Plant Ecol (2016) 217:331–342
DOI 10.1007/s11258-016-0574-0

Flammability of the keystone savanna bunchgrass *Aristida stricta*

Jennifer M. Fill · Brett M. Moule ·
J. Morgan Varner · Timothy A. Mousseau

Received: 27 July 2015 / Accepted: 30 January 2016 / Published online: 11 February 2016

Abstract Understanding the flammability of species in fire-prone or fire-dependent ecosystems is necessary for modeling and predicting ecosystem dynamics. Wiregrass (*Aristida stricta* syn. *A. beyrichiana*), a keystone perennial bunchgrass, is a dominant groundcover species in southeastern United States pine savannas. Although wiregrass flammability as a driver of pine savanna fire regimes is a fundamental paradigm in pine savanna dynamics, no studies have quantified its fuel structure and flammability at the individual bunchgrass level. We studied wiregrass flammability at the Aiken Gopher Tortoise Heritage Preserve in Aiken County, South Carolina, USA. We linked tussock fuel structure characteristics (total biomass, live:dead biomass, mass of perched litter and pine needles, moisture content, and bulk density) to flammability (flaming duration, smoldering duration, and flame length). Flame length was strongly and positively related to wiregrass biomass. Pine needles and other litter fuels perched on wiregrass tussocks were not related to flame length, but increased the duration of flaming and smoldering. Within the ranges evaluated, neither fire weather (relative humidity, wind speed, and air temperature) nor fuel moisture significantly affected tussock flammability. Our results indicate that different fuel structural properties drive separate aspects of wiregrass flammability. Together with litter from pines and other groundcover shrubs and trees, wiregrass modifies fire behavior locally, potentially influencing ecosystem dynamics at larger scales. These results have strong implications for southeastern pine savannas and more broadly where grass-dominated vegetation influences fire regimes.

Communicated by Devan Allen McGranahan.

J. M. Fill (✉) · T. A. Mousseau
Department of Biological Sciences, University of South Carolina, Columbia 29208, SC, USA
e-mail: jenna999@gmail.com

Present Address:
J. M. Fill
Center for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Matieland 7602, South Africa

B. M. Moule
Directorate of Public Works, Natural Resource Division
III Corps and Fort Hood, Fort Hood, TX, USA

J. M. Varner
Department of Forest Resources & Environmental Conservation, Virginia Tech, Blacksburg, VA 24061, USA

Present Address:
J. M. Varner
USDA Forest Service, Pacific Wildland Fire Sciences Lab, 400 N 34th Street, Suite 201, Seattle, WA 98103, USA

Keywords Fire behavior · Fuel structure · Pine savanna · Sandhills · Wiregrass

Introduction

Fire is a major process shaping terrestrial plant community composition and ecosystem function (Bond and Midgley 2005; Pausas and Keeley 2009). In many terrestrial ecosystems, fire exerts a dominant influence on transitions between savanna and forested ecosystem states (Hoffmann et al. 2009; Staver et al. 2011). By hindering seedling establishment and the transition of fire-intolerant trees from the sapling layer to the canopy via topkill, fire limits tree cover and promotes an open canopy and herbaceous understory (Beckage et al. 2009; Hoffmann et al. 2009). In turn, the likelihood of fire occurrence depends on the flammability of component species (Varner et al. 2015), which determines the ignitability, intensity, and spread rates (Bond and Midgley 1995; Kane et al. 2008; de Magalhães and Schwilk 2012). This tight association between fire effects on vegetation and fuel properties results in fire-vegetation feedbacks that contribute to ecosystem persistence (Beckage et al. 2009, 2011). Therefore, understanding species' differential flammability is necessary for understanding the behavior and effects of fires and their management in fire-prone ecosystems.

Pine savannas in the southeastern United States are representative of savannas globally that are maintained by fire-vegetation feedbacks. A high-frequency fire regime suppresses fire-intolerant tree recruitment and growth, sustaining an open canopy structure and herbaceous groundcover (Platt 1999; Hoffmann et al. 2009; Veldman et al. 2013). Savanna groundcover vegetation is dominated by fine fuels (flammable graminoids, forbs, and pine and oak leaf litter) that sustain intense and rapidly spreading surface fires (Kane et al. 2008). Heterogeneity of fine fuel complexes affects fire behavior (Thaxton and Platt 2006; Loudermilk et al. 2009; Wenk et al. 2011) and in turn, vegetation dynamics. For example, increased fuel loads can increase fire intensity and duration, thereby affecting tree mortality and resprouting (Robertson and Ostertag 2007) and thus, the likelihood of fire-intolerant seedlings transitioning to the canopy (Hoffmann et al. 2012a; Robertson and Hmielowski 2014).

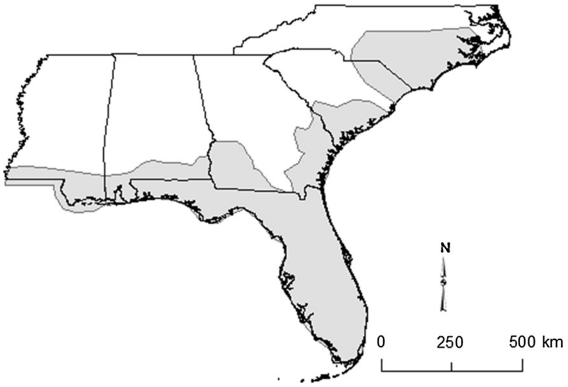

Fig. 1 The distribution of wiregrass (*Aristida stricta* syn. *beyrichiana*) in the southeastern United States

Wiregrass (*Aristida stricta* syn. *A. beyrichiana*) plays a major role in the understory flammability of many southeastern USA pine savanna ecosystems. The species occurs from North Carolina south to the Florida peninsula and westward to coastal Mississippi, often dominating and facilitating fire spread through understory environments from xeric sandhills to seasonally wet flatwoods (Fig. 1; Christensen 1977; Clewell 1989; Noss 1989; Peet 2006). Involute and fibrous tillers persist on plants (Parrott 1967; Clewell 1989), overlapping with those of neighboring tussocks to provide a continuous and well-aerated fuel bed (Clewell 1989). Bunchgrass crowns also intercept fallen litter, including flammable oak leaves and pine needles (Clewell 1989; Hendricks et al. 2002). The accumulation of slowly decomposing dead leaves and other litter (Hendricks et al. 2002) in the absence of fire can create a highly flammable fuel complex of up to ca. 800 g m^{-2} within a few years following fire (Parrott 1967; Christensen 1977). Moreover, the elevated nature of tussocks likely enhances fire spread even in seasonally wet areas (Parrott 1967; Clewell 1989).

Although wiregrass flammability likely plays a key role in our understanding of pine savanna fire regimes, we know of no studies that have quantified wiregrass fuel structure and flammability at the tussock level. Flammability is generally characterized by four components: ignitability, the time to ignition; sustainability, the duration of combustion; combustibility, the rate of fuel consumption; and consumability, the proportion of fuel consumed (Anderson 1970; Martin et al. 1993). Parrott (1967) described wiregrass fuel structure in relation to time since the last fire. Wenk et al. (2011, 2013) examined several fuel structure and flammability metrics in 4 × 4 m wiregrass “fuel complexes” (i.e., wiregrass comprised the majority of the fuel). Ellair and Platt (2013) also described temperatures reached by burning different understory fuels, with wiregrass as a component of the herbaceous fuel type. However, neither the patterns nor mechanisms of flammability at the tussock level have been examined.

In this study, we quantified the relationship between wiregrass fuel structure and flammability characteristics across a gradient of increasing time since the last fire. Our objective was to link underlying fuel and weather characteristics to differences in tussock flammability. We quantified several fuel structure variables: total biomass, live:dead biomass, moisture content, bulk density, and mass of perched pine needle litter and other litter. We examined three flammability metrics related to active combustion (Varner et al. 2015): flaming duration, smoldering duration, and flame length, which can be linked to fire behavior characteristics such as fireline intensity, reaction intensity, and spread rates (Byram 1959, 1963; Alexander 1982; Rothermel 1983; Varner et al. 2015). Fire behavior during the flaming phase, especially fire intensity and duration, affects plant mortality and resprouting patterns (Alexander 1982; Wiggers et al. 2013; Gagnon et al. 2015). Small trees and shrubs that persist via resprouts and rapid bark accumulation may be more likely to withstand intense or smoldering fires (Bond and van Wilgen 1996; Lawes et al. 2011; Hammond et al. 2015). Many understory plants that survive intense aboveground heat can resprout from belowground structures or produce seeds with smoke- or heat-stimulated germination (Bond and van Wilgen 1996; Gagnon et al. 2015). Conversely, fires of lower intensity or short duration might allow other less flammable species to recruit and alter subsequent fire dynamics. These local patterns scale up to tree:grass dynamics at the ecosystem scale, including the likelihood of overstory recruitment (Solbrig et al. 1996; Scholes and Archer 1997).

We hypothesized that wiregrass biomass, bulk density, and perched needle and broadleaf litter mass would be the predominant drivers of flame length (the length of the longest flame from base to tip; a measure of fire intensity; Alexander 1982; Rothermel 1983). Loudermilk (2010) demonstrated that at the small-plot scale, wiregrass biomass strongly and positively influenced remotely sensed temperatures generated by combustion, which are related to fire intensity. Moreover, increased amounts of available fuel should increase fire intensity (Byram 1959; Whelan 1995), assuming a constant bulk density. We therefore predicted that flame length should increase with increasing tussock biomass. Additionally, fuelbed bulk density has been supported as a strong driver of fire intensity in other savannas and woodlands (Streng and Harcombe 1982; Engber et al. 2011; Hoffmann et al. 2012b; Trauernict et al. 2012). Very low bulk density can result in low fire intensity because fuel particles are too far apart; generally, however, increasing bulk density should limit oxygen availability and decrease fire intensity (Whelan 1995). Therefore, we predicted that flame length should decrease with increasing tussock bulk density. Finally, pine and hardwood litter types in southern ecosystems vary widely in flammability (Fonda 2001; Reid and Robertson 2012; Mola et al. 2014). Longleaf pine needles have higher energy content and tend to generate higher temperatures than litter from co-occurring hardwoods (Williamson and Black 1981; Reid and Robertson 2012). Fuel loading of contrasting litter types (e.g., pine needles vs. broadleaf litter) could therefore affect fire intensity in opposite directions. Given the variability in litter flammability, we predicted that pine needle litter and broadleaf litter would generally increase flame length but to a lesser degree than tussock biomass.

We also hypothesized that bulk density, pine needle litter, and broadleaf litter mass would affect the duration of flaming and smoldering. Drivers of these flammability metrics are less well understood than those of other fire behavior characteristics (Kreye et al. 2014). In general, fuelbed bulk density tends to increase flaming and smoldering duration (Kreye et al. 2011, 2014; Varner et al. 2015). With respect to litter influences on flaming and smoldering, Wenk et al. (2011) demonstrated that duration of lethal temperatures were shorter in wiregrass fuels than in fuelbeds dominated by longleaf pine needles and turkey oak litter. Similarly, Loudermilk (2010) found pine needle litter to be a strong positive predictor of fire residence time at small scales. We therefore predicted that not only would flaming and smoldering durations increase with increasing tussock bulk density, but also that they would increase with increasing mass of pine needles and broadleaf litter.

Finally, we hypothesized that these effects would be modified by fuel moisture content and the ratio of live:dead biomass. Despite the fact that moisture is considered one of the most important influences on flammability (Gill et al. 1978), we still know little regarding its relationship with flammability metrics. Moisture dynamics (e.g., drying rates) differ widely among fuel types (Kreye et al. 2013). Increased moisture content, especially of live relative to dead fuels, decreases fire intensity by hindering ignition and limiting the amount of fuel available to burn (Whelan 1995), and is therefore negatively related to fuel consumption (Reid et al. 2012). Thus we predicted that increasing fuel moisture content and live:dead biomass should decrease flame length and potentially decrease the duration of flaming and smoldering.

Methods

We conducted this study at the Aiken Gopher Tortoise Heritage Preserve (AGTHP) in Aiken County, South Carolina, USA. AGTHP is located in the xeric sandhills of the Lower Coastal Plain (33°29′48″N, 81°25′17″W). The sparse overstory is predominantly longleaf pine (*Pinus palustris*), while the midstory has scattered oaks (dominated by turkey oak, *Quercus laevis*, bluejack oak, *Q. incana*, and blackjack oak, *Q. marilandica*). The herbaceous groundcover is dominated by *Aristida stricta*, suggesting an absence of severe soil disturbance and that the plant community is representative of the historical native community of the area (Clewell 1989; Hardin and White 1989; Noss 1989). Soils are a mix of deep, well-drained sandy soils of the Lakeland, Troup, and Fuquay series (USDA 1985). Mean monthly air temperature ranges from 8.3 °C in January to 27.1 °C in July. Mean monthly precipitation ranges from 65 mm in November to 128 mm in July (Southeast Regional Climate Center 2011). Historically, frequent fires (1–3 years; Frost 1998; Stambaugh et al. 2011) occurred predominantly in the transition from late spring to early summer (Fill et al. 2012). Prescribed fires have been conducted on AGTHP at two-year intervals or longer since 1999 and implemented primarily during the late winter and spring months.

We selected three sites (0.5–1 ha each) within AGTHP, last burned in 2005, 2010, and 2013 (9, 4, and 1 year since burning, respectively). Within each site, we delineated areas that were relatively homogenous in wiregrass and shrub and overstory density.

Biomass and fuel structure measurements

We sampled wiregrass biomass and fuel structure in the three time-since-fire sites ca. 20 days prior to burning experiments (14- and 15-May-2014). Because we were interested in modeling the fuel characteristics that drive wiregrass flammability, we considered individual tussocks as our experimental units. By sampling across this gradient of time-since-fire, our intent was to increase the temporal generality of our results.

Within each site, we used a point-quarter sampling scheme to locate 15 wiregrass tussocks. Beginning at the estimated center of each site, we located points sequentially by choosing a random azimuth (0–340°, at 20° intervals) and distance (50 m maximum) from one point to the next. If at any time during the random walk, we approached an area where the vegetation changed noticeably (e.g., high tree basal area), we turned 90° and continued the walk. At each point, we randomly selected one of the four nearest tussocks and measured the width of the clump tiller-to tiller, including tillers lying almost prostrate near ground level. We measured the height of the clump from the base to the tallest point (as opposed to tiller length, which could be longer for tillers arching downward near the tips). Additionally, we measured the distance of the clump to the nearest pine tree and hardwood shrub (sources of litter).

Because we could not simultaneously harvest the wiregrass tussock and burn it in the field, we located the nearest tussock of analogous stature (≤ 3 m away). We used the original tussock for fuel structure measurements, and the nearby analogous tussock for the flammability test. The original tussock was harvested by cutting it across the base. All aboveground material was bagged and refrigerated until processed. In the lab, we separated live and dead wiregrass tillers (categorized as “dead” if >50 % of tiller was brown; otherwise “live”), from pine needles and other litter (e.g., shrub and tree leaves, seedlings growing in the clump, and bark slough). The primary species contributing non-pine needle litter were common persimmon (*Diospyros virginiana*), sparkleberry (*Vaccinium arboreum*), and to a lesser degree, turkey oak (*Quercus laevis*). Other litter also included materials such as pine bark slough, pine cones, and woody twigs. Hereafter we refer to all non-pine needle litter as “broadleaf litter.” Once sorted, samples were oven-dried at 60 °C for 48 h (until no further weight loss), and weighed. We calculated bulk density as the mass of grass per volume via a half ellipsoid, where clump volume = (1/2) × (4/3) × Π × clump height × clump radius^2.

Field flammability experiments

We conducted field flammability experiments on 05-Jun-2014 during the historical fire season (Fill et al. 2012). To isolate each tussock for burning, we raked the perimeter surrounding each tussock (defined by the horizontal area covered by its tillers) and cut any other bunchgrasses growing within this perimeter. Isolating the tussock did not allow us to simulate fire spread from one tussock to another; however, we were careful to minimize disturbance to the experimental tussock itself. We began burning at 1030 and finished at 1600. We aimed to minimize the potential for variation in diurnal burning conditions to be confounded with our time-since-fire gradient. Therefore, we first burned seven tussocks in the 2005 unit, seven in the 2010 unit, and all 15 in the 2013 unit; we then burned the remaining eight at the 2005 site and finished with the remaining eight in the 2010 unit.

At the time of each tussock ignition, we recorded air temperature, wind speed, relative humidity, and ignition time. We collected a small sample of tillers (ca. 5 g, or about 10 tillers) to estimate fuel moisture, and stored them in pre-weighed polyethylene bags. These samples were weighed in the lab and oven-dried at 60 °C for 72 h.

Flammability was quantified in the burning experiments via measurements of flame length, flaming time, and smoldering time (Varner et al. 2015). We drizzled a small amount of fuel on each wiregrass tussock using a hand-held drip-torch with a mixture of 60 % diesel and 40 % gasoline. We ignited at the base with a hand lighter. In most cases, it took just a few seconds for the fire to increase in intensity until the whole tussock was burning, during which time maximum flame lengths were produced. Thereafter the flames decreased in length until the tussock was barely flaming and smoldering began. During each flammability test, we measured flame length (cm) using a pole marked with 1-cm gradations. Two observers stood ca. 3 m on opposite sides of the tussock (parallel to wind direction). One held the pole parallel to the flame (even if the flame was at an angle) and the other estimated maximum flame length from the base of the flame to the tip. For measuring flaming time, we started a timer at ignition and stopped it when the main flame extinguished. We did this to maintain consistency, as wind gusts intermittently caused embers to re-ignite extinguished clumps. Smoldering time was measured with another timer started at ignition and stopped when the fire was completely extinguished (i.e., no glowing embers visible).

Statistical analysis

To investigate which fuel structure characteristics predicted best each flammability metric (flame length, flaming duration, and smoldering duration), we developed a set of a priori candidate models (Table 1) that represent our hypotheses. This information-theoretic approach attempts to find the best-fit model in a set of models for which a priori support exists (Burnham and Anderson 2002). Because we were interested in the fuel characteristics that most influenced flammability, we focused on univariate drivers supported by flammability literature, rather than exploring all subsets (Burnham and Anderson 2002). Flammability metrics were modeled as count data (integers) using the negative binomial distribution.

We ran generalized linear mixed models in PROC GLIMMIX (SAS v. 9.3; SAS Institute, Inc., Cary, 2011; www.sas.com) with the Laplace approximation (Raudenbush et al. 2000), including plot (time-since-fire) as a random factor. We used the global models (the models with all parameters included) primarily to examine fit (Anderson and Burnham 2002); because “litter” (i.e., broadleaf litter) and “needles” were highly correlated ($r = 0.98$) we omitted global models in evaluating AICc values. We retained candidate models with an Akaike’s Information Criterion (corrected for small sample sizes) difference (ΔAIC_c) of <7.00 for statistical inference (Anderson and Burnham 2002; Burnham et al. 2011). We also calculated Akaike weights (w_i), which indicate the probability of a particular model being the best model given this dataset (Burnham et al. 2011). We used 95 % confidence intervals to determine the significance of parameter estimates; those that included zero were non-significant. After determining our inferential models, we investigated whether structural variables in the models differed among the three time-since-fire units. In tests for broadleaf litter and pine needle mass differences among units, we included tussock-to-

Table 1 Candidate models for wiregrass (*Aristida stricta*) flame length, including number of estimated parameters (k), Akaike's information criterion ($\mathrm{AIC_c}$), Akaike's information criterion differences ($\Delta\mathrm{AIC_c}$), and Akaike weights (w_i)

Rank	Model	k	$\mathrm{AIC_c}$	$\Delta\mathrm{AIC_c}$	w_i
Flame length					
	Biomass + Bulkdens + LDRatio + Fmc+ Litter + Needles	7	440.56		
1	**Biomass**	2	445.66	0.00	1.00
2	Fmc	2	458.42	12.76	0.00
3	LDRatio	2	463.56	17.90	0.00
4	Litter	2	466.03	20.37	0.00
5	Needles	2	467.24	21.58	0.00
6	Bulkdens	2	468.87	23.21	0.00
Flame time					
	Biomass + Bulkdens + LDRatio + Fmc + Litter + Needles	7	341.02		
1	**Litter**	2	346.76	0.00	0.48
2	**Bulkdens**	2	347.09	0.33	0.41
3	**Needles**	2	349.87	3.11	0.10
4	LDRatio	2	356.19	9.43	0.00
5	Biomass	2	356.33	9.57	0.00
6	Fmc	2	357.03	10.27	0.00
Smoldering time					
	Biomass + Bulkdens + LDRatio + Fmc + Litter + Needles	7	410.77		
1	**Litter**	2	410.23	0.00	0.60
2	**Needles**	2	411.53	1.30	0.31
3	**Bulkdens**	2	414.23	4.00	0.08
4	Biomass	2	423.49	13.26	0.00
5	LDRatio	2	424.37	14.14	0.00
6	Fmc	2	424.83	14.60	0.00

Models used for inference are in bold

nearest shrub and tussock-to-nearest pine distances as covariates, respectively.

Finally, we ran three additional models of the same structure (i.e., negative binomial regression and random plot effect) to determine if weather (air temperature, wind speed, or relative humidity) had significant effects on flame length, flaming duration, or smoldering duration. Within the bounds of the single burn day, measured air temperature, relative humidity, and wind speed had no significant effects on flammability metrics. All weather parameter estimates had confidence intervals that included zero with $P > 0.05$.

Results

We burned wiregrass tussocks across a wide span of total biomass, live:dead biomass, mass of perched broadleaf litter and pine needles, moisture content, and bulk density (Table 2). Wiregrass biomass did not differ among the units ($F = 0.505$, $df = 2$, $P = 0.61$), but bulk density was significantly greater in the 2010 unit (3 years since fire) than in the 2013 unit (1 year since fire; $\chi^2 = 15.389$, $df = 2$, $P < 0.001$). After controlling for distances of tussocks to pine trees and shrubs, neither broadleaf litter ($F_{2,35} = 2.01$, $P = 0.149$) nor needle mass ($F_{2,39} = 0.18$, $P = 0.835$) differed among plots.

All 45 wiregrass tussocks ignited, sustained visible flames, and smoldered. Flame length averaged 121 ± 6 cm, ranging from 50 to 240 cm. The tussocks flamed from 21 to 78 s (mean = 45 ± 2 s) and smoldered from 40 to 171 s (mean = 89 ± 6 s). Although fire weather varied across the experimental tussock fires, it did not vary significantly across the three time-since-fire units (air temperature, wind

Table 2 Characteristics of fire weather during experimental fires on 05-Jun-2014 and of wiregrass (*Aristida stricta*) fuel structure variables used in flammability prediction models

Variable	Average	SE	Minimum	Maximum
Air temperature (°C)	34.37	0.40	29.00	38.00
Windspeed (m s^{-1})	0.73	0.06	0.00	1.87
Relative humidity	46.94	0.99	36	56.90
Wiregrass biomass (g)	66.17	5.83	6.79	179.97
Wiregrass live:dead	0.22	0.02	0.00	0.58
Pine needle litter (g)	11.82	2.10	0.00	49.21
Other litter (g)	14.82	2.15	0.00	56.55
Bulk density (g m^{-3})	224.73	20.34	49.74	659.58
Wiregrass moisture (%)	41.51	1.85	11.17	80.00

speed, and relative humidity; all $F < 0.56$, $P > 0.57$). The global model indicated good model fit for flame length, flame time, and smoldering time (Pearson $\chi^2/df = 1.01$, 1.04, and 0.93, respectively).

We found support for the influence of fuel structure on flammability. Wiregrass biomass was the strongest predictor of flame length (Table 1). Wiregrass biomass significantly increased flame length in the univariate model (Fig. 2; Table 3). Broadleaf litter mass and bulk density were equally strongly supported univariate models of flaming duration (Table 1). Needle mass had a much lower probability but was still informative. Broadleaf litter mass, needle mass, and wiregrass bulk density increased flaming duration (Fig. 3; Table 4). Broadleaf litter and needle mass were strongly supported in models of smoldering duration, with the litter model having a higher probability than the needles model (Table 1). Bulk density was an informative model, but received lower support (Table 1). All three predictors increased smoldering duration (Fig. 4; Table 5).

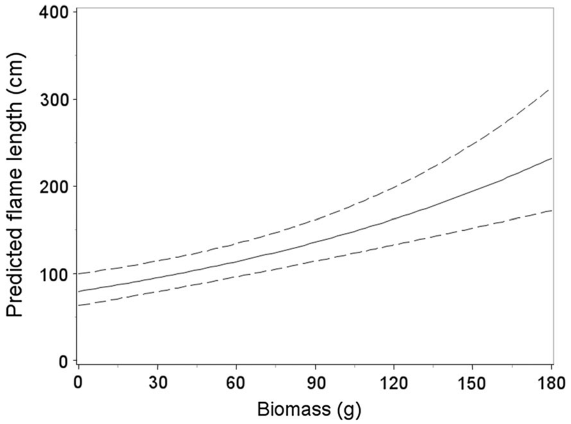

Fig. 2 The relationship between *Aristida stricta* clump flame length and biomass. *Dashed lines* represent 95 % confidence intervals

Discussion

Our results demonstrate that different aspects of wiregrass fuel structure drive various aspects of flammability. Wiregrass biomass was a strong predictor of flame length, with greater amounts of fuel generating greater flame lengths. This result suggests that greater wiregrass fuel loads support more intense fires (Wenk et al. 2011), which may also spread more rapidly through preheating of fuels at the fire front. Although wiregrass bulk density was not a supported predictor of flame length, it may be that the range of values for porous bunchgrasses like wiregrass are too low (our study: only 50–660 g m^{-3}) to affect intensity, in contrast to other grasses (Streng and Harcombe 1982), litter, or compact duff or woody fuels (Engber et al. 2011) that have much greater bulk density. Rather, in our study, increasing bulk density tended to increase wiregrass flaming and smoldering duration, likely since more compact fuels restrict inflow of oxygen (Rothermel 1983). However, it is possible that the effect of increasing fuel load diminished any negative effect of bulk density on flame length. Thus, the increase in flame length with increasing tussock biomass may have been greater had bulk density remained constant. Similarly, pine needles and other perched litter fuels were not related to wiregrass tussock flame length but increased the duration of flaming and smoldering. Our litter types may not have contributed significantly to fire intensity as coarser fuels or because of their relatively high-bulk density

Table 3 Parameter estimates and 95 % confidence intervals (CI) for the inferential model of wiregrass (*Aristida stricta*) flame length

Parameter	Estimate	SE	Lower 95 % CI	Upper 95 % CI	$P > \|t\|$
Intercept	4.3760	0.0838	4.0157	4.7363	0.0004
Biomass	0.0059	0.0011	0.0037	0.0081	<0.0001

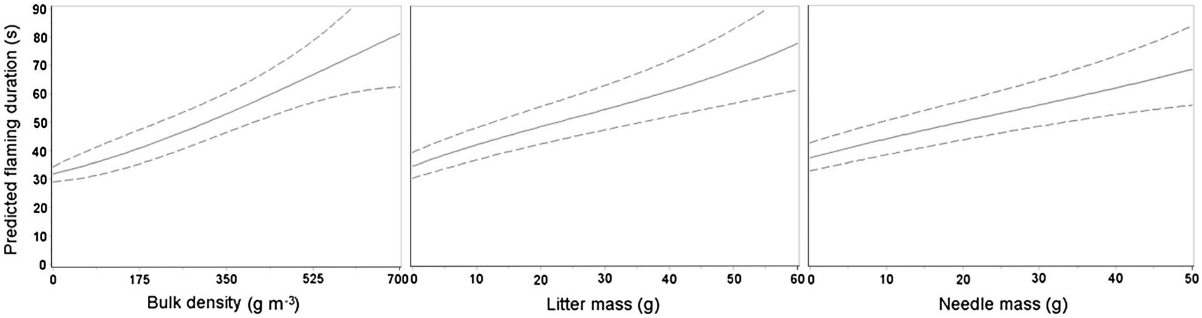

Fig. 3 The relationship between *Aristida stricta* flame time and bulk density, perched litter mass, and pine needle litter. *Dashed lines* represent 95 % confidence intervals

Table 4 Parameter estimates and 95 % confidence intervals (CI) for inferential models of wiregrass (*Aristida stricta*) flaming duration

Parameter	Estimate	SE	Lower 95 % CI	Upper 95 % CI	$P > \|t\|$
Model 1					
Intercept	3.6155	0.0722	3.2833	3.9478	0.0005
Litter	0.0111	0.0035	0.0041	0.0182	0.0027
Model 2					
Intercept	3.5341	0.0100	3.1044	3.9638	0.0008
Bulkdens	0.0011	0.0004	0.0004	0.0018	0.0035
Model 3					
Intercept	3.6737	0.0828	3.1730	4.0301	0.0005
Needles	0.0091	0.0033	0.0024	0.0158	0.0087

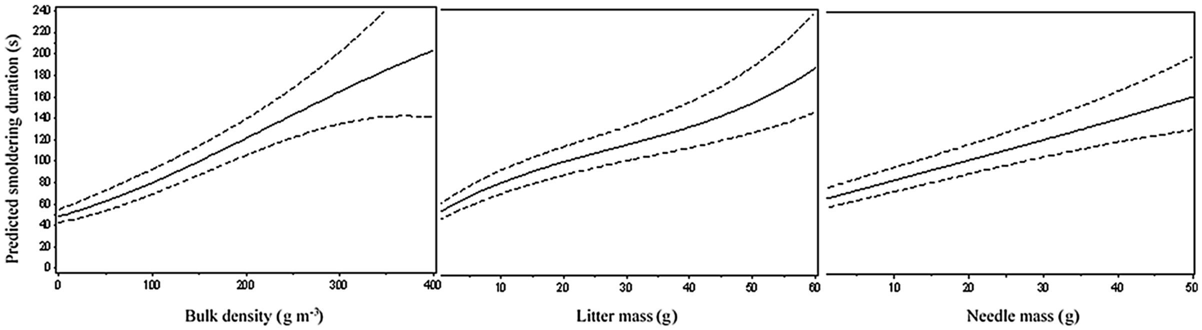

Fig. 4 The relationship between *Aristida stricta* smoldering time and bulk density, perched litter mass, and pine needle litter. *Dashed lines* represent 95 % confidence intervals

Table 5 Parameter estimates and 95 % confidence intervals (CI) for inferential models of wiregrass (*Aristida stricta*) smoldering duration

Parameter	Estimate	SE	Lower 95 % CI	Upper 95 % CI	$P > \|t\|$
Model 1					
Intercept	4.2162	0.1335	3.6419	4.7905	0.0010
Litter	0.0140	0.0033	0.0073	0.0207	0.0001
Model 2					
Intercept	4.2677	0.1422	3.6560	4.8795	0.0011
Needles	0.0132	0.0033	0.0066	0.0198	0.0002
Model 3					
Intercept	4.1426	0.1530	3.4844	4.8007	0.0014
Bulk density	0.0013	0.0004	0.0005	0.0020	0.0010

moisture content, only becoming available once dried by the initial heat from burning wiregrass. Differential litter drying rates (Kreye et al. 2013) would likely slow combustion, increasing the flaming and smoldering duration.

We found no evidence for individually significant fuel moisture, live:dead biomass, or fire weather effects on flammability, suggesting that wiregrass is capable of burning even under very moist conditions and variable weather (Table 2). Despite the high fuel moistures of our samples (up to 80 % on a dry weight basis) and relatively low wind speeds (average wind speed ranged from 0 to 1.9 m s^{-1}), wiregrass still burned with high intensity with flame lengths up to 240 cm (Table 2). These flame lengths were >3 times longer than those recorded for pure pine needles in Fonda (2001)'s study, and >3–4 times longer than those of flammable oak litter in Kane et al. (2008)'s experiment. The high surface area-to-volume ratio and low bulk density of this species may allow blades and clumps to pre-heat rapidly when exposed to flames, overcoming internal, or external inhibitory effects of moisture content on ignition. We burned wiregrass during the early summer, approximating the weather conditions under which wiregrass most often burned historically (Fill et al. 2012). The apparent lack of effects of fuel moisture and fire weather on wiregrass flammability suggest that even if fire weather is variable during this period, wiregrass may increase the likelihood of ignition (Platt et al. 2015). Thus, wiregrass should be instrumental in promoting fires even amidst the rains that accompany growing-season thunderstorms throughout its range. Wiregrass dominance in the understory should also be an important determinant of fire regime predictability across soil moisture gradients. In our study, average wiregrass fuel loads were approximately 175, 243, and 180 g m^{-2} with 1, 4, and 9 years since fire, respectively. Our values are comparable to those reported by Parrott (1967) who sampled wiregrass in soils with greater water availability (91, 120, and 100 g m^{-2}, 1, 4, and 8 years since fire, respectively), illustrating the species' role in rapid fuel recovery across soil moisture gradients.

Although we only examined the flammability of one groundcover species, our results highlight the importance of considering both grass species flammability and the flammability of other fuel types at local scales in fire-dependent savannas and woodlands. Fine scale patterns of vegetation mortality and recovery may be strongly directed by dominant groundcover species such as wiregrass (Ellair and Platt 2013). As a perennial bunchgrass capable of substantial fuel loading (784–812 g m^{-2}; Parrott 1967; Christensen 1977), wiregrass that dominates the groundcover in areas not recently burned may increase the likelihood of injury or mortality of intermixed herbs, shrubs, and small trees by increasing fire intensity (Grace and Platt 1995; Thaxton and Platt 2006; Robertson and Ostertag 2007; Ellair and Platt 2013). Moreover, extended heating attributed to increases in bulk density and fuel loading with time since the last fire could assist in topkilling woody resprouts associated with longer fire return intervals (Robertson and Ostertag 2007) and determine herbaceous vegetation composition post-fire (Gagnon et al. 2015).

In this study, we did not simultaneously or directly measure the flammability of longleaf pine needles or other litter types. Pine needles tend to increase temperatures produced by fires (Williamson and Black 1981; Grace and Platt 1995; Ellair and Platt 2013) and are also considered to limit tree recruitment via topkill and mortality, thus maintaining open savanna structure (Thaxton and Platt 2006; Ellair and Platt 2013). The relative influence of pine needles and wiregrass on local fire regimes and ecosystem dynamics will likely differ among environments (Platt et al. 1991) with variation in their distribution and abundance. For example, pine needles enhance fuel continuity where wiregrass is sparse and may be even more flammable where they are elevated in wiregrass tillers instead of forming a dense layer on the soil. Where soil moisture is high, wiregrass biomass may be much more influential than pine needles on fire intensity (Platt et al. 1991). Juvenile pine growth rates are much lower in flatwoods (Glitzenstein et al. 1995), where the local environment (fires and waterlogged soils) may result in low overstory pine density and therefore a lower potential contribution of needle cast (Glitzenstein et al. 1995; Grace and Platt 1995). Moreover, in contrast to flame lengths of <1 m for dry longleaf pine needles as measured by Fonda (2001), we observed wiregrass flame lengths under somewhat moist in situ conditions exceeding 2 m. Thus, wiregrass may be particularly important for sustaining surface fires in wetter environments and in those with low pine tree densities.

Our study is the first to quantify links between wiregrass fuel structure and its flammability that contribute to its keystone role in southeastern USA pine savannas. The predominance of wiregrass biomass as a driver of fire intensity, its capability of burning despite high fuel moisture, and its broad historical extent suggest that this species may be a major regulator of fire regime characteristics. Pine needles, pine cones, and other litter fuels also appear to locally modify dynamics through their influence on flaming and smoldering times (Fonda 2001; Kane et al. 2008; Wiggers et al. 2013). By capturing litter of other species, wiregrass tussocks facilitate a surface fire regime that varies at local scales. Fuel flammability characteristics at local scales are fundamental for modeling transitions between savannas and alternate states (Beckage et al. 2011; Mayer and Khalyani 2011; Staver et al. 2011), particularly because outcomes are strongly affected by model parameters and assumptions (Beckage et al. 2011; Reid and Robertson 2012). Accordingly, our findings emphasize the need for research into the flammability of other dominant pine savanna grasses such as little bluestem (*Schizachyrium scoparium*) and several other bluestems, (*Andropogon* spp.) in southeastern pine savannas (Peet 2006), and more broadly in fire-prone savannas and woodlands globally. Other grasses in temperate and tropical savannas with high fuel moisture similarly burn with substantial fire intensity (Setterfield et al. 2010; Engber et al. 2011; Hoffmann et al. 2012b). Australian savannas invaded by gamba grass (*Andropogon gayanus*) increased fuel loads by seven times that of native grasses, causing fires eight times more intense (Rossiter et al. 2003; Setterfield et al. 2010). Because ecosystem dynamics and resilience are ultimately driven by interactions at the species level (Solbrig et al. 1996), understanding a species' influence on fire as a keystone process should enhance our understanding and management of fire-prone ecosystems worldwide.

Acknowledgments Michael Small and Barry Kesler (South Carolina Department of Natural Resources) and Andy Johnson (South Carolina Forestry Commission) provided generous field assistance. Funding was provided by our respective institutions.

References

Alexander ME (1982) Calculating and interpreting forest fire intensities. Can J Bot 60:349–357

Anderson HE (1970) Forest fuel ignitability. Fire Technol 6:312–319

Anderson DR, Burnham KP (2002) Avoiding pitfalls when using information-theoretic methods. J Wildl Manag 66:912–918

Beckage B, Platt WJ, Gross LJ (2009) Vegetation, fire, and feedbacks: a disturbance-mediated model of savannas. Am Nat 174:805–818

Beckage B, Gross LJ, Platt WJ (2011) Grass feedbacks on fire stabilize savannas. Ecol Model 222:2227–2233

Bond WJ, Midgley JJ (1995) Kill thy neighbour: an individualistic argument for the evolution of flammability. Oikos 73:79–85

Bond WJ, Midgley JJ (2005) The global distribution of ecosystems in a world without fire. New Phytol 165:525–538

Bond WJ, van Wilgen BW (1996) Fire and plants. Chapman & Hall, London

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York

Burnham KP, Anderson DR, Huyvaert KP (2011) AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behav Ecol Sociobiol 65:23–35

Byram GM (1959) Combustion of forest fuels. In: Davis P (ed) Forest fire: control and use. McGraw-Hill, New York, pp 61–89

Byram GM (1963) An analysis of the drying process in forest fuel material. USDA Forest Service, Fire

Sciences Laboratory, Rocky Mountain Research Station Report, Missoula

Christensen NL (1977) Fire and soil–plant nutrient relations in a pine-wiregrass savanna on the coastal plain of North Carolina. Oecologia 31:27–44

Clewell AF (1989) Natural history of wiregrass (*Aristida stricta* Michx., Gramineae). Nat Areas J 9:223–233

de Magalhães RM, Schwilk DW (2012) Leaf traits and litter flammability: evidence for non-additive mixture effects in a temperate forest. J Ecol 100:1153–1163

Ellair DP, Platt WJ (2013) Fuel composition influences fire characteristics and understorey hardwoods in pine savanna. J Ecol 101:192–201

Engber EA, Varner JM, Arguello LA, Sugihara NG (2011) The effects of conifer encroachment and overstory structure on fuels and fire in an oak woodland landscape. Fire Ecol 7:32–50

Fill JM, Welch SM, Waldron JL, Mousseau TA (2012) The reproductive response of an endemic bunchgrass indicates historical timing of a keystone process. Ecosphere 3:art61

Fonda RW (2001) Burning characteristics of needles from eight pine species. For Sci 47:390–396

Frost CC (1998) Presettlement fire frequency regimes of the United States: a first approximation. In: Pruden TL, Brennan LA (eds) Fire in ecosystem management: shifting the paradigm from suppression to prescription. Tall Timbers Fire Ecology conference proceedings No. 20. Tall Timbers Research Station, Tallahassee, pp 70–81

Gagnon PR, Passmore HA, Slocum M, Myers JA, Harms KE, Platt WJ, Paine CET (2015) Fuels and fires influence vegetation via above- and belowground pathways in a high-diversity plant community. J Ecol 103:1009–1019

Gill AM, Trollope WSW, MacArthur DA (1978) Role of moisture in the flammability of natural fuels in the laboratory. Aust For Res 8:199–208

Glitzenstein JS, Platt WJ, Streng DR (1995) Effects of fire regime and habitat on tree dynamics in north Florida longleaf pine savannas. Ecol Monogr 65:441–476

Grace SL, Platt WJ (1995) Effects of adult tree density and fire on the demography of pregrass stage juvenile longleaf pine (*Pinus palustris* Mill.). J Ecol 83:75–86

Hammond DH, Varner JM, Kush JS, Fan Z (2015) Contrasting sapling bark allocation of five southeastern USA hardwood tree species in a fire-prone ecosystem. Ecosphere 6: art112

Hardin ED, White DL (1989) Rare vascular plant taxa associated with wiregrass (*Aristida stricta*) in the southeastern United States. Nat Areas J 9:234–245

Hendricks JJ, Wilson CA, Boring LR (2002) Foliar litter position and decomposition in a fire-maintained longleaf pine-wiregrass ecosystem. Can J For Res 32:928–941

Hoffmann WA, Adasme R, Haridsasan M, de Carvalho MT, Giger EL, Pereira MAB, Gotsch SG, Franco AC (2009) Tree topkill, not mortality, governs the dynamics of savanna- forest boundaries under frequent fire in central Brazil. Ecol 90:1326–1337

Hoffmann WA, Geiger EL, Gotsch SG, Rossatto DR, Silva LCR, Lau OL, Haridasan M, Franco AC (2012a) Ecological thresholds at the savanna-forest boundary: how plant traits, resources and fire govern the distribution of tropical biomes. Ecol Lett 15:759–768

Hoffmann WA, Jaconis SY, Mckinley KL, Geiger EL, Gotsch SG, Franco AC (2012b) Fuels or microclimate? Understanding the drivers of ire feedbacks at savanna-forest boundaries. Austral Ecol 37:634–643

Kane JM, Varner JM, Hiers JK (2008) The burning characteristics of southeastern oaks: discriminating fire facilitators from fire impeders. For Ecol Manag 256:2039–2045

Kreye JK, Varner JM, Knapp EE (2011) Effects of particle fracturing and moisture content on fire behavior in masticated fuelbeds burned in a laboratory. Int J Wildland Fire 20:308–317

Kreye JK, Varner JM, Hiers JK, Mola J (2013) Toward a mechanism for eastern North American forest mesophication: differential litter drying across 17 species. Ecol Appl 23:1976–1986

Kreye JK, Brewer NW, Morgan P, Varner JM, Smith AMS, Hoffman CM, Ottmar RD (2014) Fire behavior in masticated fuels: a review. For Ecol Manag 314:193–207

Lawes MJ, Adie H, Russell-Smith J, Murphy B, Midgley JJ (2011) How do small savanna trees avoid stem mortality by fire? The roles of stem diameter, height and bark thickness. Ecosphere 2:art42

Loudermilk EL (2010) Linking plant demography, forest fuels, and fire in longleaf pine (*Pinus palustris*) savannas using lidar remote sensing and simulation modeling. PhD dissertation, University of Florida, Gainesville, FL, USA

Loudermilk EL, Hiers JK, O’Brien JJ, Mitchell RJ, Singhania A, Fernandez JC, Cropper WP, Slatton KC (2009) Ground-based LiDAR: a novel approach to quantify finescale fuelbed characteristics. Int J Wildland Fire 18:676–685

Martin RE, Gorden DA, Gutierrez ME, Lee DS, Molina DM, Schroeder RA, Sapsis DA, Stephens SL, Chambers M (1993) Assessing the flammability of domestic and wildland vegetation. In: Proceedings of the 12th conference on fire and forest Meteorology. Society of American Foresters Publication 94-02, Bethesda, pp 130-137

Mayer AL, Khalyani AH (2011) Grass trumps trees with fire. Science 334:188–189

Mola JM, Varner JM, Jules ES, Spector T (2014) Altered community flammability in Florida’s Apalachicola ravines and implications for the persistence of the endangered conifer *Torreya taxifolia*. PLoS ONE 9(e103933):85

Noss RF (1989) Longleaf pine and wiregrass: keystone components of an endangered ecosystem. Nat Areas J 9:211–213

Parrott RT (1967) A study of wiregrass (*Aristida stricta* Michx.) with particular reference to fire. MS Thesis, Duke University, Durham, NC, USA

Pausas JG, Keeley JE (2009) A burning story: the role of fire in the history of life. Bioscience 59:593–601

Peet RK (2006) Ecological classification of longleaf pine woodlands. In: Jose S, Jokela EJ, Miller DL (eds) The longleaf pine ecosystem: ecology, silviculture, and restoration. Springer, New York, pp 51–93

Platt WJ (1999) Southeastern pine savannas. In: Anderson RC, Fralish JS, Baskin J (eds) The savannas, barrens, and rock outcrop communities of North America. Cambridge University Press, Cambridge, pp 23–51

Platt WJ, Glitzenstein JS, Streng DR (1991) Evaluating pyrogenicity and its effects on vegetation in longleaf pine savannas. Proc Tall Timbers Fire Ecol Conf 17:143–161

Platt WJ, Orzell SL, Slocum MG (2015) Seasonality of fire weather strongly influences fire regimes in south Florida savanna-grassland landscapes. PLoS ONE 10:e0116952

Raudenbush SW, Yang ML, Yosef M (2000) Maximum likelihood for generalized linear models with nested random effects via high-order, multivariate Laplace approximation. J Comput Graph Stat 9:141–157

Reid AM, Robertson KM (2012) Energy content of common fuels in upland pine savannas of the south-eastern US and their application to fire behavior modelling. Int J Wildland Fire 21:591–595

Reid AM, Robertson KM, Hmielowski T (2012) Predicting litter and live herb fuel consumption during prescribed fires in native and old-field upland pine communities of the southeastern United States. Can J For Res 42: 1611–1622

Robertson KM, Ostertag TE (2007) Effects of land use on fuel characteristics and fire behavior in pinelands of Southwest Georgia. In: Masters RE, Galley KEM (eds) Proceedings of the 23rd Tall Timbers Fire Ecology Conference: fire in grassland and shrubland ecosystems. Tall Timbers Research Station, Florida, pp 181–191

Robertson KM, Hmielowski T (2014) Effects of fire frequency and season on resprouting of woody plants in southeastern US pine-grassland communities. Oecologia 174:765–776

Rossiter NA, Setterfield SA, Douglas MM, Hutley LB (2003) Testing the grass-fire cycle: alien grass invasion in the tropical savannas of northern Australia. Divers Distrib 9:169–176

Rothermel RC (1983) How to predict the spread and intensity of forest and range fires. USDA Forest Service General Technical Report INT-143

Scholes RJ, Archer SR (1997) Tree–grass interactions in savannas. Annu Rev Ecol Syst 28:517–544

Setterfield SA, Rossiter-Rachor NA, Hutley LB, Douglas MM, Williams RJ (2010) Turning up the heat: the impacts of *Andropogon gayanus* (gamba grass) invasion on fire behaviour in northern Australian savannas. Biodivers Res 16:854–861

Solbrig OT, Medina E, Silva JF (1996) Determinants of tropical savannas. In: Solbrig OT, Medina E, Silva JF (eds) Biodiversity and ecosystem processes. Springer, Berlin, pp 31–41

Southeast Regional Climate Center (2011) Aiken 4 NE, South Carolina (380074): Period of Record Monthly Climate Summary [on-line]. Online at http://www.sercc.com/cgi-bin/sercc/cliMAIN.pl?sc0074 [accessed May 10, 2011]

Stambaugh MC, Guyette RP, Marschall JM (2011) Longleaf pine (*Pinus palustris* Mill.) fire scars reveal new details of a frequent fire regime. J Veg Sci 22:1094–1104

Staver AC, Archibald S, Levin SA (2011) The global extent and determinants of savanna and forest as alternative biome states. Science 324:230–232

Streng DR, Harcombe PA (1982) Why don't east Texas savannas grow up to be forest? Am Mid Nat 108:278–294

Thaxton JM, Platt WJ (2006) Small-scale fuel variation alters fire intensity and shrub abundance in a pine savanna. Ecology 87:1331–1337

Trauernict C, Murphy BP, Portner TE, Bowman DMS (2012) Tree cover–fire interactions promote the persistence of a fire-sensitive conifer in a highly flammable savanna. J Ecol 100:958–968

United States Department of Agriculture (1985) Soil survey of Aiken County Area: South Carolina. USDA Soil Conservation Service

Varner JM, Kane JM, Kreye JK, Enger E (2015) The flammability of forest and woodland litter: a synthesis. Curr For Rep 1:91–99

Veldman JW, Mattingly WB, Brudvig LA (2013) Understory plant communities and the functional distinction between savanna trees, forest trees, and pines. Ecology 94:424–434

Wenk ES, Wang GG, Walker JL (2011) Within-stand variation in understorey vegetation affects fire behaviour in longleaf pine xeric sandhills. Int J Wildland Fire 20:866–875

Wenk ES, GG Wang, JL Walker (2013) Understory fuel variation at the Carolina Sandhills National Wildlife Refuge: a description of chemical and physical properties. In: Guldin JM (ed) Proceedings of the 15th biennial southern silvicultural research conference. USDA Forest Service, Southern Research Station General Technical Report SRS-GTR-175, pp 351–356

Whelan RJ (1995) The ecology of fire. Cambridge University Press, Cambridge

Wiggers MS, Kirkman LK, Boyd RS, Hiers JK (2013) Fine-scale variation in surface fire environment and legume germination in the longleaf pine ecosystem. For Ecol Manag 310:54–63

Williamson GB, Black EM (1981) High temperature of forest fires under pines as a selective advantage over oaks. Nature 293:643–644