Effects of drought and water pulses on microbial functionality and the role of Cyanoprokaryota in the rhizospheres of gypsophytes

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Abstract

Effects of drought in semiarid Mediterranean environments are known in many aspects; however, there are others for which information is lacking. In this work, two samplings were carried out - the first during a summer drought and the second during spring - in the rhizospheres of three gypsophytes and in non-rhizospheric soil, to detect the responses, fundamentally biochemical, to the availability of water in the soil. Urease and protease showed higher values after the drought whereas the activity of the β-glucosidase was highest in the spring. This pattern was the same for all the rhizospheres tested. However, the arylsulfatase and alkaline phosphatase did not change in terms of the sampling date or the rhizosphere under study. Surprising results were obtained when water retention and water loss were studied, with the highest values being obtained for the dry season due to the association of Cyanoprokaryota (with high diversity and rarity) with the rhizospheres as a result of a water pulse. The results in our work are also explained by two water pulses that occurred before the samplings. Several parameters, whose values changed markedly due to the microbiological activation just after the drought and water pulses, are proposed as indicators of this activation: microbial biomass carbon and basal respiration rate, together with the activities of the enzymes urease and protease. However, it was the dehydrogenase activity in spring that best reflected the microbiology associated with the carbon cycle, together with the enzyme β-glucosidase. The interrelationships between carbon and nitrogen were shown through the indices: water soluble nitrogen and water soluble carbon. We propose three functional adaptation mechanisms of these plants associated with the Cyanoprokaryota in their rhizospheres and related to the water availability as determined by drought and water pulse effects. *Herniaria fruticosa* is a pioneer with the greatest diversity of Cyanoprokaryota, in both summer and spring (10 species and 11 species, respectively), and with high-medium abundance (5-30%). *Teucrium balthazaris* exhibits an intermediate strategy, with greater diversity of Cyanoprokaryota in spring (7 species) and predominance of high-medium abundance (5-30%). Finally, *Helianthemum squamatum* has lower diversity, with one species in summer (with low abundance, < 5%) and no species in spring.

Keywords: Biogeochemical cycles, Blue-green algae, Cyanobacteria, Gypsiferous community, Rhizospheric microbiota, Semiarid environment.

1. Introduction

The habitat of the gypsiferous outcrops in the Southeastern Iberian Peninsula is characterized by endemic and threatened plants (Escudero, 2009), which tend to be closely linked to the substrate distribution (Meyer, 1986) that is confined to arid and semiarid climates. The importance of the protection of these areas is manifested by the EU Habitats Directive (European Community, 1992). The Mediterranean vegetation of the gypsiferous steppes (1520* Gypsophiletalia) or *yesares* consists of formations of species of woody, small or medium sized plants, with high diversity and richness. This type of plant community usually appears as highly fragmented fertility islands, which alternate with bare soil surfaces where the biological crust supports a high coverage of species. Here, the lichen and moss communities have been widely studied and identified (Guerra et al., 1995; Egea and Alonso, 1996), while very little is known about the cyanobacterial communities (Domínguez and Asencio, 2011), although they are widely distributed in gypsiferous environments. The processes within vegetated patches and soil crusts were assumed to be relatively independent (Schlesinger et al., 1990), but evidence is now accumulating to suggest that these patches may be interconnected by networks of fungal hyphae (Collins et al., 2008).

It is considered that the Cyanoprokaryota of the arid and semiarid zones that grow in soils with high concentrations of salts are of great importance in soil stabilization and nutrient enrichment, due to their nitrogen (N) fixation and organic carbon (C) production. Cyanoprokaryota are capable of photosynthesis, respiration, decomposition, and mineralization (Mager, 2010) producing various growth promoting substances, like gibberellins, auxins, vitamin B12, free amino acids, and polysaccharides. Such substances have beneficial effects on soil structure, the growth of crop plants as well as useful bacteria (El-Enany and Issa, 2000). Baran et al. (2011) showed that the interactions with primary producers and N_2 fixers (many of them Cyanoprokaryota) and other bacteria are key for the long-term viability of N-limited environments, through a high level of microbial substrate specialization (exametabolites or exopolysaccharides).

Gypsiferous soils from semiarid environments are subjected to continuous cycles of drying and wetting due to the episodic nature of the rains, which occur during spring and autumn. The water retention in soils and reservoirs will be increasingly important under the climate change projections characterized by a decrease in precipitation and increased droughts and torrential rains in semiarid and arid areas (Eekhout et al., 2018). Native gypsophytes are generally well prepared to cope with water limitations, although changes in the timing of drought, particularly advances in the onset, can be detrimental (Matesanz et al., 2008). These plants do not seem to have a common adaptation, but rather several strategies - including the loss of leaves during the summer, a life cycle adapted to moisture sufficiency, deep roots, and even a dew collection system (Mota et al., 2011). However, the plants growing on gypsum may not be affected by water limitation since it has been seen that

Helianthemum squamatum can extract water from structural gypsum in the summer in these environments (Palacio et al., 2014). *Helianthemum* is one of the most studied genera in gypsiferous environments, much more so than others such as *Teucrium* and *Herniaria*.

Whitham et al. (2006) concluded that, in non-cultivated ecosystems, the plant community diversity and the genotypes of individual plants can influence the composition of their associated communities, both aboveground and belowground. In this sense, plants can influence the net ecosystem changes through exudates released into the rhizosphere that attract, or inhibit the growth of, specific microorganisms. This rhizodeposition is vital, not only for the plant–microbial C and N pathways (Winkler et al., 2010). Thus, the N returns to the soil (Wichern et al., 2008) and plays a significant role in N cycling (Scandellari et al., 2010), but this transfer to the soil by rhizodeposition in N-limited systems (Dijkstra et al., 2013) has received little attention (Wichern et al., 2008).

Ecological plant-microbe interactions in the rhizosphere are responsible for a number of intrinsic processes such as carbon sequestration, ecosystem functioning, and nutrient cycling (Singh et al., 2004). The composition and quantity of microbes in the soil influence the ability of a plant to obtain N and other nutrients. Cyanoprokaryota in N-limited soils of the arid and semiarid zones seem to preserve the water in the soil in summer and appear to be activated by the humidity resulting from dew and scarce rain (Lázaro et al., 2008); however, nothing is known about the participation of Cyanoprokaryota in the rhizospheres of gypsophytes. The interest in investigating the role of Cyanoprokaryota in rhizospheres arises from the fact that they are components of the biological crust and colonize gyprocks. It is known that Cyanoprokaryota

142 photosynthesize, although a small number of strains can also use hydrogen
143 sulfide (H_2S) and convert it to elemental sulfur (Cohen et al., 1986); in general,
144 they can tolerate low-oxygen conditions and concentrations of H_2S that are toxic
145 to other microorganisms. Cyanoprokaryota establish endosymbioses in Cycads,
146 in highly specialized lateral roots (in complete darkness); for instance, *Nostoc*
147 transfers fixed nitrogen to the cycad cells, and it is expected to have
148 a heterotrophic mode of carbon nutrition (Lindblad, 2008). Singh (2014)
149 conducted a review of agricultural soils, with regard to the role of possible
150 molecules that induce Cyanoprokaryota to improve plant growth and provide
151 tolerance against biotic or abiotic stress. In this sense, phytohormones,
152 polysaccharides, vitamins, amino acids and peptides- considered crucial for the
153 growth and development of plants- can be taken up by plants at the rhizosphere
154 level through the established symbiosis.

155 Some studies have demonstrated that soil moisture controls both soil
156 biological activity (Carbone et al., 2011) and nutrient availability for plant uptake
157 and growth (Sardans and Peñuelas, 2004). Soil microbial activity has been
158 assessed frequently through biological and biochemical parameters, such as
159 biomass C and enzyme activities. Soil extracellular enzyme activities are
160 sensitive and respond rapidly to environmental stresses (Sanaullah et al.,
161 2011). Although enzyme synthesis requires that both C and N be available, it
162 has been shown that neither resource alone stimulates enzyme production or
163 vigorous microbial activity (Allison and Vitousek, 2005). C and N have been
164 used as indicators of the health and sustainability of ecosystems. Water soluble
165 C (WSC), as a component of the labile C pool, may also be sensitive to
166 perturbation and stress in soil-plant ecosystems (Ghani et al., 2003) and, in a

similar way to water soluble N (WSN); therefore, they could be used as a sensitive indicators of soil quality. We hypothesized that the microbial functionality is dependent on the type of gypsophyte colonizing these environments, as well as being strongly regulated by environmental factors such as seasonal drought and water pulses. To test this, we determined soil moisture and soil microbiological and biochemical properties, especially enzymatic activities, related to the metabolic activity of the microbiota in the rhizosphere of three gypsophyte species - *Helianthemum squamatum*, *Teucrium balthazaris*, and *Herniaria fruticosa* - before and after a drought period. In addition, we also ascertained the unknown role of Cyanoprokaryota in the ecosystem functioning of the rhizospheres.

2. Materials and methods

2.1. Study site

The study was performed in a gypsum outcrop, with N90ºE direction and an average slope of 10 %, at the botanical microreserve “Yesos del Rincón” (Lorca, SE Spain, 37º 51´N, 1º 52´W. Figure 1S, supplementary material), at 739 m a.s.l. The predominant soils are Lithic Leptosols as well as Petric and Hypergypsic Gypsisols (IUSS, 2015). The dominant geological unit is the Triassic. The main characteristics of the soil are shown in Table 1. The climate type is semiarid Mediterranean, with an annual average potential evapotranspiration (ETP) of 1293 mm and an annual average rainfall of 268 mm. The mean annual temperature is 15 °C, with an average minimum

192 temperature in January of 0.4 °C and an average maximum of 30 °C in August.
193 Table 2 shows the meteorological data (at the La Paca station; 37º 51´N, 1º
194 49´W. Altitude: 713 m) corresponding to the intervals previous to each of the
195 two sampling dates. The rainfall between the two sampling dates was 81.3 mm,
196 with the following distribution: 1.9 mm until the end of September, 7.6 mm in
197 October, 44.7 mm in November, 7.6 mm in December (all 2011), 19.4 mm in
198 January 2012 (10.2 mm on 17/01/12), and 2.0 mm in February 2012.

199 The dwarf scrub community has been named *Teucrio balthazaris-*
200 *Santolinetum viscosae* (Alcaraz et al., 2008). Specifically, in the study area the
201 target habitat is characterized by gypsophytes: *Teucrium balthazaris* Sennen,
202 *Herniaria fruticosa* L. subsp. *fruticosa*, and *Helianthemum squamatum* (L.) Pers.
203 and gypsovags: *Frankenia thymifolia* Desf., *Senecio auricula* Bourg. ex Coss.
204 subsp. *auricola*, and *Chaenorrhinum rupestre* (Guss.) Maire. The bare zone is
205 covered by a biological crust and some gypsum crystals. The soil biological
206 crust is dominated by *Diploschistes diacapsis* (Ach.) Lumbsch, *Squamarina*
207 *cartilaginea* (Huds.) Poelt, *Acarospora placodiiformis* Magnusson, and *Toninia*
208 *coeruleonigricans* (Light.) Th. Fr. (Egea, 1985, Egea and Alonso, 1996), but
209 other species also occur. Among the Cyanoprokaryota found in the biocrust,
210 *Gloeocapsa rupicola*, *Tolypothrix elenkinii*, *Leptolyngbya* sp., *Microcoleus*
211 *chthonoplastes*, *Nostoc microscopicum*, *Phormidium* sp., *Schizothrix cf.*
212 *calcicola*, and *Scytonema* sp. predominate, but other species with
213 chasmoendolithic growth also occur (Asencio, unpublished data). Also, the
214 Streptophyte *Klebsormidium* sp. has been found in the biocrust.

215 Three gypsophytes were selected based on their distribution and
216 abundance: those with an habitual and exclusive presence, as is the case of

Herniaria fruticosa (H) and *Helianthemum squamatum* (HS), or with a diagnostic presence, as for HS and *Teucrium balthazaris* (T). *Herniaria fruticosa* is a typical gypsum bush with a nitrophilous tendency. *Helianthemum squamatum* is a widely studied dwarf chamaephyte in gypsum outcrops of the Iberian Peninsula (Escudero et al., 2005; Eugenio et al., 2012), and may be a good indicator of saline soils. *Teucrium balthazaris* is endemic in Almeria and Murcia, and grows in compacted soil where crystals of gypsum are often visible. At the study site it is a vulnerable species and it is a near-threatened species in the red list of the Spanish Vascular Flora (Moreno, 2008).

2.2. *Sampling procedures*

A field sampling survey was carried out in September 2011 (considered as summer drought) and May 2012 (spring) in a homogenous area, measuring approximately 3300 m^2. For this survey, 18 individual plants for each of the three target species, similar in size, were randomly chosen. Six rhizosphere soil samples of each plant species were collected. Each sample consisted of three subsamples taken in the rhizosphere of three individual plants. The rhizosphere was considered as the soil adhering to the plant root system. The non-rhizospheric soil (Table 1) was sampled in a zone without plant roots or biological crust, at a depth (0-30 cm) similar to that used in the rhizospheric sampling. The soil samples were placed in plastic bags for transport to the laboratory. Field-moist soil samples were divided into two subsamples: one was sieved at 2 mm and stored at 4 °C for microbiological and biochemical analyses

241 and the other was allowed to dry at room temperature before being sieved at 2
242 mm for the rest of the soil analyses detailed in the next section (2.3).
243
244 *2.3. Soil analyses*
245
246 The mineralogy of the rhizospheres was studied by X-ray diffraction.
247 After being ground in an agate mortar, a sample was deposited in an aluminum
248 sample holder, without favoring any preferential orientation. The X-ray
249 diffractograms were obtained with a Philips PW1700 model. The samples were
250 rolled with values of 2 θ between 3 and 80˚, at a rate of 5˚ per minute.
251 Micromorphological analysis was performed by scanning electron microscopy
252 (SEM), with an energy dispersive system (EDS). Identification of the chemical
253 composition of minerals was carried out using EDX analysis.
254 Soil pH and electrical conductivity were measured in a 1:5 (w/v) aqueous
255 extract. In this extract were measured the anions (chloride, sulfate, and nitrate,
256 using a Dionex ICS-2100 ion chromatograph) and the cations (calcium,
257 magnesium, sodium, and potassium, by ICP plasma). Gypsum was determined
258 by thermogravimetric analysis, using TGA-DTA and Differential Scanning
259 Calorimetry (DSC) in a TA Instruments SDT 2960 simultaneous analyzer and a
260 TA Instruments DSC 2920 model. The ground samples were subjected to
261 an air atmosphere with a flow of 30 cm^3 min^{-1}, heating at 10 °C min^{-1} until
262 reaching 300 °C. The water contents were measured gravimetrically at 1/3
263 (Field Capacity Point) and 15 (Permanent Wilting Point) atm using a pressure
264 plate extractor (Soil Moisture Equipment Corp., Santa Barbara, CA) as
265 described by Dirksen (1999). The difference between the values of the two

parameters was the available water content. Carbonates were estimated by the volumetric method of the Bernard calcimeter. Total phosphorus (TP) and total sulfur (TS) were quantified using Inductively Coupled Plasma Mass Spectrometry (ICP-MS) (Thermo Electron Corporation Mod. IRIS Intrepid II XDL). In soil aqueous extracts, water soluble carbon (WSC) and water soluble nitrogen (WSN) were determined with an automatic Carbon Analyser for liquid samples (Shimadzu TOC-5050A). Total organic carbon (TOC), total carbon (TC), and total nitrogen (TN) were determined with an automatic Nitrogen and Carbon Analyzer after pre-treatment with HCl to eliminate carbonates and combustion at 1020 ºC. Soil moisture content was measured by gravimetry, considering that the maximum temperature of the oven was below 50 °C (Porta, 1998) until a constant weight was obtained.

Microbial biomass C was assayed, by substrate-induced respiration, after glucose was mixed into the soil (at 60 % of its field capacity) at a rate of 0.5 % (w/w): the CO_2 production was monitored for 24 h, using the µ-Trac 4200 system (SY-LAB GmbH, P.O. Box 47, A-3002 Pukersdorf, Austria). This system is based on the variation of the electrical impedance of a 0.2 % aqueous KOH solution (Fernández et al., 2004). Respiration rates were calculated in the linear phase of the respiration curves. Basal soil respiration was assessed with the same system described for microbial biomass C but in the absence of glucose. Dehydrogenase activity was determined using INT (2-p-iodophenyl-3-p-nitrophenyl-5-phenyltetrazolium chloride) as oxidizing agent (García et al., 1997). Urease activity (EC 3.5.1.5) and N-α-benzoyl-L-argininamide (BAA) hydrolyzing protease activities were assayed according to the method of Nannipieri et al. (1980), using 1 M urea and 0.03 M BAA urea as substrates,

291 respectively. Alkaline phosphatase (EC 3.1.3.1), arylsulfatase (EC 3.1.6.1), and
292 β-glucosidase (EC 3.2.1.21) activities were determined using p-nitrophenyl
293 phosphate (disodium) (PNPP, 0.115 M), p-nitrophenyl sulfate (PNS, 0.05 M),
294 and p-nitrophenyl-β-D-glucopyranoside (PNG, 0.05 M) as substrates,
295 respectively. These assays are based on the release and detection of p-
296 nitrophenol (PNP) and were performed according to Tabatabai (1994).
297
298 *2.4 Cyanoprokaryota analyses*
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300 Cyanoprokaryota were collected in biocrust (for reference purposes),
301 where cyanobacterial growth was visible as colored patina, and in rhizhospheric
302 and non-rhizospheric soils. The material was kept dry in plastic and paper bags
303 in a cooler at 4 ºC before examination. Cultivation is usually necessary for
304 detailed taxonomic studies of subaerial cyanobacteria, since the thalli of the
305 microorganisms occurring in the patina are usually covered by large amounts of
306 inorganic material in native preparations. The morphology of the species was
307 therefore studied for both field-collected material and cultivated specimens. Part
308 of the scraped field material was spread aseptically over the surface of Petri
309 dishes containing agarized BG 11 medium (Rippka et al., 1979) and kept at
310 25.0 ºC with a light intensity of 70.0 µE m^{-2} s^{-1} and a 16-h photoperiod.
311 Microscopic examinations were made with a LAN OPTICS stereomicroscope
312 and an Olympus BX4 l compound microscope.
313 The following publications were used for the morphological identification
314 of Cyanoprokaryota: Geitler (1932), Starmach (1966), Komárek and
315 Anagnostidis (1998), Komárek and Anagnostidis (2005), and Komárek (2013).

316 In the Cyanoprokaryota results (Table 6) the diversity or richness of
317 species of Cyanoprokaryota has been considered as the number of species.
318 The abundance is indicated as low, medium, or high: + low (<5 %), ++ medium
319 (5-15 %), +++ (15-30 %) high presence.
320
321 *2.5. Statistical analyses*
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323 The normality and the homogeneity of variance of the dependent
324 variables were tested by means of the Kolmogorov-Smirnov and Levene tests,
325 respectively. The data were ln transformed to achieve normality. We used the
326 non-parametric Kruskall-Wallis test for those variables with a non-normal
327 distribution. The effects of the gypsophyte species (S), the date of sampling (D),
328 and their interaction (S x D) on the measured variables were tested by a two-
329 way analysis of variance. Correlation analysis among all the soil parameters
330 measured was carried out using Spearman's rank correlation coefficients. The
331 statistical procedures were carried out with the software package IBM SPSS
332 22.0 for Windows.
333
334 **3. Results**
335
336 It has been excluded the results of non-rhizospheric soils (shown in
337 Table 1) against rhizospheres in statistical analyses, to force the possible
338 differences between them, because if we consider it in front of the non-
339 rhizospheric soil, statistically significant differences are obtained from each one

of the rhizospheres in front of the non-rhizospheric soil, but not between the rhizospheres of gypsophytes.

3.1 Gypsum

In the study area the outcrop of primary gypsum occurs in crystalline forms of great development (massive, acicular, or fibrous) that are versicolor (with dominance of grayish and ocher tonalities) and have obvious signs of dissolution.

Microcrystalline gypsum, mainly due to gyprock weathering, can form lenticular gypsum by dissolution and reprecipitation; these gypsum forms are secondary and can be observed as whitish, powdery or crystalline, soft masses, silt-sized with a flour-like consistency or diffused in the soil matrix. The topographic setting strongly influences the type of gypsum in the soil: thus, in the high parts there is a predominance of pedogenic gypsum and in the areas on the lower slopes the diagenic gypsum predominates.

We observed the micromorphology and estimated the *in situ* chemical composition of selected samples by SEM. In the microscopic observations, globular gypsum crystals predominated, some tabular and cluster of gypsum crystal. In terms of chemical composition, the predominant elements - in accordance with the gypsiferous nature - were S and Ca, while Al, Fe, and Si appeared in minor amounts. In the non-rhizospheric samples (Figure 1a) there was a lower amount of all the elements than in the rhizospheric samples (Figure 1b), which indicates greater physical and chemical alteration of the substrate by both microorganisms and the roots of the plants. The XR diffractograms of non-

365 rhizospheric and rhizospheric soil are shown in Figure 2. The most intense
366 reflection at 7.56 Å is diagnostic for gypsum (diagnostic peaks at 7.56, 3.66,
367 4.27, and 2.53 Å). Gypsum was the dominant mineral in all samples, in
368 accordance with the electron microscopy observations.

369 Along with gypsum, the X-ray diffractograms showed the main
370 diagnostic reflections of calcite (3.04, 1.87, 2.10 Å) and dolomite (2.88, 2.19,
371 1.78 Å).

372 It can be seen that all soil samples, both non-rhizospheric (Figure 2a)
373 and rhizospheric (Figure 2b), corresponded to gypsum (analytical gypsum and
374 brushite were used as reference standards for all samples).

375 The percentage of gypsum relative to non-rhizospheric samples is shown
376 in Table 1. In the rhizospheric samples the percentage of gypsum was between
377 75 and 95 %, without statistically significant differences, neither among them
378 nor with respect to the non-rhizospheric soil (data not shown).

379

380 *3.2 Soil moisture and biochemical analysis*

381

382 The values of the physical, chemical, physico-chemical, and biochemical
383 parameters for the non-rhizospheric soil are shown in Table 1. Table 3 shows
384 the water retention capacity (Field Capacity Point, Permanent Wilting Point, and
385 Available Water Content) in the rhizosphere soil of the three gypsophytes under
386 study (H, HS, and T), as well as analytical compounds (brushite and gypsum).
387 For Field Capacity Point (1/3 atm) the highest values were for species T and H,
388 and the lowest was for HS, the differences being statistically significant for the
389 factor S and its interaction with D. However, at the Permanent Wilting Point (15

390 atm) the differences were statistically significant for the factor D, and the lowest
391 values were in spring 2012. The Available Water Content seemed to respond to
392 the trend found with regard to retention at Field Capacity Point.
393 Statistically significant differences were observed in Field Capacity Point
394 among the species studied (Table 3): H and T had higher values than HS.
395 However, Permanent Wilting Point showed statistically significant differences in
396 terms of D, being higher in the dry season (Table 3). The Available Water
397 Content differed significantly in terms of the species and their interaction with
398 the date, the highest values being for H and T (Table 3).
399 The thermograms indicated, in all cases (non-rhizospheric and
400 rhizospheric soils), multistage decomposition with relatively stable
401 intermediates, corresponding to the pattern of the analytical compound,
402 gypsum. In a more detailed description, thermograms were amplified in the 30-
403 60 ºC range, to see the corresponding dehydration. In all the rhizospheric
404 samples, the dehydration was greater than in the non-rhizospheric samples.
405 Figure 3a shows the minimum dehydration that occurred in a non-rhizospheric
406 soil sample, and Figure 3b the maximum dehydration that occurred in a sample
407 of rhizospheric soil belonging to species H; both samples belonged to the first
408 sampling after the drought.
409 The type of gypsophyte species (S) had no effect on the concentrations
410 of total P and S, water soluble C and N, total organic C and total C, and
411 carbonates. Only the total N differed significantly among species (Table 4).
412 Except for total organic C, total C, and carbonates, the soil chemical parameters
413 measured varied significantly between the two sampling dates (D). The highest
414 values of such parameters were detected in samples of the rhizosphere soil of

415 species H, HS, and T taken in September 2011, except for WSN and total N.
416 There was a significant interaction between the type of plant species and the
417 sampling date (S x D) with respect to the concentration of total N. For all three
418 gypsophytes the values of WSC were higher in September than in May. In
419 particular, the decline from September to May was more pronounced in H and T
420 (about 38 % and 44 %, respectively). By contrast, the values of WSN were
421 lower in September than in May, and the most striking change in this case was
422 for HS, with an increase of 150 %.

423 The lowest values of microbial biomass C and basal respiration were
424 recorded in the samples of May, regardless of the plant species, as shown in
425 Figure 4. For all three gypsophytes, the urease and protease activities were
426 highest in the sampling of September (Figure 5). However, the dehydrogenase
427 and β-glucosidase activities were greater in spring than in summer. Neither the
428 type of gypsophyte nor the sampling date had a significant effect on the alkaline
429 phosphatase and arylsulfatase activities.

430 In general, the values of the soil chemical parameters were significantly
431 correlated with those of some of the biochemical parameters (Table 5).
432 Excepting dehydrogenase activity, WSN, and TN, the values of the parameters
433 in the rhizosphere of the gypsophyte plants correlated positively with the basal
434 respiration rate. In the case of β-glucosidase, the correlation was negative.
435 Biomass C showed positive correlations with the urease and protease activities,
436 WSC, TOC, TP, and TS. The highest correlations for both basal respiration rate
437 and microbial biomass C were with the protease and urease activities. Also
438 notable was the correlation between basal respiration and TP (0.826***).

439 The dehydrogenase and β-glucosidase activities were correlated
440 positively with WSN and negatively with TS, while β-glucosidase exhibited some
441 negative correlations (with urease and protease activities, TP, and TS) and
442 dehydrogenase was correlated negatively only with TS. However, the
443 arylsulfatase activities showed no significant correlations, and phosphatase
444 showed positive correlations with protease activity. The urease and protease
445 activities showed positive correlations with WSC, TP, TS, TC, and carbonates.
446 The WSC was positively correlated with basal respiration, biomass C,
447 urease and protease activities, TP, and TS. However, WSN presented positive
448 correlations with dehydrogenase and β-glucosidase, and a negative correlation
449 with TS. The TOC was correlated positively with basal respiration, biomass C,
450 TP, and TS. Positive correlations existed between TC and basal respiration, the
451 urease and protease activities, TOC, and TP. However, TN was correlated with
452 TP and TS but not with basal respiration, biomass C, or any of the enzymatic
453 activities studied. The TP and TS showed positive correlations with basal
454 respiration, urease and protease activities, WSC, and TN, and negative ones
455 with β-glucosidase. Specifically, positive correlations between TP and microbial
456 biomass C were established, and negative ones between TS and
457 dehydrogenase and WSN. Finally, the carbonate values were correlated
458 positively with basal respiration, protease and urease activities, TP, and TC.
459
460 *3.3 Cyanoprokaryota*
461
462 A total of 14 species were identified in both the rhizospheric and non-
463 rhizospheric soils of the study area (Table 6). All these species were present in

464 the biocrust samples analyzed for reference purposes, with the exception of
465 *Leptolyngbya* and *Phormidium.* Of the Cyanoprokaryota studied, coccoid
466 species predominated over filamentous species (9:5); the former are included in
467 the order Chroococcales, which exhibited most diversity (64.3 %), followed by
468 the Nostocales (21.4 %) and the Oscillatoriales (14.3 %).

469 The most diverse genus was *Gloeocapsa*, with five species, whereas the
470 rest of the genera were represented by only one species each. The most
471 abundant species were *Microcoleus chthonoplastes*, *Nostoc microscopicum*,
472 *Schizothrix cf calcicola*, *and Scytonema* sp. (Figure 6)*,* whereas the least
473 plentiful were *Asterocapsa salina*, *Gloeocapsa rupestris*, and *Pseudocapsa*
474 *dubia*.

475 There were more Cyanoprokaryota species in rhizospheric soils than in
476 non-rhizospheric soils. Within the rhizospheres, the cyanobacteria were most
477 abundant in that of gypsophyte H (12 species in spring and 11 in summer),
478 followed by the rhizosphere of T (8 species in spring and 3 in summer) and,
479 finally, the rhizosphere of HS (2 species, only in summer).

480 In spring the presence and abundance of Cyanoprokaryota species were
481 very similar in the rhizospheres of H and T but lower in that of HS. However, in
482 summer there were many differences among H, T, and HS.

483 *Gloeocapsa* developed in the rhizospheres of H and T, its presence
484 being more constant over time in H, while in T it was more abundant in spring.
485 *Microcoleus chthonoplastes* (Figure 6) was the most abundant species in the
486 gypsophytes, except in the rhizosphere of HS. *Chroococcopsis* cf *fluviatilis* and
487 *Tolypothrix elenkinii* (Figure 6) had similar behavior; they appeared in the
488 rhizosphere of H in summer and spring and in the rhizosphere of T in spring.

Schizothrix cf *calcicola* only appeared in spring in the rhizospheres of H and T and in summer only in that of H. Less abundant were *Asterocapsa salina* and *Pseudocapsa dubia*, appearing only in the rhizopsphere of H. Only *M. chthonoplastes* was detected in the rhizosphere of HS in summer, whereas in spring no Cyanoprokaryota were found in the rhizosphere of HS.

In non-rhizospheric soils, *Nostoc microscopicum* and *Scytonema* sp. (Figure 6) were very abundant in spring and summer, without being affected by seasonality.

In addition to the Cyanoprokaryota, the presence of the green alga *Klebsormidium* (Table 6) was detected in the rhizospheres of HS and H in summer and in those of H and T in spring.

4. Discussion

4.1 Effects of drought and water pulses on soil properties in gypsiferous soils

It is interesting to know at a mineralogical level the composition of gypsiferous soil (non-rhizospheric and rhizospheric), since gypsum has the ability to eliminate dissolved phosphate by brushite precipitation (Pinto et al., 2009). The X-ray diffractograms (Figure 2) show that all the samples were gypsum, and all were analyzed regarding their patterns of gypsum and brushite. The micromorphology of the gypsum crystals, in both non-rhizospheric and rhizospheric soils, had a predominance of globular, tabular, and cluster-like characteristics, typical of an aridic-xeric moisture regime, according to Hashemi et al. (2011).

514

515 The differences obtained among the rhizospheres of the gypsophytes in
516 the study area in terms of water retention (Table 3), and the thermograms show
517 differences in the amount of water retained in the rhizospheres (Figure 3) in the
518 drought period. These values can be attributed to the presence and differences
519 in composition of Cyanoprokaryota, in terms of both species and date of
520 sampling (Table 6), possible due to either exopolysaccharides production
521 (Otero and Vincenzini, 2003) and/or differences in the stimulation caused by
522 rhizodeposition.

523 Most Cyanoprokaryota can resist long periods of drought, tolerating large
524 fluctuations of salinity and temperature and high radiation stress in a vegetative
525 state, and metabolic activity revives soon after rewetting (Adhikary, 2004).
526 Cyanoprokaryota are characterized by the presence of mucilaginous sheaths
527 whose volumes may vary considerably as they act as water reservoirs, thus
528 avoiding desiccation and allowing activity to persist, even in drought conditions
529 (Caiola et al., 1996; Asencio and Aboal, 2003). In adaptation to desiccation,
530 proteins play an important role (Wright et al., 2005), as indicated by the
531 influence of drought on scytonemin production, at least in some cases (Asencio
532 and Hoffmann, 2013). Exopolysaccharides may retain large amounts of water
533 and form a gel that stabilizes the macromolecular components and the cell
534 structure of the Cyanoprokaryota and other organisms that produce them. This
535 allows them to overcome long periods of drought by the formation of hydrogen
536 bonds with proteins, membrane lipids, and DNA, thereby replacing the water
537 shell surrounding these cell constituents (Caiola et al., 1996; Potts, 1999). This

538 could explain the differences in water retention and dehydration that we found in
539 rhizospheric soils, with seasonal variations, and particularly in *Herniaria*.
540 Soil organic matter mineralization is very sensitive to drought in
541 Mediterranean ecosystems (Sardans and Peñuelas, 2013). Decreases in soil
542 enzyme activity (Sardans et al., 2007; Hueso et al., 2011), and soil respiration
543 (Emmett et al., 2004; Asensio et al., 2007) have been widely observed under
544 drought conditions. During summer the soil becomes dry but upon subsequent
545 rewetting by a rain pulse there is a burst of decomposition, mineralization, and
546 release of inorganic nitrogen and CO_2 in Mediterranean environments, named
547 the Birch effect (Jarvis et al. 2007) - this is based on the conceptual paradigm of
548 pulse-reserve (Noy-Meir, 1973). Such bursts of microbiological activation are
549 dependent on the reserves of carbon (WSC), total phosphorus, and total sulfur
550 (Table 4).
551 In the semiarid area at Yesos del Rincón, after the summer drought (60
552 days with only 3.9 mm of rainfall), on 2/09/11 rainfall (27.3 mm out of a total of
553 31.2 mm shown in Table 2) triggered a pulse pattern of biological activities and
554 biogeochemical cycles (Austin et al., 2004; Huxman et al., 2004; Collins et al.,
555 2008) at the rhizosphere level. After 20 days of rain, the soils and rhizospheres
556 were sampled. The microbial biomass decreased during the drought stage but
557 was stimulated after wetting, and the wet-dry cycle itself resulted in higher net N
558 and C mineralization when compared to continuously moist soils (Austin et al.,
559 2004).
560 The Cyanoprokaryota of the rhizospheres at Yesos del Rincón (Table 6)
561 and the microorganisms of this system can be accelerated and were measured
562 as the microbial biomass C and basal respiration rate (Figure 4). The high pulse

563 of CO_2 produced can affect plants, causing rhizodeposition (Phillips et al., 2011)
564 and/or exopolysaccharides production by Cyanoprokaryota, as shown above.
565 Much, but not all, of the C in exudates can be taken up without extracellular
566 enzymatic decomposition (Weintraub et al., 2007). This fraction contains WSC
567 and nutrients (Table 4): WSC was increased significantly by the effects of
568 drought, and however WSN was decreased (Table 4). Steinweg et al. (2013)
569 showed that WSC was greater under drought than under ambient or wet
570 experimental conditions. McDaniel et al. (2013) also found higher values of
571 WSC in summer, compared to spring, under a humid continental climate, with
572 rather severe winters and warm summers (in experiments on global warming, it
573 appears that warming increases the availability of C more than that of N).
574 Prolonged drought can result in a decline in the N_2 fixation capacity of
575 Cyanoprokaryota, whereas persistent moisture results in an increase (Gundale
576 et al., 2009). This probably explains the frequent reports of decreased N_2
577 fixation rates in mid-summer, when conditions are at their driest (DeLuca et al.,
578 2002; Zackrisson et al., 2004).

579 The 27.3 mm pulse of rainfall is sufficient, in the rhizosphere system of
580 Yesos del Rincón, to produce the connectivity of the soil pores.
581 Cyanoprokaryota fix N_2 biologically and the availability of this limiting factor in
582 these environments promotes the activation of extracellular enzymes produced
583 by other microorganisms. This water pulse into the rhizospheres activated the N
584 cycle and, consequently, increased the protease and urease activities (Figure 5)
585 since water pulses are intimately related to the N cycle (Austin et al., 2004).
586 High correlations of WSC with the basal respiration rate, microbial biomass C,
587 urease, and protease were found (Table 5). However, WSN was correlated only

588 with dehydrogenase and β-glucosidase, all of these parameters having higher
589 values in the spring.

590 Enzyme activities related to N cycling were increased by the effect of
591 drought, for all three gypsophytes (Figure 5); Sanaullah et al. (2011) showed
592 similar results. It is believed that certain amounts of phosphorus (De Nobel et
593 al., 1997; Whitton et al., 2005) and sulfur (Mus et al., 2016) are required for
594 optimal N_2 fixation. After the drought there were reserves of total phosphorus
595 and sulfur (Table 4), despite the great richness of arbuscular mycorrhizal fungi
596 at Yesos del Rincón (Alguacil et al., 2012). When seasonal variations occur and
597 with respect to the decomposition and N transformation processes, these fungi
598 seem to need associations with primary producers (States et al., 2001; Porras-
599 Alfaro et al., 2008) and this could happen with respect to their uptake of
600 phosphorus forms (Singh and Kapoor, 1999).

601 At Yesos del Rincón, in spring, another 25.5 mm of rain fell in a single
602 day (20/03/2012), out of a total of 57.3 mm for this period (Table 2), and after 10
603 days of rain the soil and rhizospheres were sampled. Another type of pulse may
604 have occurred, activating the microbiological activity related to the C cycle, with
605 increases in the activities of dehydrogenase (an indicator of microbiological
606 activity) and β-glucosidase (Figure 5). It seems that the dehydrogenase enzyme
607 does not accumulate extracellularly in the soil and depends on intact cells (Das
608 and Varma, 2011). On this date the highest values of WSN were recorded
609 (Table 4).

610 Dehydrogenase activity was extremely high in the rhizospheres of all
611 three gypsophytes tested in Yesos del Rincón, even higher than in the Ah
612 horizons of Galician agricultural soils and similar to those found in soils of

613 Tabernes (Miralles et al., 2012). Dehydrogenase and β-glucosidase activities
614 were highest during spring, whereas urease and protease peaked during late
615 summer (Figure 5). Under drought stress, the activity of β-glucosidase was
616 decreased in the rhizosphere of all three gypsophytes (Figure 5).

617 No changes in alkaline phosphatase and arylsulfatase activities between
618 dates were found (Figure 5). Drought had no significant effects on the
619 phosphatase and arylsulfatase activities at Yesos del Rincón; similarly, Sardans
620 et al. (2006) obtained no changes in soil phosphatase activities in response to a
621 drought treatment under semiarid Mediterranean conditions. Phosphatase
622 enzymes are predominantly secreted by plant roots and associated mycorrhiza
623 and other fungi, as pointed out by Joner et al. (2000).

624 However, the role of Cyanoprokaryota is that of primary colonizers and
625 many species have been shown to possess the property of tricalcium
626 phosphate solubilization. Rock phosphate is abundant but, being insoluble, is
627 unavailable to crop plants. Some cyanobacteria - like *Tolypothrix*, *Scytonema*,
628 and *Hapalosiphon*, among others - have been reported to solubilize rock
629 phosphate. Moreover, extracellular phosphatase activities were detected in
630 different cyanobacterial strains (Whitton et al., 1991). It is generally considered
631 that such activities are related to the maintenance of the phosphate supply
632 (Mateo et al., 2010), but there is still a lot of uncertainty and questions
633 pertaining to enzymatic control remain unanswered. The organic P increased in
634 a drought experiment in a Mediterranean area when alkaline phosphatase
635 activity declined (Sardans et al., 2008). Perhaps, plants obtain P from their
636 interrelationships with microorganisms, in some cases through mycorrhizal
637 associations and in others through Cyanoprokaryota.

638 At Yesos del Rincón, no changes in arylsulfatase activity between the
639 sampling dates were found (Figure 5), probably because in this gypsiferous
640 environment, with very abundant sulfates, sulfur will not be limiting. With respect
641 to this element, it is known that Cyanoprokaryota incorporate it into their sheath
642 by compartmentalization, in hypersaline environments (Canfora et al., 2016),
643 and that some excrete it in the form of sulfonated exopolysaccharides (Sudo et
644 al., 1995) and also sulfur it is a essential component of nitrogenase (Mus et al,
645 2016). Additionally many algae are able to use sulfur surplus to produce
646 sulfonium compounds with different functions related with abiotic and biotic
647 stresses (Ratti and Giordano, 2008), it can be thought that the presence of
648 *Klebsormidium* may be involved in these functions.
649
650 *4.2 Role of Cyanoprokaryota in gypsiferous soils*
651
652 The gypsiferous soils of Yesos del Rincón support a high degree of
653 Cyanoprokaryota diversity and rarity. In the previous section we have seen how
654 these organisms can be stimulated by the water pulse that occur at the end of
655 drought periods and can produce exopolysaccharides, which, along with the
656 rhizodeposition of to the gypsophytes, activate the extracellular enzyme of the N
657 cycle; Cyanoprokaryota also help to maintain an optimal moisture content for
658 these enzymes. Moreover, these Cyanoprokaryota may be an important source
659 of N for plants and soils in this area since the majority of the species can fix
660 atmospheric N_2. It is considered that the species that act as N-fixing agents are
661 those that produce heterocytes, such as *Nostoc microscopicum*, *Scytonema*
662 sp., and *Tolypothrix elenkinii*. However, it has been found that some species of

663 the genus *Gloeocapsa* (Asencio and Aboal, 2009), which lack heterocytes, can
664 also fix N_2 when they are not performing photosynthesis, so that the
665 nitrogenase enzyme responsible for N_2 fixation is not inhibited by the oxygen
666 released in photosynthesis. Hence, the 14 species identified can improve soil
667 fertility, which, in turn, influences vascular plant nutrition. Cyanobacterial
668 communities can also influence the germination and establishment of vascular
669 plants in gypsiferous soils, perhaps acting as plant growth promotors (Gayathri
670 et al., 2017).

671 The presence of *Klebsormidium* in Yesos del Rincón is in accordance
672 with studies of succession on newly exposed surfaces where conditions are
673 unfavorable for rapid invasion by rooted plants; these have provided many
674 examples of Cyanoprokaryota having an important role during the early stages
675 of succession. In the case of gypsum rocks in SE Spain, succession seems to
676 start with domination by Cyanoprokaryota, followed by green algae (Dana and
677 Mota, 2006). However, this is the first time that the genus *Klebsormidium* a
678 charophyte green algae has been cited in gypsum environments, despite the
679 fact that it was detected in Los Cabecicos de Villena (Asencio, com. pers.).

680 Cyanoprokaryota species appeared in the rhizospheres of *Helianthemum*
681 *squamatum*, *Herniaria fruticosa*, and *Teucrium balthazaris* in the gypsiferous
682 soils of Yesos del Rincón, where coccoids predominated over filamentous
683 species; this coincides with the findings of Domínguez and Asencio (2011) in
684 gypsum environments.

685 Of the 10 genera identified, *Gloeocapsa* was the one with the highest
686 number of different species, five. The abundance of this genus in the study area
687 indicates that soil colonization by blue-green algae is at an initial stage since,

688 according to Fritsch (1907), Pentecost (1992), and Domínguez and Asencio
689 (2011), these blue-green algae are pioneers of the colonization of rocks.
690 *Nostoc microscopicum* is a very frequent species in the gypsum area of
691 Los Cabezos in Villena (Domínguez and Asencio, 2011), due to its capacity to
692 tolerate the osmotic stress that is a result of the dessication and concentration
693 of salts (Büdel et al., 1994).
694 These three studied gypsophytes are in a well conserved community. In
695 previous work in the study area, Muries (2017) observed that they exhibited
696 different percentages of mycorrhization: *Teucrium balthazaris* had the highest
697 percentage (exceeding 70%), *Helianthemum squamatum* had 40%, and
698 *Herniaria fruticosa* around 35%. Furthermore, these three species have differing
699 degrees of affinity for gypsum (Mota et al, 2011): it is greatest for *Helianthemum*
700 *squamatum*, moderate for *Teucrium balthazaris*, and lowest for *Herniaria*
701 *fruticosa*. Marked differences among the three gypsophyte species studied were
702 found with regard to the Cyanoprokaryota in their rhizospheres.
703 Three functional strategies or adaptation mechanisms with regard to
704 water availability could be discerned in these gypsophytes. On the one hand, *H.*
705 *fruticosa* - that can be considered as a pioneer woody species (Mota et al.,
706 2011) - had rhizospheres with a high association of Cyanoprokaryota on both
707 sampling dates (Table 6). An intermediate strategy is that of *T. balthazaris*,
708 which showed the presence of some Cyanoprokaryota, with marked differences
709 in the spring season (Table 6). Finally, for *H. squamatum* it is striking that
710 Cyanoprokaryota were not present in its rhizosphere in spring and that at the
711 end of the drought period only two species were detected (Table 6). These
712 adaptation mechanisms can explain the greater amount of water in the samples

of rhizospheres after drought in *H. fruticosa*, because they contain more Cyanoprokaryota. Since *H. fruticosa* is the species with least mycorrhization, together with a lower percentage affinity for gypsum, and is considered one of the pioneer species, it may need to be associated with Cyanoprokaryota.

5. Conclusions

The microbial functionality at a particular site is dependent on the type of gypsophyte colonizing it, as well as being strongly regulated by environmental factors such as seasonal drought and water pulses. The differences in soil moisture found in the rhizospheres of gypsophytes during drought, as a result of a water pulse, were associated with the presence and abundance of Cyanoprokaryota.

The three gypsophyte species studied seemed to have the same behavior in many of the biochemical parameters studied in their rhizospheres, with the exception of the total N that had its highest value in the rhizosphere of *Herniaria fruticosa* in spring. The pulse of water seemed to trigger the activity of soil organisms, producing an activation of the N cycle through extracellular enzymes such as urease and protease regardless of the type of gypsophyte.

The microbial biomass C and basal respiration rate appeared to be the ideal indicators of the microbiological processes that were activated after drought. In spring the water pulse boosted the C cycle. Dehydrogenase was a good indicator of the changes that occurred in the soil moisture in spring. The increase of soil moisture produced an activation of the C cycle through β-glucosidase, regardless of the type of gypsophyte.

738 This work demonstrates the tight linkage between the N and C inputs into
739 rhizospheres and the nature, magnitude, and occurrence of water pulses. The
740 WSC, WSN, and extracellular enzymes are good indicators of the responses of
741 these communities.

742 The alkaline phosphatase and arylsulfatase activities were not influenced
743 by the gypsophyte species or date.

744 In this regard, we suggest three functional strategies or adaptation
745 mechanisms related to water availability, as determined by drought and water
746 pulse effects, in gypsophytes: *Herniaria fruticosa*, a pioneer species, had the
747 greatest diversity and abundance of Cyanoprokaryota, *Teucrium balthazaris*
748 exhibited an intermediate strategy with greater diversity and abundance of
749 Cyanoprokaryota in spring, and, finally, *Helianthemum squamatum* had lower
750 diversity and abundance.

751 In this context, future research on the role of Cyanoprokaryota in
752 rhizospheres of gypsophytes could be necessary to confirm the adaptation
753 mechanisms. This would show the potential of Cyanoprokaryota to thrive and to
754 help other organisms develop under future, climate-induced changes.

755

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757

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763

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Figure captions

Figure 1. Back scattered electron microscopy images of the crystal forms of gypsum, together with Energy-Dispersive X-ray (EDX) spectra of gypsum crystals: (a) Non-rhizospheric soil, (b) Rhizospheric soil.**Figure 2.** XR diffractograms: (a) Non-rhizospheric soil, (b) Rhizospheric soil.

Figure 3. Thermograms amplified between 30 and 60ºC, corresponding to summer data of (a) Non-rhizospheric soil, (b). Rhizospheric soil of *Herniaria fruticosa.*

Figure 4. Microbial biomass C and basal respiration rate in the rhizosphere soil of the three gypsophytes (H: *H. fruticosa*, HS: *H. squamatum*, and T: *T. balthazaris*) for the different sampling dates.

Figure 5. Enzyme activities in the rhizosphere soil of the three gypsophytes (H: *H. fruticosa*, HS: *H. squamatum*, and T: *T. balthazaris*) for the different sampling dates.

Figure 6. a-f. Light micrographs [scale bar:10 µm] of a. *Gloeocapsa violascea*, b. *Gloeocapsa rupicola*, c. *Tolypothrix elenkinii*, d. *Nostoc microscopicum*, e. *Scytonema* sp., and f. *Microcoleus chthonoplaste*s.

Figure 1S. Location of study area.