Geoderma 306 (2017) 10–17

Contents lists available at ScienceDirect

Geoderma

journal homepage: www.elsevier.com/locate/geoderma

# Metabolic activity duration can be effectively predicted from macroclimatic data for biological soil crust habitats across Europe

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A R T I C L E I N F O

*Keywords:*
Biocrust
Chlorophyll fluorescence
Climate change impact modelling
Functional type
Plant-soil interactions
Soil erosion prevention

A B S T R A C T

Biological soil crusts (BSC) perform several important environmental functions such as soil erosion prevention, soil nutrient enrichment through photosynthesis and nitrogen fixation, and are receiving growing interest due to their importance in some changing habitats with soils under degradation risk. Primary producers within BSC (cyanobacteria, lichens, algae and bryophytes) are all poikilohydric and active only when wet, meaning that knowledge of the period of metabolic activity is essential to understand growth and adaptation to environment. Finding links with macroclimatic factors would allow not only prediction of activity but also the effects of any climate change over these communities. Metabolic activity and microclimate of BSC at four sites across Europe with different soils from semi-arid (Almeria, SE Spain) to alpine (Austria) was monitored during one year using a chlorophyll fluorometer. Local climatic data were also recorded. Mean monthly activity of crust within each site were strongly linked irrespective of crust type whilst, using the data from all sites, highly significant linear relationships (mean monthly values) were found for activity with incident light, air temperature and air relative humidity, and a nonlinear response to rainfall saturating at about 40 mm per month. Air relative humidity and air temperature were the best predictors of metabolic activity duration. The links observed are all highly significant allowing climate data to be used to model activity and to gain inferences about the effects of climate change over BSC communities, soil structure and fertility. Linear relationships mean that small changes in the environment will not produce massive alterations in activity. BSC also appear to behave as a single functional group, which is helpful when proposing general management policies for soil ecosystems protection.

## 1. Introduction

Biological soil crusts (BSC or biocrusts) are typically defined as a mixture of autotrophic and heterotrophic organisms that (i) live within or on top the uppermost millimeters of soil creating a consistent layer and (ii) aggregate soil particles due to their presence and activity (Belnap et al. 2003). BSC are composed of a wide range of organisms typically including cyanobacteria, algae, bacteria, fungi, lichens and bryophytes (mosses and liverworts). The proportions of these organisms present in a BSC vary depending on location, cyanobacteria can be absent from Antarctic crusts (Colesie et al. 2014) whilst they are dominant in some deserts (Belnap and Lange 2003) and alpine areas (Büdel et al. 2013). BSC have major impacts on the soil properties through stabilization, erosion limitation, and facilitation of colonization by higher plants (Issa et al. 1999; Belnap et al. 2003; Lázaro et al. 2007; Thomas and Dougill 2007; Guo et al. 2008; Belnap and Büdel 2016). BSC also appear to have global scale impacts on nutrient cycles (Wilske et al. 2009; Castillo-Monroy et al. 2011; Porada et al. 2013, 2014) and recent estimates suggest that BSC and other cryptogamic covers can be important suppliers of carbon (7% of total world $CO_2$ fixation) and nitrogen (50% of biologically fixed nitrogen) (Elbert et al. 2009, 2012).

These ecological services are especially important in extreme areas such as high mountains, polar regions or arid/semiarid regions where vascular plants are restricted by environmental constrains such as low precipitation and temperature so that BSC become the dominant vegetation. BSC inhabited areas are not only some of the more extensive on Earth, but are of growing importance in global climate change scenarios and when considering increasing soil surface erosion and massive human land-use (Reynolds et al. 2007; Maestre et al. 2012). BSC, as the major primary producers, therefore represent an important

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http://dx.doi.org/10.1016/j.geoderma.2017.07.001
Received 24 February 2017; Received in revised form 29 June 2017; Accepted 4 July 2017
Available online 14 July 2017
0016-7061/ 

experimental target to consider the impact of possible climatic changes (Field et al., 2014) when evaluating the stability of these ecosystems. BSC have been described as ecosystem engineers (Pointing and Belnap 2012), and not only have relevance in the maintenance of soil structure, but are also suggested to be global indicators of soil or ecosystems processes health (Rosentreter and Eldridge 2003). Links between BSC and soil microbial communities as well as with microfauna (protozoa, nematodes, tardigrades, rotifers, mites, collembolans, arthropods and mollusks) are evident (Maier et al. 2014; Darby and Neher 2016) and indicate that any disturbance could similarly affect all groups of organisms. Thus, the study of the impact of any environmental change over BSC communities has relevance to the whole set of soil inhabiting organisms and ecosystem processes.

The potential effects of climate change on BSC have been investigated using a variety of experimental approaches with some showing an apparent negative impact from temperature increase (Escolar et al. 2012; Maestre et al. 2013; Ferrenberg et al. 2015) whilst others did not (Grote et al. 2010; Johnson et al. 2012; Zelikova et al. 2012) although there is a general agreement on the importance of changes in quantity, temporal distribution and/or intensity of precipitation (Reed et al. 2012; Coe and Sparks 2014). All photosynthetic organisms in BSC are poikilohydric meaning that their water status tends to equilibrate with the surrounding environment and that they are wet and active when the environment is wet, and desiccated and dormant under dry conditions. Poikilohydry represents an added complexity when trying to link BSC performance to climate because, when the component organisms are active, conditions tend to be less extreme than for the general environment (Pintado et al. 2010; Schlensog et al. 2013; Raggio et al. 2014). The actual length of time when BSC are active is, therefore, a crucial piece of information when attempting to estimate their contributions to ecosystem functioning. Here we use chlorophyll fluorescence parameters as a proxy for an active metabolism so that we can determine activity periods when either photosynthesis or respiration occur. This technique, together with microclimatic and macroclimatic conditions when organisms are metabolically active provides useful tools to gain insights into adaptation to habitat and general distribution (Schroeter et al. 2011; Raggio et al. 2016).

In previous studies BSC have been classified and grouped using different approaches, e.g. species composition, functional groups, or a combination of surface appearance and functional groups (Büdel et al. 2009), and none of them were based on physiological behavior, a grouping criterion well accepted for vascular plants. We were interested in discovering linkages between activity duration of individual BSC and the environment at each site and also whether BSC composed of diverse component organisms and habitats responded similarly, so that they might be considered to be a single functional type (FT). How exactly a FT is defined has been very variable, but we will use the form adopted by Smith et al. (1997). In their definition, which was applied to vascular plants, a FT is a non-phylogenetic classification leading to a grouping of organisms that respond in a similar way to a syndrome of environmental factors (Gitay and Noble 1997). This definition is particularly useful because it aims to simplify complex communities thus making modelling of responses to be more easily achieved and improving predictions of responses to climate changes (Steffen et al. 1992). It has previously been suggested that BSC may have a constant developmental pattern with a tendency to respond similarly to the environment (Pointing and Belnap 2012).

Three major topics were studied to find answers to several specific mechanistic research questions:

(1) *Response homogeneity*. Sample and site effects need to be differentiated. How similar are the annual patterns of monthly activity of the different BSC within a study site (sample effect)? Do similar crusts types, occurring at different study sites, show diverging patterns in annual activity (site effect)?
(2) *Relationship between local climate and activity*. Is the BSC activity duration linked to local climate factors and is it possible to generalize the relationships across all sites?
(3) *Evaluation of relationships as possible climate change predictors*. How good are the relationships between activity duration and environmental factors? Is the quality such that they can provide an experimentally based model to investigate climate change scenarios?

**Table 1**
Summary of main characteristics of the four research sites involved in the study.

| | Almería | Hochtor | Homburg | Öland |
|---|---|---|---|---|
| Country | Spain | Austria | Germany | Sweden |
| Latitude | 37°00′ N, 2°26′W | 47°05′ N, 12°51′E | 50°01′N, 9°48′E | 56°32′N, 16°28′E |
| Altitude (m) | 250 | 2600 | 295 | 20 |
| Climate | Warm Mediterranean | Alpine | Warm temperate | Cold maritime |
| Annual rain (mm) | 220 | 1750–2000 | 600 | 500 |
| Annual T (°C) | 18.5 | − 3 | 8.2 | 6.5 |
| Soil type | Haplic calcisols | Calcareous regosols; rendzic leptosols | Skeletal and rendzic leptosols | Skeletal and rendzic leptosols |
| Soil depth (cm) | < 100 | 15–30 | < 10 | < 20 |
| Natural/managed | Natural | Natural | Managed | Managed |
| Particularities | Sunniest, driest area in Europe | 300 snow cover days/year | Quarry operated | Cattle grazed |

Our initial hypothesis is that, due to the poikilohydric nature of BSC, the length of the active periods in these communities could be predictable by using easily measured environmental parameters.

## 2. Materials and methods

### 2.1. Investigation sites

The four research sites, which are located along a latitudinal and altitudinal gradient in Europe, are described together with soil properties in detail in Büdel et al. (2014) and represent a variety of different climates and soil types (see Table 1 for descriptions).

### 2.2. Mesoclimate monitoring

Mesoclimate at each of the research localities was recorded at 5-min intervals using identical climate stations with data loggers (CR 1000, Campbell Scientific, Logan, UT, USA) running on batteries. Air temperature ($T_{air}$), relative humidity (RH, CS 215, Campbell Scientific, Bremen, Germany), and ambient photosynthetic photon flux density (PPFD, Quantum Sensor SKP 215, Skye, Llandrindod Wells, UK) were measured at ~1.50 m height; precipitation was recorded with a tipping bucket rain gauge (Model 52,203, Young, Traverse City, Michigan, USA) about 0.5 m above the ground. The mesoclimatic measurements made here are similar to those recorded using standard meteorological techniques.

### 2.3. BSC microclimate and metabolic activity monitoring

Monitoring of BSC activity and microclimate was carried out using automatic fluorometers (MoniDA, Gademann Instruments and Walz, Germany). Each MoniDA consists of central unit that operates the system and records the data and is connected to eight measuring heads each of which has sensors for BSC temperature and incident PPFD together with a PAM (Pulse-Amplitude-Modulation) fluorometer with a fiber optic that is placed a few mm away from the sample (Fig. 1). Sample activity and long term physiological performance was