Forest Ecology and Management 310 (2013) 54–63

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Fine-scale variation in surface fire environment and legume germination in the longleaf pine ecosystem

M. Scott Wiggers [a,b,*], L. Katherine Kirkman [b], Robert S. Boyd [a], J. Kevin Hiers [c]

[a] Department of Biological Sciences, Auburn University, 101 Rouse Life Sciences Bldg., Auburn, AL 36849, USA
[b] J.W. Jones Ecological Research Center, 3988 Jones Center Dr., Newton, GA 39870, USA
[c] Eglin Air Force Base Natural Resources, Jackson Guard, Niceville, FL 32578, USA

ARTICLE INFO

Article history:
Received 15 May 2013
Received in revised form 16 July 2013
Accepted 17 July 2013
Available online 6 September 2013

Keywords:
Fuel heterogeneity
Fine-scale fire heterogeneity
Legumes
Germination
Seed survival
Recruitment microsite

ABSTRACT

Fine-scale heterogeneity in fuels influences fire behavior and, in turn, may influence patterns of plant recruitment and regeneration from soil seed banks. In particular, hard-seeded species, such as many members of the plant family Fabaceae, may experience differential germination and mortality rates as a result of heterogeneous fire intensities mediated by variable distribution of fine and coarse fuels. Post-fire germination was examined for nine legume species native to longleaf pine (*Pinus palustris*) stands of the southeastern United States in response to fuel variation using a paired laboratory and field study. For both studies, fine fuel loads (longleaf pine needles) and coarse fuels (longleaf pine cones) were manipulated. Germination of seven species was assessed for four months in the field following experimental burns of small plots. Germination and mortality were assessed for six species after exposure to experimental laboratory fires. Burning reduced germination compared to unburned controls in both studies. Furthermore, legumes exposed to burning pine cones experienced greater reductions in germination than when exposed to burning pine needles alone. Manipulation of fine fuel loads did not affect germination in either study. Results suggest that small pieces of coarse woody debris are responsible for differential germination following fire, rather than variation in fine fuels. We present a conceptual model of fine-scale fire effects to explain how long-duration smoldering creates localized mortality events that may drive variation in recruitment from the soil seed bank for longleaf pine ecosystems.

Published by Elsevier B.V.

1. Introduction

Recurrent fires maintain the structure and diversity of numerous ecosystems worldwide (Bond and Keeley, 2005; Bond et al., 2005). Within these systems, variations in fuel loads, types, and arrangement are recognized as important determinants of fire behavior and intensity (Whelan, 1995; Bond and van Wilgen, 1996) which in turn influence the ecological effects of a given fire (Kennard and Outcalt, 2006). Only recently, however, has fine scale (i.e., <10 m^2) heterogeneity in fuels been systematically examined (Hiers et al., 2009; Rocca, 2009), especially in regard to its influence on fire behavior (Wenk et al., 2011; Loudermilk et al., 2012). Pine cones have been reported to be a particularly important source of variation of fuels in several ecosystems (Fonda and Varner, 2004; Mitchell et al., 2009; Gabrielson et al., 2012) due to their extended duration of smoldering and heat transfer to the soil relative to that of other fuels (Fonda and Varner, 2004). While fine scale variation in fuels and the impact of fire behavior is beginning to be understood, little work connects variation in fire behavior to fire effects at this scale (e.g., Rocca, 2009). A potential fire effect is its impact on soil seed banks and, thus, seedling recruitment and plant species composition.

The longleaf pine (*Pinus palustris* Mill.) woodlands of the southeastern United States is an exceptionally species rich, fire-dependent ecosystem (Peet and Allard, 1993). This ecosystem's diverse groundcover and abundant pine needle litter provide fine fuels necessary for carrying frequent fires (1–5 year return interval) across the forest floor (O'Brien et al., 2008). Bunch grasses common to this system—*Aristida* spp., *Schizachyrium* spp., and *Andropogon* spp.—are highly flammable and serve as perches for pine needles (Hendricks et al., 2002; Boring et al., 2004), which comprise the most significant contribution to fine fuel loading (Mitchell et al., 2009). Together, bunch grasses and perched fine fuels provide a continuous fuel layer and greatly enhance the pyrogenicity of longleaf pine stands. Moreover, recent work has suggested that small pieces of coarse woody debris, such as pine cones, may alter both fire behavior and fire effects at fine scales in these systems (Mitchell et al., 2009; Gabrielson et al., 2012).

In longleaf pine communities, accumulation of needles and woody litter under pine trees may increase fine-scale fire

* Corresponding author. Present address: US Fish and Wildlife Service, Mississippi Field Office, Jackson, MS 39213, USA. Tel.: +1 601 364 6910.
E-mail address: marion_wiggers@fws.gov (M.S. Wiggers).

0378-1127/$ - see front matter Published by Elsevier B.V.
http://dx.doi.org/10.1016/j.foreco.2013.07.030

intensities (Thaxton and Platt, 2006; Mitchell et al., 2009). For example, increased pine litter and associated increases in fire temperatures and intensities have been found to reduce the survival and growth of oaks (Williamson and Black, 1981; Rebertus et al., 1989). Elevated pine fuel loads also have been found to reduce the survival and resprouting of shrubs in longleaf pine stands (Thaxton and Platt, 2006) and increase mortality of longleaf pine seedlings (O'Brien et al., 2008; Jack et al., 2010).

Pine cones, which are typically between 15 and 25 cm long at maturity for longleaf pine trees (Kirkman et al., 2007), represent a potentially significant source of fuel in some situations (e.g., Mitchell et al., 2009; van Wagtendonk and Moore, 2010; Gabrielson et al., 2012) and promote the ignition of forest floor fuels (Kreye et al., 2013b). Loadings of pine cones are influenced by the distribution and density of mature pine trees (Platt et al., 1988; Mitchell et al., 2009), as well as the periodicity of mast years (Boyer, 1986, 1998; Gilliam et al., 2006) and variability of cone production by individual trees (Haymes and Fox, 2012). Thus, the impact of longleaf pine cones on fire effects is likely temporally and spatially variable, but potentially significant, particularly in mast seeding years (every 5–10 years; Boyer, 1998), when pine cones are especially abundant; however, the ecological effects of pine cones as a fuel source remain poorly understood (Fonda and Varner, 2004; Gabrielson et al., 2012).

Fine scale temporal and spatial variability in fire behavior likely contributes to the diverse longleaf pine ecosystem through influences on recruitment and survival. Theoretical explanations for community dynamics and species coexistence in species rich ecosystems include niche differentiation (Grubb, 1977; Silvertown, 2004), lottery-based seed supply (neutral theory) (Hubbell, 2001), and disturbances that limit competition (Huston, 1979, 1999). In the species rich longleaf pine ecosystem, there is increasing evidence that a complex balance of these processes regulates patterns of community assemblage, similar to the continuum hypothesis suggested by Gravel et al. (2006). For example, elimination of oaks through frequent fire in the longleaf pine ecosystem frees herbaceous species from competitive exclusion (Thaxton and Platt, 2006; Kirkman and Mitchell, 2006). Additionally, a positive correlation between soil moisture and species richness suggests that soil moisture may regulate species richness by affecting seedling recruitment (Kirkman et al., 2001). Based on the observation that water supply was more important than seed supply in determining seedling establishment, Iacona et al. (2010) concluded that appropriate sites for regeneration are a factor limiting seedling success. Moreover, in this ecosystem, the extremely high species richness that occurs at small scales with an apparent niche overlap between co-occurring species precludes niche heterogeneity as the most plausible explanation for the observed patterns of diversity (Gravel et al., 2006; Iacona et al., 2010). Thus, episodic availability of microsites for recruitment and the stochasticity of seed and seedling mortality due to fire are likely processes influencing species richness (Iacona et al., 2010).

Within ecosystems that are regularly burned, such as the longleaf pine ecosystem, the capacity for seeds to survive fires or germinate in response to these fires differs among species (e.g., Keeley et al., 1985; Clark and Wilson, 1994); thus, species-specific responses to fine-scale fuel and fire variation may contribute to patterns of species recruitment and fine-scale vegetation diversity. Fine-scale variation in fire behavior may be of particular significance in survivorship and recruitment of hard-seeded species such as many legumes, although little focus has been given to understanding this relationship. Legumes are a diverse and abundant (Drew et al., 1998; Hainds et al., 1999) groundcover component of longleaf pine communities (Ballard, 1973; Morrison et al., 1998). Hard seed coats impose a physical dormancy on seeds by limiting uptake of water by the embryo (Ballard, 1973) and thus allow for the formation of persistent seed banks (Baskin and Baskin, 1998). Exposure to fire enhances germination of some hard-seeded species by breaking the moisture barrier that imparts dormancy (i.e., the seed coat; Morrison et al., 1998). Consequently, if elevated fuel loads create patches of mortality and the resulting heat favors germination of hard-seeded species, then legume seeds within the soil seed bank should be uniquely positioned to take advantage of new gaps created by fires as recruitment sites.

The objective of this study was to examine effects of combustion of variable fine fuel loads and pine cones on germination and mortality of common legume species found in longleaf pine seed banks. First, germination and mortality of six legume species were assessed in the laboratory following experimental fires using a gradient of fuel loads. Next, post-fire germination of seven legume species were determined in the field in response to fuel (i.e., pine needles and pine cones) manipulations.

2. Materials and methods

2.1. Study site

We examined seed germination responses to fuel manipulation treatments in the laboratory and in field plots at the Joseph W. Jones Ecological Research Center at Ichauway (hereafter, Ichauway). Ichauway is a 12,000 ha research site located in Baker County, Georgia, USA and occurs within the Lower Gulf Coastal Plain ecoregion and within the historic range of longleaf pine (Ware et al., 1993). The local climate is characterized by short, mild winters and long, hot summers (Lynch et al., 1986) with average annual temperatures ranging from lows of 5 °C in winter to highs of 34 °C in summer (Goebel et al., 1997).

2.2. Study designs and data collection

2.2.1. Experiment 1: Laboratory germination

We examined seed mortality and germination in response to burning of variable fuel loads under laboratory conditions. The laboratory setting allowed for ready retrieval of the seeds for further testing. Post-treatment retrieval of seeds permitted quantification of seed mortality as a factor in the absence of germination response.

In this study, we used seeds of six legume species (nomenclature follows Wunderlin and Hansen (2003)): *Centrosema virginianum* (L.) Benth., *Crotalaria rotundifolia* Walter ex J.F. Gmel., *Desmodium floridanum* Chapm., *Lespedeza angustifolia* (Pursh) Elliot, *Mimosa quadrivalvis* L., and *Rhynchosia reniformis* DC. We selected these species based on their common occurrence within Ichauway's longleaf pine stands, their perennial life histories, and characteristics that permitted ready identification of seeds of each species during post-treatment retrieval. Additionally, these species represent a range of seed coat hardnesses, as indicated by prior scarification trials of these species (L.K. Kirkman, unpub. data). These trials indicate that *D. floridanum* is soft-seeded and does not typically require scarification for germination; *Ce. virginianum* is moderately hard-seeded, requiring some scarification; and *Cr. rotundifolia*, *L. angustifolia*, *M. quadrivalvis*, and *R. reniformis* are extremely hard-seeded, requiring more extensive scarification to elicit germination.

We harvested *R. reniformis* seeds from longleaf pine stands at Ichauway, while seeds of all other species used were harvested from a native seed production garden at Ichauway. Seeds were stored in burlap or paper bags in a climate-controlled laboratory prior to use.