UNIVERSIDAD AUTÓNOMA DE SAN LUIS POTOSÍ

FACULTADES DE CIENCIAS QUÍMICAS, INGENIERÍA Y MEDICINA

PROGRAMA MULTIDISCIPLINARIO DE POSGRADO EN
CIENCIAS AMBIENTALES

COMPOSICIÓN, ESTRUCTURA Y DINÁMICA DE LA COSTRA BIOLÓGICA DEL SUELO (CBS) EN UN ECOSISTEMA DE PASTIZAL SEMIÁRIDO

TESIS QUE PARA OBTENER EL GRADO DE

MAESTRÍA EN CIENCIAS AMBIENTALES

PRESENTA:

LIC. LAURA CONCOSTRINA ZUBIRI

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DR. JOSÉ LUIS FLORES FLORES

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SAN LUIS POTOSÍ, S.L.P. **JULIO DE 2010**

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Abstract

Biological soil crusts (BSC) (cyanobacteria, lichens and bryophytes) are key elements in dryland ecosystems. BSC enhance soil stability and fertility, and influence hydrological processes. Inadequate land use such as intensive livestock grazing may severely alter BSC composition, cover and function with potentially negative feedbacks on ecosystem processes. The degree to which communities of BSC may be affected by long-term grazing and/or be able to recover after livestock removal is overall poorly understood.

Considering the important role of BSC in arid ecosystems and severe land degradation associated with grazing, the goal of this research was to examine BSC communities under different grazing regimes (perturbation gradient) and their potential to recover (recovery gradient) after short- mid- and long-term livestock removal in grassland ecosystems of Central Mexico. We addressed two central questions: 1) How does species richness, community composition, species density and cover of BSC change along i) a perturbation gradient with different grazing regimes (moderate continuous (MCG), heavy seasonal (HSG), and heavy continuous grazing HCG) and ii) a grazing-recovery gradient with differently-aged livestock exclosures (short-term exclosure (SGE) of 6 yrs, mid-term exclosure (MGE) of 11 yrs, and long-term exclosure (LGE) of 27 yrs), considering an intra-annual drying and wetting cycle? 2) Do different species/taxa of BSC respond to or affect soil physico-chemical characteristics in grassland types that have been affected by moderate continuous (MCG), heavy seasonal (HSG), or heavy continuous grazing (HCG) when compared to a long-term grazing exclosure (LGE)?

BSC communities consisted of 26 members: a cyanobacteria dominated crust, 21 lichen, three moss, and one liverwort species. As expected, total species richness dropped from 14 species occurring in MCG and HSG sites to 10 species occurring in HCG sites. However, rather unexpectedly species richness did not differ between different differently aged exclosures. While there were no pronounced differences in species number when comparing different exclosures, species composition of BSC communities differed greatly suggesting grazing sensitive species are able to re-establish once livestock is removed, however this is a relative slow process requiring at least 11-27 years. Considering different species compositions and yet rather constant total species numbers and species densities when comparing different sites along gradients, grazing independent, inherent BSC species/taxon-specific (probably through competition and niche sharing mechanisms) controls may most likely have been responsible for shaping BSC community characteristics. Unexpectedly, BSC cover was higher in sites with heavy continuous grazing than with moderate continuous and heavy seasonal grazing. As hypothesized, total BSC cover was higher in the 27-year exclosure than in the 11-year and 6-year exclosures. Overall, cyanobacteria crust dominates the surface covered by BSC communities, however it was negatively affected by the wet season in 2009. As expected, BSC communities contributed greatly to the spatial heterogeneity of soil physico-chemical properties. By comparing specific soil physical and chemical properties associated with certain BSC species and bare soil in different grazing conditions, a complex suite of “BSC response” and “BSC effect” – types emerged suggesting soil heterogeneity in soil texture, soil fertility and chemical characteristics associated with BSC types to be a multi-dimensional phenomenon of diverse biotic and abiotic short- and long-term interaction types, which require further in-depth analysis.

We conclude that BSC species and cover may be highly vulnerable to grazing intensity, especially in the case of lichens and bryophytes. Also, species and taxa of BSC may create specific soil microsites, thereby increasing soil spatial heterogeneity. From a community perspective, organisms of BSC are remarkably resilient after livestock removal

and play a fundamental role in degraded semiarid ecosystems both from a functional and potential restoration perspective.

Keywords: biological soil crusts, perturbation gradient, recovery gradient, semiarid grassland, community structure, soil physico-chemical properties

Resumen

La costra biológica del suelo (CBS) (cianobacterias, líquenes y briófitos) es un elemento clave en los ecosistemas de zonas áridas. La costra biológica del suelo mejora la estabilidad y la fertilidad del suelo, e influye en los procesos hidrológicos. El uso de suelo inadecuado, como pastoreo de ganado intenso puede alterar severamente la composición, cobertura y función de la CBS con una retroalimentación potencial negativa en los procesos del ecosistema. Por otra parte, es limitado el conocimiento sobre (Se conoce poco en general sobre) el grado hasta el cual pueden ser afectadas las comunidades de CBS debido a pastoreo de larga duración y su capacidad de recuperación tras la eliminación del pastoreo.

Considerando el importante papel que la CBS tiene en los ecosistemas áridos y la degradación severa asociada con el pastoreo, el objetivo de esta investigación es examinar las comunidades de CBS bajo diferentes regimenes de pastoreo (gradiente de perturbación) y su recuperación potencial (gradiente de recuperación) con la eliminación del ganado en corto, mediano y largo plazo en los ecosistemas de pastizal del centro de México. En este contexto, enunciamos dos preguntas centrales. 1) ¿Cómo varía la riqueza de especies, la composición de la comunidad, la densidad de especies y la cobertura de la CBS a lo largo de i) un gradiente de perturbación con diferentes regimenes de pastoreo (moderado continuo (MCG, por sus siglas en inglés), intenso estacional (HSG) e intenso continuo (HCG)) y ii) un gradiente de recuperación del pastoreo con exclusiones de ganado de distinta antigüedad (exclusiones de corto plazo con 6 años de antigüedad (SGE, por sus siglas en inglés), de mediano plazo (MGE) con 11 años, y de largo plazo (LGE) con 27 años), considerando un ciclo intra-anual de estación seca y lluviosa? 2) ¿Distintas especies o taxones de CBS responden o afectan las características del suelo en pastizales afectados por pastoreo moderado continuo (MCG), intenso estacional (HSG) o intenso continuo (HCG) respecto a un pastizal con exclusión de ganado de largo plazo?

Las comunidades de BSC estuvieron compuestas por 26 miembros; una costra dominada por cianobacterias, 21 especies de liquen, tres de musgo y una especie de hepática. Como se esperaba, la riqueza total de especies disminuyó de 14 especies en MCG y HSG a 10 especies en el sitio HCG. Sin embargo, al contrario de lo esperado, la riqueza de especies no varió entre los sitos con distintos años de exclusión. Mientras que no existieron diferencias notables en el número de especies entre las exclusiones, la composición de especies sí varió conspicuamente sugiriendo que las especies sensibles al pastoreo pueden reestablecerse una vez que el ganado es excluido. No obstante, este proceso es relativamente lento y toma al menos entre 11 y 27 años. El control ejercido por el efecto específico de las especies de CBS, independientemente del pastoreo, puede ser el responsable de las diferencias en las características de las comunidades de CBS. Esto se refleja a su vez en diferencias en la composición de especies, más que en el número total de especies y la densidad de especies, en los distintos sitios a lo largo de los dos gradientes. Inesperadamente, la cobertura de la CBS fue mayor en sitios con pastoreo intenso continuo respecto a los sitios con pastoreo moderado continúo e intenso estacional. Como se esperaba, la cobertura total de la CBS fue más alta en la exclusión de 27 años que en las de 11 y 6 años de antigüedad. En general, las cianobacterias dominaron las comunidades de CBS en términos de cobertura. Sin embargo, este tipo de costra fue afectada negativamente por la temporada de lluvias en 2009. Como se esperaba, las comunidades de CBS se asocian considerablemente con la heterogeneidad espacial de las propiedades físico-químicas del suelo. Las propiedades físicas y químicas de ciertas especies de CBS comparadas con suelo desnudo en el gradiente de condición del pastizal estudiado, permitió elaborar un esquema de tipos de “respuesta de la CBS” y

“efecto de la CBS”. Esto permite anticipar que la heterogeneidad en las características de textura, químicas y de fertilidad del suelo, asociada con la CBS, es un fenómeno multidimensional producto de interacciones bióticas y abióticas de corto y largo plazo, que requieren de un análisis a mayor detalle.

Palabras clave: costra biológica del suelo, gradiente de perturbación, gradiente de recuperación, pastizal semiárido, estructura de la comunidad, propiedades físico-químicas del suelo.

Chapter I: Introduction

Biological soil crusts (BSC) are a complex association of soil cyanobacteria, microfungi, algae, lichens and mosses forming a biologically active film at the atmosphere - soil interface in most arid and semiarid ecosystems (Belnap, 2003a). They can be considered one of the dominant life - forms in most drylands ecosystems world-wide considering spatial extent (Belnap, 2003b). BSC communities undoubtedly increase biodiversity in dryland ecosystems. Hot and cold deserts of North America hold rich communities of BSC, with more than 50 species of cyanobacteria, more than 50 species of mosses and more than 30 species of lichens (Rivera-Aguilar *et al.* 2006). However, BSC do not only contribute to ecosystem structure and diversity but can be considered keystone taxon groups as they participate in almost all processes and functioning of dryland ecosytems (Maestre *et al.* 2005) and often beyond to what their spatial distribution and biomass content would suggest.

BSC play fundamental roles in ecosystems: they promote soil stabilization and protection against wind and water erosion at the soil surface (Belnap, 2003a), enhance water infiltration and retention (Belnap, 2006), increase organic carbon and nitrogen input (Housman *et al.* 2007), and contribute to sediment and dust trapping with their rugose surface structure (Reynolds *et al.* 2001). Both BSC structures, such as filaments in cyanobacteria, thalli and rhizines in soil lichens, and rhizoids in bryophytes, and organic exudates (e.g. polysaccharides) help protect soil physical structure and enhance soil stability (Eldridge and Kinnell 1997; Evans and Johansen 1999; Eldridge and Leys 2003; Bowker *et al.* 2008). Photosynthetic organisms forming BSC can fix between 0.4 - 2.3 (cyanobacteria dominated crust) and 12 - 37 gC/m^2/year (lichen crust) and 0.1 (cyanobacterial crust) to 1 gN/m^2/year (cyanolichen dominated crust) (Belnap, 2003b). Cyanobacteria and lichen-dominated crusts can also reduce potential nitrogen losses through leaching into surface soil (Hawkes, 2004; Veluci *et al.* 2006). Well-developed BSC cover can compensate low CO_2 uptake by sparse vascular vegetation (Wilske *et al.* 2008). Rhizines of BSC organisms, tiny anchorage structures, modify microporosity, which in turn can increase water infiltration (Belnap, 2006). Roughness of BSC enhance water retention time and surface area for infiltration (Belnap, 2006). Mosses, cyanobacteria and lichens absorb and retain water on soil surface, thereby reducing runoff; although more detailed studies of a wider variety of different BSC types need to be conducted before generalizations can be made (Eldridge and Rosentreter, 1999). Biological soil crusts can

act as a sediment trap collecting aeolian clays and silts, increasing soil absorptivity (Belnap, 2006)

In grazing ecosystems, BSC are primarily subject to mechanical disturbance and burial due to livestock trampling, soil erosion and sediment deposition. These kinds of disturbances have serious impact on BSC cover and species richness (Belnap and Eldridge, 2001) but also on the functioning of BSC (Belnap 1996). More than 50 percent of all published BSC related studies center on BSC communities in North America (ISI Web of Knowledge, 2009). Furthermore, most of the studies conducted in this region were carried out in the Desert South West and Great Basin (Muscha and Hild, 2006). These numbers highlight the necessity of promoting BSC research in semi-arid ecosystems, especially in Latin America region, where basically nothing is know on BSC species richness, composition and functional role in semiarid ecosystems (Rivera-Aguilar, 2006; Aguilar *et al.* 2009).

The aim of this study was to contribute to a better understanding of BSC community responses to grazing activity and in relation to soil physico-chemical properties, in a grazed semiarid ecosystem of Central Mexico, where BSC form abundant and highly diverse communities and overgrazing is a driving force of land degradation.

In Chapter II, we focused on those atributtes that best describe BSC communities: species composition, species richness, species density and cover, and BSC responses to grazing activity considering an intra-annual drying and wetting cycle.

In Chapter III, we investigated potential species/taxon-specific responses and/or effects that BSC species may show in relation to soil physico-chemical properties.

In Chapter IV, we synthesize the major results obtained in the present study and conclude, by highlighting that rich and diverse communities of BSC are important organisms in the grassland ecosystems of Central Mexico that contribute to spatial heterogeneity in soil properties, specially in soil fertility.

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Chapter II: Composition, structure and spatio-temporal dynamics of BSC in a semiarid grassland

a. Introduction

Overgrazing by livestock is the principal driver of land degradation in arid and semi-arid ecosystems in Mexico (Manzano *et al.* 2000). Livestock influence soil and vegetation characteristics, including communities of biological soil crusts (BSC) covering wide open interspaces between perennial vegetation (Rogers and Lange, 1971; Anderson, 1994; Aguilar *et al.* 2009). Grazing impact by trampling may lead to a change in BSC composition and reduce its cover and species richness as a consequence of disruption of soil aggregates formed by BSC, soil erosion and sediment deposition (Belnap, 1995; Belnap, 2003a; Li *et al.* 2008). However, impact of livestock grazing on BSC composition and community structure vary depending on disturbance type, intensity and timing (Belnap and Eldridge, 2001). Long-term heavy grazing and extended periods of drought have a strong negative effect on BSC community attributes (Brotherson *et al.* 1983, reviewed by Warren and Eldridge, 2001). Also, depending on the functional and morphological characteristics of BSC, vulnerability to trampling decreases in descending order: mosses < crustrose lichens < cyanobacteria (Belnap and Eldridge, 2001; Muscha and Hild, 2006; Belnap *et al.* 2006). While livestock pressure creates vegetation free interspaces and thus increases potential habitat for BSC communities (Eldridge *et al.* 2000), grazing may also have considerably negative impacts on BSC communities (Brotherson *et al.* 1983, Aguilar *et al.* 2009) yet does not always eliminate all BSC lichen and moss cover but shift community composition to more grazing tolerant and/or resistant BSC groups (Aguilar *et al.* 2009).

Natural recovery rates of BSC from livestock grazing can be monitored in long-term livestock exclosures (Anderson, *et al.* 1982). Time estimates for visually observable recovery from different disturbance types may range between 5 and 100 years (Harper and Marble, 1988) but they may last even longer (Belnap, 1993), allowing principally the re-establishment of species richness and cover of lichens and mosses but also that of cyanobacteria (Brotherson *et al.* 1983). Since BSC are only metabolically active when wet, BSC recovery depends not only on the availability of inoculation material but also on the long-term precipitation regime (Belnap and Eldridge, 2001). Recovery of BSC cover and species richness from grazing in semiarid climates varies with exclosure age, BSC morphological group and water availability (Muscha and Hild 2006, Aguilar *et al.* 2009).

In addition to external disturbance factors, internal processes associated with resource competition and community dynamics at the species level may lead to the dominance and composition of different BSC communites (Hawkes and Flechtner, 2002). Recent studies have shown that BSC communities are structured by competitive interactions (Maestre, 2008) and that depending on the scale of study and nature of biotic and abiotic stress types, co-occurrence patterns of BSC species may shift (Maestre *et al.* 2009).

Also, BSC communities may show strong differences in their attributes, especially cover, when grazing interacts with dry and wet cycles (Williams *et al.* 2008). While there are many studies, examining either grazing or drought effects on BSC cover and/or composition, few studies have evaluated simultaneously i) long-term BSC community responses to both different livestock grazing intensities and livestock removal, and ii) short-term BSC community responses to an interseasonal dry-wet cycle.

The aim of our study was to investigate the response of the local BSC species pool of semiarid grasslands in forming community types along two contrasting gradients: perturbation of and recovery from livestock grazing, and in response to a seasonal wetting and drying cycle. We asked the following questions: 1) Are BSC communities formed by different species and functional groups along the perturbation and recovery gradients? 2) Do species richness and species density (average number of species per unit area) of BSC communities decrease with grazing intensity and increase with increasing time of livestock removal? 3) Do total BSC cover and functional group cover differ along the contrasting gradients, and in response to a seasonal wetting and drying cycle?

To address these questions, we determined BSC species composition, and compared total species richness and species density of BSC communities present in the interspaces of sites exposed to varying grazing intensities (moderate continuous, heavy seasonal, and heavy continuous grazing) and sites protected from grazing using three diffently aged livestock exclosures (6, 11 and 27 years). We also compared total cover and functional group cover of BSC communities along these gradients and in reponse to a seasonal wetting and drying cycle.

We expected that BSC communities in semiarid grasslands of Central Mexico would be mainly influenced by grazing intensity and livestock removal and overall less by seasonal wetting and drying. We expected BSC community composition to differ across different sites within and between gradients. Also, we hypothesized that increasing grazing intensity will lead to both an overall decline in BSC species richness, because less BSC species are resistant to mechanical impact, and to a lower average species density

provided an increase in mechanical stress caused by livestock trampling overrides interspecific and inter-taxon competition at the interspace scale. In contrast, with increasing age of livestock exclosure BSC species richness and density will increase. Finally, we hypothesized BSC total cover may decrease along the perturbation gradient and increase along the recovery gradient, because grazing intensity affects primarly BSC crust cover. We expected BSC group-specific responses along both gradients. Relative cover of cyanobacteria will be rather consistent along the perturbation gradient, due to their resistance to mechanical impact, while cover of lichens and bryophytes are most vulnerable to mechanical impact, and thus, cover of the latter groups may decrease with increasing grazing intensity. Since bryophytes prefer and are favored by higher soil humidity, we expected bryophyte cover to increase with increasing exclosure age, since soil water retention will be increasingly higher with increasing vegetation cover. Cover of cyanobacteria and bryophytes may decrease and increase, respectively, when comparing dry and wet season, while lichen cover is expected to show no differences between seasons.

This study will contribute to our knowledge on short-term and long-term spatio-temporal responses of BSC to contrasting environmental conditions caused by land management in a semiarid grassland ecosystem of Central Mexico, where BSC communities are important elements and contribute fundamentally to ecosystem diversity and functioning.

b. Methods

i. Study site

The study area is located in the physiographic subprovince Llanos de Ojuelos (21º 49' N, 101º 37' W, 2200 m a.s.l.), Jalisco, Mexico at the southernmost part of the North American graminetum (Aguado-Santacruz and García-Moya, 1998). The climate is semiarid with mean annual precipitation of 450 mm, and mean annual temperature between 12 and 18 ℃. The main rainfall season occu rs between june and september. The topography is characterized by valleys and gentle rolling rhyolitic hills. Soils are haplic xerosols associated with lithosols and eutric planosols, and haplic phaeozems associated with lithosols, and present only in two horizons at 0-25 cm and 25-40 cm depth. Soil texture varies from silty clay to sandy loam (COTECOCA, 1979). The vegetation is a native grassland with *Bouteloua gracilis* as the dominant grass species (Aguado, 1993).

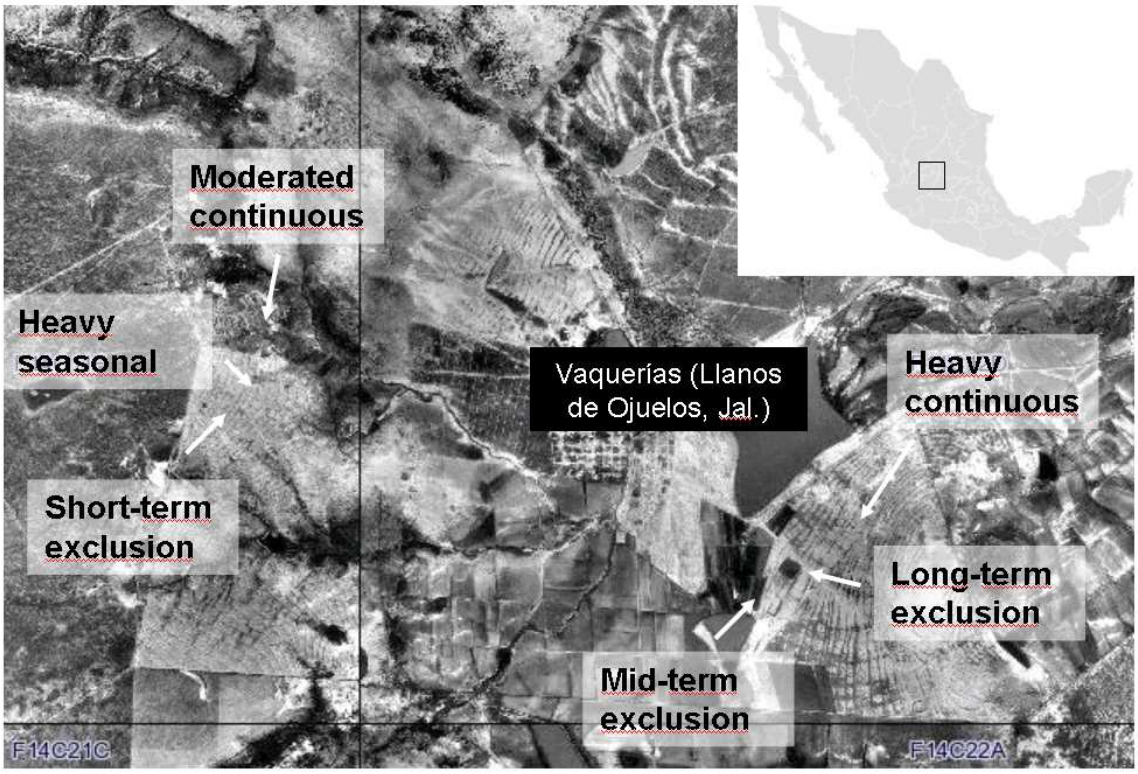


Fig. 2.1: Location of study sites in Vaquerías, Jalisco (Jal.)

Site	Dominant species	Plant cover (%)	Above ground productivity (kg dry matter/ha)	Coordinates
Pertubation gradient				
Moderate continuous grazing (MCG)	*Bouteloua gracilis, Muhlenbergia rigida*	25-30	1200	21°46' 18.493" N 101°40' 24.656" W
Heavy seasonal grazing (HSG)	*Bouteloua gracilis*	15-20	350	21°46' 10.815" N 101°40' 27.192" W
Heavy continous grazing (HCG)	*Bouteloua gracilis, Isocoma veneta, Asphodelus fistulosus*	5-10	<200	21°45' 36.36" N 101°38' 20.58" W
Recovery gradient				
Short-term grazing exclosure (SGE)	*Bouteloua gracilis*	20-25	350	21°46' 10.815" N 101°40' 27.192" W
Mid-term grazing exclosure (MGE)	*Bouteloua gracilis*	30-35		21°45' 32.42" N 101°38' 32.29" W
Long-term grazing exclosure (LGE)	*Bouteloua gracilis*	35-40	800-1200	21°45' 32.42" N 101°38' 32.29" W

Table 2.1: Characteristics of study sites.

We located the grazing and recovery gradients, each consisting of three different sites, in the natural grassland region of Vaquerias, Jalisco (Jal) in central Mexico (Table 2.1, Fig. 2.1) on private and communal (*ejido*) lands. For the perturbation gradient, sites included, 1)

“moderate continuous grazing” (MCG) with moderate grazing for over 300 years, on private land, 2) “heavy seasonal grazing” (HSG) with heavy grazing for over 70 years, during rainy season, and 3) “heavy continuous grazing” (HCG) with heavy year-around grazing on communal land, for over 70 years. For the recovery gradient, sites included a: 1) “short-term grazing exclosure” (SGE) with 6 year cattle exclusion, 2) “mid-term grazing exclosure” (MGE) with 11 year cattle exclosusion, and 3) “long-term grazing exclosure” (LGE) with 27 year cattle exclusion. Moderate and heavy grazing have lead to heavily compacted soils, reduced plant cover and large areas of interspaces without plant cover colonized by BSC (Table 2.1). As stated previously, the different long-term grazing regimes established as a consequence of different land tenure (communal land and private land and remoteness from village). Grazing exclosures were established by the Campo Experimental of the Instituto Nacional de Investigaciones Forestales, Agricolas y Pecuarias (INIFAP) in Vaquerias, Jal, Mexico.

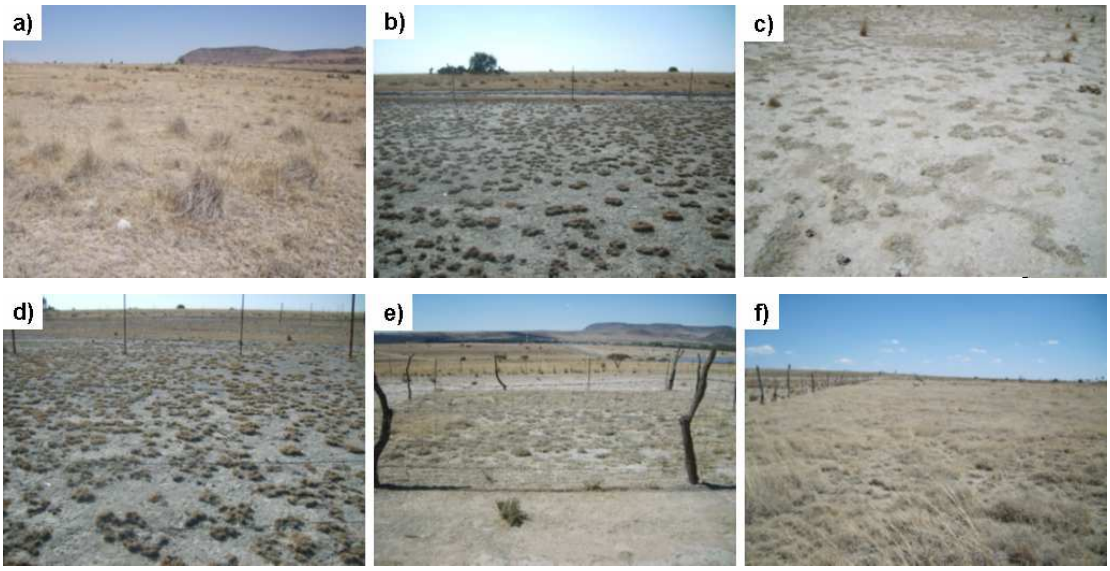


Fig. 2.2: Study sites: a) “Moderate continuous grazing” (MCG), b) “Heavy seasonal grazing” (HSG), c) “Heavy continuous grazing” (HCG), d) “Short-term grazing exclosure” (SGE), e) “Mid-term grazing exclosure” (MGE), and f) “Long-term grazing exclosure” (LGE).

ii. Monitoring and sampling procedure

In March 2009, we randomly selected four “grazed plots” (10 x 10 m) within a homogeneous 1-ha area for each of the three grazing regimes (moderate continuous grazing, heavy seasonal grazing and heavy continuous grazing). In the same study area,

INIFAP established four short-term (10 x 10 m), four medium-term (10 x 10 m) and one long-term (1-ha) grazing exclosures 6, 11 and 27 years ago, respectively serving as the "exclosure plots". We located a total of 288 (12 per plot, 48 per grazing or exclosure level) 25 x 25 cm permanent quadrats, scattered over the defined study sites on plant interspaces. Dimension of quadrats (25 x 25 cm) was determined based on the mean minimum interspace size considering both grazing and recovery gradient. Quadrats were placed non-randomly but judged by a minimum distance between quadrats of 0.5 – 1m, in vegetation-free interspaces with well-developed BSC cover, in order to capture BSC community attributes along both gradients (Maestre *et al.* 2008). Quadrat observations were made during the dry season in March 2009 and after the rain season in December 2009. To analyze BSC attributes (species richness, species density and BSC cover), BSC field identification and photographic digital recording were combined for each quadrat.

iii. BSC identification

We identified a total of 26 species and/or taxon groups of BSC. They consisted of a cyanobacteria dominated crust, 21 crustose and squamulose lichen species, three moss species, and one liverwort species. Of these 26 species/taxa, 21 occurred in the quadrats. All lichen and bryophytes were identified to the species level when possible, or assigned to different morphological groups, when field identification was not possible. Hereafter, we refer to all BSC members as "species".

Voucher specimens were collected of each BSC species for microscopical and microchemical analysis and are stored in the Laboratory of Ecology and Global Environmental Change at the Instituto Potosino de Investigación Científica y Tecnológica (IPICYT), San Luis Potosi, Mexico. Identifications of the lichen species were done using the identification keys of Lichen Flora of the Greater Sonora Desert Region (Arizona State Lichen Herbarium, 2002; 2004; 2007).

iv. Determination and analysis of BSC composition, species richness, species density and BSC cover

Field sampling.- For each of the 288 permanent quadrats (identified by colored nails), a digital photograph (Fuji FinePix A60, 12 megapixels) was taken in March and December 2009. Species presence was recorded for each quadrat and site for later comparisons in digital fotos. Each photograph was taken at a fixed distance (30 cm) from the ground and parallel to the surface.

Image processing.- Each digital foto was downloaded from the camera and converted from .jpg to .tif format. In each of the 576 (288 fotos in dry and wet season) digital images, the area of each BSC species was visually delimited with the Software Gimp 2.4 (Natterer *et al.* 2010). Area of each BSC species was determined with the image processing software SigmaScan Pro 5 (SPSS Inc., 1998). For comparisons of BSC cover between the two dates, geometric corrections were applied to second date images (ESRI, 2009).

Composition of BSC communities of each site was determined by species presence in each site of the two gradients. Total species richness of BSC for each grazing and recovery site was estimated with sample-based rarefaction analyses (EstimateS; Colwell, 2009), because rare species may not have been detected in sampling area. BSC species density, i.e. number of BSC species per quadrat, was calculated as the number of species present per sampling quadrat for each site along the two gradients. Results of species composition, species richness and species density are presented for March 2009 only, because it is unlikely that species richness and density will change between seasons of the same year.

BSC cover was calculated in percentage for total cover occupied by a certain BSC species and for each BSC functional (taxon) group in each permanent quadrats, both in the dry and the wet season.

v. Statistical analysis

To determine total species richness for each site along the perturbation and recovery gradients sample-based rarefactions were performed with the program Estimates version 8.2 (Colwell, 2009). Total species richness was estimated for the dry season only, because it is unlikely that species richness and density will change between seasons of the same year.

To analyze species density, we conducted a one-way ANOVA with gradient level as a fixed factor. This analysis was done for dry season data only, and separately for the perturbation gradient (with MCG, HSG, HCG) and for the recovery gradient (with LGE, MGE, SGE). *Post-hoc* mean comparisons were made with Tukey´s test. Four GLM procedures were run to compare total BSC cover (%) and cover of three functional groups (cyanobacteria, lichen and bryophytes) within gradient sites and considering dry and wet season. In this analysis, the fixed effects were season and gradient level nested within season (N=24). For species density (species number per unit area), total cover and by taxon, data of 12 quadrats were averaged for each of the four plots within a gradient site

(N=4). After applying Wilks' test for normality of total cover and of the different taxon groups, it was necessary to apply a log transformation to achieve normality and variance homogeneity of the data. Multiple comparisons of species density, total BSC cover and functional group cover were performed with Tukey´s test to examine between season and between gradient level (within seasons) mean differences. All ANOVAs and GLM were run with Minitab 14 (Minitab Inc., 2008).

c. Results

i. BSC species composition and community structure

BSC composition

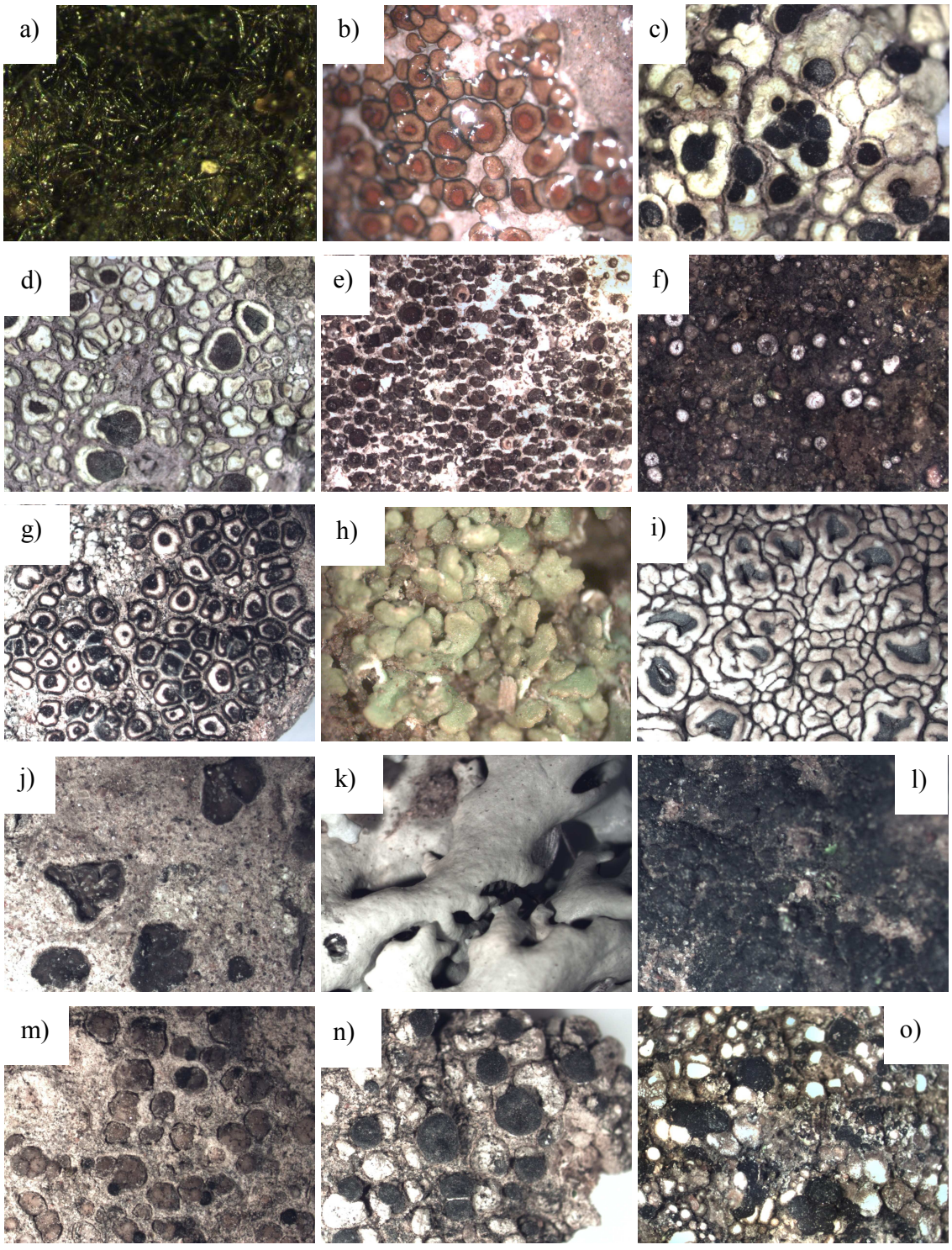
The species pool of BSC along the perturbation and recovery gradients consisted of cyanobacteria crust, 21 lichen species, 3 moss species and one liverwort species (Table 2.2; Fig. 2.3 and 2.4). Cyanobacteria were present in all study sites (Table 2.2); this group of BSC covers up to 30% of the interspaces in the perturbation gradient and 60% of the interspaces in the recovery gradient (Fig. 2.4).

Lichen crust includes the highest number of species in BSC communities at the study area (Table 2.2) and covers around 5% of interspaces in the perturbation gradient and up to 9% in the recovery gradient (Fig. 2.4). *Acarospora* was the dominant lichen genus (Table 2.2). *Acarospora scabrida*, *Acarospora socialis* and *Diploschistes diacapsis* occurred in all study sites. *Acarospora obpallens* and *Acarospora* spp., *Endocarpon pusillum*, and *Lecidella* spp. were present in all sampling quadrats, except in those of the LGE site. *Cladonia* spp., lichen spp. 2, and *Placopyrenium* spp. were only found in MCG and LGE sites. *Acarospora thelococcoides*, *Lecania* spp. and *Psora icterica* were exclusively present in the MCG site. Also, *Heteroplacidium aff. podolepsis* and *Lecidea* spp. 2 were only found in the LGE site.

Bryophytes associated with BSC communities are constitued of three moss species and one liverwort species. This group contributes the least to BSC cover in both gradients (Table 2.2; Fig. 2.4). Moss spp. 1 was present in all study sites, except HCG. Moss spp. 2 was found in all study sites. Moss spp. 3 was exclusively present in MCG site. Liverwort spp. was only found in the MCG site of the grazing gradient, and in the LGE and MGE sites of the recovery gradient.

	Perturbation gradient			Recovery gradient		
Site	MCG	HSG	HCG	SGE	MGE	LGE
Cyanobacteria						
Cyanobacteria	+	+	+	+	+	+
Lichen						
Acarospora scabrida	+	+	+	+	+	+
Acarospora schleicheri	-	+	-	+	-	-
Acarospora socialis	+	+	+	+	+	+
Acarospora obpallens	+	+	+	+	+	-
Acarospora thelococcoides	¤	-	-	-	-	-
Acarospora spp.	+	+	+	+	+	-
Cladonia spp.	¤	-	-	-	-	+
Diploschistes diacapsis	+	+	¤	+	+	+
Endocarpon pusillum	+	+	+	+	+	-
Heterodermia tropica	-	¤	-	¤	-	-
Heteroplacidium aff. podolepsis	-	-	-	-	-	¤
Lecania spp.	¤	-	-	-	-	-
Lecidea cruciaria	+	+	+	+	-	-
Lecidea spp. 1	-	-	-	-	-	+
Lecidea spp. 2	-	+	+	+	+	-
Lecidella spp.	+	+	+	+	+	-
Lichen spp. 1	¤	-	-	-	-	+
Lichen spp. 2	¤	-	-	-	-	+
Placidium lacinulatum	-	-	-	-	-	+
Placopyrenium spp.	+	-	-	-	-	+
Psora icterica	¤	-	-	-	-	-
Total lichen species	15	11	9	11	8	10
Bryophyte						
Moss spp. 1	+	+	-	+	+	+
Moss spp. 2	+	+	+	+	+	+
Moss spp. 3	+	-	-	-	-	-
Liverwort spp.	+	-	-	-	+	+
Total bryophyte species	4	2	1	2	3	3
Site total	20	14	11	14	12	14

Table 2.2: Presence (+) / absence (-) matrix of cyanobacteria, lichen and moss species within each of the three sites of the perturbation and recovery gradients in semiarid grasslands in Vaquerias, Jal. Mexico. The "¤" symbol indicates presence of the species outside of the 48 quadrats for a given site. Sites are described in Table 2.1.


a)
b)
c)
d)
e)
f)
g)
h)
i)
j)
k)
l)
m)
n)
o)

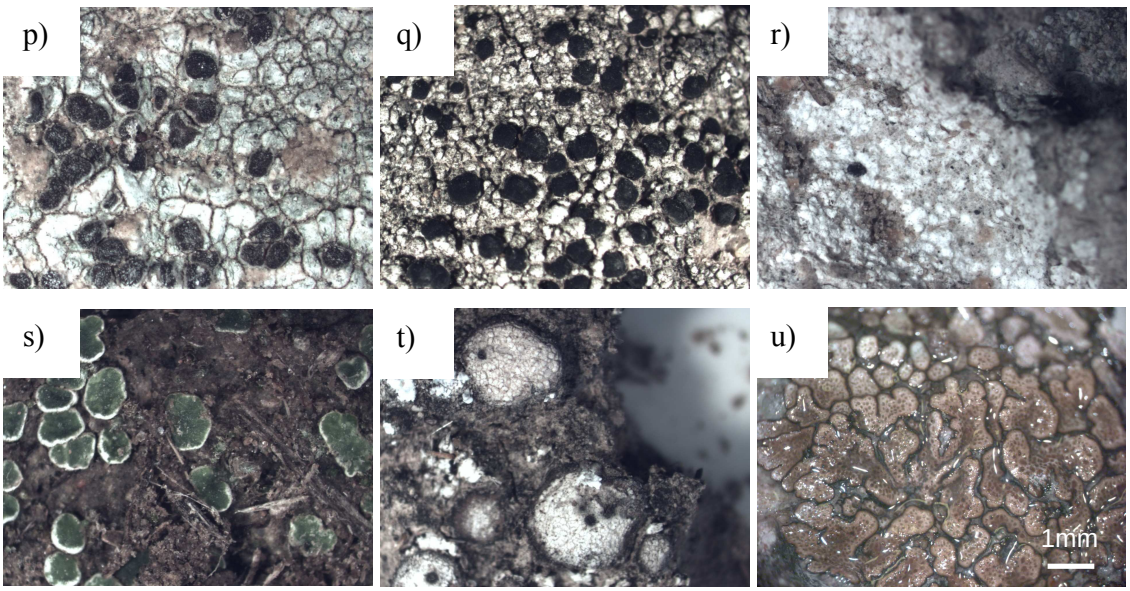


Fig. 2.3: Photographs of (a) Cyanobacteria, (b) *Acarospora scabrida*, (c) *Acarospora schleicheri*, (d) *Acarospora socialis*, (e) *Acarospora obpallens*, (f) *Acarospora thelococcoides*, (g) *Acarospora* spp., (h) *Cladonia* spp., (i) *Diploschistes diacapsis*, (j) *Endocarpon pusillum*, (k) *Heterodermia tropica*, (l) *Heteroplacidium aff. podolepsis*, (m) *Lecania* spp., (n) *Lecidea cruciaria*, (o) *Lecidea* spp. 1, (p) *Lecidea* spp. 2, (q) *Lecidella* spp., (r) Lichen spp. 1, (s) Lichen spp. 2, (t) *Placidium lacinulatum*, (u) *Placopyrenium* spp.

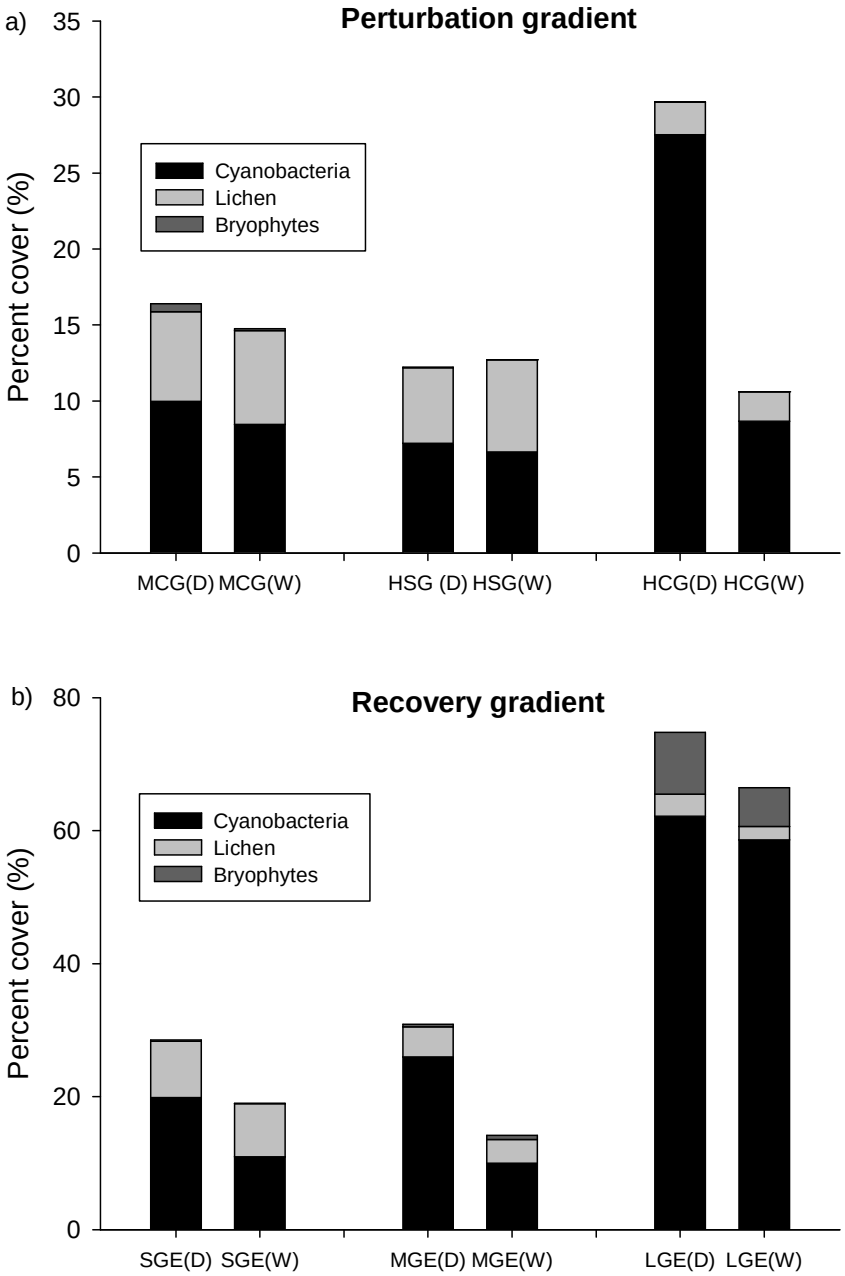


Fig. 2.4. Mean cover (%) of three functional/taxon groups (cyanobacteria, lichen and bryophytes) (a) along the perturbation gradient (MCG = moderate continuous grazing, HSG = heavy seasonal grazing, HCG = heavy continuous grazing), and (b) along the recovery gradient (SGE = short-term grazing exclosure, MGE = Mid-term grazing exclosure, LGE = long-term grazing exclosure), in the dry (“D) and the wet (“W”) season, in six sites of grasslands in Vaquerias, Jalisco, Mexico

Species richness

Grazing gradient.- Estimated total species richness was 14, 13, and 10 in MCG, HSG, and HCG sites, respectively (Fig. 2.5). Species richness did not differ significantly between MCG and HSG sites, however it was significantly higher in these sites than in HCG site (Fig. 2.5).

Recovery gradient.- Total species richness was 13, 12, and 13 in SGE, MGE, and LGE sites, respectively, and did not differ significantly among sites along this gradient (Fig. 2.5).

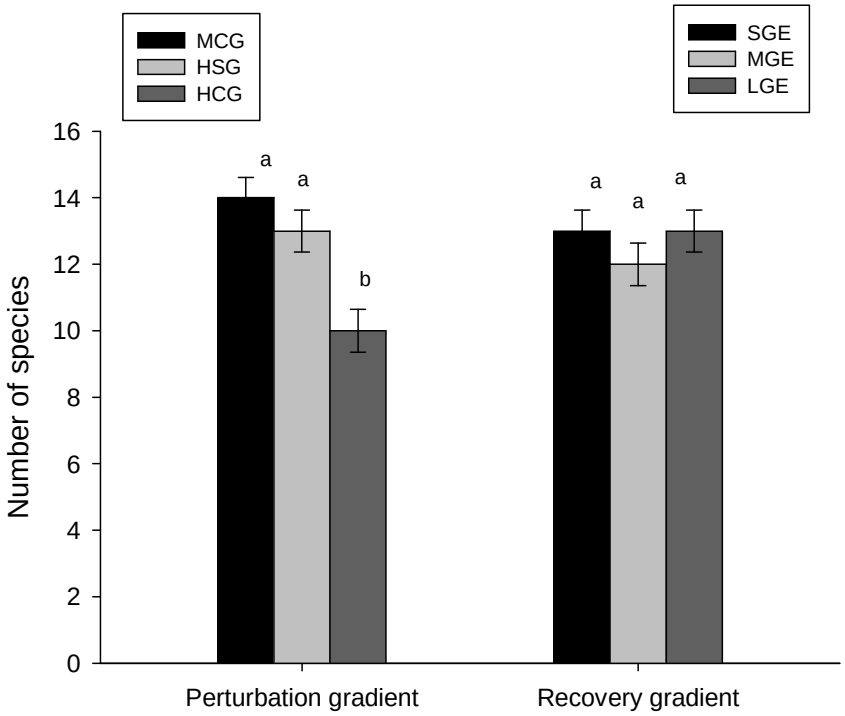


Fig. 2.5: Estimated values (± 95% confidence intervals) of total species richness at the asymptote of rarefaction curves, for different sites (gradient levels) along the perturbation (left side) and recovery (right side) gradients in March 2009. MCG = moderate continuous grazing, HSG = heavy seasonal grazing, HCG = heavy continuous grazing, SGE = short-term grazing exclosure, MGE = mid-term grazing exclosure, LGE = long-term grazing exclosure.

Species density

Mean number of species per unit area (quadrat) differed significantly among sites along the perturbation and recovery gradients (Table 2.3).

Perturbation gradient.- Species density was significantly higher in the HSG site than in MCG and HCG sites, in the dry season (Fig. 2.6).

Recovery gradient.- Species density was significantly higher in the SGE site than in MGE and LGE sites, which showed no differences, in the dry season (Fig. 2.6).

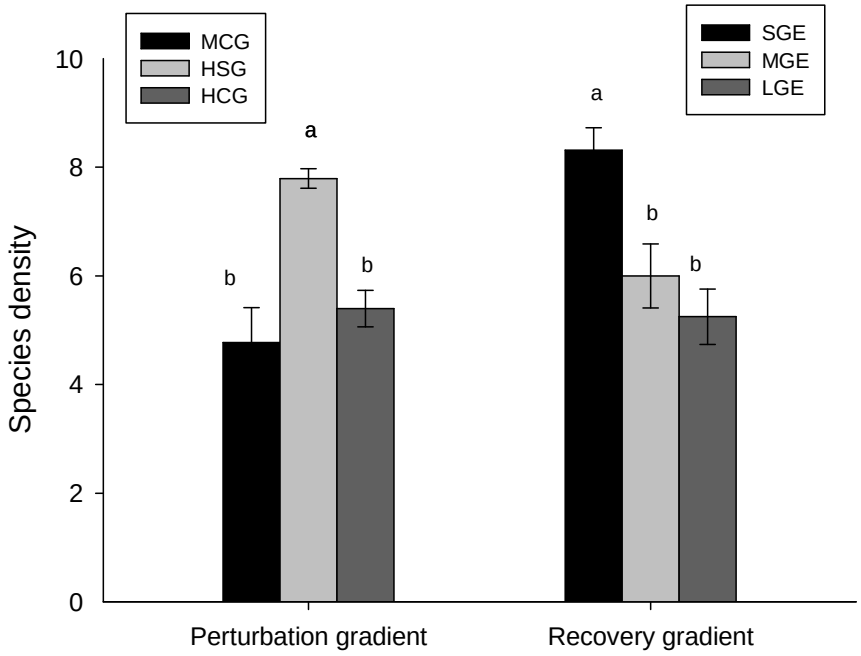


Fig. 2.6. Mean species density (mean species number per quadrat) (± 1 SE) along the perturbation (left side) and recovery (right side) gradients, in the dry season. Different letters above bars indicate significant differences between sites (gradient levels) within a gradient at the $P < 0.05$. (See text for acronyms of site gradients).

ii. Spatial and seasonal dynamics of BSC cover

Total crust cover

Grazing gradient.- There was no significant effect of season within each site. Total BSC cover was similar in all sites along the perturbation gradient both in dry and wet season (Table 2.3; Fig. 2.7).

Recovery gradient.- Total BSC cover was considerably higher in the LGE site compared with SGE and MGE sites in dry and wet season. A seasonal response occurred only in the MGE site, where BSC cover was significantly lower in the wet season than in dry season (Table 2.3; Fig. 2.7).

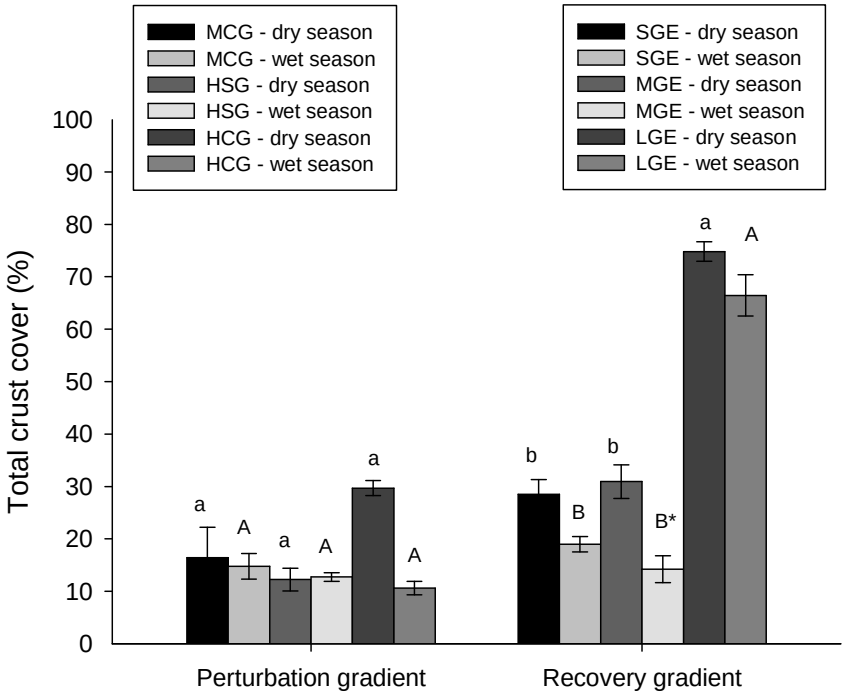


Fig. 2.7. Mean (± 1SE) total BSC cover (%) along the perturbation (left side) and recovery (right side) gradients, in dry and wet season. Different letters above bars indicate significant differences ($P < 0.05$) between sites (gradient levels) within season (small letters for dry season and capital letters for wet season) and gradient. Within site comparisons between season: asterisks indicate significant differences between wet and dry season for a particular site (gradient level) at $P < 0.05$. (See text for acronyms of site gradients).

BSC functional/taxon group cover

1. Cyanobacteria cover

Season and gradient level had a significant effect on cyanobacteria cover in both gradients (Table 2.3).

Grazing gradient.- Cyanobacteria cover was significantly higher in the HCG site compared with MCG and HSG sites in the dry season (Fig. 2.8); however, no significant differences existed among sites along the perturbation gradient in the wet season (Fig. 2.8). Comparing dry and wet season values in each site, cyanobacteria cover was significantly lower in the wet than in the dry season in the HCG site (Fig. 2.8).

Recovery gradient.- Cyanobacteria cover was significantly higher in the LGE site than in the SGE and MGE sites (dry and wet season) (Fig. 2.8). Comparing dry and wet season

values in each site, cyanobacteria cover was significantly lower in the wet season compared to the dry season in the MGE site (Fig. 2.8).

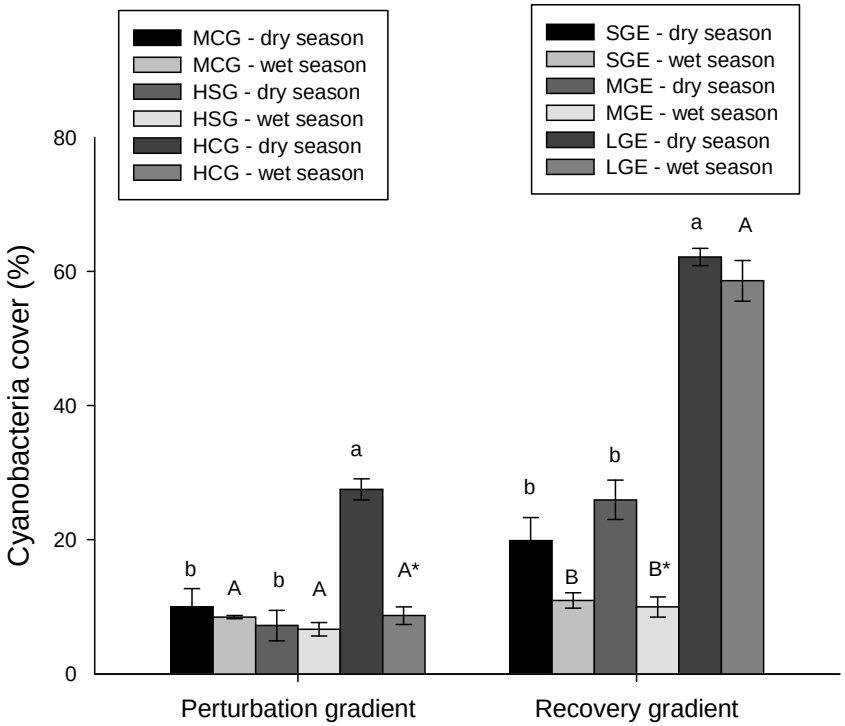


Fig. 2.8. Mean (± 1SE) cover (%) of cyanobacteria along the perturbation (left side) and recovery (right side) gradients, in dry season and wet season. Different letters above bars indicate significant differences ($P < 0.05$) between sites (gradient levels) within season (small letters for dry season and capital letters for wet season) and within each gradient. Within site comparison between season: asterisks indicate significant differences between wet and dry season for a particular site (gradient level) at $P < 0.05$. (See text for acronyms of site gradients).

2. Lichen cover

Season and site (gradient level) did not affect lichen cover in the perturbation gradient. However, site had a significant effect on lichen cover in the recovery gradient, while season did not (Table 2.3).

Grazing gradient.- Lichen cover did not differ between sites along the perturbation gradient (in dry and wet season) and there was no significant effect of season within a site (Fig. 2.9).

Recovery gradient.- Lichen cover did not differ between sites along the recovery gradient in the dry season (Fig. 2.9), however it was significantly lower in the LGE site compared with the SGE site in the wet season (Fig. 2.9). There was no significant effect of season for any of the sites (Table 2.3).

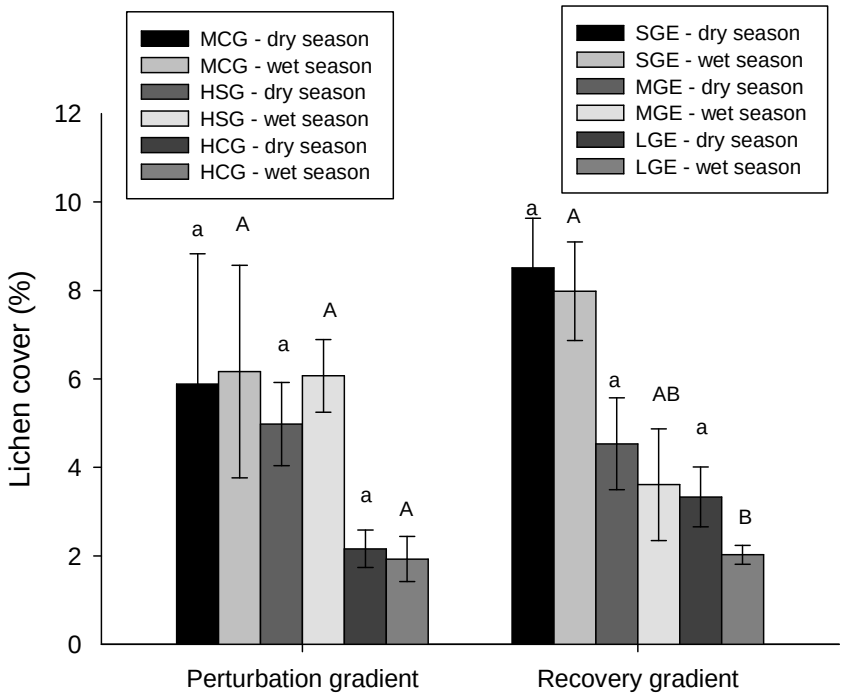


Fig. 2.9. Mean (± 1SE) lichen cover (%) along the perturbation (left side) and recovery (right side) gradients in dry and wet season. Different letters above bars indicate significant differences ($P < 0.05$) between sites (gradient levels) within season (small letters for dry season and capital letters for wet season) within each gradient. Within site comparison between seasons: asterisks indicate significant differences between wet and dry season for a particular site (gradient level) at $P < 0.05$. (See text for acronyms of site gradients).

3. Bryophyte cover

Season had no significant effect on bryophyte cover along the perturbation and recovery gradients, whereas gradient level had a significant effect on bryophyte cover; also there was a significant season by site interaction for the grazing gradient (Table 2.3).

Grazing gradient.- Bryophyte cover was significantly higher in MCG site compared with HSG and HCG sites, in the dry season (Fig. 2.10). In the wet season, bryophyte cover was

significantly higher in MCG site compared with HSG site, while it did not differ from HCG site (Fig. 2.10). There was no significant effect of season in any of the sites.

Recovery gradient.- Bryophyte cover was higher in LGE site than in SGE and MGE sites in the dry season, while it was higher both in LGE and MGE sites compared with SGE site in the wet season (Fig. 2.10). There were no significant effects of season within a each site (Table 2.3).

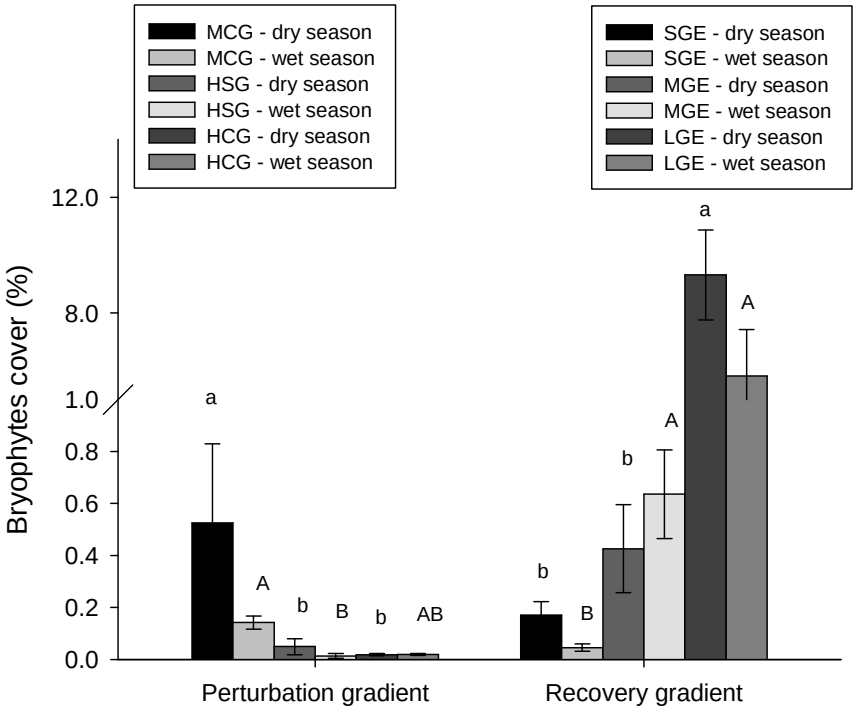


Fig. 2.10. Mean (± 1SE) bryophyte cover (%) along the perturbation (left side) and recovery (right side) gradients in dry and wet season. Different letters above bars indicate significant differences ($P < 0.05$) between sites (gradient levels) within season (small letters for dry season and capital letters for wet season) within each gradient. Within site comparison between seasons: asterisks indicates significant differences between wet and dry season for a particular site (gradient level) at $P < 0.05$. (See text for acronyms of site gradients).

Response variables		ANOVA				
		Source of variation	df	Mean square	*F*	*P*
1. Species density	Perturbation gradient	Level	2	10.728	12.60	**<0.0001**
	Recovery gradient	Level	2	10.193	9.79	**0.0060**
		General linear model				
		Source of variation	df	Mean square	*F*	*P*
2. Total crust cover	Perturbation gradient	Season	1	0.085	2.08	0.1670
		Level (Season)	4	0.112	2.75	0.0610
	Recovery gradient	Season	1	0.224	25.08	**<0.0001**
		Level (Season)	4	0.377	42.22	**<0.0001**
3. Cyanobacteria cover	Perturbation gradient	Season	1	0.170	4.91	**0.0400**
		Level (Season)	4	0.239	6.90	**0.0020**
	Recovery gradient	Season	1	0.316	24.01	**<0.0001**
		Level (Season)	4	0.533	40.53	**<0.0001**
4. Lichen cover	Perturbation gradient	Season	1	0.093	0.34	0.5690
		Level (Season)	4	0.257	0.93	0.4700
	Recovery gradient	Season	1	0.110	2.45	0.1350
		Level (Season)	4	0.283	6.33	**0.0020**
5. Bryophyte cover	Perturbation gradient	Season	1	0.744	3.84	0.0660
		Level (Season)	4	1.899	9.81	**<0.0001**
	Recovery gradient	Season	1	0.187	0.81	0.3800
		Level (Season)	4	4.521	19.55	**<0.0001**

Table 2.3. Summary of ANOVA for species density, total BSC cover, cyanobacteria cover, lichen cover and bryophyte cover along the perturbation and recovery gradient.

d. Discussion

Biological soil crusts in semiarid grassland ecosystems are composed of three principal groups of non-vascular plants: cyanobacteria, lichen and mosses. Hot and cold deserts of North America hold rich communities of BSC, with more than 50 species of cyanobacteria, more than 50 species of mosses and more than 30 species of lichens described up to date (Rivera-Aguilar *et al.* 2006). However, these numbers apply mostly to the United States of America, while BSC communities in semiarid areas of central Mexico have been poorly described thus far (but see Rivera-Aguilar *et al.* 2006). Semiarid grassland communities dominated by *Bouteloua gracilis* form the southern extension of the North American grassland biome, where BSC communities consist of more than 20 lichen species. This is in contrast to other dryland communities in Mexico, where only eight lichen species have been reported (Rivera-Aguilar *et al.* 2006). In the study region of Llanos de Ojuelos, cyanobacteria crust dominates the interspaces between grass tussocks in terms of cover (Aguilar *et al.* 2009), however thus far cyanobacteria crust has not been identified to the species level for this region with one exception. In a similar grassland, dominated by *Bouteloua scorpioides,* the dominant cyanobacteria belong to the genus *Calothrix* spp., a

taxon group indicating relatively low pH values (less than 6) (Aguilar *et al.* 2009). Low pH values have also been observed in our study area where heavy seasonal and continuous grazing dominate (see Chapter III) suggesting that in these sites *Calothrix* may also be present if not dominating; yet detailed analysis need to be conducted. Among bryophytes, three moss species and one liverwort species were found in this study site. No previous study has reported liverwort presence in arid and semiarid ecosystems of central Mexico, whereas the occurrence of three liverwort species have been reported for a secondary humid-temperate grassland in Australia (Eldridge *et al.* 2000).

As expected and previously reported, cyanobacteria crust tolerated different levels of grazing intensity and remains present after 27 years of livestock removal suggesting that succession from early stages characterized by cyanobacteria has not advanced yet in some microsites. Recovery rates depend on a wide variety of abiotic (soil fertility, soil stability) and biotic (inoculation material) factors and thus may take a very long time (reviewed in Belnap, 2003a). Among the lichen species, we identified different groups.: 1) The lichen species *D. diacapsis, A. socialis* and *Lecidella* spp. seem typical indicator species of these grassland as they occur in all sites independently of grazing intensity or age of grazing exclosure. 2) In contrast, *Heteroplacidium* aff. *podolepsis*, *Lecidea* spp. 1 and *Placidium lacinulatum* are the only three species that seem highly vulnerable to grazing and the only species that have truly recovered from grazing, as they do not occur yet in the nearby 11-year exclosure. 3) *Placopyrenium* spp., Lichen spp. 1, Lichen spp. 2 and *Cladonia* spp. occur only in LGE and MCG sites, suggesting that these lichen species do not tolerate heavy seasonal or continuous grazing, and once removed by grazing it may take a long time for these species to re-establish as they do not occur in any of the short and/or mid-term exclosures. 4) *Lecidea cruciara* is a grazing indicator, as this species occurs only in sites along the grazing gradient and the short-term grazing exclosure but is absent from mid-term and long-term exclosures. 5) *Acarospora obpallens*, *Acarospora* spp., *Endocarpon pusillum* and *Lecidella* spp. seem to greatly tolerate grazing, as they occur in all sites along the grazing gradient and in the short-term and mid-term exclosure but not in the 27 year exclosure. It should be interesting to monitor the future trajectory of these species in the short-term and mid-term exclosures and to see whether they get eventually replaced by species such as *Heteroplacidium* aff. *pololepsis*, *Lecidea* spp. 1 or *Placidium lacinulatum*. These latter taxa seem rather vulnerable to grazing or alternatively can survive under the lower light conditions that may occur beneath the relatively dense perennial vegetation in the long-term exclosure. Or it should be examined which other

potential biotic or abiotic factors may contribute to their replacement. Mosses, mostly found near grass tussocks, responded differently to grazing intensity and exclosure age, depending on the species. For instance, liverwort spp. was only found in wetter conditions present in a closer vegetation cover of tussocks in 11 and 27 year exclosures and sites with moderate grazing levels.

Species richness (11 to 14 species) of BSC did not appear to differ dramatically between sites along the perturbation and recovery gradient. However, when taking a closer look at species *identity* and when comparing exclosure sites with nearby grazing sites (i.e. comparing sites from the perturbation gradient with corresponding sites from the recovery gradient) the following shift in species composition could be observed. The HSG and SGE sites are located next to each other, meaning that the short-term exclosure was established on a site with former heavy seasonal grazing. In this case, the two sites share 14 species and none of the species is specific to one of the sites. The HCG and MGE sites are also next to each other, meaning that the mid-term exclosure was established on a site with former heavy continuous grazing. Here, the two sites share 10 species, one species occurs only in the HCG and 2 species occur only in the MGE site suggesting that a certain shift in species composition is in process. And finally, the HCG and LGE sites can also be compared as neighbour sites. In this case, it is only 5 species that these two sites have in common, additionally 6 species occur only in HCG sites and 9 species occur only in LGE sites, suggesting a rather advanced shift in species composition. While total species number does not change between exclosure sites, comparison with associated grazed sites permits to detect fundamental changes in community composition associated with the processes of natural recovery of these grassland ecosystems. Considering the large overall number of BSC species and the wide differences in abiotic and biotic characteristics of these sites (see Table 2.1; see Chapter III), the total number of BSC species (11-14) seems a rather fixed community characteristic of these grassland types that may be controlled by interspecific competition for resources or alternatively have exhausted complementary niche sharing (Loreau *et al.* 2001). Further studies on species interaction types should be conducted to corroborate the competition hypothesis as an underlying force explaining species richness of BSC in these grassland communities in Central Mexico. Also it is necessary to consider the existence of more than one species within the Cyanobacteria group, which has been considered here as only one species.

All grassland types included in this study were characterized by large areas of open interspaces ranging between 60 (long-term grazing exclosure) and 90 (heavy continuous

grazing) percent. Regardless of the relative openness and gap sizes for potential BSC colonization and development, species density ranged between 4.5 and 8 species per unit area, whereby most sites had on average 4-5 species per unit area; however HSG and SGE sites had the highest species density. As these two sites are neighbour sites, it is assumed that species density may be a site-specific characteristic rather than a consequence of grazing intensity, however more detailed studies should be conducted. Similarly, species densities in HCG, LGE and MGE sites, which all occur in the same grassland type, are similar (4-6), suggesting an overall grassland type specific effect. Alternatively, however, specific BSC species interaction types could be responsible for species density, but further analysis of species abundance is necessary to explore this potential mechanism. While species density was only determined for the rainy season, it is unlikely that species density will change between seasons.

While total BSC cover was insensitive to grazing, some BSC species seemed to be more vulnerable to grazing than others. This was reflected in a decline of total species richness with increasing grazing intensity along the grazing gradient, where under moderate and seasonal grazing, BSC was represented by a similar total number of species in MCG and HSG sites, while it was significantly lower under conditions of heavy continuous grazing (HCG). In contrast, total species richness did not change with increasing age of livestock exclosure. Yet, while species richness has remained constant along the recovery gradient, species composition is different, and as has been discussed before, recovery of some BSC species eliminated by grazing may take between 11 and 27 years as they occurred only in the LEG sites.

Total BSC cover was similar along the perturbation gradient, while it showed marked increases only in the site of long-term grazing exclosure in the recovery gradient. Cyanobacteria cover was highest under the heavy grazing regime, but only in the dry season. Contrary to what we expected, the seasonal dry-wet cycle showed small variation and so had little effect on BSC cover. These short-term temporal dynamics seem to have been caused by other variables than grazing intensity or exclosure age.

It has been shown in a previous study (Belnap *et al.* 2004) that frequent short-term precipitation pulses may drastically reduce biological activity (in particular photosynthesis) in cyanobacteria group. This is a consequence of the lack of time to develop protective pigments against high solar radiation during the short wetting period. The year 2009 was a rather wet year with short frequent precipitation events; hence, the overall reduced activity time and a net C loss by cyanobacteria may partially explain the drop in cyanobacteria

cover. In the LGE sites, an overall more humid environment (water retention in soil and nearby litter) and a more closed grass cover seem to moderate the light, temperature and soil water environment stimulating cyanobacteria development. Lichen cover did not respond differently to distinct grazing intensities, but it was significantly lower in the LGE site compared to the other exlcosures during the wet season. Meanwhile, bryophytes were negatively affected by heavy grazing intensity but responded positively to increasing age of exclosure. Hence, spatial dynamics of taxon specific BSC covers were mostly controlled by grazing pressure and by indirect effects of livestock exclosure on more favourable microenvironments that benefit the C balance of BSC components (Bowker *et al.* 2002).

e. Conclusions

High impact by livestock grazing corresponds to potentially severe mechanical damage of vegetation and soil cover. Albeit the overall intensive grazing regime characterizing the grassland ecosystems in Central Mexico, rather diverse BSC community types have established and adapted to these harsh environmental conditions. Comparing BSC communities along a perturbation (caused by grazing) and recovery gradient in nearby grasslands allowed us to identify different BSC species groups such as grazing tolerants, grazing indicators, and vulnerable to grazing. The three exclosure ages (6-27 years) allowed us also to detect BSC lichen recovery responses of most likely grazing sensitive species. This was a rather surprising result as most of the grasslands in this geographical region are overgrazed, but the inoculation material must have been conserved or even favoured in the systems. This suggests that these grassland ecosystems are rather resilient to livestock grazing, as they are no only able to recover at the level of vascular species diversity (data no shown) but also at the BSC community level. This finding may have important implications on ecosystem functioning, however further studies will have to be conducted to assess the functional role of BSC communities not only in the livestock exclosure but also in sites with different grazing histories.

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Chapter III. BSC and local soil physico-chemical properties: BSC effect along a perturbation gradient

a. Introduction

Biological soil crusts (BSC) are mainly composed of soil cyanobacteria, microfungi, lichens and mosses covering soil surfaces in arid and semiarid ecosystems (Belnap *et al.* 2001). Lichens and mosses modify soil surface roughness, reducing the impact of erosion forces, and fostering the formation of soil organic matter (Delgado-Baquerizo *et al.* 2010) and the retention of fine particles (Belnap, 2006). The filaments of cyanobacteria, hyphae of fungi and rhizines of some soil lichens physically bind soil particles forming soil aggregates at the soil surface, and thus enhance soil stability (Belnap, 2003; Bowker *et al.* 2008; Aguilar *et al.* 2009). Also, depending on the degree of thallus cohesion of lichen, some species may stabilize soil surface better than others (Aguilar *et al.* 2009). There is evidence that BSC organisms exude organic and inorganic (Hawkes, 2004; Veluci *et al.* 2006) compounds and are effective metal chelators with the capacity to modify soil pH and thereby increasing ion binding capacity, and in turn, nutrient availability. Thus, both morphological characteristics and chemical activity of BSC organisms may contribute to enhanced soil stability, protection of soil structure, and contribute to soil fertility near the surface soil. However, this effect of BSC on soil physico-chemical properties may vary between taxon group (cyanobacteria, lichen, bryophytes) and species within taxa, and is susceptible to soil surface disturbance.

Overgrazing by livestock is the principal driver of land degradation in arid and semi-arid ecosystems in Mexico (Manzano *et al.* 2000). Livestock severely influence soil and vegetation characteristics together triggering an overall depletion in soil organic matter content and nutrient concentration (through soil erosion), a reduction in cation exchange capacity, local increase in soil pH, and changes in soil texture (loss of fine particles) and structure (soil compaction) (Ganjegunte *et al.* 2005; Neff *et al.* 2005; Cui *et al.* 2005; Castellano and Valone, 2007). In addition, long-term continuous grazing greatly reduces perennial vegetation cover thereby creating large vegetation-free interspaces, which may become colonized by diverse communities of BSC (Eldridge *et al.* 2000), occasionally counteracting the directional negative effects of livestock grazing on soil properties. Physical impact and damage by livestock trampling affect BSC groups differently; they exhibit an increasing resistance to mechanical disturbance by trampling in the following increasing order: mosses < crustrose lichens < cyanobacteria (Belnap and Eldridge, 2001; Muscha and Hild 2006).

Research on cyanobateria, lichen, and bryophyte ecology has been increasing recently, due to their multi-functional roles in semiarid ecosystem structure and processes (Cornelissen *et al.* 2007). However, potential species-specific effects of BSC organisms on a wide variety of soil physico-chemical properties and considering different grazing intensities have not been assessed yet. Here, we explored the relation between BSC and soil physico-chemical properties along a grazing gradient in a semiarid grassland ecosystem in Central Mexico. We addressed the following questions: 1) Do different BSC types (cyanobacteria, lichen and mosses) and lichen species (*Diploschistes diacapsis*, *Acarospora socialis*, *Lecidella* spp.) create distinct soil microsites characterized by particular physical and chemical properties? Does grazing/trampling impact influence the formation of potential microsites? 2) In case BSC-specific soil microsites exist, what are the specific soil physical and chemical properties of these emerging microsites considering different grazing regimes? 3) Do those BSC types/species present in all sites of the grazing gradient (cyanobacteria and *D. diacapsis*) exert species-specific effects on soil microsites or does grazing intensity override BSC effects? To address these questions, we examined a wide variety of soil physico-chemical properties associated with a total of five different BSC types (cyanobacteria, 1 species of mosses, 3 species of lichens) and in bare soil along a perturbation gradient consisting of sites with different grazing histories/intensities: a long-term exclosure, and sites with moderate continuous grazing, heavy seasonal grazing and heavy continuous grazing.

We pose the following hypothesis corresponding to the specific questions: 1) Because of their biological activity, we expected soil covered by BSC to form “emerging” microsites with distinct texture, chemical properties and soil nutrient concentration compared to bare soil, independently of grazing intensity. Similarly, because of their different morphology, physiological activity and dominance during different successional stages, cyanobacteria, lichen and mosses may constitute soil microsites with different combinations of soil properties. At the lichen level, we expected potential soil microsites to differ mostly in soil texture. 2) Also, we hypothesized that for a specific grazing level, different BSC types may contribute differently to particular characteristics of soil texture, chemical properties and soil fertility. 3) Species-specific BSC effects of cyanobacteria and *D. diacapsis* on soil properties may diminish with increasing grazing intensity, since grazing pressure may alter BSC functioning, due to physiological damage exerted by mechanical impact.

The aim of this work was to contribute to a better understanding of the quality of microscale heterogeneity associated with different BSC species at the soil physico-

chemical level in relation to grazing intensity in a semiarid grassland ecosystem of Central Mexico, where BSC form abundant and highly diverse communities and overgrazing is a driving force of land degradation.

b. Methods

i. Study site

The study area is located in the physiographic subprovince Llanos de Ojuelos (21º 49' N, 101º 37' W, 2200 m a.s.l.), Jalisco, Mexico at the southernmost part of the North American graminetum (Aguado-Santacruz and García-Moya, 1998). The climate is semiarid with mean annual precipitation of 450 mm, and mean annual temperature between 12 and 18 ℃. The main rainfall season occu rs between june and september. The topography is characterized by valleys and gentle rolling rhyolitic hills. Soils are haplic xerosols associated with lithosols and eutric planosols, and haplic phaeozems associated with lithosols; they present only two horizons at 0-25 cm and 25-40 cm depth. Soil texture varies and ranges from silty clay to sandy loam (COTECOCA, 1979). The vegetation is a natural grassland with *Bouteloua gracilis* as the dominant grass species (Aguado, 1993).

Site	Dominant species	Plant cover (%)	Above ground productivity (kg dry matter/ha)	Coordinates
Long-term grazing exclosure (LGE)	*Bouteloua gracilis*	35-40	800-1200	21°45' 32.42" N 101°38' 32.29" W
Moderate continuous grazing (MCG)	*Bouteloua gracilis, Muhlenbergia rigida*	25-30	1200	21°46' 18.493" N 101°40' 24.656" W
Heavy seasonal grazing (HSG)	*Bouteloua gracilis*	15-20	350	21°46' 10.815" N 101°40' 27.192" W
Heavy continuous grazing (HCG)	*Bouteloua gracilis, Isocoma veneta, Asphodelus*	5-10	240-440	21°45' 36.36" N 101°38' 20.58" W

Table 3.1: Characteristics of study sites.

The grazing gradient consisted of four sites characterized by different histories of grazing management (Table 3.1, Fig. 3.1). Sites included: 1) "long-term grazing exclosure" (LGE): a 27 year-old cattle exclosure in a heavily grazed pasture, 2) "moderate continuous

grazing" (MCG): moderate cattle grazing for over 300 years, on private land, 3) "heavy seasonal grazing" (HSG): intensive grazing for over 70 years, during and after rainy season, on communal (*ejido*) land and 4) "heavy continuous grazing" (HCG): intensive grazing for over 70 years, all year around, currently presenting shrub encroachment, on communal land. Heavily grazed sites have lead to heavily compacted soils, reduced plant cover and large areas of vegetation-free interspaces colonized by BSC.

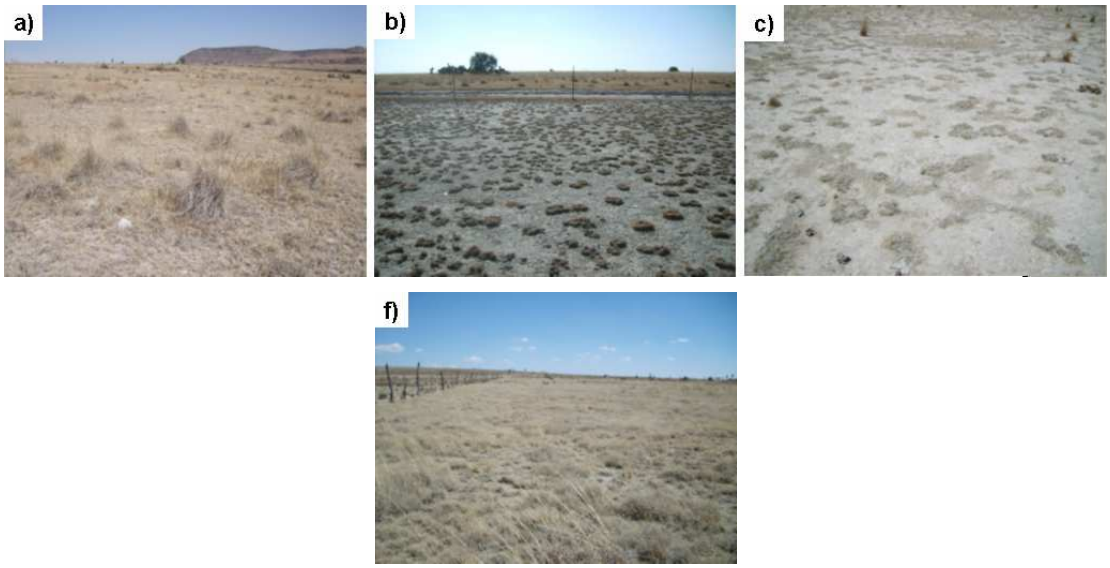


Fig. 3.1: Study sites in grasslands of Vaquerias, Jalisco, Mexico: a) "Moderate continuous grazing" (MCG), b) "Heavy seasonal grazing" (HSG), c) "Heavy continuous grazing" (HCG), and f) "Long-term grazing exclosure" (LGE). (For acronyms please see text).

ii. Soil sampling design

We examined physico-chemical properties of soil associated with five different BSC types: one moss species, cyanobacteria crust, and three crustose lichen species: *Diploschistes diacapsis* and *Lecidella* spp. with continuous thalli, and *Acarospora socialis* with semicontinuous thalli (Table 3.2). Since the objective of this study was to examine potential BSC effects on local soil physical and chemical characteristics, we selected in each site only those species with greatest abundance (number and size of thalli per BSC type per unit area) and that best represented BSC cover in the four contrasting sites. Soils were sampled beneath BSC with a minimum patch size area of 5 cm x 5 cm.

Site	Species				
	Mosses	Cyanobacteria	*A. socialis*	*D. diacapsis*	*Lecidella* spp.
LGE	x	x		x	
MCG		x		x	x
HSG		x	x	x	x
HCG		x	x	x	

Table 3.2: Species of BSC sampled in different sites along the pertubation gradient. Mosses, cyanobacteria, *Acarospora socialis*, *Diploschistes diacapsis* and *Lecidella* spp. (For site acronyms please see text)

At each grazing site, we selected three or four BSC types (Table 3.2) and a bare soil zone. Cyanobacteria crust and *D. diacapsis* occurred abundantly in all sites, mosses were abundant only in the LGE site, *A. socialis* only in sites with heavy grazing (HSG, HCG) and *Lecidella* spp. only in MCG and HSG sites (Table 3.2). For each BSC type including bare soil, we collected five composite samples each consisting of 10 subsamples. Each subsample was randomly chosen in the interspaces. At each site, we kept a constant minimum distance between BSC and grass tussocks to avoid potential interfering effects from neighboring grass roots. Within each BSC microsite, we first marked a 3.3 x 3.3 cm^2 area by inserting a spatula 1-2 mm into the soil and then carefully removed the BSC surface. We excavated a 3.3 x 3.3 x 1 cm^3 deep soil square prism after carefully removing the soil surrounding the prism. For each BSC type, we added 10 soil samples in a labelled plastic bag; all bags were stored in coolers for transportation. In the laboratory, the samples were air-dried prior to analysis. Soil samples were collected on a single day in November 2009 three days after a raining event.

iii. Soil analysis

Eighty composite soil samples were passed through a 2-mm sieve, roots were separated and oven-dried, and rocks were eliminated. For textural analysis, subsamples of 20 g of each soil sample were sent to the Soil Analysis Laboratory of the Colegio Postgraduados en Texcoco, Mexico. The following fractions were determined: sand (coarse >0.5 mm, medium 0.25-0.5 mm, fine 0.105-0.25 mm, very fine <0.25 mm), silt and clay. Soil chemical analyses were conducted in the Laboratory of Environmental Sciences of the Instituto Potosino de Investigacion Cientifica y Tecnologica. We determined soil organic matter (OM) with the calcination method (600 ºC, 2h); soil pH and electrical conductivity by using 10 g of soil in 10 ml of distilled water. Soil samples were analyzed for

ammonium acetate (NH_4OAc)-extractable calcium, potassium, magnesium, and sodium (Ca^{2+}, K^{+}, Mg^{2+} and Na^{+}), and DTPA-extractable copper, iron, manganese, and zinc (Cu^{2+}, Fe^{2+}, Mn^{2+}, and Zn^{2+}).

iv. Statistical analysis

The grazing gradient consisted of four sites (LGE, MCG, HSG, HCG). We examined seven physical soil variables (total, coarse, medium, fine and very fine sand fraction, silt, and clay fraction), three chemical variables (OM, pH, EC), four macronutrients (Ca, K, Mg, Na), and four micronutrients (Cu, Fe Mn and Zn).

Prior to analysis we tested the normality of data with Shapiro-Wilk´s test for all variables. We applied the Levene´s test for equal variances of data. We examined the possible existence of five potential BSC-specific "emerging" microsites, as soil "patches" characterized by distinct combinations of soil physico-chemical properties. For this purpose we performed four separate ordination analysis with the objective to elucidate the data structure in low dimensions using distance metrics. The four ordination analysis done were: i) between potential microsites of BSC and bare soil (cover effect), ii) among potential microsites of different BSC types (functional group effect: mosses, cyanobacteria and lichen), iii) among potential microsites of different lichen species (global species effect: *A. socialis*, *D. diacapsis* and *Lecidella* sp.), and iv) among potential microsites of bare soil and two BSC species that occur in each site of the grazing gradient (site effect: LGE, MCG, HSG and HCG). Due to violations of normality and homoscedasticity of the data, a non-parametric multivariate ordination technique was applied. We conducted non-metric multidimensional scaling (NMDS) based on Bray-Curtis distance to ordinate BSC types and bare soil (microsite) considering four levels (i-iv, see above this section) of analyses. Also, NMDS was preferred over principal component analysis, because BSC types both respond to and affect soil characteristics in a non-linear fashion. Ordination methods are techniques used to express differences in treatments (BSC taxa and recovery/perturbation grazing gradient) using simultaneously several response variables, in this case soil physico-chemical attributes. NMDS is a distance-based ordination method that finds the best possible configuration of data by reducing the number of dimensions. However, since data are considered non-metric, the distance between objects is considered distance-like in the data set, rather than an actual distance. Variance explained in NMDS axis is expressed in terms of r squared. NMDS was performed in PC-ORD version 4 (McCune and Mefford, 1999).

To examine site-specific effects of BSC types on specific soil physico-chemical properties characterizing soil texture, chemical properties and fertility, we used four separate general linear models (GLM) for each grazing site with soil cover as fixed factor (with four or five levels depending on grazing site considering three or four BSC types and bare soil; Table 3.2) and five replicates (N=20 or 25). To compare individual soil chemical and physical properties associated with different BSC types and bare soil within a site, we used Tukey´s multiple comparison test (see question 2 in introduction). To examine, whether BSC effects/responses are fixed ("emerging") for each BSC type independently of grazing intensity, or whether grazing modifies BSC effect of response pattern, we conducted a one-way ANOVA with a general linear model with soil cover (cyanobacteria, *D. diacapsis*, bare soil) nested within site (LGE, MCG, HSG, HCG) as fixed factor (N=60). To compare potential differences among cover types within and across sites, we applied Tukey´s multiple comparisons test (see question 3 in introduction).

The ANOVAs and multiple comparison tests were performed with MINITAB 14 (Minitab Inc., 2008).

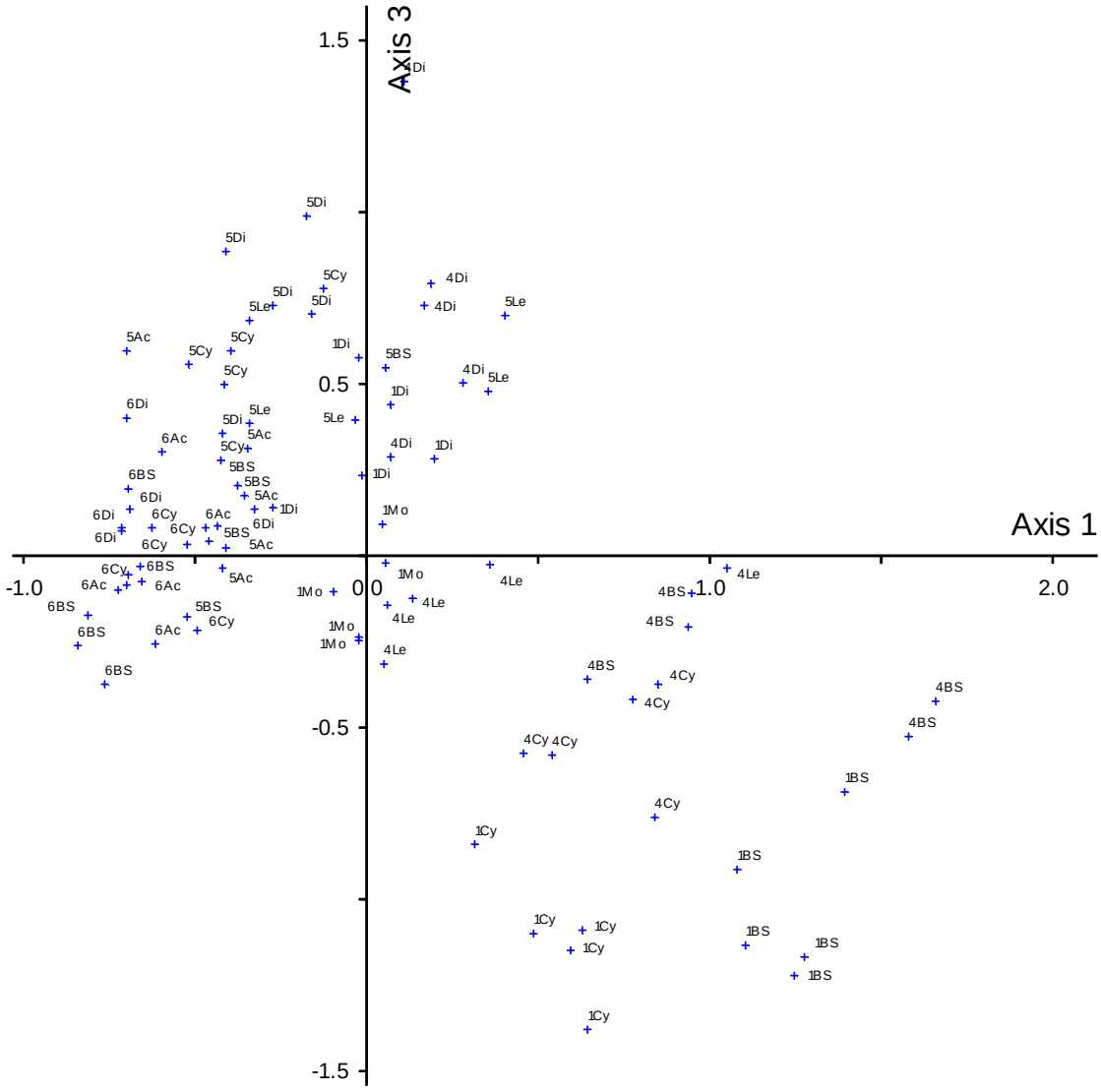
c. Results:

i. Effect of soil cover types on potential soil physico-chemical microsites

BSC cover *versus bare soil*.- To examine if BSC and bare soil form distinct microsites characterized by particular combinations of soil physical and chemical properties, we conducted a three-dimensional (best configuration) NMDS ordination (Table. 3.3) that best explained the variance of data: Axis 1 r^2=0.616, Axis 2 r^2=0.152, and Axis 3 r^2=0.186. Textural properties (coarse sand and clay fraction) were best correlated with the negative pole of Axis 1, while Na, K, and EC were highly correlated with the positive pole of Axis 1 (Table 3.3). Mg was highly correlated with the negative pole of Axis 2, and medium and coarse sand fraction with the positive pole of Axis 2 (Table 3.3). Soil pH was best correlated with the negative pole of Axis 3, while Mn, Fe and Cu were well correlated with the positive pole of Axis 3 (Table 3.3). Soil samples of bare soil and cyanobacteria separated as microsites from all other moss and lichen samples both in the positive pole of Axis 1 (Fig. 3.2a) and in the negative pole of Axis 3 (Fig. 3.2a), suggesting that microsites associated with bare soil and cyanobacteria are overall similar and that they are characterized by a relatively higher pH, higher Na and K concentration and higher EC (Table 3.3). However, these microsites of bare soil and cyanobacteria emerged only in LGE and MCG sites (Fig. 3.2a). Also, bare soil microsites in LGE sites had higher content

of coarse and medium-sized sand content as they grouped in the positive pole of Axis 2 (Fig. 3.2b), while bare soil microsites in MCG site had higher Mg and Ca concentration as they grouped separately in the negative pole of Axis 2 (Fig. 3.2b).

a)



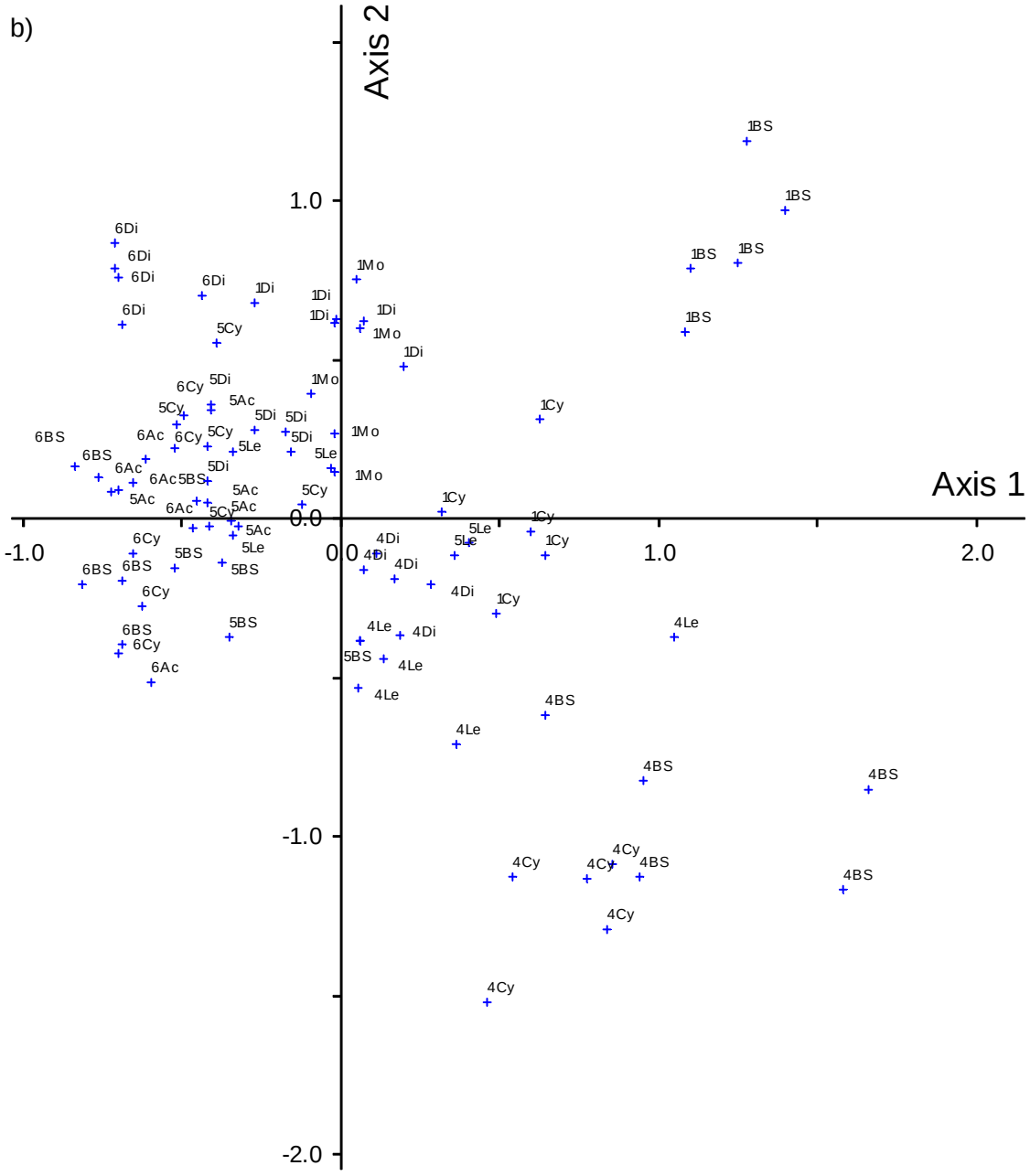


Fig. 3.2 a and b: Plot of BSC and bare soil microsites in NMDS ordination space (a) for Axis 1 vs Axis 3 and (b) for Axis 1 vs Axis 2. Each point represents a composite sample (N=85) with 1, 4, 5 and 6 corresponding to grazing sites LGE, MCG, HSG, and HCG, respectively. BS = bare soil, Mo = mosses, Cy = cyanobacteria crust, Ac = *Acarospora socialis*, Di = *Diploschistes diacapsis* and Le = *Lecidella* spp.

Potential microsites associated with different BSC types.- To examine if different BSC types form distinct microsites characterized by particular combinations of soil physical and chemical properties, we conducted a two-dimensional (best configuration) NMDS ordination (Table 3.3) that best explained the variance of data: Axis 1 r^2=0.129 and Axis 2 r^2=0.859 (Table 3.3). Soil K and Ca were highly correlated with the negative and positive pole, respectively of Axis 1 (Table 3.3). Soil Ca and most of the micronutrients were highly correlated with the negative pole of Axis 2, while Na and K were highly correlated with the positive pole of Axis 2 (Table 3.3). Cyanobacteria (only in LGE and MCG sites) and *Lecidella* spp. (only in MCG) formed microsites characterized by relatively higher K and Na concentration and EC than soil samples associated with lichen and moss soil samples (Fig. 3.3; positive pole of Axis 2; Table 3.3). *Diploschistes diacapsis,* also formed microsites with relatively higher K and Na concentration, however in HSG and HCG sites, they formed microsites characterized by relatively higher OM, Mn and Cu concentration, and silt, clay and coarse sand fraction compared to the rest of soil samples (Fig. 3.3; negative pole of Axis 1 and 2; Table 3.3). Mosses occurred only in LGE sites, where they formed microsites relatively high in Ca concentration similarly to soil microsites associated with all other BSC types (except *D. diacapsis*) occurring in HSG and HCG sites (Fig. 3.3; positive pole of Axis 1 and negative pole of Axis 2; Table 3.3).

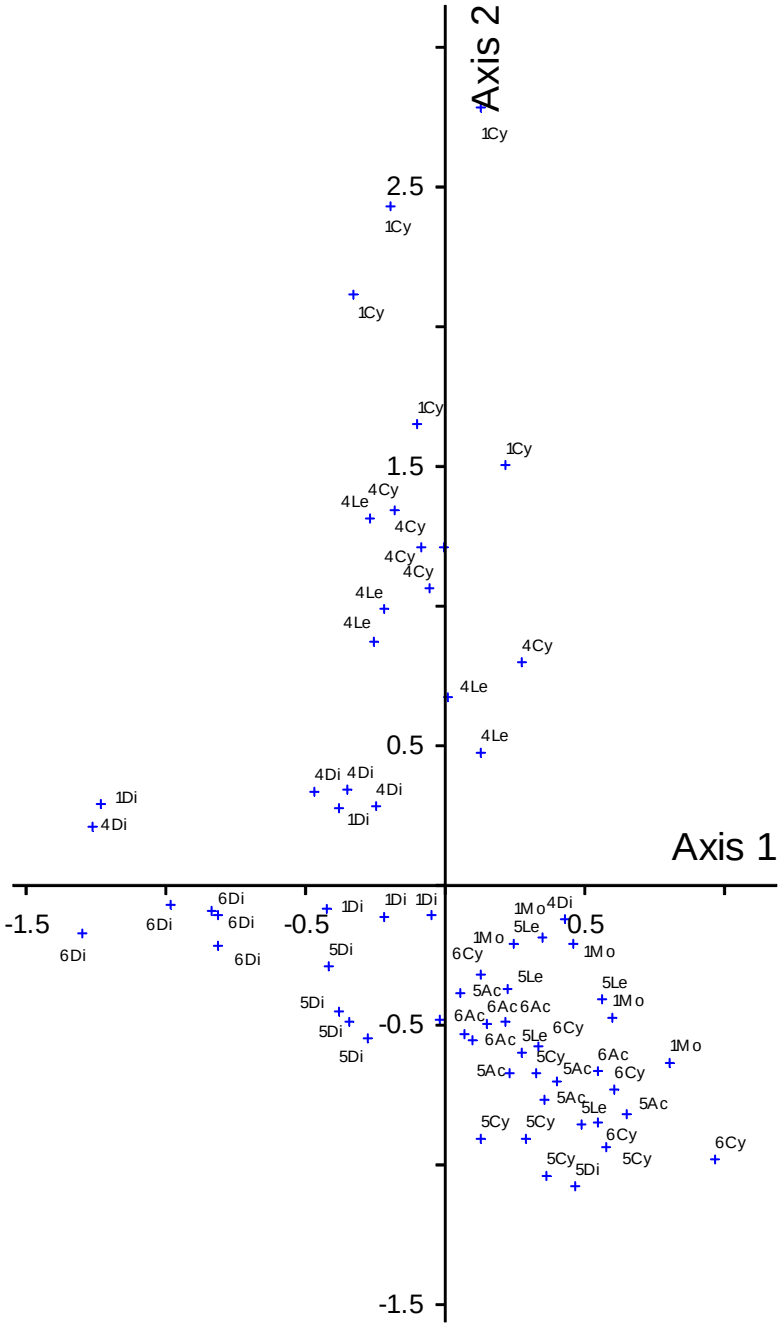


Fig. 3.3. Plot of BSC types in NMDS ordination space for Axis 1 and Axis 2. Each point represents a composite sample (N=65) with 1, 4, 5 and 6 corresponding to grazing sites LGE, MCG, HSG, and HCG, respectively. Mo = mosses, Cy = cyanobacteria crust, Ac = *Acarospora socialis*, Di = *Diploschistes diacapsis*, and Le = *Lecidella* spp.

Potential microsites associated with different lichen species.- To examine if different species within a functional group (lichen) form distinct microsites characterized by particular combinations of soil physical and chemical properties, we conducted a two-dimensional (best configuration) NMDS ordination (Table 3.3) that best explained the variance of data: Axis 1 r^2=0.701 and Axis 2 r^2=0.276 (Table 3.3). Soil Ca and K were highly correlated with the positive and negative poles of Axis 1, respectively (Table 3.3). Soil Na was best correlated with the negative pole of Axis 2, while coarse sand, silt, and clay content, OM, Mn concentration and pH were best correlated with the positive pole of Axis 2 (Table 3.3). Thus, lichen *A. socialis* occurring principally in HSG and HCG sites formed microsites with higher OM concentration, pH, Mn and Ca concentration together with higher percentage of the coarse sand fraction than the remainder of soil samples (Fig. 3.4; positive pole of Axis 1 and 2; Table 3.3). Overall, *D. diacapsis* formed microsites with relatively higher K concentrations (Fig. 3.4; negative pole of Axis 1; Table 3.2). However in the HSG and HCG, *D. diacapsis* formed microsites with higher OM, pH, Mn, Cu and Fe and coarse sand content (Fig. 3.4; positive pole of Axis 2; Table 3.3). Lichen *Lecidella* sp. formed different microsites depending on grazing condition. In MCG sites, the microsites were relatively higher in K, Na concentration and EC (Fig. 3.4; negative pole of th Axes 1 and 2; Table 3.3), while in HSG sites, microsites sites were higher in Ca and Mg concentration (Fig. 3.4; positive poles Axis 1; Table 3.3).

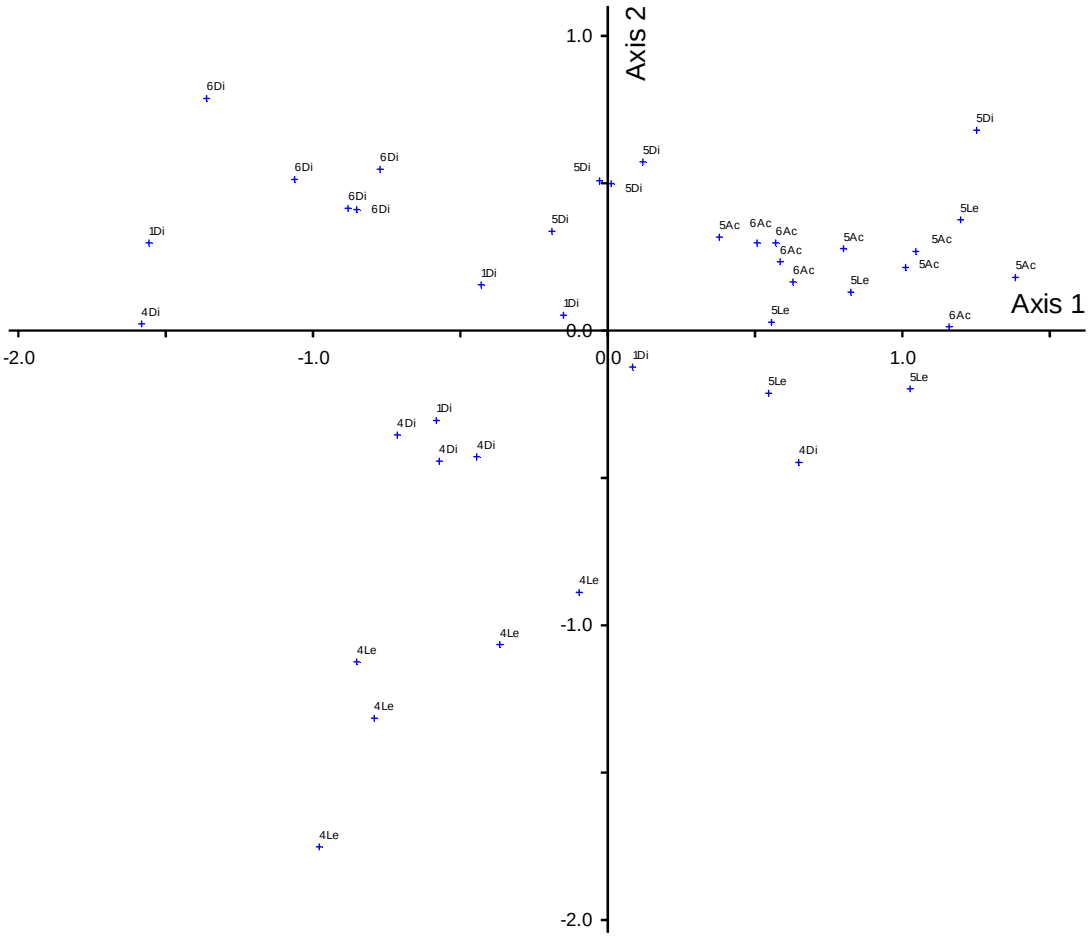


Fig. 3.4: Plot of lichen species in NMDS ordination space for Axis 1 and Axis 2. Each point represents a composite soil sample (N=40) with 1, 4, 5 and 6 corresponding to grazing sites LGE, MCG, HSG and HCG, respectively. Ac = *Acarospora socialis*, Di = *Diploschistes diacapsis* and Le = *Lecidella* spp.

Potential microsites associated with bare soil, cyanobacteria and D. diacapsis.- To examine if bare soil and two different BSC types form distinct microsites characterized by particular combinations of soil physical and chemical properties in all grazing sites, we conducted a two-dimensional (best configuration) NMDS ordination (Table 3.3) that best explained the variance of data: Axis 1 r^2=0.213 and Axis 2 r^2=0.777 (Table 3.3). Soil K, Fe, Mn, Cu, and OM concentration were the best correlates with the positive pole of Axis 1 (Table 3.3), and Ca with the negative pole of Axis 1 (Table 3.3). Soil Na, K concentration and EC were highly correlated with the negative pole of Axis 2 (Table 3.3), while Ca and Mg concentrations, OM, and fine and very fine sand and silt were highly correlated with the

positive pole of Axis 2 (Table 3.3). Characteristics of soil microsites formed by bare soil and cyanobacteria were overall quite similar within a grazing site, however microsite characteristics were different for LGE and MCG sites compared to heavily grazed sites (HSG and HCG) (Fig. 3.5). In LGE and MCG sites, bare soil and cyanobacteria formed microsites with relatively higher concentration of Na, K and EC (Fig 3.5; negative pole of Axis 2; Table 3.3), while in HSG and HCG sites, bare soil and cyanobacteria formed microsites with higher Ca, Mg and Mn concentrations, OM content and silt (Fig. 3.5; positive pole of Axis 2; Table 3.3). Also, while bare soil microsites were quite distinct between LGE and MCG sites, they were quite similar for HSG and HCG sites. *Diploschistes diacapsis* formed microsites independently of grazing intensity and they were characterized by relatively higher OM content, pH, silt and clay content, and Mn, and Fe concentrations (Fig. 3.5; positive pole of Axes 1 and 2; Table 3.3).

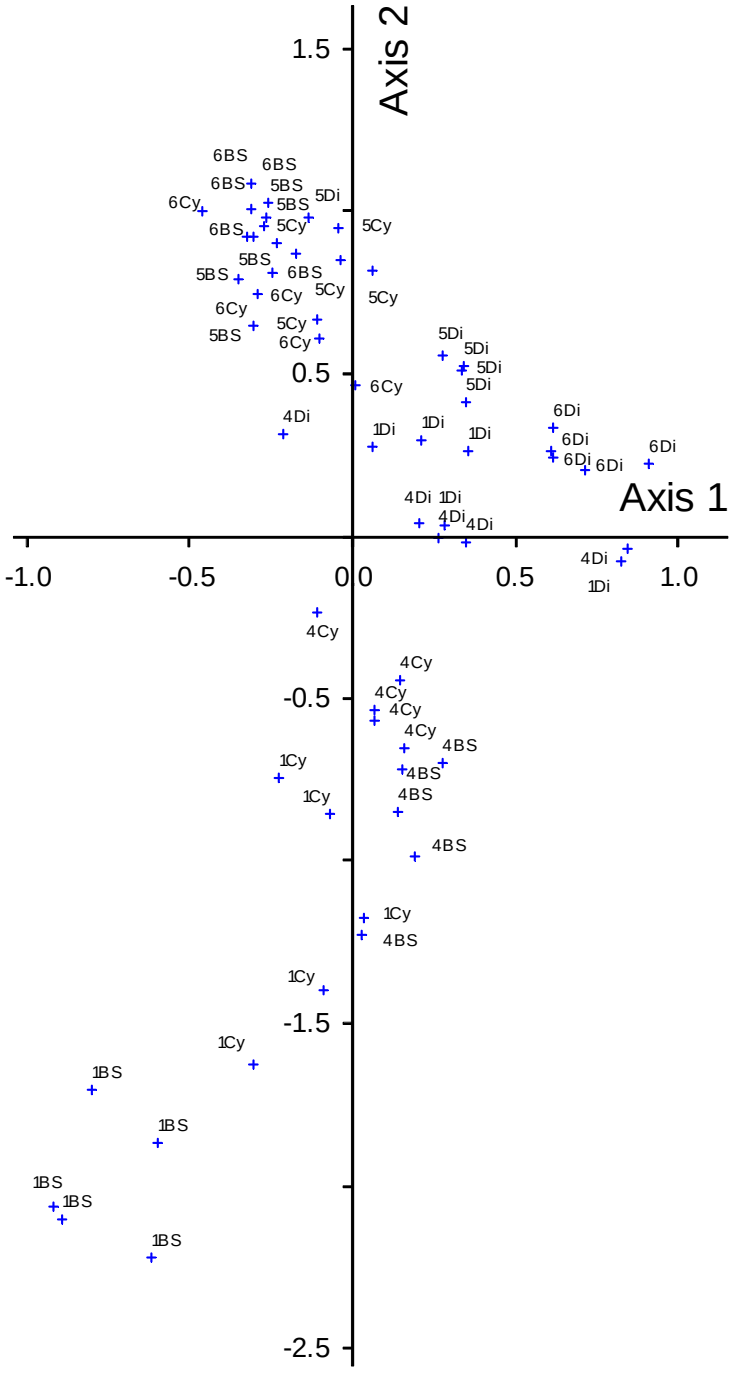


Fig. 3.5: Plot of bare soil, cyanobacteria and *D. diacapsis* composite soil samples for Axis 1 and Axis 2. Each point represents a composite soil sample (N=60) with 1, 4, 5 and 6 corresponding to grazing sites LGE, MCG, HSG, and HCG. BS = bare soil, Cy = cyanobacteria crust, Di = *Diploschistes diacapsis*.

	Correlation with ordination axis (Tau)								
	BSC types and bare soil			BSC types		Lichen species		BS-Cy-Di	
Soil property	Axis 1 (r2=0.616)	Axis 2 (r2=0.152)	Axis 3 (r2=0.186)	Axis 1 (r2=0.129)	Axis 2 (r2=0.859)	Axis 1 (r2=0.701)	Axis 2 (r2=0.276)	Axis 1 (r2=0.213)	Axis 2 (r2=0.777)
OM	0.060	-0.329	0.315	-0.196	-0.365	-0.141	0.695	0.376	0.403
pH	0.280	-0.260	-0.593	-0.156	-0.333	-0.154	0.641	0.273	0.373
EC	0.691	-0.124	-0.250	-0.354	0.421	-0.313	-0.256	0.246	-0.628
Sand	-0.090	0.388	-0.433	-0.139	-0.243	-0.156	0.562	0.201	0.355
Silt	0.180	-0.331	0.218	-0.099	-0.401	0.010	0.497	0.318	0.473
Clay	-0.239	0.057	0.156	-0.145	-0.343	-0.238	0.449	0.293	0.304
Coarse	-0.312	0.440	0.093	-0.033	-0.367	0.062	0.682	0.081	0.325
Medium	-0.147	0.577	-0.210	-0.084	-0.178	-0.087	0.508	0.156	0.201
Fine	-0.048	-0.026	-0.464	-0.161	-0.241	-0.223	0.449	0.181	0.418
V.fine	0.107	-0.221	-0.286	-0.269	-0.129	-0.287	0.333	0.228	0.395
Ca	0.229	-0.578	-0.259	0.668	-0.734	0.956	0.085	-0.227	0.873
K	0.684	-0.318	-0.361	-0.709	0.647	-0.926	-0.054	0.562	-0.528
Mg	0.150	-0.700	-0.065	0.160	-0.335	0.351	-0.131	-0.017	0.537
Na	0.743	-0.140	-0.347	-0.276	0.774	-0.405	-0.523	0.020	-0.829
Cu	0.124	0.360	0.439	-0.233	-0.204	-0.287	0.431	0.323	0.149
Fe	0.003	0.337	0.566	-0.304	-0.127	-0.390	0.344	0.447	0.138
Mn	-0.151	0.016	0.532	-0.128	-0.372	-0.023	0.608	0.275	0.345
Zn	0.472	0.133	0.021	-0.063	-0.136	-0.182	0.028	0.214	0.060

Table 3.3: Soil properties and correlations with ordination axes (Kendall's correlation coefficient, Tau) for NMDS analyses for: BSC types and bare soil, BSC types only, lichen species only and bares soil (BS), cyanobacteria (Cy) and *Diploschistes diacapsis* (Di)

ii. Soil physico-chemical properties associated with BSC types and bare soil considering different grazing intensities

1.- Long-term grazing exclosure (LGE)

Soil texture (Table 3.4).- Sand content was the only texture property which showed a significant cover type effect. Soil associated with *D. diacapsis* had overall the lowest total sand content, while it did not differ among cyanobacteria, mosses and bare soil.

Soil chemical properties (Table 3.4).- For OM there was a significant species effect. Moss cover resulted in higher soil OM content than soil of cyanobacteria and *D. diacapsis*, while it did not differ compared to OM content of bare soil. Cyanobateria soil had lower OM content than bare soil. The pH was significantly higher in soils of cyanobacteria and bare soil compared to mosses and *D. diacapsis*. EC of bare soil was significantly higher than any of the soils covered with BSC; and soils with cyanobacteria had higher EC than soils of lichen and mosses.

Soil fertility (Table 3.4).- Macronutrients: Soils of mosses and cyanobacteria had higher Ca concentration than soils of *D. diacapsis* microsites and bare soil. For the K, mosses and *D. diacapsis* microsites had a lower K concentration compared with bare soil and cyanobacteria microsites. Mg concentration did not differ between BSC cover types, however it was higher than in bare soil, except for *D. diacapsis*. Na concentration was significantly higher in bare soils compared to BSC covered soils; and among BSC, soils of cyanobacteria had a much higher Na concentration compared to mosses and *D. diacapsis*.

Micronutrients: Fe concentration in soils of *D. diacapsis* was significantly higher than in any other cover type including bare soil, while it was overall lowest in soils of cyanobacteria. Fe concentrations in moss and bare soils did not differ and had intermediate values. Soil Mn concentration in cyanobacteria was significantly lower than in soils of mosses, *D. diacapsis* and bare soil, where Mn concentration did not differ.

Response variables	GLM		LGE			
	F	*P*	Bare soil	Mosses	Cyanobacteria	*D. diacapsis*
OM	10.05	**0.0010**	6.3 ± 0.2 ab	6.6 ± 0.3 a	5.5 ± 0.4 c	6.0 ± 0.4 bc
pH	39.70	**<0.0001**	7.7 ± 0.8 a	5.7 ± 0.4 b	8.2 ± 0.5 a	5.3 ± 0.2 b
EC	225.61	**<0.0001**	1.131 ± 0.021 a	0.121 ± 0.023 c	0.321 ± 0.121 b	0.132 ± 0.068 c
Sand	5.97	**0.0060**	40.0 ± 3.6 a	38.3 ± 2.2 a	38.6 ± 3.2 a	32.3 ± 3.3 b
Silt	1.69	0.2100	35.4 ± 5.8 a	36.4 ± 4.3 a	35.4 ± 2.8 a	41.9 ± 7.4 a
Clay	0.15	0.9260	24.6 ± 3.0 a	25.3 ± 3.6 a	26.1 ± 3.2 a	25.8 ± 4.8 a
Ca	12.89	**<0.0001**	347.8 ± 75.3 b	524.4 ± 50.6 a	562.5 ± 84.9 a	325.8 ± 84.5 b
K	74.15	**<0.0001**	850.1 ± 54.7 a	406.3 ± 40.6 b	918.2 ± 124.7 a	367.2 ± 48.2 b
Mg	5.18	**0.0110**	31.6 ± 12.8 b	70.2 ± 17.6 a	66.1 ± 21.4 a	54.2 ± 15.3 ab
Na	214.00	**<0.0001**	1104.1 ± 140.1 a	60.7 ± 15.7 c	631.0 ± 162.7 b	69.8 ± 18.0 c
Cu	0.98	0.4260	0.441 ± 0.421 a	0.296 ± 0.034 a	0.215 ± 0.017 a	0.328 ± 0.021 a
Fe	24.40	**<0.0001**	35.6 ± 14.1 b	39.8 ± 12.7 b	13.4 ± 3.7 c	66.7 ± 4.3 a
Mn	14.27	**<0.0001**	38.2 ± 8.8 a	40.5 ± 3.3 a	22.9 ± 5.2 b	44.1 ± 2.7 a
Zn	0.63	0.6040	1.861 ± 0.158 a	1.770 ± 0.267 a	1.456 ± 0.868 a	1.756 ± 0.355 a

Table 3.4. Results of GLM with soil cover type (bare soil, mosses, cyanobacteria, *Diploschistes diacapsis*) as fixed effect for different soil response variables and multiple comparisons (Tukey´s test) between soil cover types in the long-term grazing exclosure (LGE). Different letters within a row indicate significant differences at the $P < 0.05$ level between cover types (columns). Analysis for Na was performed on natural log transformed data.

2.- Moderate continuous grazing

Soil texture (Table 3.5): For all soil textural fractions there was a significant species effect. Sand content in soils of *Lecidella* spp. was significantly higher than in soils of *D. diacapsis* and cyanobacteria and bare soils. Cyanobacteria and bare soil had significantly higher silt content and lower clay content than both *D. diacapsis* and *Lecidella* spp. soil.

Soil chemical properties (Table 3.5): For OM content, pH and EC, there was a significant species effect. OM content in soils of *D. diacapsis* was significantly higher than in soils of *Lecidella* spp. and in bare soils. OM content of cyanobacteria was intermediate between *D. diacapsis* and *Lecidella* spp. Soil pH was significantly higher in cyanobacteria than in any other cover type; soils of *D. diacapsis* and *Lecidella* spp. had significantly lower pH than bare soil. EC did not differ in soils of cyanobacteria, *Lecidella* spp. and bare soil, while it was significantly lower in *D. diacapsis* soils than in *Lecidella* spp. and bare soil.

Soil fertility (Table 3.5).- Macronutrients: There was a significant species effect for the Ca, K, Mg, and Na content. Overall, cyanobacteria soils had significantly higher Ca, K, Na, and Mg concentration than *D. diacapsis* and *Lecidella* spp. soils. There was no difference in macronutrient concentration between cyanobacteria and bare soils, except for Ca, which was higher in cyanobacteria than in bare soils. *Lecidella* spp. and bare soils differed only in Na and K concentrations. *Diploschistes diacapsis* soils had lower Ca concentrations than bare soil. K concentration was significantly higher in cyanobacteria than in *D. diacapsis*, and intermediate in *Lecidella* spp. For Mg, the three BSC types presented no significant differences compared to bare soil. Na concentration in cyanobacteria soil did not differ from bare soil.

Micronutrients: For Cu, Fe, and Mn concentrations, there was a significant species effect, although there was no significant species effect for Zn. Soil associated with *D. diacapsis* had overall the highest values for Cu, Fe, and Mn. Soil Cu was significantly higher in *D. diacapsis* than in all other soil types, and it did not differ between cyanobacteria, *Lecidella* spp. and bare soil. Soil Fe concentration was significantly higher in *D. diacapsis* than in *Lecidella* spp. and and cyanobacteria soils, where it was significantly lower than in the *Lecidella* spp sites. *Diploschistes diacapsis* soils had significantly higher Fe concentration than bare soil, whereas Fe concentration in cyanobacteria and *Lecidella* spp. did not differ from bare soil concentrations. Soil Mn concentration in *D. diacapsis* and *Lecidella* sp. soils was similar, yet it was significantly higher than in cyanobacteria and bare soil. Soil Mn was higher in *D. diacapsis* soils and lower in cyanobacteria microsites when compared to bare soil.

Response variables	GLM		MCG			
	F	*P*	Bare soil	Cyanobacteria	*D. diacapsis*	*Lecidella* sp.
OM	9.04	**0.0010**	6.9 ± 0.3 c	7.4 ± 0.3 ab	7.7 ± 0.2 a	7.0 ± 0.2 bc
pH	72.30	**<0.0001**	6.6 ± 0.4 b	7.6 ± 0.4 a	5.1 ± 0.2 c	5.4 ± 0.1 c
EC	6.91	**0.0030**	0.605 ± 0.225 a	0.338 ± 0.080 ab	0.189 ± 0.067 b	0.474 ± 0.176 a
Sand	3.70	**0.0340**	20.4 ± 5.3 b	25.3 ± 2.1 ab	23.9 ± 4.0 ab	28.8 ± 4.0 a
Silt	20.52	**<0.0001**	58.7 ± 4.7 a	52.8 ± 2.1 a	45.0 ± 4.8 b	39.3 ± 4.5 b
Clay	38.23	**<0.0001**	20.9 ± 1.3 b	21.9 ± 0.7 b	31.1 ± 2.9 a	31.9 ± 2.7 a
Ca	27.82	**<0.0001**	639.1 ± 89.0 b	911.3 ± 61.3 a	412.7 ± 139.5 c	541.9 ± 31.8 bc
K	52.19	**<0.0001**	1061.2 ± 157.3 a	1179.3 ± 71.6 a	503.0 ± 30.6 c	701.6 ± 83.0 b
Mg	8.54	**0.0010**	140.1 ± 41.6 ab	171.3 ± 18.4 a	93.5 ± 19.0 b	113.9 ± 14.8 b
Na	14.29	**<0.0001**	512.0 ± 170.0 a	349.3 ± 87.0 a	88.2 ± 19.9 b	248.3 ± 86.2 b
Cu	8.42	**0.0010**	0.176 ± 0.012 b	0.199 ± 0.025 b	0.365 ± 0.129 a	0.213 ± 0.012 b
Fe	87.22	**<0.0001**	23.9 ± 4.5 bc	16.7 ± 6.6 c	78.0 ± 10.1 a	34.9 ± 2.6 b
Mn	15.68	**<0.0001**	36.4 ± 9.4 b	22.2 ± 7.0 c	49.7 ± 3.3 a	45.7 ± 6.5 ab
Zn	0.72	0.5160	1.329 ± 0.379 a	0.901 ± 0.294 a	1.220 ± 0.236 a	1.333 ± 0.872 a

Table 3.5. Results of GLM with soil cover type (bare soil, cyanobacteria, *Diploschistes diacapsis, Lecidella* spp.) as fixed effects for the different response variables (mean ± 1SE) and multiple comparisons (Tukey´s test) between soil cover types in the moderate continuous grazing (MCG) site. Different letters within a row indicate significant differences at the $P < 0.05$ level between cover types (columns)

3.- Heavy seasonal grazing

Soil texture (Table 3.6).- Species significant effect was only found for silt and clay content. Considering silt, soils of *D. diacapsis* and *Lecidella* spp. had similar percentage, and these significantly higher than those for cyanobacteria, *A. socialis* and bare soil. Considering clay, soils of cyanobacteria and *A. socialis* had significantly higher clay content than soils of *D. diacapsis* and *Lecidella* spp. Clay content of BSC soils did not differ from that of bare soil.

Soil chemical properties (Table 3.6).- For OM, pH and EC there was a significant species effect. For OM content, BSC soils had not differ but *D. diacapsis* microsites had higher OM content than bare soil. Soil pH was similar for cyanobacteria, *A. socialis* and bare soils, and also, significantly higher than pH values in *D. diacapsis* and *Lecidella* spp. EC of soils of *D. diacapsis* and *Lecidella* spp. did not differ, however these values were significantly higher than those of soils of cyanobacteria. EC of bare soil, cyanobacteria, and *A. socialis* did not differ.

Soil fertility (Table 3.6).- Macronutrients: For soil Ca, Mg, K and Na concentration there was a significant species effect. Ca concentration of *Lecidella* spp. and bare soils was significantly higher than those in cyanobacteria, *A. socialis* and *D. diacapsis* soils. K concentration of *Lecidella* spp. soils was significantly higher than that of cyanobacteria soils. K concentration in BSC soils did not differ from that of bare soils (Table 3.6). Mg concentrations did not differ among soils of *A. socialis*, *Lecidella* spp. and bare soil, yet they were significantly higher than in soils of cyanobacteria and *D. diacapsis*. Na concentration of soils of *Lecidella* spp. was significantly higher than that of all other BSC and bare soil, which did not differ among each other.

Micronutrients: Soil Fe, Mn and Zn concentration had a significant species effect. Fe concentration of *D. diacapsis* soils was significantly higher than in all other BSC and bare soil, which did not differ among each other. Mn concentration was significantly higher in *D. diacapsis* and *Lecidella* spp. soils than in cyanobacteria soils, however it did not differ from *A. socialis* and bare soil In contrast, Zn concentration was significantly higher in cyanobacteria soil than in *D. diacapsis* soils, while it did not differ among cyanobacteria, *A. socialis*, *Lecidella* sp. and bare soil. For both Mn and Zn, BSC soils had similar concentrations as bare soils.

Response variables	GLM		HSG																			
	F		*P*	Bare soil			Cyanobacteria			*A. socialis*			*D. diacapsis*			*Lecidella* sp.					
OM	3.78		**0.0190**	6.8	±	0.4	b	7.0	±	0.2	ab	7.1	±	0.2	ab	7.5	±	0.2	a	7.0	±	0.3	ab
pH	23.09		**<0.0001**	5.5	±	0.1	a	5.3	±	0.2	a	5.4	±	0.1	a	4.8	±	0.2	b	4.9	±	0.2	b
EC	8.53		**<0.0001**	0.072	±	0.023	bc	0.055	±	0.012	c	0.069	±	0.043	bc	0.143	±	0.039	ab	0.269	±	0.186	a
Sand	2.02		0.1300	29.5	±	4.2	a	25.3	±	3.4	a	29.7	±	5.4	a	24.3	±	2.9	a	25.5	±	4.0	a
Silt	14.09		**<0.0001**	44.2	±	4.6	b	45.5	±	2.1	b	39.2	±	4.5	b	52.6	±	3.3	a	52.3	±	1.0	a
Clay	7.85		**0.0010**	26.2	±	2.0	ab	29.3	±	3.5	a	31.1	±	2.4	a	23.1	±	3.1	b	22.2	±	3.9	b
Ca	9.38		**<0.0001**	589.9	±	50.6	a	418.5	±	61.0	b	459.8	±	75.9	b	355.4	±	82.2	b	516.0	±	52.4	a
K	4.65		**0.0080**	362.7	±	62.4	ab	284.3	±	46.0	b	345.9	±	19.7	ab	314.4	±	35.7	ab	398.3	±	51.8	a
Mg	9.52		**<0.0001**	104.1	±	14.7	a	66.3	±	13.3	b	94.4	±	12.5	a	63.6	±	8.8	b	100.5	±	18.9	a
Na	8.24		**<0.0001**	28.1	±	14.7	b	18.6	±	3.8	b	24.7	±	5.6	b	29.1	±	3.8	b	60.7	±	26.4	a
Cu	1.86		0.1560	0.255	±	0.059	a	0.288	±	0.030	a	0.270	±	0.031	a	0.295	±	0.032	a	0.318	±	0.040	a
Fe	14.05		**<0.0001**	34.2	±	5.6	b	37.9	±	4.2	b	32.5	±	2.1	b	55.6	±	7.7	a	42.3	±	6.3	b
Mn	3.75		**0.0200**	56.9	±	12.3	ab	47.0	±	4.2	b	53.9	±	4.9	ab	60.0	±	7.6	a	65.7	±	8.5	ab
Zn	4.34		**0.0110**	1.095	±	0.299	ab	1.768	±	0.650	a	1.068	±	0.166	ab	0.899	±	0.116	b	1.144	±	0.117	ab

Table 3.6. Results of GLM with soil cover type (bare soil, cyanobacteria, *Acarospora socialis, Diploschistes diacapsis*, *Lecidella* spp.) for the different response variables (mean ± 1SE) and multiple comparisons (Tukey´s test) between soil cover types in the heavy seasonal grazing (HSG) site. Different letters within a row indicate significant differences at the $P < 0.05$ level between cover types (columns). Analyses for EC, Na and Zn were performed on natural log transformed data.

4.- Heavy continuous grazing

Soil texture (Table 3.7).- There was a significant species effect for silt and clay content. Silt content in cyanobacteria and *D. diacapsis* soils was significantly lower than in *Lecidella* spp*.* and bare soils, while clay content in cyanobacteria and *D. diacapsis* soils was significantly higher than in *Lecidella* spp*.* and bare soils.

Soil chemical properties (Table 3.7).- For soil OM and pH there was a significant species effect. Soil OM did not differ significantly among soils of BSC types. Cyanobacteria soil had significantly lower OM than bare soil. The pH of cyanobacteria, *A. socialis* and bare soils did not differ but was significantly higher than for *D. diacapsis.*

Soil fertility (Table 3.7).- Macronutrients: For Ca, K and Mg there was a significant species effect. Ca and Mg concentrations presented similar trends across microsites: cyanobacteria, *A. socialis* and bare soils had similar Ca and Mg concentrations, while soils associated with *D. diacapsis* had lower Ca and Mg. K concentration was similar in cyanobacteria and *A. socialis* soils and significantly higher than in *D. diacapsis* and bare soils.

Micronutrients: There was a significant species effect for Cu, Fe, Mn and Zn. Cu and Fe concentration was similar in cyanobacteria, *A. socialis* and bare soil, and significantly higher in *D. diacapsis* soils. Mn and Zn concentration did not differ significantly among BSC soils. However, cyanobacteria soils had significantly higher Mn concentration than bare soil, and both cyanobacteria and *D. diacapsis* soils had higher Zn concentrations than bare soil.

Response variables	GLM		HCG												
	F	*P*	Bare soil			Cyanobacteria			*A. socialis*			*D. diacapsis*			
OM	3.81	**0.0310**	7.0	± 0.5	a	6.3	± 0.4	b	6.7	± 0.4	ab	6.4	± 0.3	ab	
pH	33.38	**<0.0001**	5.5	± 0.1	a	5.5	± 0.3	a	5.6	± 0.1	a	4.6	± 0.1	b	
EC	3.88	0.0290	0.046	± 0.005	a	0.087	± 0.044	a	0.052	± 0.006	a	0.092	± 0.029	a	
Sand	0.41	0.7470	32.3	± 4.9	a	31.3	± 4.2	a	30.6	± 5.9	a	33.7	± 3.2	a	
Silt	17.90	**<0.0001**	45.7	± 5.1	a	33.5	± 3.7	b	42.6	± 3.6	a	31.4	± 1.1	b	
Clay	17.20	**<0.0001**	22.0	± 2.7	b	35.2	± 2.3	a	26.8	± 5.2	b	34.9	± 2.8	a	
Ca	20.33	**<0.0001**	480.9	± 40.5	a	502.5	± 101.4	a	422.5	± 61.5	a	219.1	± 27.1	b	
K	12.31	**<0.0001**	275.0	± 18.7	b	343.9	± 28.7	a	351.0	± 22.7	a	302.0	± 20.1	b	
Mg	11.54	**<0.0001**	79.8	± 7.6	a	87.7	± 21.2	a	83.4	± 14.4	a	42.3	± 6.3	b	
Na	2.53	0.0930	20.3	± 3.7	a	29.8	± 9.3	a	23.9	± 4.2	a	21.4	± 4.9	a	
Cu	25.72	**<0.0001**	0.156	± 0.007	b	0.197	± 0.028	b	0.187	± 0.015	b	0.280	± 0.033	a	
Fe	106.00	**<0.0001**	23.3	± 2.5	b	28.7	± 3.6	b	27.5	± 2.3	b	54.6	± 3.7	a	
Mn	3.71	**0.0340**	42.6	± 4.8	b	47.9	± 2.5	a	45.2	± 2.9	ab	40.6	± 4.2	ab	
Zn	7.88	**0.0020**	0.270	± 0.082	b	0.544	± 0.139	a	0.403	± 0.089	ab	0.574	± 0.126	a	

Table 3.7. Results of GLM with soil cover type (bare soil, cyanobacteria, *Acarospora socialis, Diploschistes diacapsis*) for the different response variables (mean ± 1SE) and multiple comparisons (Tukey´s test) between soil cover types in the heavy continuous grazing (HCG) site. Different letters within a row indicate significant differences at the $P < 0.05$ level between cover types (columns).

iii. Soil physico-chemical properties of cyanobacteria and *Diploschistes diacapsis* along the grazing gradient

To examine, whether BSC effects on and/or responses to specific soil conditions are fixed for cyanobacteria and *D. diacapsis* or differentially modified depending on grazing intensity, we conducted a GLM with soil cover type (cyanobacteria, *D. diacapsis*, bare soil) nested within site (LGE, MCG, HSG, HCG) as fixed effects (N=60) (Table 3.8). For soil texture, soil chemical properties and soil fertility, there were both significant site and species (site) effects, except for the Cu (Table 3.8).

Soil texture.- Sand content of cyanobacteria, *D. diacapsis* and bare soil was similar within sites, however, it differed significantly when comparing cover types across sites (Fig. 3.6a, Table 3.8). In bare soil, sand content in cyanobacteria and *D. diacapsis* soils was significantly higher in LGE than MCG and HSG sites, while it was intermediate in HCG site. For the silt content there was a significant species effect both within sites (except for HSC site) and across sites (Fig. 3.6b). In LGE site, *D. diacapsis* soil had higher silt content than cyanobacteria and bare soil. In MCG site, *D. diacapsis* soil had lower silt content than bare soil (Fig. 3.6b). In HSG site, there was no significant species effect (Fig. 3.6b). In HCG site, both cyanobacteria and *D. diacapsis* microsites had lower silt content than bare soil (Fig. 3.6b). Across sites, bare soil and cyanobacteria soil had higher silt content in MCG than in LGE and heavy grazed sites (HSG and HCG) (Fig. 3.6b). soil had higher silt content in HSG than in LGE and HCG sites (Fig. 3.6b). For the clay content, significant species effect within sites was only found in MCG and HCG sites, and a siginificant species effect across sites was observed along the perturbation gradient except for bare soil (Fig. 3.6c). In MCG site, soil associated with *D. diacapsis* had higher clay content than both cyanobacteria soil and bare soil (Fig. 3.6c). In HCG site, BSC microsites had higher clay content than bare soil (Fig. 3.6c). Across sites, bare soil had similar clay content along the perturbation gradient (Fig. 3.6c). Cyanobacteria soil had higher clay content in HCG site than in LGE and MCG (Fig. 3.6c). *Diploschistes diacapsis* soil had higher clay content in HCG than LGE and HSC sites (Fig. 3.6c).

Soil chemical properties.- For OM there was a significant species effect only within LGE and HCG sites, and across sites for two BSC groups. In the LGE and HCG sites, cyanobacteria soil had lower OM than bare soil (Fig. 3.7a). Across sites, bare soil had similar OM content along the perturbation gradient (Fig. 3.7a), while soil of the two BSC groups had higher OM content in MCG and HSG sites than in LGE site and HCG site (Fig.

3.7a). For soil pH, there was a species significant effect within sites and across sites (Fig. 3.7b). In the LGE and HCG sites, soil associated with cyanobacteria had similiar pH as bare soil, while *D. diacapsis* soil had lower pH (Fig. 3.7b). In the MCG site, soil pH was the highest in cyanobacteria soil, intermediate in bare soil and the lowest in *D. diacapsis* soil (Fig. 3.7b). In HSG sites, *D. diacapsis* soil had a lower pH than bare soil. Across sites, bare soil had the highest pH in the LGE site, intermediate in the MCG and lowest in the heavy grazed sites (HSG and HCG) (Fig. 3.7b). Cyanobacteria soil had similar pH in LGE and MCG sites and higher pH than in the heavy grazed sites (HSG and HCG). *Diploschistes diacapsis* soil had higher pH in the LGE than in the HCG site (Fig. 3.7b). For EC there was a significant species effect within sites (except in HCG site) and across sites (Fig. 3.7c). In the LGE site, the three microsites were significantly different from each other, bare soil had the highest EC, cyanobacteria soil had intermedite EC and *D. diacapsis* soil had lowest EC (Fig. 3.7c). In the MCG site, *D. diacapsis* soil had lower EC than bare soil (Fig. 3.7c). Across sites, bare soil had the highest EC in the LGE site, intermediate in MCG and the lowest in the heavy grazed sites (HSG and HCG) (Fig. 3.7c). Cyanobacteria soil had higher EC than in LGE and HCG sites than in heavy grazed sites (HSG and HCG) (Fig. 3.7c). *Diploschistes diacapsis* soil had higher EC in MCG than in HCG site (Fig. 3.7c).

Soil fertility.- Macronutrients: for Ca there was a significant microsite/species effect within sites and across sites (Fig. 3.8a). In the LGE site cyanobacteria soil had higher Ca than both *D. diacapsis* soil and bare soil (Fig. 3.8a). In MCG site, Ca concentration was significantly different across microsites with cyanobacteria soil having the highest Ca concentration, bare soil intermediate and *D. diacapsis* soil the lowest Ca concentration (Fig. 3.8a). In HSG site, *D. diacapsis* soil had lower Ca than bare soil (Fig. 3.8a). In HCG site, bare soil and cyanobacteria soil had higher Ca concentration than soil associated with *D. diacapsis*. Across sites, bare soil had higher Ca in MCG and HSG than in LGE site (Fig. 3.8a). Soil associated with cyanobacteria had higher Ca in MCG than in the LGE and heavy grazed sites (HSG and HCG), which had similar Ca (Fig. 3.8a). Soil *D. diacapsis* was higher in MCG than in HCG (Fig. 3.8a). For soil K concentration there was a significant species effect within site in LGE and MCG sites, and across sites (Fig. 3.8b). In the LGE and MCG sites, K was similar in bare soil and cyanobacteria soil, and higher than in soil associated with *D. diacapsis* (Fig. 3.8b). Across sites, bare soil had similar K values in LGE and MCG sites, although they were higher than in heavy grazed sites (HSG and HCG) (Fig. 3.8b). BSC microsites had higher K in MCG site than in LGE and heavy grazed

sites (HSG and HCG), which had similar values (Fig. 3.8b). For Mg concentration, there was a significant species effect within site in continuous grazed sites (MCG and HCG), and across sites (Fig. 3.8c). In MCG site, bare soil and cyanobacteria soil had similar Mg concentration and it was higher than in soil associated with *D. diacapsis* (Fig. 3.8c). In the HCG site, cyanobacteria soil had higher Mg than *D. diacapsis* soil (Fig. 3.8c). Across sites, bare soil had highest Mg in MCG site, intermediate in HCG site, and lowest in LGE site (Fig. 3.8c). Cyanobacteria soil had higher Mg in the MCG than in the LGE and heavy grazed sites (HSG and HCG), which presented similar Mg (Fig. 3.8c). *Diploschistes diacapsis* soil had similar Mg in LGE, MCG and HSG sites, while values in MCG site were higher than in HCG (Fig. 3.8c). For Na concentration there was a significant species effect within site (excecpt in the HSG site), and across sites (Fig. 3.8d). In LGE site, three microsites were significantly different from each other; bare soil had the highest Na, cyanobacteria soil intermediate and *D. diacapsis* soil lowest Na concentration (Fig. 3.8d). In MCG site, bare soil and cyanobacteria soil had similar Na, and it was higher than in soil associated with *D. diacapsis* (Fig. 3.8d). In HCG site, cyanobacteria soil had higher Na concentration than *D. diacapsis* soil. Across sites, bare soil and cyanobacteria had the highest Na concentration in LGE site, intermediate in MCG site and lowest in the heavy grazed sites (HSG and HCG) (Fig. 3.8d). *Diploschistes diacapsis* soil had higher Na in LGE and MCG sites than in the heavy grazed sites (HSG and HCG) (Fig. 3.8d).

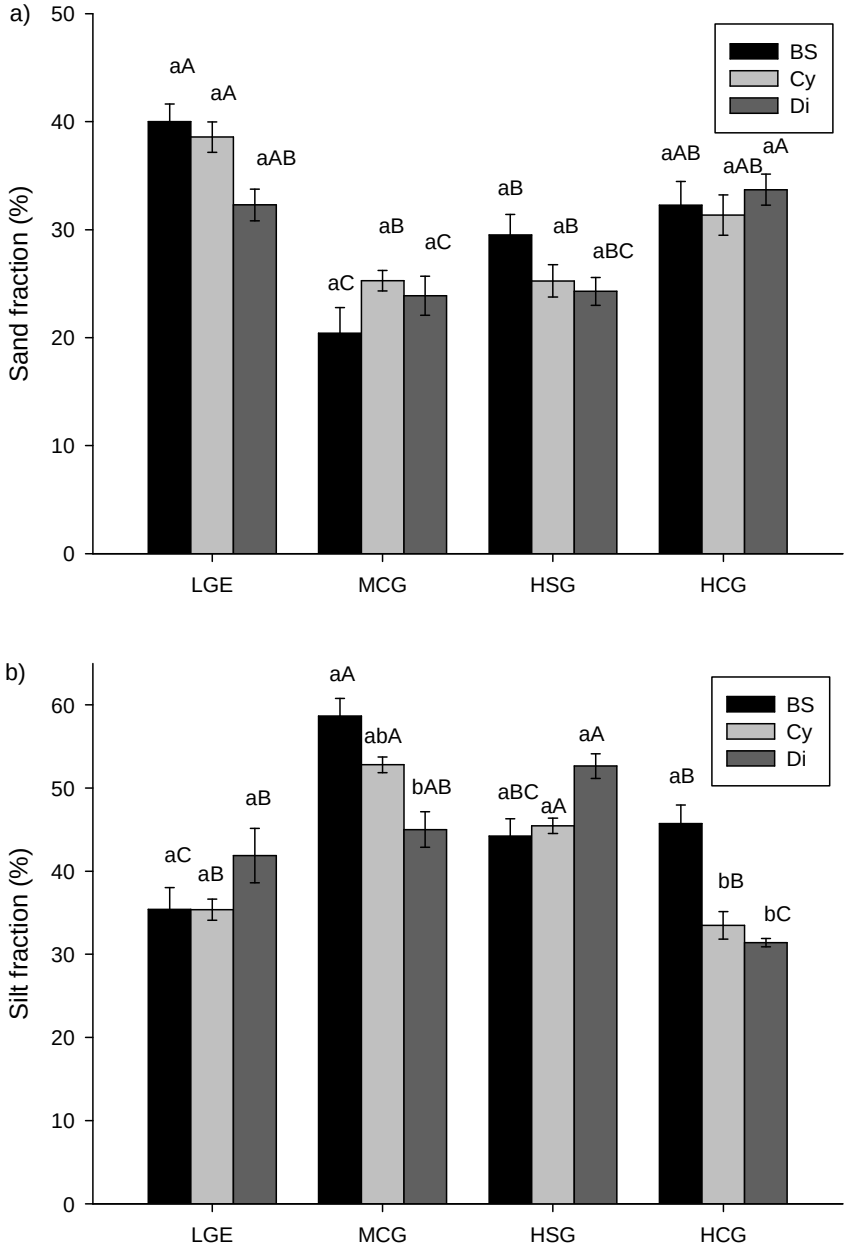
Micronutrients: For Cu concentration, there were no significant species effect within site or across sites (Fig. 3.9a). For Fe concentration, there was a significant species effect within site and across sites (Fig. 3.9b). In the LGE site, soil *D. diacapsis* had the highest Fe, bare soil intermediate and cyanobacteria the lowest Fe concentration (Fig. 3.9b). In the grazed sites (MCG, HSG and HCG), bare soil and cyanobacteria soil had similar Fe concentration, which was lower than in soil associated with *D. diacapsis* (Fig. 3.9b). Across sites, bare soil had similar Fe concentrations along the perturbation gradient (Fig. 3.9b). Cyanobacteria soil had higher Fe in heavy grazed sites than in LGE site (Fig. 3.9b). *Diploschistes diacapsis* soil had higher Fe in MCG site than in the heavy grazed sites (HSG and HCG) (Fig. 3.9b). For Mn concentration, there was a significant species nested within site effect in the LGE and MCG sites and across sites (Fig. 3.9c). Bare soil had higher Mn in HSG site than in LGE and MCG sites (Fig. 3.9c). Cyanobacteria soil had higher Mn in heavy grazed sites (HSG and HCG) than in the LGE and MCG sites (Fig. 3.9c). *Diploschistes diacapsis* soil had higher Mn in MCG than in LGE site and

continuously grazed sites (MCG and HCG) (Fig. 3.9c). For Zn concentration, there was a significant species nested within site effect. In HSG site, cyanobacteria soil had higher Zn than soil associated with *D. diacapsis* (Fig. 3.9d). Across sites, bare soil had higher Zn concentration in LGE and MCG than in HCG site (Fig. 3.9d). Cyanobacteria soil had higher Zn in HSG site than in continuously grazed sites (MCG and HCG). *Diploschistes diacapsis* soil had higher Zn in LGE site than in heavily grazed sites (MCG and HCG) (Fig. 3.9d).

	General linear model				
Response variables	Source of variation	df	Mean square	*F*	*P*
OM	Site	3	5.74	53.04	**<0.0001**
	Species (Site)	8	0.72	6.70	**<0.0001**
pH	Site	3	0.34	133.96	**<0.0001**
	Species (Site)	8	0.14	55.69	**<0.0001**
EC	Site	3	11.45	110.10	**<0.0001**
	Species (Site)	8	2.44	23.47	**<0.0001**
Sand	Site	3	568.03	39.61	**<0.0001**
	Species (Site)	8	40.43	2.82	**<0.0001**
Silt	Site	3	849.68	45.68	**<0.0001**
	Species (Site)	8	176.66	9.50	**<0.0001**
Clay	Site	3	109.45	13.25	**<0.0001**
	Species (Site)	8	122.61	14.84	**<0.0001**
Ca	Site	3	209657.00	32.73	**<0.0001**
	Species (Site)	8	148806.00	23.23	**<0.0001**
K	Site	3	4.04	319.99	**<0.0001**
	Species (Site)	8	0.63	49.57	**<0.0001**
Mg	Site	3	19724.90	55.00	**<0.0001**
	Species (Site)	8	3673.80	10.24	**<0.0001**
Na	Site	3	32.51	468.26	**<0.0001**
	Species (Site)	8	3.86	55.56	**<0.0001**
Cu	Site	3	0.04	2.18	0.1020
	Species (Site)	8	0.03	2.07	0.0580
Fe	Site	3	125.70	2.81	**0.0490**
	Species (Site)	8	2813.60	62.92	**<0.0001**
Mn	Site	3	1230.76	27.74	**<0.0001**
	Species (Site)	8	461.54	10.40	**<0.0001**
Zn	Site	3	3.88	26.49	**<0.0001**
	Species (Site)	8	0.41	2.81	**0.0120**

Table 3.8. Summary of data analysis of GLM with site (LGE= long-term grazing exclosure, MCG = moderate continuous grazing, HSG = heavy seasonal grazing, HCG = heavy continuous grazing) as main effect and species (bare soil, cyanobacteria, *D. diacapsis*) as nested effect for different response variables (soil properties); analyses for pH, EC, K, Na

and Fe were performed on natural log transformed data. OM=organic matter, EC= electrical conductivity.



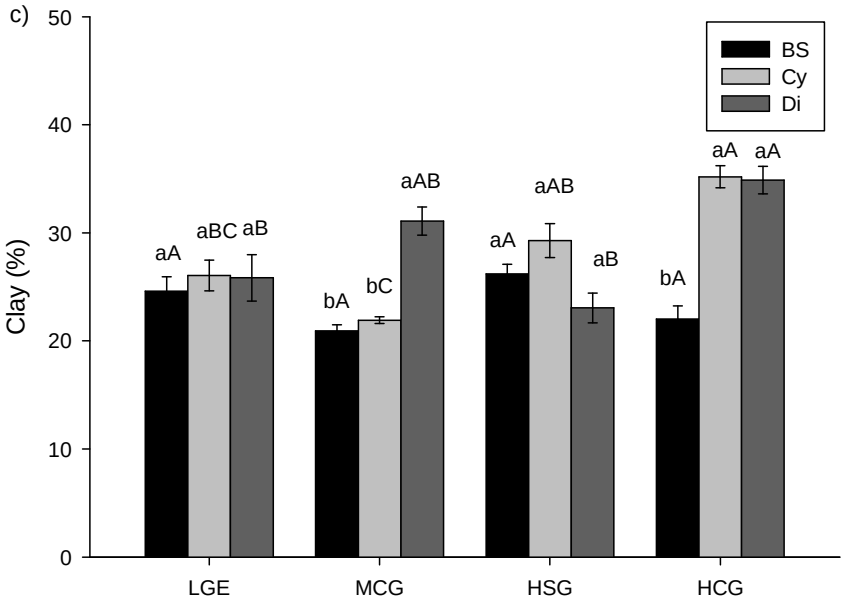
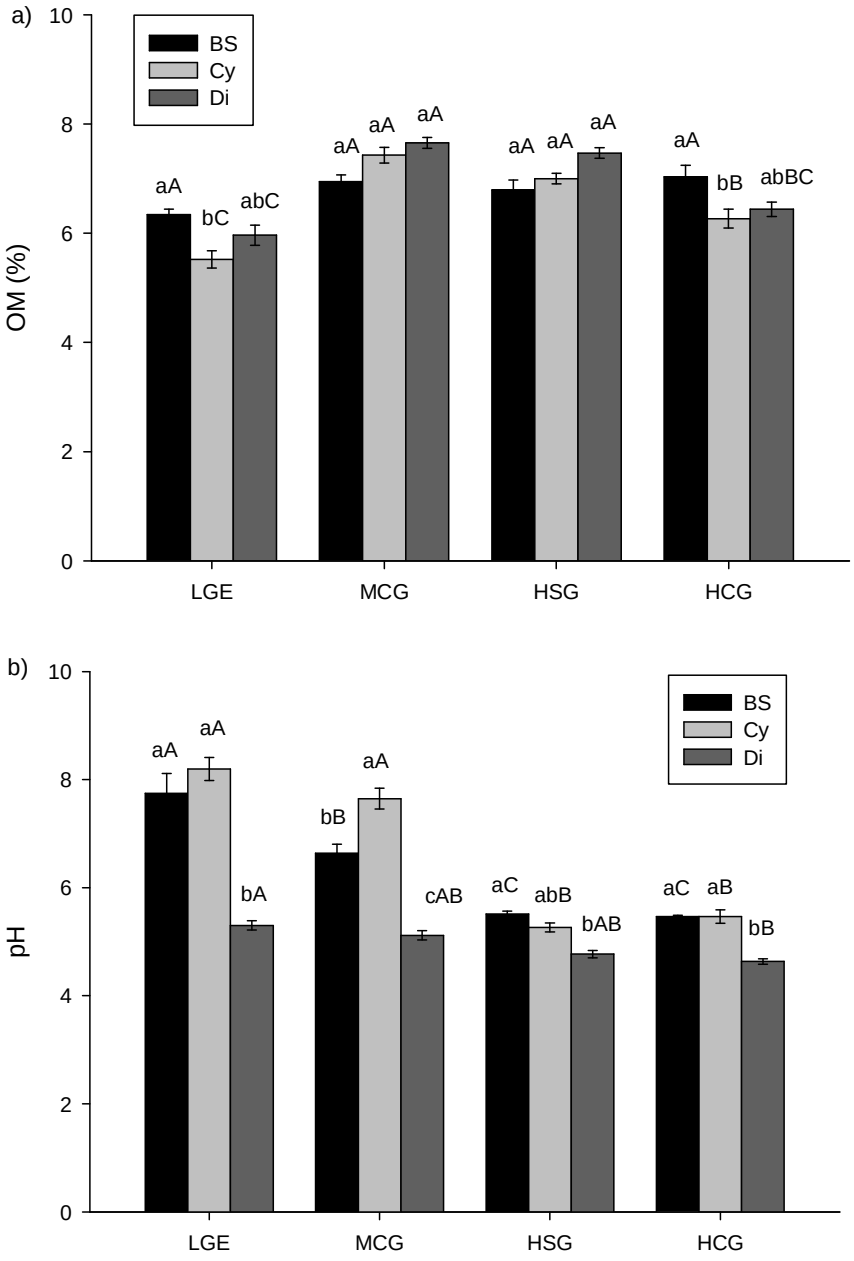


Fig. 3.6: Mean (± 1 SE) of soil (a) sand content (%), (b) silt content (%) and (c) clay content (%) of bare soil (BS), cyanobacteria crust (Cy) and *D. diacapsis* (Di) microsites. Significant differences between species (sites) were determined from Tukey´s multiple comparisons test at $P < 0.05$. Different small letters above bars indicate significant differences between species (microsites) within a site. Different capital letters above bars indicate significant differences between species (microsites) across sites. (For acronyms see text).


a)
OM (%)
BS
Cy
Di
aA
bC
abC
aA
aA
aA
aA
aA
aA
aA
bB
abBC
LGE
MCG
HSG
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cAB
aC
abB
bAB
aC
aB
bB

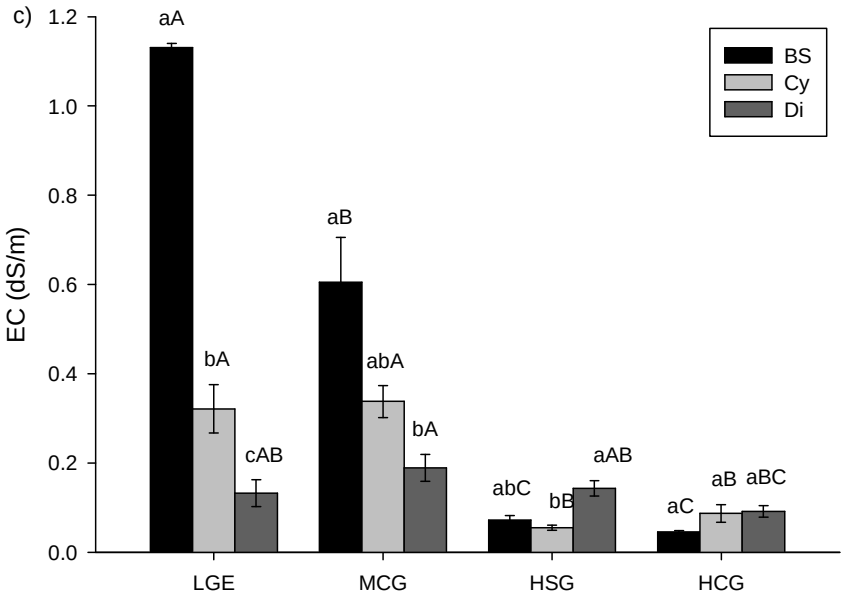
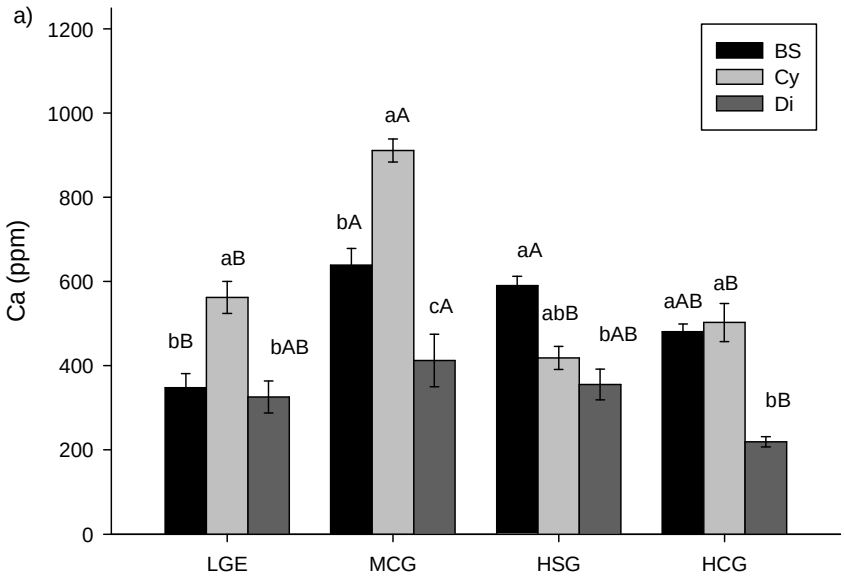
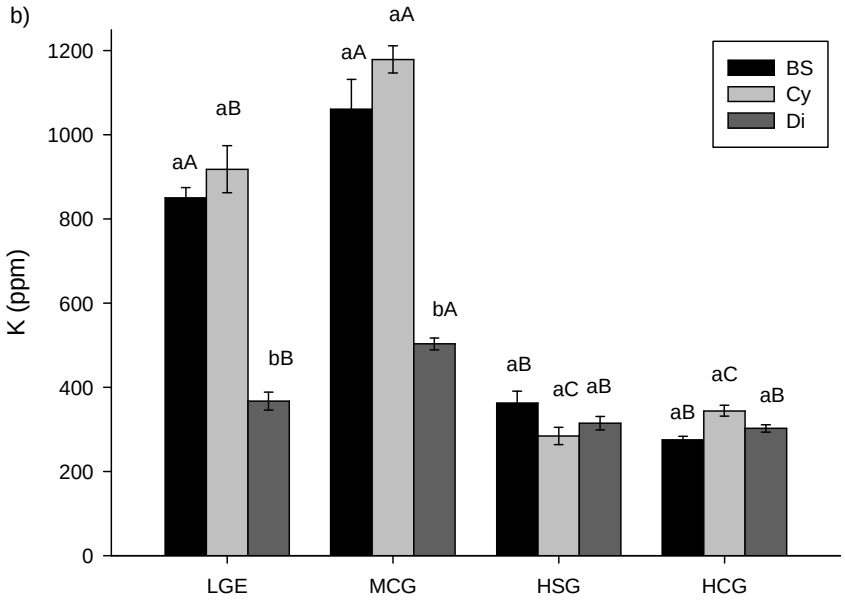


Fig. 3.7: Mean (± 1 SE) of soil (a) OM content (%), (b) pH and (c) EC of bare soil (BS), cyanobacteria crust (Cy) and *D. diacapsis* (Di) microsites. Significant differences between species (sites) were determined from Tukey´s multiple comparisons test at $P < 0.05$. Different small letters above bars indicate significant differences between species (microsites) within a site. Different capital letters above bars indicate significant differences between species (microsites) across sites.




b)
K (ppm)
1200
1000
800
600
400
200
0
BS
Cy
Di
aA
aB
aA
aA
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bA
aB
aC
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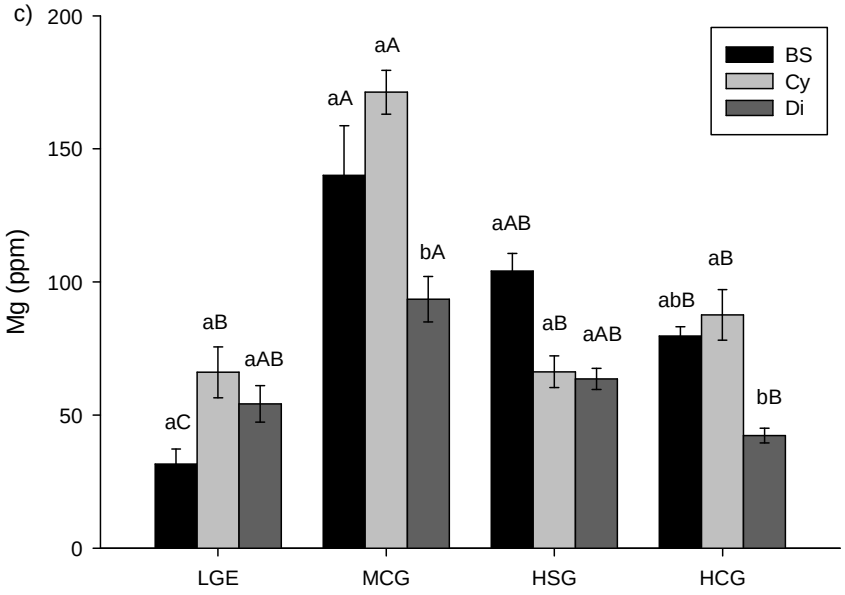
aB
aC
aB
LGE
MCG
HSG
HCG


c)
Mg (ppm)
200
150
100
50
0
BS
Cy
Di
aC
aB
aAB
aA
aA
bA
aAB
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aAB
abB
aB
bB
LGE
MCG
HSG
HCG

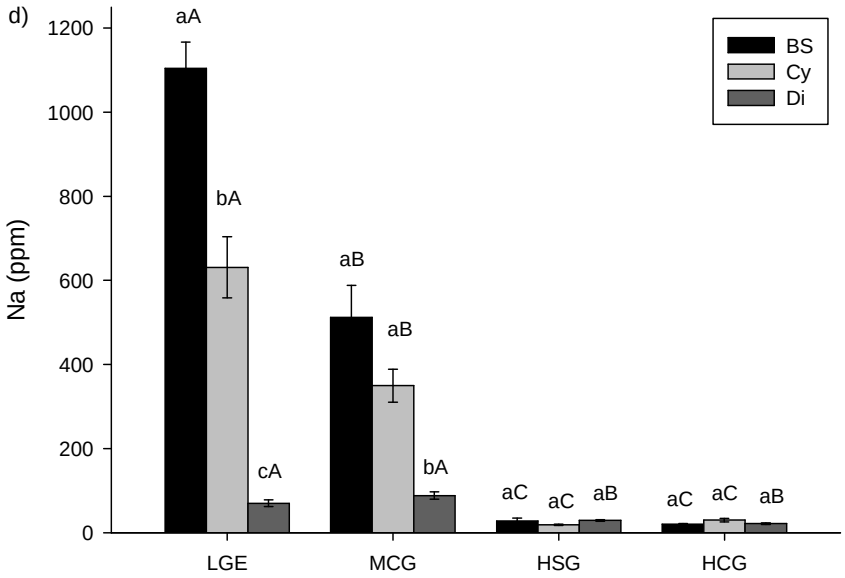
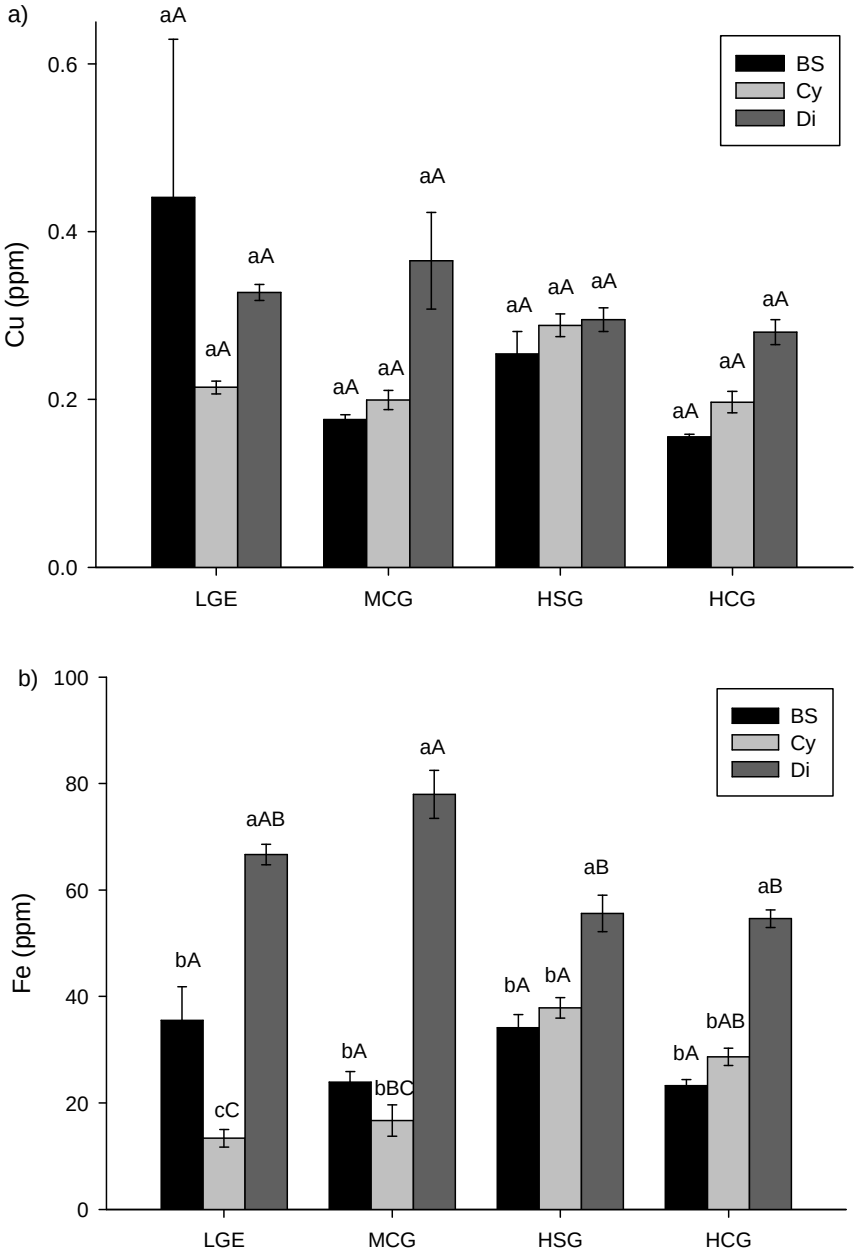


Fig. 3.8: Mean (± 1 SE) of (a) Ca (ppm), (b) K (ppm), (c) Mg (ppm) and (d) Na (ppm) concentration of bare soil (BS), cyanobacteria crust (Cy) and *D. diacapsis* (Di) microsites. Significant differences between species (sites) were determined from Tukey´s multiple comparisons test at $P < 0.05$. Different small letters above bars indicate significant differences between species (microsites) within a site. Different capital letters above bars indicate significant differences between species (microsites) across sites.


a)
Cu (ppm)
0.0
0.2
0.4
0.6
BS
Cy
Di
aA
aA
aA
aA
aA
aA
aA
aA
aA
aA
aA
LGE
MCG
HSG
HCG
b)
Fe (ppm)
0
20
40
60
80
100
BS
Cy
Di
bA
cC
aAB
bA
bBC
aA
bA
bA
aB
bA
bAB
aB
LGE
MCG
HSG
HCG

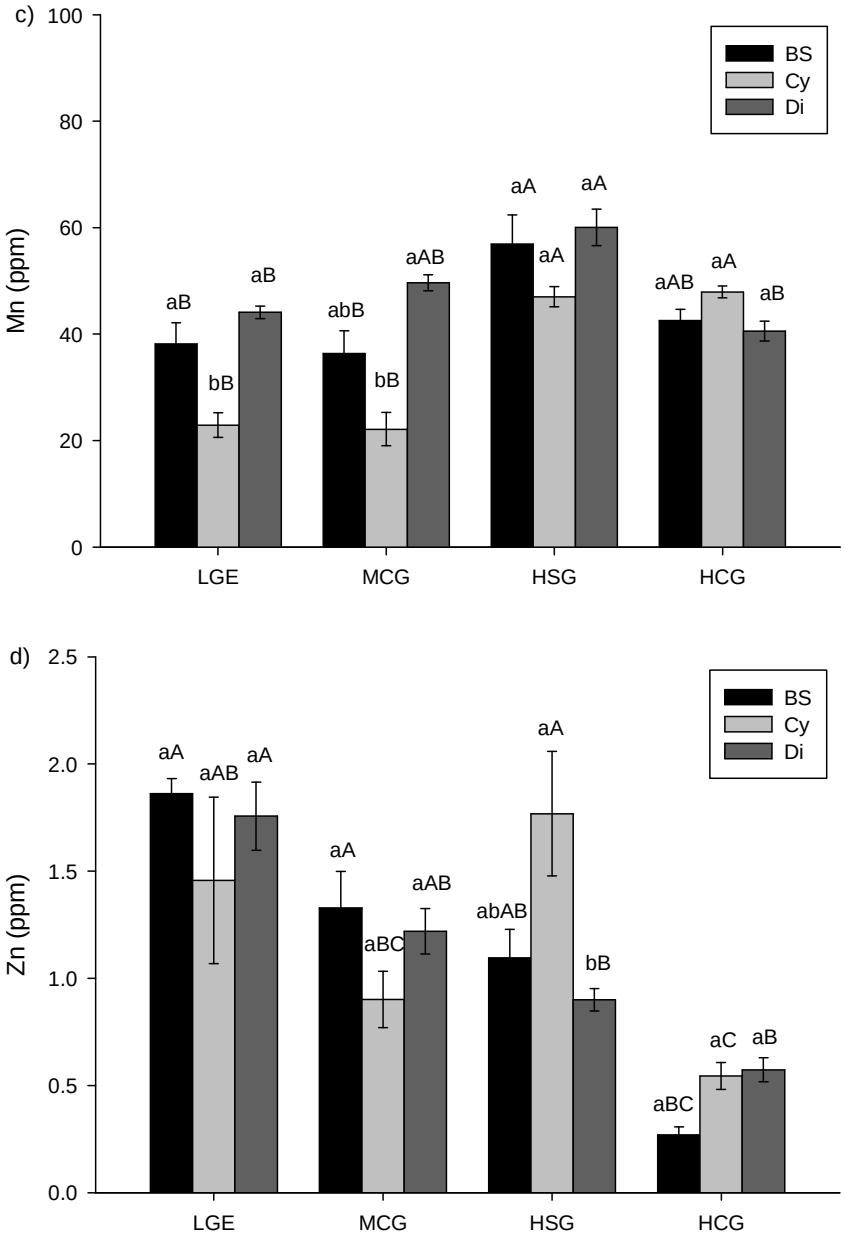


Fig. 3.9: Mean (± 1 SE) of (a) Cu (ppm), (b) Fe (ppm), (c) Mn (ppm) and (d) Zn (ppm) concentration of bare soil (BS), cyanobacteria crust (Cy) and *D. diacapsis* (Di) microsites. Significant differences between species (sites) were determined from Tukey´s multiple comparisons test at $P < 0.05$. Different small letters above bars indicate significant differences between species (microsites) within a site. Different capital letters above bars indicate significant differences between species (microsites) across sites.

iv. Discussion:

Biological soil crusts in semiarid ecosystems alter soil fertility, soil stability and hydrologic processes (Belnap, 2003). BSC alter soil surface chemistry in several ways: 1) when exuding polysaccharides, organic acids and other organic and inorganic compounds (e.g. NO_3^-, phosphorus) and chelate elements into the soil surface (Lange, 1974; Kleiner and Harper, 1977; Harper and Pendleton, 1993; Thiet *et al.* 2005; Veluci *et al.* 2006; Johnson *et al.* 2007), 2) when taking up soil nutrients (Lange, 1974), and 3) by forming microhabitats for diverse soil bacterial and fungal communities (Garcia-Pichel *et al.* 2003; Bates and Garcia-Pichel, 2009), and micro- and meso-faunal (Belnap and Phillips, 2001; Bamforth, 2004; Bamforth, 2008) communities in surface soils. E.g. when soil lichens exude organic acids into the soil surface to chelate elements essential for their growth, they decrease locally soil pH and consequently increase the solubility and availability of soil nutrients (mostly of micronutrients). Biological soil crusts also modify soil physical characteristics by penetrating the top millimetres to centimetres with rhizines, rhizoids, hyphae, or gelatinous filaments that enhance the formation of both soil aggregates (Schulten, 1985) and a cohesive crust that stabilizes the soil surface and traps fine dust particles containing bioessential nutrients (e.g. N, P, K, Mg, Cu, Fe, Mn) (Black, 1968; Reynolds *et al.* 2001) additionally enhancing soil fertility and locally changing soil texture. Also, during the rapid wetting and drying cycles in arid and semiarid climates, lichen thalli, moss stems and cyanobacterial filaments go through expansion and contraction cycles that may greatly influence soil surface microtopography and soil structrure (Belnap and Gardner, 1993). Obviously, the extent to which BSC activities may exert species-specific effects on soil physico-chemical characteristics depends on the taxon-specific morphology and external disturbance factors that may influence the activity, structure, morphology and composition of BSCs. All these factors may potentially lead to a physico-chemically active and diverse BSC - substrate interface and contribute to a distinct fine-scale soil surface heterogeneity. This may not only have important implications on soil fertility and hydrological processes, but on plant productivity and cover and spatial patterns of ecosystem function (Belnap and Harper, 1995; Maestre *et al.* 2005; Belnap, 2006). While the spatio-temporal heterogeneity of soil characteristics in association with perennial plants has been well described for arid and semiarid ecosystems (Jackson and Caldwell, 1993; Ryel and Caldwell,1998) little is known of the nature and dynamics of soil spatial heterogeneity caused by the interaction between different BSC organisms and surface

soils and to which degree external sources of perturbation such as trampling by livestock may alter this soil heterogeneity.

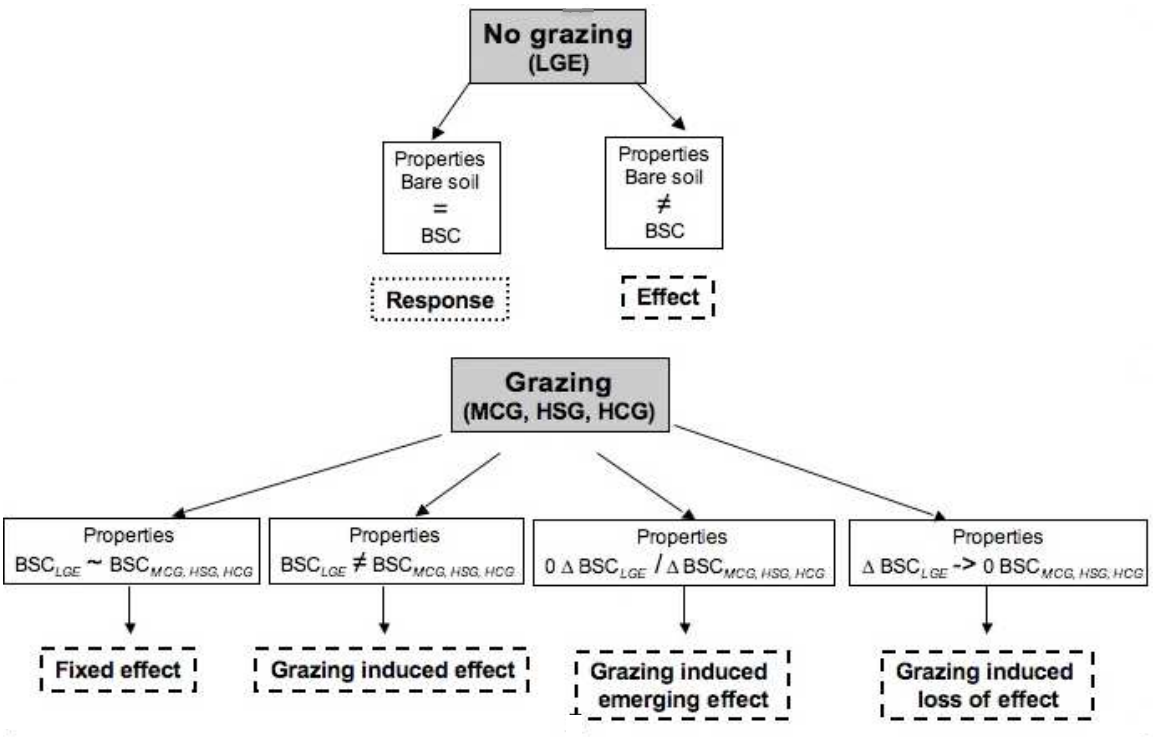


Fig. 3.10. Conceptual model of biological soil crust (BSC) response and/or effect patterns on soil physico-chemical properties in long-term exclosure (LGE) (top) and fixed effects, grazing induced effects, grazing induced emerging effects, and grazing induced loss of effect in sites with moderate continuous grazing (MCG), heavy seasonal grazing (HSG) and heavy continuous grazing (HCG) (bottom). $BSC_{LGE,MCG,HSG,HCG}$ = any soil physical and/or chemical property associated with different BSC species in different grazing sites.

In this study, we could elucidate the ecological/functional role of cyanobacteria, soil lichen and bryophytes in contributing to soil heterogeneity in a semiarid grassland ecosystem of Central Mexico. By comparing soil physical and chemical properties in soil associated with different BSC types and those found in bare soil we could demonstrate whether BSC presence is responding to and/or influencing local soil physical and chemical characteristics. Also, by setting up the study along a grazing gradient including a long-term grazing exclosure, and seasonal and continuous, moderate and heavy grazing regimes,

we could assess and separate the following BSC patterns: 1) When individual soil characteristics of bare soil are similar to those associated with different BSC types, then BSC types exhibit a “response” pattern to the overall soil characteristics typical for an ungrazed or grazed site. 2) When individual soil characteristics of bare soil differ from those associated with BSC types, then BSC types exhibit an “effect” pattern where BSC characteristics modify certain soil properties for an ungrazed or grazed site. 3) When a certain “BSC – effect” is maintained under different grazing regimes, then BSC types exhibit a “fixed effect”, i.e. BSC could be an indicator for a certain soil variable. 4) When a certain “BSC – effect” in any of the grazed sites is different from the BSC – effect from the LGE sites, then BSC types exhibit a “grazing-induced BSC effect”. 5) When there are no differences in soil properties between BSC types and bare soil in LGE sites, and they appear in response to a certain grazing regime, then BSC exhibit a “grazing induced emerging BSC effect”. This differs from a “grazing-induced BSC effect”, where a BSC effect is present in ungrazed sites but gets altered under different grazing regimes.

We found several “fixed effects” pattern of different BSC species on soil chemical and fertility characteristics, however some properties were “more fixed” than others. E.g. Soil OM in soil associated with cyanobacteria was lower compared to bare soil, however only in HCG sites, while in the other grazing sites (MCG, HSG) grazing effects seem to override BSC effects. For pH, however, there was a consistent strong “fixed effect” associated with *D. diacapsis,* in that it drastically reduced pH levels in all sites independently of grazing intensity. Similarly, *D. diacapsis* increased Fe concentration in all sites. Cyanobacteria and *D. diacapsis* reduced EC only in MCG sites, while under heavy grazing this “fixed” effect disappeared. Fixed effects were also observed with macronutrients (Ca and K) and Na but only in MCG site; cyanobacteria increased Ca and decreased Na, while *D. diacapsis* reduced K and Na. “Grazing-induced effects” were observed in *D. diacapsis,* which reduced Ca only in HSG and HCG sites but not in LGE and MCG sites. We detected two “grazing-induced emerging BSC effects” associated with soil physical characteristics and one with macro and micronutrients: in moderately grazed and heavily grazed sites (MCG, HCG), where both cyanobacteria (only in HCG) and *D. diacapsis* (in MCG and HCG) accumulated relatively more clay particles (and relatively less silt particles) than bare soil. This effect was not observed in the LGE site. Further, *D. diacapsis* reduced Mg concentration in MCG and HCG sites and cyanobacteria accumulated Zn in soils in HSG sites. Hence, BSC cover in grazed sites may either have a passive effect on soil, such as

fine particle retention or modify macro or micronutrient concentration. We did not find a global loss of an "effect" response due to grazing (in general), but we did see that most species-specific effects disappeared under the HSG and HCG conditions (K, OM, EC, etc,). Further studies should be conducted to examine the effect of BSC species on soil P, NH_4^+ and NO_3^-.

Soil physicochemical environment associated with BSC

While vegetation free soil interspaces are often described as nutrient depleted sites and contrasted to islands of fertility formed by vascular plants, our study showed that cyanobacteria, and four lichen species in the soil interspaces greatly contributed to soil fertility (macronutrients and micronutrients). However, high grazing impact (heavy grazing regimes; HSG, HCG) may greatly reduce these ecological roles. At a small scale, most soil physical and chemical characteristics differed more clearly between different BSC types and bare soil within a grazing site than among grazing sites (see Results section 2 and 3). However, these differences were not as apparent under high grazing intensity. E.g., pH values in bare soil along the grazing gradient ranged between 7.7 (LGE) and 5.5 (HCG), while within grazing sites between 8.2 (cyanobacteria) and 5.3 (*D. diacapsis*) (in LGE site) and 5.6 (*A. socialis*) and 4.6 (*D. diacapsis*) (in HCG site). Similarly, soil OM in bare soil ranged between 6.3% (LGE) and 7% (HCG) along the grazing gradient, while within grazing sites between 5.5% (cyanobacteria) and 6.6% (mosses) (in LGE site) and 6.3% (cyanobacteria) and 7.0% (bare soil) (in HCG site). Soil texture of the different grazing sites are silt loams, where fine material in bare soils ranged between 60 (LGE) and 80 (MCG) percent. While in LGE site, different BSC types did not modify local soil texture, in grazed sites, it was mostly the lichens *D. diacapsis* and *Lecidella* spp. that accumulated up to 10 percent more clay or silt particles (MCG, HSG) than bare soil. For soil macronutrients, Ca concentration in bare soil ranged between ca. 350 ppm (LGE) and 640 ppm (MCG) along the grazing gradient, while it ranged between ca. 355 (*D. diacapsis*) and 516 ppm (*Lecidella* spp.) in HSG site and between ca. 410 (*D. diacapsis*) and 910 (cyanobacteria) ppm in MCG sites.

In contrast, concentration of soil potassium (K) and magnesium varied more among grazing sites (for K: 275 ppm in HCG and 1060 ppm in MCG sites; for Mg: 31 ppm in LGE and 104 ppm in HSG site) than within grazing sites, where K concentration ranged between 300 (*D. diacapsis*) and 350 ppm (*A. socialis* spp.) in HCG sites and between 500

(*D. diacapsis*) and 1180 ppm (Cyanobacteria) in MCG sites; and where Mg concentration ranged between 54 (*D. diacapsis*) and 72 ppm (Mosses) in LGE site.

For micronutrients, also within-site (between- BSC type) differences were more pronounced than between sites with different grazing regimes. Hence, this spatial assessment (within site vs. between site) suggests that BSC lichen and cyanobacteria contribute to important soil heterogeneity.

Grazing effects on BSC activity

Cyanobacteria are the dominant BSC types in the semiarid grasslands and occur in all grazing sites. Actively N_2 fixing cyanobacteria have been shown to increase soil pH leading to a greater solubility and availability of macronutrients (Belnap, 2002). Nitrogenase activity is enhanced by Mn, Fe and Zn availability, although may be severely affected by physical damage of BSC through trampling, etc. (Belnap and Eldridge, 2001). A comparison of micronutrient concentration (Fe, Mn, Zn) and pH values in association with cyanobacteria among different grazing regimes suggests that in ungrazed (LGE) and moderately grazed (MCG) sites, cyanobacteria were actively fixing N_2, while in heavily grazed sites (HSG, HCG) they were negatively influenced by trampling. When seemingly active in low-impact sites, pH values in cyanobacteria soils ranged between 7.6 (MCG) and 8.2 (LGE) – and were significantly higher than in bare soils of respective sites. However, in high-impact sites, pH values ranged between 5.3 (HSG) and 5.5 (HCG) – and did not differ from bare soils. Also, in low-impact sites (LGE, MCG), soil Fe and Mn concentration associated with cyanobacteria were significantly lower than in bare soils, while in high-impact soils Fe and Mn concentration in cyanobacteria was significantly higher than in bare soil concentrations. Hence, nitrogenase activity seems to tolerate some level of grazing, although there is a threshold beyond which cyanobacteria do not seem to contribute to soil N.

e. Conclusion

Grazing intensity has been related to both higher and lower soil heterogeneity, and the nature of the effect depends on the scale (Steffens *et al.* 2009). In low-impact grazing sites (LGE, MCG), at the microscale, cyanobacteria and bare soil were similar in that they were associated with rather alkaline microsites compared to mosses and lichen rather leading to local soil acidification. However, high-impact sites (HSG, HCG) seemed to reduce local

soil heterogeneity associated with different BSC types and bare soil. *Diploschistes diacapsis* is the only lichen species that occurred along the whole grazing gradient and contributed rather consistently to soil heterogeneity suggesting a fixed effect pattern (see Fig 3.9 - conceptual model). In contrast, *Lecidella* spp. soils seemed to constitute highly different combinations of soil properties depending on grazing intensity. Both bare soil and cyanobacteria microsites showed different soil property combinations along a gradient consisting of macronutrients (Ca, Mg and Na) on the one side, and micronutrients (Cu, Fe) and OM on the other side. Instead, *D. diacapsis* soil conserved microsite identity, regardless of grazing intensity, suggesting a fixed species-specific effect on soil properties.

As expected, mosses, cyanobacteria and lichen microsites presented differences in most of the soil properties related to chemical characteristics and soil fertility, and also, it differed from bare soil characteristics. However, these differences diminished or even disappeared under heavy grazing intensity (see Fig 3.9 – conceptual model: grazing induced loss of BSC effect), suggesting a homogenization of topsoil properties due to disturbance of BSC activity and functioning.

BSC organisms can bind sulfides of copper, Zn, zinc dust, and ferric hydroxide (Belnap, 2003), increasing nutrient availability. However, when soil is covered by BSC, nutrient translocation may occur from soil surface to crust organisms body (Goyal and Seaward, 1981; Brown and Bates 1990), and may result in a depletion of nutrients compared with uncrusted soil (Beraldi-Campesi *et al.* 2009). In this study, macronutrients (Ca, K, Mg) and micronutrients (Fe, Mn) showed differences between different soil microsites (BSC and bare soil) regardless of grazing intensity. However, the nature and strength of these changes depended on BSC type and species. Higher Cu, Zn and Fe concentration in soil beneath lichen cover, compared with bare soil, has been found by Bowker and coworkers (2006).

Diploschistes diacapsis microsites exhibited a more consistent effect-response pattern along the perturbation gradient concerning most of the soil chemical and fertility properties, while bare soil and cyanobacteria microsites tended to vary mostly with grazing intensity.

Trampling activity and wind erosion combined may lead to a loss of fine-grained material in grazing semi-arid ecosystems (Neff *et al.* 2005). The thick and continuous thalli of *D. diacapsis* protect soil surface and seem to buffer soil erosion, maintaining a higher percentage of clay fraction and thus fertility under continuous grazing. *Diploschistes diacapsis* microsites are consistently acidic along the perturbation gradient, and buffer EC.

Also, soil of *Diploschistes diacapsis* presented higher concentration of Cu in continuously grazed sites (MCG, HCG), and a consistent increases in Fe concentration along de perturbation gradient, compared with bare soil. This suggest that *Diploschistes diacapsis* increases micronutrient availabitlity.

Our study is one of the first to demonstrate quantitatively that BSC species/taxa contribute to soil heterogeneity in the vegetation free interspaces between tussock grasses in the semiarid grassland ecosystem of Central Mexico. Our results provide new insights into species-specific (spatial) effects on soil physico-chemical characteristics and their potential functional role on ecosystem processes. These interactive relations are currently discussed also for vascular plants (Suding and Hobbs, 2009) in an functional group context.

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Chapter IV: Synthesis, Conclusions and Future work

BSC should be considered a key structural and functional element of semi-arid ecosystems, due to their ubiquity, their contribution to ecosystem diversity and their role in soil conservation. Several species and taxa of BSC have shown to be rather resistant to grazing, which is a dominant driver in almost all semiarid ecosytems worldwide. BSC colonize vegetation free interspaces, playing several functional/ecological roles that have been traditionally assigned to vascular plants only. Here, we explored BSC community attributes such as species composition, species richness and cover, and their potential functional role related to local soil physico-chemical properties. Grassland ecosystems of Central Mexico constitute a complex spatio-temporal mosaic of differently managed grassland sites and differently aged exclosures, thus providing an excellent framework to study BSC communities.

BSC species composition, species richness, and cover of BSC communities were differentially determined by grazing intensity and seasonal wetting. Depending on grazing intensity and BSC attributes (especially species composition and cover), these communities contribute differently to soil heterogenity, which may also vary between seasons. In summary, long-term exclosure site presented more than one species that occurred only in this particular site, suggesting that natural recovery of most likely highly grazing vulnerable species is faster than expected. While along the perturbation gradient species richness changed and cover did not, species richness did not change along the recovery gradient yet cover change, suggesting that grazing pressure selects more against certain species (highly vulnerable) that may establish (resistant to trampling impact) and grazing release affects more the degree of cover development (probably through other variables such as greater water availability, change in microclimate by presence of a more dense perennial vegetation). Semiarid grasslands of Vaquerias, Jalisco hold rich communities of biological soil crust communities, in a wide variety of biotic and abiotic conditions, that contribute to soil spatial heterogeneity, increasing soil fertility and mantaining fine particles in vegetation free interspaces, otherwise poor-nutrient eroded areas, specially under grazing activity.

BSC organisms exhibited a species-specific response to and/or effect on certain individual or combined soil physico-chemical properties. *Diploschistes diacapsis* soil showed interesting and particular characteristics in terms of texture, chemical properties

and soil fertility, having a potentially important role in soil conservation, and these patterns were observed all along the grazing gradient. In general (considering both bare soil and crusted soil), grazed sites presented higher organic matter, lower pH and EC than long-term exclosure, also, lower sand content and higher concentrations of Mg and Mn, but lower concentrations of Na and Zn.

Future research on BSC community composition and functional role should focus on in-depth analysis of the underlying mechanisms of the controls of species composition (niche complementarity and resource competition theory) in different grazing sites. In this context, it is highly recommended that the members of the “cyanobacteria crust” will be identified with molecular techniques, as they may be composed also of microfungi and algae, and most likely differ between sites. Lichen taxa showed an unusually high number of species in these grassland ecosystems of central Mexico. Since lichens are formed by continuous or semi-continuous thalli, in future studies the size and spatial arrangement of lichen fragments should be incorporated into the analysis of community dynamics of BSC such as diversity and evenness along the perturbation and recovery gradient. Also, a more in-depth analysis of the temporal dynamics of medium-sized lichen patches may reveal fragmentation processes in lichen cover due to livestock trampling and thus should be monitored in future studies.

Essential nutrients such as C, N and P should be included in soil fertility assessments associated with BSC presence. In order to corroborate the functional role of BSC in soil fertility, nutrient concentration in lichen thallus and bryophyte tissue should be determined. To corroborate the nature and quality of soil chemical properties in association with BSC cover as well as the rate of exudation of chemical compounds released by BSC into the soil, detailed studies with resin-bags should be implemented along the recovery and perturbation gradient; the latter, to see if any physiological damage (by trampling) has interfered with BSC activity.