Biological soil crust development affects physicochemical characteristics of soil surface in semiarid ecosystems

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ABSTRACT

Water and nutrients are scarce resources in arid and semiarid ecosystems. In these regions, biological soil crusts (BSCs) occupy a large part of the soil surface in the open spaces surrounding patches of vegetation. BSCs affect physicochemical soil properties, such as aggregate stability, water retention, organic carbon (OC) and nitrogen (N) content, associated with primary ecosystem processes like water availability and soil fertility. However, the way BSCs modify soil surface and subsurface properties greatly depends on the type of BSC. We hypothesized that physicochemical properties of soil crusts and of their underlying soils would improve with crust development stage. Physicochemical properties of various types of soil crusts (physical crusts and several BSC development stages) and of the underlying soil (soil layers 0-1 cm and 1-5 cm underneath the crusts) in two semiarid areas in SE Spain were analysed. The properties that differed significantly depending on crust development stage were aggregate stability, water content (WC) (at -33 kPa and -1500 kPa), OC and N content. Aggregate stability was higher under well-developed BSCs (cyanobacterial, lichen and moss crusts) than under physical crusts or incipient BSCs. WC, OC and N content significantly increased in the crust and its underlying soil with crust development, especially in the first centimetre of soil underneath the crust. Our results highlight the significant role of BSCs in water availability, soil stability and soil fertility in semiarid areas.

Keywords: physical crust, cyanobacteria, lichen, moss, aggregate stability, water content, organic carbon, nitrogen.

1. Introduction

Biological soil crusts (associations of soil particles with cyanobacteria, algae, fungi, lichens or bryophytes) are common ground cover in open spaces surrounding vascular plants in arid and semiarid areas. Biological soil crusts (BSCs) significantly influence primary ecosystem processes (Maestre et al., 2011), and have been described as ecosystem engineers in drylands, as they cause changes in soil surface conditions that affect the habitat for other organisms (Bowker et al., 2005, 2006). Some of the functions that BSCs perform are: 1) The microtopography associated to the BSCs and the polysaccharides secreted by BSC organisms make soil particles adhere to each other, increasing soil aggregation and stability, thereby reducing erosion by water and wind (Belnap and Gardner, 1993; Mazor et al., 1996) and increasing the retention of nutrients in the top soil, thus making soil more fertile (Reynolds et al., 2001). 2) BSCs modify soil surface features such as roughness (Rodríguez-Caballero et al., 2012), porosity (Miralles et al., 2011), water retention (Chamizo et al., 2012a) and aggregation (Shulten, 1985), all of which affect the way water moves into and through soils. This BSC layer in the boundary between atmosphere and soil therefore plays a major role in infiltration and runoff, evaporation and soil moisture (Belnap, 2006). It regulates vertical and horizontal fluxes of water and critically influences water availability and redistribution, as well as sediment and nutrient resources, in arid and semiarid ecosystems (Belnap et al., 2003a; Chamizo et al., 2012b). 3) BSCs are capable of C and N fixation (Beymer and Klopatek, 1991; Evans and Ehleringer, 1993), and also of decomposing and mineralizing organic compounds (Mager, 2010). While distribution of soil nutrients in semiarid areas is concentrated under the plant canopy (Pugnaire et al., 1996), BSCs occupy the nutrient-poor zones surrounding patches of vegetation, so that most nutrient inputs and losses in interplant spaces are regulated by them (Belnap et al., 2003a). Thus, BSCs strongly affect nutrient cycling (Maestre et al., 2011) and represent major sources of C and N in arid ecosystems (Housman et al., 2006). 4) BSCs affect the germination, emergence and survival of vascular plants, either through competition with cover and biomass, or changes in soil properties (Eldridge and Greene, 1994; Belnap et al., 2003b).

When BSC organisms colonize the soil, they spread until they occupy extensive areas of soil surface, and later, as development continues one species replaces others (Lázaro et al., 2008). In arid and semiarid ecosystems, which represent around 40% of the Earth´s land surface, BSCs can cover up to or more than 70% of the soil surface (Belnap et al., 2003a). Cyanobacterial BSCs represent the earliest successional stages of BSCs, whereas lichens and mosses appear during the later stages (Lange et al., 1997). Some of the factors that have been reported to condition BSC cover and composition are radiation intensity and topographic attributes, such as slope aspect, which affect soil moisture (Eldridge and Tozer, 1997; Lange et al., 1997) and soil surface stability (Lázaro et al., 2008), vascular plant structure (Maestre and Cortina, 2002), environmental variables, such as soil pH, texture, soil organic matter (SOM), and soil nutrients (Anderson et al., 1982; Eldridge and Tozer, 1997; Bowker et al., 2005, 2006), and disturbances and their intensity (Dougill and Thomas, 2004). For instance, Martinez et al. (2006) related the abundance of lichen and moss in two semiarid gypsiferous areas of Spain to soil-aggregate stability, soil respiration and potassium content. Bowker et al. (2005) demonstrated a positive correlation between lichen and moss abundance and higher moisture and manganese and zinc availability. These authors also suggested the existence of feedback between crust and nutrient availability in the soil, so that lichen (*Collema spp*.) was more abundant where manganese and zinc were available, but as a consequence of the modification of the soil environment by lichens, more micronutrients were available in the soil.

Soil stability and fertility losses are two of the most pressing problems involved in the degradation of ecosystem functioning and desertification in drylands (Bowker et al., 2006, 2008). Given the key role of BSCs in increasing soil stability, reducing erosion, and retaining soil nutrients, their loss is considered a major cause of land degradation (Belnap, 1995). In addition, BSCs are considered essential components of healthy, functional ecosystems and both local and regional biodiversity (Eldridge, 2000). Some studies have suggested total BSC cover as an indicator of ecological health (Tongway and Hindley, 1995; Pellant et al., 2000). Less in the literature is BSC composition as such an indicator. However, this could only be taken into consideration, as the rate and type of vital ecosystem services that BSCs perform greatly vary depending on species abundance and crust composition (Housman et al., 2006).

Thus, the presence of one BSC or another can affect soil properties, such as water retention, aggregate stability, and nutrient availability, among other variables, differently, and in turn, soil surface properties can affect the presence of one type of BSC or another by making habitat conditions more favourable for the establishment of one species than another. Moreover, how or how much the crust type, or development stage, might modify soil properties or these might favour the growth of specific BSC species can vary from one ecosystem to another. However, no study has yet simultaneously analysed the physicochemical characteristics of different types of soil crusts, including both physical and biological crusts, and BSC stages of development, as well as their underlying soils, in two different ecosystems with similar BSC composition. Even if an association between the crust type and soil properties were to be found, the crust type could potentially be used as an indicator of soil quality.

The aim of this study was to find out whether the physicochemical characteristics of soil crusts and the soil beneath them varied with physical or biological crust type and BSC development stage, in two semiarid ecosystems with contrasting lithology where BSC development stages are well-represented. More specifically, our objectives were to: 1) determine whether physicochemical properties of the crust improve with development stage, 2) analyse how crust development affects the physicochemical characteristics of the underlying soils, and 3) analyse the vertical variation in soil physicochemical characteristics (from the crust to a soil depth of 5 cm) by crust development. We hypothesized that the quality of the physicochemical properties of the crust and their underlying soils would increase with crust development, from the physical crusts to the most highly developed BSCs, and that these properties would decrease with depth, from the uppermost to the deepest layer. In addition, the ratio between the crust and the underlying soil was determined in order to find out the relative importance of the crust with respect to the underlying soil, and to examine the ratio's trend with crust development.

2. Material and methods

2.1. Study sites and types of soil crust

A progressive classification of soil crust types from physical through various BSC development stages were selected in two semiarid ecosystems in SE Spain characterised by different lithologies and soil crust distributions, “El Cautivo” in the Tabernas desert and “Las Amoladeras” in the Cabo de Gata-Níjar Natural Park.

El Cautivo is located in the Tabernas Basin, a badlands catchment surrounded by the Alhamilla, Filabres, Nevada and Gador Mountain Ranges. The catchment is mainly filled with Neogene marine sediments, consisting of gypsum-calcareous mudstones and calcaric sandstones. The climate is characterised by hot, dry summers and mild temperatures the rest of the year, with rain falling mostly in winter (mean annual rainfall of 235 mm). Soil types are classified as Epileptic, Endoleptic or Calcaric Regosols and Eutric Gypsisols, and soil texture is silty loam (Cantón et al., 2003). Ground cover in the area is strongly controlled by topographic attributes (Cantón et al., 2004). The area is characterised by a mosaic of discontinuous perennial plant cover, some annuals and very abundant physical crusts and BSCs. Both physical crusts and BSCs cover around 80% of the soil surface. Four of the most abundant crust types as described in previous studies at this site (Lázaro et al., 2008; Chamizo et al., 2012a, b, c) were selected: 1) a physical soil crust, 2) a light-coloured BSC with incipient colonisation by cyanobacteria (incipient-cyanobacterial BSC; 3) a dark BSC mainly dominated by cyanobacteria (cyanobacteria-dominated crust or well-developed cyanobacterial BSC), which also contained numerous pioneer lichens, including *Placynthium nigrum*, *Collema spp.*, *Endocarpon pusillum*, *Catapyrenium rufescens* and *Fulgensia spp.*, and 4) a light-coloured BSC mainly composed of the *Diploschistes diacapasis* and *Squamarina lentigera* species of lichens (lichen BSC). This selection was based on a sequence of increasing crust development, from abiotic (physical crusts) to wide BSC cover by late-successional species. BSC developmental stages were identified based on Lázaro et al. (2008).

Las Amoladeras, located in the Cabo de Gata-Níjar Natural Park, is a dissected caliche in a flat alluvial fan. The climate is also semiarid, with an average annual temperature of 19°C and a mean annual rainfall of 200 mm, falling mainly in winter. Soils are Calcaric Leptosols and Haplic Calcisols, and the texture is sandy loam. The vegetated surface consists of scattered shrubs covering around 30% of the area, predominately *Macrochloa tenacissima.* Due to the coarse soil texture, physical crusts are not abundant, and BSCs are the most representative crust types found. BSCs occupy around 30% of the open areas surrounding shrubs. The remaining area is occupied by a calcaric outcrop and stones. The three main types of BSCs identified at this site were (Chamizo et al., 2012b, c): 1) a cyanobacteria-dominated BSC, 2) a lichen-dominated BSC, and 3) a moss-dominated BSC, which also contained around 15% of cyanobacterial cover. The species composition of the first two crust types was similar to the same BSC types in El Cautivo. The cyanobacterial BSCs represent an early-successional stage, whereas the lichen and moss BSCs represent late-successional stages (Lange et al., 1997).

2.2. Sampling and determination of physicochemical characteristics of the crusts and their underlying soils

Four samples per crust type were collected in the field from the following soil layers: 1) the “crust layer” (around 0.5 cm thick), 2) the “top layer” (1-cm layer of soil immediately underneath the crust), and 3) the “deep layer” (1-5-cm-deep layer of soil underneath the crust). As BSCs are expected to strongly influence aggregate stability in the top millimetres of soil, aliquots were carefully separated from the top-layer samples for later determination of aggregate stability. Sampling sites in each study area were near each other, ensuring similar topography and the same soil type.

In the laboratory, the crust and soil samples were air-dried and sieved to 2 mm to acquire the fine earth fraction. Aliquots of these samples were taken and mashed in a mechanical agate mortar to obtain 0.5-mm particle size necessary for determination of organic carbon, exchangeable cations and cation exchange capacity.

The following physical properties were determined in the samples: a) particle size distribution underneath crusts in the top and deep layers by the Robinson's pipette method (Gee and Bauder, 1986); b) water content (WC) at -33 kPa and at -1500 kPa in intact and repacked crusts, and sieved fine earth samples from the top and deep layers, with a Richard´s pressure-membrane extractor, and c) aggregate stability of 4-5 mm aggregates by the drop test (Imeson and Vis, 1984). Due to the high variability in aggregate stability in semiarid regions (Cantón et al., 2009), this test was replicated in 40 aggregates per crust type.

The following chemical properties were analysed in all three layers per crust type: a) organic carbon (OC) by the Walkley and Black method modified by Mingorance et al. (2007), b) total nitrogen (N) by the Kjeldhal method (Bremner, 1996), and c) exchangeable cations (Ca, Mg, Na, K) and cation exchange capacity (CEC) by formation of Cu(II) complexes with triethylenetetramine followed by photometric analyses (Meier and Kahr, 1999). Exchangeable cations and CEC in the crust samples were determined by analysing soil particles scraped off the crust, referred to as “crust-layer soil particles”. Electrical conductivity, pH, and calcium carbonate in the soil samples were also determined from the top and deep layers underneath the different crust types. The electrical conductivity and pH were measured in a 1:1 soil-water suspension (Thomas, 1996), and calcium carbonate was determined by Bernard's calcimeter (Loeppert and Suarez, 1996). Finally, as the parent material in El Cautivo is gypsiferous mudstone, total sulphates were analysed as a measure of soil gypsum using the gravimetric method based on sulphate ion precipitation, in acid medium, as barium sulphate (Porta et al., 1986). As this method is not reliable when gypsum content is less than 1%, and its content in the top-layer samples was negligible, gypsum was only determined in the deep layer below the different crust types. Due to the high gypsum content found underneath the physical and lichens crusts, average Ca content under these crusts was overestimated and therefore not taken into account in the results or the statistical analyses.

2.3. Statistical analysis

To find out whether the site characteristics and crust development stage, or type, affected soil physicochemical properties, and whether these properties varied significantly among soil layers (crust layer, top layer, deep layer), general linear models (GLMs) were performed for the properties determined, using site, crust type and soil layer as predictors (the last factor was not included in the analysis when the variable was determined in only one layer). First, to examine the influence of the site on the dependent variables, GLM analyses were performed only for the crusts that were common to both study sites, and using site, crust type and soil layer as predictors. Then, to test for the significance of the predictor factors (crust type and layer) at a site, GLM analyses were done separately for each study site. When the factors or their interaction were significant for the dependent variables, planned orthogonal contrasts (see Quinn and keough, 2002) were performed to test the significance of our *a priori* hypothesis about the horizontal (crust type or development) and vertical (layers) trends of the variables determined. We tested the hypothesis that there would be a horizontal increase in the variable with crust development, i.e., physical < incipient-cyanobacterial < cyanobacterial < lichen crusts in El Cautivo, represented by the contrast vector [-2 -1 1 2], and cyanobacterial < lichen and moss crusts in Las Amoladeras, represented by the contrast vector [-2 1 1]. We also tested the hypothesis of a vertical decrease of the variable with depth, i.e., crust layer > top layer > deep layer, represented by the contrast vector [-1 0 1]. The exception was soil texture, which, as a very stable property, was not expected to vary significantly under the crust types.The level of significance was established at $P<0.05$. STATISTICA 8.0 was used to perform the analyses (StatSoft, Inc., Tulsa, Oklahoma, USA).

Soil property means underneath the crust were weighted by the thickness of the top (1 cm) and deep (4 cm) soil layers, and then the crust-to-underlying soil (top and deep layers) ratio was determined. Ratios over 1 would indicate that the crust was more influential on the property, whereas ratios lower than 1 would indicate that the underlying soil was more important.

3. Results

3.1. Physical properties

The study site was a significant factor for all the physical properties determined. Soil texture, aggregate stability and WC at -33 and -1500 kPa significantly differed between sites (Table 1). Table 2 shows the percentage of sand, silt and clay in the top and deep layers underneath the crust types at both study sites. Silt was predominant at El Cautivo, whereas the particle size at Las Amoladeras was mainly sand. Contrary to expectations, sand, silt and clay content varied significantly under the crust types in El Cautivo (Table 1). Sand content was lower and clay content was higher under physical crusts and lichen BSCs than under incipient and well-developed cyanobacterial BSCs (Table 2).

No significant difference in soil texture was found between the top and deep layers. At Las Amoladeras, no difference was found in soil particle distribution underneath the crust types. The soil layer influenced silt content (Table 1), which was higher in the top than in the deep layer underneath the BSCs (Table 2).

Aggregate stability was lower at El Cautivo than at Las Amoladeras (Table 2). Crust development influenced aggregate stability at the first site, but not at the second (Table 1). At El Cautivo, the planned contrast revealed an increase in the number of drops needed to break down the aggregates with crust development (Table 2). At Las Amoladeras, although the planned contrast was not significant, more drops were needed under the lichen and moss than under the cyanobacterial BSCs.

WC at -33 and -1500 kPa was higher at El Cautivo than at Las Amoladeras (Table 3). At El Cautivo, the planned contrast indicated a significant increase in WC at -33 kPa from the least to the most developed crusts in all the layers. At -1500 kPa, the crust types showed similar WC (Table 3). The soil layer affected WC at -33 kPa and -1500 kPa (Table 1). However, WC did not follow a decreasing trend with soil depth, as was hypothesised. At -33 kPa, the top layer showed higher WC than the other layers, and at -1500 kPa, WC was generally higher in the deep soil than in the other layers. At Las Amoladeras, the interaction between crust type and soil layer was significant for WC at -33 and -1500 kPa (Table 1). The planned contrast showed that WC at both pressures was higher in the lichen and moss BSCs than in the cyanobacterial BSCs. WC was also higher in the top layer under the lichen and moss BSCs than under the cyanobacterial BSCs at -33 kPa, but similar at -1500 kPa in the top layer under the BSCs. No difference in WC was found at either pressure in the deep layer under the BSCs (Table 3). Differences among layers were observed in the most developed BSCs (lichen and moss BSCs), where the crust layer showed higher WC at -33 and -1500 kPa than the underlying soil layers. WC at both pressures was similar in the crust and the underlying soil layers in the cyanobacterial BSCs (Table 3).

The crust-to-underlying soil ratio for WC at -33 and -1500 kPa (Table 3) was around 1 at El Cautivo, with the exception of the lichen BSCs at -1500 kPa, where the ratio was over 1. These ratios indicated that on fine-textured soils, WC in the crusts and their underlying soils was similar. At Las Amoladeras, the WC ratio at both pressures was over 1 in all BSCs and increased in order from cyanobacterial to lichen and moss BSCs, thus indicating higher WC in the crust with respect to its underlying soil with increasing BSC development.

3.2. Chemical properties

The study site was a significant factor for OC and N content (Table 1). As seen in Fig. 1, the content of both were higher in the crusts and soils at Las Amoladeras than at El Cautivo. The interaction between crust type and soil layer was significant for OC and N at both sites (Table 1). At El Cautivo (Figs.1a and 1b), the planned contrast indicated an increase in OC and N from the least to the most developed crusts in all the soil layers. Nevertheless, differences among crusts were especially significant in the crust layer and decreased in the underlying soil layers. For instance, lichen BSCs had twice as much OC as cyanobacterial BSCs, six times as much as physical crusts and over twice as much N as physical crusts. OC and N content did not differ among soil layers in the physical crusts and incipient-cyanobacterial BSCs, but did in the cyanobacterial and lichen BSCs, where the contents in both decreased with soil depth (Fig. 1a and 1b). At Las Amoladeras (Figs. 1c and 1d), the planned contrast indicated that lichen and moss BSCs had higher OC and N content than cyanobacterial BSCs in the crust and top layers, but that their content did not differ in the deep layer under the BSCs. Lichen and moss BSCs had nearly twice as much OC and around 1.5 times more N than cyanobacterial BSCs. OC content was higher in the crust than in the underlying soil layers in all the BSC types. N content was higher in the crust than in the underlying soil layers in the lichen and moss BSCs, but similar in the crust and underlying soil layers in the cyanobacterial BSCs.

The crust-to-underlying soil ratio for OC and N (Fig.1) was around 1 in the physical crusts. In the BSCs, this ratio was over 1, and increased with BSC development at each site, meaning higher OC and N content in the crust with respect to its underlying soil as the BSC was more developed.

Fig. 2 shows the average exchangeable cations and CEC in the crust-layer soil particles, and top and deep layers at both study sites. The site was significant for Na ($P=0.02$), K ($P=0.05$) and CEC ($P=0.00$). These properties were higher in crusts and soils at Las Amoladeras than at El Cautivo (Fig. 2). Contrary to what was expected, crust type did not have a significant effect on exchangeable cations at either of the two sites, with the exception of Ca content at Las Amoladeras, where moss BSCs showed higher content of this element than the other BSCs (data not shown). The soil layer significantly affected Ca, Mg and K content at both sites (Table 1). These properties were higher in the crust-layer soil particles than in the underlying soil (top and deep layers) (Fig. 2), except for Ca content in El Cautivo, which was higher in the top and deep layers than in the crust-layer soil particles (Fig. 2a). Crust type and layer significantly influenced CEC at El Cautivo (Table 1). This property increased with crust development stage in all layers (e.g., average CEC in the crust-layer soil particles was 3.32 ± 0.22 in the physical crust and 4.18 ± 0.61 in the lichen BSCs), and was higher in the crust-layer soil particles than in the soil underneath the crusts (Fig. 2a). At Las Amoladeras, crust type only significantly influenced CEC in the crust-layer soil particles, where CEC increased with BSC development, from cyanobacterial (mean 4.27 ± 0.49 cmol kg^{-1}) to lichen (mean 4.38 ± 0.28 cmol kg^{-1}) and moss BSCs (mean 5.12 ± 0.92 cmol kg^{-1}). No difference in CEC was found in the top or deep layers under the BSCs. Differences in CEC between layers were only significant in the moss BSCs, where the crust-layer soil particles showed higher CEC (P=0.00) than the soil underneath the crust.

Soil pH did not vary between sites (Table 1). Crust development influenced pH at El Cautivo, but not at Las Amoladeras. However, contrary to expected, pH did not increase with crust development at El Cautivo, although it was higher in the soil under BSCs than under physical crusts. No difference in pH was found between the top and deep soil layers at either of the two sites (Table 1).

Calcium carbonate content, which differed between sites (P=0.00)), was higher at El Cautivo than at Las Amoladeras (Table 4). Neither crust development nor soil layer influenced calcium carbonates at either of the two sites.

Electrical conductivity also differed between sites (Table 1). This property was much higher in the soils at El Cautivo than at Las Amoladeras (Table 4). Crust development and soil layer influenced electrical conductivity at El Cautivo, but not at Las Amoladeras (Table 1). At the first site, electrical conductivity was higher in the soils under the physical crusts and lichen BSCs than under the incipient and well-developed cyanobacterial BSCs, and higher in the deep layer than in the top one underneath those crusts (physical crusts and lichen BSCs). Gypsum was also higher in the soil underneath the physical crusts and lichen BSCs than under the incipient and well-developed cyanobacterial BSCs (Table 4).

4. Discussion

BSCs affect many soil properties involved in primary ecosystem processes in drylands, such as nutrient cycling and hydrological processes. Although numerous studies have reported an increase in water retention (Malam Issa et al., 2009), aggregate stability (Shulten, 1985) and OC and N content (Rogers and Burns, 1994; Gao et al., 2010) due to the presence of BSCs separately, to our knowledge, no previous publication has simultaneously reported on the changes in all these properties in the crust and their underlying soils considering a sequence from less to more developed crust types. We examined all these changes in soil properties with crust development in two ecosystems with contrasting lithologies and representative of the most common BSC habitats and spatial distributions in semiarid areas. Our results fill in these gaps and demonstrate that the type of soil crust, in terms of crust development stage, significantly influences soil physicochemical properties.

4.1. Influence of crust development on physical soil properties

Soil particle-size distributions in the two study sites contrasted considerably (Table 2). Due to the complex topography of El Cautivo, soil texture underneath the crust types differed significantly in this area. Incipient and well-developed cyanobacterial BSCs often colonize depositional landforms with coarser soils due to the transport of fine sand from the top of the hillslopes where the rest of the overlying calcaric sandstone remain, while physical crusts and lichen BSCs develop on hillslope positions over mudstone regolith that is composed of 80% silt (Cantón et al., 2003) and with hardly any calcaric sandstone deposition (Cantón et al., 2004). Thus, silt content was higher and sand content lower in the soils underneath the physical crusts and lichen BSCs than under the incipient and well-developed cyanobacterial BSCs (Table 2). On the flat sandy loam soils at Las Amoladeras, soil texture did not vary with crust type.

Aggregate stability was higher under well-developed BSCs (cyanobacterial, lichen and moss BSCs) than under physical crusts or poorly-developed BSCs (incipient-cyanobacterial BSCs) (Table 2). The importance of BSCs in enhancing the stability of soil aggregates has been widely described (Shulten, 1985; Belnap and Gardner 1993; Eldridge and Greene, 1994; Mazor et al., 1996). Mechanically, fungal hyphae, cyanobacteria filaments, and lichen and moss attachment structures form a network in the upper soil layers that greatly enhances aggregate stability. Chemically, the sticky polysaccharides secreted by BSC organisms bind soil particles, favouring soil aggregation (Schulten, 1985; Belnap and Gardner, 1993). This is especially significant within the first millimetres of the soil surface and strongly contributes to reducing erosion by water and wind (Eldridge and Greene, 1994). McKenna Neuman et al. (1996), studying the influence of BSCs on wind transport of sand particles, pointed out that the mechanical entanglement of particles by cyanobacteria filaments was more effective in increasing surface shear stresses and decreasing wind speed than the chemical entrapment of particles by polysaccharides. Soil cohesion by algae has been reported to be indispensable at early stages, while later growth of lichens, mosses and fungi improve cohesion by changes in soil physicochemical properties (Hu et al., 2002). Chamizo et al. (2012b) also found, under simulated extreme rainfall, that physical crusts generated much higher sediment yield than BSCs and that sediment yield significantly decreased with BSC development. Furthermore, the removal of BSCs dramatically increased erosion by water (Chamizo et al., 2012b). The higher aggregate stability found under the most developed BSCs and in the soils at Las Amoladeras than at El Cautivo can also be attributed to the higher soil OC content (Fig. 1). Rogers and Burns (1994) also reported a positive correlation between increased soil carbohydrate C induced by inoculation of soil with BSCs and increased soil aggregate stability.

Because of the textural differences between sites, WC at -33 and -1500 kPa were higher in the finer-textured soils at El Cautivo than at Las Amoladeras (Table 3). WC at each site increased with BSC development stage (Table 3). Cyanobacterial sheaths, moss stems and lichen thalli trap airborne silt and clay particles that increase water retention at the surface (Verrecchia et al., 1995; Malam Issa et al., 1999). We found that silt content on coarse-textured soils (Las Amoladeras) was higher in the top layer underneath the BSCs than in the deep layer (Table 2). Moreover, BSCs are able to absorb large amounts of water in a short period of time. Cyanobacteria polysaccharide sheaths can absorb up to 10 times their volume of water (Verrecchia et al., 1995). Moss can absorb water directly through hair-points on their leaves and expand their cover and biomass up to 13 times (Galun et al., 1982). On fine-textured soils (El Cautivo), the presence of BSCs compared to physical crusts and increased BSC development resulted in increased WC in the crust and its underlying soil at -33 kPa, but not at -1500 kPa (Table 3). As fine soils have a high water retention capacity, the soil underneath the crust generally had a higher WC than the crust itself and the crust-to-underlying soil ratio was close to or lower than 1 (crust-to-underlying soil ratio, Table 3). At Las Amoladeras, where soil texture was coarser, WC at -33 and -1500 kPa was higher in the crust than in the underlying soil, and significantly increased in order from cyanobacterial to lichen to moss BSCs (Table 3). Furthermore, the increase in WC in the crust with respect to its underlying soil increased with BSC development stage (ratio over 1; Table 3). Malam Issa et al. (2009) reported that WC at -33 kPa in sand dunes was twice as high in samples with dense microbial cover and four times as high as in samples thinly covered or devoid of microbial cover. However, no differences were found between samples with and without microbial cover at -1500 kPa. We also found that the presence of well-developed BSCs (lichens and mosses) on coarse soils increased WC in the underlying top layer at -33 kPa, but did not induce significant differences in WC in the top and deep layers at -1500 kPa. Our results suggest that greater BSC development increases WC at the soil surface, especially on coarse-textured soils, and that the improvement in WC of the underlying soil is mainly restricted to the upper layer. In deeper soils (5 cm deep), the difference in WC is mainly between well-developed (cyanobacterial and lichen BSCs) and poorly-developed (physical and incipient-cyanobacterial BSCs) crusts. Thus the presence of well-developed BSCs, in addition to increasing WC in the top layer, is also able to increase WC in deeper soil layers.

4.2. Effect of crust development on soil chemical properties

OC and N stocks were substantially larger at Las Amoladeras than at El Cautivo. The Las Amoladeras site has better conditions, characterised by higher infiltration rates and less erosion due to its coarser soil texture, and less hydric stress because of its proximity to the Mediterranean Sea than El Cautivo, which is located in a badlands on a highly erodible lithology with fine-textured soils and higher runoff and erosion rates (Chamizo et al., 2012b; Cantón et al., 2011). Both sites showed the same pattern of higher OC and N content in the crust and its underlying soil as development progressed (Fig. 1). Previous studies have shown that BSCs mainly affect nutrient cycling in the top soil (Mager and Thomas, 2011). We also found that the effect of the crust on soil OC and N was especially significant in the top layer. In the deep layer, differences were mainly between soils under poorly (physical crusts and incipient-cyanobacterial BSCs) and well-developed (cyanobacterial and lichen BSCs) crusts (Figs. 1a and 1b), which is why no differences in OC and N were found in the deep layer underneath the BSCs at Las Amoladeras (Figs. 1c and 1d).

Several publications have reported up to a 300% increase in soil C content (Rao and Burns, 1990; Rogers and Burns, 1994) and an increase in soil N of up to 200% (Rogers and Burns, 1994; Harper and Belnap, 2001) due to the presence of BSCs. Malam Issa et al. (1999) found that the presence of BSCs improved surface OC over bare and litter-covered soils. Thomas and Dougill (2007) reported that cyanobacterial BSCs significantly increased soil N and SOM compared to unconsolidated surfaces. Gao et al. (2010) also found that BSCs significantly increased OC and N in the surface soil layer (0–5 cm) under wet conditions, although no difference was found in the soil profile at a depth of 60 cm.

BSCs are able to fix atmospheric C (Beymer and Klopatek, 1991) and increase the soil C pool by producing extracellular polysaccharides (Mager and Thomas, 2011). Polysaccharide content may be 1.5 to 3 times higher in samples of dense BSC cover than sparse cover (Malam Issa et al., 2001). Belnap et al. (2008) found a significant relationship (R^2 = 0.71) between cyanobacteria-dominated BSC development and exopolysaccharide content. Moreover, Mager (2010) reported that in the south-west Kalahari, surface carbohydrate content produced by cyanobacterial BSCs may represent up to 75% of total soil OC. Exopolysaccharide content in the crusts at our study sites has also been shown to significantly increase from the least (physical crusts) to the most developed (lichens and mosses) crusts (Chamizo et al., in press, a). The higher OC found in the more developed BSCs and their underlying soil can be attributed to this increased polysaccharide content.

After water, soil N availability is another critical limiting factor for semiarid ecosystem functioning (Gebauer and Ehleringer, 2000). N inputs occur through atmospheric deposition and N fixation (Hawkes, 2003), whereas N outputs occur through N mineralization and subsequent gaseous losses by volatilization, nitrification, and denitrification (Evans and Lange, 2003). BSCs largely regulate N input and losses in arid regions. In xeric and N-limited ecosystems, N fixation by BSCs has been reported to be the dominant source of N input (Evans and Ehleringer, 1993; Evans and Lange, 2003). Cyanobacteria and cyanolichens fix atmospheric N (Evans and Ehleringer, 1993) and make it available for vascular plants and other microorganisms (Hawkes, 2003; Veluci et al., 2006). Ammonium is the preferred form of combined-N for cyanobacteria. In the absence of ammonium, cyanobacteria can use other N forms (i.e. nitrate) that are then reduced to ammonium (Luque and Forchhammer, 2008). Only during depletion of combined-N forms through mineralization, volatilization or leaching, cyanobacteria use atmospheric N-fixation (Luque and Forchhammer, 2008; Mager and Thomas, 2011). N fixation by BSCs varies considerably depending on temperature, moisture, light and BSC composition (Belnap, 2003). In general, later successional BSCs have higher N fixation rates and therefore contribute higher N content to surrounding soils than early successional cyanobacterial BSCs (Housman et al., 2006; Belnap et al., 2008). However, high N fixation rates do not necessarily imply enhanced productivity. Recent studies have reported higher nitrate content in areas with low BSC cover than in areas dominated by well-developed lichen BSCs (Castillo-Monroy et al., 2010; Delgado-Baquerizo et al., 2010). In contrast, Veluci et al. (2006) found more ammonium leaching in lichen BSCs than moss and bare soils, while nitrate leaching was lower in lichen than in moss BSCs and bare soils. Cyanobacterial BSCs are also thought to limit loss of N by leaching (Mager, 2009). Thus, BSCs are able to increase nutrient availability in the soil surface by reducing nutrient losses to the subsoil (Mager and Thomas, 2011). BSCs also increase nutrient inputs by trapping aeolian dust enriched in micro and macronutrients. Physical crusts exhibit low N content due to the absence of microorganisms capable of fixing and retaining N. Because well-developed

BSCs are more effective in fixing N, trapping nutrient-enriched dust and reducing erosion than less developed BSCs, we found higher N content in more developed lichens and moss BSCs than in less developed incipient-cyanobacterial BSCs (Fig. 1). This is also supported by the crust-to-underlying soil ratio found, which showed that OC and N were higher in the crust than in the underlying soil, and that the increase in the crust with respect to the underlying soil rose with BSC development (Fig. 1).

In the rest of the variables analysed, differences were found only among some of the crust types. Crusted surfaces often trap silt and clay particles which bind positively charged particles such as Ca, Mg, Na and K cations. Polysaccharides also cause these cations to be bound more strongly (Belnap et al., 2003b). Although exchangeable cations did not differ significantly among crusts (Table 1), CEC did increase with BSC development in all layers at El Cautivo and in the crust-layer soil particles at Las Amoladeras, which seems to indicate that well-developed BSCs especially improve CEC in lesser-quality soils. This increase in CEC can be attributed to a parallel increase in OC with BSC development. A positive relationship between increased soil CEC and SOM was reported by Miralles et al. (2007, 2009) in other semiarid environments.

BSCs have been reported to increase pH in the top soil from 8 to 10.5 (García Pichel and Belnap, 1996). Rivera-Aguilar et al. (2009) found a positive correlation between lichens and soil pH, attributed to calcium carbonates and the preference of some lichen species for an alkaline pH (Bowker et al., 2006). Increased soil pH could also be related to increased SOM (Miralles et al., 2009). Although calcium carbonates in the soils under the crust types from our study sites did not differ significantly, their content was higher underneath BSCs than physical crusts, which together with the also higher OC under BSCs, could explain the higher pH in soils underneath BSCs than physical crusts (Table 4).

Gypsum was higher in the soils underneath physical crusts and lichen BSCs than under incipient and well-developed cyanobacterial BSCs at El Cautivo (Table 4). At this site, runoff and erosion rates on physical soil crusts are very high (Cantón et al., 2001). This limits soil development, making that many soil properties underneath them, like the gypsum content, are inherited from the parent material, a gypsiferous mudstone (Cantón et al., 2003). On the other hand, the lichens *Diploschistes diacapsis* and *Squamarina lentigera* are gypsum specialists (Martínez et al., 2006). Some studies have also suggested that lichen cover grows with increased soil gypsum (Büdel and Lange, 2003). The higher electrical conductivity in soils under physical crusts and lichen BSCs is associated to the higher gypsum content underneath these crusts (Table 4).

Our results demonstrate that BSCs have a major role in soil water content, soil stability and fertility in drylands, and that these functions become more significant as the BSC is more developed. For instance, in the badlands, mean OC and N in the lichen-covered soil profile including the crust and underlying 5 cm of soil was 9.04 ± 1.77 g kg^{-1} and 1.23 ± 0.12 g kg^{-1} , respectively, whereas it was 4.99 ± 0.76 g kg^{-1} and 0.85 ± 0.07 g kg^{-1}, respectively, in soils underneath physical crusts. Well-developed BSCs are therefore able to increase soil OC and N up to twice as much as soils covered by physical crusts. The better quality of soil physicochemical properties with BSC development also supports our progressive classification of BSCs based on their development stage. Nevertheless, it should be noted that these results could be interpreted as either the improvement of soil properties due to the presence of well-developed BSCs or as the establishment of well-developed BSCs in soils with better physicochemical properties. We suggest a feedback process by which more developed BSCs colonize soils with better soil properties and in turn, the presence of well-developed BSCs improves soil surface physicochemical properties in the long-term. As also reported by other studies, the relationship between BSC development and soil physicochemical properties could potentially be used to develop a qualitative (or even quantitative) soil quality indicator in semiarid areas based on total BSC cover (Chaudhary et al., 2009), the presence of well-developed BSCs, such as lichens and mosses, or on attributes associated with BSCs, such as exopolysaccharides (Belnap et al., 2008), chlorophyll *a* (Bowker et al., 2008), or OC and N content (this study). Moreover, remote sensing applied to mapping of BSCs (see Weber et al., 2008; Chamizo et al., 2012c), could provide a powerful tool for estimating soil surface conditions and critical information about soil stability, C and N stocks, and associated hydrological and erosive dynamics in arid and semiarid regions.

5. Conclusions

After determining the physicochemical properties of different types of soil crusts, we found that the main properties which showed significant differences with crust development were aggregate stability, WC, OC and N. Aggregate stability was higher under well-developed BSCs than under physical crusts and poorly-developed BSCs. BSCs increased WC, especially in coarse-textured soils, and OC and N compared to physical crusts. The more developed the BSC stage was, the better the quality of these properties in the crust and its underlying soil. However, the improvement in physicochemical properties of the soil underneath the crusts was especially important in the top soil layer (1 cm of soil under the crust) and diminished in deeper soil (1-5 cm), where differences among crusts were mainly between physical crusts or incipient-cyanobacterial BSCs and well-developed cyanobacterial and lichen BSCs. The improvement in the physicochemical characteristics of BSCs with their development supports our BSC development stage classification. From these findings, we can infer that the presence or type of BSCs could be used as a qualitative indicator of soil surface properties in arid ecosystems. Thus, well-developed BSCs (lichens and mosses) would be indicators of better-quality soils (more aggregate stability, WC, OC and N) than soils dominated by physical crusts or incipient-cyanobacterial BSCs. Therefore, BSCs play a crucial role in water availability, soil stability and reduction of erosion, and represent significant stocks of C and N in arid and semiarid areas, where these sources are important limiting factors.

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Table 1

Table 1. Result of the GLM showing the effect of the predictor factors on physicochemical soil properties. It is only shown the variables for which the crust type or the layer had a significant effect in one of the two sites. p-value for the interaction is only shown when interaction between the two predictor factors at each site (crust type and layer) resulted significant for one property.

	Site factor			El Cautivo		Las Amoladeras	
	F	P		F	P	F	P
Sand	320.72	**0.000**	Crust type	9.65	**0.000**	1.15	0.338
			Layer	0.54	0.472	1.76	0.200
Silt	347.43	**0.000**	Crust type	5.21	**0.007**	3.45	0.054
			Layer	0.00	0.945	6.42	**0.021**
Clay	19.29	**0.000**	Crust type	6.84	**0.002**	1.38	0.278
			Layer	1.25	0.277	2.95	0.103
Aggregate stability	10.15	**0.005**	Crust type	6.99	**0.002**	1.02	0.399
WC at -33kPa	1262.21	**0.000**	Crust type	14.52	**0.000**		
			Layer	3.44	**0.043**		
			Crust type*Layer			4.84	**0.005**
WC at -1500 kPa	16.88	**0.000**	Crust type	2.01	0.130		
			Layer	13.63	**0.000**		
			Crust type*Layer			21.37	**0.000**
OC	11.71	**0.001**	Crust type*Layer	21.64	**0.000**	5.73	**0.001**
N	12.78	**0.001**	Crust type*Layer	4.41	**0.002**	8.30	**0.000**
*Ca	---	---	Crust type			6.09	**0.007**
			Layer			16.38	**0.000**
			Crust type*Layer	6.98	**0.000**		
Mg	1.81	0.187	Crust type	0.45	0.716	0.22	0.803
			Layer	6.62	**0.004**	4.11	**0.028**
K	4.11	**0.050**	Crust type	0.78	0.511	1.39	0.265
			Layer	7.88	**0.001**	9.07	**0.001**
CEC	22.72	**0.000**	Crust type	3.62	**0.022**		
			Layer	6.58	**0.004**		
			Crust type* Layer			5.15	**0.003**
pH	1.56	0.226	Crust type	3.28	**0.038**	0.61	0.563
			Layer	0.74	0.398	0.00	0.972
Electrical conductivity	25.29	**0.000**	Crust type	47.28	**0.000**	0.99	0.404
			Layer	9.77	**0.005**	1.97	0.191
Gypsum content	---	---	Crust type	6.20	**0.018**	---	---

* The GLM for this variable was performed only for each site separately. Due to the high gypsum content under physical crusts and lichen BSCs at El Cautivo, Ca content in these soils was overestimated and therefore, not taken into account in the statistical analysis.

Table 2

Table 2. Mean (± SD, *n*=40) number of drops needed to break down the aggregates (4-5 mm size) under the different crust types, and mean (±SD, *n*=4) percentage of sand, silt and clay in the top and deep soil layers under the crust types, at both study sites. The crust types are: P, physical crust; IC, incipient-cyanobacterial BSC; C, cyanobacteria-dominated BSC; L, lichen-dominated BSC; M, moss-dominated BSC. Differences among crust types in aggregate stability were analysed using planned contrasts. As soil texture significantly varied under the crust types (see table 1) and no planned contrast was hypothesised for this variable, differences in soil texture under the crust types were analysed with the LSD post hoc test. Different letters indicate significant differences within a column.

		Top layer (soil layer 0-1cm underneath the crust)				Deep layer (soil layer 1-5cm underneath the crust)		
Site	Crust type	Aggregate stability*	Sand (%)	Silt (%)	Clay (%)	Sand (%)	Silt (%)	Clay (%)
El Cautivo	P	14.6 ± 7.4	15.4 ± 1.3^{b}	62.8 ± 1.5^{b}	21.8 ± 2.8^{a}	13.9 ± 4.0^{b}	63.8 ± 1.1^{ab}	22.3 ± 3.3^{a}
	IC	16.9 ± 8.2	27.9 ± 8.9^{a}	58.9 ± 5.9^{ab}	13.2 ± 4.2^{b}	32.6 ± 2.9^{a}	54.0 ± 3.8^{c}	13.4 ± 3.6^{b}
	C	42.1 ± 9.1	31.3 ± 9.2^{a}	54.5± 6.0^{a}	14.2 ±3.3 ^{b}	28.1 ± 7.1^{a}	57.2 ± 5.5^{bc}	14.7 ± 1.8^{b}
	L	32.1 ± 9.6	26.4 ± 4.1^{a}	59.7 ± 3.1 ^{ab}	13.9 ± 1.4^{b}	20.3 ± 4.2^{b}	61.9 ±2.8^{b}	17.8 ± 6.5^{ab}
		Aggregate stability	Sand (%)	Silt (%)	Clay (%)	Sand (%)	Silt (%)	Clay (%)
Las Amoladeras	C	49.3 ± 20.2	58.4 ± 3.7^{a}	30.4 ± 4.2^{a}	11.2 ± 2.8^{a}	61.6 ± 2.0^{a}	27.1 ± 3.7^{a}	11.2 ± 3.2^{a}
	L	65.3 ± 15.8	56.5 ± 3.7^{a}	36.6 ± 4.2^{a}	6.9 ± 1.0^{a}	58.8 ± 2.8^{a}	29.4 ± 2.7^{a}	11.8 ± 0.2^{a}
	M	56.6 ± 9.8	60.1 ± 7.3^{a}	29.1 ± 4.3^{a}	10.8 ± 3.3^{a}	62.8 ± 7.9^{a}	26.3 ± 5.9^{a}	10.9 ± 2.0^{a}

* Significant planned contrast (i.e. significant increase in the variable with crust development).

Table 3

Table 3. Mean (±SD, *n*=4) water content (WC) at -33 kPa and-1500 kPa, in the three soil layers per crust type: the crust layer (0.5 cm thickness), the top layer (soil layer 0-1 cm underneath the crust) and the deep layer (soil layer 1-5 cm underneath the crust). The crust-underlying soil (top and deep layers) ratio for WC at -33 kPa and-1500 kPa for each crust type is also shown. The crust types are: P, physical crust; IC, incipient-cyanobacterial BSC; C, cyanobacteria-dominated BSC; L, lichen-dominated BSC; M, moss-dominated BSC.

	Water content at -33 kPa (%)					Water content at -1500 kPa (%)				
	Crust type	Crust*	Top layer*	Deep layer*	Crust-underlying soil ratio	Crust type	Crust	Top layer	Deep layer	Crust-underlying soil ratio
El Cautivo	P	23.2 ± 2.0	23.9 ± 0.8	23.5 ± 0.7	0.99 ± 0.07	P	9.3 ± 0.1	9.3 ± 1.3	12.2 ± 1.1	0.81 ± 0.08
	IC	23.6 ± 4.8	27.3 ± 3.7	24.9 ± 4.3	0.95 ± 0.06	IC	9.4 ± 1.6	8.9 ± 3.4	11.6 ± 1.6	1.05 ± 0.40
	C	28.7 ± 2.2	30.8 ± 3.0	27.8 ± 3.7	1.02 ± 0.08	C	11.2 ± 0.5	9.0 ± 0.7	11.9 ± 2.2	1.01 ± 0.20
	L	27.9 ± 1.7	30.8 ± 0.6	28.9 ± 1.4	0.95 ± 0.08	L	14.0 ± 3.3	7.9 ± 1.0	13.2 ± 1.1	1.14 ± 0.34
		Crust*	Top layer*	Deep layer	Crust-underlying soil ratio		Crust*	Top layer	Deep layer	Crust-underlying soil ratio
Las Amoladeras	C	16.8 ± 2.3	14.6 ± 2.3	14.1 ± 2.1	1.22 ± 0.14	C	8.9 ± 1.9	7.2 ± 1.7	7.0 ± 1.4	1.28 ± 0.05
	L*	25.5 ± 1.9	21.0 ± 1.8	16.5 ± 0.9	1.43 ± 0.07	L*	16.3 ± 2.2	9.5 ± 1.0	8.8 ± 0.8	1.86 ± 0.30
	M*	26.8 ± 4.0	16.8 ± 3.5	14.6 ± 1.1	1.80 ± 0.29	M*	21.9 ± 4.1	8.3 ± 1.5	7.0 ± 1.1	2.80 ± 0.27

*Significant planned contrast. An asterisk (*) next to the name of the soil layer indicates a significant increase in the variable with crust development in that layer. The same symbol next to the name of the crust type indicates a significant decrease in the variable with depth (from the crust towards the 5-cm-deep soil layer) in the specified crust type.

Table 4

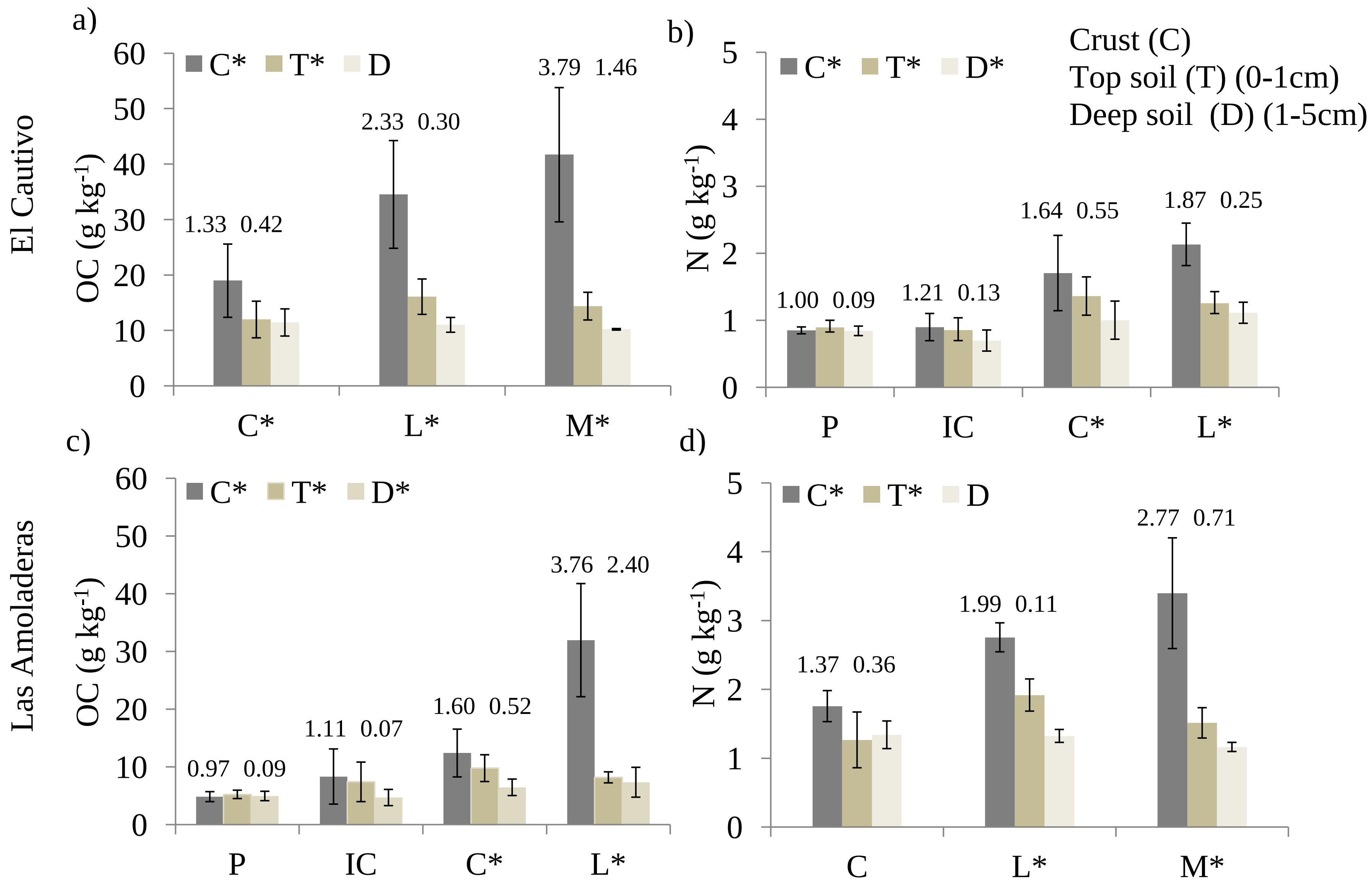
Table 4. Weighted mean (±SD, *n*=4) of calcium carbonate, pH and electrical conductivity, for the top (soil 0-1 cm underneath the crust) and deep (soil 1-5 cm underneath the crust) layers under the different crust types. As the parent material at El Cautivo is gypsiferous mudstone, gypsum was only determined in the soils from this site. The value of gypsum shown corresponds just to the deep layer (soil 1-5 cm underneath the crust), as its content in the top layer was negligible (<1%). The crust types are: P, physical crust; IC, incipient-cyanobacterial BSC; C, cyanobacteria-dominated BSC; L, lichen-dominated BSC; M, moss-dominated BSC.

Site	Crust type	Calcium carbonate (g kg^{-1})	pH	Electrical conductivity (S m^{-1})	Gypsum (g kg^{-1})
El Cautivo	P	226.0 ± 4.1	7.3 ± 0.1	1.94 ± 0.04	53.5 ± 3.8
	IC	245.9 ± 28.7	7.8 ± 0.4	0.49 ± 0.29	1.6 ± 1.1
	C	265.5 ± 17.7	7.6 ± 0.4	0.25 ± 0.07	0.7 ± 0.1
	L	242.2 ± 35.0	7.7 ± 0.3	1.68 ± 0.19	47.8 ± 39.4
Las Amoladeras	C	128.0 ± 9.5	7.9 ± 0.1	0.25 ± 0.04	---
	L	129.7 ± 15.1	7.7 ± 0.2	0.21 ± 0.06	---
	M	140.8 ± 9.7	7.8 ± 0.1	0.16 ± 0.02	---

Figure 1

Fig. 1. Mean (± SD, *n*=4) organic carbon content (OC) (a) and total nitrogen (N) (b) at El Cautivo, and OC (c) and N (d) at Las Amoladeras, in the three soil layers per crust type. Numbers correspond to the crust-underlying soil (including the top and deep soil layers) ratio for each crust type. The crust types are: P, physical crust; IC, incipient-cyanobacterial BSC; C, cyanobacteria-dominated BSC; L, lichen-dominated BSC; M, moss-dominated BSC.

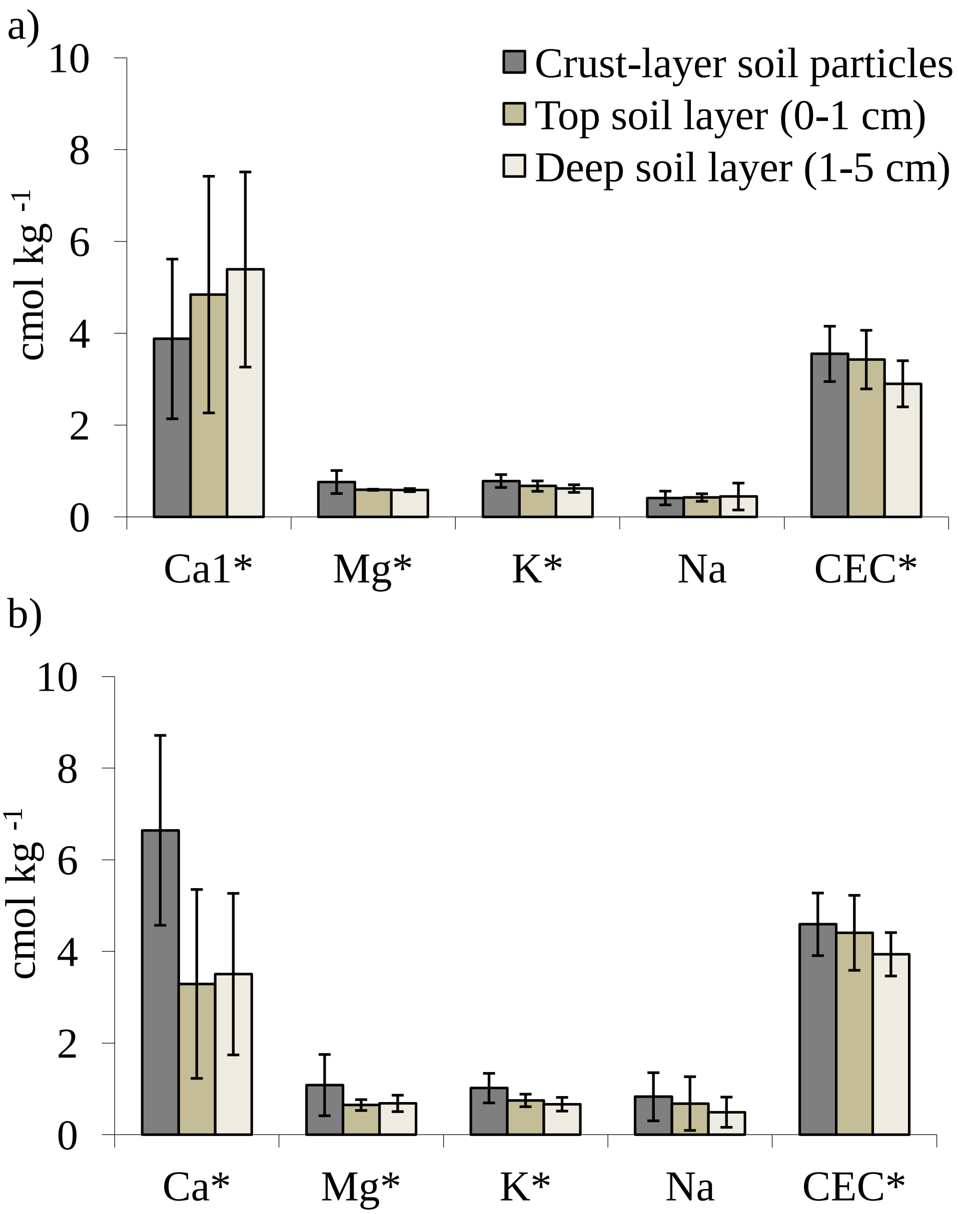
*Significant planned contrast. An asterisk (*) next to the name of the soil layer indicates a significant increase in the variable with crust development in that layer. The same symbol next to the name of the crust type indicates a significant decrease in the variable with depth (from the crust towards the 5-cm-deep soil layer) in the specified crust type.



a)
El Cautivo
OC (g kg-1)
C* T* D
1.33 0.42
2.33 0.30
3.79 1.46
C* L* M*
b)
N (g kg-1)
C* T* D*
Crust (C)
Top soil (T) (0-1cm)
Deep soil (D) (1-5cm)
1.00 0.09
1.21 0.13
1.64 0.55
1.87 0.25
P IC C* L*
c)
Las Amoladeras
OC (g kg-1)
C* T* D*
0.97 0.09
1.11 0.07
1.60 0.52
3.76 2.40
P IC C* L*
d)
N (g kg-1)
C* T* D
1.37 0.36
1.99 0.11
2.77 0.71
C L* M*

Figure 2

Fig. 2. Mean (± SD, *n*=4) Ca, Mg, K, Na and CEC in the three soil layers per crust type, at El Cautivo (a) and Las Amoladeras (b). The crust types are: P, physical crust; IC, incipient-cyanobacterial BSC; C, cyanobacteria-dominated BSC; L, lichen-dominated BSC; M, moss-dominated BSC. Crust type only had a significant effect on CEC, which increased with crust development in all layers at El Cautivo, but only in the crust-layer soil particles at Las Amoladeras. An asterisk (*) next to the variable indicates a significant decrease in the variable with depth (from the crust towards the 5-cm-deep soil layer).



[1]Ca in the crust-layer soil particles in the physical crusts and the top and deep layers under the physical crusts and lichen BSCs was excluded for determination of Ca content in each layer, due to the higher gypsum content in these soils.