Biological soil crusts promote N accumulation in response to dew events in dryland soils

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ABSTRACT

Dew is an important source of water in drylands, particularly for biological soil crusts (BSCs), which are soil communities dominated by lichens, mosses and cyanobacteria that are prevalent in these environments and play important roles in nutrient cycling. While BSCs can retain and use water from dew, the effects of dew events on the cycling of nitrogen (N) and carbon (C) in BSC-dominated ecosystems are largely unknown. We conducted an experiment to evaluate the effects of BSCs and dew on N and C cycling; intact soil cores from either bare ground or BSC-dominated microsites were incubated over 14 days under control and artificial dew addition treatments. A positive increment in the amount of total available N and phenols was observed in response to dew events under BSCs. We also found an increase in the concentration of dissolved organic N, as well as in the pentoses:hexoses ratio, under BSCs, suggesting that dew promoted an increase in the decomposition of organic matter at this microsite. The increase in the amount of available N commonly observed under BSCs has been traditionally associated with the fixation of atmospheric N_2 by BSC-forming cyanobacteria and cyanolichens. Our results provide a complementary explanation for such an increase: the stimulation of microbial activity of the microorganisms associated with BSCs by dew inputs. These effects of dew may have important implications for nutrient cycling in drylands, where dew events are common and BSCs cover large areas.

1. Introduction

Drylands (arid, semi-arid and dry-subhumid ecosystems) are a key terrestrial biome, covering 41% of the Earth's land surface and supporting over 38% of the total global population (Reynolds et al., 2007). In these ecosystems, where water availability is the most important factor limiting biological processes (Whitford, 2002), dew events are a common source of water for plants, biological soil crusts dominated by mosses, lichens and cyanobacteria, invertebrates, and small vertebrates (Kidron et al., 2002; Zhang et al., 2009). Information about dew events and their biological implications is still scarce as they have been traditionally considered a minor component of the water balance (Wallin, 1967). However, studies conducted during the last decades indicate that dew plays a significant role in the local water balance of semi-arid vegetation in

drylands as they may provide up to 40% of the water inputs received every year (Kidron, 2000; Jacobs et al., 2002; Moro et al., 2007; Lekouch et al., 2011). For instance, up to 195 days of dew and foggy mornings were recorded in the Negev Desert of Israel, providing an annual mean of 33 mm of dew and fog precipitation (Evenari, 1981). Water pulses from dew differ from those of rainfall events in their size and frequency; while dew events are common throughout the year, and typically range from 0.15 mm to 0.30 mm per day (Kidron, 2000; Jacobs et al., 2000; Moro et al., 2007), the smallest rainfall events in arid/semiarid ecosystems are less than 5 mm (Loik et al., 2004), and show irregular patterns of distribution both intra- and inter-annually (Westoby, 1972; Noy-Meir, 1973). Water inputs from rainfall events play a critical role on biogeochemical processes in drylands as even small pulses can activate processes such as nitrification, soil respiration and denitrification (Cui and Caldwell, 1997; Smart et al., 1999; Austin et al., 2004). However, not much is known about the influence that very small water pulses, such as those from dew events, have on biogeochemical cycles in drylands.

Biological soil crusts (BSCs) play key functional roles in drylands worldwide, where they are a prevalent biotic component (Eldridge

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and Greene, 1994; Belnap and Lange, 2003; Maestre et al., 2011). These crusts control the carbon (C) cycle in drylands by fixing atmospheric C through photosynthesis (Belnap et al., 2004), by contributing to soil CO_2 efflux (Castillo-Monroy et al., 2011a), and by affecting the activity of β-glucosidase (Bowker et al., 2011). Key processes of the nitrogen (N) cycle, such as N fixation (Belnap, 2002), mineralization–depolymerization (Castillo-Monroy et al., 2010), and gaseous N losses (Barger et al., 2005), are also driven by BSCs. The influence of BSCs on C (i.e. photosynthesis) and N (i.e. mineralization) processes in response to small rainfall events (around 2 mm) has been previously observed (e.g., Belnap et al., 2004; Delgado-Baquerizo et al., 2012). By increasing the roughness and microtopography of the soil surface, BSCs can increase its area, and augment the amount of dewfall reaching the soil (Rao et al., 2009). Therefore, BSCs are likely to determine potential effects of dew events on soil biogeochemical processes.

The effects of BSCs on soil N and C dynamics in response to water inputs from dew have not apparently been reported to date. We aimed to do so by evaluating how simulated dew conditions affect multiple variables related to N (ammonium, nitrate, dissolved organic nitrogen [DON], amino acids, total available N) and C (carbohydrates, phenols, pentoses:hexoses ratio and carbohydrates:available N ratio) cycling in soils from microsites differing in the degree of BSC development (bare ground and well-developed BSCs areas). These cryptogams have been observed to be physiologically active during dew events (Veste et al., 2008; Wilske et al., 2008; Rao et al., 2009; Pintado et al., 2010), and maintain abundant and rich fungal communities underneath them (Bates et al., 2010). Thus, we hypothesized that the microbial communities associated with BSCs may carry out microbial decomposition and N mineralization in response to dew events, taking up C labile sources, and producing N available to plants and microorganisms (Schimel and Bennett, 2004) at a faster rate than those present in bare ground areas.

2. Methods

2.1. Sampling design and laboratory analyses

Soils and BSCs for this study were collected at the Aranjuez experimental station, located in central Spain (40°02′ N − 3° 37′W; 590 m a.s.l.; 8° slope Facing SE). The climate is Mediterranean semi-arid, with an average annual rainfall and temperature of 349 mm and 14.5 °C, respectively (1986–2012 period). Perennial plant cover is below 40%, and is dominated by the tussock grass *Stipa tenacissima* L. (18% of plant cover) and the N-fixing shrub *Retama sphaerocarpa* (L.) Boiss (6% of plant cover). Open areas between plant patches host well developed BSCs dominated by lichens such as *Diploschistes diacapsis* (Ach.) Lumbsch, *Squamarina lentigera* (Weber) Poelt, *Fulgensia subbracteata* (Nyl.) Poelt, *Toninia sedifolia* (Scop.) Timdal, and *Psora decipiens* (Hedw.) Hoffm. (see Castillo-Monroy et al., 2010 for a full checklist). Bare ground and BSC-dominated areas cover 28% and 32% of the total area of the study site, respectively. The soil is classified as Xeric Haplogypsid (Marqués et al., 2008), and has a fine texture dominated by the presence of gypsum. See Appendix A for further information on the soils from the study site.

Soil sampling was carried out during the spring of 2010. Twelve intact soil cores (5 cm depth, 7.5 cm diameter) were collected under each of two microsites: well-developed BSCs (cover of lichens and mosses > 75%; see Appendix B of Castillo-Monroy et al., 2010) and bare ground areas (BG hereafter) devoid of vascular vegetation and visible BSC components (cover of mosses and lichens < 15%; see Appendix B of Castillo-Monroy et al., 2010). This depth was chosen to keep the influence of BSCs in its entirety (usually top 0–4 cm of

soil, Castillo-Monroy et al., 2010; Delgado-Baquerizo et al., 2010). After sampling, soil cores were transported to the laboratory and air-dried at room temperature for four weeks.

Air-dried soil cores with and without BSCs (with six replicates each) were incubated in a plant growth chamber for 14 days under two treatments: with and without (control) dew. Day (9 h of light, 20% relative humidity, 20 °C) and night (15 h darkness, 80% relative humidity, 10 °C) conditions simulated in this chamber follow climatic conditions typically found in early spring in the study area, when BSCs and soil microbial communities are most active (Castillo-Monroy et al., 2011a). In the dew treatment, soils were watered automatically three times during the darkness period to keep soil humidity constant at a rainfall equivalent of 0.15 mm per pot (1% of soil water content in our soils). The amount and duration of dew events were selected according to the number and duration of dew events observed in ecosystems similar to that studied here (Jacobs et al., 2002; Kidron, 2000; Moro et al., 2007). The amount of dew added to the soil was monitored by weighting all the cores every 12 h (Appendix B). In the control treatment, soils were not watered at any time during the experiment.

Before and after the experiment, we collected 2.5 g of soil (0–2 cm depth) from each replicated core. This depth was chosen because the effects of BSCs on soil properties are mainly noticeable in the first two cm of the soil profile (e.g., Bowker et al., 2011; Castillo-Monroy et al., 2011b; Maestre et al., 2012). Soil samples were extracted with K_2SO_4 0.5 M in a ratio 1:5. Soil extracts were shaken in an orbital shaker at 200 rpm for 1 h at 20 °C and filtered to pass a 0.45-μm Millipore filter (Jones and Willett, 2006). The filtered extract was kept at 2 °C until colorimetric analyses, which were conducted within 24 h following the extraction. Sub-samples of each non-incubated (air-dried) extract were taken for measurements of amino acids, phenols and carbohydrates (sum of pentoses and hexoses) according to Chantigny et al. (2006). The pentoses:hexoses ratio was calculated from these variables. Ammonium, nitrate, DON were measured by following Delgado-Baquerizo et al. (2011). Potentially available N (total available N hereafter) was calculated as the sum of ammonium, nitrate and DON as described in Delgado-Baquerizo and Gallardo (2011). We used the ratio carbohydrates:total available N as an indicator of the relative C and N availability for soil microorganisms in drylands, as this ratio can provide additional insights compared to the classic total C-to-N ratio (Gallardo and Schlesinger, 1992, 1995).

We also collected samples of BSC-forming lichens to measure their respiration in response to simulated dew events. We weighed 12 samples (∼5 g) of BSCs (without soil) in Petri dishes. Six of these samples were subjected to each treatment (control and dew, as described above), and were placed in the plant growth chamber. Lichen respiration was measured multiple times during a 12 h period, including measurements of night and light conditions, by using an Infra-Red Gas Analyzer (SBA-4, *PP-Systems*, *Hitchin*, *U.K*).

2.2. Numerical and statistical analyses

We calculated the absolute increment in the values of soil C variables (hexoses, pentoses, phenols, and hexose:pentose ratio) and N variables (ammonium, nitrate, DON, amino acids, total available N, C-phenols: available N and carbohydrates:available N ratio) after 14 days of incubation (regarding initial concentrations). One-way ANOVAs were used to evaluate differences between microsites (BSC and BG) in the initial values (before incubations) of C and N variables. Differences in the increment of these variables were evaluated using two-way ANOVAs, with microsites (BSC and BG) and treatments (control and dew) as fixed factors. Separate ANOVAs were conducted for each variable. To investigate interactions, data were divided into subsets based on one of the

Table 1
Initial concentration of carbon and nitrogen variables in both biological soil crust (BSC) and bare ground (BG) microsites. Data represent means (SE), $n = 12$. Significance levels between microsites are as follows: $^*p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

Variable	BG	BSC
NH_4^+ (mg N kg^{-1} soil)**	5.23 (0.50)	3.22 (0.18)
NO_3^- (mg N kg^{-1} soil)	5.98 (0.70)	4.78 (0.80)
DON (mg N kg^{-1} soil)	26.31 (1.96)	21.28 (1.56)
Amino acids (mg N kg^{-1} soil)**	0.76 (0.09)	0.35 (0.07)
Total available N (mg N kg^{-1} soil)*	37.52 (2.62)	29.07 (2.01)
Carbohydrates (mg C kg^{-1} soil)	110.22 (9.83)	95.60 (12.64)
Phenols (mg C kg^{-1} soil)**	23.31 (2.59)	11.07 (1.06)
Ratio pentoses:hexoses	0.66 (0.20)	0.45 (0.13)
Carbohydrates:total available N	3.00 (0.28)	3.53 (0.59)
Phenols:carbohydrates	0.22 (0.03)	0.15 (0.03)

factors of interaction, and then were subjected to ANOVA. Differences in the respiration of BSC-forming-lichens between control and dew treatments were evaluated by using repeated-measures ANOVA. All statistical analyses were carried out using IBM SPSS 15.0 (SPSS Inc, Chicago, IL, USA). The experiment-wide error rate was not adjusted for multiple testing, as this approach is considered excessively conservative (Gotelli and Ellison, 2004).

3. Results

Before incubation, the concentration of ammonium, amino acids, total available N and phenols was higher in BG than in BSC microsites ($p < 0.05$; Table 1). At this time, differences in the concentration of nitrate, DON, carbohydrates, and in the hexoses:pentoses, carbohydrates:total available N and phenols:carbohydrates ratios, were not found between microsites ($p > 0.05$; Table 1).

A significant Microsite $\times$ Treatment interaction was found for the increment in DON ($p < 0.05$; Appendix C, Fig. 1A). The addition of dew increased DON (regarding control) in the BSC microsite ($p < 0.05$; Fig. 1A; Appendix C). Soils under BSCs showed a greater decrease in DON than BG soils in the control treatment ($p = 0.05$; Appendix C), but the inverse result was found under dew
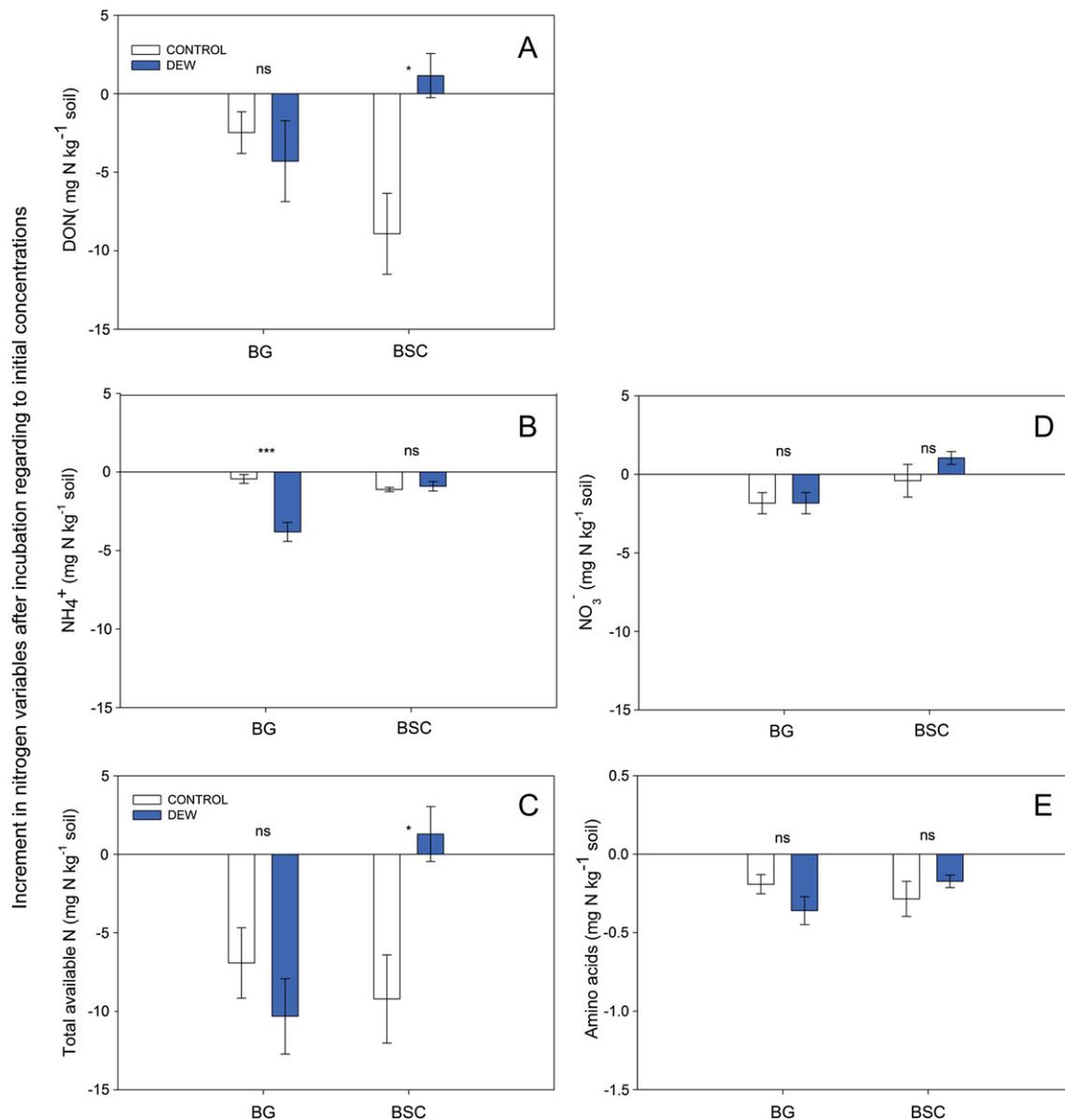

Fig. 1. Increment in the studied nitrogen variables after 14 days of incubation under control and simulated dew conditions for biological soil crust (BSC) and bare ground (BG) soils. Data are means $\pm$ SE ($n = 6$). Significance levels between treatments (control and dew) are as follows: $^a p < 0.1$ (marginally significant); $^*p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

Fig. 2. Increment in the studied carbon variables after 14 days of incubation under control and simulated dew conditions for biological soil crust (BSC) and bare ground (BG) soils. Data are means ± SE ($n = 6$). Significance levels between treatments (control and dew) are as follows: [a]$p < 0.1$ (marginally significant); *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.
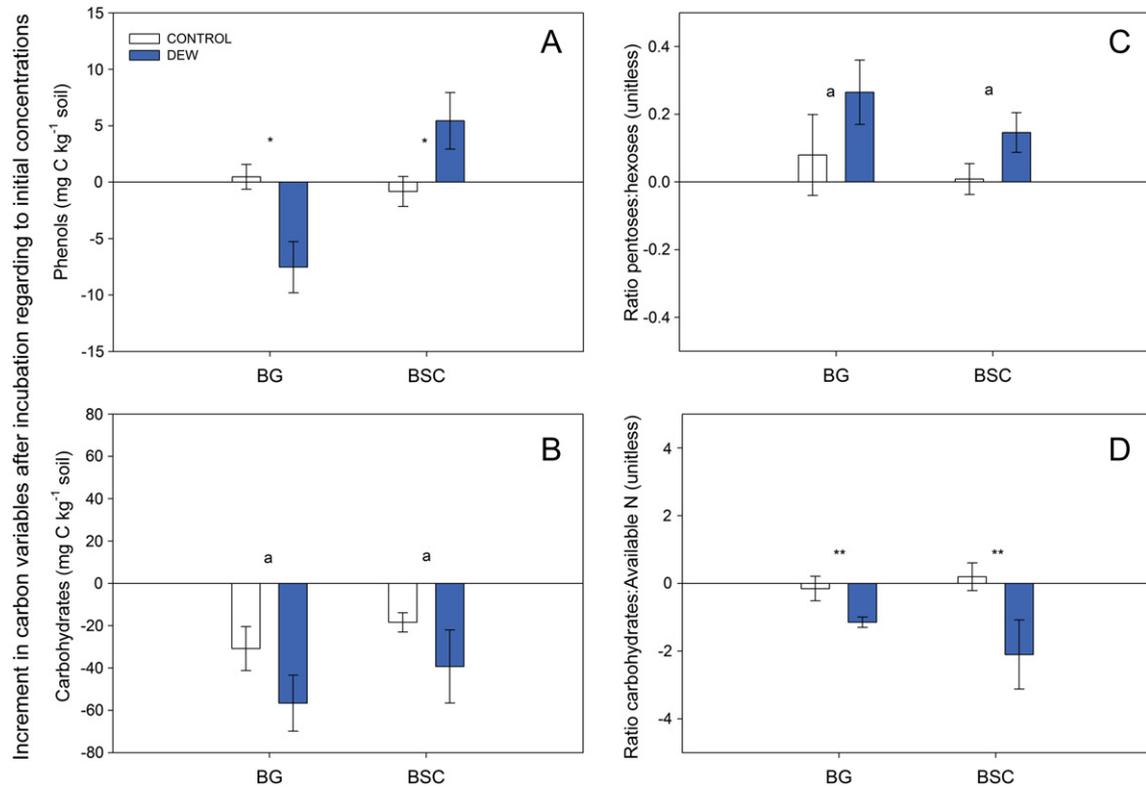
conditions ($p < 0.01$; Fig.1A; Appendix C). A Microsite × Treatment interaction was also found when analyzing the increment in ammonium ($p < 0.01$; Appendix C). In the dew treatment, soils from bare ground areas showed a greater decrease in ammonium than those from the BSC microsite ($p < 0.05$), which was not observed in the control treatment ($p > 0.05$; Fig. 1B; Appendix C). A Microsite × Treatment interaction was observed for the increment in total available N ($p < 0.01$; Appendix C). Dew additions increased total available N with respect to control in the BSC microsite ($p < 0.01$), a response that was not observed in the BG microsite ($p > 0.05$; Fig. 1C; Appendix C). Significant differences between microsites were not found in the control treatment ($p > 0.05$), albeit BSC soils had a higher increase in the total available N than BG soils with dew ($p < 0.01$; Fig. 1C; Appendix C). Significant differences were not observed between the microsites or treatments when analyzing the increment in nitrate and amino acids ($p > 0.05$; Fig. 1D and E; Appendix C).

A Microsite × Treatment interaction was found for the increment of phenols ($p < 0.01$; Appendix C). The addition of dew promoted a significant increase in phenols for the BSC and a decrease in phenols for the BG microsites ($p < 0.05$; Fig. 2A; Appendix C). Dew decreased the amount of carbohydrates found ($p < 0.01$) regardless of the microsite considered ($p > 0.05$; Fig. 2B; Appendix C). The increment in the pentoses:hexoses ratio showed a marginally significant tendency ($p = 0.08$) to increase in response to dew additions at both BSC and BG microsites (Fig. 2C; Appendix C). Dew decreased the carbohydrates:total available N ratio ($p < 0.01$), regardless of the microsites considered ($p > 0.05$; Fig. 2B; Appendix C).

The respiration of BSC-forming-lichens was always higher in the dew treatment than in the control, where respiration was not detected ($p < 0.01$; Fig. 3; Appendix C), with the highest peak of crust respiration found after the first dew pulse (Fig. 3).

4. Discussion

Our results show that water pulses similar to those provided by dew events under field conditions can activate the microbial communities associated with BSCs, promoting microbial mineralization and decomposition of soil-organic matter (Schwinning and Sala, 2004). They also indicate that well developed BSCs change the response of C and N variables to dew pulses, which could be mediated by the activity of bacteria and fungi. The observed positive increment in the total available N under BSCs in response to dew events may be promoted by higher fungi:bacteria ratios
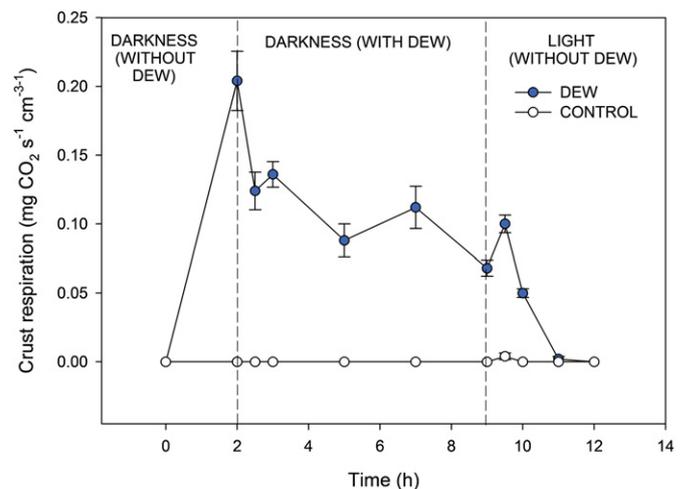

Fig. 3. Monitoring of the respiration of biological soil crust-forming lichens over a 12 h period for both control and dew treatments. Data are means ± SE ($n = 6$).

observed at this microsite (compared to bare ground areas) in our study area (Appendix A). Similarly, well-developed fungal communities under BSCs have been reported in other dryland ecosystems (Bates et al., 2010). Fungi-dominated communities have a higher microbial N-use efficiency than bacterial-dominated communities, producing biomass with a higher C:N ratio (Paul and Clark, 1996), and immobilizing less N per unit of assimilated C (Austin et al., 2004). In addition, cyanobacteria and green algae communities, which are usually linked to BSCs (Belnap and Lange, 2003; Belnap et al., 2004), could also be responsible for the higher N availability observed under BSCs due to their high capacity in fixing atmospheric N (Belnap and Lange, 2003).

The immobilization of total available N, ammonium and amino acids observed in the control treatment under BSCs, as well as the decrease of carbohydrates and the carbohydrates:available N ratio observed in both BG and BSC microsites, suggests that even the 80% relative humidity present in the plant growth chamber during the incubation period in the control treatments may be enough to activate N cycling processes under BSCs. Both green algae and the lichens containing them as photobionts have been shown to use atmospheric moisture to carry out photosynthesis and growth (Thomson and Iltis, 1968; Belnap and Lange, 2003). Thus, bacterial populations with rapid expansion may be active under these conditions, promoting an initial phase of immobilization followed by a mild phase of mineralization under dew conditions, as suggested by Austin et al. (2004). The observed trend toward a positive increase in the pentoses:hexoses ratio in both microsites, and the increase of DON under BSCs in response to dew events, suggests a higher plant-derived decomposition of organic matter in this microsite (Chantigny et al., 2006; Schimel and Bennett, 2004). Thus, fungal-dominated microbial communities, which are more desiccation-tolerant than those dominated by bacteria (Adebayo and Harris, 1971; Austin et al., 2004), may be more efficient promoting decomposition under dew events (Austin et al., 2004; Butterbach-Bahl and Per Gundersen, 2011).

Furthermore, the wilting point in soils of the area studied is reached near 30% of water holding capacity (Marqués et al., 2008), whereas surface soils (0–5 cm) at BS and BSC microsites in the study area commonly experience low soil moisture values (below 15%) during a significant part of the year (Castillo-Monroy et al., 2011a). This fact emphasizes the idea that soil moisture levels limiting plant production are not limiting microbial function. This allows soil microorganisms associated with BSCs operating without nutrient plant competition to accumulate N, which can be used by plants during their main activity periods (Singh et al., 1989).

Moreover, the increment in phenols observed under BSCs may be the result of either organic matter decomposition or active microbial synthesis. In either case, such increment may suggest an allelopathic effect that may prevent other groups of microorganisms from occupying a microsite with high total available N as a result of the positive impacts of BSCs on this variable (Chantigny et al., 2006; Zhang et al., 2009). For example, catechol and hydroxamate siderophores, produced by some groups of microbes have been implicated in microbial competition through the chelation of Fe (Martinez et al., 1990; Diarra et al., 1996).

Finally, the respiration detected in the BSC-forming lichens when dew was added, together with the observed changes in C and N variables, supported the idea that even small water pulses can activate soil microbial communities associated to BSCs in drylands and the metabolism of C and N in soils (Schwinning and Sala, 2004). In addition, the highest peak in crust respiration observed immediately after a dew event agree with previous studies showing rapid physiological responses of BSC-forming lichens to small water pulses (Veste et al., 2008; Wilske et al., 2008; Rao et al., 2009). Our results also showed a decrease in soil carbohydrates with dew,

suggesting that the crust respiration responses to dew events may be modulated by the reserve of labile soil carbohydrates.

To conclude, we found that dew-like water inputs can promote the activation of microorganisms involved in the C and N cycles in dryland soils, and that this response is modulated by well developed BSC communities. Increases in the availability of N under BSCs have been commonly observed in many drylands worldwide (Belnap, 2002; Zaady, 2005; Delgado-Baquerizo et al., 2010; Su et al., 2011). Such an increase is often associated with the fixation of atmospheric N_2 by BSC-forming cyanobacteria and cyanolichens (Belnap, 2002). Our results provide an alternative explanation for the increase of N typically observed under BSCs: the stimulation of microbial activity of the microorganisms associated with BSCs by dew inputs. Given the degree of development of BSCs in drylands worldwide, and the importance of water inputs from dew, the production of N under dew conditions can make an important contribution to the total N available for plants and microorganisms in these regions. The different response found in BSC and BG microsites suggest that different microbial communities may modulate the hierarchical response to soil moisture pulse events commonly observed in drylands (Schwinning and Sala, 2004). Our results complement those of previous studies highlighting the key role of BSCs as modulators of C and N dynamics in dryland ecosystems, and indicate that the conservation of well-developed BSC communities is crucial to maintain and increase N availability in drylands.

Acknowledgments

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2013.02.015.

References

Adebayo, A.A., Harris, R.F., 1971. Fungal growth responses to osmotic as compared to matric water potential. Soil Science Society of America Proceedings 35, 465–469.

Austin, A.T., Yahdjian, L., Stark, J.M., Belnap, J., Porporato, A., Norton, U., Ravetta, D.A., Schaeffer, S.M., 2004. Water pulses and biogeochemical cycles in arid, and semiarid ecosystems. Oecologia 141, 221–235.

Barger, N.N., Belnap, J., Ojima, D.S., Mosier, A., 2005. NO gas loss from biologically crusted soils in Canyonlands National Park, Utah. Biogeochemistry 75, 373–391.

Bates, S.T., Nash, T.H., Sweat, K.G., Garcia-Pichel, F., 2010. Fungal communities of lichen-dominated biological soil crusts: diversity, relative microbial biomass, and their relationship to disturbance and crust cover. Journal of Arid Environments 74, 1192–1199.

Belnap, J., 2002. Nitrogen fixation in biological soil crusts from southeast Utah, USA. Biology and Fertility Soils 35, 128–135.

Belnap, J., Lange, O.L., 2003. Biological Soil Crusts: Structure, Function, and Management. Springer-Verlag, Berlin.

Belnap, J., Phillips, S.L., Miller, M.E., 2004. Response of desert biological soil crusts to alterations in precipitation frequency. Oecologia 141, 306–316.

Bowker, M.A., Mau, R.L., Maestre, F.T., Escolar, C., Castillo-Monroy, A.P., 2011. Functional profiles reveal unique roles of various biological soil crust organisms in Spain. Functional Ecology 25, 787–795.

Butterbach-Bahl, K., Per Gundersen, 2011. Nitrogen Processes in Terrestrial Ecosystems. The European Nitrogen Assessment, Sources, Effects and Policy Perspectives. Cambridge University Press, New York, USA.

Castillo-Monroy, A.P., Delgado-Baquerizo, M., Maestre, F.T., Gallardo, A., 2010. Biological soil crusts modulate nitrogen availability in semi-arid ecosystems: insights from a Mediterranean grassland. Plant and Soil 333, 21–34.

Castillo-Monroy, A.P., Maestre, F.T., Rey, A., Soliveres, S., García-Palacios, P., 2011a. Biological soil crust microsites are the main contributor to soil respiration in a semiarid ecosystem. Ecosystems 14, 835–847.

Castillo-Monroy, A.P., Bowker, M.A., Maestre, F.T., Rodríguez-Echeverría, S., Martinez, I., Barraza-Zepeda, C.E., 2011b. Relationships between biological soil crusts, bacterial diversity and abundance, and ecosystem functioning: insights from a semi-arid Mediterranean environment. Journal of Vegetation Science 22, 165–174.

Chantigny, M.H., Angers, D.A., Kaiser, K., Kalbitz, K., 2006. Extraction and characterization of dissolved organic matter. In: Carter, M.R., Gregorich, E.G. (Eds.), Soil Sampling and Methods of Analysis, second ed. Canadian Society of Soil Science, pp. 617–635.

Cui, M., Caldwell, M.M., 1997. A large ephemeral release of nitrogen upon wetting of dry soil and corresponding root responses in the field. Plant and Soil 191, 291–299.

Delgado-Baquerizo, M., Gallardo, A., 2011. Depolymerization and mineralization rates at 12 Mediterranean sites with varying soil N availability A test for the Schimel Bennett model. Soil Biology and Biochemistry 43, 693–696.

Delgado-Baquerizo, M., Castillo-Monroy, A.P., Maestre, F.T., Gallardo, A., 2010. Plants and biological soil crusts modulate the dominance of N forms in a semi-arid grassland. Soil Biology and Biochemistry 42, 376–378.

Delgado-Baquerizo, M., Covelo, F., Gallardo, A., 2011. Dissolved organic nitrogen in Mediterranean ecosystems. Pedosphere 21, 302–308.

Delgado-Baquerizo, M., Maestre, F.T., Gallardo, A., 2012. Biological soil crusts increase the resistance of soil nitrogen dynamics to changes in temperatures in a semi-arid ecosystem. Plant and Soil, 1–13.

Diarra, M.S., Dolence, J.A., Dolence, E.K., Darwish, I., Miller, M.J., Malouin, F., Jacques, M., 1996. Growth of Actinobacillus pleuropneumoniae is promoted by exogenous hydroxamate and catechol siderophores. Applied and Environmental Microbiology 62, 853–859.

Eldridge, D.J., Greene, R.S.B., 1994. Microbiotic soil crusts e a review of their roles in soil and ecological processes in the rangelands of Australia. Australian Journal of Soil Research 32, 389–415.

Evenari, M., 1981. Ecology of the Negev Desert, a critical review of our knowledge. In: Shuval, H. (Ed.), Developments in Arid Zone Ecology and Environmental Quality. Balaban ISS, Philadelphia, PA, pp. 1–33.

Gallardo, A., Schlesinger, W.H., 1992. Carbon and nitrogen limitations of soil microbial biomass in desert ecosystems. Biogeochemistry 18, 1–17.

Gallardo, A., Schlesinger, W.H., 1995. Factors determining soil microbial biomass and nutrient immobilization in desert soils. Biogeochemistry 28, 55–68.

Gotelli, N.J., Ellison, A.M., 2004. A Primer of Ecological Statistics. Sinauer Associates, Sunderland, USA.

Jacobs, A.F.G., Heusinkveld, B.G., Berkowicz, S.M., 2000. Dew measurements along a longitudinal sand dune transect, Negev Desert, Israel. International Journal of Meteorology 43, 184–190.

Jacobs, A.F.G., Heusinkveld, B.G., Berkowicz, S.M., 2002. A simple model for potential dewfall in an arid region. Atmospheric Research 64, 285–295.

Jones, D.L., Willett, V.B., 2006. Experimental evaluation of methods to quantify dissolved organic nitrogen (DON) and dissolved organic carbon (DOC). Soil Biology and Biochemistry 38, 991–999.

Kidron, G.J., 2000. Analysis of dew precipitation in three habitats within a small arid drainage basin, Negev Highlands, Israel. Atmospheric Research 55, 257–270.

Kidron, J.G., Herrnstadt, I., Barzilay, E., 2002. The role of dew as a moisture source for sand microbiotic crusts in the Negev Desert, Israel. Journal of Arid Environments 52, 517–533.

Lekouch, I., Kabbachi, B., Milimouk-Melnytchouk, I., Muselli, M., Beysens, D., 2011. Dew, fog, and rain as supplementary sources of water in south-western Morocco. Energy 36, 2257–2265.

Loik, M.E., Breshears, D.D., Lauenroth, W.K., Belnap, J., 2004. Climatology and ecohydrology of precipitation pulses in arid and semiarid ecosystems of the Western USA. Oecologia 141, 269–281.

Maestre, F.T., Bowker, M.A., Cantón, Y., Castillo-Monroy, A.P., Cortina, J., Escolar, C., Escudero, A., Lázaro, R., Martínez, I., 2011. Ecology and functional roles of biological soil crusts in semi-arid ecosystems of Spain. Journal of Arid Environments 75, 1282–1291.

Maestre, F.T., Castillo-Monroy, A.P., Bowker, M.A., Ochoa-Hueso, R., 2012. Species richness effects on ecosystem multifunctionality depend on evenness, composition and spatial pattern. Journal of Ecology 100, 317–330.

Marqués, M.J., Bienes, R., Pérez-Rodríguez, R., Jiménez, L., 2008. Soil degradation in Central Spain due to sheet water erosion by low-intensity rainfall events. Earth Surface Processes and Landforms 33, 414–423.

Martinez, J.L., Delgado-Iribarren, A., Baquero, F., 1990. Mechanisms of iron acquisition and bacterial virulence. FEMS Microbiology Reviews 75, 45–56.

Moro, M.J., Were, A., Villagarcia, L., Canton, Y., Domingo, F., 2007. Dew measurement by Eddy covariance and wetness sensor in a semiarid ecosystem of SE Spain. Journal of Hydrology 335, 295–302.

Noy-Meir, I., 1973. Desert ecosystems: environment and producers. Annual Review of Ecological Systems 4, 25–51.

Paul, E.A., Clark, F.E., 1996. Soil Microbiology and Biochemistry. Academic Press, San Diego, California.

Pintado, L.G., Sancho, J.M., Blanquer, T.G., Green, A., Lázaro, R., 2010. Microclimatic factors and photosynthetic activity of crustose lichens from the semiarid southeast of Spain: long-term measurements for *Diploschistes diacapsis*. Bibliotheca Lichenologica 105, 211–224.

Rao, B., Liu, Y., Wang, W., Hu, C., Li, D., Lan, S., 2009. Influence of dew on biomass and photosystem II activity of cyanobacterial crusts in the Hopq Desert, northwest China. Soil Biology and Biochemistry 41, 2387–2393.

Reynolds, J.F., Smith, D.M., Lambin, E.F., Turner, B.L., Mortimore, M., Batterbury, S., 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.

Schimel, J.P., Bennett, J., 2004. Nitrogen mineralization: challenges of a changing paradigm. Ecology 85, 591–602.

Schwinning, S., Sala, O.E., 2004. Hierarchy of responses to resource pulses in arid and semi-arid ecosystems. Oecologia 141, 211–220.

Singh, J.S., Raghubanshi, A.S., Singh, R.S., Srivastava, S.C., 1989. Microbial biomass act as a source of plant nutrients in dry tropical forest and savanna. Nature 338, 499–500.

Smart, D.R., Stark, J.M., Diego, V., 1999. Resource limitations to nitric oxide emissions from a sagebrush-steppe ecosystem. Biogeochemistry 47, 63–86.

Su, Y., Zhao, X., Li, A., Li, X., Huang, G., 2011. Nitrogen fixation in biological soil crusts from the Tengger desert, northern China. European Journal of Soil Biology 3, 182–187.

Thomson, J.W., Iltis, H.H., 1968. A fog-induced lichen community in the coastal desert of southern Peru. The Bryologist 71, 31–34.

Veste, M., Heusinkveld, B.G., Berkowicz, S.M., Breckle, S.-W., Littmann, T., Jacobs, A.F.G., 2008. Arid Dune Ecosystems Ecological Studies, vol. 200, pp. 305–318.

Wallin, J.R., 1967. Agrometeorological aspects of dew. Agricultural Meteorology 4, 85–102.

Westoby, M., 1972. Problem-oriented Modelling: a Conceptual Framework. In: IBP/Desert Biome, Information Meeting, Tempe, Ariz.

Whitford, W.G., 2002. Ecology of Desert Systems. Academic Press, San Diego, CA.

Wilske, B., Burgheimer, J., Karnieli, A., Zaady, E., Andreae, M.O., Yakir, D., Kesselmeier, J., 2008. The CO_2 exchange of biological soil crusts in a semiarid grass-shrubland at the northern transition zone of the Negev desert, Israel. Biogeosciences 5, 1411–1423.

Zaady, E., 2005. Seasonal change and nitrogen cycling in a patchy Negev Desert: a review. Arid Land Research and Management 19, 111–124.

Zhang, J., Zhang, Y.M., Alison, D., Cheng, J., Zhou, X., Zhang, B., 2009. The influence of biological soil crusts on dew deposition in Gurbantunggut Desert, Northwestern China. Journal of Hydrology 379, 220–228.