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Short communication

The response of the moss *Campylopus lamellatus* (Leucobryaceae Schimp.) post El Niño: a case study in the Caatinga

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Abstract
Biological soil crusts (biocrusts) are important biological components in arid and semi-arid regions because they can serve as ecological facilitators for the vascular flora. Biocrusts of rocky outcrops of the Caatinga biome in the semiarid region of Northeast Brazil are comprised mainly of populations of the pioneer moss *Campylopus lamellatus*. Meanwhile, the Caatinga is undergoing progressive desertification, which is likely to continue for the next 100 years. Therefore, the physiological responses of *C. lamellatus* to climate change should be included in predictions regarding the future of the flora of these rocky environments. We evaluated a population of *C. lamellatus* during a prolonged drought brought about by El Niño, and during the first subsequent rainy season. We used biomass (dry mass) and proportion of chlorophyll as measures of tolerance. We identified decreased investment in biomass allocation and the degradation of photosynthetic pigments during the drought event. In contrast, we observed a rapid increase of chlorophyll during the rainy season, which represents biomass investment via chlorophyll regeneration. We conclude that the resilience of *C. lamellatus* is rapid, even for a photophilic plant, and should ensure its facilitative function under conditions of water saturation of the environment.
Key words: Biomass, stress, photosynthesis, pigments, semiarid.

Resumo
Biological soil crusts (*biocrusts*) são componentes importantes em regiões áridas e semiáridas, comumente associados à facilitação da flora vascular. Os *biocrusts* em afloramentos rochosos da Caatinga, no semiárido nordestino, são representados principalmente por populações do musgo pioneiro *Campylopus lamellatus*. Entretanto, a Caatinga está sob progressivo processo de desertificação, que deve se prolongar pelos próximos 100 anos. Assim, entender a resposta fisiológica de *C. lamellatus* sob um cenário de mudanças climáticas, deve basear previsões sobre o rumo da flora de ambientes rochosos em cenário futuro. Aqui, nós avaliamos uma população do musgo *C. lamellatus* durante o efeito prolongado de seca, causado pelo El Niño, e durante a primeira estação chuvosa após o fenômeno. Nós utilizamos a biomassa (massa seca) e proporção de clorofilas como medidas de vigor. Nós identificamos a diminuição do investimento em alocação de biomassa e a degradação dos pigmentos fotossintéticos durante o evento de seca. Em contrapartida, constatamos o rápido aumento das clorofilas durante a estação chuvosa, i.e., investimento em biomassa via regeneração de clorofilas. Desse modo, nós concluímos que a resiliência do *C. lamellatus* é rápida até mesmo para uma planta fotófila, o que deve assegurar sua função facilitadora em condições de saturação ambiental.
Palavras-chave: Biomassa, estresse, fotossíntese, pigmentos, semiárido.

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The Caatinga is a Brazilian dry forest that is experiencing drastic desertification, with predictions of decreasing rainfall and increasing temperatures for at least the next 100 years (Vieira *et al.* 2015). This scenario should alter the distribution of species and, consequently, the dynamics of ecosystems. The rocky outcrops represent floral refuges with a wide variety of habitats (*e.g.*, depressions, bare rock, cracks and soil islands) and diverse microclimates (Porembski *et al.* 1998). They are unique environments with many endemic and rare Brazil plant species with limited distributions (Schneider & Boldrini 2012; Silva & Germano 2013; Pereira *et al.* 2016; Silva *et al.* 2014). Despite this, studies on the ecology of rocky outcrops are still incipient in Brazil (see Silva 2016).

Bryophytes represent one of the most expressive components of biological soil crust in arid environments, such as rocky outcrops (Belnap & Lange 2001). Biocrusts are associations between avascular organisms and soil particles, with the organisms living in or just above the ground (*e.g.*, cyanobacteria, algae and bryophytes; Benalp & Lange 2001). These associations can affect microclimates, facilitate germination, and alter nutritional status and survival of vascular plants (Benalp & Lange 2001). These functions are especially important in arid and semi-arid regions and environments, such as the rocky outcrop ecosystems located in the dry forests of the Caatinga.

Among mosses common to biocrusts, *Campylopus lamellatus* Mont. (= *Campylopus pilifer* Brid. according Gama *et al.* 2017) stands out as an abundant species on rocky outcrops (Silva *et al.* 2014, 2018; Penãloza-Bojacá *et al.* 2018). It is an acrocarpic pioneer moss of rocky outcrops (Oosting & Hess 1956; Scarano 2002), and is widely distributed worldwide. In the Neotropics the species occurs at high elevations, reaching up to 3500 m (Gradstein & Sipman 1978). According to Gradstein & Sipman (1978), the species requires a humid climate, at least periodically, for population persistence. It is recognized as being adapted to xeric climates, possessing morpho-anatomical attributes that allow it to colonize and persist therein. Such attributes include well-developed and internally-differentiated strands arranged in stereochemical bands that decrease mechanical stress during desiccation events (Frahm 1990). Its costa, occupying more than two-thirds of the width of the leaves, is the main site for photosynthesis, and acts in gas exchange and effective water conduction (Frahm 1985, 1990). Its tall lamellae allow the photosynthetically active period to be extended in dry environments (Frahm 1985). Thus, understanding the responses of *C. lamellatus* to climate change can facilitate predictions regarding the flora of dry environments and allow inferences to be made regarding the dynamics of plant communities.

Catimbau Valley National Park (PARNA Catimbau; 08º24'–08º36'S × 37º09'–37º14'W), possesses a horizontal gradient of rainfall with extremes differing by 500 mm (Rito *et al.* 2017). Considering the effects of climatic change on the Caatinga (Vieira *et al.* 2015), changes in the spatial distribution of plant species are expected, particularly so for bryophytes, which should accompany the moisture gradient and move towards more humid extremes (Tng *et al.* 2009; Sun *et al.* 2013). This pattern should be intensified by the broad geographic distribution of many bryophyte species (i.e., long-distance dispersion via spores), with shifts in the distribution of plants according to the rate of the climate change. New records for bryophyte species have come from some very unlikely locations [*e.g.*, *Crossidium crassinerve* (De Not.) Jur., *Dicranella howei* Ren. et Card., *Frullania inflata* Gottsche - Pócs (2011)]. Although it is difficult to pinpoint the causes of changes in the distributions of bryophytes (see Frahm & Klaus 2000; Kürschner 2002), Pócs (2011) suggests that at least some of these records are potentially due to the influence of climatic change.

We collected two 10 × 10 cm samples of *C. lamellatus* from the same population (approximately 1 m²): one in July 2016 during drought season (El Niño effect) and one during the first rainy season post El Niño in June 2017. In July of 2016, the mean daily rainfall for the month was approximately 0.93 mm, with rain concentrated in only two days, while the mean monthly temperature was 22.9 °C. The El Niño event of 2015–16 exhibited relatively high anomalies and had major impacts on the dynamics and structure of the tropical ecosystems worldwide (Brito *et al.* 2017). In Brazil, this event caused an extreme dry climate in the semiarid region. In June 2017, the mean daily rainfall for the month was approximately 3 mm, with rains on every day, while the mean monthly temperature was 19.4 °C (National Institute of Meteorology INMET <http://www.inmet.gov.br>). The response of the moss population to the differing climates of the two periods was evaluated using variation in dry mass and pigment parameters [i.e., amounts of chlorophyll a (Chl a) and chlorophyll b (Chl b) and the proportion chlorophyll a:chlorophyll b (Chl a:b)], according to Marschall & Proctor (2004). We packed the samples in ziplock bags to conserve moisture and they were maintained in the dark at 10 ºC.

We measured the mass of 50 gametophytes for each climatic period on a precision scale (0.0001 g). We then dried the samples at 80 °C for 72 h, and then reweighed them to obtain dry mass (adapted from Marschall & Proctor 2004), which we treat as biomass here. For the pigment parameters, we macerated 100 mg of botanical material in a darkened environment and added 10 ml of 80% acetone. The solution was allowed to settle for 24 h in the dark in a test tube enveloped with paper and foil for the complete separation of possible substrate particles and for measuring the amount of pigments (Lichtenthaler 1987). The amounts of the photosynthetic pigments Chl a and Chl b were measured (in triplicate) using a spectrophotometer at absorbances of 645 and 663 nm, respectively (Lorenzen 1967; Peñuela 1984; Martínez & Sánchez 1987; Marschall & Proctor 2004). We removed the acetone effect by calculating the difference between the pigment solution and the acetone content by reading the pure acetone at each absorbance. We transformed the results using the following typical equations in bryophyte's physiology: $Ca = 12.3 * E663 - 0.86 * E645$; $Cb = 19.3 * E645 - 3.6 * E663$; $Ca + Cb = 8.7 * E663 + 18.4 * E645$, where Ca and Cb indicate the concentrations of chlorophyll a and b, respectively. Since these results are in mg/L, we converted them to mg/g wet weight by the following equation: $C = (Ca * V)/g$, where Ca indicates the value for chlorophyll a in mg/L; V indicates the volume of the extraction in L; and g indicates the weight of the moss sample (G.M. Gecheva - personal communication).

Biomass (mean ± SD: dry = 14.04 mg ± 8.48 mg, rainy = 16.70 mg ± 9.80 mg) did not vary significantly between sampling periods (t-student test, $t = -1.453$, n.s.). This can be explained by the lack of adequate weather and climate for investment in growth between the end of the drought season and the next sampling period (subsequent rainy season) about six months later. Nonetheless, biomass increased slightly in the rainy season, which may be indicative of initial investment in the accumulation of dry mass by gametophytes.

Chlorophyll a levels were generally higher in the rainy season (Mann-Whitney test: $Z = -1.963$, $P = 0.049$), but there was no significant difference in chlorophyll b levels ($Z = -1.385$; n.s.) or in the chl a:b ratio ($Z = -0.654$; n.s.). It should be noted that Chl a levels increased by a factor of four times during the rainy season and that Chl b levels also increased during the rainy season, but not significantly so (Table 1). Although the pigment levels are considered normal for species of bryophytes adapted to xeric environments (Martín & Churchill 1982; Marshall & Proctor 2004), the increase of chlorophyll levels in the rainy season shows that variation in rainfall is a determinant for the development of the bryophytes (Ueno *et al.* 2006). On the other hand, the non-significant difference in chlorophyll b levels and chl a:b between the two climatic extremes indicates investment in protective processes, such as photoinhibition, as has been documented for *Campylopus introflexus*, another species of the genus (García *et al.* 2016).

Chlorophyll degradation is a well-known process. One of the elementary factors for triggering this process is environmental stress, such as prolonged drought (Hendry *et al.* 1987). The increase in chlorophyll content in *C. lamellatus* may be linked to decreased available sunlight during the rainy season (due to increased cloudiness) and to increased biomass of gametophytes. The investment in biomass must be accompanied by increased leaf production, which thereby increases the concentration of chlorophyll. This explanation is consistent with the data presented by Carvalho *et al.* (2007) for vascular plants of open and closed Cerrado. Although there are differences in the concentrations of chlorophyll molecules between vascular and avascular plant groups, there is also great overlap (Marschall & Proctor 2004). This is explained by the fact that increased or decreased concentrations vary according to the level of solar radiation, for example (Marschall & Proctor 2004).

The proportion of chlorophylls a:b (1.65, s.d. ± 1.13) of this species in the dry season is much lower than that found for other species in exposed environments (2.51, s.d. = 0.22 – Martín & Churchill (1982); 2.39, s.d. = 0.51 – Marschall & Proctor 2004). This indicates that the level of solar radiation experienced in dry seasons in the Caatinga in rocky outcrops is particularly higher than in the surrounding matrix. *Campylopus lamellatus* presents Type 3 light curves (Bates *et al*. 2009), which indicates a photoprotective response to light intensities above normal including maintaining the trans-thylakoid pH gradient necessary for zeaxanthin-PSBS-mediated quenching (Gerotto *et al.* 2012; Proctor & Smirnoff 2015; Proctor & Bates 2018).

Bryophytes cushion susceptibility to erosion and aid in the uptake and retention of nutrients, and thus affect the structure of vascular plant communities (Belnap & Weber 2013). These plants constitute one of the least studied plant groups in xeric environments, especially in the case of rocky outcrop ecosystems (see Silva 2016). Because they are poikilohydric, conditions of high aridity may hinder establishment. Although the growth rates of bryophytes in dry environments are low when compared to those in mesic environments, their contribution to these ecosystems (*e.g.*, structuring of sandy soils, and biomass accumulation) at the global level is of fundamental importance (Stark *et al.* 2011). We report a significant increase in chlorophyll a levels during the rainy season in a pioneering moss from a fragile Caatinga ecosystem. We suggest that during the rainy season, when there is greater water accumulation in the gametophytes due to poikilohydrism, the productivity of the population increases, which produces a discrete increase in biomass in a few months. A reduction in rainfall intensity or an increase in the duration of the rainy season, either due to climatic events such as El Niño or to global climatic changes, may alter the physiology of the studied species of moss, which may have drastic consequences for the dynamics and vegetation associated with rocky outcrops.

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