UNLOCKING USES OF MOSSES IN POST-FIRE RESTORATION: BETTER GROWING PRACTICES

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ABSTRACT

UNLOCKING USES OF MOSSES IN POST-FIRE RESTORATION: BETTER GROWING PRACTICES

HILINA YOHANNES KEBEDE

This study explores the utilization of mosses, particularly "fire mosses" such as *Bryum, Ceratodon, and Funaria*, as integral components in post-fire restoration efforts. The research investigates optimal growing practices in both soil-based (Bryotron system) and soil-less (Fog chamber) environments through a two-way factorial design. The study evaluates the impact of Knop solution fertilization and the introduction of live or sterile soil on moss percent cover over time.

Results indicate the feasibility of achieving substantial moss cover for all three species in both growing systems. *Ceratodon* exhibits enhanced cover with Knop solution and live soil inoculum, while Funaria responds positively to Knop solution addition. However, the study recommends further randomized and replicated experiments across growing systems at the individual species level to better understand variations in responses to treatment factors and growing conditions.

In summary, this research provides valuable insights into cultivating "fire mosses" and underscores their potential significance in post-fire ecosystem restoration. The findings emphasize the need for specific considerations in growing practices, paving the way for informed strategies in leveraging mosses for effective restoration after wildfire incidents.

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DEDICATION

I dedicate this to my Husband and Son.
Thank you for standing by my side, for your sacrifices, and for being my pillars of strength.

PREFACE

This document's second chapter is prepared for publication in peer-reviewed ecological literature, therefore there is some repetition of material between chapters.

CHAPTER I

Fire is a crucial component of the Earth system, although the origins and influences of this process vary substantially on different time and space scales. It is a dynamic force that reacts to and shapes ecosystems, functioning as a transformative agent, encouraging species variety in fire-dependent ecosystems, recycling nutrients, and removing vegetation to promote ecological renewal (Bond *et al.*, 2005; Pyne, 1997). Additionally, fire is necessary to preserve some types of landscapes, such as savannas and grasslands, where periodic burning is a normal part of the cycle. Fire has also affected human cultures throughout history, having an impact on land management, agriculture, and even the dynamics of climate change (Pausas & Keeley, 2009). As such, its significance goes beyond ecological aspects (Bowman *et al.*, 2009; Marlon *et al.*, 2012). (Marlon *et al.*, 2012)

Globally, forest fires are becoming more frequent and severe as a result of climate change and other factors (Bowman *et al.*, 2009). Many fires have caused extensive damage, affecting not just forests but also human communities, the environment, and wildlife (Williams *et al.*, 2019; Pivello *et al.*, 2021). Whether considered from an ecological or economic standpoint, fire damage can have significant and far-reaching effects. In terms of the environment, uncharacteristically severe wildfires can cause instantaneous vegetation loss, habitat disruption, and harm to wildlife populations (Alexander & Thomas, 2000). They can hurt the long-term health of the impacted areas by upsetting natural ecosystems, and causing soil erosion and water quality problems (Gajendiran *et al.*, 2024). These disruptions have the potential to trigger a series of ecological changes that will manifest for years to come (Keeley *et al.*, 2011).

Economically speaking, fire damage costs communities, businesses, and governments a great deal. Additionally, fire damage can have an effect on tourism and agriculture, which can have long-term negative economic effects on areas that depend on these industries. Given the increasing frequency and severity of wildfires caused by variables such as climate change, it is imperative to comprehend the dual ecological and economic aspects of fire damage to effectively prepare for, mitigate, and recover from these events (Pausas & Keeley, 2014).

To lessen the ecological effects of wildfires and encourage ecosystem recovery, ecological restoration is an essential activity after a fire. The foundation of ecological restoration is the application of ecological knowledge to comprehend the functioning of ecosystems and to restore conditions within them that preserve their structure and function (Martin,2017). Many different strategies for post-fire ecological restoration exist. For example, research by Mandujano & Ramírez (2022) highlights how crucial it is to follow a holistic approach encompassing social, ecological, and economic components while working on restoration projects. Furthermore, the importance of spontaneous regeneration processes in post-fire ecosystems has been emphasized by researchers such as Vieira & Scariot (2006), which may lessen the requirement for active interventions. According to Whelan (2004), adaptive management techniques are important because they enable continuous modifications to restoration plans in response to ecological input. The significance of a natural regeneration method, which enables ecosystems to heal on their own over time, is shown by studies like that of Chazdon (2017). This tactic aids in safeguarding and utilizing native species and the current seed bank. According to Dimson and Gillespie (2020), active restoration, which includes reseeding and planting native species, has had great success in several instances. Additionally, invasive species management techniques are essential for ensuring that non-native plants do not outcompete native vegetation during the recovery period, as mentioned in (D'Antonio & Meyerson, 2002). Studies like Kwan & Swanson (2014) describe soil and watershed management strategies that focus on stabilizing soil and reducing erosion, which can help with the restoration of biological processes. Adaptive management enables continuing adjustments to restoration measures, ensuring the resilience and health of ecosystems impacted by fire and informed by constant monitoring and assessment (Gillson & Whitlock, 2019). These methods, which are supported by scientific research, work together to aid ecosystem recovery and sustainability after a fire.

In various parts of the world, including the western United States, mosses including *Ceratodon purpureus, Funaria hygrometrica, and Bryum argenteum* colonize the top millimeters of burned soil surfaces, ash, and char. For ease of usage, these species are referred to as "fire mosses." This is a widely used term, particularly as a common name for *Ceratodon purpureus.* Depending on the habitat, fire moss communities may reach very high coverage within months to a few years following a fire, making them among the earliest colonizing primary producers (Brasell & Mattay 1984; Cremer & Mount 1965; Silva *et al.* 2019). Reducing soil erosion, boosting soil fertility and water retention (Xiao *et al.* 2015; Seitz *et al.* 2017; Silva *et al.* 2019), and maintaining soil biota—all factors of soil health—are ways that moss cover supports the functionality of recovering ecosystems. Grover *et al.* (2020) found out that post-fire colonization by fire mosses in southwestern USA forests after high-severity wildfires demonstrated improved soil stabilization, with increased water infiltration (55%), shear strength (106%), compressive strength (162%), and aggregate stability (195%) compared to bare soil. The research highlights the predictability of post-fire moss colonization and its positive impact on soil resistance to erosion and hydrological function, offering insights for managing landscapes affected by severe wildfires. All of these activities might eventually help vascular plants recover (Antoninka *et al.*, 2016; Bowker *et al.*, 2017). Intentional application of fire mosses as an ecological restoration technique has not been thoroughly explored, despite the apparent advantages. This oversight represents a missed chance to restore ecological processes in forests following a stand-destroying fire. The benefits of fire mosses in post-fire situations have been highlighted in studies like (Carmona, 2022). Researchers like Silva *et al.* (2019) showed the presence of a dense moss covering can operate as a powerful insulator in moss-dominated locations, shielding the underlying soil and helping post-fire recovery. In contrast, non-moss-dominated settings can experience less plant diversity and higher soil erosion due to the absence of such insulation. Additionally, moss-dominated areas tend to recover more quickly because of their ability to catch and hold moisture, creating an ideal environment for seed germination and plant growth, according to Li *et al.* (2021). These results highlight the essential function of mosses in post-fire ecosystem recovery and resilience as well as the difficulties non-moss-dominated areas encounter when trying to recover from fire disturbances.

Over the years, few studies have been done to better understand these processes. For instance; Grover *et al.* (2020) highlights the potential of fire mosses for ecological restoration in wildfire-affected areas. Through successful greenhouse cultivation and optimization of growth conditions, the study addresses propagule limitations, offering a scalable approach for utilizing these mosses in post-wildfire rehabilitation. Ives's (2016) research addresses gaps in understanding the effectiveness of fire mosses for post-fire stabilization and restoration, pioneering investigations in this unexplored field.

The overarching objective of this thesis is to investigate, refine, and develop artificial moss cultivation techniques to enhance our understanding of fire mosses and their potential utilization in ecological restoration and rehabilitation efforts. The remainder of the thesis includes a manuscript chapter (Chapter 2) describing a moss cultivation experiment in the greenhouse, as well as a chapter describing the management implications of the research (Chapter 3).

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CHAPTER II

GREENHOUSE CULTIVATION AND MOSS COVER RESPONSE TO DIFFERENCES IN SOIL TYPE AND APPLICATION OF FERTILIZER

Abstract

Certain species of mosses, “fire mosses,” are primary colonizers of burned areas appearing on surfaces of soil, ash, and char. They grow as quickly as within a few months after severe fire incidence and may facilitate the re-introduction of soil microbiota back to the soil. We tested greenhouse techniques to identify the best-growing methods for fire mosses *(Bryum, Ceratodon*, and *Funaria).* The experiment had a two-way factorial design assessing changes in moss percent cover over time as a response variable with two factors: fertilization with Knop solution and a soil addition composed of either live soil or sterile soil. The experiments are set up in two growing systems; a soil-based (Bryotron) and a soil-less system (Fog chamber). We found that it is possible to achieve a significant amount of cover in both growing systems for all three species. *Ceratodon increased* in cover with the addition of Knop and live soil inoculum. *Funaria* increased in cover with the addition of Knop solution at some time points. Further studies should be randomized across replicated growing systems at the individual species level to better understand differences in response to the growing systems. This study holds significance in unraveling the cultivation techniques for "fire mosses" (*Bryum*, *Ceratodon*, and *Funaria*), crucial primary colonizers in post-fire landscapes.

Keywords: Fire Moss, Bryophytes, Ecosystem restoration

Introduction

A well-documented cause of increasing fire size and intensity is the accumulation of woody fuels in forests of the Western United States as a result of historical fire suppression practices (Bowman *et al.*, 2009). Fuel conditions and climate conditions interact to determine fire regime characteristics. The risk of large or intense fire has recently increased due to dramatically increased fuel aridity in Western U.S. forests brought on by anthropogenically induced temperature rises and vapor pressure deficits (Abatzoglou & Williams, 2016). Westerling *et al.*, (2006) found a marked rise in the frequency and severity of big wildfires in the western US as a result of higher temperatures and earlier snowmelt, while Dennison, Brewer & Arnold (2014) found evidence of more frequent and widespread wildfires in the same region. The research by Williams *et al.* (2019) highlighted the compounding effects of numerous climate-related elements and emphasized the cumulative effect of climate change on wildfires. Moritz *et al.* (2012) also highlighted how regional differences in wildfire patterns are driven by climate change. There is also an upward trend in the annual number of large fires, total fire area, and area burned at high severity (Singleton *et al.*, 2019). These trends coincide with long-term drought and predictions for increased drought and warming through the 21st century (Williams *et al.*, 2019). Further disturbances to the fire regimes in the Western United States and other areas of the world that are prone to fire will be caused by ongoing climatic changes, invading species, and the effects of previous fire management fields (Dennison, Brewer & Arnold, 2014).

The intentional introduction of fire mosses, a group of hardy moss species noted for their capacity to form protective biological soil crusts, or biocrusts, on the burned soil surface, is a potentially effective method of restoring wildfire-affected areas. Ecosystem services and functions can be potentially recovered through biocrust restoration (Antoninka *et al.*, 2020). Biocrusts stabilize soil surfaces, supply carbon, fix nitrogen, and moderate the hydrological cycle, all of which may support restoration efforts (Bowker *et al.*, 2018; Heindel *et al.*, 2019). Fire moss biocrusts are quicker to develop than other types of biocrusts in other environments, forming in a few months to a few years according to Clement & Touffet (1981), Duncan & Dalton (1982), and Grover *et al.* (2020), and they frequently appear before most vascular plants recover. Thus, focusing restoration intervention on these mosses provides a plausible pathway to get ecological restoration projects off the ground quickly and accelerate ecosystem recovery in areas devastated by wildfires. Carmona *et al.* (2020) highlighted the important function of mosses as early colonizers in fire-affected areas, supporting crucial ecological processes such as soil stabilization and nutrient cycling. Though not yet tested, it is plausible that fire mosses can also foster favorable microenvironments for seed germination and vascular plant establishment in the wake of wildfires (Havrilla *et al.*, 2019).

Ex-situ moss cultivation in controlled settings, such as greenhouses, has come to be recognized as a successful approach for producing mosses to be reintroduced to disturbed field sites, among other goals (Doherty, 2014; Bowker & Antoninka, 2016). Ex-situ cultivation has the ability to achieve a variety of goals. For instance, Sabovljević *et al.* (2014) looked into the effective ex-situ cultivation of rare moss species, highlighting its significance for maintaining biodiversity and genetic diversity. Furthermore, Proctor and Tuba (2002) shed light on ex-situ cultivation by investigating the physiological and ecological aspects of moss development under controlled conditions. Two unique growing systems—soil-based and soil-less fog-based techniques—have been studied in several ground-breaking publications, including those by Ives (2016), Doherty *et al.* (2016), Grover *et al.* (2020), and others. The "Bryotron" automated system was utilized by Doherty *et al.* (2016) to grow biocrusts in soil using the soil-based technique. This system supplies water pulses to growing biocrust organisms from below via capillary action through a soil substrate, usually sand (Ives, 2016). Grover (2020) introduced major modifications of this approach, using an organic soil layer over a wicking layer of mineral wool, resulting in highly successful moss growth in only about 8 weeks. Doherty *et al.* (2020) later introduced a soil-free method, growing mosses directly on fabrics inside of a greenhouse-based fog chamber, using fog emitters to circulate sub-micron water droplets to hydrate the mosses. Our research, which built on this previous work, began with parallel studies with two growth systems to examine various treatments for the best moss production: a bryotron-system (modified for compatibility with organic soils), and a soil-less fog chamber method. We investigated the value of supplemental fertilization and the addition of live soil.

We established ***two growing systems in parallel experiments in which the factors of live soil and fertilization (two levels each) were compared in terms of the growth of three fire moss species.*** The live soil factor introduced a small amount of soil from unburned forests as a source of soil microbiota. The fertilization factor applied a growth medium containing multiple nutrients. Therefore, the primary objective of this study is ***to identify and choose the best treatment combination for the growth of fire mosses***. *To* test the best methods to grow fire mosses, we conducted a greenhouse experiment using *Bryum argenteum, Funaria hygrometrica and Ceratodon purpureus,* all considered pioneers in disturbed areas helping succession and stabilization of the environment. Our goals were to: ***(1) explore the existing interaction effects on the overall moss cover over time.***

(2) identify whether live soil addition promotes moss growth overtime. We hypothesized that live soil would cause faster moss growth due to the availability of potentially beneficial soil microbiota (3) to identify whether the addition of nutrients promotes moss cover over time. We hypothesized that the addition of fertilizer (Knop solution) would cause faster moss growth due to the enhanced availability of nutrients.

Methods

Experimental design

We set up two parallel two-factor experiments in the greenhouse in the Fog chamber and Bryotron following a full factorial randomized design encompassing 2 factors with 2 levels for soil and fertilizer: (***Factor:*** Soil inoculum ***Levels:*** Live soil and Sterile soil; ***Factor:*** Fertilizer ***Levels:*** Knop addition or water with 6 replicates including controls resulting in a total of 192 experimental units (96 units=Fog chamber, 96 units=Bryotron experiment).

Moss addition

We collected fire mosses from pile burn scars at Bud Tank near Flagstaff, Arizona. We selected patches of three species: *Funaria hygrometrica*, *Ceratodon purpureus*, and *Bryum argenteum.* Although there was often some contamination of these patches by the other species, we verified that each patch was at least 95% dominated by the target species. The source site was selected based on slash piles burned in the winter of 2017, four years after the burn before the collection of moss samples and the availability of all three target mosses. The mosses were cleaned on a 2 mm sieve to remove underside soil and then sieved through a 4mm sieve to break them up and then homogenized. The inoculation phase included weighing the moss (10ml) and the soil ready for culture.

Fertilizer treatment

Knop medium (24ml) was added in each unit every 15 days using a hand-held pump sprayer which began on day 15 after the experimental setup. The Knop medium was prepared in the lab by mixing the following: 1 mg of Potassium nitrate (KNO_3), 1 mg of Magnesium sulfate ($MgSO_4$), 1 mg of Potassium phosphate dibasic (K_2HPO_4), 3 mg of Calcium nitrate ($Ca(NO_3)_2$) and 5 Liters of distilled water (Ives, 2016).

Soil addition

We collected forest soil from unburned adjacent areas every 5 meters along a transect line. We obtained 0-10cm deep subsamples of soil and homogenized it. Our collections encompassed areas with woody and herbaceous vegetation to ensure that a wide variety of soil biota were present in our homogenized soil. We double steam-sterilized a portion of the soil, leaving another portion unsterilized.

Experimental elements: Soil, Growing system, and Monitoring moss cover

Cultivation Systems

The Bryotron experimental setup is an irrigation system that works by wicking, where irrigation lines feed into nested basins, where the bottom basin receives water directly which wicks into the top basin through small holes, watering to field capacity (Doherty et al. 2015). In the basin is a layer of weed cloth, and then sand to encourage wicking, then a sterilized organic soil substrate, then small quantity of live or sterile forest soil, and finally moss. This setup also involves sanitizing the plastic food storage containers (Gladware, 12*12 cm, hereafter, "containers") and synthetic weed cloths, checking whether the irrigation and blockage holes are properly set, and connecting the container units to the irrigation line. In the Bryotron experiment, a layer of sterilized pool sand of 100 ml, sterilized organic mulch soil of 330 ml, and 70 ml of live or sterile forest soil were added on top of the sand and organic soil. Sterilized soil was used to: avoid outside contamination of moss units, allow us to more clearly observe the effects of live soil addition, and because soil surfaces in naturally burned environments are often sterilized by the fire-generated heat.

As also described by Grover *et al.* (2020), the Fog chamber uses sonicators in a basin of water inside of a PVC frame covered with row cover cloth to retain humidity and exclude fungus gnats, while still allowing light to reach growing mosses. Fans blow the fog across trays situated inside of the chamber. Six trays made of PVC frames with window screen covering were stacked within the chamber, each holding squares of a synthetic cloth (15*15 cm^2) on which the mosses grew. To implement the soil biota factor in this growing system, a thin layer of either live or sterile soil was added to the cloth surface with the moss inoculum.

Monitoring

We tracked changes in moss cover over time using a Grid-Point Intercept (GPI) method. This involved systematically placing a grid or point frame over the containers and recording the presence or absence of the target moss species at 25 specific points within the grid. Monitoring was undertaken once every month and for a total of 5 months, from December 2021 to April 2022, for a total of five consecutive observation points.

Statistical analysis

Repeated measures ANOVA was used to examine data in which the same experimental units are measured more than once through time. Our model included the factors: Soil, and Fertilizer with time as a non-independent factor. We were not able to statistically compare the results of the two growing systems because they were not replicated.

Prior to performing the repeated measures ANOVA, we checked the dataset for normality, homogeneity of variance, and outliers. We used boxplots, histograms, QQ plots, and the Shapiro-Wilk test to test these assumptions. Data met assumptions without transformation. Analysis was conducted in R using the lme4 package (Friedrich *et al.*, 2019).

Results

Combination of effects and overall trends in moss cover

Results from repeated measures ANOVA are given in Table 1. The results provide the cover data of *Bryum, Ceratodon, and Funaria* as they changed over time in both the Bryotron and Fog chamber growing systems. As time progressed, we observed an upward trend in the growth of these moss species, though for some species the increase was more consistent in the soil-based system.

The overall trends indicated in Fig (1) showed that initial cover was similar in the two growing systems around 15% in the Bryotron experiment and 10% in the Fog chamber experiment. Generally, moss cover in the Bryotron experiment had a steady increase from monitoring event 1 (day 15) through day 75 which was nearly 3 months from the initial monitoring period. This was especially true for *Ceratodon* and *Bryum*. Fig (1) shows moss cover increased to nearly 84% at most for *Bryum* (K- and L); in the Fog chamber experiment the same treatment combination reached 62% cover. For *Ceratodon*, moss cover increased by 80% (K+, L) in the bryotron experiment and 57% in the Fog chamber experiment for the same treatment.

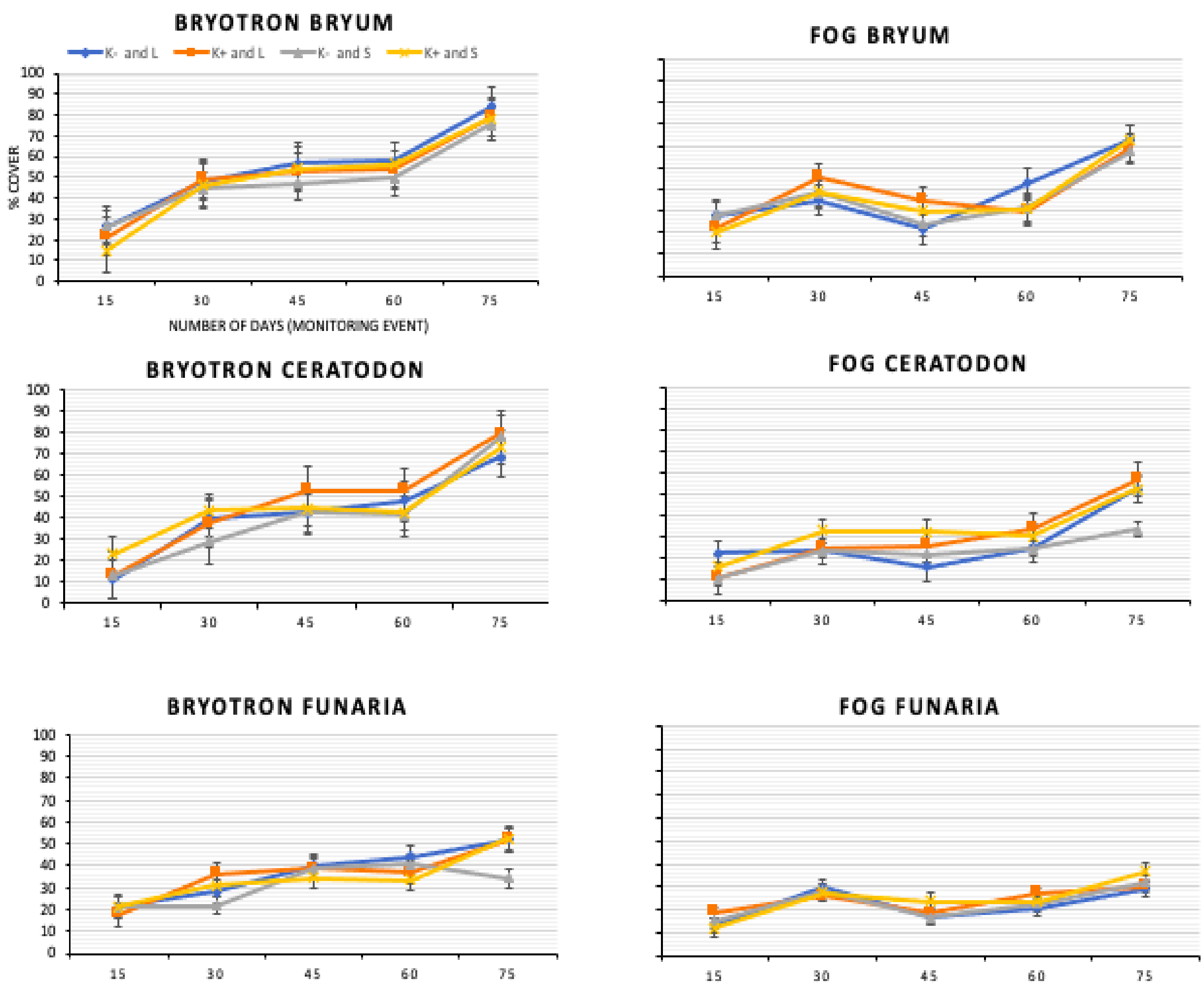

Figure 1 Overall trends in moss cover over time. The X-axis represents the number of days, denoted as Monitoring Events, which were conducted at regular intervals. These events span the duration of the study and capture the progression of moss cover. The Y-axis represents the moss cover percentage, indicating the extent of moss growth observed during each monitoring event. This graph illustrates how moss cover evolves, providing valuable insights into the growth dynamics of the studied moss species in response to varying conditions and treatments. Colored lines indicate treatments. Blue represents (K-, L), orange represents (K+, L), Grey represents (K-,S), Yellow represents (K+, S). Standard error bars represent the range within which the true value of the data point is likely to fall.

Soil type (Live and Sterile) and Knop addition

There were some differences noticed on the live soil with increased cover of some mosses in both of the growing systems, hinting at the potential influence of soil conditions on moss development. Substantiating these observations, the repeated measures ANOVA underscored a statistically significant interaction between soil type and Knop solution ($p < 0.05$) regarding moss cover.

In both growing systems, the repeated measures ANOVA didn't indicate any significant differences on cover as a result of Knop or live soil addition or their interaction; only monitoring period was a significant influence on growth.

In the Bryotron experiment, Knop solution had a significant main effect on *Ceratodon* cover ($p=0.006$). In the Fog chamber experiment, the combined effect of Knop solution and soil type was statistically significant for *Ceratodon* ($p=0.03$), resulting in increased cover. The overall trend indicates a positive influence of Knop solution on *Ceratodon* cover in both growing systems, leading to an increase in cover.

Knop solution interacting with time had a significant positive effect on Funaria cover ($p=0.03$) in the Bryotron, but not the Fog chamber. In the Fog chamber, only the monitoring period affected *Funaria* growth.

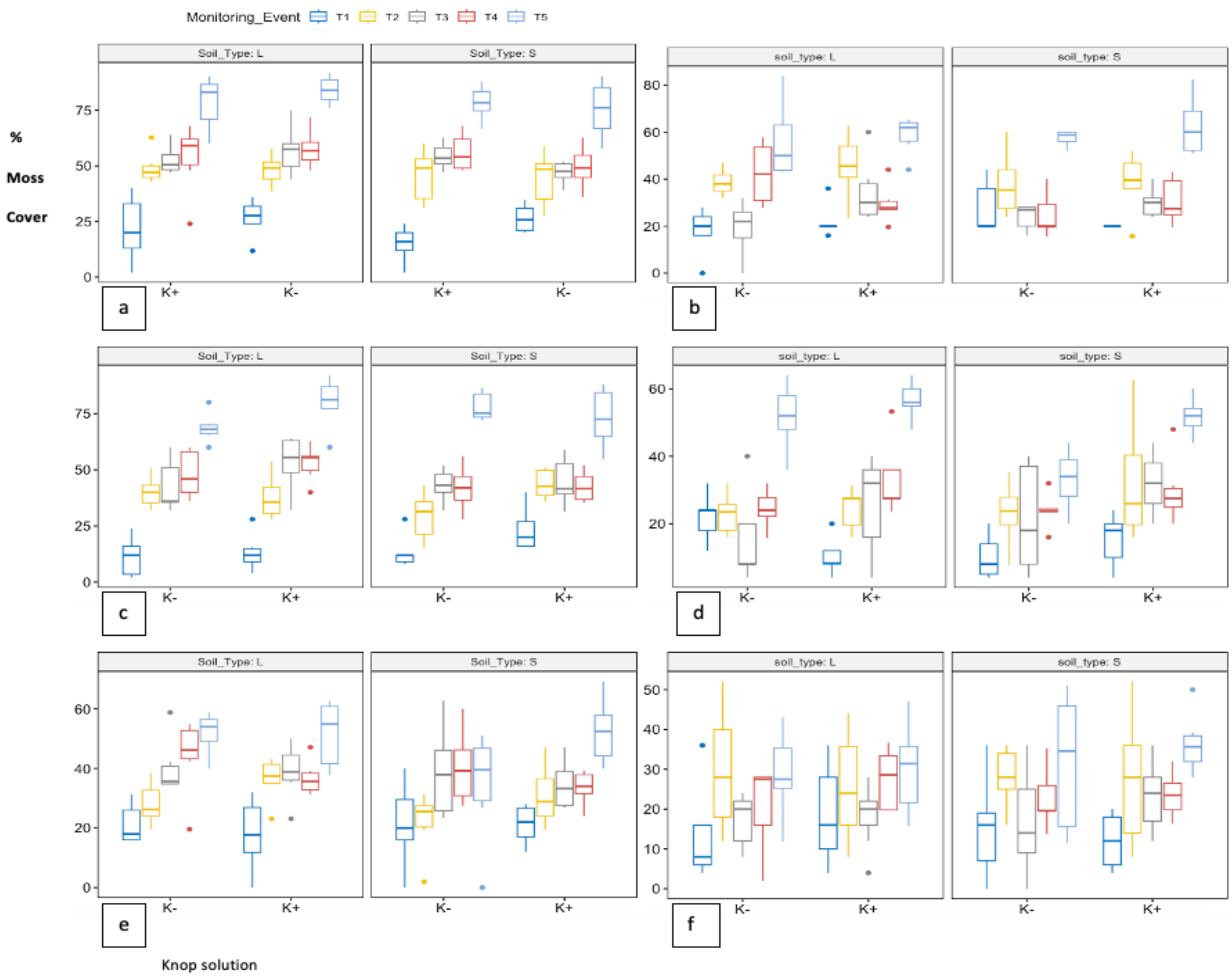

Figure 2. Differences in treatments of the Bryotron experiment and Fog chamber experiments *(Growing period is represented by Time one (number of days) in dark blue, Time 2 in Yellow, Time 3 in black, Time 4 in Red, Time 5 in light blue (a) Bryum in the Bryotron experiment, (b) Funaria in the Bryotron experiment, (c) Ceratodon in the Bryotron experiment, (d) Bryum in the Fog chamber experiment, (e) Funaria in the Fog chamber experiment, (f) Ceratodon in the Fog chamber experiment. x-axis represents both the treatment factors (soil type= L (Live soil) and S (Sterile soil) and Knop solution (K- (control), K+ (addition of Knop). The line in the center of the box plot is the median representing the middle value when the data is sorted, boxes are divided in*

two parts representing one of the quartiles, lines/Whiskers represent the range of the data, and points outside of the plot represent outliers beyond the whiskers.

Table 1 Repeated measures ANOVA outputs for cover in Bryotron (***df =degree of freedom)***

Moss Type	Interaction	Df	Sum Sq	Mean Sq	F_value	Pr(>F)
Bryum						
	Knop Solution	1	4.00	4.00	0.05	0.81
	Soil inoculum	1	285	285	3.34	0.07
	Monitoring Event	4	39319	9830	115.16	**<2e-16**
	Knop Solution: Soil inoculum	1	59.00	59.00	0.69	0.41
	Knop Solution: Monitoring Event	4	399.00	100.00	1.16	0.32
	Soil inoculum: Monitoring Event	4	8.00	2.00	0.02	0.99
	Knop Solution: Soil inoculum: Monitoring Event	4	367.00	92.00	1.07	0.37
	Residuals	99	8450.00	85.00		
Ceratodon						
	Knop Solution	1	702.00	702.00	7.76	**0.00**
	Soil inoculum	1	53.00	53.00	0.58	0.44
	Monitoring Event	4	43829	10957	121.23	**<2e-16**
	Knop Solution: Soil inoculum	1	7.00	7.00	0.07	0.77
	Knop Solution: Monitoring Event	4	75.00	19.00	0.21	0.93
	Soil inoculum: Monitoring Event	4	706.00	177.00	1.95	0.11
	Knop Solution: Soil inoculum: Monitoring Event	4	1023	256.00	2.83	**0.02**
	Residuals	97	8767.00	90.00		
Funaria						
	Knop Solution	1	65.00	65.1	0.56	0.45
	Soil inoculum	1	399	398.9	3.48	0.06
	Monitoring Event	4	10222	2555.6	22.29	4.13e-13
	Knop Solution: Soil inoculum	1	130.00	129.8	1.13	0.28
	Knop Solution: Monitoring Event	4	1261	315.3	2.75	**0.03**
	Soil inoculum: Monitoring Event	4	342.00	85.6	0.74	0.56
	Knop Solution: Soil inoculum: Monitoring Event	4	422.00	105.5	0.92	0.45
	Residuals	98	11233	114.60		

Table 2 Repeated measures ANOVA outputs for cover in the Fog chamber (***Note df =degree of freedom)***

Moss type	Interaction	Df	Sum Sq	Mean Sq	F_value	Pr(>F)
Bryum						
	Knop Solution	1	26	26	0.23	0.63
	Soil inoculum	1	121	121	1.09	0.29
	Monitoring Event	4	19219	4805	43.567	**<2e-16**
	Knop Solution: inoculum	1	6	6	0.05	0.82
	Knop Solution: Monitoring Event	4	779	195.00	1.76	0.14
	Soil inoculum: Monitoring Event	4	284	71.00	0.64	0.63
	Knop Solution: Soil inoculum: Monitoring Event	4	1023	256.00	2.31	0.06
	Residuals	91	10036	110		
Ceratodon						
	Knop Solution	1	1132	1132	11.94	**0.00**
	Soil inoculum	1	107	107	1.13	0.28
	Monitoring Event	4	14652	3663	38.65	< 2e-16
	Knop Solution: Soil inoculum	1	412	412	4.34	**0.04**
	Knop Solution: Monitoring Event	4	786	196	2.07	0.09
	Soil inoculum**: Monitoring Event**	4	1261	315	3.32	**0.01**
	Knop Solution: Soil inoculum: Monitoring Event	4	428	107	1.12	0.34
	Residuals	99	9381	95		
Funaria						
	Knop Solution	1	197	196.6	1.74	0.18
	Soil inoculum	1	37	36.9	0.32	0.56
	Monitoring Event	4	4656	1164.10	10.33	**3.89e-07**
	Knop Solution: Soil inoculum	1	45	45.2	0.40	0.52
	Knop Solution: Monitoring Event	4	179	44.6	0.39	0.811
	Soil inoculum: Monitoring Event	4	201	50.2	0.44	0.77

Knop Solution: Soil inoculum: Monitoring Event	4	276	69.00	0.61	0.65
Residuals	109	12273	112.6		

Discussion

In this study, we determined that fire mosses can be grown using both soil-based and soil-less (fog chamber) methods, further demonstrating the feasibility of growing mosses as a bio-inoculant for burned areas. We found that addition of supplemental nutrients was not strictly necessary to achieve positive moss growth, but some species did benefit from nutrients somewhat in certain contexts. We did not detect any main effect of the addition of live soil on moss growth in our cultivation systems, though live soil did interact with other factors to produce detectable effects.

Fire mosses grow in soil-based and soil-less (fog based) environments:

Clonal propagation of mosses dates to the early twentieth century (Hohe & Reski, 2005), but methods to grow large quantities of moss for restoration or other purposes are relatively new endeavors and are rapidly advancing (Doherty *et al.*, 2020a; Grover *et al.*, 2022). One key consideration for developing moss cultivation techniques is the substrate used. Mosses have been grown on agar, in liquid culture, or on solid surfaces such as soils (Servettaz,1913; Knop 1884; Ashton & Cove, 1977, Schween *et al*.,2003; Johri & Desai 1973).

Since fire mosses are primarily observed on burned soil and associated burned materials, it is logical to attempt to grow them on various types of soil. On the other hand, because the soil is heavy, it may be desirable to cultivate mosses free of soil, for example, to transport to and disperse in burned locations to enhance ecosystem recovery. Our results show that mosses may be successfully grown in either soil-based (bryotron) or soil-less (fog chamber) systems, lending considerable flexibility to researchers or restoration practitioners wishing to produce moss biomass.

Multiple soil-based growing systems have been used to produce fire mosses in restoration-relevant quantities. Collectively, these works illustrate the importance of manipulation of some growing conditions. Two key parameters are the type of soil used and other additives. A study by Gross (2009) used topsoil, sand, potting, and a mix in addition to different cloths on top of the soil and with this *Ceratodon purpureus* showed the highest growth on topsoil attaining > 90% cover in only 70 days. Ives's work on automated wicking through a sand substrate tested a useful approach for taking advantage of the pore-size distribution of sand to deliver water to growing mosses. Fire moss also demonstrated rapid and substantial growth, achieving high coverage within just two months on an organic substrate, utilizing constant wicking hydration, and being provided with protective shade cover (Grover *et al*.,2020). These experiments collectively showed growth on organic-rich soil was better for these species than various types of sand. But, a drawback of organic soils is that they do not have the same favorable wicking properties that sand has. By skillfully merging the advantages of Ives and Gross's earlier studies, our experiment demonstrates a novel methodology. Our bryotron experiment brought together the organic substrate for its benefits in supporting fire moss growth and sand for its beneficial wicking properties.

Various additives have been investigated by Gross (2009), Ives (2016), and Grover (2020), for instance adding ash or char to promote short-term growth, or adding hormones. These studies found no strong evidence that the addition of these components helped in promoting growth. To further study this, our version of the experiment used live or sterile soil substrates on top of sand and also concentrated on moss establishment without these inputs, which may make the experimental setup simpler and offer insights that are more widely applicable to a range of moss species and settings.

Our experiment indicated that all three mosses also grew successfully in a soil-less environment, hydrated by fog. All mosses exhibited growth from day 15 to 30, indicating successful establishment during the early stages of cultivation. However, the intriguing aspect arises in the subsequent period from day 45 to 75, particularly within the fog chamber system, where moss growth appeared to slow down or even exhibit negative trends. This phenomenon could be attributed to several factors, one of which might be the challenge of maintaining consistent hydration levels in the fog chamber, especially when subjected to fluctuations in weather conditions. Mosses are highly dependent on adequate moisture for growth, and variations in humidity levels, along with potential drying events, could have adversely affected their development during this period.

Fog-based systems hold great promise for the mass production of fire mosses, despite that they did not always outproduce soil-based systems on the basis of growing surface area for all of the species. Fog systems can have multiple layers of growing surface; up to 10 layers have been tested by our lab's previous research works (Doherty *et al.*2020). Therefore, even if they are less productive, the vertical stacking means we can produce much more moss per greenhouse bench area. Previous studies by (Doherty *et al.*, 2020b) suggest that the fog chamber production system, which uses fog to cultivate moss on burlap substrates, holds promise for efficient and rapid biocrust establishment. Another advantage of fog culture is that fire mosses can be attached to something (e.g., burlap cloth Doherty, 2014) when desired, but can also be grown on a surface and then completely detached when desired. The advantages of this strategy have been examined in several recent studies. Doherty *et al.* (2020) focused on the advantages of attachment to cloth, including less loss of material to wind and the potential use of the cloth to shelter the biocrusts. These studies highlight how versatile fog culture is for using fire mosses for a range of purposes, which makes it an important tool for scientific research, ecological restoration, and sustainable moss management.

Variable Effects of Soil Microbes on Fire Moss Cultivation Rate

The response of fire mosses in our experiment presents a nuanced relationship with soil microbes, as reflected in the variable effects observed on the different mosses and growing systems. While some instances show the potential for soil microbes to enhance fire moss cover, for instance for *Ceratodon*, other scenarios reveal limited or even inconsequential impacts. The simplest explanation is that in our experimental systems, mosses are obtaining a sufficient supply of resources, including moisture and nutrients, limiting the importance of microbial facilitators and symbionts. This might be especially true in our bryotron system, in which a nutrient-rich organic soil serves as the substrate. In contrast, these mosses could have a greater dependence on soil microbes in natural or less regulated environments. In the literature, there are conflicting results on whether mosses benefit from soil biota. Numerous scholars have investigated the connections between moss and microbes and have come to various conclusions (Eppley *et al.*, 2018; Doherty *et al.*, 2018). Possibly, these mosses have a very low reliance on mineral nutrients, or they have additional mechanisms to obtain nutrients that are not dependent on the biota in the live soil. This may be explained by the distinct ecological niche that mosses hold. Future studies in understanding the intricate nature of moss-microbe interactions will be greatly aided by additional examination into the intriguing phenomenon of mosses' relative indifference to live soil inoculum and the degree to which that variation depends on species or the settings.

Fire mosses can be grown without nutrient amendments:

A crucial component of moss biology and ecosystem management is comprehending how receptive fire moss species are to nutrient additions. Numerous studies conducted recently have revealed the varied ways in which various moss species interact with and gain from nutrient supplementation.

Our experiment indicated knop is influential for *Ceratodon* but less so for the other species. The impact of Knop solution on the cover of mosses was variable at different time points and between different species. For instance, in *Funaria, the* cover appeared to be higher at some time points and lower at others when Knop solution was added. In contrast, *Ceratodon* had a more consistent response to the addition of Knop solution.

Ceratodon and Funaria may have certain growth habits or nutrient needs that complement the features of this system combined with nutrient additions. The Bryotron system's configuration and surroundings might also produce a microcosm that is particularly favorable to their growth. It might also imply that *these mosses* might be more sensitive to outside nutrients and have strategies to make the most of the extra fertilizers.

Knop solution addition also resulted in an increase in moss cover in *Ceratodon* in the Bryotron growing system and when combined with live soil inoculum in the Fog chamber growing system. A possible explanation for such effects could be that certain moss species, like *Ceratodon*, have microbial dependencies that support their growth, but the microbes are nutrient-limited. Thereby, the moss would respond favorably to nutrient supplementation and live soil contact. This moss may have developed mutualistic connections with soil microbes, which when paired with extra nutrients, lead to a rise in moss cover. According to Gross (2009); the impact of nutrient supplementation on the response may be shaped by both the biological characteristics of the species and the specific type of nutrients introduced. For instance, differentiated growth methods are used by different species, and characteristics including growth rate, competitiveness, and reproductive tactics influence how well a species responds to nutrient supplementation. While slow-growing species might not exhibit as strong of a reaction, fast-growing species might benefit more from nutrient availability. The growth of moss can also be expedited or inhibited by nutrients, contingent on the particular species as well as the type and concentration of the nutrients involved (Burkholder 1959; Glime 1988).

Our results in which different mosses have a different growing system-dependent response to nutrient supplementation through fertilizer addition, are in line with those of several other studies. Mosses can survive in nutrient-poor conditions according to some authors (Smith *et al.*, 2017, Johnson *et al.*, 2019). On the other hand, other researchers (Baldarelli *et al.*, 2021; Gross 2009; Antoninka *et al.*2015), have published studies with conflicting findings that show some moss species can benefit from nutrient supplementation. These contradictory results highlight the complexity of moss ecology and imply that different moss species from various ecosystem types may respond differently to Knop solution input. Such differences underline the need for a more complex comprehension of moss responses to nutrients and the significance of taking particular circumstances into account when interpreting these results. In our case, it was valuable to test the effects of fertilizers separately for the three species because any result from one of the species or a mixture may not represent what would have been found for another species.

Conclusion

This study demonstrates that fire mosses can be successfully grown without the addition of extra nutrients, though they may have some benefit for some species if also grown in the presence of live soil biota. Our parallel studies using soil-based and soil-less growing systems further show that mosses start successfully in both systems but maintain a steadier rate of growth in soil-based systems. Additional study is required to compare the two growing systems side by side with replication in the growing system to assess the variations in production between the two systems. The results of this study also unquestionably demonstrate the adaptability of mosses, which thrive in both soil-based and soil-less growing situations. The ability to grow these mosses in soil-less systems is as important as growing them on soil-based media because it offers production efficiency, especially when numerous stacked vertical layers are used for growth. Overall, our findings emphasize these plants' versatility and amenability to cultivation, emphasizing their potential for study and production in a range of contexts.

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CHAPTER III

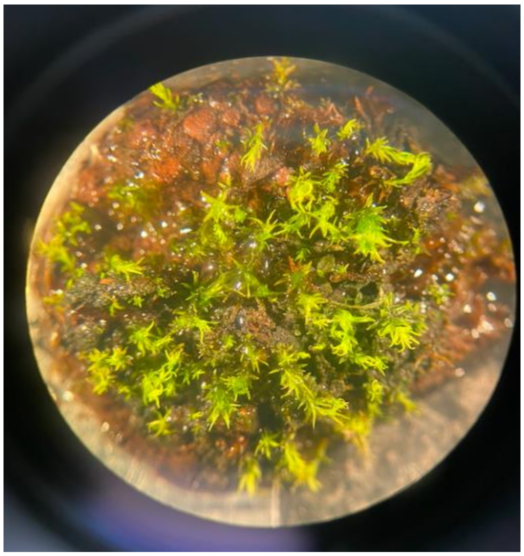
Management implications

Southwest Fire Changes: Adapting to the New Fire Reality

Fire trends in the Southwest of the United States have seen a major change throughout time. In the past, numerous, low-intensity fires shaped the region's vegetation as a natural component of its ecosystems. An accumulation of fuels and the potential for more intense wildfires resulted from human interference and a century of fire suppression practices, which interrupted this natural fire regime (Swetnam *et al.*, 2016). The area has seen an increase in large, uncharacteristically severe wildfires recently, which have been made worse by protracted droughts and warming temperatures linked to climate change (Abatzoglou & Williams 2016; Singleton *et al*. 2018). In a study by Dennison, Brewer, and Arnold (2014) in the western US there is an annual increase in the number of fires and the total area that affects the yearly expansion of the fire-affected area is 355 km^2, and the average number of big fires is increasing by roughly seven fires annually.

The Southwestern United States will likely continue to experience problems related to water scarcity, rising temperatures, and extended dry seasons; therefore, this pattern is predicted to persist (Dettinger *et al.*, 2015). Increased public awareness, adaptive fire control tactics, and steps to lessen the effects of climate change will all be necessary to address these fire trends. In order to balance ecological restoration, wildfire prevention, and protecting populated areas, forest and land management practices will also need to change. The current research has provided valuable information that can help ecological restoration strategies be more specialized and targeted. It has explicitly looked into the complexities of producing fire moss on a smaller scale, providing a sophisticated understanding of the methods and approaches required for fruitful restoration projects.

Greenhouse Magic: Growing Mosses for Post-Fire Recovery



The use of greenhouses to cultivate mosses such as *Funaria, Bryum and Ceratodon* appears to be a good answer to the problem of wildfires that are becoming more severe and the wider effects of climate change. Mosses are crucial in the recovery of landscapes damaged by fire since they are frequently disregarded but biologically vital (Smith, 2001; Viles, 2008). With exact circumstances that closely resemble the natural habitat of these plants, regulated greenhouse environments can be transformed into centers of creativity and regeneration. Here, the tiny yet strong mosses take the stage in the rebuilding of ecosystems, providing hope in this era of wildfire devastation.

Tailored Greenhouse approaches for *Ceratodon, Funaria, and Bryum* Growth

For *Ceratodon:*

Recommendation: Continue incorporating Knop solution and live soil inoculum in the growth medium for *Ceratodon*.

Rationale: *Ceratodon* responds positively to either Knop solution alone or in combination with live soil inoculum. These treatments should be consistently applied to support the growth and development of *Ceratodon* in greenhouse conditions.

For *Funaria:*

Recommendation: Focus on the addition of Knop solution to the soil-based growth systems for *Funaria*.

Rationale: *Funaria* shows a positive response to the addition of Knop solution in one growth system, but not the other. Live soil inoculum does not appear to affect *Funaria*, therefore it is simpler to omit it.

For *Bryum:*

Recommendation: Bryum does not show a significant response to either Knop solution addition or live soil inoculum.

Rationale: Given that *Bryum* cover remains consistent regardless of these treatments, greenhouse managers may consider optimizing resource use by not applying Knop solution or live soil inoculum when cultivating *Bryum*.

Monitoring and Adaptation:

Recommendation: Implement a monitoring program to assess the effects of the recommended treatments on moss cover over longer growing periods.

Rationale: Regular observations will help greenhouse managers adapt cultivation practices based on the evolving needs and responses of *Ceratodon, Funaria, and Bryum* over time.

Exploring the use of a fog chamber for moss production can offer significant advantages, particularly when considering economic and spatial constraints in moss culture. Implementing a fog chamber allows for controlled environmental conditions, optimizing moisture levels essential for moss growth. When calculating production on a greenhouse area basis, it becomes evident that efficient use of space is crucial for economic feasibility. The major limitation in moss cultivation often lies in the cost and availability of space. Fog chambers can enhance space utilization by promoting vertical growth and allowing for increased stacking, thereby maximizing the productive capacity within a confined area. Additionally, adopting soil-free cultivation methods, such as aeroponics or hydroponics, further optimizes space and reduces weight. This approach not only contributes to economic efficiency but also aligns with sustainable practices by minimizing resource use and potentially opening new avenues for commercial moss cultivation in urban or limited-space environments. Consideration of these factors is pivotal for the development of economically viable and environmentally sustainable moss cultivation practices.