

THE EFFECTS OF MOWING AND FIRE ON  
BRYOPHYTE COMMUNITIES IN OKLAHOMA, AND  
A BRYOPHYTE FLORA FROM SOUTHEASTERN  
OKLAHOMA

By

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Abstract: This thesis is composed of four chapters, exploring the effects of mowing and fire on bryophyte communities in Oklahoma and providing a bryophyte flora from southeastern Oklahoma. First, I addressed whether mowing frequency and seasonality affect bryophyte communities within a C4-dominated grassland. All plots were mown under all combinations of the months March, June, September, and unmown for the previous 12 years. Bryophyte cover by species was visually estimated in early 2010. Bryophytes were absent from all unmown plots and present with low cover in all mowed plots. Season of mowing significantly affected bryophyte cover and composition, with the lowest cover in June-only mowings. I conclude that mowing regime has significant and subtle effects on bryophyte communities, even in a relatively xeric, C4-dominated grassland. Second, I ask the question: will epiphytic bryophytes in frequently disturbed areas have a high resilience to fire in terms of cover, species composition, and species richness? To address this question, I sampled bryophytes on three tree species (*Acer rubrum*, *Quercus alba*, and *Q. rubra*) at two study sites located within the Homer L. Johnston Wildlife Management Area in the Ouachita National Forest, LeFlore County, Oklahoma, prior to and following a 2012 prescribed fire. The majority of bryophytes present before the fire suffered extensive or mortal damage from the fire but the species richness of bryophytes did not significantly change. Species composition of epiphyte communities was more affected by phorophyte host species than by the effects of time since fire. These results suggest weakly that bryophytes are not particularly resilient to fire. Third, I provide a bryophyte flora of a 6047 ha portion of the Homer L. Johnston Wildlife Management Area in the Ouachita National Forest. I made collections of bryophytes from spring 2012 to early spring 2014. I found 50 families and 74 genera represented by 87 moss, one hornwort, and 29 liverwort species. This includes 22 state records and 37 county records. This large number (18%) of species newly reported for the state of Oklahoma demonstrates the need for more bryophyte surveys to be conducted in this understudied region.

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## CHAPTER I

### INTRODUCTION

Disturbance affects most ecological communities (Belsky 1992; Connell 1978; Denslow 1980) including bryophyte communities (Engelmann and Weaks 1985; Fenton and Bergeron 2008; Jonsson and Esseen 1990), potentially affecting both species composition and species richness. In some cases, there is a positive relationship between bryophyte species richness and disturbance (Hart and Chen 2006). In other cases, species richness decreases following disturbance (Werner and Gradstein 2009). The reason why we see these conflicting patterns remains unclear. It is possible that the type of disturbance plays a role in this disparity. Both mowing and fire are common types of disturbance affecting vegetation communities in Oklahoma.

Mowing removes plant biomass in a manner similar to herbivory, and these forms of disturbance are well studied. While the response of vascular plants to mowing is relatively well studied, much less is known about the response of bryophytes to this type of disturbance. At least one study (Vantoreen et al. 1990) found increased species richness of bryophytes with increased mowing frequency, but another study (Vanderpoorten et al. 2004) failed to show the same effect. Memmott et al. (1998) and Vanderpoorten et al. (2004) suggest that timing of this type of disturbance (seasonality) may have an important effect on the response of communities. This leads to the question: does mowing regime, particularly season of mowing, affect bryophyte communities in an Oklahoma grassland?

Fire is a dominant form of disturbance in dry oak communities (Allen and Palmer 2011; Hallgren et al. 2012) and grasslands, such as those found in Oklahoma. The effects of fire on vascular plants are well studied (Whelan 1995). However, few studies have been conducted to determine the effects of fire on bryophyte communities. What is known is that many forest communities are resilient to fire (Andersen et al. 2005; Hallgren et al. 2012; Pausas et al. 2008), especially vascular plant communities that experience frequent fire disturbances (Andersen et al. 2005; Hallgren et al. 2012). However, it is unclear whether similar patterns will exist in bryophyte communities. But we see both vascular plant and bryophyte communities demonstrating a similar pattern of a low resiliency to fire in forests with long fire return intervals. In this study (Chapter III) we ask whether bryophytes in frequently disturbed areas have a high resiliency similar to that seen in vascular plants experiencing a high fire frequency.

The purpose of this thesis is to determine the effects of mowing and fire disturbance on bryophyte communities in Oklahoma, and to report on a bryophyte flora of a natural area, as reported in the following chapters.

In Chapter II, I conduct an analysis of the effects of mowing regime on bryophyte communities in Oklahoma. In Chapter III, I conduct an experiment to determine the effects of fire on epiphytic bryophytes in Oklahoma. In Chapter IV, I conduct a survey of bryophytes in a fire-disturbed region of Oklahoma.

The link between these three chapters is a focus on the effects of disturbance on bryophyte communities. Overall, my findings suggest that mowing significantly affects bryophyte cover and composition, with bryophytes completely absent from unmown plots, and that fire significantly affects epiphytic bryophyte cover but not species richness. Despite the prevalence of disturbance in Oklahoma, and the aridity of Oklahoma in relation to better studied areas, Oklahoma features a diverse bryophyte flora that is apparently able to cope with stressful conditions.

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## CHAPTER II

# MOWING REGIME AFFECTS BRYOPHYTE COMMUNITIES IN AN OKLAHOMA GRASSLAND

### ABSTRACT

Many grasslands experience disturbance in the form of mowing, and even though the effect of mowing on vascular plants is well studied, studies exploring the effects of mowing on bryophytes is lacking. In this study, I addressed whether mowing frequency and seasonality affect bryophyte communities within a C4-dominated grassland. This study was conducted in a tallgrass prairie, Payne County, north central Oklahoma, USA. All 144 1m<sup>2</sup> plots were mown under all combinations of the months March, June, September, and unmown for the previous 12 years resulting in 18 replicates per treatment. Bryophyte cover by species was visually estimated in early 2010. A Canonical Correspondence Analysis (CCA) was performed to determine treatment effects on species composition. Bryophytes were absent from all unmown plots and present with low cover in all mowed plots. Season of mowing significantly affected bryophyte cover and composition, with the lowest cover in June-only mowings. There is a significant compositional gradient with September mowing favoring *Archidium ohioense*, while discouraging *Fissidens sublimbatus*; the most frequent species (both in the genus *Weissia*) occur in all treatments. This compositional gradient is consistent with the limited knowledge available of the life history strategies of the most frequent species. I conclude that mowing regime has significant and subtle effects on bryophyte communities, even in a relatively xeric, C4-dominated grassland.

KEYWORDS: Moss; Mowing Season; Mowing Frequency; Long Term Mowing; Xeric Mosses

## INTRODUCTION

Many grasslands are subject to frequent disturbance in the form of fire (Towne & Owensby 1984; Allen et al. 2009), grazing, (Axelrod 1985) and in some cases mowing (Losvik 1988). In the absence of disturbance grassland bryophytes are likely to be outcompeted by vascular plants (Lobel et al. 2006). However, different disturbance types will likely have different effects on grassland bryophyte community structure. In a calcareous grassland in Europe, mowing increased species richness more than burning (Jeschke et al. 2008). Bergamini et al. (2001) found grazing to increase species richness more than mowing in montane calcareous fens. It is not only the type of disturbance that can alter grassland bryophyte communities but their seasonality as well. In cold desert environments, season of grazing by cattle had a significant effect on bryophyte cover in cryptogamic crusts (Memmott et al. 1998). Vanderpoorten et al. (2004) found species composition to differ in plots mown annually at different seasons. The stress gradient hypothesis (Bertness and Hacker 1994; Bertness and Callaway 1994) could be employed to describe why season of mowing affects bryophyte species composition in Oklahoma grasslands. According to the stress gradient hypothesis, positive species interactions, such as facilitation, are more likely to occur in stressful environments than in benign environments. Thus, in xeric grasslands, bryophytes likely require vascular plant cover during the hottest part of the year to facilitate growth.

There have been several studies on the effects of mowing on grassland communities, but studies including bryophytes have mostly involved European grasslands (Vantooren et al. 1990; Vanderpoorten et al. 2004; Ingerpuu & Kupper 2007; Jeschke et al. 2008) and wetlands (Bergamini et al. 2001; Peintinger & Bergamini 2006; Hajkova et al. 2009). Vantooren et al. (1990) found in a short term study that Dutch chalk grasslands bryophyte species richness was positively correlated with number of mowings per year. In contrast, Vanderpoorten et al. (2004) found that bryophyte species richness did not significantly differ between mowing regimes. It is perhaps not surprising that bryophytes are either unaffected or positively affected when herbaceous biomass is removed in moist C3 grasslands. However, in understudied drier C4-dominated grasslands, it is possible that removal of herbaceous biomass is detrimental to poikilohydric organisms such as bryophytes (*sensu* stress gradient hypothesis, Bertness and Hacker 1994; Bertness and Callaway 1994). In this paper, I test whether mowing regime, and in particular season of mowing, affects bryophyte communities in a C4-dominated North American grassland.

## METHODS

### STUDY SITE AND PLOTS

The study site is owned by Oklahoma State University and is located 17km WSW of Stillwater in Payne County, Oklahoma USA (36.073°N 97.248°W). Prior to the initiation of this study the site experienced grazing by horses and cattle. There are 144 1x1m plots arranged in 12 rows and 12 columns with 1m walking lanes between them. These plots were mowed (with removal of clippings) under all combinations of the months of March, June, and September with an additional unmown treatment. Treatments were randomly assigned to plots. This resulted in 18 replicates for each of the eight treatments. This mowing regime began in 1998 and continued every year for 12 years.

## SAMPLING

During January and February 2010, I visually estimated percent cover of bryophytes by species within the 1x1m plots with abundance categories of <0.1%, 0.1-1%, and increments of 1% thereafter. For specimens difficult to identify to species in the field, I collected and identified them in the laboratory with the aid of compound and dissecting microscopes. Sterile members of the genus *Bryum* were not identified to species. Nomenclature follows Crum and Anderson (1981) and Flora of North America Editorial Committee (FNA; 2007).

## STATISTICAL ANALYSIS

Because the data were non-normally distributed, I tested the correlation between overall bryophyte cover and bare soil within the plots using a Spearman rank correlation test; significance of treatment effects on bryophyte cover was tested by a Kruskal-Wallis test; both tests were performed using R 9.2 (R Development Core Team 2009).

To determine the effect of mowing treatments on bryophyte species composition, I performed a canonical correspondence analysis (CCA) using CANOCO for Windows 4.5 on square-root transformed bryophyte cover in the mowed plots, with treatments as nominal variables (ter Braak & Šmilauer 2002; Lepš & Šmilauer 2003). Significance of all axes combined was tested using a Monte Carlo permutation test with 1000 permutations.

## RESULTS

Mowing had a strong effect on bryophyte cover. Season of mowing had a significant effect on bryophyte cover (Fig. 2.1). My finding of complete absence of bryophytes in unmown plots, and presence in all mowed plots, contrasts with the idea that herbaceous cover provides protection for poikilohydric bryophytes in a dry climate. In other words, the stress gradient hypothesis does not provide a tenable model for the relationship between vascular plants and bryophytes in this system. In my study, bare soil is strongly correlated with bryophyte cover (Spearman Rank coefficient 0.636, p-value < 0.00001). Only five unmown plots had exposed bare soil, with a maximum of 1% cover. This is in contrast to mowed plots, all of which contained bare soil with a mean of 10.9% and a range of 1-75% cover. Plots mown only in June had a significantly lower bryophyte cover than all other mowed plots (Fig. 2.1).

Overall, species richness was low. Mosses, represented by 10 taxa, were the only bryophytes encountered. Drought-tolerant acrocarpous species dominated, with *Weissia controversa* being the most abundant and *W. muehlenbergiana* being second most abundant species (Table 2.1).

Canonical Correspondence Analysis (CCA; Fig. 2.2) and Table 2.1 reveal an effect of season of mowing on species composition. Centroids of treatments mowed in September appear towards the left of the CCA biplot, while those not mowed in September are towards the right. September mowing appears to favor *Archidium ohioense* and *Funaria hygrometrica* and to discourage *Fissidens sublimbatus* (Fig. 2.2). However, *Funaria hygrometrica* was only present in a single plot and thus this species' relationship to September mowing should not be strongly interpreted. While the second CCA axis might indicate a gradient of mowing frequency, its eigenvalue is much lower than that of the first and is thus probably not worth interpreting.

## DISCUSSION

My finding of complete absence of bryophytes in unmown plots, and presence in all mowed plots, contrasts with the idea that herbaceous cover provides protection for poikilohydric bryophytes in a dry climate. The lack of bryophytes in the unmown plots is likely due to the buildup of vascular plant litter on the soil surface eliminating bare soil patches required for bryophyte colonization. This absence of bryophytes in control plots is in contrast to Vanderpoorten et al. (2004) and Ingerpuu & Kupper (2007) who found that bryophyte cover in their mowed plots did not differ significantly from their unmown controls. These different results can likely be attributed to the difference in study systems. Vanderpoorten et al. (2004) looked at the effects of mowing in a calcareous grassland in Belgium and Ingerpuu & Kupper (2007) examined the effects of mowing in a Dutch chalk grassland; both of these study sites have a more humid climate than Oklahoma. This higher level of moisture allows for larger growth forms of bryophytes to develop resulting in a much higher bryophyte cover. The bryophyte communities at both of these European sites consisted primarily of pleurocarpous species in contrast to our Oklahoma grassland site, which was dominated by drought-tolerant acrocarpous species. Additionally, my study and that of Ingerpuu and Kupper (2007) differed in the length of mowing treatment implementation, which may explain some of the differences in our findings. My experimental treatments were implemented for 12 years whereas the experimental plots in Ingerpuu and Kupper (2007) were only mown in one year. My longer mowing regime may have caused species that were moderately sensitive to disturbance, and not initially excluded by mowing, to become extirpated while allowing the dominance of species, which are more tolerant of disturbance such as *Weissia controversa*.

My results are similar to Vanderpoorten et al. (2004), in that I found seasonality of mowing significantly affected bryophyte community composition. Mowing in September likely favors *Archidium ohioense* because it has spores that mature in the fall (Crum and Anderson 1981). Allowing the sensitive protonema to develop and mature throughout winter when vascular plant shading is reduced by September mowing. The two species of *Weissia* were found in all mowing treatments. This is likely because they can produce two crops of spores per year in Oklahoma: one in the fall and another in the spring (Crum and Anderson 1981). June mowing probably favors *Fissidens sublimbatus* because it is apparently adapted to xeric conditions: it predominantly occurs in the arid western US where it thrives in hot dry climates (FNA 2007).

Mowing during June removes vascular plant shading to the soil during the hottest period of the year in Oklahoma. Zibilske and Makus (2009) showed that mowing during the summer in Texas can increase soil surface temps by 15° C. This drastic increase in soil temperature probably accounts for the significant decrease in bryophyte cover, which occurred in plots mown only in June. Plots mown only in June also have high herbaceous cover from fall through spring, so there is no time period advantageous for moss growth. For those plots that are mowed in June in addition to another time, it is likely that winter-active bryophytes can remain dormant in summer in a desiccated state.

My results show that in the absence of other forms of disturbance mowing will allow bryophytes to exist in Oklahoma grasslands. In addition, the season of mowing has significant effects on bryophyte species composition that is interpretable with respect to life history

strategies associated with poikilohydry.

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TABLE

Table 2.1. Frequency (% of plots occupied) of each bryophyte species for each mowing treatment along with mean ( $\pm$  s.d.) species richness.

	Treatment							
	Unmown	M	J	S	M,J	M,S	J,S	M,J,S
<i>Weissia controversa</i>	-	100	89	83	100	56	83	89
<i>Weissia muhlenbergiana</i>	-	56	22	78	72	89	89	83
<i>Archidium ohioense</i>	-	28	11	56	11	83	78	33
<i>Bryum</i> sp.	-	17	6	28	22	28	17	22
<i>Physcomitrium pyriforme</i>	-	6	6	28	-	39	33	-
<i>Fissidens sublimbatus</i>	-	22	22	-	28	-	-	-
<i>Barbula convoluta</i>	-	-	-	6	6	-	22	-
<i>Ctenidium molluscum</i>	-	-	6	6	-	-	-	-
<i>Funaria hygrometrica</i>	-	-	6	-	-	-	-	-
unidentified protonema	-	11	-	-	-	-	-	-
<i>Campylium chrysophyllum</i>	-	6	-	-	-	-	-	-
Mean Species Richness	-	3.8 $\pm$ 2.1	1.9 $\pm$ 1.5	4.8 $\pm$ 1.4	3.5 $\pm$ 1.7	5.3 $\pm$ 1.4	5.2 $\pm$ 1.3	3.3 $\pm$ 1.5

## FIGURES

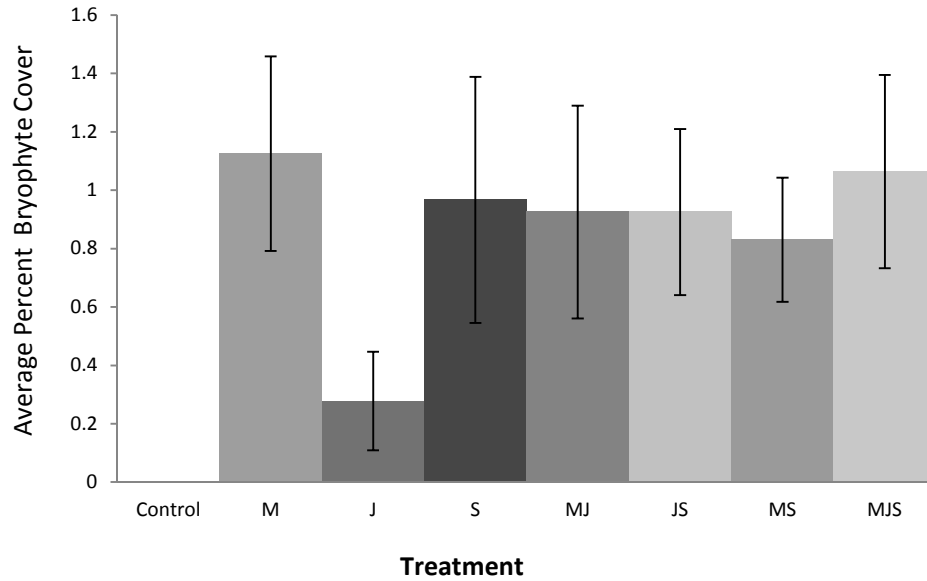


Figure 2.1. Average percent cover of bryophytes by mowing treatment with 95% confidence intervals. Treatment letters refer to months of mowing (M=March, J=June, S=September). Control was unmown. Treatment effects are significant (Kruskal-Wallis  $K = 67.1$ , d.f. = 7,  $p < 0.0001$ ).

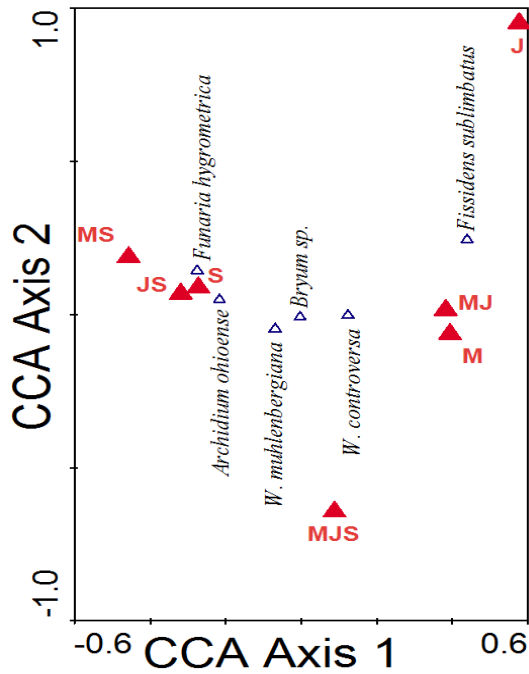


Figure 2.2. CCA biplot of bryophyte species and centroids of mowing treatments, with letters indicating the month(s) of mowing. All ten bryophyte taxa were included in the analysis, even though only the six most common bryophyte species are shown in this figure. Unmown plots are excluded from analysis because no bryophytes were present. The first and second eigenvalues are 0.1651 and 0.0251 respectively. The first axis and all combined axes are highly significant ( $p < 0.001$ ).

## CHAPTER III

### THE EFFECTS OF PRESCRIBED FIRE ON EPIPHYTIC BRYOPHYTES WITHIN THE OUACHITA NATIONAL FOREST, OKLAHOMA

#### ABSTRACT

Although the effects of fire on vascular plant communities are relatively well studied, little research exists on the effects of fire on bryophyte communities. Epiphytic bryophyte communities are particularly poorly studied. Thus, I ask the question: will epiphytic bryophytes in frequently disturbed areas have a high resilience to fire in terms of species composition, similar to that seen in vascular plants experiencing a high fire frequency? To address this question, I sampled bryophytes on three tree species (*Acer rubrum*, *Quercus alba*, and *Q. rubra*) at two study sites located within the Homer L. Johnston Wildlife Management Area along the north slope of Winding Stair Mountain in the Ouachita National Forest, LeFlore County, Oklahoma, prior to and following a 2012 prescribed fire. I performed a Canonical Correspondence Analysis (CCA) on the relative abundance of bryophytes, a partial CCA (pCCA) using the relative abundance of bryophytes as in the previous CCA but factoring out phorophyte host species, and three separate pCCAs (one for each phorophyte species). Because I sampled only trees affected by fire, the majority of bryophytes present before the fire suffered extensive or mortal damage from the fire and bryophyte cover decreased significantly following fire the species richness of bryophytes did not significantly change. Furthermore, only two epiphytic bryophyte species were eliminated following fire. Species composition of epiphyte communities was more affected by phorophyte host species than by the effects of time since fire. These results suggest weakly that bryophytes are not particularly resilient to fire.

## INTRODUCTION

Disturbance is a major driver of biological diversity (Connell 1978). While there are many types of disturbance with varied effects, fire is the dominant form of disturbance in many forests (Bond and Keeley 2005), including Oklahoma oak forests (Allen and Palmer 2011; Hallgren et al. 2012).

The effects of fire on vascular plants are relatively well studied (Whelan 1995). For example, without at least two fires per decade, the sapling layer of dry oak forests of the Southern Great Plains will become dominated by non-oak tree species (Burton et al. 2010). These non-oak species have more rapidly decaying litter and will replace oaks in the canopy over time, creating a feedback of oak decline and fire suppression (Nowacki and Abrams 2008). Additionally, increased fire frequency within the herbaceous layer of oak forests leads to an increase in both richness and cover of forbs, C3 graminoids, and summer-flowering herbs (Bowles et al. 2007; Burton et al. 2011).

Vascular plant communities that experience long return intervals between fires often have low resilience, i.e., it takes a very long time for the community to revert to a species composition similar to that prior to the disturbance event (Gromtsev 2002). In contrast, we see a high resilience to fire in vascular plant communities that experience frequent disturbances (Andersen et al. 2005; Hallgren et al. 2012). Even though resilience can describe the response of cover, species richness, or species composition to disturbance in a particular community, the term 'resilience' is used in the current study to describe the response of species composition to disturbance unless otherwise specified.

Despite this well-studied influence of fire on vascular plant community structure, there have been relatively few studies examining the effects of fire on bryophyte communities. Their lack of a cuticle, small size, and low moisture content during dry conditions suggest that bryophytes should be adversely affected by fire. We know that bryophytes are potentially heat-tolerant: a moss, *Syntrichia caninervis*, can survive temperatures of 120°C for 30 minutes when it is in a desiccated state (Stark et al. 2009). However, it is not known if bryophytes can withstand yet higher temperatures for a shorter duration, which are typical of natural fire events, nor whether they are capable of resisting combustion. Nevertheless, because bryophytes regularly occur in fire-prone forests, they must have mechanisms to either tolerate fire or to recolonize after fire events.

It is unclear if bryophyte communities are similar to vascular plant communities in their resilience to fire. Most studies on the resilience of forest bryophyte communities have occurred in boreal forests (Caruso et al. 2011; Dynesius and Hylander 2007; Landhausser and Wein 1993; Ross-Davis and Frego 2002), which naturally have very long fire return intervals. It may take bryophyte communities centuries to reestablish to predisturbance levels following a fire in these systems with infrequent fires (e.g. Turetsky et al. 2012). We see both vascular plant and bryophyte communities demonstrating a similar pattern of a low resilience to fire in forests with long fire return intervals. Conversely, in forests with frequent fire disturbances, members of the vascular plant community often have mechanisms to tolerate or rapidly resprout following fire (i.e., long lived diaspore banks, underground storage structures, etc.). Similarly, bryophyte communities might also be resilient after fire, and bryophyte species occurring in these habitats may have mechanisms allowing for this high resilience. This begs the question: will species

composition of bryophyte communities in frequently disturbed areas have a high resilience similar to that seen in vascular plants experiencing a high fire frequency?

One possible mechanism by which bryophytes may have a high resilience after fire is by surviving in unburned habitat refugia. Among vascular plants, those species occurring in “fire refugia” typically are fire intolerant and restricted to these unburned areas (Camp et al. 1997; Clarke 2002). Conversely, vascular plants that inhabit fire prone habitats typically have mechanisms to resprout or tolerate fire (i.e., underground bud banks, protection of meristematic tissues, etc.) (Heyward 1939; Appezzato-Da-Gloria et al. 2008). This pattern is not the same for bryophyte species in refugia, which are typically the same species that were present in the surrounding matrix and can recolonize the surrounding burned matrix following fire (Hylander and Johnson 2010). These refugia can be in the form of boulders, deep bark crevices, or simply unburned patches on the landscape. Intact bryophytes from these refugia can potentially act as source populations for recolonization following fire. However, the significance of refugia in recolonization of the forests by bryophytes is unclear.

Nearly all studies concerning fire and forest bryophytes have investigated ground layer bryophytes. Additionally, environmental factors such as microtopographic position are more important than diaspore availability in determining which species recolonize after fire in boreal forest bogs, suggesting again that substrate suitability is more important than dispersal limitations for bryophyte colonization (Benscoter 2006). Furthermore, fire can play an important role for many species of bryophytes by removing dominant competitors and altering the substrate chemistry to make it more favorable for their establishment (Bradbury 2006). These burnt-soil specialists are commonly referred to as “fire mosses”. Across many biomes we see this same pattern of fire removing dominant competitors and altering substrate conditions so that disturbance-loving ruderal species, and in some cases ash and charcoal specialists, colonize first. These communities then go through a succession to more competitively superior perennial species typical of their habitat in an unburned state. This same pattern occurs in boreal forests (Marozas et al. 2007; Puche and Gimeno 2000; Thomas et al. 1994), in Mediterranean forests (Heras et al. 1990; Heras et al. 1994; Heras et al. 1995), and in grasslands (Ferguson et al. 2009), often with the same species of early colonizing “fire mosses”.

In their review of after-fire bryophyte recolonization of soil and logs, Ryoma and Laaka-Lindberg (2005) noted that little research exists studying after-fire colonization of coarse woody debris by bryophytes. However, it seems that this same pattern of initial colonization by fire mosses following fire seems to hold on coarse woody debris as well (Ryoma and Laaka-Lindberg 2005; Schmalholz et al. 2011; Vanha-Majamaa et al. 2007). It is also interesting to note that in many cases, it is the same species (i.e., *Ceratodon purpureus* and *Funaria hygrometrica*) that colonize both soil and burnt logs after a fire (Duncan and Dalton 1982). There are many specialist epixylic liverwort species that cannot colonize burnt coarse woody debris; in some cases, it can take these burnt substrates hundreds of years to become suitable again for the epixylic (i.e. decorticated wood) liverworts (Ryoma and Laaka-Lindberg 2005). This suggests that fire alters the substrate of coarse woody debris making it more favorable for a few cosmopolitan species, while making it unfavorable for more specialized epixylic species. While some bryophyte species specialize on burnt substrates or decorticated logs, others prefer the bark of living trees; these bryophytes are known as epiphytic bryophytes.

Among epiphytic bryophytes, strict phorophyte (i.e. the substrate plant species) host specialization is rare (Schmitt and Slack 1990). However, epiphytic bryophytes do make the distinction between gymnosperm and angiosperm phorophyte hosts (Cleavitt et al. 2009; Palmer 1986). However, when species composition is taken into account, individuals of specific phorophyte species harbor similar epiphytic bryophyte communities (Palmer 1986; Peck et al. 1995; Schmitt and Slack 1990; Sim-Sim et al. 2011). It is therefore probable that within Oklahoma forests, different tree species will harbor different communities of bryophytes. It is not known if any species of epiphytic bryophytes specialize on burnt bark.

To my knowledge there have been only three studies regarding the effects of fire on epiphytic bryophytes (Boudreault et al. 2000; Pharo et al. 2013; Ohlson et al. 1997). Two of these studies were conducted in northern forests with extremely long fire return intervals of stand-replacing fires. The first study (Ohlson et al. 1997) inventoried all bryophytes (presumably including epiphytes), and showed that stands that had experienced fire in the past had higher species richness than those untouched by fire. The forests they examined were swamp forests with at most two to three fires per millennium. Swamp forests burn much less frequently than the surrounding landscape and are important source refugia for both epiphytic bryophytes and lichens to recolonize the surrounding landscape following fires (Kuusinen 1996). The second study (Boudreault et al. 2000) examined epiphytes in a chronosequence of forests of different ages (i.e., time since fire), corresponding to 278, 125, 79, and 51 year-old stands. They found a higher species richness in the oldest stands. In both of these studies, the forests had established following a catastrophic fire event. The third study (Pharo et al. 2013) was conducted in an Australian eucalypt forest. In this study, the researchers examined all bryophytes in plots placed in areas that experienced three fire intensities (i.e., unburned, moderately burned, and severely burned). These researchers included epiphytes on the lower 2m of tree trunk in their study; even though they did not examine the effects of fire on epiphytes separately, they did find that 60% of the variation in species richness and composition between the plots was explained by fire severity. Also, within the severely burned plots there were no epiphytes recorded.

No known studies have explicitly examined epiphytes on the lower tree trunk, nor have any examined the effects of frequent, low-intensity ground fires. Nevertheless, oak forests in the Southern Plains experience frequent burns, and epiphytic bryophyte species are frequent. Therefore I predict that the species composition of epiphytes that occur in this system will display a high resiliency to fire, as is seen in vascular plants occurring in systems that experience frequent fires.

The purpose of this study is to determine if the species composition of epiphytic bryophyte communities display a high resiliency after a 2012 fire in the Ouachita National Forest of Oklahoma.

## METHODS

### STUDY SITES

Two study sites were located within the Homer L. Johnston Wildlife Management Area along the north slope of Winding Stair Mountain in LeFlore County, Oklahoma. These two were randomly selected from all of the upper reaches of the north-facing ephemeral drainages in the area (chosen because they were likely to contain *Acer rubrum*, *Quercus alba*, and *Quercus*



*rubra*). Both sites burned in early spring of 2012. After the fire there was almost no leaf litter or coarse woody debris remaining. Several mature trees were killed and most of the fine branches on the remaining mature trees died. There was an abundance of epicormic sprouts coming out of the remaining living trees.

## FIELD METHODS AND SAMPLING

Within each of the two study sites, I randomly chose five trees of each of three species: *A. rubrum*, *Q. alba*, and *Q. rubra* totaling 30 trees. After selecting a random starting point using ArcGIS; I followed a transect due north for 100 m. The first five suitable trees of each species that fell within 5 m of either side of these transects and met certain criteria were included. These criteria were that the trees were at least 15cm in diameter and showed fire damage to epiphyte communities. Any browning or blackening of bryophyte stems, which could reasonably be assumed to be due to fire, was considered damage. Due to the intensity of the fire, nearly every tree in the area suffered damage due to the fire, with many individual trees being killed by the fire.

Initial sampling of epiphytes occurred in summer 2012, followed by resampling in summer 2013. I estimated percent cover of living and dead epiphytic bryophytes by species in 10 x 10 cm quadrats on vertical belt transects on the north and east side of each tree up to a height of 1 m. Because the first sampling period followed a prescribed fire and fire-damaged taxa retained enough three-dimensional structure to be identified to species level, I used the combined living and dead epiphyte cover from 2012 to represent the before fire community composition. The living epiphytes from 2012 represent the first post-fire community composition sampling. I resampled the trees in summer 2013, recording only living cover by species; due to their degradation, it was no longer possible to identify dead stems to species level in 2013. The 2013 living epiphyte composition represents the second post-fire sampling.

## DATA ANALYSES

The cover of epiphytes on all aspects and heights were summed for each tree by sampling time combination, creating a composite “tree” sample. Using these composite “tree” samples, I then calculated the relative abundance of each species of bryophyte for each tree. To determine the importance of tree species and sampling period on the relative abundance of bryophytes, I performed a Canonical Correspondence Analysis (CCA) on the relative abundance of bryophytes for the combined height and aspect measures of each tree, using tree species by sampling period as the environmental variables (ter Braak 1986). Then I conducted a partial CCA (pCCA) using the relative abundance of bryophytes as in the previous CCA. I used individual trees as my covariable to more directly see the effects of fire on the epiphytes. Additionally, I conducted three separate partial CCAs (pCCAs; Borcard et al. 1992), one for each phorophyte species (*A. rubrum*, *Q. alba*, and *Q. rubra*). I used sampling time as an environmental factor and individual tree identity as a factor covariate. Significance of all ordinations and axes was tested using Monte Carlo permutation tests with 9999 iterations and with the covariable as permutation blocks (for the pCCA) (Legendre & Legendre 1998; Šmilauer and Lepš 2014).

## RESULTS

While the flora of the study site contains 117 bryophyte species (Chapter IV; Appendix A), only twenty-three bryophyte taxa were found on the experimental trees. In the current study, taxa in the genera *Frullania* (except *F. asagrayana*), *Orthotrichum* (*O. ohioense* or *O. pumilum*) and *Brachythecium* (*B. acuminatum*, *B. oxycladon*, *B. plumosum*, *B. rotaeantum*, or *B. rutabulum*) were not identified to species level in the field. Most of the bryophytes present before the fire suffered extensive damage or mortality due to the fire.

Bryophytes on all sampled heights on the tree bole experienced an initial decrease in cover following the fire, with all but the lower height classes on *Acer rubrum* losing more than 50% of their cover (Figure 3.1). Only epiphytes on *Acer rubrum* had a larger decrease in cover at intermediate heights, whereas epiphyte cover was reduced to similar levels for all heights on both *Quercus* species (Figure 3.1). Recovery following the fire seems to be strongest close to the ground, indicating that cover of the basal communities may be more resilient to fire. More interestingly, there was a significant recovery in bryophyte cover one year after fire on the *Quercus* trees, but not on the *Acer* trees (Figure 3.2). Even though there was a significant decrease in cover following fire, there was not a significant change in species richness after fire (Figure 3.3). Only two very infrequent species were eliminated from the sampled trees during the study period.

Phorophyte host species had a much larger effect on species composition of epiphyte communities than did the effects of time since fire (Figure 3.4). Except for rarely encountered species restricted to a single sampling time, my results indicate no epiphytic species that are clearly favored by fire.

If the 2013 sampling centroid had fallen between the prefire and immediately post fire centroids for all of the tree species, we could have inferred that these communities are resilient (that is, they would be on a trajectory back to their original conditions). However, these are not the results that we see. For *Acer rubrum*, the 2013 centroid is quite different from both the other sampling time centroids; for *Quercus alba* the 2013 centroid is close to the prefire centroid indicating (weakly so) that composition of *Q. alba* epiphyte communities may be resilient to fire; and for *Quercus rubra* the 2013 centroid is nearest the immediately post fire centroid, indicating a change in composition after the fire, but very little further change after that (Figure 3.4). Therefore, my data do not support the idea of a highly resilient epiphyte community composition in these forests with respect to fire.

When the effects of phorophyte host species are factored out in pCCA, we see that there is a cohort of species that are associated with the 2013 sampling period. These are *Fissidens dubius*, *Weissia controversa*, and *Atrichum angustatum* (Figure 3.5). These species are all relatively uncommon in the sample dataset, and they are typically terricolous taxa, only occurring at the very base of the tree when epiphytic.

The pCCAs performed separately for each individual phorophyte host species (not shown) all show a similar weak pattern of an initial decrease in relative species abundance of epiphytes following fire, followed by regrowth and a recovery towards the original sampling centroid along the second axis one year following fire. However, the 2013 centroids are still located far from the prefire centroids along the first axis. Time since fire was only significant for *Q. rubra*, (*A. rubrum*  $p=0.300$  for first axis, 0.740 for all axes; *Q. alba*  $p=0.280$  for first axis,

0.280 for all axes; *Q. rubra*  $p= 0.002$  for first axis, 0.003 for all axes) though low sample sizes limit statistical power.

## DISCUSSION

Even though there are no published growth rates for most epiphyte species, my data suggest that individuals within Ouachita National Forest epiphyte communities can grow relatively quickly in the presence of ample rainfall. The year of this study had higher than average rainfall. The study occurred during a particularly wet year following two years of drought. The long-term average annual precipitation and temperature for LeFlore County, Oklahoma are 118.2cm and 16.1°C, whereas the total rainfall and average temperatures for 2013 were 149cm and 14.2°C, respectively. It is possible that the effect of this anomalously wet and cool year (2013) swamped out the effects of fire on the epiphyte communities. However, if this were the case I would still expect to see a strong effect of sampling time on the epiphyte communities, unless all species increased simultaneously, and this is not seen. Another possibility is that it may take more than one year for these communities to recover entirely from the effects of fire. It is likely that the species composition of these communities is generally quite resistant to fire; in other Oklahoma forests epiphytes can survive leaf litter fires with no noticeable damage (Richardson, unpublished). However, when conditions favor very hot fires, it appears that a threshold is reached and there is a shift in the communities caused by the fire.

I expected to see a decrease in percent cover immediately following fire because I purposely selected trees with epiphyte communities damaged by fire. Not surprisingly, almost all sampled heights on the tree bole experienced an initial decrease in bryophyte cover following the fire. Cole (1992) found the maximum temperatures in oak forest fires to be near 20cm above the ground. Therefore, I expected to see the largest decrease in cover due to fire at an intermediate height near the location of the hottest part of the flame. This pattern was only observed on *Acer* individuals. Although the bryophyte communities are different between the two *Quercus* species, the pattern of a significant recovery in overall bryophyte cover for almost all heights is shared between them. Both of the *Quercus* species showed a significant increase in cover between the 2012 after-fire sampling and the 2013 sampling. This increase in cover seen on the *Quercus* species is reasonable due to the ability of bryophytes to regenerate from any living cell (totipotency). However, the bryophytes on *Acer* individuals showed a continued decrease in cover in the basal portions during this same time period. This could mean that there are legacy effects of the fire on *Acer* individuals that continue to manifest one-year after-fire. The *Quercus* species also had a much larger initial decrease in overall cover following fire than did *Acer*. This may be because there was lower bryophyte cover before the fire on the *Acer* individuals, leading to less bryophyte biomass to burn or to carry fire to neighboring bryophyte colonies on the tree. The difference in after-fire cover may also be simply because the fire was less intense around the *Acer* individuals. *Acer* litter decays more rapidly and is less flammable than *Quercus* litter, and there was a lower proportion of *Quercus* oak litter beneath the *Acer* trees than there was beneath the *Quercus* trees. The lower initial decrease in epiphyte cover on *Acer* trees may also be because they are more sensitive to fire and the surviving *Acer* trees experienced less intense fire than the surviving *Quercus* trees.

The miniscule effects of sampling time compared to phorophyte host species on bryophyte species composition are surprising. Even though we often see the pattern of individuals of a single phorophyte host species harboring very similar epiphyte communities (Palmer 1986; Peck et al. 1995; Schmitt and Slack 1990; Sim-Sim et al. 2011), one would expect dramatic effects of fire on the species composition of these tiny, often single cell layer thick epiphytes. In terrestrial bryophyte communities that are very different before fires (i.e., boreal and Mediterranean forests), we see a strong similarity in the initial post fire community composition due to the presence of the “fire moss” community (Puche and Gimeno 2000; Ryoma and Laaka-Lindberg 2005). This initial rapid colonization of burned substrates following fire by the “fire moss” community is a nearly ubiquitous phenomenon in terricolous bryophyte communities (Marozas et al. 2007; Puche and Gimeno 2000; Ryoma and Laaka-Lindberg 2005; Thomas et al. 1994). Based on these studies, I expected to see a strong effect of sampling time on the epiphyte communities due to new species colonizing the tree bark after fire. However, this is not the case. My data do not support the idea that there are “fire mosses” in epiphyte communities in an Oklahoma oak forest as there are in terricolous bryophyte communities.

Further, both Palmer (1986) and Schmitt and Slack (1990) found that the epiphyte communities on host congeners were more similar than the communities between phorophyte hosts of different genera. Therefore, it is very surprising to see that the bryophyte communities on the two *Quercus* species are as dissimilar to one another as they are to the communities on the *Acer* species in my study. Despite the strong differences in the communities between the different phorophyte species, I expected to see new species colonizing the tree after fire as is seen in terricolous communities. Even though it appears that a few uncommonly epiphytic taxa were more associated with the 2013 sampling time, it is important to note that these are all typically terricolous taxa that only rarely are epiphytic in Oklahoma. In more mesic conditions they become more abundant as epiphytes. Therefore, I strongly suspect that their association with the 2013 sampling time is due to climate related factors and not fire.

## CONCLUSIONS

Even though epiphytic bryophytes commonly occur in forested, fire-prone landscapes, the results of my study suggest weakly that the species composition of bryophyte communities is not particularly resilient to fire over the span of one year. Interestingly, there do not appear to be any epiphytic “fire mosses” as are found amongst terricolous bryophyte taxa. My experimental results show that phorophyte host species has a stronger effect on epiphyte community composition than does time since fire, even though there is a short-term shift in epiphytic bryophyte communities after fire, and that the responses of individual bryophyte species vary with phorophyte host species. However, even though almost all species showed a decline in abundance after the fire, it is important to note that there were only two epiphyte species (which were infrequent in this study) eliminated from the system during the study period. This could have been due to fire, or simply due to stochastic environmental effects. These results must be interpreted with caution since they were possibly influenced by the wetter and cooler than average year that occurred during this study.

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TABLE

Table 3.1. Labels used in ordination biplots and average percent cover for each phorophyte by time combination shown for all bryophyte species. pre= pre fire samples, post1= 2012 post fire samples, post2= 2013 post fire samples.

Species	Species code	<i>Acer rubrum</i>			<i>Quercus alba</i>			<i>Quercus rubra</i>		
		pre	post1	post2	pre	post1	post2	pre	post1	post2
<i>Amblystegium varium</i>	<i>AmblVari</i>	0.38	0.18	0.54	0.35	0.22	0.89	0.40	0.29	1.30
<i>Atrichum angustatum</i>	<i>AtriAngu</i>	0.00	0.00	0.02	0.00	0.00	0.03	0.00	0.00	0.04
<i>Brachythecium</i> sp.	<i>BrachSp</i>	0.01	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00
<i>Brotherella</i>	<i>BrotTenu</i>	0.10	0.25	0.00	0.10	0.30	0.00	0.11	0.39	0.00
<i>Clasmatodon parvulus</i>	<i>ClasParv</i>	0.01	0.03	0.08	0.01	0.03	0.10	0.01	0.03	0.09
<i>Drummondia</i>	<i>DrumPror</i>	2.64	0.51	1.19	3.17	0.61	2.76	4.15	0.74	3.28
<i>Entodon seductrix</i>	<i>EntoSedc</i>	0.00	0.00	0.01	0.01	0.00	0.01	0.01	0.00	0.02
<i>Fabronia ciliaris</i>	<i>FabrCili</i>	0.91	0.40	0.09	1.05	0.48	0.11	1.13	0.59	0.13
<i>Fissidens dubius</i>	<i>FissDubi</i>	0.00	0.00	0.01	0.00	0.00	0.02	0.00	0.00	0.01
<i>Frullania asagrayana</i>	<i>FrullAsag</i>	0.02	0.05	0.12	0.02	0.06	0.15	0.02	0.07	0.19
<i>Frullania</i> sp.	<i>FrullSp</i>	1.67	0.66	0.42	1.24	0.80	0.68	1.28	0.90	0.75
<i>Anomodon tristis</i>	<i>HaplTrist</i>	0.35	0.00	0.00	0.39	0.01	0.01	0.40	0.01	0.01
<i>Hedwigia ciliata</i>	<i>HedwCili</i>	0.01	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00
<i>Leskea gracilescens</i>	<i>LeskGrac</i>	0.06	0.10	0.06	0.06	0.13	0.24	0.06	0.16	0.32
<i>Leucodon julaceus</i>	<i>LeucjulC</i>	1.93	1.22	0.45	2.38	1.46	0.67	3.01	1.84	0.84
<i>Orthotrichum</i> sp.	<i>OrthtSp</i>	0.00	0.01	0.00	0.00	0.01	0.01	0.00	0.00	0.01
<i>Plagiomnium affine</i>	<i>PlagAffn</i>	0.24	0.59	0.00	0.23	0.72	0.00	0.25	0.93	0.00
<i>Platygyrium repens</i>	<i>PlatRepen</i>	3.54	2.34	3.37	3.23	2.81	4.05	3.42	3.28	4.72
unidentified	<i>Protonem</i>	0.00	0.00	0.04	0.00	0.00	0.04	0.00	0.00	0.05
<i>Pylaisiella selwynii</i>	<i>PylaSelw</i>	2.51	0.61	1.31	3.12	0.76	1.55	3.44	0.93	1.84
<i>Schwetskeopsis</i>	<i>SchwFabr</i>	0.00	0.00	0.26	0.05	0.05	0.32	0.05	0.07	0.27
<i>Syntrichia laevipila</i>	<i>SyntLaev</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<i>Thelia asprella</i>	<i>ThelAspr</i>	0.33	0.33	0.18	0.32	0.40	0.22	0.25	0.51	0.28
<i>Thelia hirtella</i>	<i>ThelHirt</i>	0.56	0.43	0.37	0.54	0.53	0.45	0.59	0.68	0.57
<i>Tortella humilis</i>	<i>TortHuml</i>	0.31	0.17	1.46	0.71	0.27	1.76	0.67	0.27	2.17
<i>Weissia controversa</i>	<i>WeisCont</i>	0.00	0.00	0.11	0.00	0.00	0.14	0.00	0.00	0.00

FIGURES

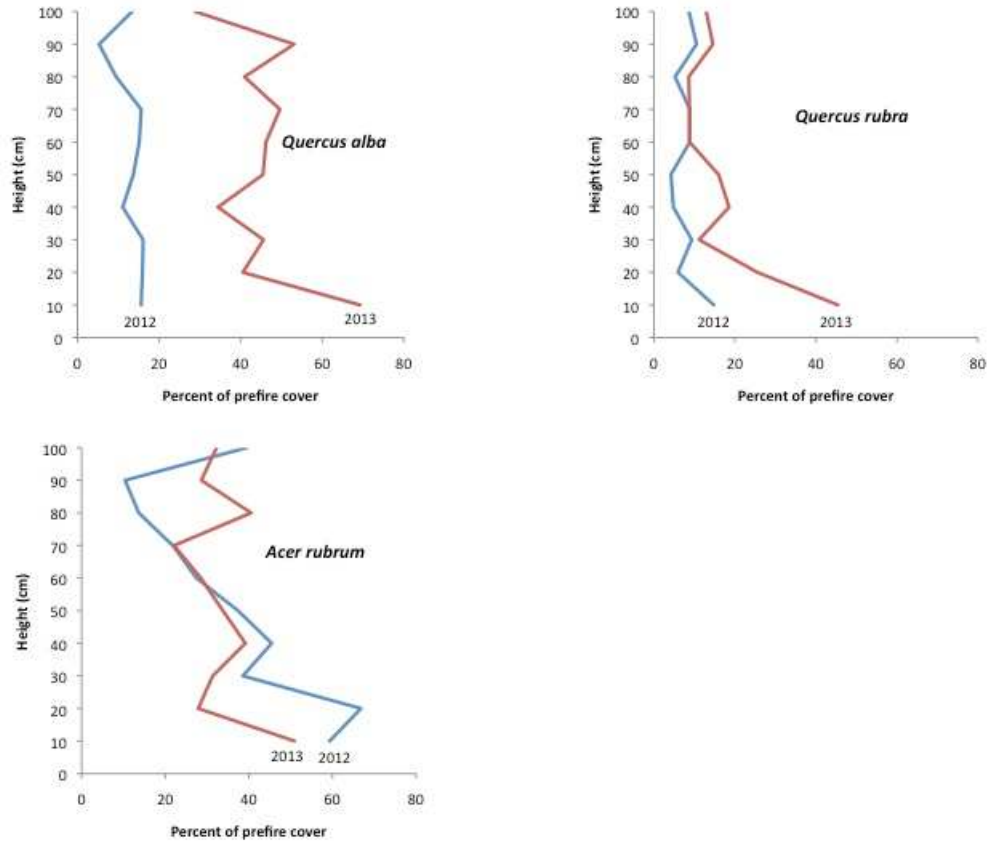


Figure 3.1. Average percent cover, expressed as a proportion of total prefire cover, of epiphytic bryophytes in 10 x 10cm quadrats on the lower 1m of tree trunk on ten individuals of *Acer rubrum*, *Quercus alba*, and *Quercus rubra* in the Homer L. Johnston Wildlife Management Area study site of the Ouachita National Forest, LeFlore County, Oklahoma. There are 2 sampling times shown, 2012 post fire and 2013. Confidence intervals are not plotted because we summed cover across all trees and calculating the average would involve dividing by zero.

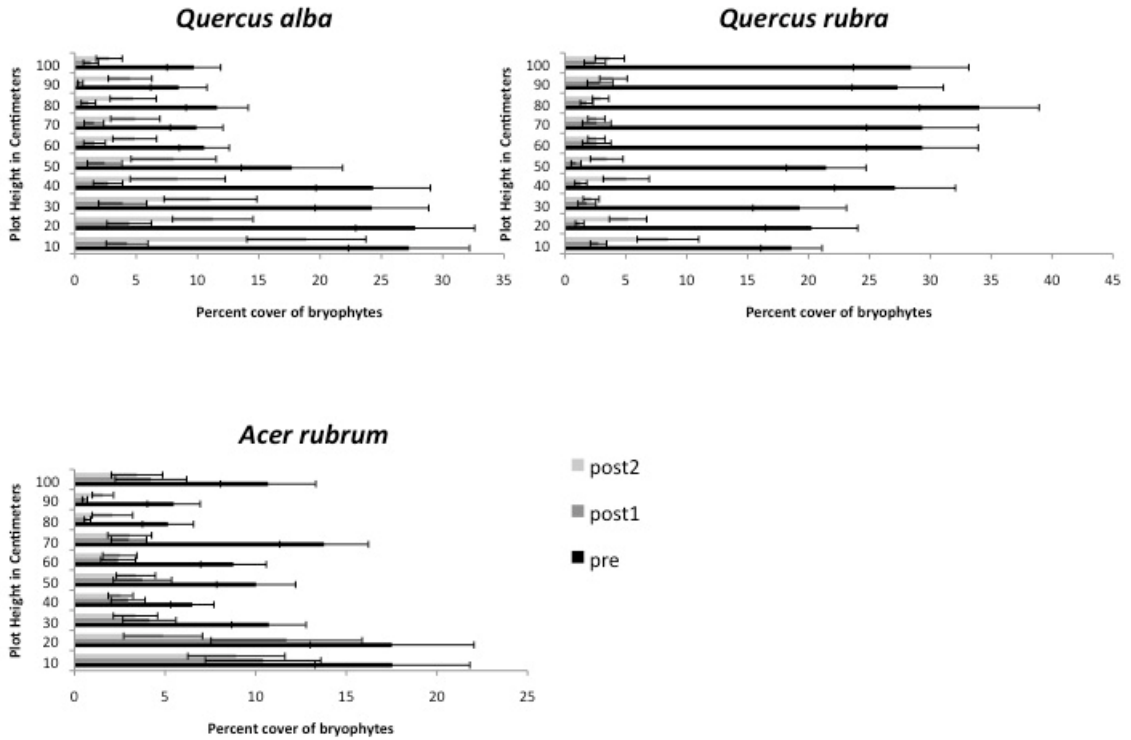


Figure 3.2. Average percent cover of epiphytic bryophytes in 10 x 10cm quadrats on the lower 1m of tree trunk on ten individuals of each of three tree species (*Acer rubrum*, *Quercus alba*, and *Quercus rubra*) in the Homer L. Johnston Wildlife Management Area study site of the Ouachita National Forest, LeFlore County, Oklahoma. There are 3 sampling times shown, pre=2012 prefire, post1= 2012 post fire, and post2=2013 post fire, with 95% confidence intervals shown. Confidence intervals were calculated on the square root transformed data then back transformed.

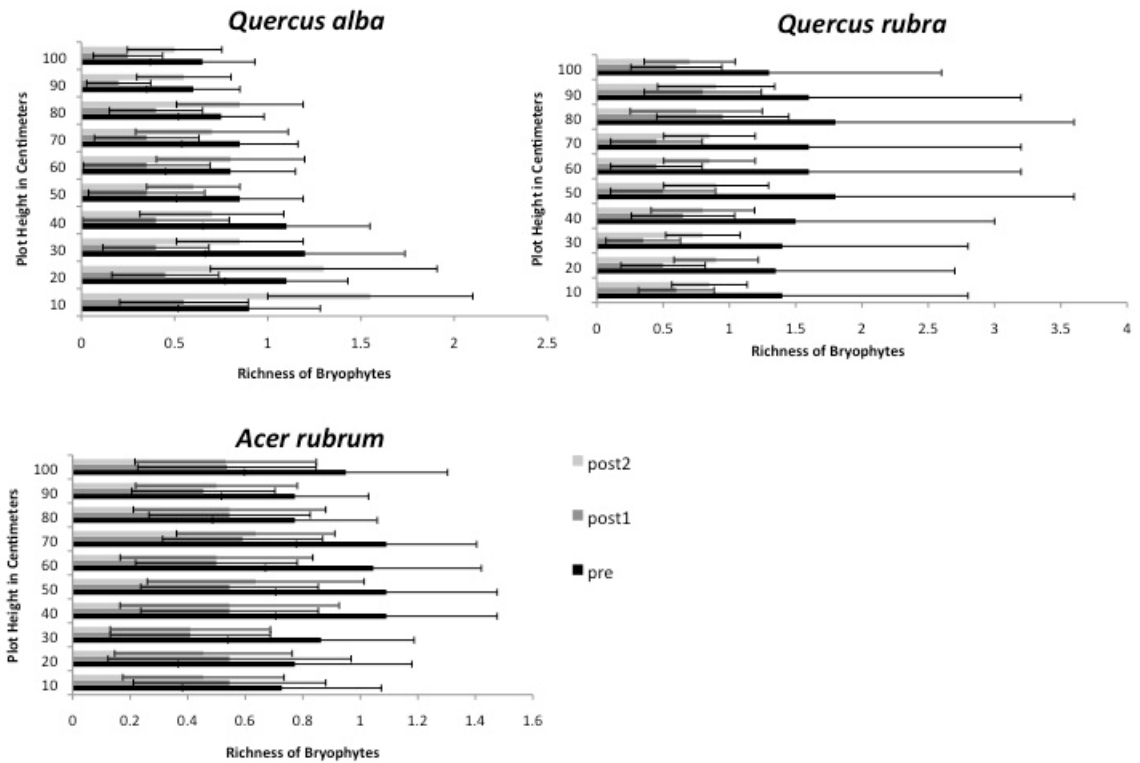


Figure 3.3. Average species richness of epiphytic bryophytes in 10 x 10cm quadrats every 10 cm on the lower 1m of tree trunk on ten individuals each of three tree species (*Acer rubrum*, *Quercus alba*, and *Quercus rubra*) in the Homer L. Johnston WMA study site of the Ouachita National Forest, LeFlore County, Oklahoma. There are 3 sampling times shown, pre=2012 prefire, post1=2012 post fire, and post2=2013 post fire, with 95% confidence intervals shown.

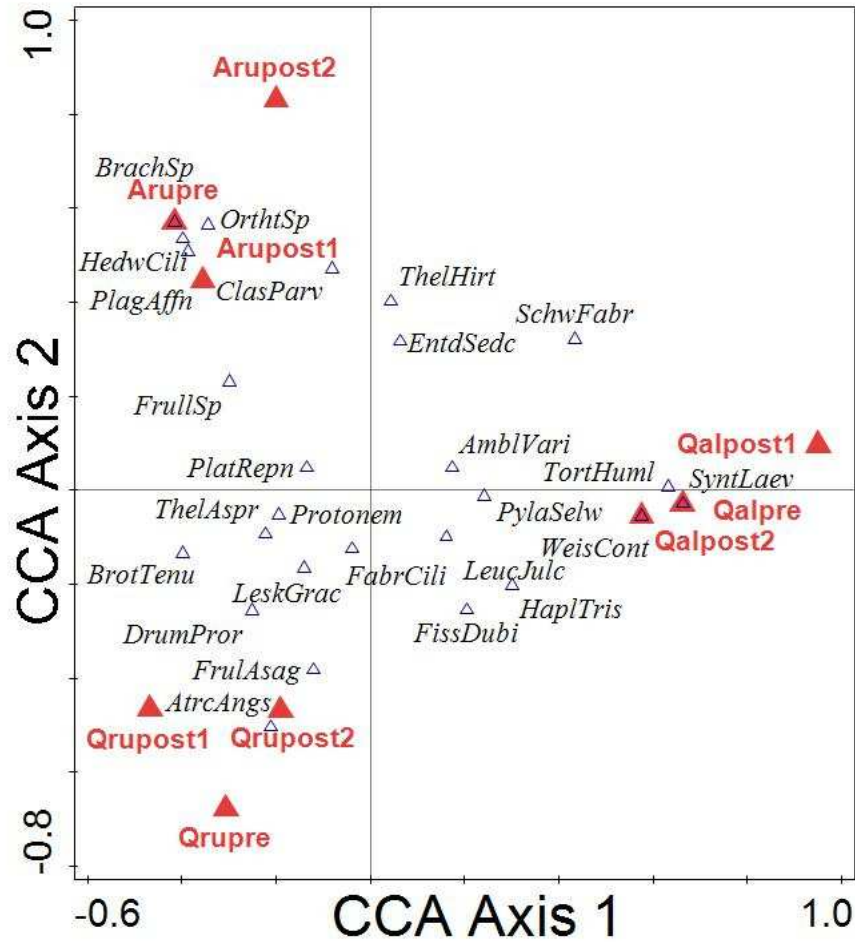


Figure 3.4. Canonical correspondence analysis (CCA) biplot showing centroids for relative species abundance and phorophyte host species by sampling time. Aru = *Acer rubrum*, Qru = *Quercus rubra*, Qal = *Quercus alba*, pre= pre fire samples, post1= 2012 post fire samples, post2= 2013 post fire samples. Labels for species codes are provided in Table 3.1. Significance of the ordination axes was calculated using a Monte Carlo permutation test (for the 1<sup>st</sup> axis  $p= 0.0001$ , for all axes combined  $p= 0.0002$ ).

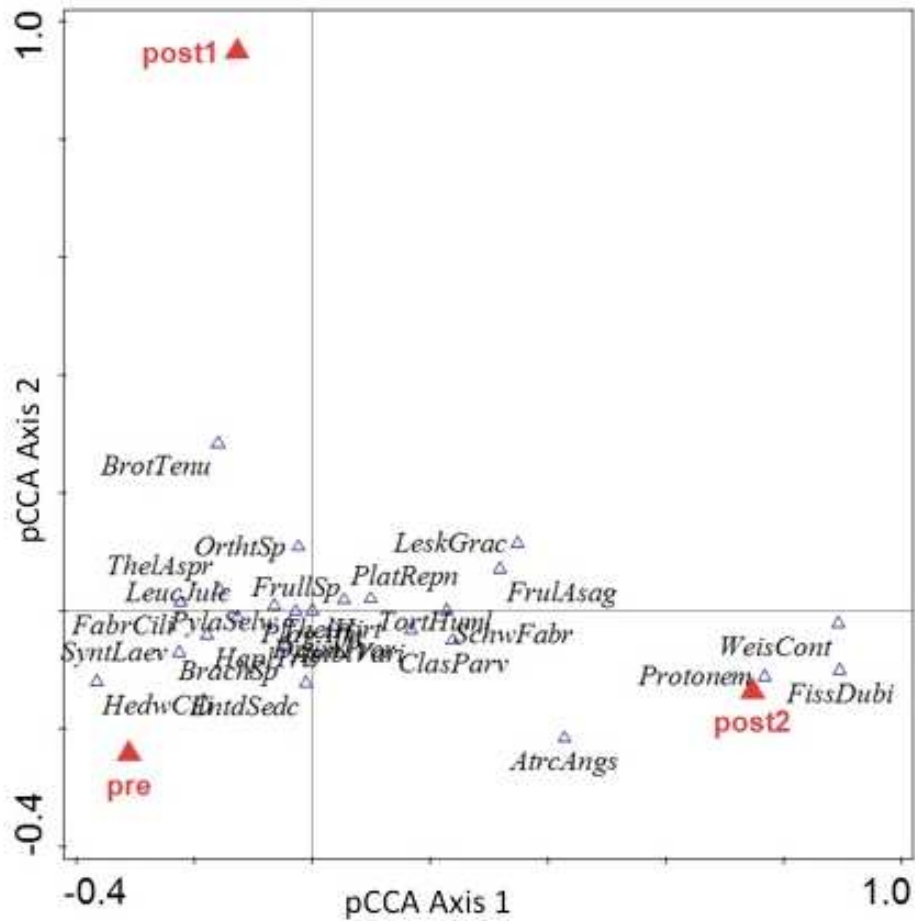


Figure 3.5. Partial canonical correspondence analysis (pCCA) biplot showing centroids for sampling times, for all phorophyte species combined. I used individual tree ID as the sole covariable. Pre= pre fire samples, post1= 2012 post fire samples, post2= 2013 post fire samples. Labels for species codes are provided in Table 3.1. Significance of the ordination axes was calculated using a Monte Carlo permutation test (for the 1<sup>st</sup> axis  $p=0.0003$ , for all axes combined  $p=0.0059$ ).

## CHAPTER IV

### THE BRYOPHYTE FLORA OF THE HOMER L. JOHNSTON WILDLIFE MANAGEMENT AREA AND WINDING STAIR MOUNTAIN NATIONAL RECREATION AREA OF THE OUACHITA NATIONAL FOREST, LEFLORE COUNTY, OKLAHOMA

#### ABSTRACT

The 6047 ha study site is a portion of the Homer L. Johnston Wildlife Management Area in the Ouachita National Forest. The area is located in LeFlore County, Oklahoma, and is jointly managed by the National Forest Service and the Oklahoma Department of Wildlife Conservation. I made collections of bryophytes from spring 2012 to early spring 2014. I found 50 families and 74 genera represented by 87 moss, one hornwort, and 29 liverwort species. This includes 22 state records and 37 county records. This large number (18%) of species newly reported for the state of Oklahoma demonstrates the need for more bryophyte surveys to be conducted in this understudied region.

KEY WORDS: Bryophytes, liverworts, mosses, Oklahoma, Ouachita National Forest, state records

#### INTRODUCTION

The Ouachita Mountains of southeastern Oklahoma contain many endemic or disjunct vertebrate and vascular plant species (e.g., *Plethodon ouachitae*, *Amorpha ouachitaensis*, and *Solidago ouachitaensis*). Other groups of organisms, such as bryophytes, are poorly studied within southeastern Oklahoma. It is likely that there are many interesting bryophyte taxa waiting to be discovered in the Ouachita Mountains. The purpose of this study is to document the bryophyte flora of a portion of the Ouachita National Forest as a baseline inventory to expand our knowledge of the current bryophyte flora of Oklahoma, and to be a tool with which we can document any future floristic changes.

## STUDY SITE

The study site is part of the Ouachita National Forest and is jointly managed with the Oklahoma Division of Wildlife Conservation, with the majority being a portion of the Homer L. Johnston Wildlife Management Area (WMA). The highest elevation southern portion of the study site is part of the Winding Stair Mountain National Recreation Area (WSMNRA). The WMA portion of the study area is managed for timber harvest, wildlife, and outdoor recreation, while the WSMNRA is managed using a “progressive ecosystem management policy” which focuses on maintaining biodiversity and ecosystem services (USDA Forest Service 2004b). The study area has been managed with prescribed fire since at least the early 1900s, with annual burning being common in the early part of the 20<sup>th</sup> century (Strausberg and Hough 1997). The study site is currently primarily managed with prescribed burning and selective timber harvest (USDA Forest Service 2004a). The area was burned by prescribed fire during the spring of 2012.

The Ouachita Mountains represent a unique geomorphic province within Oklahoma (Curtis and Ham 1979). This study area is entirely contained within the Ouachita Mountains province. The site lies along the north slope of Winding Stair Mountain and contains a portion of the Winding Stair Mountain National Recreation Area. The study site is a single 6047ha parcel that is bordered by Forest Service Rd. 6014 to the east, Oklahoma State Rt. 1 to the south, Forest Service Rd. 6010 to the west, and Holson Valley Road to the north; the latitude ranges from 34.8110 to 34.7251 and longitude ranges from -94.8797 to -94.6938. There are a few small private inholdings, in the NW corner of the study area, with one additional small inholding in the SE portion of the study area. All private inholdings were excluded from the study. The study site contains several 1<sup>st</sup> and 2<sup>nd</sup> order streams and two 3<sup>rd</sup> order streams, the largest of which is Cedar Creek. The study site is underlain with Pennsylvanian sandstones and shales (Hatcher et al. 1989), with the sandstone forming outcrops and cliffs near the top of Winding Stair Mountain and along several of the 1<sup>st</sup> order streams. Elevation ranges from 201m above sea level where Stark Hollow leaves the NW portion of the study area to 684m along a portion of OK Rt. 1 at the top of Winding Stair Mountain.

The study site is mostly forested (>90%). The northern portions of the study area consist mostly of gently rolling slopes and flat bottomlands dominated by *Pinus echinata* away from the streams and *Quercus stellata* closer to the streams. The elevation rises steeply to the south where the forest transitions into one with a more mesic northern affinity dominated by *Quercus alba*, *Carya tomentosa*, *Q. rubra*, and *Acer rubrum*. The most interesting and bryologically diverse areas are the higher elevation 1<sup>st</sup> order stream drainages. There are also boulder fields, which are the result of previous mass wasting events in the higher elevation areas of the study area. Surprisingly, bryophytes are nearly absent from these areas.

Areas of high human impact include a number of multiuse horse/hiking trails, unimproved forest service access roads, and the Horsethief Springs Recreation Area. The trails and roads provide higher disturbance areas and increase the bryophyte flora by providing habitat for otherwise un-encountered terricolous (i.e. soil dwelling) ephemeral taxa (i.e. *Fossombronina* sp., *Anthoceros laevis*). The old watering trough at The Horsethief Springs Recreation Area provides a small amount of habitat for calcicolous bryophyte taxa on the cement mortar of the structure. There are several (~12) wildlife food plots along the gravel USFS roads in the northern portion of the study site. There are several small anthropogenic ponds, which were created as wildlife habitat.



## METHODS

I systematically collected bryophytes between Spring 2012 and early spring 2014. I made trips during all seasons. Google earth imagery (Google Inc. 2013) and topographic GIS layers using ArcMap 10.0 (ESRI 2011) were used to insure that all representative habitats were visited. Habitat information, substrate, and geographic coordinates for each voucher specimen were recorded in the field. Specimens are deposited in the Oklahoma State University Herbarium (OKLA) with duplicates of some taxa deposited in the Morehead State University Herbarium (MDKY). I conducted a thorough search of published literature to determine state and county records (Sharp 1929, Little 1936, Bird 1960, Mahler and Mahler 1980, Churchill et al. 1981, Talbot and Ireland 1982, Timme and Redfearn 1997, FNA 2007). Collections accessible online at The Missouri Botanical Garden (MO) and The New York Botanical Garden (NY) were searched for additional collections from other collectors. I did not find any from the current study area.

All bryophyte specimens were identified in the lab using compound and dissecting microscopes. Moss specimens were identified using The Flora of North America (FNA) volume 27 (2007) for included taxa, and Crum and Anderson (1981) for groups not included in FNA volume 27. Liverworts and Hornworts were identified using the appropriate volume of The Anthocerotae and Hepaticae of North America East of the Hundredth Meridian (Schuster 1966, Schuster 1969, Schuster 1974, Schuster 1980, Schuster 1992a, Schuster 1992b.). Nomenclature of mosses follows the FNA volume 27 (2007) for included taxa, and Tropicos.org (2014) for taxa that were not included in FNA volume 27. Liverwort and hornwort nomenclature follows Stotler and Crandall-Stotler (1977), except *Frullania appalachiana* and *F. ericoides*, which follow Schuster (1992b) and *Chiloscyphus profundus*, which follows Engel and Schuster (1984). This bryophyte flora follows the standards set forth by Palmer and Richardson (2012).

## RESULTS AND DISCUSSION

I found 50 families and 74 genera represented by 87 moss, one hornwort, and 29 liverwort species for a total of 117 taxa (Table 4.1; Appendix A). There were no species with more than one infraspecific taxon. Prior to this study there were 194 species of mosses verified for Oklahoma (Mahler and Mahler 1980, Churchill et al. 1981, Talbot and Ireland 1982). Also, prior to this study there were 43 species of liverworts and 2 species of hornworts known from Oklahoma (Sharp 1929, Little 1936, Bird 1960, Talbot and Ireland 1982, Timme and Redfearn 1997). This study includes 22 state records and 37 county records. Nineteen percent of the species found in this flora are newly reported for the state. This study increases the known bryophyte flora of Oklahoma to 206 species of mosses, and 56 species of liverworts. This highlights the need for further biodiversity inventories of bryophytes and other understudied organism groups.

The most common genera were *Frullania* with 6 species (5%), *Fissidens*, and *Brachythecium* with 5 species each (4%). The most common species of bryophyte was the moss *Platygyrium repens*. There was little coarse woody debris in the study area, thus several epixylic species of bryophytes that would be expected to occur there were rare or absent. The abundance

status of individual bryophyte species was not recorded. There were no exotic species found. All species found are considered native to Oklahoma. The most interesting taxa found were *Plagiochila dubia*, which is typically a subtropical coastal plain species, and *Frullania applachiana*, which was previously thought to be restricted to the region of the south central Appalachian Mountains.

#### ACKNOWLEDGEMENTS

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TABLE

Table 4.1. The taxonomic distribution of the bryophyte flora of a portion of the Ouachita National Forest in Oklahoma. There were no species with more than one infraspecific taxon found.

	Families	Genera	Species
Anthocerothyta	1	1	1
Marchantiophyta	16	19	29
Bryophyta	33	54	87

FIGURE

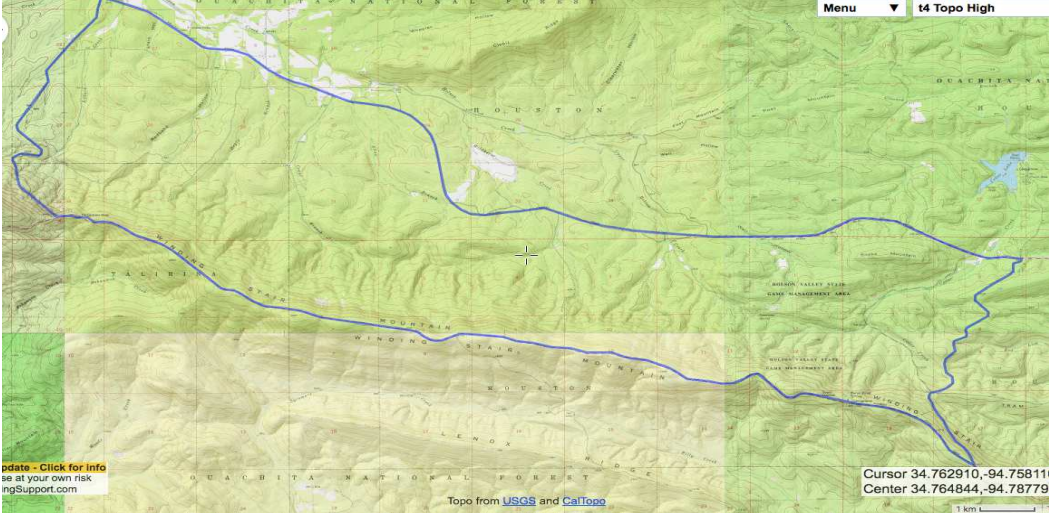


Figure 4.1. Map showing the study area outlined on the north slope of Winding Stair Mountain within the Ouachita National Forest.

## APPENDIX

**APPENDIX A.** Catalogue of bryophyte specimens collected from the Homer L. Johnston Wildlife Management Area and Winding Stair National Recreation Area of the Ouachita National Forest, LeFlore County, Oklahoma. The species and genera are listed alphabetically by family. Family ordering of the Marchantiophyta follows Crandall-Stotler et al. (2009). Family ordering for the Bryophyta follows Goffinet et al. (2009). Some difficult specimens were annotated by Allen Risk (Morehead State University Department of Biology and Chemistry) and Paul Davison (University of North Alabama Department of Biology). Taxa newly reported for the state of Oklahoma are preceded by a double asterisk (\*\*). Taxa known to occur in Oklahoma, but newly reported for LeFlore County are preceded by a single asterisk (\*). All collection numbers are those of J.C. Richardson.

### ANTHOCEROPHYTA

#### **Anthocerotaceae**

- \* *Anthoceros laevis* L. 2259

### MARCHANTIOPHYTA

#### **Aytoniaceae**

- \* *Asterella tenella* (L.) P. Beauv. 2366
- \* *Reboulia hemisphaerica* (L.) Raddi 2229, 2272

#### **Fossombroniaceae**

*Fossombronia* sp. 2367

#### **Pallaviciniaceae**

- \* *Pallavicinia lyellii* (Lindb.) Gray 2210

#### **Metzgeriaceae**

- Metzgeria furcata* (L.) Dum. 2258, 2362, 2301, 2253
- \*\* *Metzgeria myriopoda* Lindb. 2170

#### **Aneuraceae**

\*\* *Riccardia chamedryfolia* (With.) Grolle 2265

\*\* *Riccardia multifida* (L.) S. F. Gray 2260

### **Porellaceae**

*Porella pinnata* L. 2066, 2113, 2137, 2357, 2359

*Porella platyphylla* (L.) Pfeiff 2087

### **Radulaceae**

\*\* *Radula complanata* (L.) Dum 2335, 2358

### **Frullaniaceae**

\*\* *Frullania applachiana* R.M. Schust. 2353, 2205, 2237, 2394

*Frullania tamarisci* subsp. *asagrayana* (Mont.) Hatt. 2085

\*\* *Frullania brittoniae* Evans 2350

*Frullania eboracensis* Gott. 2085, 2110

\* *Frullania ericoides* (Nees ex Mart.) Mont. 2352, 2209, 2233

\* *Frullania inflata* Gott. 2171, 2330, 2331, 2353, 2361, 2180, 2169

\*\* *Frullania kunzei* Lehm. and Lindenb. 2300, 2351, 2249

### **Lejeuneaceae**

\* *Leucolejeunea clypeata* (Schwein) A. Evans 2112, 2172, 2134, 2138, 2182, 2223

*Cololejeunea biddlecomiae* (Aust.) Evans 2190, 2263, 2256, 2275

### **Lophocoleaceae**

\*\* *Chiloscyphus profundus* (Nees) Eng. and Schust. 2073, 2192, 2347, 2181, 2200

### **Plagiochilaceae**

\*\* *Plagiochila dubia* Lind. & Gott. 2276

### **Cephaloziaceae**

\*\* *Cephalozia bicuspidata* (L.) Dum. 2069

### **Cephaloziellaceae**

\*\* *Cephaloziella hyalina* Douin 2198

### **Scapaniaceae**

\* *Diplophyllum apiculatum* (Evans) Steph. 2194, 2262

\* *Scapania nemorosa* (L.) Dum. 2090

### **Calypogeiaceae**

- \*\* *Calypogeia fissa* (L.) Raddi 2306  
*Calypogeia muelleriana* (Schiffn.) K. Muell. 2079
- Jungermanniaceae**
- \*\* *Jungermannia atrovirens* Dum. 2134.1
- BRYOPHYTA**
- Sphagnaceae**
- Sphagnum lescurii* Sull. 2280
- Polytrichaceae**
- Atrichum angustatum* (Brid.) Bruch and Schimp. 2111, 2318, 2116, 2278
- \* *Atrichum altecristatum* (Ren. and Card.) Smyth and Smyth 2213, 2214
- \* *Polytrichum commune* Hedw. 2228
- Polytrichastrum ohioense* (Ren. and Card.) G.L. Smith 2245
- Diphysciaceae**
- Diphyscium foliosum* (Hedw.) D. Mohr 2193
- Funariaceae**
- Unidentified Funariaceae 2369
- Drummondiaceae**
- Drummondia prorepens* (Hedw.) E. G. Britt 2080, 2075
- Grimmiaceae**
- Grimmia pilifera* P. Beauv. 2322, 2255, 2303, 2130, 2175
- \* *Schistidium agassizii* Sull & Lesq. 2328, 2336
- \* *Schistidium apocarpum* (Hedw.) Bruch. & Schimp. 2286, 2323, 2281
- \*\* *Schistidium dupretii* (Ther.) W.A. Weber 2342
- \* *Schistidium rivulare* (Brid.) Podp. 2288
- Ptychomitriaceae**
- Ptychomitrium incurvum* (Schwägr.) Spruce 2241, 2243, 2313
- Archidiaceae**
- \*\* *Archidium alternifolium* (Dickson ex Hedwig) 2368
- Fissidentaceae**
- \* *Fissidens bryoides* Hedw. 2132, 2179, 2186, 2304



- \* *Fissidens bushii* (Card. and Ther.) Card. and Ther. 2244  
*Fissidens dubius* P. Beauv. 2078, 2277, 2325
- \* *Fissidens subbasilaris* Hedw. 2311  
*Fissidens taxifolius* Hedw. 2119, 2125

#### **Ditrichaceae**

*Ditrichum pallidum* (Hedw.) Hampe 2084, 2346

#### **Dicranaceae**

- Dicranella heteromalla* (Hedw.) Schimp. 2247, 2338, 2345  
*Dicranum condensatum* Hedw. 2197, 2250, 2354
- \* *Dicranum flagellare* Hedw. 2355  
*Dicranum montanum* Hedw. 2166, 2349, 2303, 2314, 2319  
*Dicranum scoparium* Hedw. 2246, 2251, 2296

#### **Leucobryaceae**

*Leucobryum glaucum* (Hedw.) Angstr. 2195

#### **Pottiaceae**

- \* *Molendoa sendtneriana* (Bruch & Schimp.) Limpr. 2243  
*Syntrichia laevipila* Brid. 2285  
*Tortella humilis* (Hedw.) Jenn 2284  
*Weissia controversa* Hedw. 2183, 2220

#### **Mniaceae**

- \* *Plagiomnium affine* (Blandow ex Funck) T.J. Kop. 2072, 2089, 2189, 2234
- \* *Plagiomnium ciliare* (Mull. Hal.) T.J. Kop. 2356  
*Plagiomnium cuspidatum* (Hedw.) Kop. 2199, 2290
- \* *Pohlia wahlenbergii* (Web. and Mohr) Andr. 2188
- \* *Rhizomnium punctatum* (Hedw.) T.J. Kop. 2279

#### **Bartramiaceae**

*Bartramia pomiformis* Hedw. 2115, 2261

#### **Orthotrichaceae**

- Orthotrichum ohioense* Sull. and Lesq. 2207
- \* *Orthotrichum pumilum* Sw. 2204

- \* *Orthotrichum strangulatum* P. Beauv. 2289
- Ulota hutchinsiae* (Sm.) Hamm. 2299, 2310

#### **Hedwigiaceae**

*Hedwigia ciliata* (Hedw.) P. Beauv. 2240, 2333

#### **Aulacomniaceae**

*Aulacomnium heterostichum* (Hedw.) Bruch and Schimp. 2118, 2128, 2269, 2141

#### **Fontinalaceae**

- \* *Fontinalis flaccida* Ren. and Card. 2071
- \* *Fontinalis missourica* Card. 2332
- \* *Fontinalis sullivantii* Lindb. 2363

#### **Climaciaceae**

*Climacium americanum* Brid. 2196

#### **Amblystegiaceae**

- \* *Amblystegium varium* (Hedw.) Lindb. 2142, 2282
- Campylium chrysophyllum* (Brid.) J. Lange 2317
- Campylium hispidulum* (Brid.) Mitt. 2221, 2226, 2309
- \*\* *Hygroamblystegium fluviatile* (Hedw.) Loeske. 2131, 2295
- Hygroamblystegium tenax* (Hedw.) Jenn. 2266, 2365

#### **Leskeaceae**

- Leskea gracilescens* Hedw. 2074, 2083, 2287
- \*\* *Leskea obscura* Hedw. 2211, 2212
- \*\* *Platylorella lescurii* (Sull.) A.L. Andrews 2124, 2140, 2187, 2327

#### **Thuidiaceae**

*Thuidium delicatulum* (Hedw.) BSG 2307, 2173, 2268

#### **Brachytheciaceae**

- Brachythecium acuminatum* (Hedw.) Aust. 2345, 2339
- \* *Brachythecium oxycladon* (Brid.) Jaeg and Sauerb. 2324, 2230, 2238.1
- \* *Brachythecium plumosum* (Hedw.) BSG 2121
- \*\* *Brachythecium rotaeantum* De Not. 2308
- Brachythecium rutabulum* (Hedw.) Schimp. 2364

- \* *Bryhnia graminicolor* (Brid.) Grout 2129
- \*\* *Bryhnia novae-angliae* (Sull & Lesq. ex Sull) Grout 2120
- Bryoandersonia illecebra* (Hedw.) H. Rob. 2184, 2360, 2067, 2107, 2117
- Clasmatodon parvulus* (Hampe) Hook. and Wils. ex Sull. 2232, 2208, 2202
- Eurhynchium pulchellum* (Hedw.) Jenn. 2238, 2242
- \*\* *Steerecleus serrulatus* (Hedw.) H. Rob 2176, 2218, 2321, 2136, 2344

#### **Fabroniaceae**

- \* *Fabronia ciliaris* (Brid.) Brid. 2191, 2337

#### **Hypnaceae**

- Homomallium adnatum* (Hedw.) Broth. 2348, 2122, 2135, 2224, 2257
- \* *Platydicta subtile* (Hedw.) Crum 2293
- \* *Taxiphyllum deplanatum* (Bruch and Schimp. ex Sull) Fl. 2091
- Taxiphyllum taxirameum* (Mitt.) Fleisch. 2315

#### **Hylocomiaceae**

- Ctenidium molluscum* (Hedw.) Mitt. 2108, 2114, 2271, 2316

#### **Entodontaceae**

- Entodon cladorrhizans* (Hedw.) C. Mull. 2264, 2248
- \* *Entodon macropodus* (Hedw.) C.M. 2270
- Entodon seductrix* (Hedw.) Mull. Hall. 2254, 2267, 2320, 2215, 2217

#### **Pylaisiadelphaceae**

- \*\* *Brotherella tenuirostris* (Bruch. and Schimp. ex Sull.) Fl. 2225
- Platygyrium repens* (Brid.) BSG2076, 2297, 2174, 2185, 2201, 2203, 2235, 2239, 2252

#### **Sematophyllaceae**

- Sematophyllum demissum* (Wils.) Mitt. 2068, 2123, 2168, 2298, 2302, 2329

#### **Leucodontaceae**

- Leucodon julaceus* (Hedw.) Sull. 2206, 2291, 2088

#### **Anomodontaceae**

- Anomodon attenuatus* (Hedw.) Hub. 2109, 2222, 2177, 2219, 2212
- \* *Anomodon rostratus* (Hedw.) Schimp. 2273, 2274, 2294

*Anomodon tristis* (Ces.) Sull. and Lesq. 2178, 2236, 2077

\* *Schwetschkeopsis fabronia* (Schwaegr.) Broth. 2231, 2283, 2292

**Theliaceae**

*Thelia asprella* Sull. 2082

*Thelia hirtella* (Hedw.) Sull 2081

*Thelia lescurii* Sull. 2070, 2312

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