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Effects of Temperature on Seed Viability of Six Ozark Glade Herb Species and Eastern Redcedar (Juniperus virginiana)

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ABSTRACT.—Although prescribed fires are commonly used in management, little is known about how temperatures generated during fires affect the seed viability of species of conservation concern. We measured seed viability of six herbaceous forbs native to Ozark glade ecosystems and the glade-invading shrub *Juniperus virginiana* (eastern redcedar) after exposure to four temperature treatments for 15 min: 24 C, 50 C, 100 C and 150 C. Viability of *Allium canadense* and *Ruellia humilis* was reduced to near zero after exposure to temperatures of 100 or 150 C, whereas viability of *Echinacea simulata* and *J. virginiana* was only significantly reduced at 150 C. *Lespedeza virginica*, *Oenothera macrocarpa,* and *Silphium terebinthinaceum* maintained substantial viability after exposure to 150 C, with the proportion of viable seeds ranging from 0.3–0.5. Our results suggest that interspecific differences in tolerance to heat-related mortality of seeds may be an important factor mediating post fire patterns of plant regeneration.

INTRODUCTION

Grasslands provide a variety of ecosystem services but are among the world's most fragmented and degraded ecosystems (Bond and Parr, 2010). Prescribed fire has become one of the most commonly used tools for promoting native plant establishment and reducing encroachment by undesirable invasive and woody plants (Briggs *et al.*, 2005) but without fully appreciating the myriad of effects that fire has on altering ecosystems. Understanding which species are affected by fire and whether certain species that are impediments to restoration are more susceptible to deleterious effects of burning relative to grassland species, will ultimately enhance the utility of prescribed fires in a restoration and management context (Pyke *et al.*, 2010).

Using Ozark glade grasslands as a study system, we examined the relative effect of heat on the viability of six herbaceous species, that are indicators of glade grasslands, as well as the problematic woody species eastern redcedar (*Juniperus virginiana*). We focused on seed viability for two reasons. First, because establishment of many grassland species is limited by the presence of viable seeds (Clark *et al.*, 2007), recruitment from the seed bank may be important for determining plant population dynamics and community composition following prescribed burning. Second, although the Ozark glades are a fire-maintained system (Batek *et al.*, 1999; Ware, 2002) and fire can have profound effects on seed viability and germination (*e.g.,* Baskin and Baskin, 2001), little is known about how heat affects the viability of many native glade species. Our goal is to test the relative effects of heat on the seed viability of six species that are characteristic of Ozark glade plant communities (Baskin and Baskin, 2000) and the undesirable woody shrub *J. virginiana* (Briggs *et al.*, 2002).

METHODS

STUDY SYSTEM

Ozark glades are highly diverse grassland ecosystems found on shallow soils surrounded by hardwood forests (Baskin and Baskin, 2000). Herbaceous forbs, including several

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endemics, constitute a significant fraction of glade plant diversity and are considered of high conservation value (Ware, 2002). Historic fire return intervals (pre-1940s) ranged from 1 y to 2 dec (Batek *et al.*, 1999), where shorter fire return intervals maintained herbaceous vegetation (Ware, 2002). More recently, fire suppression has been a primary mechanism of glade conversion to shrubland, particularly by *Juniperus virginiana* encroachment (Briggs *et al.*, 2002), because frequent fires generally kill *J. virginiana* seedlings and saplings (Ortmann *et al.*, 1998).

HEAT SHOCK EXPERIMENT

We purchased seeds from commercial suppliers: *Allium canadense* L. and *Ruellia humilis* Nutt. (Prairie Moon Nursery, Winona, MN), *Echinacea simulata* R.L. McGregor (Easyliving Wildflowers, Willow Springs, MO), *Lespedeza virginica* (L.) Britton, *Oenothera macrocarpa* Nutt., *Silphium terebinthinaceum* Jacq. (Hamilton Native Outpost, Elk Creek, MO) and *Juniperus virginiana* L. (Sheffield's Seeds, Locke, NY). Nomenclature follows the USDA, NRCS (2012). Seeds were stored at room temperature and ambient relative humidity. The native species were selected based on their status as indicator species of Ozark glades habitat (see Baskin and Baskin, 2000). We heated seeds on aluminum trays (ten seeds per tray) in an oven for 15 min at four treatment temperatures: 24 C, 50 C, 100 C, and 150 C. We selected our treatments to represent temperatures and duration near the soil surface during grassland fires (Archibold *et al.*, 1998; Wally *et al.*, 2006), which are most likely to affect seeds near the soil surface. Grassland fires can reach temperatures upwards of 400 C for short durations (a few min or less) in grass and shrub canopies (Gibson *et al.*, 1990; Archibold *et al.*, 1998) but tend to be lower (50–200 C, depending on litter substrate) and of longer duration (>5 min, depending on litter substrate) at the soil surface (Archibold *et al.*, 1998; Wally *et al.*, 2006). Because seeds near the soil surface are most likely to experience these lower, prolonged temperatures, we opted to use a 15 min duration time in order to produce a conservative estimate of the effect of temperature on seed viability.

Each species had three replicate trays except for *A. canadense* and *R. humilis* at 100°C and *E. simulata* and *J. virginiana* at 150 C, which had eight replicate trays. Expansion of aluminum trays during heating resulted in the loss of a small number of seeds per replicate; 39 of the 109 trays lost at least one seed, but on average, trays had 9.5 seeds per tray (±1.0 SD, n = 109), and all trays had at least five seeds. After heating, a standard tetrazolium chloride (TTC) assay was used to assessing seed viability (Peters, 2000).

Three species (*L. virginica*, *O. macrocarpa*, and *S. terebinthinaceum*) seemed to be tolerant of our temperature treatments, so we exposed them to additional heat treatments: 175 C (only for *O. macrocarpa* and *S. terebinthinaceum*) and 200 C (for all three species) using the same methods described above.

STATISTICAL ANALYSIS

We used a generalized linear model (GLM) with a binomial response distribution to examine the proportion of viable seeds (Littell *et al.*, 2006). Our model included two factors, temperature treatment (four levels: 24 C, 50 C, 100 C, and 150 C) and seed species (seven levels), as well as their interaction. We present the results for the three species in which we conducted additional temperature treatments as means (± 95% CI) for comparison to the main trial. We used an inverse link function to present means and confidence intervals on a linear scale. All analyses were performed using PROC GLIMMIX in SAS 9.2 (SAS Institute Inc., Cary, NC, U.S.A).

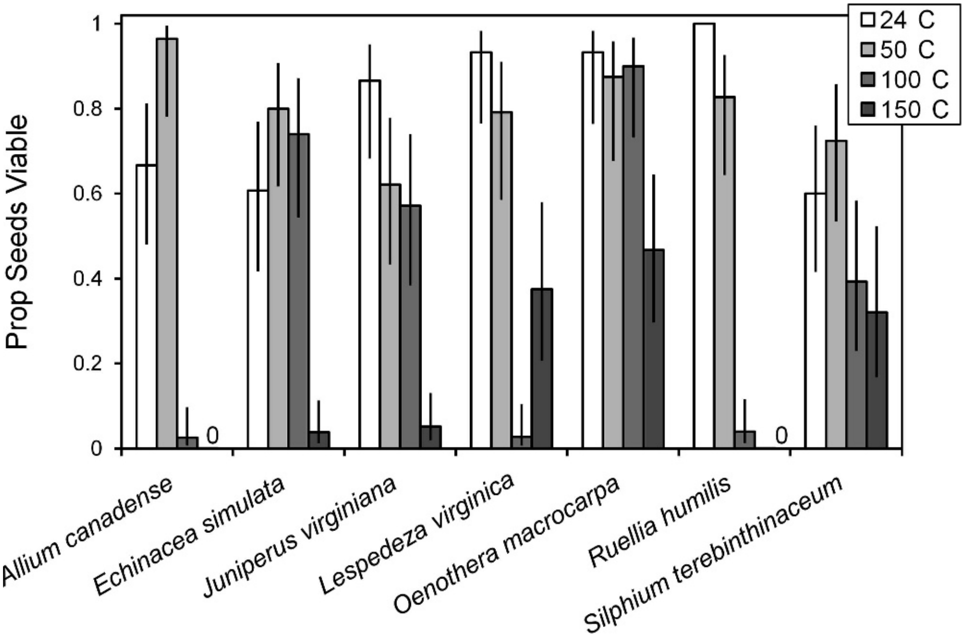

FIG. 1.—Proportion of seeds viable after a 15 min exposure to various temperatures. Six herbaceous species are indicative of glade grassland ecosystems (*Allium canadense, Echinacea simulata, Lespedeza virginica, Oenothera macrocarpa, Ruellia humilis, Silphium terebinthinaceum*); *Juniperus virginiana* is a woody species that often establishes in glade ecosystems following fire suppression. We used a GLM and applied an inverse link function in order to report the estimated means on a linear scale. Error bars are 95% confidence intervals. Variance estimates for treatments where all replicates had either all seeds viable or no seeds viable (indicated by a zero in the figure) are not included

RESULTS

The species main effect ($F_{6,81} = 4.68$, $P = 0.0004$), the temperature treatment main effect ($F_{3,81} = 24.01$, $P < 0.0001$), and the interaction term ($F_{18,81} = 6.49$, $P < 0.0001$) were all highly significant, suggesting that species' seed viability varies in response to heat shock. Most species had highest viability between 24 C and 100 C and lowest viability at 150 C (Fig. 1). *Juniperus virginiana* seed viability was reduced from 0.87 (0.68, 0.95; 95% CI) at room temperature (24 C) to 0.62 (0.43, 0.78; 95% CI) at 50 C, 0.57 (0.38, 0.74) at 100 C, and to 0.05 (0.02, 0.13; 95% CI) at 150 C. Seed viability of *A. canadense, L. virginica,* and *R. humilis* was reduced to nearly zero after 15 min of heat exposure at 100 C. However, the 150 C treatment for *L. virginica* increased to 0.38 (0.21, 0.58; 95% CI) proportion of viable seeds, although this result may be driven by one replicate that had complete viability. *Echinacea simulata* had high viability (>0.60) between 24 C–100 C but was reduced to nearly zero at 150 C. In contrast the proportion of *O. macrocarpa* and *S. terebinthinaceum* seed viability remained moderate at 150 C with 0.47 (0.30, 0.65; 95% CI) and 0.32 (0.17, 0.52; 95% CI), respectively.

Heating to 175 C reduced the proportion of viable seeds of *O. macrocarpa* to 0.04 (0.009, 0.16; 95% CI) and that of viable *S. terebinthinaceum* seeds to 0.08 (0.003, 0.21; 95% CI) at 175 C. All three of the species that were subjected to additional heat treatments (*L. virginica, O. macrocarpa,* and *S. terebinthinaceum*) at 200 C had zero viable seeds.

DISCUSSION

Our work suggests that heat differentially affects the viability of seeds of glade plant species. Seeds of some native forbs (*e.g., Oenothera macrocarpa* and *Silphium terebinthinaceum*) were relatively heat tolerant and may be able to survive and establish after fires. In contrast other species were susceptible to heat at low (*e.g.,* above 50 C: *Allium canadense* and *Ruellia humilis*) or high (*e.g.,* above 100 C: *Echinacea simulata, Juniperus virginiana,* and *Lespedeza virginica*). Field studies from grasslands suggest that at sites with high plant diversity, the seed bank seems to be an important source of post-fire regeneration for many species of forbs (Taft, 2003). However, the seed bank may contribute little to the distribution of grasses, which are of often the dominant plant cover in glades, or other species that resprout from belowground organs (Benson and Hartnett, 2006). Thus, heat tolerance of seeds may be an overlooked mechanism contributing to post-fire regeneration of some forbs, which constitute a large portion of overall plant diversity. Additional studies are needed to assess the degree to which different methods of regeneration (*i.e.,* vegetative or seed) are most important for structuring post-fire glade diversity.

Spatial variation in burn intensity and duration can create spatial patterning in plant communities (Gagnon *et al.,* 2012). Our results illustrate that differential susceptibility of seeds to high temperatures may be an underappreciated mechanism by which variance in fire intensity generates spatial variation in plant communities. For example, fires that are uniformly hot can effectively homogenize vegetation because the elimination of many viable seeds leads to communities dominated by perennial plants that resprout following fire (Benson and Hartnett, 2006; Collins *et al.,* 2006). However, if fire produces low or heterogeneous temperatures across the landscape, this can promote spatial heterogeneity in plant regeneration (Turner *et al.,* 1994; Gagnon *et al.,* 2012). Patch characteristics (*e.g.,* edges, patch size, and connectivity) that influence fire intensity also may affect the composition of the subsequent plant community. For example conservation corridors that connect patches of disjunct habitat and edges can alter spatial patterns of burn temperatures by affecting both fuel loads and wind speed or direction (Brudvig *et al.,* 2012). Changes in fire intensity or duration could then give rise to corridor- or edge-mediated changes in plant recruitment via differential susceptibility of species to temperature (Fig. 1). Finally, seed moisture can affect heat tolerance (Le Fer and Parker, 2005; Stephan *et al.,* 2010), so variation in soil moisture could also generate spatial patterns in post-fire regeneration.

Our results also have implications for management of *J. virginiana,* particularly by targeting the seed bank. Prescribed fires that target the seed bank have been effective in controlling invasive species in other systems. Temperatures greater than 125 C reduced seed germination of *Genista monspessulana* (Terraga *et al.,* 1992), an invader of fire maintained chaparral systems in California, and prescribed burns may contribute to reducing the *G. monspessulana* seed bank (Alexander and D'Antonio, 2003). In Hawaiian grasslands, D'Antonio *et al.,* (2001) found that *Melinus minutiflora* invades after fires due, in part, to tolerance of seeds to heat shock. These authors suggest that high-intensity fires (>120 C) may deplete the seed bank, although they question if this will adequately control this species because the vertical distribution of seeds in the litter and soil can change the efficacy of fire-induced heat shock. Emery *et al.* (2011) found that high-intensity fires may reduce seed viability of both native and nonnative plants in eastern deciduous forest herb layers. However, if nonnative seeds are more tolerant of heat shock, prescribed fire could actually facilitate invasion. Since *J. virginiana* does not form long-lived seed banks (Holthuizen and Sharik, 1984), most recruitment likely is from seeds that have been recently dispersed and are near the soil surface. Our study suggests that high-intensity fires (>150 C) should effectively kill *J. virginiana* seeds and that if combined with other removal methods (*e.g.*, cutting adults) could contribute to controlling multiple life stages.

Our results reveal there is considerable variation in the susceptibility of seeds to relatively low temperatures (Fig. 1). Because many grassland species do not form long-lived seed banks (*e.g.*, Young *et al.*, 1989; Coffey and Kirkman, 2006; Orrock and Hoisington-Lopez, 2009), post-fire recruitment in these systems is likely to be driven by recently dispersed seeds that are present in the litter duff and soil, and so are likely to experience longer heating periods similar to temperatures studied here. As a result, our work suggests that future studies may benefit from examining how longer duration times and lower temperatures affect seed viability, because this may be an important source of variation in seed survival (Fig. 1). Furthermore, differences in the effect of temperature on seed viability like the ones we observed between native glade plants and the undesirable invasive *J. virginiana* (Fig. 1) may have implications for management and restoration of many ecosystems (Pyke *et al.*, 2010). Thus, studying the effects of fire on seed viability will improve our understanding of how fire shapes plants communities in both basic and applied ecological contexts.

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LITERATURE CITED

ALEXANDER, J. M. AND C. M. D'ANTONIO. 2003. Seed bank dynamics of French broom in coastal California grasslands: effects of stand age and prescribed burning on control and restoration. *Restor. Ecol.*, **11**:185–197.

ARCHIBOLD, O. W., L. J. NELSON, E. A. RIPLEY, AND L. DELANOY. 1998. Fire temperatures in plant communities of the northern mixed prairie. *Can. Field-Nat.*, **112**:234–240.

BASKIN, J. M. AND C. C. BASKIN. 2000. Vegetation of limestone and dolomite glades in the Ozarks and Midwest regions of the United States. *Annals MO Bot. Garden*, **87**:286–294.

BASKIN, C. C. AND J. M. BASKIN. 2001. Seeds: Ecology, biogeography, and evolution of dormancy and germination. Academic Press, San Diego, CA, USA.

BATEK, M. J., A. J. REBERTUS, W. A. SCHROEDER, T. L. HAITHCOAT, E. COMPAS, AND R. P. GUYETTE. 1999. Reconstruction of early nineteenth-century vegetation and fire regimes in the Missouri Ozarks. *J. Biogeogr.*, **26**:397–412.

BENSON, E. J. AND D. C. HARTNETT. 2006. The role of seed and vegetative reproduction in plant recruitment and demography in tallgrass prairie. *Plant Ecol.*, **187**:163–177.

BOND, W. J. AND C. L. PARR. 2010. Beyond the forest edge: ecology, diversity and conservation of the grassy biomes. *Biol. Conserv.*, **143**:2395–2404.

BRIGGS, J. M., G. A. HOCH, AND L. C. JOHNSON. 2002. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. *Ecosystems*, **5**:578–586.

BRUDVIG, L. A., S. A. WAGNER, AND E. I. DAMSCHEN. 2012. Corridors promote fire via connectivity and edge effects. *Ecol. App.*, **22**:937–946.

CLARK, C. J., J. R. POULSEN, D. J. LEVEY, AND C. W. OSENBERG. 2007. Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. *Am. Nat.*, **170**:128–142.

COFFEY, K. L. AND L. K. KIRKMAN. 2006. Seed germination strategies of species with restoration potential in a fire-maintained pine savanna. *Nat. Areas J.*, **26**:289–299.

COLLINS, S. L. AND M. D. SMITH. 2006. Scale-dependent interaction of fire and grazing on community heterogeneity in tallgrass prairie. *Ecology*, **87**:2058–2067.

D'ANTONIO, C. M., R. F. HUGHES, AND P. M. VITOUSEK. 2001. Factors influencing dynamics of two invasive C_4 grasses in seasonally dry Hawaiian woodlands. *Ecology*, **82**:89–101.

EMERY, S. M., J. UWIMBABAZI, AND S. L. FLORY. 2011. Fire intensity on seed germination of native and invasive eastern deciduous forest understory plants. *Forest Ecol. Manage.*, **261**:1401–1408.

GAGNON, P. R., K. E. HARMS, W. J. PLATT, H. A. PASSMORE, AND J. A. MYERS. 2012. Small-scale variation in fuel loads differentially affects two co-dominant bunchgrasses in a species-rich pine savanna. *PLoS One*, **7**:e29674.

GIBSON, D. J., D. C. HARTNETT, AND G. L. S. MERRILL. 1990. Fire temperature heterogeneity in contrasting fire prone habitats: Kansas tallgrass prairie and Florida sandhill. *Bull. Torrey Bot. Club*, **117**:349–356.

HOLTHUIJZEN, A. M. A. AND T. L. SHARIK. 1984. Seed longevity and mechanism of regeneration of eastern redcedar (*Juniperus virginiana* L.). *Bull. Torrey Bot. Club*, **111**:153–158.

LE FER, D. AND V. T. PARKER. 2005. The effect of seasonality of burn on seed germination in chaparral: the role of soil moisture. *Madrono*, **52**:166–174.

LITTELL, R. C., G. A. MILLIKEN, W. W. STROUP, R. D. WOLFINGER, AND O. SCHABENBERBER. 2006. SAS for mixed models. SAS Institute, Cary, NC, U.S.A.

ORROCK, J. L. AND J. L. HOISINGTON-LÓPEZ. 2009. Mortality of exotic and native seeds in invaded and uninvaded habitats. *Acta Oecol.*, **35**:758–762.

ORTMANN, J., J. STUBBENDIECK, R. A. MASTERS, G. H. PFEIFFER, AND T. B. BRAGG. Efficacy and costs of controlling eastern redcedar. *J. Range Manage.*, **51**:158–163.

PETERS, J. 2000. Tetrazolium Testing Handbook. Contribution No. 29 to the Handbook on Seed Testing revised 2000. Association of Official Seed Analysts.

PYKE, D. A., M. L. BROOKS, AND C. D'ANTONIO. 2010. Fire as a restoration tool: a decision framework for predicting the control or enhancement of plants using fire. *Restor. Ecol.*, **18**:274–284.

STEPHAN, K., M. MILLER, AND M. B. DICKINSON. 2010. First-order fire effects on herbs and shrubs: present knowledge and process modeling needs. *Fire Ecol.*, **6**:95–114.

TAFT, J. B. 2003. Fire effects on community structure, composition, and diversity in a dry sandstone barrens. *J. Torrey Bot. Soc.*, **130**:170–192.

TERRAGA, R., L. CALVO, AND L. TRABAUD. 1992. Effect of high temperatures on seed germination of two woody Leguminosae. *Vegetatio*, **102**:139–147.

TURNER, M. G., W. W. HARGROVE, R. H. GARDNER, AND W. H. ROMME. 1994. Effects of fire on landscape heterogeneity in Yellowstone National Park, Wyoming. *J. Veg. Sci.*, **5**:731–742.

USDA, NRCS. 2012. The PLANTS Database. (http://plants.usda.gov) National Plant Data Team, Greensboro, NC, U.S.A.

WALLY, A. L., E. S. MENGES, AND C. W. WEEKLEY. 2006. Comparison of three devices for estimating fire temperatures in ecological studies. *App. Veg. Sci.*, **9**:97–108.

WARE, S. 2002. Rock outcrop plant communities (Glades) in the Ozarks: A synthesis. *Southwest. Nat.*, **47**:585–597.

YOUNG, J. A. AND R. A. EVANS. 1989. Seed production and germination dynamics in California annual grasslands, p. 39–45. *In:* L. F. Huenneke and H. A. Mooney (eds.). Grassland Structure and Function: California Annual Grassland. Kluwer Academic Publishers, Boston. 232 p.

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