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Thermotolerance in Miniature: Heat Resilience of Moss Propagules From Brazilian Ferruginous Rocky Outcrops

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ABSTRACT

Harsh environments present substantial challenges to most organisms, making survival and thriving difficult. Such conditions often include extreme temperatures, intense radiation, strong winds, and very low or high humidity levels, resulting in a limited availability of resources like water and nutrients. Deserts, with their extreme heat and scarce water, and Brazilian ferruginous rocky outcrops (*Cangas*), known for their extreme temperatures, nutrient-poor soils, wildfire events, and limited water, are prime examples. Despite these harsh conditions, *Cangas* host specialised flora, including rare angiosperm species, and diverse mosses and liverworts adapted to water scarcity and high solar radiation. However, their adaptations to heat stress are not well understood. Our study is the first to investigate the thermotolerance of bryophyte asexual propagules in two common moss species found in *Cangas*, in the context of forest fires, focusing on *Bryum atense* R.S. Williams (Bryaceae) and *Campylopus savannarum* (Müll. Hal.) Mitt. (Dicranaceae). We subjected *B. atense* tubers and *C. savannarum* detached leaves to heat treatments at 120°C, 140°C, and 160°C for 5 and 30 min, alongside a control group. Results showed that *C. savannarum* leaves lack thermotolerance, whereas *B. atense* tubers exhibited notable resilience, as evidenced by protonemata production up to 54 days after treatment, with 60.4% regeneration at 120°C for 30 min and 58.3% at 160°C for 5 min. This study represents the first record of thermotolerance in bryophyte asexual propagules in *Cangas*, documenting the highest level of thermotolerance known for moss propagules. It offers valuable insights into moss resilience in harsh environments and their potential responses to wildfires and global warming.

1 | Introduction

Rocky outcrops are geological formations in which a hard core of parental rocks protrudes above the surface of the surrounding land and can be found on all continents (Fitzsimons and Michael 2017), with a conspicuous number of these ecosystems being registered in southeastern Brazil (Scarano 2007). A unique Brazilian outcrop type is the *Canga*, a ferruginous rocky outcrop characterised by severe environmental conditions for plant establishment, including high UV exposure, low water retention, constant winds, impermeable soils (Jacobi et al. 2007;

Jacobi and Carmo 2008) and high daily temperatures (average soil temperature ~38°C; Ferrari et al. 2016). Another stress factor for the plants in *Cangas* is wildfires, which can cause habitat destruction, alter soil structure, induce thermal stress (soil temperature, during wildfires, can reach ~548°C; Rodrigues et al. 2021), and result in the death of numerous specimens (Conceição et al. 2016; Figueira et al. 2016).

Despite all these stress factors, the *Cangas* support a diverse range of plant species that have developed specific survival and reproductive strategies, from seed plants (Carmo and

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Jacobi 2013; Souza et al. 2018) to bryophytes (Oliveira-da-Silva and Ilkiu-Borges 2018; Peñaloza-Bojacá et al. 2018a, 2018b; Oliveira et al. 2021). Indeed, the majority of bryophytes exhibit desiccation tolerance (Proctor et al. 2007; Stark 2017; Oliver et al. 2005; Proctor 2001), presenting also traits that favour water absorption (Proctor 1982; Vanderpoorten and Goffinet 2009). Additionally, many bryophyte species employ both sexual (e.g., spores) and asexual (e.g., aerial gemmae, tubers, caducous propagules) reproduction to colonise harsh environments (e.g., Stark et al. 2000, 2007).

However, with regard to heat tolerance, bryophytes from *Cangas* have yet to be studied. In fact, it is already known that mosses from ecosystems with high temperatures can exhibit thermotolerance, which may suggest that mosses from the *Cangas* also possess this capability. For example, the populations of the cosmopolitan moss *Bryum argenteum* Hedw. (Bryaceae) collected in the Gurbantunggut Desert (soil temperature ~44°C; Jing et al. 2009) present heat tolerance, surviving at 120°C for 10 min (Zhuo et al. 2020). Plants from the Mojave Desert (soil temperature ~52°C; Bai et al. 2014), such as *Microbryum starckeanum* (Hedw.) Zand. (Pottiaceae) and *Syntrichia caninervis* Mitt. (Pottiaceae), also exhibit inherent heat tolerance in the gametophyte (McLetchie and Stark 2006; Stark and McLetchie 2006). Additionally, *S. caninervis* holds the record for the highest thermal tolerance among adult eukaryotes, with the ability to regenerate after exposure to 120°C for 30 min (Stark et al. 2009). The majority of the studies conducted have focused on the gametophyte and/or sporophyte structures of the plants, with diaspores (e.g., spores and gemmae) being less studied in terms of heat tolerance (Yusup et al. 2022; Marchetti et al. 2020).

Given that bryophytes inhabiting *Cangas* are exposed to high thermal stress due to elevated soil temperatures and wildfire events, we hypothesise that certain terricolous moss species may exhibit heat tolerance, similar to other bryophytes in different harsh ecosystems. We specifically investigate the thermotolerance of two common moss species found in *Cangas*, utilising their asexual propagules. We utilised detached leaves of *Campylopus savannarum* (Müll. Hal.) Mitt. (Dicranaceae) and tubers of *Bryum atenense* R.S. Williams (Bryaceae). Additionally, the detachable leaves of *C. savannarum* exhibit normal photosynthetic function. To date, to our knowledge, this study represents the first investigation into heat tolerance in bryophyte asexual propagules, in the context of *Cangas*. Additionally, this study provides important insights into bryophyte heat tolerance not only within Brazilian ecosystems but also opens possibilities for exploring similar adaptations in bryophytes from other environments where high temperatures act as an important evolutionary driver.

2 | Material and Methods

2.1 | Studied Site and Species Selection

Our study focused on mosses found in a *Canga* located at *Monumento Natural Serra da Calçada* in Brumadinho, Brazil (20°05'43" S, 43°58'59" W; Figure 1A). The study site is situated in the *Quadrilátero Ferrífero* region, a transition zone between two globally recognised biodiversity hotspots: the *Cerrado* and

the Atlantic Forest (Mittermeier et al. 2004; Fernandes 2016). This area is acknowledged as one of the world's most significant iron ore deposits (Dorr 1969). The average annual temperature in the study site varies between 11.8°C and 23.9°C, with an average total annual precipitation of approximately 1559 mm (WorldClim 2).

Based on the floristic survey by Oliveira et al. (2021), we selected two abundant moss species from the *Monumento Natural Serra da Calçada*: *Campylopus savannarum* (Müll. Hal.) Mitt. and *Bryum atenense* R.S. Williams (Figure 1B), respectively belonging to Dicranaceae and Bryaceae, the most representative moss families in the region. The selected species have contrasting propagation strategies: *C. savannarum* (Figure 1C,D) reproduces via caducous branches and leaves (Frahm 1991), whereas *B. atenense* (Figure 1E,F) via subterranean tubers (i.e., rhizoidal gemmae; Ochi 1980), a specialised asexual propagule that plays a key role in soil diaspore banks (During 2001).

2.2 | Moss Sampling and Preparation

Moss sampling occurred in October 2022 during the early rainy season in the *Canga* of our study site. We gathered 15 samples (ca. 100 cm²) for both *B. atenense* and *C. savannarum* patches, at least 2 m apart each. Samples were collected from the topsoil layer by gently inserting a spatula into the substrate, then placed in small plastic bags and transported to the laboratory. Each sample was divided into two portions: one portion was transferred to a paper bag for taxonomic identification, while the other was immediately placed at 10°C and in darkness for one week to keep the plants fresh for the experiment. Taxonomic identification of the mosses was conducted using specific literature (Ochi 1980; Frahm 1991) and using a stereomicroscope and light microscope. Specimen vouchers were deposited in the BHCB herbarium at Universidade Federal de Minas Gerais (voucher numbers 211375–211389).

We selected non-sex expressing gametophytes of *C. savannarum* larger than 3 cm for leaf detachment. From the 15 collected samples, we chose a minimum of five gametophytes from each for the experiment. Before detaching the leaves, we separated the moss gametophytes from the substrate and cleaned them using an ultrasonic bath (two cycles of 480 s each into distilled water). Excess water from the plants was removed by placing them on a Petri dish lined with paper towels. Approximately 4–5 leaves were removed from each of the 75 clean gametophytes of *C. savannarum*, which had their 1 cm apical regions defoliated. Only the greenest and largest leaves (>4 mm and fully developed) were selected for the experiment.

For *B. atenense*, we observed that all collected colonies produced tubers. We chose to extract a minimum of 20 tubers per sample, selecting only those with a diameter >0.2 mm and a reddish colour. The tubers were separated using a stereomicroscope. The colonies were positioned upside down, and we excavated the substrate with sterilised tweezers and needles. When a tuber was visible, we carefully removed it using the moistened tip of the needle, taking extreme care to avoid perforating or damaging it. We always ensured that the tuber was free of rhizoids. Finally, we cleaned it with distilled water. Excess water from

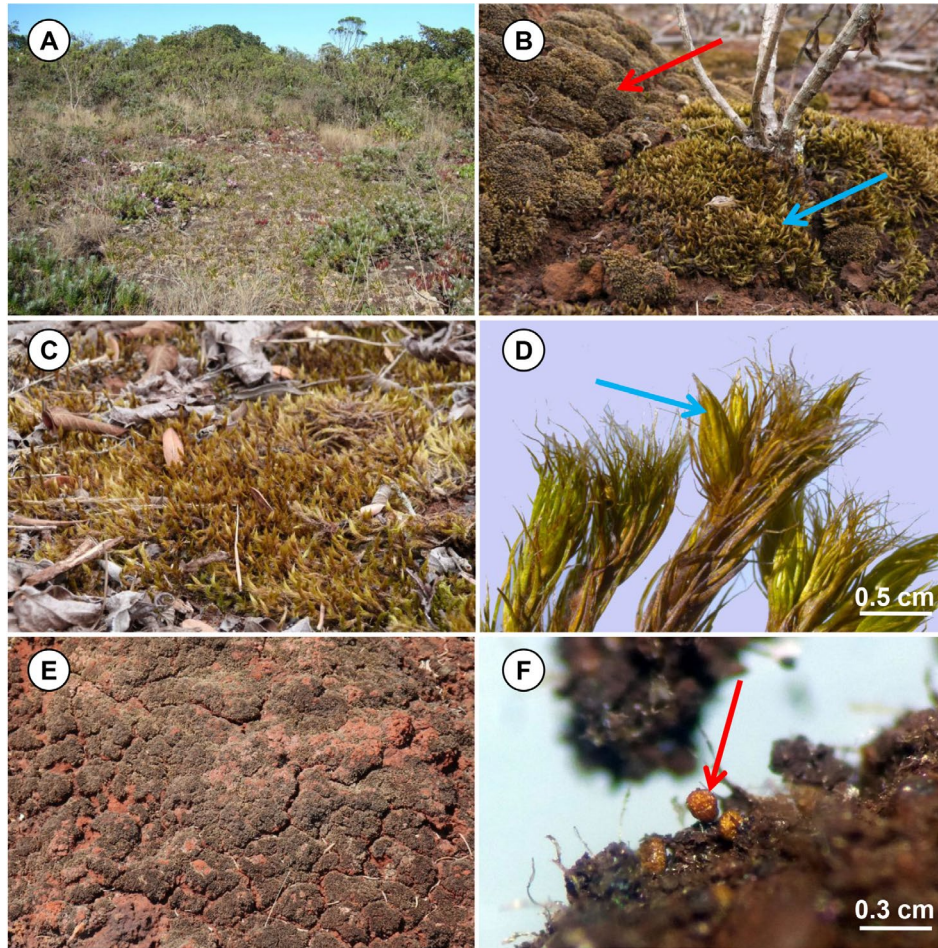


FIGURE 1 | Studied site and selected species for the heat tolerance experiment. (A) *Canga* of the Monumento Natural Serra da Calçada, Brazil. (B) *Campylopus savannarum* (indicated by the blue arrow) and *Bryum atense* (indicated by the red arrow). (C) Colony of *C. savannarum*. (D) Caducous branches and leaves of *C. savannarum* (indicated by the blue arrow). (E) Colony of *B. atense*. (F) View of the underside of a *B. atense* colony, highlighting its tubers along with soil (indicated by the red arrow).

the tubers was removed by placing them on a Petri dish lined with paper towels.

The selected tubers and leaves (ca. 400 each) were carefully stored in Petri dishes lined with filter paper and wrapped in aluminium foil to prevent light exposure. We opted to do this to prevent the stimulation of asexual structure regeneration. Until the day of the experiment setup, the plant structures were kept refrigerated at 10°C for another week to maintain their freshness.

2.3 | Experimental Design

The experiment was set up following a factorial design ($2 \times 7 \times 48$), with two kinds of bryophyte propagules (detached leaves and tubers), seven heat treatments, and 48 replicates for each propagule (i.e., our sampling units). The heat treatments were designed based on the upper thermal limits tolerated by mosses, with reference to Stark et al. (2009), who reported survival at temperatures up to 120°C for 30 min. We adopted the 30-min exposure to replicate the conditions tested by Stark et al., while the 5-min exposure was intended to simulate brief, low-intensity wildfire events. Accordingly, the experimental treatments included a control condition (room temperature, 26°C) and three

elevated temperatures (120°C, 140°C, and 160°C), each applied for both 5 and 30 min.

We used 336 tubers of *B. atense* and 336 detached leaves of *C. savannarum* for the whole experiment. Each treatment (control, 120°C, 140°C, and 160°C for 5 min, and 120°C, 140°C, and 160°C for 30 min) received 48 propagules of each species. We emphasise that all structures were air-dried at room temperature (c. 25°C) for at least 2–3 h prior to the heat treatments and were handled using properly sterilised tweezers to minimise environmental contamination.

To test heat tolerance, we prepared 48 *C. savannarum* detached leaves and 48 *B. atense* tubers for each treatment. For each species and asexual structure, two Petri dishes (each containing 48 propagules arranged on filter paper) were used. The dishes were placed in a preheated laboratory oven (Bransdonto model 3) at the designated temperature. After 5 min, one dish per structure (i.e., leaves and tubers) was removed from the oven and allowed to cool at room temperature for 30 min.

The second dish per structure remained in the oven for an additional 25 min (total exposure time of 30 min), after which it was also cooled for 30 min before inoculation. This procedure

was repeated for three temperatures: 120°C, 140°C, and 160°C. Temperature was monitored throughout the exposure using a precision thermometer. As a control, a set of 48 propagules per structure was not subjected to heat.

As a next step, all propagules (both heat-treatment and control groups) were individually inoculated into the wells of pre-labelled multiwell culture plates, each containing a filter and 1 mL of distilled water, and wrapped in plastic film to prevent contamination. Each propagule was evaluated as an individual event in the statistical analyses, following similar previous studies (Stark et al. 2009). The plates were placed in a cultivation room with a photoperiod of 12 h (average irradiance of $74 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and a temperature of 16.2°C–22.7°C. Every 7 days, we watered the plants with 1 mL of distilled water. Additionally, we rearranged the culture plates on the shelf to minimise the effects of spatial variations in light intensity, and we assessed the regeneration of *C. savannarum* detached leaves and *B. atenense* tubers using a stereomicroscope, considering that the production of protonemata and new shoots indicates the survival of the structure and its regenerative capability. When we observed that the structures had stabilised in terms of regeneration rate, we decided to conclude the experiment, totalling 54 days of incubation.

2.4 | Data Analysis

To assess the regeneration rates of moss species under heat treatments, we employed a Generalised Linear Mixed-Effect Model (GLMM) using the glmer function from the lme4 package (Bates et al. 2015) in R version 4.0.2 (R Development Core Team 2013). The binary response variable “regeneration” (0/1) was recorded for leaves and tubers. The GLMM incorporated the fixed effects “heat treatment” and “asexual structure” and initially included “time” as a random effect to account for repeated measures. However, the model showed near-zero variance for the random effect, resulting in a singular fit warning. Consequently, we removed “time” as an effect.

We then used a Generalised Linear Model (GLM) via the glm function to assess the effects of heat treatment, asexual structure, and their interaction. We specified the binomial family with a logit link function due to the binary nature of the response variable. Model fit and selection were evaluated based on overdispersion (residual deviance/null deviance) and the Akaike Information Criterion (AIC).

Additionally, we analysed the potential effects of heat treatments and asexual structure on fungal growth using a separate GLM, specifying the same binomial family. This model evaluated the main effects and their interaction to determine whether fungal presence was associated with the experimental conditions. All statistical analyses were conducted using a significance level of $p\text{-value} < 0.05$.

3 | Results

The GLM model indicated that heat treatments did not have a statistically significant effect on the regeneration of bryophyte

TABLE 1 | Summary of the generalised linear model (GLM) evaluating the effect of heat treatment, asexual structure (detached leaves of *Campylopus savannarum* and tubers of *Bryum atenense*), and culture time on the probability of regeneration.

Effect	Estimate	Standard error	Z	p
Intercept	−3.9406	0.5439	−7.245	< 0.0001
Treatment	−0.0477	0.1263	−0.378	0.7056
Tuber structure	4.4463	0.5634	7.891	< 0.0001
Heat × tuber structure	−0.2472	0.1312	−1.884	0.0596
Residual deviance		1394.5		
Null deviance		1916.1		
AIC		1402.5		

Note: p -values ($p < 0.05$) are highlighted in bold.
Abbreviation: AIC, Akaike information criterion.

propagules (Table 1). In contrast, the type of asexual structure had a highly significant effect, with tubers showing a substantially higher probability of regeneration compared to detached leaves (Table 1 and Figures 2C and 3C). Neither the exposure duration nor the interaction between heat treatment and asexual structure reached statistical significance. However, the interaction showed a marginal trend, potentially indicating a modulatory effect of heat, particularly on the tubers of *B. atenense*.

Detached leaves of *C. savannarum* were capable of regenerating (i.e., producing protonemata in the form of rhizoids, green filaments of early gametophytes) after heat treatments (Figure 2A,B), specifically following exposure to 160°C for 5 min and 120°C for 30 min. However, the proportion of leaves that regenerated was very low after 54 days, with only 6.3% of samples regenerating in each of these treatments (Figure 2C). Curiously, the first signs of regeneration were observed after 2 days of the experiment. Additionally, after 54 days, we observed that no regeneration occurred in the control group of *C. savannarum* leaves, as well as in those treated at 120°C and 140°C for 5 min or at 140°C and 160°C for 30 min.

In contrast, tubers of *B. atenense* demonstrated higher efficiency in regeneration (i.e., producing protonemata and/or new leafy shoots), specifically following exposure to 160°C for 5 min and 120°C for 30 min (Figure 3A,B) with over 50% of samples regenerating in both treatments. The first protonemata produced by the tubers were observed after 2 days of the experiment, with at least two samples in each treatment showing signs of regeneration. The control group exhibited an average regeneration of approximately 37.5% by day 54 (Figure 3C), which was surpassed by tubers exposed to heat at 120°C for 5 min (41.7% regeneration), 160°C for 5 min (58.3%), and 120°C for 30 min (62.5%).

Fungal growth was observed in both the leaves of *C. savannarum* and the tubers of *B. atenense*, with a notably higher incidence in the former, particularly at 120°C and 140°C for 30 min, compared to higher temperatures. In tubers, fungal presence was also recorded, but without pronounced variation among

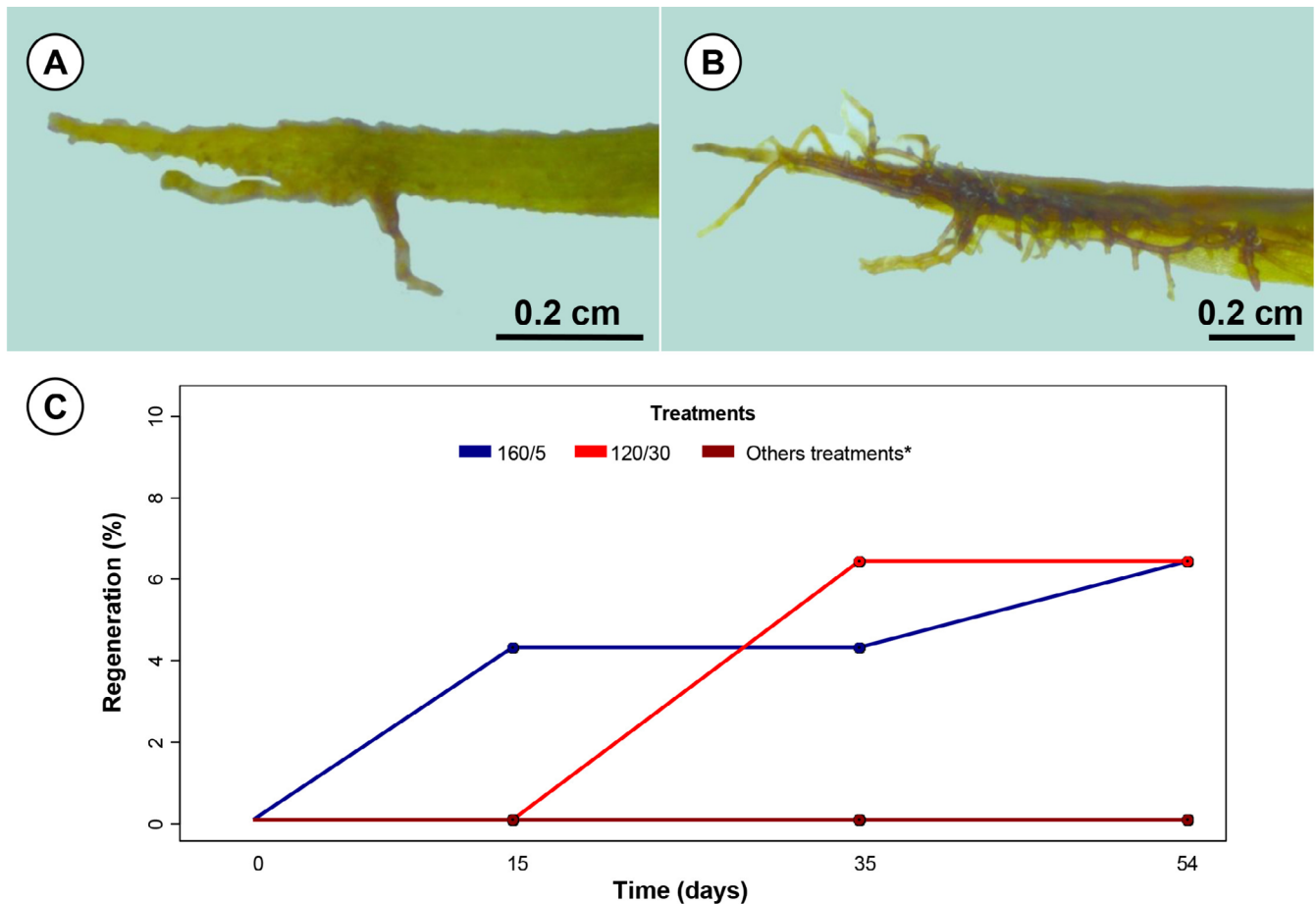


FIGURE 2 | Leaves of *Campylopus savannarum* after heat tolerance experiment: (A) Protonemata in leaves subjected to 120°C for 30 min, observed after 15 days. (B) Appearance of protonemata in leaves subjected to 160°C for 5 min, observed after 54 days. (C) Regeneration of detached leaves subjected to various heat treatments. *Control leaves, as well as those treated at 120°C and 140°C for 5 min, and at 140°C and 160°C for 30 min, did not regenerate and are therefore represented by a single line in the graph.

heat treatments. The GLM analysis revealed significant main and interaction effects ($p < 0.0001$), indicating that heat treatment and asexual structure influenced fungal occurrence (Null deviance: 788.94; Residual deviance: 441; AIC: 469).

4 | Discussion

Our results support our hypothesis that mosses from the Brazilian *Cangas* can exhibit heat tolerance through vegetative structures such as propagules, which contribute to the thermotolerance of the gametophyte. This pattern is similar to other moss species from different harsh environments, such as *Bryum argenteum* and *Syntrichia caninervis* from deserts (Stark et al. 2009; Zhuo et al. 2020). Additionally, this represents the highest thermotolerance reported for any bryophyte propagule, with *B. atense* tubers dry heated not only surviving in treatments of 160°C for 5 min and 120°C for 30 min, but also successfully generating protonemata and new leafy shoots. We believe that the tubers achieved this result due to their lipid storage and low water content, which acts as a thermal insulator, providing resilience against extreme temperatures and high desiccation levels (Frey and Kürschner 2011; Proctor et al. 2007; Tiloca et al. 2022).

In contrast, our results indicate that *C. savannarum* detached leaves showed limited regeneration under heat stress, with minimal survival. The primary function of bryophyte leaves is photosynthesis (Goffinet and Shaw 2000). We believe that heat treatments impair the photosynthetic apparatus, as optimal temperatures for net photosynthesis in tropical mosses have an upper limit of 25°C (He et al. 2016). Additionally, the main areas affected by thermal damage in plants include critical components of the photosynthetic machinery, which are essential for oxygen production, carbon fixation, and energy generation (Allakhverdiev et al. 2008; Hüve et al. 2011).

Interestingly, the control treatment of both species exhibited low regeneration rates ($< 37.5\%$ for *B. atense* and 0% for *C. savannarum*). Despite the known density-dependent effects on growth and regeneration in certain moss species—where higher shoot density can improve microclimatic conditions within colonies and enhance survival (Bates 1988)—detached leaves may show greater stabilisation and regenerative capacity under both laboratory and field conditions when compared to intact gametophytes or isolated shoots (e.g., Maciel-Silva 2017). However, the low regeneration rates of *C. savannarum* leaves, even in the control group, suggest that they may not serve as efficient propagative structures to establish new populations of these plants in the field.

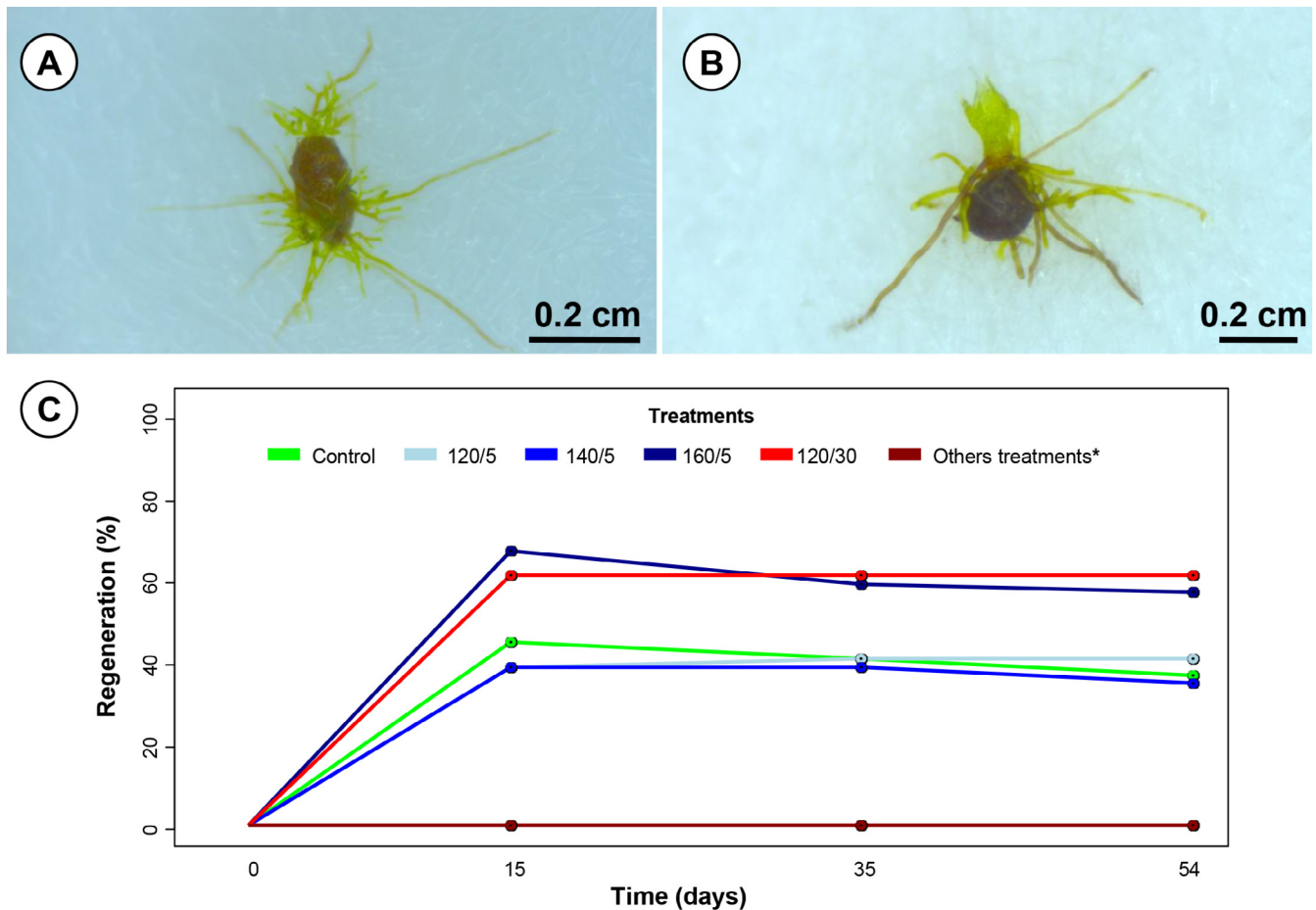


FIGURE 3 | Tubers of *Bryum atense* after the heat tolerance experiment: (A) Protonema in tubers subjected to 160°C for 5 min, observed after 15 days. (B) Appearance of protonemata and shoots in tubers subjected to 120°C for 30 min, observed after 54 days. (C) Response of tubers to various heat treatments. *Tubers treated at 140°C and 160°C for 30 min did not regenerate and are therefore represented by a single line in the graph.

Fungal growth was detected in both *C. savannarum* leaves and *B. atense* tubers, with a notably higher incidence in leaves—particularly under moderate heat treatments (120°C and 140°C for 30 min). This may be due to the lack of efficient morphological barriers in leaves compared to tubers. In contrast, fungal occurrence in tubers remained relatively low across all treatments, possibly reflecting structural defences such as thick cell walls (Frey and Kürschner 2011). As underground resistant structures, tubers are naturally more resistant than chlorophyllous vegetative leaves (Duckett et al. 2004). It is important to note that the fungi observed were likely opportunistic and did not appear to influence the overall regeneration percentages in our study. For future research, exploring interactions with potential symbionts could provide further insights.

With soil surface temperatures reaching higher than 42°C on hot days (Ferrari et al. 2016) and up to 548°C during wildfires (Rodrigues et al. 2021), the tubers of *B. atense* may represent a significant evolutionary advantage for coping with these extreme conditions, both in *Cangas* and other ecosystems. Indeed, vegetative propagation structures present in the soil are well documented in angiosperms that also contend with these adverse conditions, like *Tabebuia alba* (Cham.) Sandwitt (Bignoniaceae) that forms underground vegetative propagules that germinate after wildfires (Bond and Scott 2010). Furthermore, given that

tubers of *B. atense* tolerated both high-intensity short-term (160°C for 5 min) and moderate-intensity long-term (120°C for 30 min) heat exposure, it is reasonable to infer that similar tolerance may be present in other moss species bearing tubers (e.g., species within the Bryaceae family; Spence 2015), may also possess a similar strategy to cope with heat stress. This suggests potential for testing heat tolerance in tuber-bearing mosses globally.

The mechanisms behind moss heat tolerance are actively being studied. Thermal recovery in bryophytes involves both constitutive and inducible production of heat shock proteins, which stabilise and renature damaged proteins during recovery (Gao et al. 2018; Marchetti et al. 2020; Zhou et al. 2023). Additionally, stress- and drought-responsive genes modulate their expression under extreme temperatures, indicating the presence of signal transduction pathways that facilitate gene expression adjustments in these plants (Elzanati et al. 2020; Zhuo et al. 2020; Yang et al. 2022). Given that *B. atense* exhibits considerable heat tolerance and shares a close phylogenetic relationship with *B. argenteum*—a species known to increase transcription factors regulating desiccation stress genes such as *BaABI3A* and *BaABI3B* (e.g., Gao et al. 2018; Leng et al. 2024) to adapt to extreme environments—we anticipate similar adaptive processes in *B. atense*.

However, it is important to note that changes in gene expression do not necessarily indicate an adaptive advantage or a survival strategy (Des Marais and Juenger 2010). While transcriptional responses undoubtedly occur, their functional significance in terms of adaptation and survival can only be fully understood through assessments of fitness or survival under changing environmental conditions (López-Maury et al. 2008). In our study, we evaluated the effectiveness of such responses by analysing regeneration rates under different heat stress conditions. To further investigate whether transcriptional changes translate into adaptive advantages, future studies could integrate RNA sequencing with physiological assessments, such as chlorophyll fluorescence, relative electrolyte leakage, and measure the oxidative stress after heat treatments (Wen et al. 2019; Chen et al. 2017; Zhang et al. 2019). A comparative analysis of gene expression before and after heat treatment, coupled with survival rates and regeneration capacity, would provide valuable insights into the functional relevance of these molecular responses.

In the case of *Syntrichia caninervis*, researchers are exploring its potential as a model organism for studying desiccation and stress tolerance in mosses. Notably, studies are investigating the functions of the *ATG8* gene, which is linked to autophagy and plays a role under multiple abiotic stresses (Cao et al. 2024). Moreover, other bryophyte species, such as the liverwort *Marchantia polymorpha* L., possess transcriptional regulators that respond to temperature stress, including heat shock factor genes *MpHSFA1* and *MpHSFB1* (Wu et al. 2022). These genetic mechanisms are likely integral to modulating phenotypic expression and ensuring plant stabilisation in challenging environments.

In addition to the natural heat of the *Cangas* and the effects of wildfires (Ferrari et al. 2016; Schaefer et al. 2016), it is crucial to recognise that studies like ours can provide valuable insights into global warming issues. Understanding how plants respond to climate change is one of the major challenges in biodiversity conservation and sustainable ecosystem management. Many bryophyte species thrive in cooler climates and have limited ability to acclimate to rising temperatures, especially when hydrated (Clausen 1964; Meyer and Santarius 1998). Consequently, global warming may impact bryophyte diversity, particularly in species-rich regions like boreal forests, alpine environments, and high-altitude tropical sites, where temperature increases may alter species distributions and ecological interactions (He et al. 2016). However, other studies, such as Perera-Castro et al. (2022), have provided a more comprehensive review of the optimum temperatures for bryophyte photosynthesis and found no clear latitudinal trends. Exploring thermotolerance in propagules may help predict which species are more likely to survive in a warming world and guide conservation efforts to protect those at greater risk.

Author Contributions

Guilherme Freitas Oliveira: conceptualization, data curation, formal analysis, investigation, methodology, writing – original draft. **Mateus Fernandes Oliveira:** conceptualization, data curation, formal analysis, investigation, methodology, writing – review and editing. **Cintia Aparecida Teixeira Araújo:** conceptualization, methodology, validation. **Adaisés Simone Maciel-Silva:** methodology, resources, supervision, validation, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The authors confirm that the data supporting the findings of this study are available within the article. Additionally, vouchers are deposited in the BHC Herbarium at the Instituto de Ciências Biológicas da Universidade Federal de Minas Gerais (UFMG).

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