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The Effects of Fire on *Lycopodium digitatum* strobili

Stephanie I. Vogel*, Bryan T. Piatkowski*, Alton C. Dooley, Jr.**, and DorothyBelle Poli *

ABSTRACT

Lycopodium is a commonly ignored plant in the forest understory and in fire ecological studies in spite of the well-documented explosive nature of their spores. Therefore, in order to understand how fire may affect *Lycopodium*, burn studies were carried out on varying sporophyte life cycle stages. Strobili exhibited varying degrees of sporophyll opening and closing in response to the burning and age was directly correlated to the length of the burn. Spores that were burned and plated on axenic media showed a decrease in germination time, from 9 months to 3 weeks, after being subjected to fire. Beyond providing baseline understanding of the effects of fire on *Lycopodium* and its reproduction, these studies also provide clues about the possible role of fire in Paleozoic forests.

INTRODUCTION

One of the most seen and memorable uses of lycopod spores is in the movie "The Wizard of Oz" (MGM 1939) during the famous scene when the Wicked Witch, after threatening to get Dorothy and her little dog too, disappears into a ball of orange-red dust and fire. The cloud of dust is dyed *Lycopodium* spores. However, the knowledge that modern lycopod spores were flammable was first noted in the Victorian Era. Spores were referred to as "vegetable sulfur" because of their explosive capabilities, commonly used in fireworks, but during the same time period the spores were also used to coat pills for easier swallowing and for dusting babies (like a talc powder) (Orton 1896).

Today, *Lycopodium* spores are known to be highly flammable (see the Material Safety Data Sheet), as is typical of airborne organic particulates (Proust 1993, van der Wel 1993, Krause and Kasch 1996). For example, when Krause and Kasch (1996) examined different kinds of organic dust, concentration particles, and flow velocity, *Lycopodium* powder had a greater burning velocity than wheat flour or cornstarch. *Lycopodium* spores (10 µm) were smaller than either of the other two materials tested (30 µm) but the caloric value was approximately 1.5 times higher (30,554 kJ/kg) which resulted in the smallest approximate activation energy necessary of the three organics. As a result, *Lycopodium* powder has the fastest burn reaction (Krause and Kasch 1996) and ignites at lower temperatures than other organic standards (Mintz 1991). Additionally, as spore concentrations increase, flammability decreases showing there are upper limits to ignition (Powell 1962). Today many chemistry departments use *Lycopodium* spores to demonstrate the power of organic burns (for an example see North Carolina State University Lecture Demonstrations).

While the burn properties of *Lycopodium* spores have been well studied, very little consideration has been given to the effects of burning on *Lycopodium* plants themselves. *Lycopodium* and other lycopods are a relatively minor component of modern floras; the group was much more abundant and

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diverse during the late Paleozoic Era, and included numerous arborescent forms (Frankenberg and Eggert 1969; Thomas and Watson 1976; Stewart 1983). As the peak of lycopod diversity overlaps with the origin and early diversification of fire-adapted gymnosperms, further examination of fire's impact on extinct lycopods may shed some further light on the origins of fire ecology.

Today, fire has a strong role in habitat ecology. It can not only modify wildlife conditions and alter the number of trees susceptible to disease and insects, but it can also influence vegetation types and ages and it impacts the nutrient cycles available to plants (Kilgore 1973). Modern species use fire to induce germination of thick-skinned seeds (e.g. *Ceanothus*, *Arctostaphylos*, and *Rhus*) (Daubenmire 1959; Kauffman and Martin 1991). In other plants, like *Pinus* sp. fire induces rapid growth and development (Daubenmire 1959; Kauffman 1990; Perry 1991) while others have fire-resistant foliage and bark (Philpot 1970; Nord and Green 1977). Given the explosive nature of lycopod spores and that lycopod diversity peaked simultaneously with the origins of gymnosperm fire ecology, the presence of fire adaptations in lycopods might be expected.

MATERIALS AND METHODS

Developmental Stage Determination

Whole plants of *Lycopodium digitatum* (Dill) [pseudoname *Lycopodium flabelliforme* (Fern.) Blanch] were collected from Wilderness Adventures at Eagle Landing in New Castle, Virginia, from September to October 2010. Plants were examined and photographed under a Leica EZ4D microscope with a built-in camera before they were burned to determine different life cycle stages. Young stage strobili had green unopened sporophylls (leaves) that were held tightly together in a cone shape with no spores exposed or the sporophylls were slightly pulled back, revealing small numbers of spores. The stems had a dark green color. Mature stage strobili had sporophylls pulled back, exposing intact or open spore capsules with large numbers of spores. Mature stems still have the dark green color but the tips of the sporophylls were turning brown. Old stage plants had the strobili sporophylls completely opened, intact spore capsules were absent (because they have fully opened and the spores have been released), and the stems had a yellow-green to brown color.

Burning Experiments

After determining strobili life stage, the strobili tips were burned. The stems were placed in forceps, with the strobili untouched. The strobili were then passed through the flame of a cigarette lighter. Once the strobili tip caught fire, the flame was removed and the plant was allowed to burn until the fire went out. Life stage and the burn distance were noted. Burned plants were examined and photographed under the Leica EZ4D microscope. This process was repeated on 5 plants at each life stage described (10 trials for each life stage).

Culture

After burning, the spores were plated on lycopodium culture, with or without the inclusion of a mycorrhizal component, as described by Whittier et al. (2005). After spores were shaken onto the plates, the plates were individually wrapped in aluminum foil and stored in a drawer for darkness as suggested by Whittier et al. (2005). Cultures were inspected for growth weekly underneath the dissection Leica EZ4D microscope and pictures were taken. Once growth was found, the spores were kept in darkness for an additional week and then transferred to the growth culture chamber as described by Whittier et al. (2005).

RESULTS

Strobili Burn Lengths: Patterns by Life Stage

After setting the tip of each strobilus on fire and letting it burn out naturally, it was clear that the life stage correlates to the total charred length (Table 1). Young strobili were staged based on having closed strobili that were not actively releasing spores. The young strobili burned an average length of 0.9 ±

Table 1: The burn distance of each life stage strobili from *Lycopodium digitatum*. Each distance represents at least 10 plant trials ± standard error.

Developmental Stage	Burn Distance from Tip
Young	0.9 ± 0.1 cm
Early Mature	1.6 ± 0.2 cm
Mature	2.7 ± 0.1 cm
Old	5.0 ± 0.1 cm
Re-burn and Dried of Mature	4.8 ± 0.0 cm

0.1 cm; early mature strobili with open sporophylls and intact sporangia burned a distance of 1.6 ± 0.2 cm. Mature strobili, containing open sporophylls, numerous spores present, but lacking obviously intact sporangia, burned the greatest length at 2.7 ± 0.1 cm. Completely absent of spores, the old strobili burned down completely to the sporophyte at approximately 5.0 ± 0.1cm in length. Each set of measurements resulted from a mean of at least 10 strobili burns of each life stage from 5 different plants ± standard error of burn total distance calculations.

Observations on Strobilus Appearance after Burning

After strobili were burned the sporophylls reacted differently depending upon life stage. Young stage strobili had tightly closed sporophylls prior to burning but post-burn the sporophylls opened slightly in the areas most severely burned, but the end edge of the burn had sporophylls that remained open, even if slightly burned, to reveal fresh spores. The sporophylls directly under the burn edge remained tightly closed. Early mature stage strobili show a different sporophyll pattern prior to burning; sporophylls were open and sporangia were visible but not actively releasing spores. Previously opened sporophylls burned from the apex of the sporophyll inward; the most severely burned sporophylls closed tightly during burning but those on the edge of the burn remained open. Exposed sporangia that were still exposed post-burn, experienced slight charring but began releasing spores; this is shown by the splitting of the sporangium and individual spores. If an early mature strobilus sporophyll did not experience direct burning it did not change its position; non-charred sporangia did not release spores. Mature strobili were represented by the absence of intact sporangia and the presence of numerous spores. Mature stage strobili showed similar reactions to burning as the early mature strobili; the most damaged spores were retained by sporophyll closure while spores found at the edge of the burn were still released. Unlike the other three stages, the old stage strobili burned the entire distance of the reproductive organ and the burned sporophylls did not close as tightly; no spores were present prior to burning trials.

Tissue Culture Experiments

It has been suggested that growing *Lycopodium* spores in the dark will decrease growth time from 4-5 months to as little as 3 weeks, depending on species (Whittier et al. 2005). Therefore, once strobili were burned, spores from each life stage were placed in tissue culture as described by Whittier et al. (2005). Of early mature spores plated on the mycorrhizal supportive or non-supportive culture media post-burn, 30% germinated in 3 weeks when placed in the dark, a total of 35% germinated in one month. Early mature spores were the only ones to develop after a burn.

DISCUSSION

While *Lycopodium* spores are highly flammable, the plant itself is not. Even the strobilus is resistant to ignition until it has actually opened. Spores appear to remain viable even after the strobilus containing them has burned. Moreover, our field observations suggest that plants seem to stagger spore release, so that large numbers of strobili may not typically be open simultaneously. The fire resistance of *Lycopodium* is most likely due to presence of lignin and possibly other chemical or physical characteristics. Comparative biochemical studies of lignin indicate that modern *Lycopodium* has a gymnospermous-type lignin while other lycopods produce more advanced lignin precursor compounds (Towers and Maass 1964; White and Towers 1966;

White et al. 1967; Logan and Thomas 1985).

Upon initial burning experiments, the lengths that different age plants burned were statistically different, suggesting that development and the ability to burn are related. It appears that youngest plants with the most immature spores were the most fire resistant but as the plant aged, the plant burned to longer lengths. Additional studies should demonstrate whether the higher fire resistance of younger plants is due to greater hydration levels or some ontogenetic physiological change.

Lycopodium has proven to be a difficult plant to culture. A long series of experiments (Whittier 1977, 1981, 1998; Whittier and Webster 1986; Peterson and Whittier 1990; Maden et al. 1986; Whittier et al. 2005) greatly expanded the understanding of germination requirements for *Lycopodium*. Through these studies germination times were reduced from seven years to three weeks through increased understanding of basic axenic culture nutrients and possible mycorrhizal symbionts. Different species of *Lycopodium* show substantially different germination times under given conditions. According to Whittier (1998) *L. deuterodensum* germinates in 3 weeks in the dark in an axenic culture, while *L. clavatum* germinates in 3 months and *L. digitatum* germinates in 9 months under these conditions. All three taxa have substantially longer germination times (> 1 year) when exposed to light.

After being burned, germination times for *L. digitatum* spores in this experiment were reduced from 9 months to as little as 3-4 weeks. This suggests that *Lycopodium* may have a developmental response to fire similar to that seen in some gymnosperms (Daubenmire 1959; Kauffman 1990; Perry 1991).

Implications for the evolution of lycopods

Lycopodium appear to have several fire-related adaptations, including general fire resistance of the sporophylls, fire-induced responses in strobili, and increased spore development rates after burning. Given these adaptations, it is perhaps surprising that modern *Lycopodium* does not seem to have any particular fire-related associations, either in environment or associated species, and it is not generally considered to be important in fire ecology. This suggests an earlier evolutionary origin for fire resistance, rather than an adaptation specific to *Lycopodium*.

While all modern lycopods are small plants, this has not been true through their entire history, with some Carboniferous lycopods exceeding 30 m in height (Thomas and Watson 1976). Orton (1896) noted that the extinct *Lepidodrendron* produced large quantities of spores, so much so that entire seams of high quality coal are almost entirely made of up of these. With these giant lycopods producing large numbers of potentially explosive spores, fire may have been an important component in Carboniferous terrestrial ecosystems.

The lack of modern arborescent lycopods presents a challenge when attempting to interpret the ecology of fossil forms. The closest living relative to the ancient arborescent lycopods is generally considered to be the quillwort *Isoetes* (Taylor et al. 1983), a highly specialized aquatic form that has a small number of elongate leaves, no strobilus, and which releases its spores below the water. For these reasons we believe that *Isoetes* is a particularly poor ecological model for arborescent lycopods. In contrast, *Lycopodium* releases its spores into the air from a distinct strobilus, so it may provide a superior (if imperfect) model for arborescent lycopods even though it is more phylogenetically distant than is *Isoetes*.

Microspore samples from *Lepidostrobus* have been reported to be between 15-50 µm in width, with the average around 30 µm (Balbach 1966; Taylor and Eggert 1969; Willard 1989a,b; Raine 2008); in contrast, megaspores have been reported to be hundreds of micrometers (Phillips 1979) yet the sporangium-sporophyll unit does appear to be specialized for wind and aquatic dispersal (Dimichele and Phillips 1985). This microspore size is comparable to that of *Lycopodium*, and suggests that *Lepidostobus* spores may have been just as susceptible to ignition (Proust 1993, van der Wel 1993, Krause and Kasch 1996; Cashdollar 2000). A potential contributing factor to the flammability of *Lycopodium* spores appears to be their high oil content (Langer, 1889; Cline, 1939; Tulloch, 1965). Interestingly, this high oil content may result in the spores being hydrophobic and buoyant (Cline, 1938; Balick and Beitel 1989), even though *Lycopodium* is not generally associated with aquatic environments.

Frequent Carboniferous wildfires are suggested by the presence of abundant charcoal during this time (Falcon-Lang et al. 2001). During the Carboniferous atmospheric oxygen content was as high as 35%, which may have contributed to wildfires (Berner et al. 2000; Berner et al., 2003). Lignin concentrations are also thought to have increased during the Carboniferous across multiple lineages, although they subsequently decreased due to an increase in lignin-degrading organisms (Robinson 1990a, b), suggesting an evolutionary response to an increase in wildfires (Wildman et al. 2004; Schwilk and Ackerly 2001).

The wetlands settings in which many arborescent lycopods are found would have provided only limited protection from fires. Fires are a significant phenomenon in modern wetlands environments, especially during droughts but sometimes even during wet seasons (Garren 1943; Rollins et al. 1993). Moreover, the terminal location of the strobili in arborescent lycopods would result in the majority of the spores being released at altitudes of up to 40 meters above the swamp.

Given their potential explosive qualities and the radiation of fire-prone gymnosperms during the Pennsylvanian, how did lycopods reach high levels of success under these conditions? The fire resistance adaptations observed in *Lycopodium* suggests a solution to this problem. These features may have developed in early lycopods both as a means of protecting the plant against fires fueled by gymnosperms, and to protect themselves from the explosive nature of their own spores. With at least some level of fires being unavoidable, it seems that lycopods even incorporated adaptations to take advantage of fires, including the more rapid germination rate of spores after light burning, and in dark conditions that could occur under a layer of newly-formed ash.

This interpretation of lycopod ecology has a number of implications for understanding Carboniferous ecosystems. There is some level of segregation between gymnosperms and lycopods in these deposits, which has been variously attributed to either a preference by lycopods for marshy lowlands and by gymnosperms for drier uplands, or that the fire ecology introduced by gymnosperms precludes the extensive growth of lycopods. In addition, Glasspool (2003) noted that lycopods are among the rarest components of Carboniferous charcoal deposits. The fire resistance of lycopods indicates that they were likely quite capable of thriving in forests with a large percentage of fire-adapted gymnosperms, and their absence from these deposits may rather be due to abiotic environmental factors such as water availability. Alternatively, given the fire resistance of lycopods there is a possible bias against preserving these plants in charcoal deposits, so the scarcity of lycopods in these deposits cannot necessarily be taken as evidence of their absence from the living flora in those ecosystems.

The highly flammable nature of lycopod spores raises another intriguing possibility. There surely must have been occasions when a large number of giant lycopods released their spores simultaneously, perhaps during severe storms with high winds. This could have led to conditions favorable to an explosive firestorm, in which even the lycopods' fire resistance was insufficient to protect them. Rare lycopod charcoal deposits, which have been interpreted as intense crown fires that burned through the trunk and into the ground (Peterson 1998; Falcon-Lang 1998, 1999a, 1999b, 1999c; Falcon-Lang and Scott 2000; Falcon-Lang and Cantrill 2000; Falcon-Lang et al. 2001), may represent such catastrophic lycopod-firestorms.

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Figure 1: Developmental index of strobili development before and after burning of *Lycopodium digitatum.* A) Young, tightly closed strobili and no spores present. B) Young, burned tips. C) Enlarged section of young burned tip showing opened sporophylls at burn edge and releasing spores. D) Early mature, opened sporophylls with intact sporangia. E) Early mature, burned . F) Enlarged section of burned early mature. Can see open leaves with spores about to be released. G) Mature, sporophylls completely open and spores present. H) Mature burned, spores being released. I) Enlarged section of mature burned with charred spores present and being released. J) Old, completely developed without spores present. K) Old, burned completely. No spores present.

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