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Short Communication

Moisture activation and carbon use efficiency of soil microbial communities along an aridity gradient in the Atacama Desert

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ABSTRACT

Due to their extreme aridity, high rate of UV irradiation and low soil carbon (C) content, the soils of the Atacama Desert represent one of the world's most hostile environments for microbial life and its survival. Although infrequent, climatic conditions may, however, prevail which temporarily remove these stresses and allow life to briefly flourish. In this study we investigated the response of soil microbial communities to water and C availability across an aridity gradient (semi-arid, arid, hyper-arid) within the Atacama Desert. We simulated the impact of hyper-dry spells, humid fogs and precipitation events on the activation of the microbial community and the subsequent mineralization of low (glucose) and high (plant residues) molecular weight C substrates. Our results showed that mineralization rate followed the trend: semi-arid > arid > hyper-arid. Some glucose mineralization was apparent under hyper-arid conditions (water activity, a_w = 0.05), although this was 10-fold slower than under humid conditions and ca. 200-fold slower than under wet conditions. A lag phase in CO_2 production after glucose-C addition in the hyper-arid soils suggested that mineralization was limited by the low microbial biomass in these soils. No lag phase was apparent in the corresponding semi-arid or arid soils. In contrast, the breakdown of the plant residues was initially much slower than for glucose and involved a much longer lag phase in all soils, suggesting that mineralization was limited by low exoenzyme activity, particularly in the humid and hyper-dry soils. Our results also showed that microbial C use efficiency followed the trend: hyper-arid > arid > semi-arid. In conclusion, we have shown that even under hyper-arid conditions, very low levels of microbial activity and C turnover do occur. Further, the microbial communities are capable of rapidly responding to available C once water becomes more abundant, however, this response is both biomass and metabolically limited in hyper-arid soils.

The hyper-arid soils of the Atacama experience some of the most severe climatic conditions on Earth, and are often used to understand the potential for life on exoplanets such as Mars (Valdivia-Silva et al., 2012; McKay, 2014). These soils contain very low organic carbon (OC) concentrations, with labile OC values varying from 2 to 73 μg C g^{-1} (Valdivia-Silva et al., 2012; Fletcher et al., 2011, 2012). The role of (hyper)arid conditions on soil OC processing vs. stabilization continues to be debated (e.g. Skelley et al., 2007; Ewing et al., 2006, 2008; Ziolkowski et al., 2013; Wilhelm et al., 2017).

Microbial soil communities in the hyper-arid core of the Atacama Desert are of low abundance and express numerous xero-tolerance traits (Azua-Bustos et al., 2012, 2015; Connon et al., 2007; Drees et al., 2006; Lebre et al., 2017; Navarro-González et al., 2003). Their activity is primarily limited by water, although other factors such as C limitation, high salinity and UV irradiation may also impose constraints on life (Warren-Rhodes et al., 2006; Cockell et al., 2008; Gómez-Silva et al., 2008; Paulino-Lima et al., 2013). Although extremely infrequent, the microbial biomass can be subject to precipitation events (Jordan et al., 2015) or more likely to high humidity and fog-derived water (Cáceres et al., 2007). In this context, our aims were to (1) determine the re-activation speed of the soil microbial community to moisture and OC addition, (2) compare the relative mineralization rate of low and high molecular weight OC substrates in soil, and (3) investigate the C use efficiency (CUE) of these communities.

The Atacama is a temperate desert and extends from ca. 15 to 35°S and between 70 and 72°W along South America's Pacific Coast.

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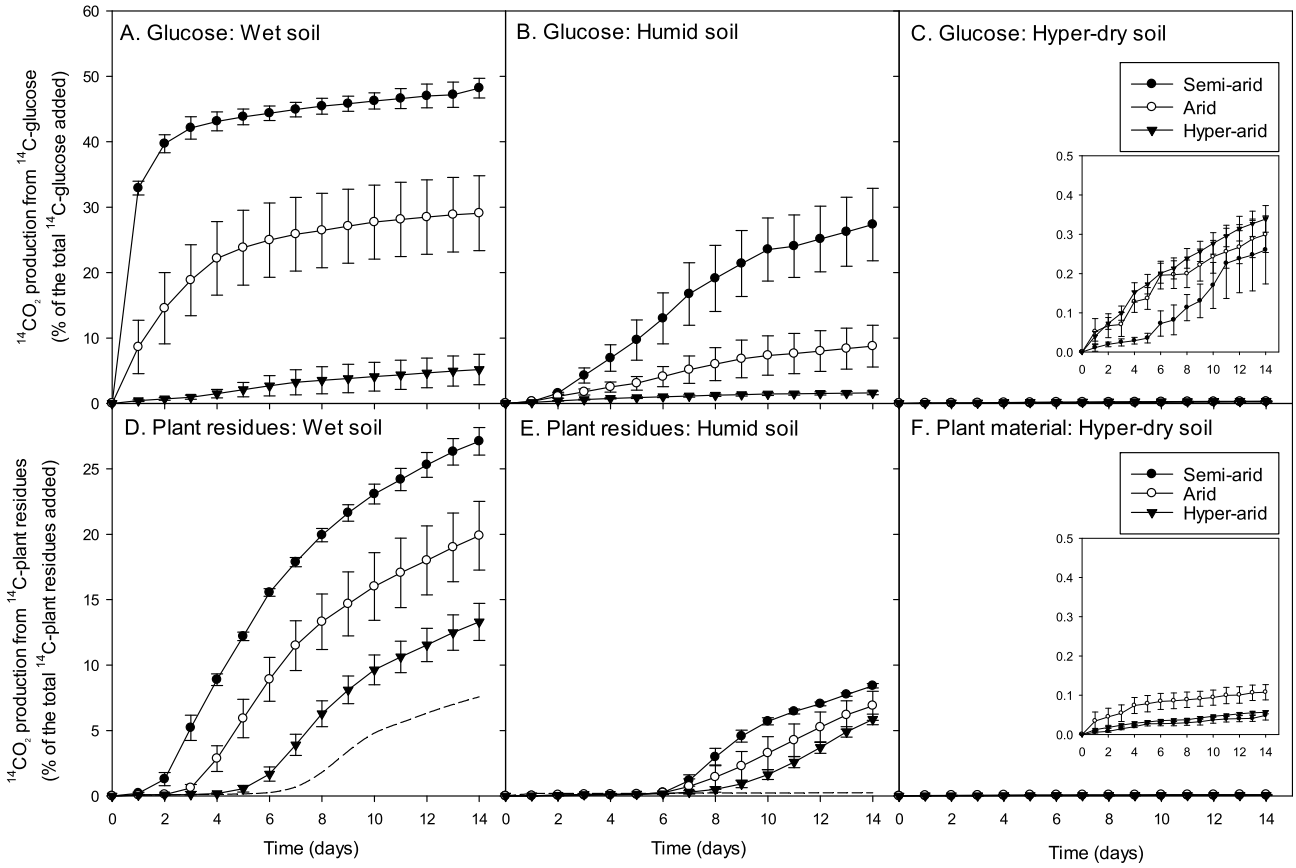

Fig. 1. Mineralization of either ^{14}C-labelled glucose (Panels A-C) or ^{14}C-labelled plant material (Panels D-F) under three imposed moisture regimes (wet, humid or hyper-arid) in semi-arid, arid or hyper-arid soils of the Atacama Desert. Values represent means ± SEM. The dotted line in the plant residue panels represents the intrinsic mineralization of the plant residues in the absence of soil. The inset panels in the hyper-dry treatment represent the same data but with an expanded y-axis scale.

Hyperarid conditions have existed in the Atacama desert for ca. 25 Ma (Dunai et al., 2005). The mean annual rainfall in the hyperarid core is < 1 mm y^{-1}; a single rainfall event of 1–20 mm may occur once in a decade (Warren-Rhodes et al., 2006; McKay et al., 2003).

Field sampling was undertaken in the Atacama region of Chile in February 2014. Soil samples were taken from the surface soil (0-10 cm; n = 3) and subsoil (20-40, 120-140 cm; n = 1) were collected from the hyper-arid site at Yungay (1020 m a.s.l.; 24°8′54.67″S; 70°7′32.48″W). Yungay is probably the most frequently studied hyper-arid region of the Atacama Desert, having an extremely low water availability (Navarro-González et al., 2003; Azua-Bustos et al., 2015). Surface samples (0-10 cm, n = 3 at 5 sites) were also taken in the Andean Precordillera at Quebrada Aroma (19°31′42.7″S; 69°22′43.2″W to 19°46′53.1″S; 69°40′02.4″W). This precipitation gradient transect was characterized by decreasing vegetation cover and plant diversity from arid (2020-2720 m a.s.l.; 3 sites) to hyper-arid sampling sites (1340-1660 m a.s.l.; 2 sites). Finally, additional surface (0-10 cm, n = 3) and subsurface soils (n = 1) were sampled down to 2 m near Paposo in the semi-arid Coastal Cordillera (570 m a.s.l.; 25°00′43.02″S; 70°26′47.50″W). The samples from all sites had a low intrinsic moisture content at the time of collection (20.4 ± 4.1 g kg^{-1}). All samples were homogenised by sieving (< 2 mm) and stored in sealed tubes prior to use. Based on their moisture regime, the sites were divided into 3 levels of aridity, namely, semi-arid, arid and hyper-arid (see Supplementary information for further details and basic chemical data).

The experiments used two contrasting forms of C to determine how microbial activity was regulated by substrate quality: (1) low molecular weight (MW) substrate (^{14}C-labelled glucose); (2) high MW substrate (^{14}C-labelled dry *Lolium perenne* L. shoots; Hill et al., 2007; Simfukwe et al., 2011). In addition, to explore their response to moisture availability we used three moisture regimes: (1) *wet*, in which water was added directly to the soil surface to simulate desert rainfall, (2) *humid*, in which the soil samples were maintained at a high relative humidity to simulate desert fogs, and (3) *hyper-dry*, in which the soil samples were incubated at a low relative humidity to simulate typical conditions in the hyper-arid region of the Atacama Desert.

For each sample, 1 g of field soil was placed into sterile 50 cm^3 polypropylene containers. Either ^{14}C-labelled glucose (72 mg C kg^{-1} soil; 0.44 MBq kg^{-1} soil) or 100 mg of ^{14}C-plant material (100 g kg^{-1} soil; 42 g C kg^{-1} soil; 3.6 MBq kg^{-1} soil) was then added to the soil. For the *humid* treatments, the ^{14}C-glucose was first dried down under N_2 onto a sterile quartz sand carrier before addition to the soil (100 g sand kg^{-1} soil), while the dried ^{14}C-labelled plant material was added directly to the soil. The relative humidity in the *humid* (simulated fog) containers was 67 ± 3% at the start and was 83 ± 3% at the end. For the *wet* treatments (simulated rainfall), the ^{14}C substrates were added as described above, but together with 100 µl of distilled water. For the *hyper-dry* treatments (simulated normal conditions), the method was identical to the *humid* treatment, except that the containers also contained a small vial of desiccant (1 cm^3; Drierite®; Sigma-Aldrich, Poole, UK) to maintain a relative humidity of 1–5% (Reis et al., 2009). In the *wet* and *humid* treatments, $^{14}CO_2$ evolved from the soil was captured with a vial of 1 M NaOH trap placed inside the container (Glanville et al., 2016), while in the *hyper-dry* treatment it was trapped with a vial containing 40 mg of solid $Ba(OH)_2{\cdot}8H_2O$. After addition of the ^{14}C-substrates and $^{14}CO_2$ traps, the containers were hermetically sealed and incubated at 20 °C. The $^{14}CO_2$ traps were replaced daily for 14 d. The length of experiment reflects the typical time that water may remain in soil after a rare precipitation event (McKay et al., 2003). The $^{14}CO_2$ in the traps was determined by liquid scintillation counting using