climate Gradient

Soil respiration responses in the gravel plains to patch type appear to reflect topographic patterns that influence water and organic matter accumulation. The lower-lying watercourses accumulate water when rainfall is sufficient for runoff to occur. This water movement may influence soil respiration rates both through transport of organic matter into watercourses, which serves as a substrate for microbial metabolism, and through enhancing plant productivity. It is not surprising that the difference in soil respiration between upland and watercourse was most prominent at Ganab as at this site large amounts of fluvially-transported litter were apparent in[^]watercourse. The minimal differences between patch types at Kleinberg may reflect limited transport and organic matter accumulation in these poorly defined watercourses. Alternatively, there may be increases in organic matter accumulation in the watercourses but the difference may be offset by respiration from lichens, which are abundant in the uplands but absent in the watercourse. Similarly, the lack of difference between uplands and watercourse at Gobabeb Plains may reflect the limited organic matter accumulation in the watercourse or may be a function of greater surface microbial activity in the uplands than the watercourse. At Gobabeb Plains we observed evidence of biological soil crusts and hypoliths (cyanobacteria colonies on the underside of translucent quartz rocks) in the uplands but not the watercourse. These organisms may have been respiring in the soil chamber, which does not permit any light transmission. Soil respiration differences between patch types in the dunes reflects patterns of vegetation cover and presumably patterns of soil organic matter accumulation. Rates of soil respiration on the bare patches were among the lowest measured in the study, and this was partic-

ularly true at Swartbank and Gobabeb Dunes where bare patches were large with little or no evidence of organic inputs into bare areas. Greater respiration at Far East in both bare and hummock patches likely reflects higher productivity in this relatively high moisture site. The small bare patches at Far East likely are interspersed with roots extending out from hummocks; these roots would contribute to soil respiration (Cable et al. 2008).

Soil Respiration Responses to Simulated Rainfall

In the gravel plains, responses to simulated rainfall were clear and consistent at the two extremes in the climate gradient. Positive responses to rainfall in both patch types at these two sites provide evidence that organic matter substrates were not limiting. In contrast, apparent saturation response at 5 mm simulated rainfall suggests that carbon substrates may be limiting in these soils, such that additional water did not further stimulate respiration (Fernandez et al. 2006).

Soil respiration responses to simulated moisture in the dunes reflected expected patterns of soil organic matter accumulation, at least at the two extremes of the climate gradient. Strong positive responses to simulated rainfall in both patch types at Far East are in line with large amounts of visible organic matter accumulation in soils at this site. Rainfall responses even in bare patches suggest that there is significant burial of litter in bare patches (no visible litter on surface) and/or roots from hummocks extend out into the bare patches; both are likely given that bare patches were much smaller relative to the other sites. Furthermore, substantial organic matter accumulation at Far East may enhance soil moisture retention (Gupta & Larson 1979), prolonging the impact of simulated rainfall. The lack of moisture response in Swartbank bare patches appears to reflect a near complete lack of biological activity in the bare areas, presumably due to limited litter and root inputs. The patterns at Gobabeb were unexpected and are difficult to explain. There is no reason that rainfall would typically decrease respiration, suggesting the possibility that the shorter measurement time used in at this study site than other sites could have ~~reflected~~ affected the results. Transient increases in respiration immediately following rainfall may be a result of flushing of accumulated CO₂ from soil pores (the 'Birch effect'; Jarvis et al. 2007); dissimilarities in the overall time series of the data would make transient initial patterns more important in the Gobabeb Dunes dataset. Another possibility for inconsistent patterns is the high termite activity at this site; a few soil respiration collars had visible termites in them and data from these collars were discarded. However, subsurface termite activity would not be apparent and thus we may have some spuriously high values as termites would drastically increase rates of respiration. Further studies at Gobabeb are warranted to better understand respiration responses at this site.

Conclusions

Our results show high variation in rates of soil respiration from Namib Desert soils, with differences among patch types, soil surfaces, and sites along the climate gradient ostensibly reflecting differences in soil texture, topography, and soil organic matter accumulation. Relative increases in respiration with precipitation varied with location, but were highest in sites where rain, fog, and soil conditions favoured organic matter accumulation. Understanding the controls over soil respiration, which is the largest transfer of C from the earth to the atmosphere is soil respiration, will help increase scientific understanding of what controls the land surface - atmosphere exchange of C. Given the limited understanding of how climate change influences C cycling (de Graaff et al. 2014) and the potentially large role that drylands play in the global C cycle (Ahlström et al. 2015, Lal 2004), this information is critical for helping advance global C cycle predictions and informing future global climate models.

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Literature Cited

- AHLSTRÖM A., RAUPACH M.R., SCHURGERS G., SMITH B., ARNETH A., JUNG M., REICHSTEIN M., CANADELL J.G., FRIEDLINGSTEIN P., JAIN A.K., KATO E., POULTER B., SITCH S., STOCKER B.D., VIOVY N., WANG Y.P., WILTSHIRE A., ZAEHLE S., ZENG N. 2015. The dominant role of semi-arid ecosystems in the trend and variability of the land CO₂ sink. *Science* 348:895-899
- AULT T.R., COLE J.E., OVERPECK J.T., PEDERSON G.T., MEKO D.M. 2014. Assessing the risk of persistent drought using climate model simulations and paleoclimate data. *Journal of Climate* 27:7529-7549



- AUSTIN A.T., YAHDJIAN L., STARK J.M., BELNAP J., PORPORATO A., NORTON U., RAVETTA D.N.A., SCHAEFFER S.M. 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia* 141:221-235
- BARGER N.N., ARCHER S.R., CAMPBELL J.L., HUANG C.H., MORTON J.A., KNAPPA.K. 2011. Woody plant proliferation in North American drylands: a synthesis of impacts on ecosystem carbon balance. *Journal of Geophysical Research - Biogeosciences* 116:G00K07
- BARRON-GAFFORD G.A., SCOTT R.L., JENERETTE G.D., HUXMAN T.E. 2011. The relative controls of temperature, soil moisture, and plant functional group on soil CO₂ efflux at diel, seasonal, and annual scales. *Journal of Geophysical Research* 116:G01023
- CABLE J., OGLE K., WILLIAMS D., WELTZIN J., HUXMAN T. 2008. Soil texture drives responses of soil respiration to precipitation pulses in the Sonoran Desert: implications for climate change. *Ecosystems* 11:961-979
- DE GRAAFF M.-A., THROOP H.L., VERBURG P.S.J., ARNONE J.A., CAMPOS X. 2014. A synthesis of climate change and elevated atmospheric CO₂ impacts on biogeochemical cycling of carbon and nitrogen in shrub-dominated drylands. *Ecosystems* 17:931-945
- DEL GROSSO S.J., PARTON W.J., MOSIER A.R., HOLLAND E.A., PENDALL E., SCHIMEL D.S., OJIMA D.S. 2005. Modeling soil CO₂ emissions from ecosystems. *Biogeochemistry* 73:71-91

- ECKARDT F.D., LIVINGSTONE I., SEELY M., VON HOLDT J. 2013. An introduction to the surface geology and geomorphology around Gobabeb, Namib Desert, Namibia. *Geografiska Annaler: Series A, Physical Geography* 95:271-284
- FERNANDEZ D., NEFF J., BELNAP J., REYNOLDS R. 2006. Soil respiration in the cold desert environment of the Colorado Plateau (USA): Abiotic regulators and thresholds. *Biogeochemistry* 78:247-265
- FIELD C., BEHRENFELD M., RANDERSON J., FALKOWSKI P. 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* 281:237-240
- GUPTA S.C., LARSON W.E. 1979. Estimating soil water retention characteristics from particle size distribution, organic matter percent, and bulk density. *Water Resources Research* 15:1633-1635
- IPCC (ed) 2013. *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom
- JARVIS P., REY A., PETSIKOS C., WINGATE L., RAYMENT M., PEREIRA J., BANZA J., DAVID J., MIGLIETTA F., BORGHETTI M., MANCA G., VALENTINI R. 2007. Drying and wetting of Mediterranean soils stimulates decomposition and carbon dioxide emission: the “Birch effect”. *Tree Physiology* 27:929-940
- KING A.W., HAYES D.J., HUNTZINGER D.N., WEST T.O., POST W.M. 2012. North American carbon dioxide sources and sinks: magnitude, attribution, and uncertainty. *Frontiers In Ecology And The Environment* 10:512-519
- LAL R. 2004. Carbon sequestration in dryland ecosystems. *Environmental Management* 33:528-544
- LANCASTER J., LANCASTER N., SEELY M.K. 1984. Climate of the Central Namib Desert. *Madoqua* 14:5-61
- MILLY P.C.D., DUNNE K.A., VECCHIA A.V. 2005. Global pattern of trends in streamflow and water availability in a changing climate. *Nature* 438:347-350
- NOY-MEIR I. 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4:25–51
- OVERPECK J., UDALL B. 2010. Dry times ahead. *Science* 328:1642-1643
- POULTER B., FRANK D., CIAIS P., MYNENI R.B., ANDELA N., BI J., BROQUET G., CANADELL J.G., CHEVALLIER F., LIU Y.Y., RUNNING S.W., SITCH S., VAN DER WERF G.R. 2014. Contribution of semi-arid ecosystems to interannual variability of the global carbon cycle. *Nature* 509:600–603
- REYNOLDS J.F., SMITH D.M.S., LAMBIN E.F., TURNER B.L., MORTIMORE M., BATTERBURY S.P.J., DOWNING T.E., DOWLATABADI H., FERNANDEZ R.J., HERRICK J.E., HUBER-SANNWALD E., JIANG H., LEEMANS R., LYNAM T., MAESTRE F.T., AYARZA M., WALKER B. 2007. Global desertification: Building a science for dryland development. *Science* 316:847-851

- SCHLESINGER W.H., BERNHARDT E.S. 2013. Biogeochemistry, An Analysis of Global Change, 3rd Edition edn. Academic Press
- SPONSELLER R.A. 2007. Precipitation pulses and soil CO₂ flux in a Sonoran Desert ecosystem. *Global Change Biology* 13:426-436
- SULZMAN E.W., BRANT J., BOWDEN R., LAJTHA K. 2005. Contribution of aboveground litter, belowground litter, and rhizosphere respiration to total soil CO₂ efflux in an old growth coniferous forest. *Biogeochemistry* 73:231-256
- WANG D., GOUHIER T.C., MENGE B.A., GANGULY A.R. 2015. Intensification and spatial homogenization of coastal upwelling under climate change. *Nature* 518:390-394
- WANG L., D'ODORICO P., EVANS J., ELDRIDGE D., MCCABE M., CAYLOR K., KING E. 2012. Dryland ecohydrology and climate change: critical issues and technical advances. *Hydrology and Earth System Sciences* 16:2585-2603

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