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Pyrogenic fuels produced by savanna trees can engineer humid savannas

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Abstract. Natural fires ignited by lightning strikes following droughts frequently are posited as the ecological mechanism maintaining discontinuous tree cover and grass-dominated ground layers in savannas. Such fires, however, may not reliably maintain humid savannas. We propose that savanna trees producing pyrogenic shed leaves might engineer fire characteristics, affecting ground-layer plants in ways that maintain humid savannas. We explored our hypothesis in a high-rainfall, frequently burned pine savanna in which the dominant tree, longleaf pine (*Pinus palustris*), produces resinous needles that become highly flammable when shed and dried. We postulated that pyrogenic needles should have much greater influence on fire characteristics at ground level, and hence post-fire responses of dominant shrubs and grasses, than other abundant fine fuels (shed oak leaves and grass culms). We further reasoned that these effects should increase with amounts of needles. We managed site conditions that affect fuels (time since fire, dominant vegetation), manipulated amounts of needles in ground-layer plots, prescribed burned the plots, and measured fire characteristics at ground level. We also measured characteristics of ground-layer oaks and grasses before, then 2 and 8 months after fires. We tested our hypotheses regarding effects of pyrogenic pine fuels on fire characteristics and vegetation regrowth and explored direct and indirect effects of fuels on fire characteristics and vegetation using a structural equation model. Pine needles influenced fire characteristics, elevating maximum temperature increases, durations of heating above 60°C, and fine fuel consumption considerably above measurements when fuels only included other savanna plants. Presence of pine needles depressed post-fire numbers of oak stems and grass culms, especially in the interior of grass genets, as well as post-fire flowering of grasses. The structural equation model indicated strong direct and indirect pathways from pine needles to post-fire responses of oaks and grasses. The experimental field tests of hypotheses, bolstered by structural equation modeling, indicate pyrogenic fine fuels modify characteristics of prescribed fires at ground level, negatively affecting dominant ground-layer oaks and grasses. Frequent fires fueled by pyrogenic needles should maintain humid savannas and generate spatial pyrodiversity that affects composition and dynamics of pine savanna ground-layer vegetation.

Key words: community organization; duration of heating; fine fuel combustion; fire-engineering; ground-layer oaks and grasses; maximum temperature increase; Pinus palustris; *post-fire regrowth and flowering; pyrodiversity; pyrogenic fuels; structural equation models.*

Introduction

Savannas are terrestrial ecosystems in which trees and grasses are co-dominant life forms. As documented by Sankaran et al. (2005) and Bucini and Hanan (2007), savannas occur over wide ranges of mean annual precipitation, including mesic (>650–800 mm) and high-rainfall (>1200 mm) regions (Platt 1999, Beckage et al. 2003, Slocum et al. 2010*b*, Lehmann et al. 2011, Ratnam et al. 2011, Hoffmann et al. 2012). Thus, savannas occur worldwide in some regions where closed-canopy forests would be expected based on rainfall alone (e.g., Woinarski et al. 2004, Bond et al. 2005, Bowman 2005, Beckage et al. 2009, Staver et al. 2011, Accatino and De Michele 2013). Since the initial appearance of C_4-grass-dominated savannas in the mid-Cenozoic (Beerling and Osborne 2006, Scheiter et al. 2012), humid savannas have occurred worldwide. Endemic savanna trees, grasses, and other plants indicate a long evolutionary history during which savanna conditions have been maintained (Simon et al. 2009, Maurin et al. 2014, Pennington and Hughes 2014, Noss et al. 2015).

Fire has often been proposed as the ecological process that maintains humid savannas. Acting alone or with other disturbances (Higgins et al. 2000, Platt et al. 2000, 2002, 2006*b*), recurrent fires can block formation of a closed canopy, maintaining grass-dominated ground layers, even in mesic and high-rainfall regions (Beckage et al. 2006, 2009, 2011, Lehmann et al. 2011, Platt et al. 2015, Dantas et al. 2016). Particularly high fire frequencies occur in humid savannas (e.g., Richards et al. 2012, Fill et al. 2015, Bond 2016). In these savannas, lightning ignited fires characteristically burn ground-layer vegetation

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during annually predictable fire seasons. These fire seasons follow dry seasons during which moisture content of fine fuels is reduced, and they occur before moisture increases substantially in ensuing wet seasons (Platt et al. 2015). Post-fire regrowth of C_4 grasses during these wet seasons results in widespread abundant fine fuel that is loosely packed (sensu Simpson et al. 2016), contains abundant air space, and dries quickly (Robertson and Hmielowski 2014). Spread of fires becomes likely when moisture content of the rapidly drying vegetation and associated litter (total fine fuels) is reduced to the point that combustion becomes self-sustaining across landscapes (e.g., Sarmiento et al. 1985, Slocum et al. 2010*a*, Platt et al. 2015). Ignition and spread of fires occurs almost every year in some humid warm temperate and subtropical savannas (e.g., Platt 1999, Slocum et al. 2003, 2007, Huffman 2006, Stambaugh et al. 2011, Ryan et al. 2013, Platt et al. 2015).

Frequent fire-season fires should affect grass-tree dynamics in mesic and high rainfall savannas. Such fires reduce litter and self-shading, enhancing high light conditions that facilitate rapid growth of C_4 grasses and generate new fine fuels (Uys et al. 2004, Sankaran et al. 2005, Bond 2008, Accatino et al. 2010, Beckage et al. 2011, Accatino and De Michele 2013). Fires also top-kill small woody plants with underground suffrutices that subsequently resprout (Sarmiento et al. 1985, Bond and Midgley 1995, Glitzenstein et al. 1995, Olson and Platt 1995, Higgins et al. 2000, 2007, Hoffmann et al. 2009, Werner and Prior 2013). Recurring fires fueled by C_4 grasses thus produce "fire traps," demographic bottlenecks that reduce chances that woody plants will reach the overstory (e.g., Bond and Midgley 1995, Higgins et al. 2007, Werner and Franklin 2010, Grady and Hoffmann 2012, Ellair and Platt 2013, Werner and Prior 2013). Nonetheless, variation in fire weather conditions (e.g., rainfall and drought conditions; Beckage et al. 2006, Slocum et al. 2010*b*) can influence fuel accumulations (e.g., Platt and Gottschalk 2001) and change fire regimes, especially in high rainfall regions, resulting in periodic escape of woody species from fire traps (Beckage et al. 2009, Ellair and Platt 2013).

Some savanna trees produce highly flammable fine fuels that might enhance frequent fire-season fires, reducing uncertainty in fire regimes of humid savannas. Shed leaves that are larger and/or longer tend to result in increased flammability, especially if leaves do not pack or decompose readily in the litter (e.g., Scarff and Westoby 2006, Schwilk and Caprio 2011, Murray et al. 2013, Grootemaat et al. 2015). Depending on patterns of leaf fall around trees, leaves of some species may become distributed throughout ground-layer vegetation, as well as on the ground surface, effectively decreasing bulk density and increasing volume of the fuel bed, enhancing likelihoods of ignition by lightning strikes and subsequent fire spread. In addition, leaves that contain volatile compounds should affect fire characteristics more than other flammable fuels (e.g., Ormeño et al. 2009, van Altena et al. 2012, de Magalhäes and Schwilk 2012, Ellair and Platt 2013). Pyrogenicity could reduce chances that small trees of species sensitive to increased fire intensity escape the fire trap, and thus prevent growth into the canopy by forest trees in the vicinity (Platt 1999, Beckage et al. 2009). Both juveniles and adults of savanna trees that produce pyrogenic fuels tend to be protected from fires (e.g., Platt et al. 1988, Jackson et al. 1999, Grace and Platt 1995, Lawes et al. 2011, 2013), and so increases in densities might result in "woodlands" as one extreme of a continuum in savanna tree density (Fill et al. 2015). In such cases, fuels shed beneath and around savanna trees could replace those fuels normally provided by grasses. Moreover, trees producing pyrogenic fuels could modify fires in ways that reduce chances of humid savannas/woodlands transitioning to forest, especially if grasses maintain fuel continuity in treeless areas (Platt 1999, Ellair and Platt 2013, Veldman et al. 2015). Thus, pyrogenic fuels produced by savanna trees might fire-engineer humid savannas and woodlands.

We propose that shed pyrogenic fuels engineer characteristics of fires, influencing ground-layer vegetation in humid savannas. We expect fires fueled by pyrogenic shed leaves to depress dominant groundcover plants (e.g., woody plants and grasses). Effects might include increased likelihoods that woody stems are girdled and dormant buds at the soil surface are damaged, so that resprouting occurs from a reduced bud bank located belowground (Glitzenstein et al. 1995, Olson and Platt 1995, Drewa et al. 2002). Hence, repeated fires fueled by pyrogenic shed leaves should influence genets of woody plants with underground storage organs. Effects also might involve mortality of culms of savanna grasses, although genet architecture (especially of bunch grasses) has been proposed to reduce effects of pyrogenic fuels on meristems at ground level (Gagnon et al. 2010, 2012). These proposed effects should depend on the presence and amounts of pyrogenic fuels, and thus variation in pyrogenic fuels could result in spatial heterogeneity in the dominance of shrubs and grasses in the ground layer of savannas (Ellair and Platt 2013).

We explored our general hypothesis using a field experiment in a frequently burned, high-rainfall North American coastal plain pine savanna. The dominant tree, longleaf pine (*Pinus palustris*) produces resinous needles that, when shed and dried, are more flammable and burn at higher temperatures than leaves of other pines and hardwoods (Williamson and Black 1981, Fonda 2001, Ellair and Platt 2013). We postulated that needle deposition in fuels influences fire characteristics at ground level, and consequently, post-fire responses of groundcover shrubs and grasses more than other fine fuels (shed leaves of savanna oaks and grass culms). We further reasoned that as amounts of pyrogenic needle fuels increases, effects on fire characteristics should augment depressant effects on oaks and grasses. We anticipated that effects of pyrogenic pine needles should be manifest post-fire in regrowth of shrub genets, maintaining an effective fire trap, and in survival of grass culms, affecting clonal structure and genet architecture.

To examine these hypotheses, we manipulated amounts of longleaf pine needles in natural pine savanna groundcover, conducted prescribed fires under natural conditions, and measured fire characteristics and responses of groundcover oaks and grasses. Prior to each fire, we measured fuels present in situ and then experimentally manipulated amounts of pine needles in plots containing ground-layer oaks and grass clumps. During fires, we measured fire characteristics at ground level; after fires, we resampled fuels to estimate combustion. We measured regrowth of oaks and grasses before and at 2 and 8 months (at the end of the growing season) after fires. We used parametric analyses (MANOVA, MANCOVA) to test a priori hypotheses and structural equation models (SEM) to examine how the presence and different amounts of pyrogenic pine needles and other fine fuels might affect fire characteristics and groundcover vegetation in different environmental contexts. We then explored consequences of engineering of fuels by savanna trees on the ground-layer vegetation in humid savannas.

Methods

Conceptual model, included/excluded variables, and field design of the experiment

Fire is a complex process. Cause-effect relationships are multivariate and hierarchical, often resulting in variable effects at small scales. We use a structural equation model (SEM) to depict potential contributors to variation in fires and fire effects in the ground layer of a pine savanna. Such linear models enable hypothesized relationships to be explored in the context of a complex, interacting environment (Fox 2006, Grace 2006, Grace et al. 2010).

We designed our field experiment to manage variation in amounts, structure, and types of fuels. We linked site conditions, fuels, fire, and ground-layer plants using a network of hypothesized directional pathways (Fig. 1). We embedded our hypothesized effects of pyrogenic longleaf pine fuels within this network as a set of hierarchical relationships. Our manipulations of pyrogenic pine needles, depicted in a treatment compartment, are linked, through fuels, to potential direct effects on fires (Fig. 1).

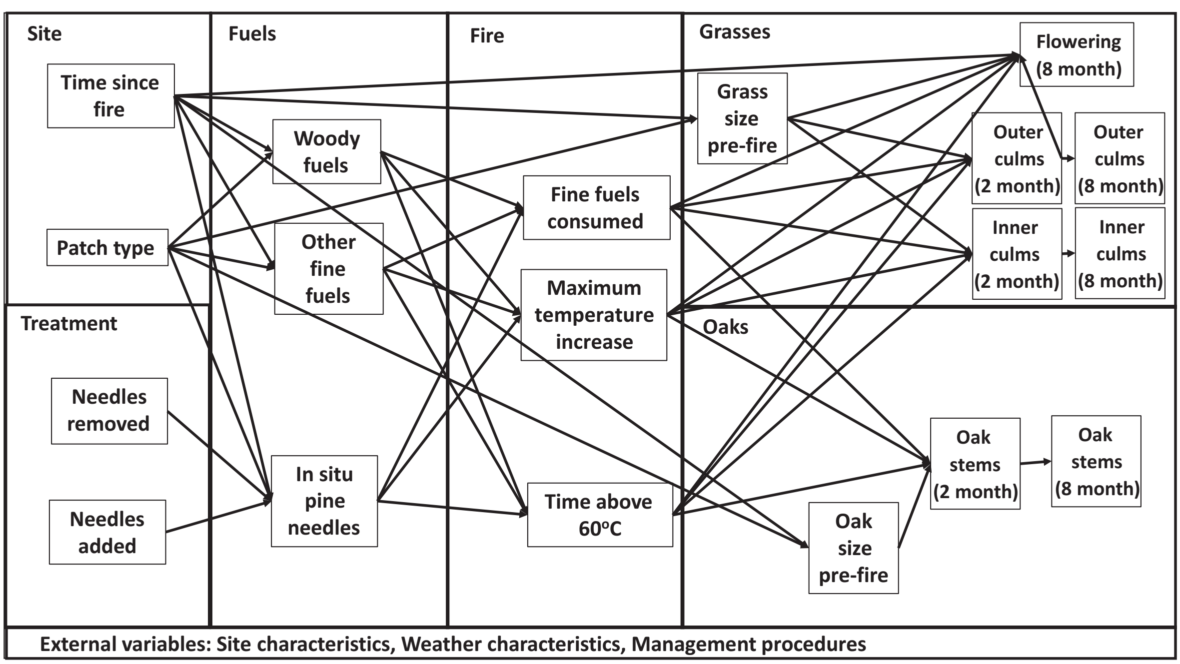

Fig. 1. Directional conceptual model used for field study of effects of pyrogenic pine needles on characteristics of fires at ground level and ground-layer oaks and grasses in a pine savanna. Six boxes (site, treatment, fuels, fire, grasses, and oaks) indicate major components of the study. Site indicates local conditions (time since fire, different patches of vegetation) potentially affecting fuels and groundcover vegetation at the time of fires. Treatment refers to experimental manipulation of pine needle fuels that involved additions to and removals from in situ fuels. Fuels include dead and live vegetation in the ground layer that potentially combusts during a fire, grouped as pine needles, other fine fuels, and woody fuels. Fire includes the combustion of fine fuels, the maximum temperatures at ground level, and the duration of heating above 60°C. Grasses and oaks are the dominant lifeforms in the ground layer. Characteristics of the grasses measured include pre-fire size (basal diameter of clumps), as well as the density of culms in the interior and surrounding exterior of the clump, and number of flowering culms at 2 and 8 months post-fire. Measurements of oaks include pre-fire size (basal diameter), and numbers of stems comprising genets at 2 and 8 months post-fire. Arrows denote potential connections between measured variables that characterize the different components and are directional from left to right. External variables not explored as part of the study and in which we reduced variation via control of site location and prescribed fires are indicated in a box without arrows.

Local variation in site conditions, weather prior to and during fires, and procedures used to conduct prescribed fires influence variation in fire characteristics (e.g., Thaxton and Platt 2006, Hiers et al. 2009, Platt et al. 2015). We reduced variation in external variables by conducting fires under similar weather and management conditions; we indicate external components that we managed or excluded from our conceptual model at the bottom of Fig. 1. This hybrid approach involving experimental testing of a priori hypotheses and SEM resulted in more robust conclusions than using either approach alone.

Field study site.—We conducted our study using Girl Scout Camp Whispering Pines (30°41′ N; 90°29′ W) in Tangipahoa Parish, Louisiana, USA. This site, moderately dissected upland terrain 25–50 m above sea level in the Tangipahoa River drainage, contains well-drained silty soils mixed with and capped by loess (fragiudults; McDaniel 1990). Camp Whispering Pines contains ~400 ha of pine savannas/woodlands that have remained intact over the past century (Platt et al. 2006). Overstory longleaf pines ~100 yr old form a non-contiguous matrix (Noel et al. 1998), within which are embedded scattered patches of overstory oaks and hickories (*Quercus falcata*, *Q. stellata*, *Carya tomentosa*) and grass-dominated patches without overstory trees. Ground-layer vegetation is dominated by C_4 grasses (*Schizachyrium scoparium* and *S. tenerum*), but also contains a wide diversity of herbaceous and woody plants. Since 1990, management has included prescribed fires that mimic the 1–2 yr frequency and timing (fire season) of natural lightning-ignited fires in pine savannas (Platt 1999, Platt et al. 2015). A more detailed history of Camp Whispering Pines, its restoration and prescribed fire management, is presented in Platt et al. (2006) and updated in Appendix S1.

Local site context.—We managed local variation in fuels and vegetation through location of experimental units, providing a local site context for the experiment. We anticipated differences in fuels resulting from differences in total amounts (time since fire), as well as location in different vegetation patches (arrows from Site to Fuels in Fig. 1). We further expected site differences to affect ground-layer oaks and grasses directly independent of effects on fuels (arrows from Site to Grasses and Oaks in Fig. 1). We did not expect site-related differences to influence fire characteristics independent of effects on fuels. Moisture content of pine, oak, and grass fuels in patches with different overstory conditions did not differ greatly at times of prescribed fires (W. J. Platt, *unpublished data*), and so we did not include direct site–fire relationships in our conceptual model (Fig. 1).

We controlled time since fire by conducting the study in two fire management units separated by a road. Both units, each ~100 ha of upland longleaf pine savanna, had been prescribed burned on a biennial schedule in alternate years for the past 20 yr as part of the restoration program (Platt et al. 2006, Ellair and Platt 2013). When we conducted our field experiment in 2011, the units had last been burned in May 2009, and May 2010, resulting in 1 and 2 yr since the last fire, respectively. We anticipated greater amounts of fuels with a longer time since fire. We also hypothesized that fuel structure would differ with time since fire, as fuels become more layered and concentrated closer to the ground over time. Thus, as indicated in Table 1, the experimental design incorporated time since fire as a complex natural categorical variable (and hence coded in SEM) including both amounts and structure.

We also controlled some heterogeneity in fuel composition. Live and dead fine fuels comprise almost all fuels consumed in frequent pine savanna fires (Platt et al. 1991, Robertson and Ostertag 2007, Hiers et al. 2009, Reid et al. 2012, Ellair and Platt 2013). To reduce variation in these fine fuels (Thaxton and Platt 2006, Hiers et al. 2009, O'Brien et al. 2013), we located patches with different dominant vegetation in each fire management unit: longleaf pine, savanna oaks, or warm-season grasses. These patches contained flammable fine fuels dominated by savanna trees (pines and oaks) and grasses. In each fire unit, we selected one patch of each type with a radius of at least 10 m. Although all patches contained fine fuel mixtures of pine needles, oak leaves, and warm-season grasses, we anticipated that relative composition of fuels in patches would differ, reflecting dominant vegetation. Thus patch type was also incorporated as a categorical variable and coded for SEM (Table 1). Our field design also generated potential interactive effects due to differences in fuel production in vegetation patches over the two lengths of time since fire.

Weather and prescribed fire management.—We standardized weather conditions and used the same prescribed fire techniques to burn both fire management units. Fire management units were burned at similar times since rainfall, at similar times of day, and under similar conditions of air temperature, humidity, and wind. The 2-yr fire unit was burned on 2 May 2011, 6 d since last rainfall, starting around 10:00; fires reached vegetation patches 2.0–2.5 h after ignition. The 1-yr fire unit was burned on 11 May 2011, 7 d since last rainfall, starting around 10:00; fires reached vegetation patches 1.0–1.5 h after ignition. On 2 May and 11 May, air temperatures during fire were, respectively, 30°C with 67% relative humidity and 29°C with 59% relative humidity. Winds were from the south-southeast both days, 21–26 km/h on 2 May and 15–18 km/h on 11 May. Weather data were taken at Hammond, Louisiana, ~18 km south of the study site, at the National Climatic Data Center operated by the National Oceanic and Atmospheric Administration (data *available online*).[4] We used similar procedures to conduct both prescribed fires. Fires were ignited with a drip torch; experimental units burned with flanking and head fires. We assume that using similar weather

[4] http://www7.ncdc.noaa.gov/CDO/dataproduct

Table 1. Summary of variables and transformations included in MANOVA and SEM analyses; empty cells indicate absence of variable in analysis.

Variable name	MANOVA type/ transformation	SEM Code/ Transformation	Description
Time since fire	categorical	1 yr = 0; 2 yr = 1	1 or 2 yr since last fire; amounts and structure of fuels
Patch	categorical	P = 1, O = 0, G = 0; P = 0, O = 1, G = 0	different patches: pine (P), oak (O), or grass (G) dominated patches
Treatment	categorical	R = 0, IS = 1, A = 1	Unaltered in situ (IS) fuels, addition (A) or removal (R) of pine needles
Pine needle fuels	natural log	none	fuel load (g/m^2) of pine needles sampled before fire (after treatments applied)
Other fine fuels	natural log	natural log	fuel load (g/m^2) of fine fuels other than pine needles (oak leaves, grass, forbs, litter) sampled before fire
Woody fuels	natural log	natural log	fuel load (g/m^2) of woody fuels sampled before fire
Fine fuels consumed	natural log	none	difference in load (g/m^2) of fine fuels collected pre- and post-fire; the amount of fuels consumed by fire
Maximum temperature increase	none	none	difference in temperature (°C) between maximum recorded during fire and ambient recorded pre-fire
Time above 60°C	natural log	natural log	amount of time (minutes) that temperatures remained elevated above 60°C
Oak size pre-fire	square root	square root	area (cm^2) of root crown of target oak genet before fire
Oak stems (2 months)	square root	natural log(no. stems + 1)	number of oak stems within the target genet, sampled 2 months after fire
Oak stems (8 months)	square root	natural log(no. stems + 1)	number of oak stems within the target genet, sampled 8 months after fire
Oak height (2 months)	none	none	height (cm) of tallest oak stem per genet, sampled 2 months after fire
Oak height (8 months)	none	none	height (cm) of tallest oak stem per genet, sampled 8 months after fire
Grass size pre-fire	none	natural log	area (cm^2) of target grass clump before fire
Inner grass culms (2 months)	square root	natural log(no. stems + 1)	number of grass stems within a central 2 × 2 cm square inside the target genet, sampled 2 months after fire
Inner grass culms (8 months)	square root	natural log(no. stems + 1)	number of grass stems within a central 2 × 2 cm square inside the target genet, sampled 8 months after fire
Outer grass culms (2 months)	square root	natural log(no. stems + 1)	difference between total number of grass culms and culms in center, sampled 2 months after fire
Outer grass culms (8 months)	square root	natural log(no. stems + 1)	difference between total number of grass culms and culms in center, sampled 8 months after fire
Flowering grass culms (8 months)	square root	natural log(no. stems + 1)	number of flowering culms within the target genet, at 8 months after fire

Notes: The pre-burn MANOVA had seven response variables (each type of fine and woody fuel) and two independent categorical variables (time since fire, patch) with interaction. The MANOVA on burn effects included grass clump basal area as a control variable; three categorical independent variables (time since fire, patch, treatment) with all interactions; and 12 dependent variables (maximum temperature increase, duration of heating, fine fuel consumption, number and height of oak stems at 2 and 8 months, number of grass culms inside and outside the clump center at 2 and 8 months, flowering culms at 8 months). Codes for categorical variables are discussed further in Appendix S4.

conditions and methods for conducting prescribed fires likely reduced confounding effects otherwise expected. Thus, we excluded weather and fire management effects from our model (Fig. 1). We recognize that reducing variation in fire characteristics could limit generality of our results if more extreme variation in fire characteristics influences effects of pyrogenic fuels.

Experimental plots and treatments.—At the onset of the study, we located nine plots within central regions of each of the six combinations of time since fire and patch type. Plot locations within patches were random, except that no plot contained large pieces of wood; also, any wood >2 cm in diameter was removed that fell into a plot. This eliminated extreme variation in fuel characteristics (e.g., increases in fuels from hurricane-downed trees; Thaxton and Platt 2006, Gagnon et al. 2012). Each plot was 2 × 2 m, with a central 1 × 1 m quadrat around which the remaining 3 m^2 comprised a border 0.5 m in width (Fig. 2).

We located each plot so that each central 1 × 1 m quadrat contained at least one oak genet and one grass clump. Target ground-layer oaks in two-thirds of the plots in time-since-fire–patch combinations were *Quercus falcata* (southern red oak) and in one-third were *Q. nigra* (water oak). These oaks had not developed thick bark; all had live and dead stems present, indicating prior top-kill and resprouting from a root crown. Sizes of oaks varied, with root crown surface areas of 2–266 cm^2, 2–16 stems, and heights of 17–123 cm. *Schizachyrium scoparium* (little bluestem) was our target grass; grass clumps, composed of 2–92 culms, ranged from 3 to 456 cm^2 in basal area. Measurements of plant size were correlated; we used oak root crown area and grass basal area as covariates in analyses. The nine plots in each time-since-fire–patch combination were grouped into three replicated sets based on oak species and sizes of oaks.

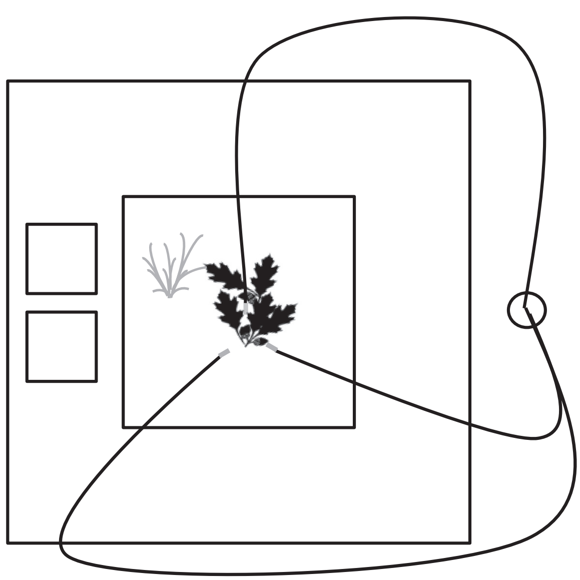

Fig. 2. Diagram representing 4-m^2 plot, with inner 1 × 1 m quadrat containing an oak and grass, two adjacent 30 × 30 cm fuel sampling plots, and the location of data loggers buried outside plot, with three thermocouples and cables positioned around the target oak stem and connected to data loggers.

Each of the three plots in the three replicated sets was randomly assigned to one of three pine needle fuel treatments. One treatment (Table 1) was in situ mass of pine needles (no alteration of natural fuel loads); in these plots, pre-fire mass of pine needles averaged 369 ± 42 g/m^2. The other treatments, applied to in situ pine needles several weeks prior to fires were fuel manipulations (decrease/increase in pine needles; Table 1). Decreases involved removal of all pine needles located in fuel-removal plots, resulting in pine needle mass of ~0 g/m^2. Needle-by-needle extraction minimized disruption of fuel structure and vegetation. We based increases in pine needle fuels (300 g/m^2) on prior studies (Thaxton and Platt 2006, Ellair and Platt 2013). Pine needle mass in fuel-addition plots averaged 672 ± 40 g/m^2, slightly less than double the mean of in situ fuel plots. Fuel additions resulted in pine needle fuel loads well within the range of natural variation at Camp Whispering Pines (Thaxton and Platt 2006). Pine needles collected in the vicinity were hand-distributed across the surface of fuel-addition plots in a way that simulated increased needlefall; the amounts used did not generate a deep fuel bed of needles.

Our field design involved a total of 54 plots. These were arrayed in the field as 2 fire units (times since fire) × 3 patch types/fire unit × 3 treatments/patch type/fire unit and each of the 18 combinations was replicated three times. The fuel manipulations altered pine needle fuels independently of site characteristics. Thus, treatment effects, as described in Table 1 and depicted in Fig. 1, are independent of site effects, which are presumed to affect in situ pine needles. We conducted the experiment under controlled and standardized environmental conditions, reducing chances that external effects might blur effects of treatments. The field design thus enabled parametric data analyses within the context of an experiment designed to explore relationships among different hierarchical components. The potential pathways connecting left and right sides (Fig. 1) enabled us to explore effects of time since fire, patch type, and presence/absence and amounts of pine needles on amounts and composition of fine fuels, characteristics of prescribed fires at ground level, and responses of groundcover vegetation.

Measured variables

Characteristics of fuels.—We sampled ground-layer fuels for each plot, measuring amounts and composition of fuels before and after prescribed fires. About 2 weeks prior to fires, post-treatment, we collected all aboveground vegetation and litter from one (randomly selected) of two paired 30 × 30 cm quadrats randomly located along the border of each plot (Fig. 2). We sorted fuels into fine and woody fuels. We sorted fine fuels into groups: pine needles, hardwood leaves, grasses, forbs, and litter (fragments too decomposed to be categorized). Woody fuels (bark, stems, cones, acorns) were sorted into pine and hardwood fuels. We dried and weighed fuel samples to obtain total and component pre-fire fuel mass for each plot. Arithmetic and geometric means and confidence intervals of pre-fire fuels were calculated based on time since fire, patch type, and treatment (pine needle manipulation). Data were natural log-transformed to increase homogeneity, so we present geometric means and 95% confidence intervals.

A few hours after fires, we returned to each plot and collected residual fuels from the other 30 × 30 cm quadrat. These post-fire fuel samples were sorted into fine (ash, fragments of needles and leaves, litter) and woody (discernible pieces of bark, stems, branches, cones, acorns) fuels. We used the pre- and post-fire measurements in each plot to estimate consumption of fine, woody, and total groundcover fuels in prescribed fires. We analyzed effects of site conditions and treatment on these estimates of fuel consumption.

Characteristics of prescribed fires.—We measured a suite of variables to characterize fires. A number of these variables extracted from or derived from field data were not included in analyses. Fire variables that were excluded are summarized in Appendix S2: Table S1.

We measured temperatures at ground level over time during fires within each 1-m^2 quadrat. Thermocouples attached to data loggers by cables (Fig. 2) recorded temperatures every second at the soil surface around oak stems. Data loggers were constructed as described in Ellair and Platt (2013) and Gagnon et al. (2015). We used three thermocouples in each plot in case there were outliers or logger failures during fires. Prior to fire, thermocouple probes were positioned on the soil surface beneath fuels at 10-cm distances at angles of 0°, 120°, and 240° from target oaks (Fig. 2). Data loggers attached to thermocouples were enclosed in plastic bags and buried outside plots. Loggers were retrieved about 3 h after fires, and data were downloaded.

Two variables extracted from temperatures recorded over time by data loggers were used in analyses. Maximum temperature increase was calculated as the difference between maximum temperature reached during fire and the ambient temperature before fire. Duration of heating was calculated as the time (minutes) that the temperature at the soil surface remained elevated above 60°C. Other studies have indicated that temperatures above 60°C in non-prolonged fires are lethal to plant tissues (e.g., Costa et al. 1991, Gutsell and Johnson 1996, Dickinson and Johnson 2001, Bova and Dickinson 2005, Choczynska and Johnson 2009). Data collected from different data loggers within each plot were averaged to yield single values for analyses. Values greater than three standard deviations from the mean of fire characteristics were considered outliers and were excluded from analyses. Other variables not used are listed in Appendix S2: Table S1. Final data sets were used to calculate means and in parametric analyses.

Characteristics of vegetation.—We measured characteristics of oaks and grasses in the ground layer of central 1 × 1 m quadrats before and after fires. A month before prescribed fires, we measured sizes of oaks and bunchgrasses. We measured right-angle diameters of root crowns of target oaks and of bluestem grass clumps and estimated ground surface area occupied by each genet. These genet sizes were used to group plots in treatment combinations so that they had somewhat similar sizes of target plants and were used as covariates in analyses. We measured additional characteristics of target oaks and grasses prior to fires and at 2 and 8 months after fires. We counted stems and measured diameters at ~0.5 cm and height from ground to the tip of the apical meristem for each stem in oak genets. Stem diameter was highly correlated with stem height, so was excluded from further analyses; number of stems and maximum height were used to analyze oak growth responses to fire. These variables provide adequate characterization of resprouting in hardwoods (Schafer and Just 2014). For grasses, we counted vegetative and flowering culms, both in the entire genet and in a 2 × 2 cm marked section in the interior of each clump. During the first post-fire census, we examined each oak and grass genet for fire damage; we noted patterns of regrowth at each post-fire census. No measurement varied significantly when the two species of oaks used in the study were separated in analyses; thus, data were pooled for oaks. Appendix S2 includes further description of variables measured, but later excluded, for both oaks (Appendix S2: Table S2) and grasses (Appendix S2: Table S3). Final data sets were used to estimate means and in parametric analyses.

Analyses

Parametric data analyses.—Strengths of directional relationships in this study's underlying conceptual model (Fig. 1) were tested with multivariate (PROC GLM) and univariate (PROC REG) analyses using SAS 9.4 (SAS Institute 2014). Concurrent variation of seven pre-fire fuels among aspects of local site context (time since fire and patch type) was analyzed with a 2 × 3 factorial multivariate analysis of variance (MANOVA). The simultaneous variation of nine post-fire vegetation effects and three fire characteristics among local site context (time since fire, patch type, and pine needle treatment), controlling for additive effects of grass clump basal area and oak root crown basal area, was analyzed with a 2 × 3 × 3 factorial multivariate analysis of covariance (MANCOVA). A priori orthogonal contrasts for the MANCOVA tested significance between pine treatments for both absence vs. presence of pine needles and in situ vs. added pine needles. The influences of individual response variables on significant effects in both analyses were indicated using squared standardized canonical correlation coefficients (R^2 values for linear correlations that denote the strength of correlation and percentage of variance explained for each response). Large values denote response variables responsible for significant effects. Variables included in the MANOVA and MANCOVA were transformed for linearity, normality of residuals, and homogeneity of variance (Table 1). Normality of residuals was tested using the Shapiro-Wilk statistic (PROC UNIVARIATE). Homogeneity of variance was tested with chi-square tests (PROC DISCRIM). Additional information is presented in Appendix S3.

Univariate regressions were used to describe relationships between pine needle mass across sites on influential fire characteristics. Effects of fire characteristics and pre-fire vegetation on post-fire vegetation were investigated in PROC REG. Final model covariates were determined by stepwise variable selection, with 0.15 entry significance criterion.

Structural equation model.—Our SEM contained continuous and categorical metrics associated with site, treatment, fuels, fire, and vegetation. Descriptions of variables and how they were incorporated into the SEM are denoted in Table 1 and described in Appendix S4. All variables were checked for normality and transformed when necessary to obtain normality and reduce skewness (Table 1), and all bivariate relationships were examined for linearity (Grace 2006). We used SPSS AMOS 21 (Arbuckle 2010) to evaluate the SEM using maximum likelihood ratio tests. The initial SEM (Appendix S4: Figure S4-1) reflected our initial conceptual model (Fig. 1). Model selection is presented in Appendix S4.

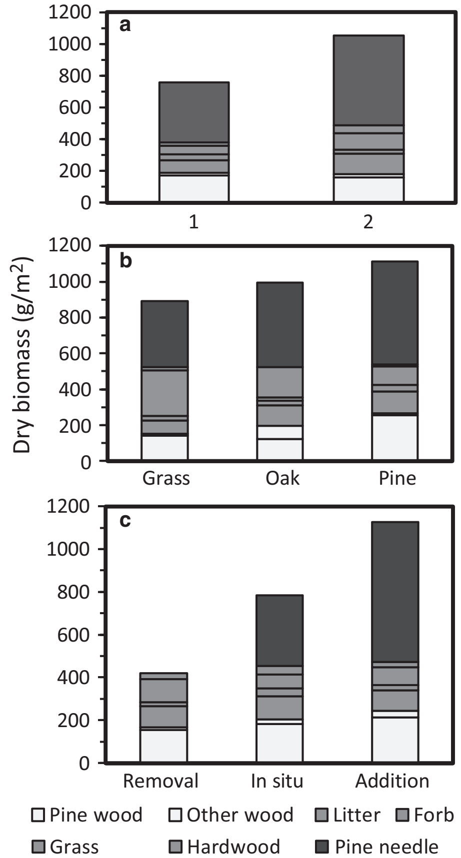

Fig. 3. Effects of site characteristics and treatment on pre-fire fuel loads. (a) Time (1 and 2 yr) since fire. (b) Patch type: no trees (grass), hardwood trees (oak), and pine (pine). (c) Treatment: pine needle removal, in situ, and addition (300 g). Data for time since fire and patch type are based on in situ and addition plots (subtracting 300 g from pine biomass). Data for treatment involve all plots. Shades are coded to represent pine fuels (black), other fine fuels (dark gray), and wood fuels (light gray). Data are presented in Appendix S3: Table S3-1. Statistical tests are presented in Appendix S3: Table S3-2 and summarized in *Results*.

Results

Pre-fire fuels

Site characteristics influenced amount and composition of fuels present post-treatment and prior to fires. Geometric means and 95% confidence intervals for fuel categories are presented in Appendix S3: Table S1 separately for time since fire and patch types. Mean fuel masses for the different categories as a function of site characteristics separately are presented in Fig. 3.

Fuel mass was greater the second year after fire. Mean total mass of fine + woody fuels was 38% greater 2 yr (1341 g/m^2) than 1 yr (973 g/m^2) since fire; 95% confidence intervals indicated highly significant pairwise differences (Appendix S3: Table S1.1). Most of this difference resulted from fine fuels (Fig. 3); mean fine fuel biomass increased 44% (737–1063 g/m^2) from 1 to 2 yr since fire. All fine fuels except forbs increased in the second year after fire (Appendix S3: Table S1.1), and again 95% confidence intervals indicate highly significant differences. In contrast, mean mass of woody fuels was only 8% greater 2 yr (230 g/m^2) than 1 yr (213 g/m^2) after fire, and 95% confidence intervals indicated no significant differences.

Total pre-fire fuel mass differed slightly among patch types. Patches dominated by grasses, oaks, or pines had similar mean total fuel biomass (range 911–994 g/m^2), as well as similar mean fine fuel biomass (range 654–718 g/m^2), as indicated in Fig. 3. The 95% confidence intervals overlapped the means for total fine, total wood, and total fuel biomass (Appendix S3: Table S1.2). Local patch types were reflected in the composition of fine fuels (Appendix S3: Table S1.2); grass and hardwood fuels were most prominent in grass and oak patches, respectively, while pine fuels were prominent in all patch types (Appendix S3: Table S1.3). Woody fuel biomass means were higher for pine (250 g/m^2) and oak patches (234 g/m^2) than for treeless grass patches (173 g/m^2), but 95% confidence intervals indicated substantial overlap in woody mass (Appendix S3: Table S1.2).

MANOVA indicated that site characteristics influenced composition and amounts of post-treatment, pre-fire fuels. Accounting for correlations among response variables, both time since fire ($F_{7,42}$ = 5.59;

$P < 0.001$) and patch type ($F_{14,84} = 10.28$; $P < 0.001$) had significant effects (Appendix S3: Table S2). The nonsignificant interaction between time since fire and patch type indicated that changes over time in fuels did not vary greatly among patch types (Appendix S3: Table S2). Fine fuels were more influential than woody fuels; R^2 values for effects of site characteristics on fine fuels tended to be much larger for fine fuels than woody fuels (Appendix S3: Table S2). Positive effects on fine fuel biomass comparing 1–2 yr post-fire were most notable for litter. Variation in fuel mass among patch types was strongly influenced, and in different directions, by variation in oak and grass fuels, which were positively associated with their patch type. The small standardized canonical correlation coefficients relating pine needle biomass to site characteristics (Appendix S3: Table S2) underscored the treatment-site independence with respect to fuels.

Manipulations of pine needle fuels resulted in large differences in pine needle biomass at the time of fire, independent of site characteristics. Mean total other fine fuel biomass and total wood biomass were similar across treatments (Fig. 3), and confidence intervals for fuel categories other than pine needles overlapped considerably (Appendix S3: Table S1.3). Mean biomass of pine needles fuels were 0, 329, and 652 g/m^2 in removal, in situ, and addition plots (Appendix S3: Table S1.3), comprising, on average, 0% (removal), 43% (in situ), and 64% (addition) of total fine fuels.

Post-fire results

MANCOVA, controlling for pre-fire effects of sizes of oak and grass genets, indicated effects of site characteristics and treatment on fire characteristics and post-fire vegetation. Statistical analyses are presented in Appendix S3. As indicated in Appendix S3: Table S3, there were strong effects of pine needle fuel treatment ($F_{26,46} = 6.90$; $P < 0.001$), as well as weaker influences of time since fire ($F_{12,23} = 2.21$; $P = 0.035$) and patch type ($F_{24,46} = 2.27$; $P = 0.008$). Nonsignificant two- and three-way interactions of main effects on fire characteristics and post-fire vegetation underscored independence of treatment and site characteristics (Appendix S3: Table S3). Pre-fire sizes of oaks ($F_{12,23} = 5.06$; $P < 0.001$) and grasses ($F_{12,23} = 14.80$; $P < 0.001$) also influenced responses of plants (Appendix S3: Table S3).

Fire characteristics.—Pine needle fuel treatments affected fire characteristics. Structural canonical coefficients indicated that effects of fuel treatment on fine fuel consumption ($R^2 = 0.64$), maximum temperature increase ($R^2 = 0.56$), and time above 60°C ($R^2 = 0.48$) had by far the largest effect on all three fire characteristics (Appendix S3: Table S3). Considerably larger proportions of fine fuels were consumed in fires when pine needles were present (Fig. 4a), and added pine needles resulted in almost complete combustion of fine fuels (Fig. 4a). On average, removing pine needles resulted in only 36% of

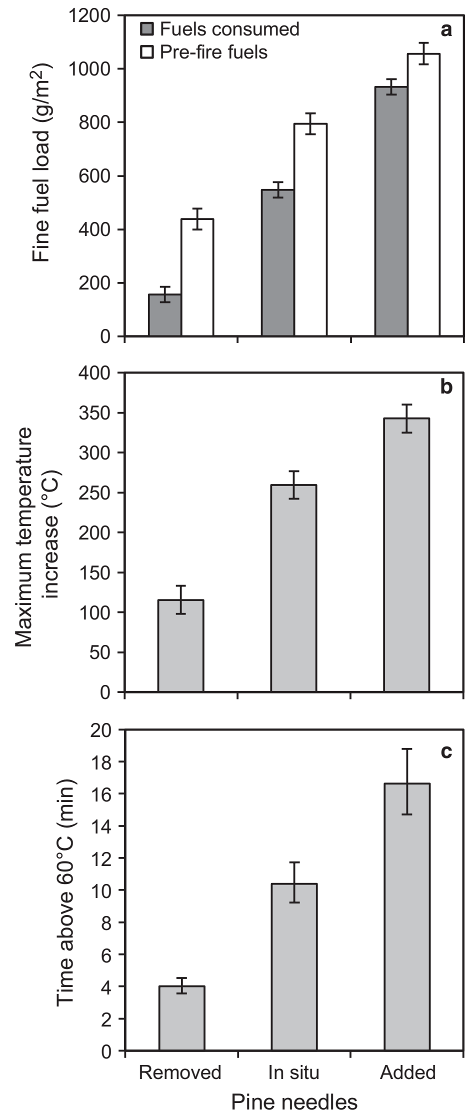

FIG. 4. Responses of (a) fine fuel consumption, (b) maximum temperature increase, and (c) time above 60°C to three pine needle fuel treatments. Values are means ± standard errors. Statistical tests associated with these figures are presented in Appendix S3: Table S3-3 and summarized in *Results*.

fine fuels being consumed, compared to 69% for in situ pine needle fuels, and 88% when additional pine needles were added (Fig. 4a). Temperatures (Fig. 4b) and durations of heating (Fig. 4c) also increased when pine needles were added, and decreased when pine needles were removed. Overall effects of treatments, based on orthogonal contrasts (Appendix S3: Table S3), were stronger when comparing absence (removal) and presence (in situ and addition) of pine needles ($F_{12,23} = 17.89$; $P < 0.001$) than comparing in situ and addition of pine needles ($F_{12,23} = 6.26$; $P < 0.001$). Structural canonical coefficients indicated that this pattern applied to fine fuel consumption, maximum increases in temperatures, and

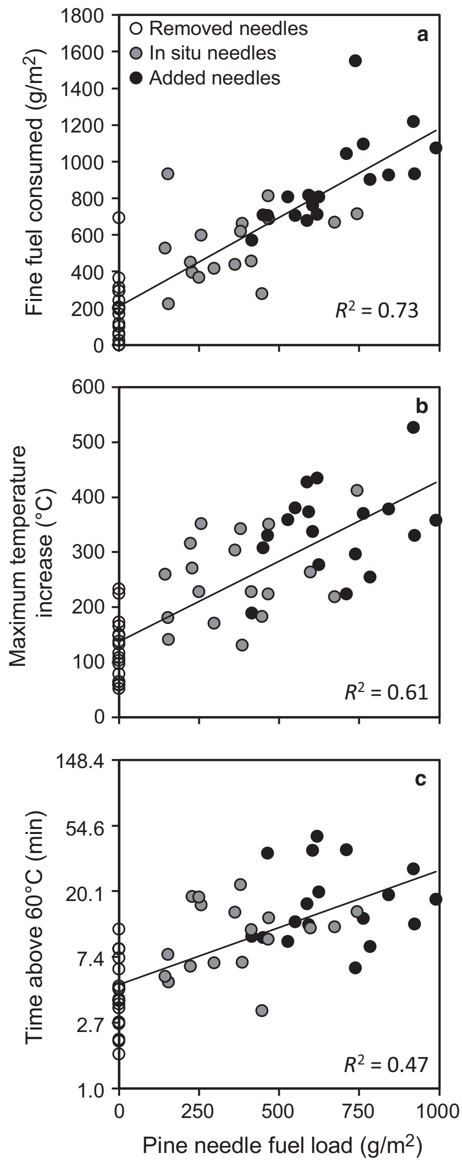

FIG. 5. Responses of (a) fine fuel consumption, (b) maximum temperature increase, and (c) time above 60°C to pine needle fuel loads. R^2 are partial regression coefficients. Statistical tests are presented in Appendix S3: Table S3-4 and summarized in *Results*.

time above 60°C (Appendix S3: Table S3). Neither measured covariate was related to fire characteristics (Appendix S3: Table S3).

Fire characteristics were linearly related to amounts of pine needles. Fine fuel consumption, maximum temperatures at ground level, and time above 60°C all increased as the amount of pine fuels increased (Fig. 5). Regressions indicated significant overall effects of pine needles on fire characteristics ($F_{3,50}$ = 66.06; P < 0.001). Amount of pine needles explained a large proportion of the variance for fine fuel consumption (R^2 = 0.73), maximum temperature increase (R^2 = 0.61), and the natural log of time above 60°C (R^2 = 0.47). Individual univariate regressions of fire characteristics on pine needle fuels indicated similar patterns (Appendix S3: Table S4).

Site characteristics (patch, time since fire) did not appear to influence fire characteristics at ground level. Partial regression coefficients indicated no substantial relationships with fire characteristics of main effects (time since fire or patch type), their interactive effects, or interactive effects with treatments (Appendix S3: Table S3). The only exception to this pattern was an indication that there might be a weak interaction between treatment and time since fire ($F_{24,46}$ = 1.75; P = 0.051; Appendix S3: Table S3); weak partial regression coefficients indicated that fine fuel consumption, maximum temperatures, and time above 60°C may have increased more in the second year after fire, perhaps reflecting greater amounts of pine needles (Fig. 4).

Responses of oaks.—Oaks were weakly affected by treatments. Effects on the two species were similar, and so species were pooled. At both 2 and 8 months post-fire, there tended to be more oak stems per genet when pine needle fuels were removed than when pine fuels were present (Fig. 6a). Partial regression coefficients indicated weak positive effects of fuel treatment (Appendix S3: Table S3). In addition, there was indication of an interaction between treatment and time since fire on numbers of oak stems 2 and 8 months after fire (Appendix S3: Table S3). As indicated in Fig. 6a, numbers of stems 2 months after fire were reduced considerably when pine needles were present, compared to when they were absent, but by 8 months after fire, more additional stems were present in pine needle plots than in removal plots. Orthogonal contrasts for a priori hypotheses indicated weak effects on numbers of oak stems at 2 months with pine needles absent or present and for added compared to in situ pine needles (Appendix S3: Table S3). By 8 months after fire, there were no notable effects of fuel treatments (Appendix S3: Table S3), either comparing effects of pine needles absent vs. present, or pine needles in situ vs. added (Appendix S3: Table S3). Heights of oak stems at 2 or 8 months after fire were not significantly related to fuel treatment or fire characteristics (Appendix S3: Tables S3 and S5). At 2 and 8 months after fire, numbers of oak stems were strongly positively related to pre-fire sizes (root crown area), and oak stem heights were positively related to time since fire (Appendix S3: Table S3).

Responses of grasses.—Numbers of culms in central regions of grass clumps were affected by treatments. Centers of clumps contained more grass culms post-fire when needles were removed and fewer when needles were added (Fig. 6b). Structural canonical coefficients indicated relationships between fuel treatments and numbers of culms in centers of clumps both at 2 (R^2 = 0.52) and 8 (R^2 = 0.55) months after fire (Appendix S3: Table S3). The effects were similar for absence vs. presence of pine

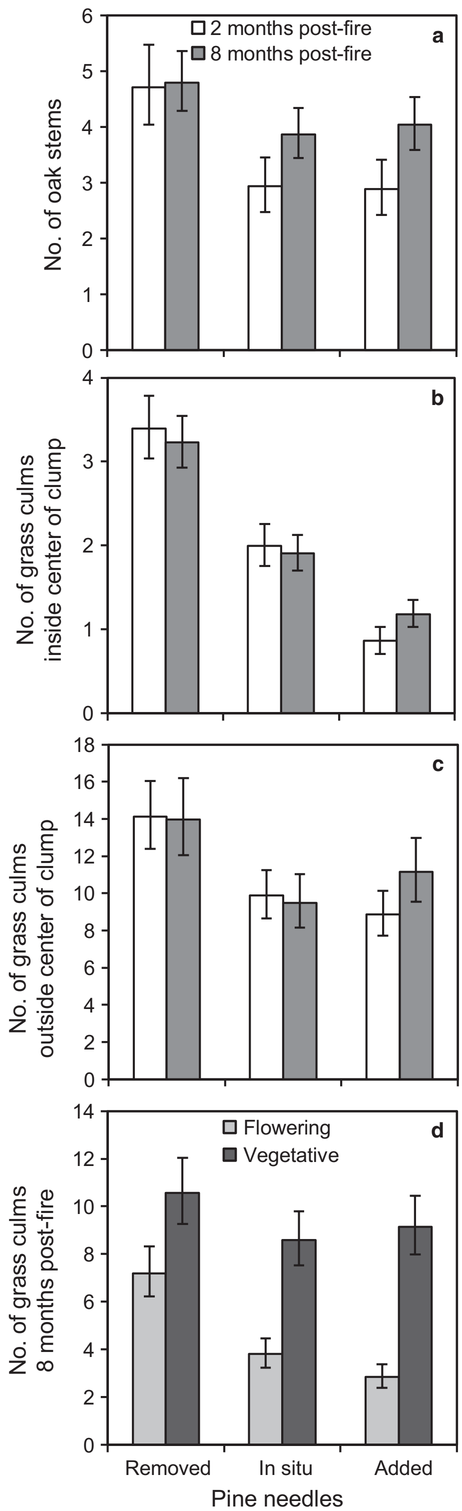

FIG. 6. Responses of (a) number of oak stems, (b) number of inner grass culms, (c) number of outer grass culms at 2 and 8 months, and (d) number of flowering and vegetative culms at 8 months to three pine needle fuel treatments. Values are means ± standard errors. Statistical tests are presented in Appendix S3: Tables S3-5, S3-6, S3-7 and summarized in *Results*.

needles and in situ vs. added pine needles at 2 and 8 months after fire (R^2 = 0.51–0.55; Appendix S3: Table S3). In addition, numbers of culms in centers of clumps at 2 months were related to the interaction between time since fire and treatment (R^2 = 0.64; Appendix S3: Table S3). Numbers of culms in the centers of clumps tended to be similar in plots burned 1 and 2 yr after fire, but when pine needles were present, fewer culms tended to be present in the center of grass clumps in plots burned 2 yr after fire than in plots burned 1 yr after fire.

Numbers of grass culms outside the central 4 cm^2 were weakly related to fuel treatments. More grass culms occurred in the outer portion of the clump at 2 and 8 months when pine needles were removed than when pine needles were present (Fig. 6c). Structural canonical coefficients for numbers of outer culms at 2 and 8 months were weakly related to fuel treatments, and also were strongly influenced by patch and time since year effects (Appendix S3: Table S3). Weak positive treatment effects occurred for absence vs. presence of pine needles and in situ vs. added pine needles at 2 and 8 months after fire (R^2 = 0.27–0.46; Appendix S3: Table S3). In addition, structural canonical coefficients indicated that numbers of outer culms in clumps at 2 (R^2 = 0.73) and 8 (R^2 = 0.67) months were strongly related to the interaction between time since fire and treatment (Appendix S3: Table S3).

Pre-fire pine needle fuel treatments influenced post-fire reproduction of grasses. There were more flowering culms in needle-removal plots than in plots with pine needles (Fig. 6d). The partial regression coefficients indicated that treatment was associated with numbers of flowering culms 8 months after fire (R^2 = 0.47), and site characteristics also were associated with flowering culms (Appendix S3: Table S3). The partial regression coefficients also suggested that numbers of flowering culms were associated with absence vs. presence of pine needles and in situ vs. added pine needles (R^2 = 0.47,0.54; Appendix S3: Table S3).

Pre-fire size of grass clumps influenced characteristics of grasses. Structural canonical coefficients indicated strong positive effects of pre-fire size on the numbers of outer culms at 2 and 8 months and on flowering stems (Appendix S3: Table S3).

Relationships between post-fire vegetation and fire characteristics.—Stepwise variable selection resulted in models (Appendix S3) with different fire and pre-fire vegetation variables selected for different vegetation characteristics: oaks (Appendix S3: Table S5), and grasses at 2 (Appendix S3: Table S6) and 8 months (Appendix S3: Table S7). Time above 60°C was significantly and negatively associated with most post-fire vegetation characteristics. These included numbers of oak stems at 2 ($F_{1,50}$ = 8.66; P = 0.005) and 8 ($F_{1,50}$ = 4.05; P = 0.05) months (Appendix S3: Table S5), number of grass culms inside the center at 8 months ($F_{1,50}$ = 28.66; P < 0.001), number of grass culms outside the center at 2 ($F_{1,51}$ = 5.12; P = 0.03) and 8 ($F_{1,51}$ = 4.25; P = 0.04) months, and total vegetative grass culms at 8 ($F_{1,50}$ = 6.32; P = 0.02) months (Appendix S3: Tables S6 and S7). Maximum temperature increase was only weakly negatively related to number of grass culms inside the center at 2 months (Appendix S3: Table S6). Fine fuel consumption was weakly and negatively related to number of flowering grass culms at 8 months (Appendix S3: Table S7). Maximum heights of oak stems at 2 and 8 months were not significantly related to any measured fire characteristics. There also were positive effects of pre-fire vegetation on post fire vegetation, both for oaks and grasses (Appendix S3: Tables S5, S6, and S7).

Structural equation models.—The preliminary model, based on Fig. 1, is depicted in Fig. S4-1: Appendix S4. After modifications of components (described in Appendix S4), a final model was obtained (Appendix S4: Fig. S2). This SEM contained pathways involving control variables (time since fire, patch, and pre-fire vegetation). These pathways reflected effects of site conditions, but as predicted, did not interact with treatments. Because they did not influence assessment of effects of pine needles relative to other fine fuels, site conditions were not included in subsequent exploration of hypotheses regarding effects of different fine fuels (Fig. 7). Regression weights (Appendix S4: Table S1), covariances (Appendix S4: Table S2), and squared multiple correlations (Appendix S4: Table S3) associated with the final model also are presented in Appendix S4.

Pine needle treatments were primary drivers of fire characteristics at ground level in the SEM. Pathways involving pine needles (Fig. 7) indicate strong effects relative to those produced by oak and grass fuels. The relative predicted importance of different pathways can be ascertained by multiplying sequences of standardized regression weights (β). For example, effects of added pine needles were almost twice those of in situ pine needles, both for fine fuel consumption (1.03 × 0.90 = 0.93 vs. 0.57 × 0.90 = 0.51) and maximum temperatures (1.03 × 0.78 = 0.80 vs. 0.5 × 0.78 = 0.44). Pine needle fuels did not directly affect time above 60°C, but had a strong indirect effect through maximum temperature increase, especially for added compared to in situ pine needles (1.03 × 0.78 × 0.80 = 0.64 vs. 0.57 × 0.78 × 0.80 = 0.36). Fine fuel consumption was more strongly affected by pine needle fuels (0.90) than by other fine fuels (0.40). The strong effect of maximum temperature increase on time above 60°C and positive correlation with fine fuel consumption indicate that fire characteristics at round level were driven primarily by effects of pine needles on fire temperatures (Fig. 7).

SEM indicated effects of pine needles on groundcover oaks (Fig. 7). Fuel treatments weakly and negatively

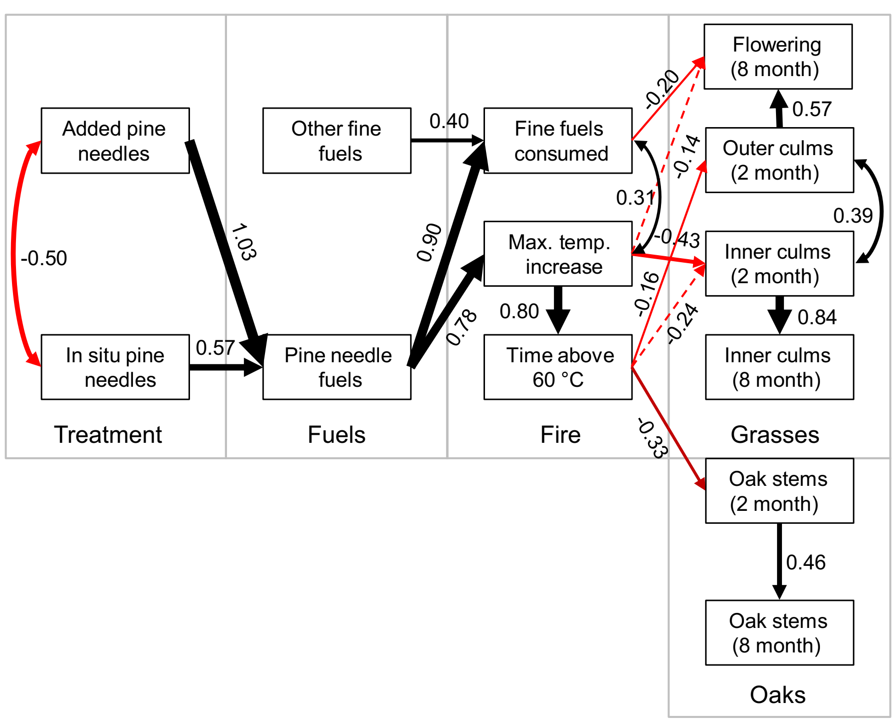

Fig. 7. Subsets of the final structural equation model (SEM) showing effects of treatments and fuels on fire characteristics, and effects of fire characteristics on oaks and grasses. Line weights are proportional to standardized regression weights (β), which are given next to lines. Black lines indicate positive regression weights; red lines negative regression weights. Dashed lines indicate nonsignificant pathways. Numbers on lines are standarized regression coefficients. Control variables (time since fire, patch type, pre-fire vegetation) and error terms of endogenous variables are omitted because they did not affect fuel-fire-vegetation relationships. Probabilities of standardized regression weights (β) are presented in Appendix S4: Table S4-1 and summarized in *Results*.

affected oaks 2 months after fire via duration of heating at ground level (added needles, 1.03 × 0.78 × 0.80 × −0.33 = −0.21; in situ needles, 0.57 × 0.78 × 0.80 × −0.33 = −0.12). Numbers of oak stems at 2 months were fairly strongly associated with numbers of stems at 8 months (0.46); thus pine needles had persistent, but weak negative effects 8 months after fire (added needles, −0.21 × 0.46 = −0.10; in situ needles, −0.12 × 0.46 = −0.05). SEM suggested that the most prominent effects of pyrogenic fuels on groundcover oaks were delayed resprouting after fire; these effects were mediated via indirect effects of pine needles (increases in temperatures that increased duration of heating). These effects diminished during the growing season, but persisted, especially with added pine needles. There were no significant effects of fine fuel consumption on numbers of oak stems; hence, variation in oak and grass fuels had little effect on oaks.

Grasses were affected by pine needle fuels, as indicated by SEM. Combinations of direct and indirect effects were likely to influence numbers of culms in central and outer regions of clumps, with strongest effects occurring in the center 2 months after fire (Fig. 7). Both added and in situ pine needles were directly associated with decreases in numbers of culms in clump centers 2 months after fire via effects of maximum temperature increases (added needles, 1.03 × 0.78 × −0.43 = −0.35; in situ needles, 0.57 × 0.78 × −0.43 = −0.19). There also were indirect effects via time above 60°C (Fig. 7). The strong association of inner culms at 2 months and 8 months (0.84) resulted in persistent, weak and negative effects of added (−0.29) and in situ (−0.16) pine fuels compared to oak and grass fuels on numbers of inner culms. Again, effects were potentially greater due to indirect effects (Fig. 7). Increases in time above 60°C were associated with a significant, but smaller decreases (−0.16) in numbers of culms outside the center of the clump, again indicating that pine needle fuels had greater direct effects than oak and grass fuels (Fig. 7).

Pine needle fuels directly and indirectly decreased flowering. Direct negative effects of pine needles resulted from increased consumption of fine fuels (0.90 × −0.20 = −0.18), and indirect effects involved increases in time above 60°C and numbers of outer culms at 2 months (0.78 × 0.80 × −0.16 × 0.57 = −0.06), as indicated in Fig. 7. Maximum temperature increase also had a small direct negative effect (0.78 × 0.8 × −0.14 = −0.09) on flowering. SEM thus indicated that pine needle fuels could result in decreases in grass flowering caused by different characteristics of fires, but in total as much as one-third greater than effects of oak and grass fine fuels.

Discussion

Pyrogenic fine fuels produced by longleaf pine resulted in negative effects on oaks and grasses in the ground layer. These effects increased with amounts of pine needles in fuels. The SEM indicated that effects mediated through fire characteristics at ground level were increased greatly by pine needles relative to oak and grass fuels. Thus, pyrogenic fuels of longleaf pine should engineer pine savannas via effects on recurrent frequent fires (i.e., 1–3 yr pre-settlement fire return intervals indicted by tree-ring studies; Huffman 2006, Stambaugh et al. 2011).

Effects of pyrogenic fuels on ground-layer plants in pine savannas

Ground-layer oaks.—Pine needles affected oak genets. In fires without pine needles, stems were killed back close to, but above, ground level. Resprouting often occurred within weeks from dormant buds 1–5 mm above ground; stems rapidly elongated to pre-fire height and produced leaves (also see Ellair and Platt 2013). When pine needles were present, stems of oaks were killed back to the ground and often the root crown was charred. Fewer stems were present 2 months post-fire; resprouting stems, often slightly fewer than before fire, were produced over several months by buds deeper in the soil below root crown surfaces. These negative effects of pine needles on numbers of oak stems were reflected in patterns of post-fire regrowth.

Savanna hardwood tree populations have been postulated to contain two states: ground-layer genets in a fire trap and overstory trees that escaped the fire trap. Fires top-kill genets, blocking growth into the overstory (e.g., Hoffmann et al. 2009, Ellair and Platt 2013, Werner and Prior 2013). Top-killed plants survive via resprouting meristems located below heat-killed portions of the plants, typically at/below ground level on underground storage organs (Bellingham and Sparrow 2000, Drewa et al. 2002, Hoffman and Moreira 2002, Clarke et al. 2013, Maurin et al. 2014, Schafer and Just 2014). Our study indicates that recurrent fires fueled by pyrogenic pine fuels not only maintain the fire trap, but depress genets by effects on bud banks on underground structures. We expect successive fires fueled by pine needles, especially with short return intervals, to produce compounded negative effects that eventually result in mortality, as noted in long-term studies (see review in Robertson and Hmielowski 2014, also Gonzalez-Benecke et al. 2015). Under such fire regimes, few oaks should be expected to survive beneath pines that grow into the overstory and live for centuries (Platt et al. 1988).

Spatial relationships between pines and oaks should be influenced by effects of pyrogenic fuels on regeneration. Pines can transition through ground-layer stages with minimal effects of fires on the transition from groundcover to overstory trees (i.e., no fire trap), but only in open areas away from overstory pines (Platt et al. 1988, Platt and Rathbun 1993). Thus, both oaks and juvenile pines should occur in open areas away from overstory longleaf pines (cf., Grace and Platt 1995, Veldman et al. 2013). Competition between oaks and juvenile pines in open areas should depend on conditions influencing immigration and growth, as well as effects of pyrogenic fuels (e.g., Rebertus et al. 1993), all of which should vary with size of opening and local distributions of overstory pines and oaks. Long-lived oak genets might capture some openings and suppress pines by shading (also see Greenberg and Simons 1999). We envision natural pine savannas as a dynamic spatial mosaic in which savanna oaks that persist clonally in the ground layer capture some open space, persisting until patches are recolonized by pines that reach the overstory. Such patch dynamics would lengthen hypothesized return intervals for patches based on pines alone (e.g., Platt et al. 1988, Platt and Rathbun 1993, Noel et al. 1998).

Ground-layer grasses.—Fires fueled by pine needles alter clonal structure of genets of dominant C_4 grasses. Effects are mediated through those parts of plants at or just below the surface, the meristem or bud banks (sensu Harper 1977, Klimešova and Klimeš 2007). Negative effects on meristems of *S. scoparium* were greater for culms in interior than outer regions of genets. We note that interiors of grass genets are likely to contain bases of older dead culms, which if ignited (i.e., when pine needles are present), then burn and kill live meristems. Thus combustion of fuels containing pine needles should result in fragmentation of genets (sensu Wilhalm 1995, Briske and Derner 1998), and genets near pines may not reach sizes they do away from pines. Because most culms are in outer regions of genets, overall numbers may not change greatly in any fire. With recurrent fires, however, genet size should shift toward smaller units (ramet hierarchies; Briske and Butler 1989, Welker et al. 1991, Williams and Briske 1991, Derner and Briske 1998). Such smaller separated ramet units may comprise less aboveground mass, reducing aspect dominance of grasses in the ground layer close to trees in savannas.

Flowering by grasses also was suppressed by more intense fires. We note that flowering by little bluestem, like other savanna and prairie grasses in the southeastern United States, is strongly and positively associated with fires during the growing season (e.g., Streng et al. 1993, Main and Barry 2002, Fill et al. 2012, Shepherd et al. 2012). In our study, average numbers of flowering culms (adjusted for pre-fire genet size) when no pine needles were present were about twice the number when pine needles were present. Thus, our study indicates negative effects of fires fueled by longleaf pine needles on both patterns of genet structure and sexual reproduction of *S. scoparium.* Larger intact genets with flowering culms and recruitment of new genets should be more likely in open areas away from pines than close to or underneath pines.

Ground-layer plant assemblages.—In our study, only a few oaks and grasses with added pine needles were killed by fires that smoldered in root crowns of oaks or tightly packed bases of grass genets. Nonetheless, individual genets of ground-layer oaks and grasses typically were damaged by fires fueled by pyrogenic needles (also see Gagnon et al. 2012, 2015, Ellair and Platt 2013). Delays in resprouting (oaks), reductions in sizes (oaks and grasses), and reductions in flowering (grasses) should result in reductions in sizes and abundances of genets over successive short-return interval fires. Hence, dominance of ground-layer vegetation by oaks and grasses might well not occur near, and especially beneath overstory longleaf pines. Instead, composition of ground-layer vegetation likely reflects consequences of pyrogenic fuels of longleaf pine.

One important consequence of effects of pyrogenic pine fuels should be heterogeneity in ground-layer vegetation. Away from pines, oaks should be dominant shrubs with some reaching overstory tree sizes (Ellair and Platt 2013, Veldman et al. 2013). Genets of C_4 grasses should tend to reach large size, remain intact, and flower after fires. We propose that depictions of pine savanna ground-layer vegetation as dominated by C_4 grasses and savanna hardwoods locked in the fire trap actually may be most applicable to the ground layer away from pines. In contrast, ground-layer species tolerant of high-intensity fires should be favored under pines. Common shrubs under large pines might include those with meristems on belowground rhizomes (e.g., Laycock 1967). Some shrubs might have underground storage organs that produce aboveground branches with highly flammable evergreen leaves (e.g., Shafizadeh et al. 1977, Rodgers et al. 1986, Burgan and Susott 1991, Behm et al. 2004). The short-statured, branched architecture of genets of these species (see also Bond 2016) tend to trap pine needles in their foliage, and thus heat released during combustion should occur primarily above ground level (e.g., Gagnon et al. 2010). Shrub species composition and dynamics thus might reflect longleaf pine patch dynamics (also see Veldman et al. 2013). Similar shifts may occur among herbaceous species in pine savannas. Suppression of caesipitose clump-forming grasses by high-intensity fires should open space that can be colonized by other grasses (e.g., with deeply buried rhizomes or a short-term seed pool that can withstand increased fire intensity at ground level) or by forbs with underground storage organs or seeds that survive fires. These indirect effects of pyrogenic fuels should facilitate local heterogeneity, increasing landscape-level biodiversity in the ground layer.

Pyrogenicity of longleaf pine

Like other pines, longleaf pine produces needles that, once shed and dried, are highly flammable (sensu Anderson 1970, Martin et al. 1994, Fernandes and Cruz 2012, Schwilk 2015), characterized by high energy content (Reid and Robertson 2012). Such pyrogenicity results from high concentrations of oils and resins (Kramer and Kozlowski 1960). Relative to most pines, longleaf pine needles contain high concentrations of monoterpenes (i.e., α- and β-pinene), which occur with oleoresins in five longitudinal ducts (Schorger 1914, 1916, 1919, Franklin and Snyder 1971). Once dried, monoterpenes volatilize at temperatures just above 100°C (Schorger 1914); the highly combustible needles increase flame lengths and rates of consumption (Fonda 2001). Such flammability has been proposed to increase energy release and thus fire intensity (Platt et al. 1988, 1991, Gagnon et al. 2010, Ellair and Platt 2013). Our study and others of fuel-fire relationships involving longleaf pine support this idea (Williamson and Black 1981, Rebertus et al. 1989*a*,*b*, Drewa et al. 2002, Thaxton and Platt 2006, Hiers et al. 2009, Wenk et al. 2011). Similar effects of terpenes on flammability have been noted in other ecosystems (e.g., Alessio et al. 2008).

Pyrogenic and flammable fine fuels have different effects on fires.—Our study provides an indication of how pine needles modify fire characteristics at ground level. Temperature increases occur rapidly following ignition of fine fuels; maxima commonly occur within a few minutes after ignition when fuels contain longleaf pine needles. Slow declines in temperatures result in substantial durations of elevated temperatures when pine needles are present, sometimes many minutes after flaming combustion has ended (also Ellair and Platt 2013). Such effects may result from glowing combustion of pine needles and other fine fuels ignited by pine needle combustion after consumption of most fine fuels. In our study, increases in temperatures and durations of heating in plots with in situ pine needles were on average more than twice those occurring when pine needles were not present; increases and durations after needle additions tended to be three to four times those when pine needles were not present. Fine fuel combustion of 95%, increases in ground-level temperatures exceeding 500°C, and durations above 60°C for nearly 1 h can result from mass of pine needles equivalent to amounts occurring under canopies of large pines.

Other savanna plants also are flammable. Many savanna grasses, as well as some savanna trees, are notable for their production of readily combustible fine fuels (e.g., Bragg 1982, Platt and Gottschalk 2001, Gill and Zylstra 2005, Kane et al. 2008, Wenk et al. 2011, Overholt et al. 2014, Simpson et al. 2016). In some environments (e.g., pronounced and extended dry seasons ending with fires ignited during thunderstorms), fuels produced by such savanna plants might facilitate fires, reducing likelihoods that savannas will transition to closed-canopy forests (sensu Hoffmann et al. 2009, 2012, Beckage et al. 2009, 2011, Veldman et al. 2013, Werner and Prior 2013). Indeed, most studies of savanna–forest dynamics postulate that grasses are the primary fuels (Sankaran et al. 2004, Beckage et al. 2011, Lehmann et al. 2011, Ratnam et al. 2011, Werner and Prior 2013, Bond 2016). In our study, fine fuels comprised of warm-season grasses and savanna oak leaves resulted in much less fine fuel consumption than fuels containing pine needles, as also noted by Reid and Robertson (2012). Furthermore, our study showed that, compared to fuels containing longleaf pine fuels, fuels comprised of oaks and grasses resulted in much lower increases in temperatures and much shorter durations of heating at ground level. We propose that grasses and savanna trees whose leaves tend to be held above ground and not decompose rapidly (e.g., Kane et al. 2008) should contribute flammable fuels to the ground layer and thus increase total heat production during fires (also see Reid and Robertson 2012, Fill et al. 2016). Fine fuel production by such species (Kane et al. 2008, Hiers et al. 2014) appears more consistent, however, with concepts of flammability as protection from fire than engineering of fire (cf., Gagnon et al. 2010). Such differences may result in flammability of heterogeneous fuel mixtures that reflects primarily presence/absence of pyrogenic species (cf. Varner et al. 2015).

Engineering of fires by longleaf pine.—We propose that longleaf pines modify savanna fires to a far greater extent than other pine savanna plants that produce flammable fuels. Pyrogenic combustion of fuels containing longleaf pine needles reflects strong non-additive effects of the different fuels present (sensu de Magalhäes and Schwilk 2012) and likely result from chemicals, monoterpenes in the case of longleaf pine (and other pines). The much higher concentrations of monoterpenes in longleaf pine needles than most pines seems to be the primary cause of rapid increases in temperatures, while other oleoresins and oils may result in long durations of heating. Similar suggestions for volatile chemicals have been made for other systems (Madrigal et al. 2012, Pausas et al. 2012). Such effects involve both rapid and sustainable combustion, which tend to be inversely related in most fuels (de Magalhäes and Schwilk 2012). Pyrogenic fuels produced by longleaf pines thus influence fuel combustion differently than flammable fuels produced by other vegetation in pine savannas (Veldman et al. 2013) and in many other grasslands and savannas (e.g., Beckage et al. 2011, Lehmann et al. 2011, Hoffmann et al. 2012).

Strong pyrogenic effects of longleaf pine likely are magnified by patterns of deposition and slow decomposition of shed needles. Pyrogenic fine fuels are almost continuously present in the vicinity of pines. Southeastern savanna pines retain needles on trees for only 2 yr and shed needles throughout the year, with peak needlefall occurring in the spring prior to natural fires (Wiegert and Monk 1972, Gholz et al. 1985, Landers 1991). Fires often scorch lower branches of overstory pines, resulting in a post-fire layer of needles on the ground prior to regrowth of vegetation and before litter accumulates. Further, a tripartite needle structure results in shed needles being trapped and embedded in regrowing vegetation such as shrubs and grass clumps. The pervasive presence among strata comprising the ground-layer vegetation/fuels results in vertical continuity of pyrogenic fuels. Decomposition is slow (Hendricks et al. 2002), and while monoterpenes in needles decrease over time (Schorger 1914), pyrogenic fuels accumulated post-fire are capped by freshly shed needles at the time natural fires are most likely (Platt et al. 2015).

Variation in amounts and types of other fuels did not alter pyrogenic effects of pine needles in our study. Thus, as suggested by Reid and Robertson (2012) and de Magalhäes and Schwilk (2012), pyrogenic fuels should be incorporated into fire models. Such models use standard energy content levels and ignore effects of pyrogenic fuels on total heat production (Rothermel 1972, Forestry Canada Fire Danger Group 1992; Scott and Burgan 2005, Andrews 2009); more importantly, they are poor predictors of pyrogenic effects related to fire characteristics at ground level, where meristems of ground-layer plants are located. Improvement of models based on characterization of pyrogenic fuels should be useful and applicable to fire-prone ecosystems (also see Fernandes and Cruz 2012).

A conceptual model for pine savannas

Pyrodiversity.—Our study suggests that fires produce natural pyrodiversity in pine savannas. Most prior studies have considered post-fire variation due to differences in management (e.g., Martin and Sapsis 1992, Sapsis and Martin 1993, Parr and Andersen 2006, Faivre et al. 2011). We focus on how pyrogenic fuels modify post-fire conditions naturally within humid savannas, generating alternate states within savannas.

We envision two pre-fire states, with and without pine needles. Each state is based on amounts and composition of fine fuels generated by local distributions of pines and other vegetation. Characteristics of naturally burning fires should be altered based on fuels present. Where needles are present, we expect increases in maximum temperatures, durations of heating at ground level, and fine fuel consumption. As amounts of needles increase, greater fuel consumption and effects on vegetation should result in "blacker landscapes" with decreased residual upright and ground-layer fuels. Without pine needles we expect smaller increases in fire temperatures and durations of heating, as well as less complete combustion of fine fuels. These "lightly burned" areas should contain residual fuels on the ground and ground-layer vegetation that has been damaged and perhaps top-killed, but not as consumed by the lower intensity fires.

There should be two major post-fire states that result from natural fires in the ground layer of pine savannas. These two states should reflect the presence/absence of pyrogenic fuels, although post-fire states also may be influenced by other aspects of fuels (e.g., total fine fuels, other flammable fuels, continuity across landscapes, etc.) and weather conditions (e.g., time since rainfall, moisture content, relative humidity, etc.) that influence flammability, combustion, and consumption of fuels. Other shed components of fuels (e.g., pine cones, shed bark, small branches) also might contribute to localized high-intensity fires (e.g., Fonda and Varner 2004).

Natural pyrodiversity should reflect patch structure and dynamics of pine populations. Local populations of longleaf pine in old-growth stands (e.g., Platt et al. 1988, Platt and Rathbun 1993, Noel et al. 1998), as well as some second-growth stands (e.g., Greenberg and Simons 1999, Ellair and Platt 2013, Veldman et al. 2013, 2015) generate patterns in vegetation consistent with such pyrodiversity. The spatial distribution of recruitment away from overstory pines and high-intensity fires (Grace and Platt 1995) also suggests pyrodiversity generated via dispersal patterns of shed needles (Platt et al. 1991, Ellair and Platt 2013). We propose that natural pyrodiversity as a landscape pattern changes at temporal/spatial scales generated by pine population dynamics.

Consequences of pyrodiversity.—Engineering of fires by savanna trees producing pyrogenic fuels should have important consequences for locally pyrodiverse ecosystems. First, species like longleaf pine should drive characteristics of fire regimes in ways that preclude transition to forests, maintaining a savanna physiognomy (sensu Gilliam et al. 2006, Beckage et al. 2009). Effects of rapidly drying pyrogenic fuels on fire regimes, in conjunction with fire weather producing predictable patterns of ignition following short-term droughts (Platt et al. 2015), may be the primary reason for savannas in high rainfall warm-temperate and subtropical regions. Second, spatial variation in fire regimes generated by pyrogenic shed leaves should affect plant community dynamics. Pyrogenic fuels should increase understory light levels (e.g., Platt et al. 2006), as well as generate and maintain conditions facilitating fire-resistant plant species when fires occur frequently. Small-scale heterogeneity in biodiversity has been noted in savannas (e.g., Stott 1988, Schmitz et al. 2002, Uys et al. 2004, Myers and Harms 2009, Sankaran 2009, Ratnam et al. 2011, Veldman et al. 2013). Local pyrodiversity, in conjunction with a diversity of local environmental conditions (e.g., Laliberté et al. 2013, Parr et al. 2014, Peet et al. 2014, Veldman et al. 2015) expressed through engineering of fire by pyrogenic fuels, might well set the stage for mesic and high rainfall savannas becoming high diversity landscapes. Such savannas should be heterogeneous, containing patches of unique biotically engineered high biodiversity woodlands dominated by savanna trees that produce pyrogenic fuels, interspersed with more open areas characterized by more traditional shared tree-grass dominance.

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Supporting Information

Supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecm.1224/suppinfo

Data Availability

Data associated with this paper have been deposited in Dryad: http://dx.doi.org/10.5061/dryad.bm4v7.