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REGULAR ARTICLE

Biological soil crusts increase the resistance of soil nitrogen dynamics to changes in temperatures in a semi-arid ecosystem

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Abstract
Aims Biological soil crusts (BSCs), composed of mosses, lichens, liverworts and cyanobacteria, are a key component of arid and semi-arid ecosystems worldwide, and play key roles modulating several aspects of the nitrogen (N) cycle, such as N fixation and mineralization. While the performance of its constituent organisms largely depends on moisture and rainfall conditions, the influence of these environmental factors on N transformations under BSC soils has not been evaluated before.
Methods The study was done using soils collected from areas devoid of vascular plants with and without lichen-dominated BSCs from a semi-arid *Stipa tenacissima* grassland. Soil samples were incubated under different temperature (T) and soil water content (SWC) conditions, and changes in microbial biomass-N, dissolved organic nitrogen (DON), amino acids, ammonium, nitrate and both inorganic N were monitored. To evaluate how BSCs modulate the resistance of the soil to changes in T and SWC, we estimated the Orwin and Wardle Resistance index.
Results The different variables studied were more affected by changes in T than by variations in SWC at both BSC-dominated and bare ground soils. However, under BSCs, a change in the dominance of N processes from a net nitrification to a net ammonification was observed at the highest SWC, regardless of T.
Conclusions Our results suggest that the N cycle is more resistant to changes in T in BSC-dominated than in bare ground areas. They also indicate that BSCs could play a key role in minimizing the likely impacts of climate change on the dynamics of N in semi-arid environments, given the prevalence and cover of these organisms worldwide.

Keywords Semiarid ecosystem · N depolymerization rate · N mineralization rate · DON

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Introduction

Arid, semi-arid and dry-subhumid ecosystems (commonly referred to as drylands) are a key

terrestrial biome, covering 41 % of Earth's land surface and supporting over 38 % of the total global population (Reynolds et al. 2007). These areas are highly vulnerable to global change and desertification (Korner 2000; Reynolds et al. 2007). Despite their importance and extent, the global change literature is dominated by work carried out in other ecosystems (Schimel 2010), and there are important gaps in our knowledge on how global change will impact key soil processes in drylands.

The availability of resources for primary producers and soil microorganisms largely controls ecosystem performance and its capacity to respond to global change (Finzi et al. 2011). Nitrogen (N) is, after water, one of the most important factors limiting primary production in dryland ecosystems (Whitford 2002). Biological soil crusts (BSCs) are communities dominated by mosses, lichens and cyanobacteria, which constitute a key biotic component of these areas (Belnap and Lange 2003). These crusts have been found to play a prevalent role in important aspects of the N cycle, such as N fixation (Belnap 2002), nitrification (Castillo-Monroy et al. 2010; Delgado-Baquerizo et al. 2010), and gaseous N losses (Barger et al. 2005).

Climate change is expected to cause important changes in the temperature and rainfall dynamics of drylands, including a higher frequency of intense precipitation events, increases in extreme high temperatures, decreases in extreme low temperatures, heat waves and drought (IPCC 2007). The performance of BSC constituents, such as lichens and associated microorganisms, depends up to a large degree on soil water content (SWC) and temperature (T) conditions (Lange 2003; Del Prado and Sancho 2007; Maestre et al. 2009). Thus, expected changes in rainfall and temperature can strongly affect the functioning of BSC-forming organisms (Belnap et al. 2008; Grote et al. 2010) and the ecosystem processes that are affected by them, such as soil respiration (Maestre et al. 2010; Castillo-Monroy et al. 2011a). However, the resistance (*sensu* Orwin and Wardle 2004) of soils located under BSCs to changes in temperature and soil water content has never been tested before. Indeed, traditional laboratory studies of N mineralization have been carried out under optimal SWC and T conditions, but only a few studies have studied the influence of the physiological range of temperature and SWC on net N mineralization and depolymerization (dissolved organic nitrogen [DON] production) rates (Schimel and Bennett 2004; Szukics et al. 2010; Bregliani et al. 2010). Depolymerization, rather than ammonification, seems to be a key controller of the N cycle, but the effects of soil temperature and moisture on the production of DON are still poorly known (Schimel and Bennett 2004; Bregliani et al. 2010).

In this study, we evaluated how different combinations of T (5–30 °C) and SWC (30–80 % of water holding capacity [WHC]) affected key variables from the N cycle (ammonium, nitrate, inorganic-N, dissolved organic nitrogen [DON]; aminoacids, and N in the microbial biomass), as well as the relative dominance of the N transformation rates, in soils from microsites differing in the degree of BSC development (bare ground and well-developed BSCs areas). We also applied the Orwin and Wardle Resistance Index (2004) to evaluate how BSCs modulate changes in these variables in response to variations in T and SWC. Previous studies have suggested that nitrification rates should increase with augments in T until moderate SWC values (30–60 %; Szukics et al. 2010; Bregliani et al. 2010), while ammonification might be less limited by lower temperatures (Szukics et al. 2010). However, the influence of these environmental factors on N transformation rates under BSCs has been scarcely studied before (Grote et al. 2010). We hypothesize that the influence of BSCs on the organic and inorganic N forms will determine a different response to changes in temperature and SWC to that found in areas without well-developed BSCs. Thus, an increase in the microbial metabolic rates should be expected with increases in SWC and T, decreasing the organic N and increasing the inorganic N as a result of increasing both decomposition and mineralization rates. Drawing upon previous studies (Castillo-Monroy et al. 2010; Delgado-Baquerizo et al. 2010), we tested the hypothesis that BSCs, which confer physical protection to the soil (e.g. Belnap 2006), can also increase the resistance of the N cycle to changes in SWC and T. Thus, microbial communities under BSCs may slow down the alteration of the N dynamics under future climatic scenarios.

Methods

Study site

Soils for this study were collected from the Aranjuez experimental station, located at the centre of the

Iberian Peninsula (40 °02′ N–3 ° 37′W; 590 m a.s.l.; 8 ° slope Racing SE). The climate is Mediterranean semi-arid, with average annual rainfall and temperature of 349 mm and 14.5 °C, respectively (1986–2012 period). Perennial plant cover is lower than 40 %, and is dominated by the perennial grass *Stipa tenacissima* L. Open areas between plant patches contain a well developed BSC community 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). The soil is classified as Xeric Haplogypsid (USDA 2003), and has a fine texture dominated by the presence of gypsum. The main soil properties of the study area are shown in Table 1.

Sampling design and laboratory analyses

Soil sampling was carried out during spring of 2008, the most biologically active season at the study area (Castillo-Monroy et al. 2011a). Five soil samples from the top 4 cm of mineral soil profile 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) devoid of vascular vegetation and visible components of BSCs (cover of mosses and lichens <5 %; BG hereafter; see Appendix B of Castillo-Monroy et al. 2010). Cyanobacteria are present at both microsites, but we have not quantified them. Nonetheless, the biotic communities are very different between BSC and BG microsites, and given the higher degree of BSC development in the former microsite, we expect that cyanobacteria should be much more abundant there (Yeager et al. 2004; Maestre et al. 2006). Soils were transported to the laboratory and air-dried at room temperature for 4 weeks. Previous studies have found that the biochemical properties are hardly affected by air-drying in semiarid Mediterranean soils (Zornoza et al. 2009), which otherwise are under dry conditions most of the year (e.g., Maestre et al. 2002).

Air-dried soil samples were incubated in the laboratory for 14 days by using different T (5 °C, 10 °C, 20 °C and 30 °C) and SWC (30 %, 50 % and 80 % of WHC) levels in a factorial design for both BSC and BG microsites. Five replicates were used for each combination of treatments. The incubation was performed in a closed chamber to keep SWC constant during the incubation time. The chamber was closed with polyethylene film allowing gas exchange, but avoiding water losses. Soil samples were incubated in dark conditions. Incubated and initial (air-dried) 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 the 24 h following the extraction. Sub-samples of each non-incubated (air-dried) extract were taken for measurements of phenols, pentoses and hexoses according to Chantigny et al. (2006). Incubated and non-incubated samples were analyzed from K_2SO_4 extract subsamples following the same methods for all measurements, including inorganic N, DON, and amino acid concentrations (Chantigny et al. 2006; Jones and Willett 2006; Delgado-Baquerizo et al. 2011). Ammonium concentration in the extract was directly estimated by

Table 1 Main soil characteristics of soils under biological soil crusts (BSC) and in bare ground areas (BG). Phenols were expressed as equivalents of 2-hydroxybenzoic acid, hexoses as equivalents of glucose, pentoses as ribose equivalents, and amino acids as equivalents of leucine. Data are means±SE (n=5)

	BSC	BG
pH	7.4±0.1	7.2±0.1
Silt (%)	30.0±2.7	38.0±1.1
Clay (%)	6.3±0.0	6.3±0.0
Sand (%)	63.7±2.7	55.7±1.1
C:N ratio	10,11±0.7	11.24±0.1
NH_4^+-N (mg Nkg^{-1} soil)*	11.97±1.4	1.86±0.1
$N0_3$_N (mg Nkg^{-1} soil)*	55.28±5.4	21.42±2.5
DON (mg Nkg^{-1} soil)	43.04±7.9	35.27±2.1
Aminoacids (mg kg^{-1} soil)**	19.59±3.0	5.57±1.7
MB-N (mg Nkg^{-1} soil)	14.63±6.0	3.31±1.7
Phenols (mg kg^{-1} soil)	26.6±5.1	24.93±4.1
Hexoses (mg kg^{-1} soil)	145.3±24.6	202.8±39.8
Pentoses (mg kg^{-1} soil)	138.5±39.8	115.8±33.1

*Significant differences between microsites in the initial soil variables concentrations are as follows: * p<0.05 and ** and p<0.01. pH, soil texture and the C:N ratio data were not analyzed

colorimetry (indophenol blue method) using a microplate reader (Sims et al. 1995). Nitrate was first reduced to NH_4^+ by keeping overnight 250 μl of extract with ca. 20 μg of Devarda alloy in a microplate. The supernatant was transferred to other microplate and analyzed colorimetrically as explained above. Nitrate concentration (NO_3^-) in the extracts was calculated as the difference between Devarda-incubated and unincubated samples. Inorganic-N is expressed as the sum of ammonium and nitrate. DON in the extracts was first oxidized to NO_3^- with $K_2S_2O_8$ in an autoclave at 121 °C for 55 min, and then reduced to NH_4^+ with Devarda alloy (Sollins et al. 1999). DON values were calculated as total dissolved N minus inorganic N. Ammonium, nitrate, inorganic-N, DON and amino acid concentration were also determined for each incubated K_2SO_4 extract subsample.

Potential net depolymerization, ammonification and nitrification rates were estimated as the difference between air-dried and incubated DON, NH_4^+-N and NO_3^--N concentrations for each combination of T and SWC divided by the number of days of incubation (Delgado-Baquerizo and Gallardo 2011). The sum of ammonification and nitrification rates was defined as the N mineralization rate (production of inorganic-NN), and the sum of this rate and depolymerization was defined as the N transformation rate (production of total available N). The relative dominance of potential net depolymerization, ammonification and nitrification rates was calculated as a percentage relative to the sum of these three metabolic rates (Castillo-Monroy et al. 2010; Delgado-Baquerizo and Gallardo 2011). All results were expressed on a dry soil basis.

In parallel, the N in microbial biomass (MB-N) was determined using the fumigation-extraction method following Brookes et al. (1985). Non-incubated and incubated soil subsamples were fumigated with chloroform for 5 days. Non-fumigated replicates were used as controls. Fumigated and non-fumigated samples were extracted with K_2SO_4 0.5 M in a ratio 1:5 and filtered through a 0.45-μm Millipore filter. Total N in the extracts was converted to NO_3^--N using the persulphate oxidation technique (Sollins et al. 1999), and the concentration was estimated by the colorimetric method described above. Microbial biomass-N concentration was estimated as the difference between total N of fumigated and unfumigated digested extracts divided by a Kn (fraction of biomass N extracted after the CHC_{13} treatment) of 0.54 (Brookes et al. 1985).

Statistical and numerical analyses

To evaluate how BSCs affected the resistance of the soil to changes in T and SWC, the Orwin and Wardle Resistance Index (2004) was calculated for all N variables using the following equation:

$$RS = 1 - \frac{2 \cdot |D_0|}{(C_0 + |D_0|)}$$

where (D_0) is the difference between the control (C_0) and the disturbed (P_0) soil at the end of the disturbance. Disturbance is used here as the period of time that the soils were exposed to different treatments of T and SWC (14 days in our case). This index has the advantage to be standardized by the control, being bounded between −1 (less resistance) and +1 (maximal resistance); it remains bounded even when extreme values are encountered (Orwin and Wardle 2004). We evaluated how the resistance index was influenced by the different treatments separately for BSC and BG soils.

Our data did not meet ANOVA assumptions (normality and homogeneity of variances). Thus, differences between BSC and BG soils in each initial (air-dried) soil variable were tested by using the semi-parametric PERMANOVA approach developed by Anderson (2001), with BSC presence/absence as a fixed factor. PERMANOVA uses permutation tests to obtain *P* values, does not rely on the assumptions of traditional parametric ANOVA, and can handle experimental designs such as employed here. The effects of T, SWC and microsite (BSC vs. BG) on the different variables evaluated were also evaluated using PERMANOVA; in these analyses, all the factors were considered fixed. When significant interactions between factors were found, separate PERMANOVA analysis were conducted for the different factor levels. However, we interpreted the main effect in the presence of interaction when the analysis suggested that interaction only moderated the strength of the main effect and did not flip over its direction (ordinal interaction; Reinard 2006). When significant differences between SWC levels were not detected, the data were pooled among SWC levels for visualization purposes. PERMANOVA analyses were carried out using 99999 permutations (permutation of raw data) and the Euclidean distance with the PERMANOVA+for PRIMER statistical package (PRIMER-E Ltd., Plymouth Marine Laboratory, UK). *P* values were not

adjusted for multiple testing because this approach is considered overly conservative (Gotelli and Ellison 2004).

Results

N concentrations (before and after incubation)

Before the incubation, BSC soils had higher values of NH_4^+-N, NO_3^- -N and amino acids than BG soils ($P<0.05$; Table 1, Appendix 1). No significant differences were found in any of the other variables evaluated ($P>0.05$; Appendix 1).

After the incubation, NH_4^+-N, NO_3^- -N, DON, amino acids, and MB-N had higher values under BSCs than in BG microsites ($P<0.01$; Appendix 1; Figs. 1 and 2). The concentration of NH_4^+-N significantly decreased with increases in T at both BSC and BG microsites ($P<0.01$; Appendix 1; Fig. 1). However, significant T×SWC, T×MI, SWC×MI and T×SWC×MI interactions were found for this variable ($P<0.01$; Appendix 1). In the BG samples, neither temperature nor SWC affected the concentration of NH_4^+-N (Appendix 2); however, in the BSC samples, this variable responded to changes in WHC only in the 30 °C treatment (Appendix 2). At this temperature, NH_4^+-N decreased in the 50 % of WHC treatment, and increased in the highest SWC treatment (80 % of WHC; $P<0.01$; Appendix 2).

The MB-N was higher in the 50 % of WHC treatment at both BSC and BG microsites ($P<0.01$; Appendix 1; Fig. 1). A significant T×MI interaction was also found when analyzing this variable ($P<0.01$; Appendix 1). MB-N increased with T in the BG microsite ($P<0.01$; Appendix 2; Fig. 1), but not in the BSC microsite (Appendix 2; Fig. 1). Nitrate increased with temperature in both BSC and BG microsites ($P<0.01$; Appendix 1; Fig. 2), but did not change with SWC in any microsite (Appendix 1; Fig. 2). Inorganic N was not affected by changes in either SWC or T, regardless the microsite considered ($P>0.05$; Appendix 1; Fig. 2). DON decreased at intermediate T values in both BSC (20 °C) and BG (10 °C and 20 °C) microsites ($P<0.01$; Appendix 1; Fig. 2), but was not affected by changes in SWC (Appendix 1, Fig. 2). The concentration of amino acids decreased with T in both BSC and BG microsites ($P<0.01$; Appendix 1; Fig. 2), but was not affected by SWC (Appendix 1, Fig. 2).

N transformation rates

Variations in T and SWC did not affect the potential net mineralization rate observed in the BSC microsite ($P>0.05$; Appendix 2; Fig. 3). This variable, however, increased with augments in T in the BG microsite ($P<0.01$; Appendix 2; Fig. 3). BSC soils only had a higher potential net mineralization rate than BG soils at the 30 % WHC ($P<0.01$; Appendix 2; Fig. 3). Significant T×SWC×MI and T×MI interactions were found when analyzing the N transformation (production of total available N) and potential net ammonification rates (Appendix 1, Fig. 3). When analyzing

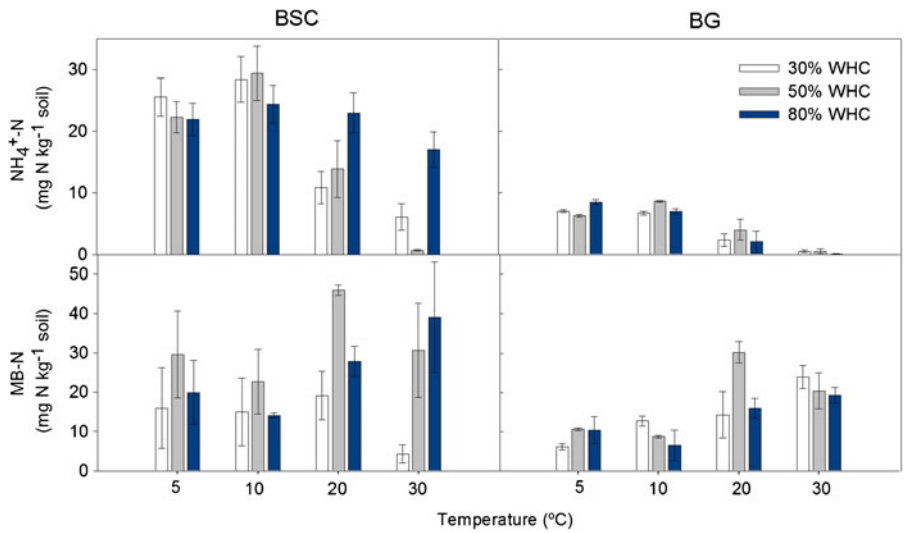

Fig. 1 Concentration of NH_4^+-N and MB-N (after incubation) under the different combinations of soil water content and temperature in biological soil crust (BSC) and bare ground (BG) soils. Data are means±SE ($n=5$)

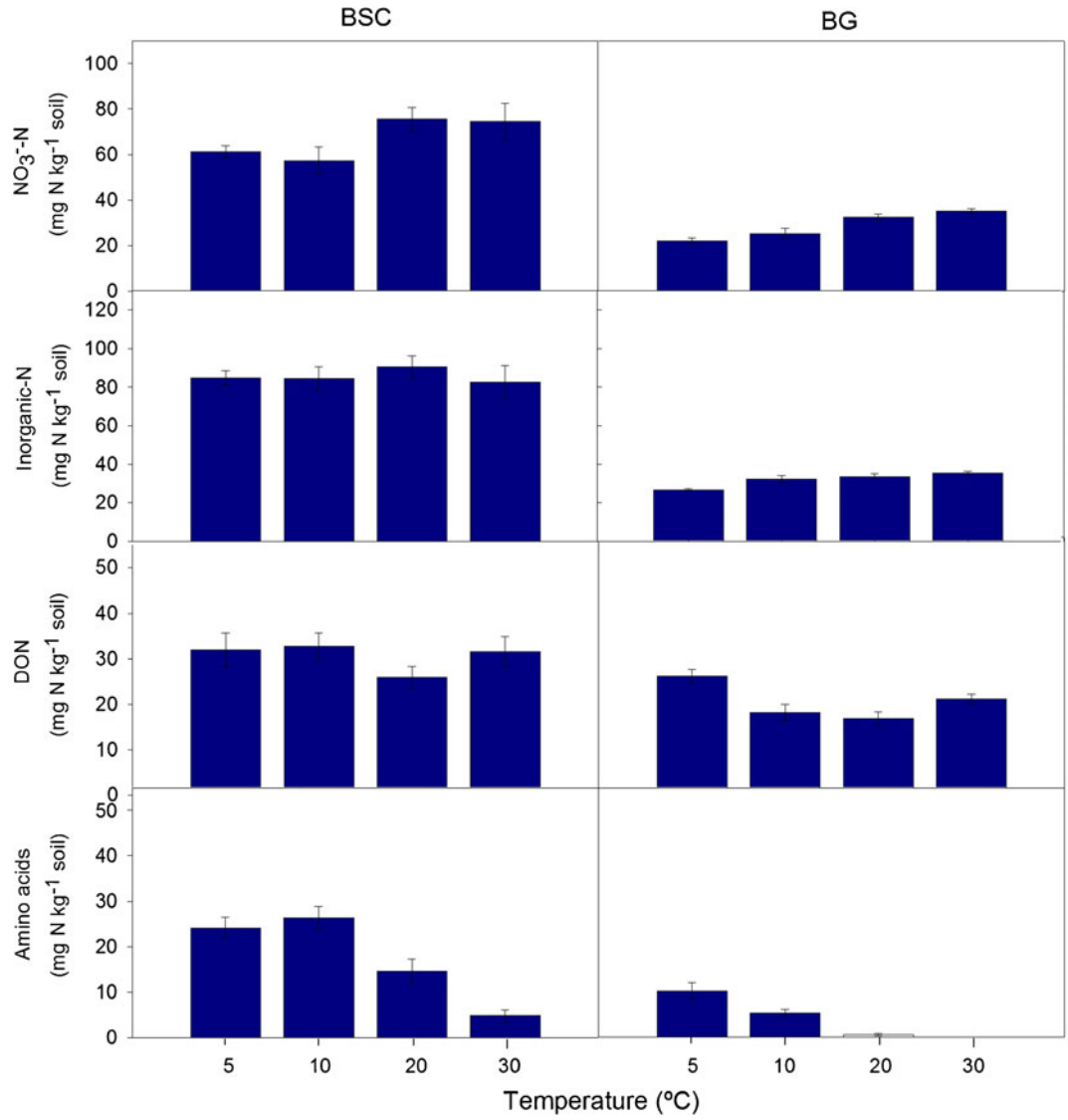

Fig. 2 Concentration of NO_3^--N, inorganic-N, DON and amino acids (after incubation) under the different temperature levels evaluated in biological soil crust (BSC) and bare ground (BG) soils. Data are means±SE (n=5)

the data separately for different T values, we did not find differences in the N transformation rate between either microsite type or SWC at 5 °C (P <0.01; Appendix 2, Fig. 2). At intermediate T values (10–20 °C), soils under BSC had a higher N transformation rate than BG (P<0.01; Appendix 2). At 30 °C, a significant SWC×MI interaction was found (P<0.01; Appendix 2). At this temperature, changes in the N transformation rate were not observed for the BG microsite (P>0.05; Appendix 2; Fig. 3) but this variable significantly decreased under BSCs in the 80 % of WHC treatment. At 30–50 % WHC, higher N transformation rates were found under BSCs (P<0.001), but no significant effects of T were found. In the 80 % of WHC treatment, the N transformation rate decreased under BSCs, but not in the BG microsite (P<0.01; Appendix 2; Fig. 3).

The dominance of ammonification decreased with temperature in both BSC and BG microsites between 30 % and 50 % WHC (P<0.01; Appendix 2; Fig. 4). For the 80 % of WHC, the dominance of this process keep decreasing for the BG but did not show significant differences under BSCs (Appendix 2; Fig. 4). At this SWC, the dominance of potential net ammonification was

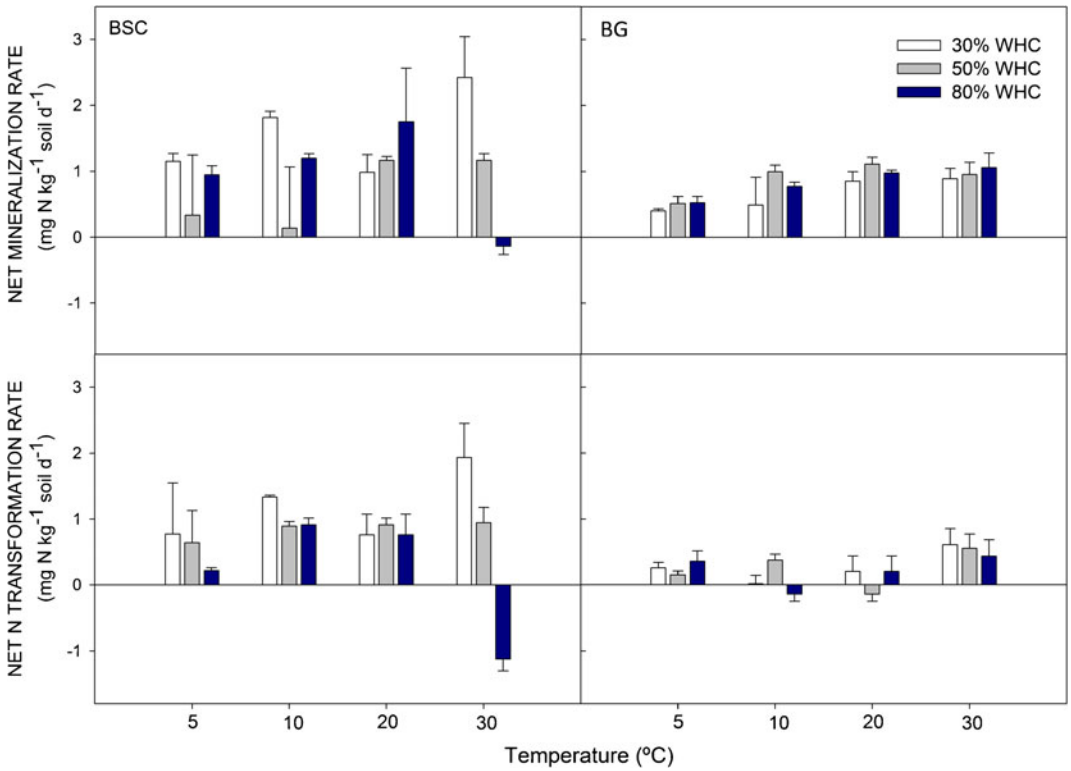

Fig. 3 Changes in the net nitrogen mineralization and transformation rates under the different combinations of soil water content and temperature in biological soil crust (BSC) and bare ground (BG) soils. Data are means±SE (n=5)

higher in the BSC than in the BG microsite (P<0.01; Appendix 2; Fig. 4). The nitrification rate increased with T in both BG and BSC microsites between 30 % and 50 % WHC (P<0.01; Appendix 1; Fig. 4). Differences between microsite were not observed for these WHC (P>0.05; Appendix 2; Fig. 4). However at the 80 % of WHC treatment, the nitrification dominance kept increasing in the BG (P<0.01; Fig. 4) but stopped increasing in the BSC microsite (P>0.05; Appendix 2). At this point, the potential net nitrification dominance was higher for the BG than for the BSC microsite (P<0.01; Appendix 2; Fig. 4) In contrast, depolymerization rates were not affected by any of the treatments evaluated (P>0.05; Appendix 1).

Orwin and Wardle Resistance index

Soils under BSCs showed higher levels of ammonium resistance that those from the BG microsite (P<0.01; Fig. 5; Appendix 1 and 2). Resistance for this variable increased with T in both microsites (P<0.01; Appendix 1 and 2). Differences between SWC were observed in both BSC and BG microsites, but only at 10 °C and 20 °C and without showing a particular pattern (P<0.01; Appendix 1 and 2).

We did not find changes with SWC for the rest of the variables studied: resistance in NO_3^- -N, inorganic-N, DON, amino acids and MB-N (Appendix 1).

The resistance of nitrate, inorganic-N, MB-N and amino acids was higher in the BSC than in the BG microsite (P<0.01; Fig. 6; Appendix 1 and 2). The resistance of nitrate decreased with T for the BG microsite (P<0.01), but did not change under BSCs (Fig. 6; Appendix 1). The resistance of inorganic N decreased with T in both microsites (P<0.01; Fig. 6; Appendix 1). No significant differences between microsites were found when analyzing the resistance of DON; this variable showed its lowest values in the intermediate T (10 and 20 °C; P<0.01; Appendix 1). The resistance of MB-N and amino acids did not change with T in either BG or BSC microsites (Fig. 6).

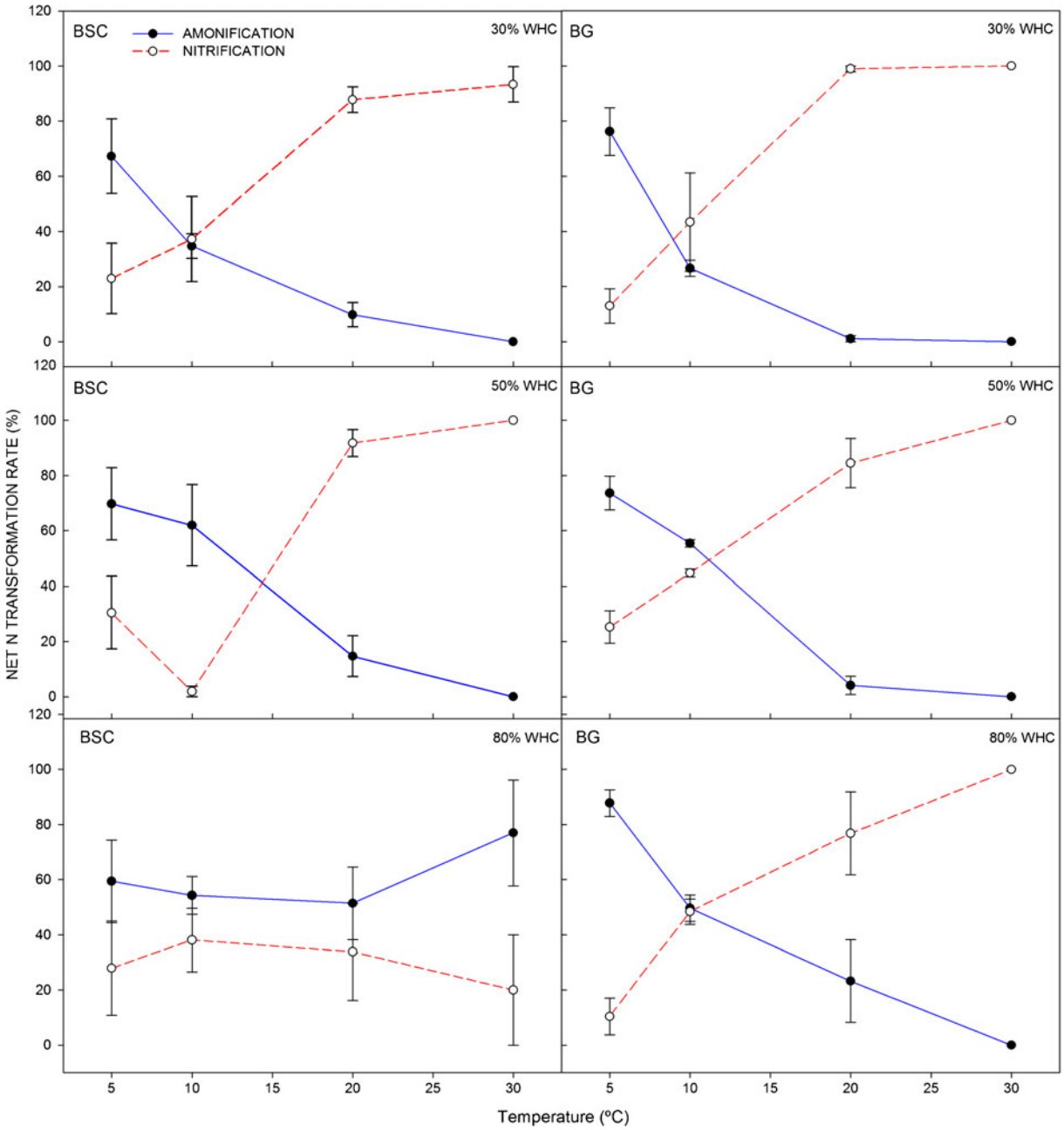

Fig. 4 Changes in the relative dominance of nitrogen transformation processes (net ammonification and nitrification rates) under the different combinations of soil water content and temperature in biological soil crust (BSC) and bare ground (BG) soils. Data are means±SE (n=5)

Discussion

N concentrations

According to our hypothesis, we found that virtually all of the N variables studied had a different response to changes in temperature when BSCs were present, as indicated by the significant temperature×microsite interactions found. However, similar interactions were not observed for soil water content. The different variables evaluated were highly sensitive to changes in temperature, but not to the later variable within the range evaluated in this study (30–80 % of water holding capacity). Thus, the observed increase of microbial

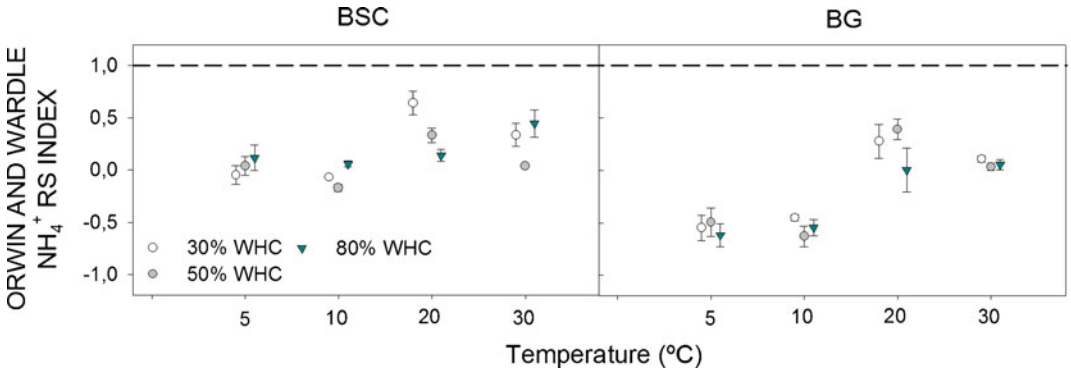

Fig. 5 Changes in the Orwin and Wardle Resistance index for NH_4^+-N under different combinations of soil water content and temperature in biological soil crust (BSC) and bare ground (BG) soils. Data are means±SE (n=5)

biomass-N and NO_3^- and the decrease of NH_4^+ and amino acids with the increase in temperature would suggest an increased use by microorganisms of these reduced substrates, increasing nitrification and microbial immobilization. We expected a higher influence of soil water content on N transformations and concentrations, given the influence of this variable on most soil processes in drylands, such as soil respiration (e.g., Fernandez et al. 2006; Almagro et al. 2009; Castillo-Monroy et al. 2011a), N mineralization (Kladivko and Keeney 1987; Gallardo and Merino 1998) and microbial biomass (Gallardo and Schlesinger 1993; 1995). The low influence of soil water content in our study may reflect the adaptation of the soil microbial community to the dry conditions typically maintained during long periods of time in the study area (Castillo-Monroy et al. 2011a). Thus, these microorganisms may be more responsive to the more continuously changing temperature than to changes in soil water content. However, we cannot discard that our minimum soil water content (30 % of WHC) was not low enough to produce metabolic stress in our microbial populations. While 30 % of WHC has been found to be the wilting point in soils such as those studied (Marqués et al. 2008), surface soils (0–5 cm) at BS and BSC microsites at the study area commonly experience very low soil moisture values (below 20 % of WHC during dry periods; Castillo-Monroy et al. 2010, 2011a). Thus, significant microbial functioning exists at 30 % of WHC, with no apparent response to increasing soil moisture, emphasizing the idea that levels of soil humidity limiting plant production are not necessary coupled with limitation of microbial functioning, the latter being extended during longer periods of time in semi-arid ecosystems. The lack of response to 80 % WHC as compared to lower WHC levels observed in our studied variables may be the consequence of the hierarchy of responses to water pulses size suggested for arid and semi-arid ecosystems (Schwinning and Sala 2004). Soil microbes involved in processes such as N mineralization and decomposition can be physiologically active in small amounts of water, while other microbes driving processes not measured in this study, such as microbialN fixation and predation, may require higher amount of water to be active (Cui and Caldwell 1997; Austin et al. 2004; Schwinning and Sala 2004).

It is interesting to note that there were not significant differences between BSC and BG soils in the initial conditions of C and N sources such as hexoses, pentoses, DON, and MB-N. We also did not find differences between nitrification inhibitors such as phenols, and other soil variables such as pH or the C:N ratio. We would expect that these initial differences between BSC and BG microsites may have resulted in divergent microbial community compositions (e.g. Ben-David et al. 2011). The lack of differences in these initial soil variables between these microsites suggests that the different responses to changes in temperature and soil water content of the variables evaluated can only be explained by the different microorganism communities under BSCs with regard to those existing in BG areas. While particular differences in microbial communities between BSC and BG microsites in our study area have not explored yet, these are likely to occur, as recent studies that have shown important effects of BSC composition, richness and degree of development on the abundance and composition of soil microorganisms (Yeager et al. 2004, Housman et al. 2007, Soule et al. 2009; Castillo-Monroy et al. 2011b).

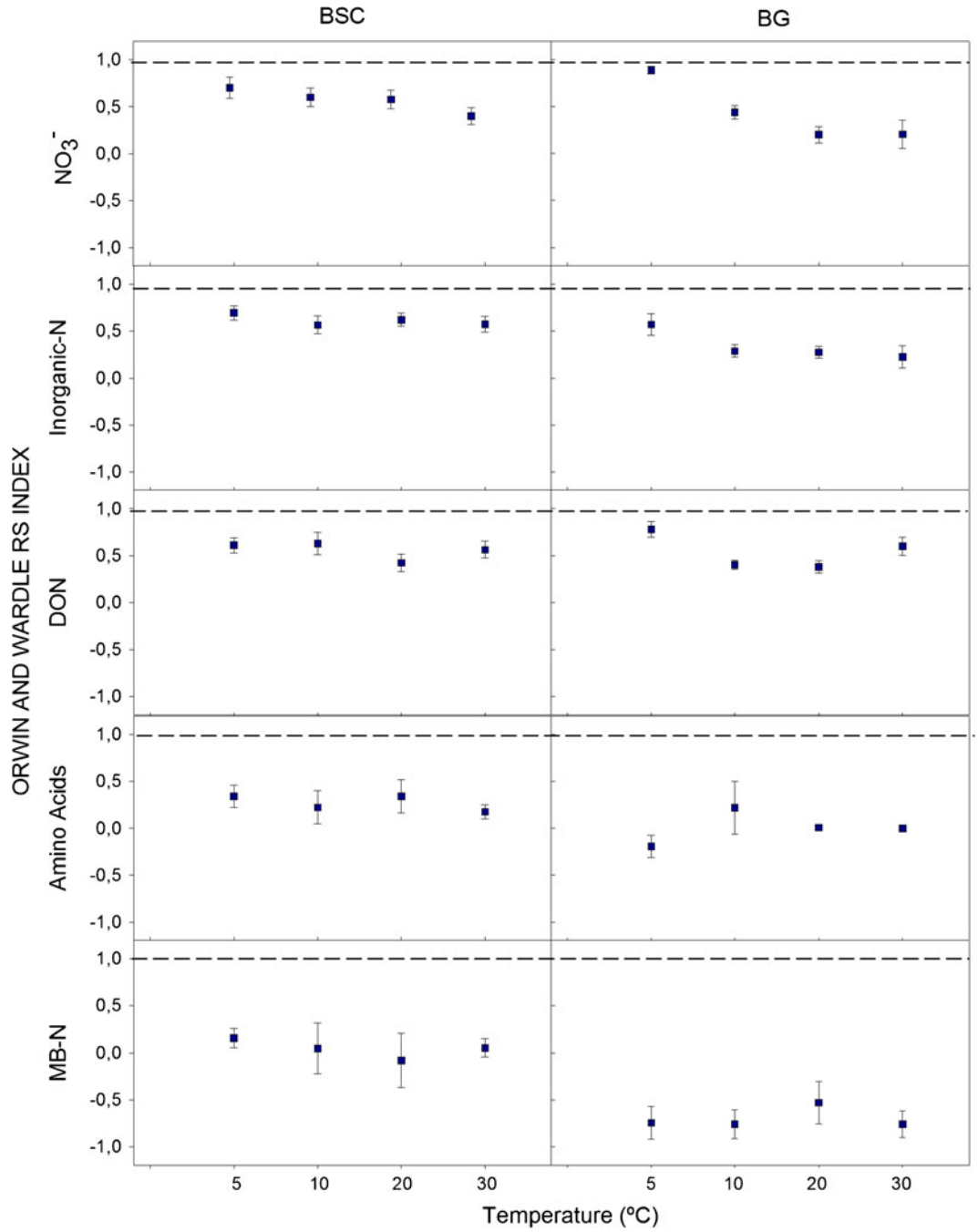

Fig. 6 Changes in the Orwin and Wardle Resistance index for NO_3^--N, inorganic-N, DON and amino acids (after incubation) under the different temperature levels evaluated in biological soil crust (BSC) and bare ground (BG) soils. Data are means±SE ($n=5$)

N transformation rates

Ammonification was the dominant N transformation process at both BSC and BG microsites under low temperatures and 30–50 % WHC, whereas nitrification was the dominant process at high temperatures. An increase in nitrification parallel to augments in temperature up to moderate water content (30–60 % WHC) has also been observed by other authors (Szukics et al. 2010; Bregliani et al. 2010). However, at higher water content

levels, the prevalence of nitrification was turned into a dominance of ammonification in BSC soils at the highest temperatures, whereas in BG soils nitrification continued to be the dominant process at this temperature (Fig. 3). These results suggest a differential response of microorganisms in BSC and BG microsites under these conditions. Previous studies have observed an accumulation of ammonium in cyanobacteria-covered soils, which was not observed under well-developed and lichen-dominated BSC soils (Housman et al. 2007). While denitrification can substantially differ depending on the degree of development of the BSC community (Barger et al. 2005), we assume it was not an important process in our experiment. As we applied the same treatments to both BSC and BG soils, and our soils were maintained under their water holding capacity, we do not expect anaerobic conditions to be prevalent in either treatment, even if they occur in some soil micropores. The abundance of nitrate in both treatments also indicated that denitrification was not important in our experiment. Our results suggest that, in semi-arid soils like those studied, small-scale spatial differences in factors like soil temperature, water content and the microbial community, which are strongly modified by BSCs (Castillo-Monroy et al. 2011a, b; Maestre et al. 2011; Gundlapally and García-Pichel 2006), may have more influence on the relative dominance of N transformation processes than differences in the overall availability of N (Schimel and Bennett 2004).

Orwin and Wardle Resistance index

The RS index obtained with variables such as DON, ammonium, nitrate and inorganic N showed a high sensitivity to changes in temperature at both BSC and BG microsites. However, changes in soil water content did not have any impact on the RS index for these variables. Thus, temperature, rather than water content, seems to be the main factor affecting the resistance of the N variables in the studied ecosystem.

Our results showed that soils under well-developed BSCs had a higher RS index than BG soils for most of the variables evaluated (ammonium, nitrate, inorganic-N, amino acids and MB-N), although a significant interaction with T appeared for ammonium and nitrate. These significant interactions can also be seen for DON, concluding that the presence of BSCs influenced alone, or in combination with temperature, all the studied variables. This effect may be a consequence of the more stable environment provided by BSCs versus the BG microsite. Because the RS index was predominantly higher for most N variables under BSCs, well-developed BSC communities may contribute to protect the N cycle in arid and semi-arid ecosystems by making their soils more resistant to the expected changes in climatic variability expected under the ongoing climatic change, helping to maintain soil functioning and fertility under future climatic conditions. These results highlight the importance of BSCs as a key player of N cycling in drylands, and complement and expand the findings of previous studies showing the influence of these organisms over the N cycle (Belnap 2002; Housman et al. 2007; Delgado-Baquerizo et al. 2010; Castillo-Monroy et al. 2010)

Concluding remarks

Our results showed that changes in temperature (between 5 °C and 30 °C) were more important than variation in soil water content (between 30 % and 80 % of field capacity) to determine the relative dominance of N transformation rates in a semi-arid grassland. Biological soil crusts significantly increased the resistance of the N variables studied to changes in temperature. Our results complement those of previous studies highlighting the key role of BSCs as modulators of N dynamics in dryland ecosystems, and indicate that the maintenance of well-developed BSC communities can minimize the impacts of expected increase in temperature variability with climate change on important variables of the N cycle.

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