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Effects of heat and smoke on the germination of six Florida scrub species

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ABSTRACT

Ecological disturbances in ecosystems are often essential for the continued success of many species, acting to increase resource availability and allowing recruitment of new individuals. Fire, a common disturbance, has been shown to influence seed germination in many ecosystems worldwide. The goal of this study was to determine the effects of fire, in the form of heat and smoke, on seed germination of six Florida scrub species (*Chrysopsis highlandsensis*, *Eryngium cuneifolium*, *Hypericum cumulicola*, *Lechea cernua*, *Liatris tenuifolia*, and *Polygonella polygama*). We applied dry heat, wet heat, and aqueous smoke treatments to the target species with control, low, and high levels for each treatment, using a novel approach with individual seeds closely monitored for germination time in microplate wells. Smoke treatments resulted in significantly higher germination percentages for three Florida scrub species, *C. highlandsensis*, *E. cuneifolium*, and *L. cernua*, as well as decreased time to germination for *C. highlandsensis*, but had no effect on the other three species. Dry heat treatments either had no effect or reduced percent germination in all species, while wet heat treatments resulted in virtually no germination. These results show fire effects in Florida scrub do include smoke-stimulated germination in some species, and most of our study species would not have reduced germination due to heat, especially if located within the insulating sands. Determining how fire influences seed germination will allow for more effective management techniques and higher success in propagating native plants.

1. Introduction

Ecological disturbance plays an important role in shaping ecosystems worldwide (Sousa, 1984; White and Pickett, 1985; Hobbs and Huenneke, 1992). Wind, fire, landslides, grazing, and floods are a few of the many ecological disturbances that are important (Hobbs and Huenneke, 1992). As one of the most common disturbances across a variety of ecosystems, fire affects vast areas of land, influences the global distribution of pyrogenic ecosystems, has important feedbacks to vegetation dynamics, and is under partial control by humans (Sousa, 1984; Bond et al., 2002; Certini, 2005; Bowman et al., 2009). Fire is an essential part of landscape function, as fire exclusion often results in increased woody biomass and affects ecosystem processes such as carbon storage and nutrient cycling (Rykiel, 1985; Carrington and Keeley, 1999; Bond and Keeley, 2005; Certini, 2005; Pausas and Keeley, 2009). Additionally, fires open up space for recruitment (Johnstone and Chapin, 2006), cycle nutrients back into the soil (Thonicke et al., 2001), and help maintain appropriate habitat for many plant and animal species (Breininger and Schmalzer, 1990; Menges et al., 2008). Which species are favored by fire depend on their responses to the fire itself and to post-fire conditions.

Species that inhabit pyrogenic ecosystems possess a variety of responses to fire. While some plant species are able to survive fires because of thick bark or strong resprouting (Clarke et al., 2013), species that are killed by fire must recruit new individuals from seed to replenish their populations (Pausas et al., 2004; Slapcinsky et al., 2010). The increase in resource availability and reduced competition make the post-fire habitat particularly suitable for germination (Carrington, 1999; Keeley and Fotheringham, 2000; McConnell and Menges, 2002; Carrington, 2010). Additionally, specific fire cues such as smoke, heat, ash, charcoal, and nutrient pulses can stimulate seed germination in plant species around the world (Drewes et al., 1995; Brown and Van Staden, 1997; Keeley and Fotheringham, 1997; Thomas et al., 2003; Williams et al., 2003; Flematti et al., 2004; Dayamba et al., 2010; Kulkarni et al., 2011). Heat stimulates germination by breaking physical dormancy in seeds, usually in species with hard seed coats that are impermeable to water and require scarification for germination (Thomas et al., 2003; Chou et al., 2012). Smoke is now known to contain karrikins, chemicals that are powerful germination promoters (Flematti et al., 2004; Van Staden et al., 2004; Chiwocha et al., 2009). Other chemicals found in smoke, such as ethylene and nitrogen dioxide, may also stimulate germination (Sutcliffe and Whitehead, 1995; Keeley and Fotheringham, 1998). However, high doses of either heat or smoke

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can result in decreased germination as well (Williams et al., 2003; Moreira et al., 2010). Although both smoke and heat can promote germination, for many species the effects of heat and smoke on germination remain unknown.

The Florida scrub is a pyrogenic shrubland, with fires occurring at various frequencies in different Florida scrub habitats (Menges, 2007), usually ignited by the frequent lightning strikes in the region. This study focused on rosemary scrub, dominated by *Ceratiola ericoides* (Florida rosemary) and *Pinus clausa* (sand pine), and scrubby flatwoods, dominated by a mixture of oaks (*Quercus* spp.), palmettos (*Serenoa repens* and *Sabal etonia*), and other shrubs (Abrahamson et al., 1984). Historically, fire returned more frequently to scrubby flatwoods (5–20 years) than rosemary scrub (15–100 years) (Menges, 1999), which has favored plant communities that differ in their response to fire. Communities with shorter fire return intervals (e.g. scrubby flatwoods) have higher concentrations of resprouting species, fewer obligate seeders, and smaller, more transient gaps (Menges and Kohfeldt, 1995; Clarke et al., 2013; Dee and Menges, 2014). In contrast, rosemary scrub has a longer fire return interval and obligate seeders occur more frequently as the dominant vegetation (rosemary, sand pine) is killed by fire, increasing the persistence of open gaps (Menges et al., 2008). Compared to scrubby flatwoods, rosemary scrub species are often xeric-site specialists, gap-specialists, herbs, endemics, and obligate seeders, recovering from a dormant seed bank post-fire (Menges, 1999; Navarra et al., 2011). Both dominants of the rosemary scrub (rosemary and sand pine) as well as many subordinate species, including some narrow endemics specializing in Florida scrub (e.g. *Dicerandra* spp., *Eryngium cuneifolium*), are obligate seeders. Post-fire seed germination is an advantage for these species to quickly reclaim space in the post-fire ecosystem, which may be cued to germinate directly by fire or indirectly through increased light or altered nutrient availability (Lindon and Menges, 2008; Haller et al., 2012). However, it is not generally known whether the increase in post-fire germination in those species is affected by specific fire cues.

Two previous studies of Florida scrub species have demonstrated fire-stimulated germination in a few species. *Dicerandra christmanii* showed increased germination when treated with charate water as opposed to de-ionized water (Haller et al., 2012). Lindon and Menges (2008) revealed smoke stimulated germination in *Polygala lewtonii* and *Liatris chapmanii*, but not in 18 other species. However, these studies did not examine the effects of smoke and heat in combination, whereas some studies outside of Florida scrub have revealed germination responses not evident from single factors alone (Thomas et al., 2003). The combination of smoke and heat is also a more realistic approximation of field conditions (Williams et al., 2003; Dayamba et al., 2010; Moreira et al., 2010). Additionally, the previous studies in Florida scrub did not consider the potentially different effects of wet and dry heat, which has been shown to have different effects on germination in other studies (e.g. Martin et al., 1975; Baskin and Baskin, 1998). Combining smoke and heat treatments and comparing different methods of heat application is necessary for more accurately understanding germination responses to fire.

This study aimed to determine whether heat and/or smoke stimulated germination in six Florida scrub species. We used a novel setup, following individual seed germination in microplate wells. The specific questions posed by this study were: (1) Do heat, smoke, or a combination of the two stimulate germination in these species? (2) Does the type of heat (wet or dry) affect germination? (3) Do species with different life history strategies (seeders vs. resprouters) respond differently to fire cues?

2. Materials and methods

2.1. Study area

This study was conducted at Archbold Biological Station (ABS) located on the southern end of the Lake Wales Ridge in Highlands County, Florida, in the southeastern United States (Swain, 1998). The climate is subtropical and humid, with annual rainfall exceeding 1200 mm and mean temperatures ranging from 8 °C in winter to 34 °C in the summer (Archbold Weather Data, 1932–2009). The majority of precipitation falls between June and September, and the area experiences frequent thunderstorms with 70–90 thunderstorm days annually (Fernald and Purdum, 1992). Fires were historically ignited by lightning, with the peak fire season in late spring before the onset of the rainy season (Platt et al., 2015). The soils in the area are deep and sandy, with low clay and silt content, and range from excessively well-drained to poorly drained (Abrahamson et al., 1984). Vegetation associations of ABS include southern ridge sandhill, several types of Florida scrub (e.g. rosemary scrub, scrubby flatwoods), flatwoods, swale, bayhead, seasonal ponds, and permanent ponds (Abrahamson et al., 1984; Menges, 1999).

2.2. Seed collection

We collected seeds of six Florida scrub species between mid-October and the end of November 2012. Species were selected based on several factors, including: (1) presence in Florida scrub habitats; (2) adequate seed production for experiments; (3) membership in a plant family that is likely to have a fire response (Keeley and Fotheringham, 2000; Chou et al., 2012); and (4) lack of previous study of fire effects using germination trials. We also selected some species that have been shown to exhibit a strong post-fire population increase (Quintana-Ascencio et al., 2003; Menges and Quintana-Ascencio, 2004) and seeds found in the soil seed bank (Navarra et al., 2011), as they may be indicators of a fire germination response. We chose six species: *E. cuneifolium* Small, *Lechea cernua* Small, *Polygonella polygama* (Vent.) Engelm. & A. Gray, *Chrysopsis highlandsensis* DeLaney & Wunderlin, *Hypericum cumulicola* (Small) W. P. Adams, and *Liatris tenuifolia* Nutt. Of these species, *C. highlandsensis*, *H. cumulicola*, *P. polygama*, and *E. cuneifolium* are obligate seeders (generally unable to resprout after top-killing fires), while *L. cernua* and *L. tenuifolia* are primarily resprouters (Menges and Kohfeldt, 1995). Following seed collection, seeds were stored in paper bags at room temperature until they were cleaned of chaff and debris. We removed damaged or poorly developed seeds and sorted healthy seeds into packets of 100 seeds for treatments.

2.3. Experimental design and treatments

In this study, we used a combination of three smoke treatment levels and three heat treatment levels, with an additional two types of heat treatment (wet vs. dry heat), for a total of 18 treatment combinations for each species. We used 100 replicate seeds per treatment combination, for a total of 1800 seeds per species. Smoke was applied as an aqueous solution after Drewes et al. (1995). To make the smoke water we collected plant litter (pine needles, twigs, oak leaves, etc.) from around ABS and burned it in a bee smoker. We bubbled the smoke through a clear, polypropylene tube into a container filled with 1 L of water until the water had turned a yellow color indicating the presence of the smoke's water soluble compounds (~8 h). Using this smoke water, we created 1:10 (high) and 1:100 (low) dilutions for the smoke water treatments. We used de-ionized water for the control. The heat treatment temperatures were 100 °C for 5 min, 60 °C for 30 min, and no heat application (room temperature). We selected heat treatment levels to mimic fire temperature residence times in soil, based on data taken by Carrington (2010). Dry heat treatments were applied in a drying oven, while the wet heat treatments were applied by placing seeds in water heated to the appropriate temperature. Seeds in the wet heat treatment were removed from the water immediately after the appropriate time to avoid extended high temperatures. We applied smoke treatments following the heat treatments by soaking the seeds in the appropriate solution for 24 h. While certain species may require

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