

**BIOCRUST-FORMING LICHENS INCREASE SOIL AVAILABLE
PHOSPHORUS UNDER SIMULATED CLIMATE CHANGE**

Running title (50 characters): Biocrusts and climate change modulate P cycling

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ABSTRACT

Drylands are important reservoirs of soil phosphorus (P) at the global scale, although large uncertainties remain regarding how climate change will affect P cycling in these ecosystems. Biocrust-forming lichens are important regulators of abiotic and biotic processes occurring in the soil surface, including nutrient availability and redistribution, across global drylands. However, their role as modulators of climate change impacts on soil P cycling is poorly known. We conducted a manipulative microcosm experiment to evaluate how six biocrust-forming lichens (*Buellia zoharyi*, *Diploschistes diacapsis*, *Fulgensia subbracteata*, *Psora decipiens*, *Squamarina lentigera*, and *Toninia sedifolia*) with diverse morphology and chemistry affect soil available P concentration and the activity of acid phosphatase after 50 months of simulated ~2°C warming and 35% rainfall reduction. Lichens increased soil available inorganic and total available P, and the activity of acid phosphatase, although the magnitude of these effects was highly species-specific. Climate change treatments increased available organic P regardless of lichen species. Our findings provide novel experimental evidence on the importance of biocrusts as modulators of P cycling in drylands and highlight the necessity to take into account the identity of biocrust constituents when evaluating their effects on soil fertility.

KEYWORDS

Biological soil crusts, climate change, drylands, lichens, soil fertility

HIGHLIGHTS

- Biocrust-forming lichens effects on soil phosphorus under simulated climate change were evaluated
- A microcosm experiment with warming and rainfall reduction and six lichen species was conducted
- Multiple lichens increased available inorganic and total available P, and the activity of acid phosphatase
- Biocrust-forming lichens have species-specific effects on phosphorus cycling in dryland soils

INTRODUCTION

Drylands store more than half of total phosphorus (P) present in global soils, and contains more labile inorganic P than humid areas (Plaza *et al.*, 2018). Although biological activity in drylands is strongly limited by their low water availability, processes such as plant and microbial nutrient uptake and release are important regulators of P availability and redistribution in these areas (Delgado-Baquerizo *et al.*, 2013, 2015).

Biocrusts, diverse communities of lichens, mosses and other organisms (e.g., cyanobacteria) living in the soil surface (top first 1-2 cm), are a major biotic component of drylands worldwide, where they can cover up to 70% of the soil surface (Ferrenberg *et al.*, 2017). They are well-known drivers of carbon and nitrogen cycling and storage in these ecosystems (Belnap, 2002; Maestre *et al.*, 2013; Delgado-Baquerizo *et al.*, 2014), and can also play a major role in regulating soil P cycling (García-Velázquez *et al.*, 2020). Specifically, biocrust-forming lichens, one of the most conspicuous and abundant biocrust constituents in global drylands (Weber *et al.*, 2016), promote the retention of fine-textured sediments, which are typically enriched in P (Reynolds *et al.*, 2001; Concostrina-Zubiri *et al.*, 2013). In addition, lichens segregate multiple secondary compounds (e.g., organic acids), which contribute to mineral bioweathering (e.g., solubilizing P compounds; Belnap, 2011), and regulate soil microbial activity and diversity (Castillo-Monroy *et al.*, 2011; Maier *et al.*, 2014), thus influencing soil nutrient cycling. However, lichens also require P for several photosynthetic processes, which may decrease soil P via nutrient uptake (Bowker *et al.*, 2006). Although previous studies indicate that biocrust-forming lichens can exert important and highly species-specific effects on soil P cycling, they are scarce and mostly observational (Concostrina-Zubiri *et al.*, 2013; Delgado-Baquerizo *et al.*, 2015).

Ongoing climate change is causing a profound alteration in the structure and functioning of global drylands (see Maestre *et al.*, 2016 and references therein). In particular, increases in temperature and reductions in precipitation affect biocrust abundance and diversity (Ferrenberg *et al.*, 2015; Ladrón de Guevara *et al.*, 2018), with important consequences to dryland C and N nutrient cycling (Zelikova *et al.*, 2012; Concostrina-Zubiri *et al.*, 2021a). In contrast, our understanding of how ongoing climate change impacts the effects of biocrusts on soil P cycling is still very limited. Since abiotic and biotic processes involved in soil P mineralization and release are highly dependent on soil moisture (Sardans *et al.*, 2006; Belnap, 2011), it is expected

that climate change drivers such as warming and altered rainfall regime will have negative and interactive effects on soil P cycling under biocrusts. However, and to the best of our knowledge, no previous study has experimentally evaluated how climate change drivers impact biocrust-forming lichen effects on soil P, and whether these effects are species-specific.

Here we report results from a manipulative microcosm experiment where we evaluated how six biocrust-forming lichens with diverse morphology and chemistry affect soil P cycling (i.e., available organic and inorganic and total available P, and acid phosphatase activity) under simulated climate change (~2°C warming and 35% rainfall reduction). We hypothesized that: i) biocrust-forming lichens increase soil P concentration and cycling, and ii) the magnitude of this effect will be species-specific and diminished under warming and reduced rainfall.

MATERIALS AND METHODS

Experimental design

We conducted a microcosm experiment in the Climate Change Outdoor Laboratory (CCOL) located in central Spain (Rey Juan Carlos University, Móstoles, 40°20'37''N, 3°52'00''W, 650 m a.s.l.). Its climate is Mediterranean semi-arid, with mean annual temperature of 16.6°C, mean annual precipitation of 362 mm and mean annual relative humidity of 61.3%. Microcosms were made with 8 cm depth plastic pots (diameter 20 cm, Fig. S1) filled with 3 cm of stones at the base and 4.5 cm of gypsum soil with a total P concentration ranging between 134-162 mg P/Kg soil. Soil and lichen thalli lacking visible damage of six lichen species (*B. zoharyi* Galun, *D. diacapsis* (Ach.) Lumbsch., *F. subbracteata* (Nyl.) Poelt, *P. decipiens* (Hedw.) Hoffm., *S. lentigera* (Weber) Poelt, and *T. sedifolia* (Scop.) Timdal, Table S1) were collected in gypsum outcrops 50 km south of the CCLOL (40°20'N–3°32'W; 590 m a.s.l., Fig. S1). The species selected dominate biocrust communities in Mediterranean drylands but are also common in other drylands worldwide (Galun & Garty, 2001; Maestre *et al.*, 2011; Weber *et al.*, 2016). These species have been successfully used in manipulative experiments before (Maestre *et al.*, 2012a; Castillo-Monroy *et al.*, 2014). This study was carried out between March 2013 and May 2017.

We established a factorial design with two factors. First, climate change; with three levels: control, warming (~2.3°C annual temperature increase) and warming x rainfall reduction (warming and 35% rainfall reduction combined). Second, lichen

species; with seven levels: bare soil without lichens as a control and monocultures of the six lichen species selected. Each level of lichens species was replicated four to six times (always four in the case of bare soil) for each level of climate change treatments. A total of 107 microcosms were established. The temperature increased was achieved using open-top chambers and the rainfall reduction treatment consisted of passive rainfall shelters (Fig. S1), and these treatments are in line with forecasted climate change for central Spain in the second half of the 21st century (De Castro *et al.*, 2005; Rhein *et al.*, 2013). See Concostrina-Zubiri *et al.* (2021a) for additional details on the experiment.

Soil harvest and analyses

Soil samples (2 cm depth) were collected after 50 months (May 2017) in each microcosm after carefully removing biocrusts. Soils were sieved (2 mm mesh), air-dried at room temperature (one month) and then stored in sealed plastic bags in the dark until further analysis (Maestre *et al.*, 2012b). Available inorganic P was analysed using 1g of soil samples and 20 ml aliquots of 0.5M NaHCO₃ (adjusted to pH 8.5) as extractable solution (Olsen and Sommers, 1982). Total carbonate-extractable P (hereafter, available P) in the NaHCO₃ extracts was determined using an alkaline digestion with 0.148M K₂S₂O₈ and 3M NaOH. The digestion was made in the autoclave at 121°C for 1h. Available organic P was calculated as the difference between total available P and available inorganic P. We used the Malachite Green Method (Hess & Derr, 1975; Fernández *et al.*, 1985) to estimate PO₄³⁻-P concentration in the extracts. The activity of acid phosphatase and soil pH in distilled water (1:1) were also measured as described in Maestre *et al.* (2012b) to better understand changes in P concentration as mediated by microbial communities (e.g., via organic P mineralisation) and in response to climate change treatments (Margalef *et al.*, 2017).

Data analyses

To test the effects of biocrust species and climate change treatments on available organic and inorganic P and total available P and on the activity of acid phosphatase, we conducted a two-way semiparametric permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001) for each P variable. In these models, species (seven levels; bare soil and lichens) and treatments (three levels; control, warming and the combination of warming and rainfall reduction), were fixed factors. We also initially

included the interaction between species and treatments, as it may have important effects on soil functioning in drylands (Concostrina-Zubiri *et al.*, 2021). We compared the model including the interaction and the model without the interaction using backward selection based on the Akaike Information Criteria (AIC; Akaike, 1973), to obtain the best model (i.e., the model with lowest AIC). Best models were those not including the interaction in all cases, so this term was removed. To detect differences between levels of lichen species and climate change treatments, we conducted PERMANOVA pairwise tests when these factors were significant. All PERMANOVA analyses were run using Euclidean distance and based on unrestricted permutations (999 permutations) because of a small sample size (n = 4-6 per species and treatment) and the unbalanced design (Anderson, 2001) using the “adonis” function from the vegan R package (Oksanen *et al.*, 2019). All analyses were performed with R version 3.6.1 (R Core Team, 2019). Data are available from Figshare (Concostrina-Zubiri *et al.*, 2021b).

RESULTS

Biocrust species had a significant effect on available inorganic and total available P, and on the activity of acid phosphatase, while climate change treatments increased organic P and soil pH. In particular, *B. zoharyi* increased available inorganic P relative to bare soil. Also, *S. lentigera* had higher available inorganic P than *P. decipiens*, while this species increased available inorganic P compared to *B. zoharyi*, *D. diacapsis* and *F. subbracteata* (Fig. 1a, Table S2). In addition, *B. zoharyi*, *D. diacapsis*, *S. lentigera* and *T. sedifolia* increased total available P relative to bare soil. *Squamarina lentigera* also had higher total available P compared to *F. subbracteata* (Fig. 1b, Table S2). The activity of the acid phosphatase was higher in *F. subbracteata* and *P. decipiens* compared to bare soil, *B. zoharyi*, *D. diacapsis* and *T. sedifolia* (Fig. 1c, Table S2). Warming and its combination with rainfall reduction increased available organic P and soil pH compared to the control treatment (Fig. 1d,e, Table S2).

DISCUSSION

Our results, obtained with a manipulative experiment, indicate that some biocrust-forming lichens contribute to soil P accumulation and cycling. Moreover, we found that these effects are species-specific and maintained regardless of climate change treatments in the case of available inorganic and total available P, and the activity of acid phosphatase.

Multiple differences were found among lichen species regarding their effects on soil available P. For instance, soil available inorganic P was higher in *S. lentigera* compared to *P. decipiens* and in *P. decipiens* compared to *B. zoharyi*, *D. diacapsis* and *F. subbracteata*. Such species-specific effects may be due to the great differences in lichen morphology and secondary chemistry among the studied species (Table S1), together with differences in biocrust tissue nutrient content (Delgado-Baquerizo *et al.*, 2015). For example, the dark coloured, discontinuous thallus of *P. decipiens* and its lack of secondary compounds (Table S1) may have favoured the microbial activity (i.e., mineralization) via temperature increase and the allowance of higher in the superficial soil layer (George *et al.*, 2003; Raggio *et al.*, 2014), compared to the other species. Indeed, *P. decipiens* showed one of the highest values for acid phosphatase activity (Fig. 1c). Our results are partially in agreement to a previous study reporting that only some of the studied species (i.e., *F. subbracteata*, *P. decipiens* and *S. lentigera*) effectively increased soil dissolved inorganic P in the field, and this effect seemed to be related to their P tissue content (Delgado-Baquerizo *et al.*, 2015). Contrary to our results, *D. diploschistes* increased inorganic P, compared to bare soil, in a grazed ecosystem, suggesting that this species acts as a dust trap and/or protects the soil surface from mechanical erosion (Concostrina-Zubiri *et al.*, 2013), and thus, retain P-rich compounds in the soil. However, this mechanism does not seem to be operating in our experiment; i.e., only *B. zoharyi* increased inorganic P compared to bare soil. By contrast, *D. diacapsis* had a negative effect on soil inorganic P in a long-term grazing exclusion (Concostrina-Zubiri *et al.*, 2013), indicating that under more favourable conditions this species and/or the microbial communities under its influence were more active, and thus, require a higher P uptake. We found no evidence suggesting that the lichens studied uptake important amounts of available inorganic P from the soil, or at least not at a higher rate than they promote it. Rather, the higher total available P concentration and the relatively similar acid phosphatase activity found in bare soil and under most biocrusts species, together with an increasing trend in available organic P under biocrusts compared to bare soil (Fig. S2), suggest that soil P mineralization rates were generally low, or, conversely, that microbial communities under biocrusts were able to uptake and immobilize certain amounts of available inorganic P.

We found increased acid phosphatase activity under *F. subbracteata* and *P. decipiens* compared to bare soil and to other species such as *B. zoharyi* and *T. sedifolia*. A plausible explanation for these results is that both *F. subbracteata* and *P. decipiens*

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produce anthraquinones, which have metal-chelating capacity (Hauck *et al.*, 2009). The release of such compounds into the soil may enhance both micronutrient and P availability for microbes, resulting in increased microbial activity. However, anthraquinones in *P. decipiens* are only produced in the fruiting bodies (i.e., generally scarce and not always present; Table S1), and some anthraquinones and other secondary compounds (e.g., usnic acid) produced by the species included in our study can also have antimicrobial effects (Manojlovic *et al.*, 2002). Therefore, our results may be alternatively explained by *F. subbracteata* and *P. decipiens* secreting greater amounts of extracellular phosphatases into the surrounding soils (Belnap, 2011), compared to bare soil and other lichen species (Delgado-Baquerizo *et al.*, 2015; Concostrina-Zubiri *et al.*, 2021a).

Soil available organic P and pH were consistently higher under warming and warming and rainfall reduction treatments than in the control treatment regardless of biocrust species (Fig. 1d,e). The higher available organic P found under warmer and more arid conditions contrast with the general idea that aridity reduces the concentration of organic P forms (Plaza *et al.*, 2018), likely due to a negative effect exerted on soil organic matter content (Delgado-Baquerizo *et al.*, 2013). However, the simultaneous increase of soil pH and soil evapotranspiration under warming and warming and rainfall reduction treatments (Lafuente *et al.*, 2018), may have promoted nutrient imbalance (Jiao *et al.*, 2016) and decreased nutrient availability (Moreno-Jiménez *et al.*, 2019) under more arid conditions, negatively affecting soil microbial communities (Maestre *et al.*, 2015a; Chen *et al.*, 2019). The eventual death of microbes would imply a reduction in the consumption of organic P or even the liberation of organic P contained in their biomass, explaining the higher available organic P concentration under climate change treatments.

Although we did not evaluate the effects of rainfall exclusion alone due to logistic limitations, we wouldn't expect this treatment to impact P variables in our soils because the major impacts of simulated climate change on other nutrient cycles (i.e., C and N) under the influence of biocrusts are related to warming (Maestre *et al.*, 2013, 2015; Delgado-Baquerizo *et al.*, 2014). Notwithstanding, further research is needed to evaluate the impact of changes in other climatic variables such as precipitation frequency and form (e.g., liquid vs. dew), which are also important drivers of biocrust physiology and subsequent effects on soil fertility and functioning in drylands (e.g., Baldauf *et al.*, 2018).

CONCLUSION

Using a microcosm approach, we found that multiple biocrust-forming lichens increase soil available inorganic and total available P amounts and cycling in a highly species-specific manner. Also, more arid conditions resulted in higher soil available organic P concentration. Our findings thus provide novel experimental evidence on the importance of biocrusts as modulators of P cycling in drylands, with important implications for their primary productivity and functionality. They also highlight the necessity to consider the identity of biocrust-forming lichens when evaluating their effects on soil fertility. Future research is required to evaluate the capacity of biocrust secondary compounds to reach the soil surface and their role in P fertility and associated bioweathering processes.

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DATA SHARING AND DATA ACCESSIBILITY STATEMENT

Data are available from Figshare, doi: 10.6084/m9.figshare.13498371.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interests.

AUTHORSHIP AND AUTHOR CONTRIBUTIONS

F.T.M. planned and designed the experiment, E.V., V.O., B.G. and B.J.M. set up and maintained the experiment and conducted laboratory analyses, L.C.Z., E.V., V.O., B.G. and B.J.M. processed and analysed data, L.C.Z, E.V. and F.T.M. wrote the manuscript and all authors contributed to the final review.

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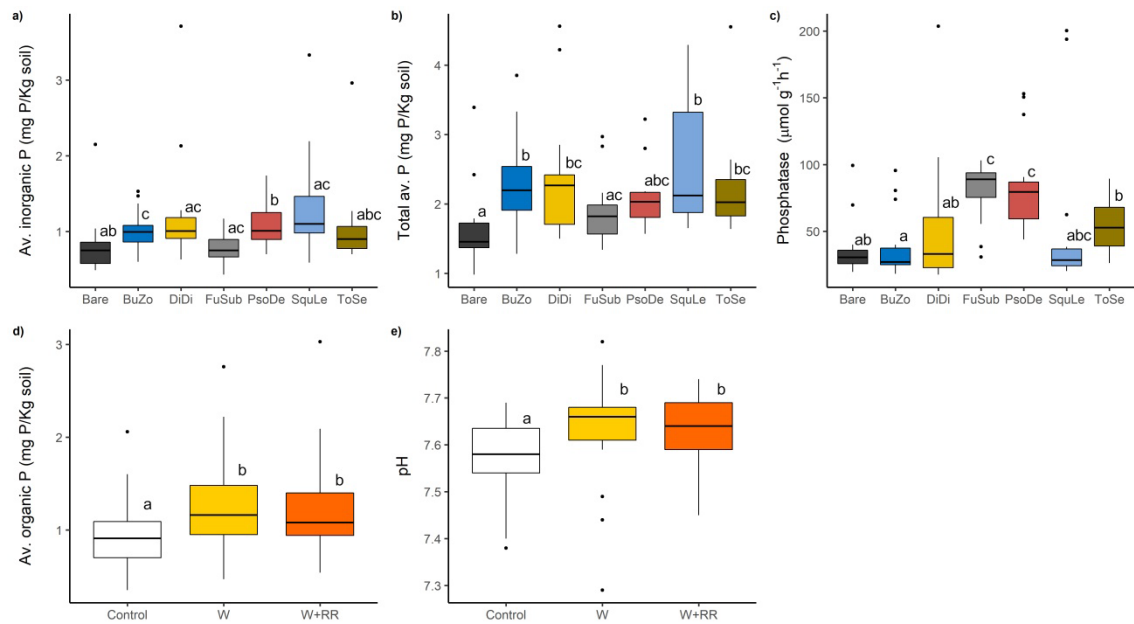


Fig. 1. Concentration of soil available inorganic P (a), total available P (b), acid phosphatase activity (c), available organic P (d) and pH (e) in bare soil and soils under different biocrust-forming lichen species (a-c) and under different climate change treatments (d-e). Boxes show the median, 25th and 75th percentiles; vertical lines show the minimum and maximum values that fall within 1.5 times the height of the box. Different letters next to boxes indicate differences between species or treatments ($P < 0.05$, after PERMANOVA analysis, Table S2). Bare, bare soil ($n=12$); BuZo, *Buellia zoharyi* ($n=18$); DiDi, *Diploschistes diacapsis* ($n=18$); FuSub, *Fulgensia subbracteata* ($n=15$); PsoDe, *Psora decipiens* ($n=15$); SquLe, *Squamarina lentigera* ($n=15$); ToSe, *Toninia sedifolia* ($n=14$). W, warming and W+RR, warming and rainfall reduction. Phosphatase, acid phosphatase activity.