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Original Research

Smoke and Ash Effects on Seedling Emergence from Germinable Soil Seed Bank in Fescue Prairie[☆]

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ABSTRACT

Seedling recruitment plays a crucial role in recovering plant communities after disturbance. As a natural disturbance, fire can mediate species composition in fescue prairie. However, little was known about the effects of important fire cues on seedling recruitment in fescue prairie. Soil seed bank samples were taken from the top 5 cm of the soil profile and separated into litter, 0- to 1-cm, and 1- to 5-cm layers. Seedlings emerging from soil seed banks incubated in the greenhouse were examined after applying smoke, ash, and smoke plus ash in 2013 and 2014, to assess their effects on the density, richness, and composition of seedlings emerging from the soil seed bank in fescue prairie. Smoke plus ash significantly increased the number of *Artemisia ludoviciana* Nutt. seedlings emerging from 0- to 1-cm soil layer and *Conyza canadensis* (L.) Cronquist seedlings emerging from the litter layer ($P < 0.05$), while ash significantly increased the number of *Artemisia frigida* Willd. seedlings emerging from 0- to 1-cm soil layer ($P < 0.05$). Densities of total seedlings emerging from the 0- to 1-cm soil layer were increased by smoke plus ash in 2013 and by ash in 2014 ($P < 0.05$). Smoke plus ash and ash alone had more prominent effects on seedling density and richness of native forbs. Species composition was altered by ash in the 0- to 1-cm, 0- to 5-cm, and all layers combined in 2013 ($P < 0.05$). Direct fire cues appear to stimulate recruitment of some species, especially native forbs, contributing to potential changes in species composition of fescue prairie.

Introduction

Fescue prairie is one of the most threatened ecosystems in Canada, located in central and southwestern Alberta and west central Saskatchewan (Moss and Campbell 1947; Coupland and Brayshaw 1953). Due to urbanization and cultivation, 95% and 85% of fescue prairie in Saskatchewan and Alberta has been severely degraded, respectively. In addition, fire suppression leaves fescue prairie susceptible to invasion by shrubs (Anderson and Bailey 1980). Reintroducing fire is critical in maintaining diversity in remnant fescue prairie (Romo 2003), but effects of fire on plant community composition in fescue prairie vary with burning season (Bailey and Anderson 1978; Redmann et al. 1993) and fire frequency (Anderson and Bailey 1980). Species composition shifted in favor of perennial forbs for at least 3 years after burning in a fescue prairie in Alberta, Canada (Bailey and Anderson 1978). High germination and seedling establishment occurred immediately after burning (Keeley et al. 2012).

Soil seed bank is regarded as a biodiversity reservoir in restoring degraded or invaded ecosystems (Thompson and Grime 1979). Romo and Gross (2011) concluded that species composition of seedlings that emerged from the soil seed bank in fescue prairie was affected by burning history and season of burning. Although seedling recruitment from the soil seed bank is fundamental to predicting plant species composition in response to disturbances, only limited attention has been given to the effects of burning on seedling emergence from the soil seed bank in fescue prairie.

Burning alters soil nutrients, light availability, temperature fluctuations on the soil surface, and competitiveness among species (Keeley et al. 1985; Auld and Bradstock 1996). Altered environmental conditions account partly for the surge in regeneration from soil or canopy-stored seed bank after burning. In addition, solitary or combinations of direct fire cues, such as heat shock (Keeley et al. 1985), plant-derived smoke (Roche et al. 1997; Abella 2009), and ash (Gonzalez-Rabanal and Casal 1995; Izhaki et al. 2000) have been reported to exert promotive, inhibitive, or neutral effects on seedling emergence from soil seed banks. Smoke can break seed dormancy and stimulate seed germination (De Lange and Boucher 1990; Keeley and Fotheringham 1997) and has been shown to increase seedling densities and richness of seedlings emerging from the soil seed bank in mesic grasslands in South Africa (Ghebrehiwot et al. 2012). With increasing soil depth, the extracted content of 3-methyl-2H-furo[2,3-c]pyran-2-one (KAR_1), the major active compound in smoke, decreased (Ghebrehiwot et al. 2011). Smoke also increases germination of species native to semiarid grasslands in North America (Schwilk and Zavala 2012). Inhibiting effects of ash on seed germination and seedling establishment have been reported in

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herbaceous (Sweeney 1956), shrub (Gonzalez-Rabanal and Casal 1995), and tree species (Izhaki et al. 2000). However, germination of four montane species in Mexico was positively affected by ash (Zuloaga-Aguilar et al. 2011). The combination of fire cues, specifically heat and smoke, can influence germination independently or synergistically. However, the interactive effect of smoke and ash on seedling emergence from the soil seed bank remains relatively unknown.

Despite the importance of the seed bank in vegetation dynamics, roles of different fire cues in general, and smoke and ash specifically, on seedling emergence from the soil seed bank in fescue prairie are poorly understood. The objective of this study was to determine the effects of smoke, ash, and their combination on the density and composition of seedlings emerged from the soil seed bank in fescue prairie. The following hypotheses were tested: 1) smoke, ash, and smoke plus ash alter species composition and promote seedling emergence from the soil seed bank in fescue prairie; 2) seedlings emerging from upper soil layers of the soil seed bank respond stronger to smoke, ash, and smoke plus ash; and 3) smoke, ash, and smoke plus ash favor seedling density and species richness of forbs and native species emerging from the soil seed bank.

Material and Methods

Study Site

Field work was conducted at Kernen Prairie, an approximately 130-ha parcel near Saskatoon, SK, Canada (52°10′N, 106°33′W, elevation 510 m) in 2013 and 2014. The long-term annual temperature averages 2.2°C (Environment Canada 2013), while the long-term average temperatures in May, June, July, and August (growing season) are 11.5°C, 16.0°C, 18.2°C, and 17.3°C, respectively (Environment Canada 2013). The long-term annual precipitation averages 350 mm, with more than half of it occurring from May to August (Environment Canada 2013). In 2013, temperatures averaged 13.0°C in May, 15.5°C in June, 17.4°C in July, and 18.9°C in August. Total precipitation was 15.2 mm in May, 115.9 mm in June, 35.2 mm in July, and 14.7 mm in August (Environment Canada 2013). In 2014, temperatures averaged 10.1°C in May, 14.1°C in June, 18.3°C in July, and 17.9°C in August. Total precipitation was 61.1 mm in May, 94.8 mm in June, 44.5 mm in July, and 18.5 mm in August (Environment Canada 2014). Kernen Prairie is dominated by *Fescuta hallii* Vasey and other C3 plants (Coupland and Brayshaw 1953). Soils in Kernen Prairie are Bradwell and Sutherland Orthic Dark Brown Chernozems (Acton and Ellis 1978). The growing season has approximately 110 frost-free days.

Experimental Design

Fifty 3 × 3 m experimental plots were established on 17 April 2012 for this study. Twenty-five plots were used for study in 2013, and another 25 plots were used for study in 2014. Four subplots of the same size (25 × 25 cm) were randomly selected within each plot. Twenty-five 25-cm^2 soil core samples were collected from the top 5 cm of the soil profile in each subplot using iron cylinders with diameter of 5.6 cm and were subjected to one of four treatments: control, smoke, ash, and smoke plus ash. Soil samples were collected on 4 May 2013 and 10 May 2014. Except for the control, soil cores were collected after clipping the phytomass to the ground in each subplot. Clipped phytomass was collected and dried in an 80°C oven for 2 days to determine dry weight. Dry weight averaged at 87 ± 4.9, 94 ± 7.2, and 99 ± 8.0 g for smoke, ash, and smoke plus ash treatments in 2013, respectively. It averaged at 74 ± 4.5, 73 ± 5.9, and 75 ± 6.7 g for smoke, ash, and smoke plus ash treatments in 2014, respectively. Phytomass from each subplot was then combusted to generate smoke solution or ash. The apparatus to produce smoke solutions and ash was constructed from a wooden board fixed with an electric ring heater. A sufficient gap was left under the board for the power cord of the ring heater to exit. A metal, 75-L garbage can with two holes drilled on either side was inverted over the heater. Pressure gauges connecting an air-supplying hose on one side and a silicon tube on the other side were affixed to the two holes. A pot for holding plant material and two weights to hold the garbage can in place completed the apparatus. Each smoke, ash, or smoke plus ash sample was produced by smouldering phytomass that was put into a container and placed on the electric ring heater. The garbage can was inverted over the wooden board enclosing the ring heater and the metal container containing plant materials. The weights were placed on top of the garbage can to eliminate smoke leakage. Air was forced into the combustion chamber at a pressure of 70 − 100 kPa. Smoke produced from the samples was continuously passed through the silicon tube and bubbled into 500 mL of distilled water in a water bottle to make smoke solutions. Ash was left in the container after combustion. In total, 25 smoke solution samples, 25 ash samples, and 25 smoke plus ash samples were produced within each year in this way.

Each soil core sample collected from the top 5 cm of the soil profile was divided into the litter layer on the soil surface, 0-1 cm, and 1-5 cm depths. Common layers for the 25 soil cores from each subplot were combined, mixed, and spread onto plastic trays (52 × 26 × 7 cm) to < 1 cm in depth. Root fragments, rhizomes, and plant materials were removed. The litter layer was spread on a 1-cm layer of sterile sand placed at the bottom of plastic trays measuring 26 × 26 × 6 cm. Trays containing soil cores from the same plot were randomly placed as blocks in a greenhouse. The air temperature during the growing season in the greenhouse averaged 27 ± 3°C during the day and 21 ± 4°C at night. Natural light was supplemented with two 400-W, high-pressure sodium lights (18-h photoperiod, average of 600 μmol · m^{-2} · s^{-1}) for each bench. Each of the 25 blocks had four treatments including soil cores without any treatment, soil cores treated with smoke, soil cores treated with ash, and soil cores treated with smoke plus ash.

The amount of smoke, ash, or smoke plus ash applied to the litter layer and two soil layers was based on the volumetric ratio among these three layers. More specifically, we calculated the volumes of 0- to 1-cm and 1- to 5-cm soil layers of 25 soil cores collected from same subplot, which was 625 cm^3 (25 × 25 cm^2 × 1 cm) and 2 500 cm^3 (25 × 25 cm^2 × 4 cm), respectively, in both years. We used volumetric cylinder to measure the litter volume of 25 soil cores collected from the same subplot. In total, we had 100 (25 × 4) subplots in each year. The litter volume within each subplot averaged at 220 and 270 mL in 2013 and 2014, respectively. Hence, the ratios for applying smoke, ash, or smoke plus ash obtained from the phytomass collected from a specific subplot to the litter, 0- to 1-cm, and 1- to 5-cm soil layers collected from the corresponding subplot were 220: 625: 2 500 and 270: 625: 2 500 in 2013 and 2014, respectively. Water was applied immediately after applying different treatments. All trays were watered manually to field capacity every day. Extra water was drained through small holes at the bottom of each tray. Seedling emergence was recorded weekly for 14 weeks, and new seedlings were transplanted in pots until they were identified. In total, data from five layers (litter layer, 0- to 1-cm depth, 1- to 5-cm depth, 0- to 5-cm depth) and all layers combined (litter layer plus 0- to 5-cm depth soil layer) were analyzed.

Data Analysis

Analysis was conducted on individual species' seedling densities, total seedling densities, species richness, seedling densities and species richness of functional groups of forbs, graminoids, native, and non-native plants, species diversity (Diversity indices), and seedling emergence rate from the soil seed bank in the greenhouse. Data were square root, log, or log (× + 1) transformed and subjected to analysis of variance (ANOVA) in a split plot in a complete randomized design with 25 replicates. Transformations were applied to meet normality assumptions. Twenty-five plots within each year were the whole plot experimental unit, with year as the whole-plot factor, while each plot within each year was the subplot experimental unit, with different treatments