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Within-stand variation in understorey vegetation affects fire behaviour in longleaf pine xeric sandhills

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Abstract. The frequent fires typical of the longleaf pine ecosystem in the south-eastern USA are carried by live understorey vegetation and pine litter. Mature longleaf pine stands in the xeric sandhills region have a variable understorey vegetation layer, creating several fuel complexes at the within-stand scale ($20\,m^2$). We identified three fuel complexes found in frequently burned stands on the Carolina Sandhills National Wildlife Refuge, and used prescribed fire to test whether distinct sets of fire conditions were associated with each fuel complex. Study plots were dominated by either turkey oak or wiregrass in the understorey, or lacked understorey vegetation and contained only longleaf pine litter. Turkey oak-dominated plots had the highest fuel loads, and during burns they had higher total net heat flux than wiregrass- or longleaf pine litter-dominated plots, and longer burn durations than wiregrass-dominated plots. Across all plots, the quantity of litter fragments had the greatest effect on fire temperature and duration of burn. These results show that the patchy understorey vegetation within longleaf pine stands will create heterogeneous fires, and areas dominated by turkey oak may have increased fire intensity and soil heating compared with the other two fuel complexes.

Additional keywords: fire temperature, fuel complex, fuel heterogeneity, turkey oak, wiregrass.

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Introduction

Understorey vegetation and fuels vary at the within-stand scale (Keane *et al*. 2001) with significant effects on fire behaviour (Hough and Albini 1978; Molina and Llinares 2001; Price *et al*. 2003; Thaxton and Platt 2006; Hiers *et al*. 2009) and fire effects on vegetation (Williams *et al*. 1994; Odion and Davis 2000; Rocca 2009). However, in many fire-adapted ecosystems there are concerns that prior land-use and fire exclusion have altered the understorey vegetation. One effect can be more homogeneous fuel distributions and forest structures that may burn with different fire effects (Knapp and Keeley 2006; Dodson and Peterson 2010). In other cases, changes in the fire regime, species composition and cover can create a positive feedback cycle where reintroduction of fire can further expand the cover of certain plant communities (Mermoz *et al*. 2005). Identifying patterns in fuel distribution and fire behaviour at the within-stand scale becomes necessary to assess how changes in vegetation can create new fuel complexes that may change the way fire behaves within an ecosystem.

In longleaf pine (*Pinus palustris* Miller) ecosystems of the south-eastern USA, 2–8 year fire return intervals were characteristic (Christensen 1981). This short fire return interval supported the regeneration of longleaf pine and many herbaceous species (Christensen 1981; Brockway and Lewis 1997). Fire exclusion and past land-use has lead to substantial changes in fuels and fire regimes in this ecosystem. There has been an increase in both hardwood cover (Christensen 1981; Williamson and Black 1981; Gilliam *et al*. 1993; Provencher *et al.* 2001*a*, 2001*b*) and surface fuels (Provencher *et al.* 2001*a*, 2001*b*; Varner *et al*. 2005). Rebertus *et al.* (1989*a*) found that the reintroduction of fire following extended fire exclusion resulted in the spatial segregation of longleaf pine and turkey oak (*Quercus laevis* Walter), creating persisting patches of turkey oak. Changes in vegetation and fuels can alter the fire regime and subsequent response of the vegetation to fire in the longleaf pine ecosystem (Varner *et al*. 2005).

Within the longleaf pine ecosystem, pine, oak and grass species vary in their energy content and flammability (Golley 1961; Hough 1969; Fonda 2001; Kane *et al*. 2008; Wenk 2009), and drying rates (Nelson and Hiers 2008). Field studies using manipulated fuel loads have shown that within-stand variation in pine fuels affects fire intensity, shrub abundance (Thaxton and Platt 2006) and longleaf pine regeneration (O'Brien *et al*. 2008). Variation in pine and oak densities affects fire temperature and subsequent turkey oak mortality (Williamson and Black 1981; Rebertus *et al.* 1989*b*; Platt *et al*. 1991). Spatial

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segregation and interaction of these fuels create distinct fuel complexes (or fuel cells) and sets of fire conditions at the small and even fine scale (Hiers *et al*. 2009).

Through our study we sought to establish relationships between understorey fuel complexes and fire behaviour in the xeric sandhills region of the longleaf pine ecosystem. On Carolina Sandhills National Wildlife Refuge (NWR), the upland longleaf pine forest is characterised by a longleaf pine overstorey and a patchy understorey with small areas dominated by wiregrass (*Aristida stricta* Michaux) or shrub layer turkey oak that grade into each other. Management plans for habitat restoration of the endangered red-cockaded woodpecker (USFWS 2003) have created land management goals to reduce hardwood cover, restrict hardwoods to the understorey and increase the cover of a graminoid-dominated understorey on Carolina Sandhills NWR (USFWS 2009). Prescribed fire is the primary land management tool used on Carolina Sandhills NWR to accomplish these goals, and understanding whether vegetation and fuel variability change the fire behaviours and effects desired by land managers is necessary.

The variation in understorey vegetation existing within areas of comparable pine canopy cover creates conditions ideal for studying the effects of variable understorey vegetation on fire behaviour under field conditions. We identified three fuel complexes, all with longleaf pine needle litter, but varying in other fuel components. The objectives of our study were to (1) quantify and compare the pre-fire fuel conditions of each fuel complex and (2) determine how these fuel complexes affect fire behaviour. If fuel complexes burn with significantly different fire behaviours, results would help identify a source of small-scale heterogeneity in ecosystems influenced by frequent fire, as well as benefit land managers in understanding the effects of understorey vegetation cover patterns on fire.

Materials and methods

Study area

The study site was at Carolina Sandhills NWR (34.58°N, 80.23°W) in Chesterfield County, South Carolina. Carolina Sandhills NWR is in the xeric sandhills region of the longleaf pine ecosystem (Fig. 1*a*), situated on the fall-line of the Upper Atlantic Coastal Plain. Elevations for this area range from 70 m along Black Creek to 180 m on the highest ridges. Soils are excessively well drained sands of the Alpin series. The parent material for these soils is sandy marine deposits, and the available water capacity is 0.08 cm cm^{-1} (NRCS 2010). The mean annual precipitation is 1212 mm and mean annual temperature is 16.1°C (USFWS 2009). All study locations were upland sites with a longleaf pine canopy and slopes ranging from 1 to 7%.

Experimental design

We identified three distinct fuel complexes in stands with variable understorey vegetation, and used these fuel complexes as a replicable treatment across several stands. We did not attempt to describe the full variation of fuels present, but focussed on fuel complexes either including or excluding one species (wiregrass) desired by land managers and another species (turkey oak) whose cover land managers wish to decrease, within natural understorey vegetation cover patterns. The first fuel complex was dominated by longleaf pine needle litter, with live fuels nearly absent ('longleaf pine litter' plots), the second by turkey oak stems and litter ('turkey oak' plots) and the third by wiregrass ('wiregrass' plots). Longleaf pine needle litter was present in all fuel complexes, and all plots were located in areas with a mature longleaf pine canopy (mean basal area = 11.9 m^2 ha^{-1}). We installed 4 × 4-m plots for each fuel complex. At the within-stand spatial scale we sought to describe, fuels were relatively homogenous within the 16 m^2 compared with the heterogeneity found across the stands. Significant fine-scale heterogeneity is still present within plots of this size, which can affect fire behaviour at an even smaller spatial scale (Hiers *et al*. 2009).

We included 10 plots of each fuel complex, with two plots of each fuel complex present in each of five burn units. Because burn units included several stands and we were describing variability within a stand, we blocked plots at the stand level, rather than the burn unit level (Fig. 1*b*) and refer to each stand as a site. We had seven sites in this experiment, with three sites containing two plots of each fuel complex and four sites

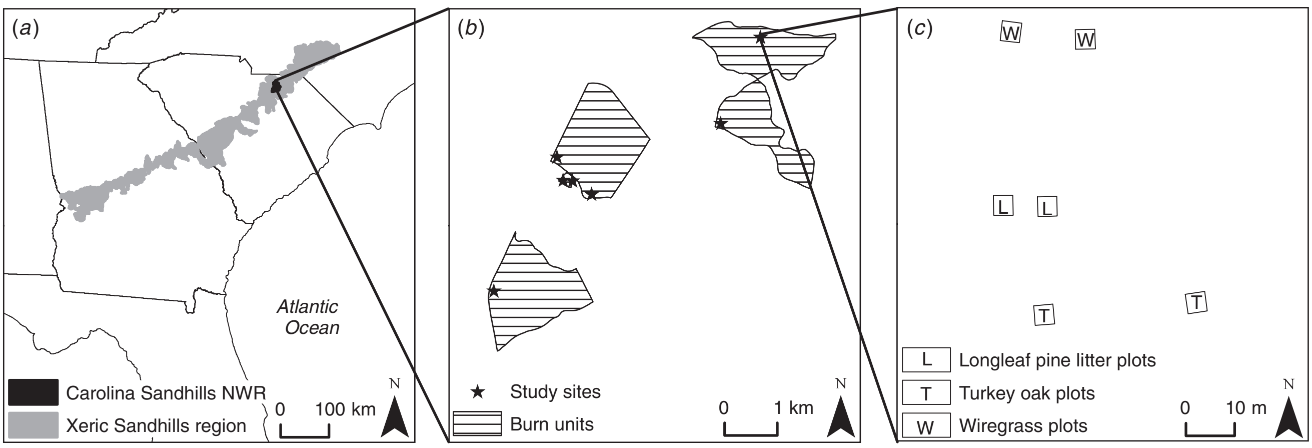

Fig. 1. (*a*) The xeric sandhills region in the south-eastern USA, (*b*) the study site and burn unit locations on the Carolina Sandhills National Wildlife Refuge (NWR) and (*c*) approximate plot locations at one study site.

containing one plot of each fuel complex. Fuel complexes were in close proximity to each other on a site (Fig. 1*c*). Burn units were similar in recent burn history, with the last prescribed burn conducted in the spring of 2003 or 2004. Though fire return intervals may be shorter in other parts of the longleaf pine ecosystem, this interval is within the range noted for the xeric sandhills region (Christensen 1981) and was typical for this time period on Carolina Sandhills NWR.

Fuel complex descriptions

In February and March of 2008 we sampled all plots to estimate potential fuel weight by measuring the dominant standing vegetation (live and dead) less than 2 m tall and estimating all surface litter and fuels. The fuel components measured for all fuel complexes included turkey oak stems, wiregrass plants and litter (including 1- and 10-h pine fuels, pine cones, and dead, horizontal, turkey oak stems). Plots with 100- or 1000-h longleaf pine fuels were excluded to minimise the influence of confounding factors on fire temperature and behaviour. Our goal was to understand the effects of understorey vegetation and associated fuels, not to describe the full range of conditions present. In addition, fires are carried by fine fuels in the longleaf pine ecosystem (Clewell 1989; Noss 1989; O'Brien *et al.* 2008) and fuel complexes with large quantities of woody debris are uncommon (Hiers *et al.* 2009). Furthermore, a previous study has already reported some effects of longleaf pine fuel (needle litter and woody fuel) on fire intensity and fire effects (Thaxton and Platt 2006).

We destructively sampled turkey oak stems outside the study plots to construct height *v.* weight regressions, which we used to estimate the weights of all standing stems within plots. All regressions were performed using 'Proc Reg' in SAS Ver. 9.2 (SAS Institute Inc., Cary, NC, USA). Leaves were not attached to stems at the time of burn and the regressions estimate the weight of stems without leaves: live stems 0–50 cm (biomass (g) = $(0.132 + 0.050\,\text{height (cm)})^2$, $R^2 = 0.885$, $n = 6$), live stems > 50 cm (biomass = $(-3.555 + 0.124\ \text{height})^2$, $R^2 = 0.948$, $n = 28$), dead stems 0–50 cm (biomass = $(-0.158 + 0.074\ \text{height})^2$, $R^2 = 0.756$, $n = 12$), dead stems > 50 cm (biomass = $(-6.682 + 0.182\ \text{height})^2$, $R^2 = 0.825$, $n = 15$). As not all turkey oak stems were consumed during burns, actual potential fuel weight was corrected based on post-burn estimates of remaining turkey oak stem weight. We destructively sampled wiregrass plants outside of the study plots to develop a relationship between plant basal area and weight: wiregrass (biomass = $(2.014 + 0.001\ \text{basal area (mm}^2))^2$, $R^2 = 0.745$, $n = 47$). Plant basal area was estimated by taking two perpendicular measurements of plant crown diameter. Basal area and weight were estimated for all plants in each plot.

Litter weight was estimated from samples collected adjacent to study plots. Litter samples from a 1 × 1-m area were used to estimate the litter weight of the longleaf pine litter and wiregrass plots, and samples from a 1 × 2-m area were used to estimate the litter weight of the turkey oak plots. Different areas were used owing to higher variability in litter cover at the smaller 1-m^2 scale in turkey oak plots. Similar variability in litter cover was observed within all fuel complexes using our sampling method (a Levene's test for homogeneity of variance across all treatments did not fail for total litter weight, $P = 0.227$). We sorted the litter samples into three components: longleaf pine litter, turkey oak litter and litter fragments (small litter particles, not identified to species), and obtained oven-dry weights for each. Within each species, types of litter (e.g. needle, bark, twig and cone) were not separated. Duff was absent at the sites we studied, owing to the short fire return interval and xeric conditions. Cone densities were low, with fewer than 10 cones observed per 16 m^2, and their weight was included in litter weight estimates, in addition to recording the number of intact cones. Longleaf pine cones support flaming combustion and may be largely consumed during burns (Fonda and Varner 2004).

Other herbaceous species, namely dwarf huckleberry (*Gaylussacia dumosa* Andrews), little bluestem (*Schizachyrium scoparium* Michaux) and splitbeard bluestem (*Andropogon ternarius* Michaux) made up a minimal proportion of the fuels. For example, there were an average of 1.4, 1.3 and 5.2 bluestem plants in longleaf pine litter, turkey oak and wiregrass plots respectively compared with 11.3, 12.0 and 87.5 wiregrass plants in respective plot types. Weights of these minor fuels were not estimated for this study.

Litter depth was measured before burns in all plots, with measurements taken at five regular points per plot. Litter depth was measured as the highest point with litter that was part of the continuous litterbed. For example, longleaf pine needles lodged in a wiregrass plant were included in litter depth, because they were part of the litterbed. Needles caught on a turkey oak branch above the litterbed were not included in litter depth measurements because they were disjoint from the litterbed, whereas those vertically oriented at the base of a stem were be included. Few needles were observed on turkey oak branches at our study sites. Bulk density measures were used to characterise litter and fuelbed aeration (Rothermel 1983). Litterbed bulk density represents the ratio of litter weight-to-litter depth and fuelbed bulk density represents the ratio of ground-layer fuels (litter and wiregrass) to litterbed depth.

Just before and during burns, we collected fine fuel samples for fuel moisture content. We collected recently cast longleaf pine needle litter (a combination of horizontally and vertically oriented needle litter), recently cast turkey oak leaf litter, wiregrass (a combination of live and dead leaf blades representative of sampled plants) and turkey oak twigs (less than 0.64 cm in diameter). Samples were placed in zip-lock plastic bags and refrigerated and weighed for wet weight at first convenience. Following 48 h in an oven at 65°C we determined their dry fuel weight. These samples were collected from burn units, although not always near study plot locations owing to personnel and active burning. Fuel moisture content samples corresponding most closely to plot burn times were used to estimate fuel moisture content during burns (Table 1).

Prescribed burns

Study areas were burned by Carolina Sandhills NWR staff between 28 February and 23 April 2008. All burns used a spot-grid ignition pattern. Four of the five burns were ignited aerially, with balls dropped from a helicopter at an approximate spacing of 24 m. In those four burns, the study sites were in burn units

Table 1. A summary of weather and fuel moisture content on Carolina Sandhills National Wildlife Refuge during prescribed burns
Plot burn time is shown to the nearest 15 min. All values displayed were recorded within one hour of plot burn time except for fuel moisture content during the 23 April 2008 burn, which was recorded 2 h before plot burn time. –, missing data

Burn date	Plot burn time (hours)	Temperature (°C)	RH (%)	Wind speed (km h^{-1})	Precipitation in last 3 days (mm)	Longleaf pine litter moisture content (%)	Wiregrass blade moisture content (%)	Turkey oak leaf litter moisture content (%)
28-Feb-08	1300	6	31	16	8	13.7	11.0	10.3
1-Mar-08	1500	21	27	14	0	12.3	15.8	9.0
1-Mar-08	1545	21	27	14	0	12.3	15.8	9.0
21-Mar-08	1245	17	21	6	23	9.9	12.8	9.2
21-Mar-08	1300	18	19	8	23	9.9	12.8	9.2
22-Mar-08	1045	13	79	14	23	–	–	–
23-Apr-08	1400	22	67	11	4	13.2	22.5	14.2

between 150 and 250 ha. The burn on 22 March was ignited by hand, using a 15-m grid spacing for ignition. This burn unit was ~5 ha. This variation in firing method was necessary because of a change in Carolina Sandhills NWR burn plans after the installation of our project. In spot-grid fires, heading, backing and flanking fires occur simultaneously, and it was possible for a plot to be burnt by multiple flame fronts at once. Though this increases the variability of burning conditions present in our study plots, this is the most common firing method used on Carolina Sandhills NWR. Thus, it is representative of how these stands are regularly burned. All burns were understorey burns, with only small areas of torching (contained to locations outside of the study sites). Fine fuel consumption was nearly complete for these burns, and understorey turkey oak stems in burn units were largely top killed. Hourly weather data were obtained from a weather station on Carolina Sandhills NWR, located at most 12.5 km from a study site (Table 1).

Fire monitoring

We used thermocouple probes (TCPs) and HOBO data loggers (Onset Computer Corporation, Bourne, MA, USA) to record temperature during burns. The TCPs were 4.8 mm in diameter and 30.5 mm long, with a type K thermocouple at the tip. Five TCPs were placed in each 4×4-m plot, with one at the centre and one on each diagonal, 1.8 m from the plot centre. TCPs were buried at the base such that the probe tips were 25 cm above the soil (Iverson *et al*. 2004). Any disturbed litter was replaced following TCP installation to mimic natural conditions. Data loggers recorded temperature at 1.5-s intervals for 12 h, to within 5°C. TCPs and data loggers performed well, with only a 3% failure rate.

Post-burn fuel measurements

Following burns, litter depth was measured at the same locations used for pre-burn measurements. Post-burn litter depth measurements were only taken on four of the seven sites, and made before TCP removal. The litter fragments remaining after burns were too small to make collection possible, and no estimates were made of post-burn litter weight. Turkey oak stems were destructively sampled after burns from outside of the study plots to create post-burn stem height-to-weight regressions: stems 0–50 cm (biomass = $(0.034 + 0.054$ stem height$)^2$, $R^2 = 0.613$, $n = 14$), stems > 50 cm (biomass = $(-3.883 + 0.127$ stem height$)^2$, $R^2 = 0.918$, $n = 41$). The weights of all stems in study plots were estimated from height measurements. Owing to high litter consumption (an average of 95% litter depth consumption) and complete consumption of above-ground wiregrass biomass, fuel consumption weights were estimated based on the assumption that the only fuels remaining were the unconsumed turkey oak stems.

Analysis of fire data

TCP data were used to create time–temperature curves, which were analysed to determine peak temperature, duration of burn above ambient temperature, duration of burn above 60°C and total net heat flux (integrated area under the time–temperature curve) above two thresholds: ambient temperature and 60°C. Peak temperature was determined as the highest temperature the TCP recorded, but is not equal to peak flame temperature owing to the heating lag time of the probe (the approximate heating lag time of a 4.8-mm diameter TCP is 1.2 s (Omega Engineering Inc. 2010)). A 60°C threshold was used in duration and net heat flux calculations because 60°C is the lethal heating temperature for plant cells (Alexandrov 1964). Again, owing to the heating lag time of the TCPs, our estimates of duration above 60°C may be viewed as a conservative index of the actual values. Ambient temperature varied by site, and occasionally by plot, and was based on the TCP readings, not fire weather data. Integration was done using the trapezoidal rule, with 1.5-s time increments.

Statistical analysis

We used mixed model analyses of variance (ANOVA) in Proc Mixed (SAS Institute Inc.) to test for significant differences in fuel and fire properties among fuel complexes. For each model, we included the site location as a random effect, and used weighting to account for the different number of plots at each site. We used least-squares means tests to calculate means and pooled estimates of standard error to make specific comparisons between fuel complexes. We used Proc Means (SAS Institute Inc.) to calculate the means and standard errors of the mean presented in tables and figures. All levels of significance displayed in tables are based on level of $\alpha = 0.05$.

Table 2. A summary of fuel measurements before and after prescribed burns in longleaf pine xeric sandhills

Means are shown for each fuel complex (longleaf pine litter, turkey oak and wiregrass) followed by the (s.e.) of the mean. Means followed by the same superscript letter are not significantly different

Fuel measurement	Longleaf pine litter	Turkey oak	Wiregrass	*F*-value	*P*-value
Potential fuel (Mg ha^{-1})	7.0 (0.64)^b	9.9 (1.36)^a	6.3 (0.73)^b	4.50	0.035
Consumed turkey oak stems (Mg ha^{-1})	0.00 (0.00)^b	1.0 (0.4)^a	0.03 (0.02)^b	5.48	0.020
Total turkey oak stems (Mg ha^{-1})	0.03 (0.02)^b	3.6 (0.4)^a	0.06 (0.04)^b	84.91	<0.001
Litter depth, pre-burn (cm)	4.8 (0.70)^b	8.3 (0.94)^a	7.2 (0.98)^a	6.37	0.013
Litterbed bulk density (kg m^{-3})	16.1 (2.45)^a	11.3 (1.91)^b	7.9 (1.33)^b	7.32	0.008
Fuelbed bulk density (kg m^{-3})	16.4 (2.45)^a	11.4 (1.89)^b	10.0 (1.39)^b	5.17	0.024
Litter depth, post-burn (cm)	0.2 (0.06)	0.4 (0.10)	0.2 (0.06)	1.14	0.380
Litter depth consumption (%)	93.3 (2.73)	94.8 (1.56)	97.2 (0.43)	0.85	0.472

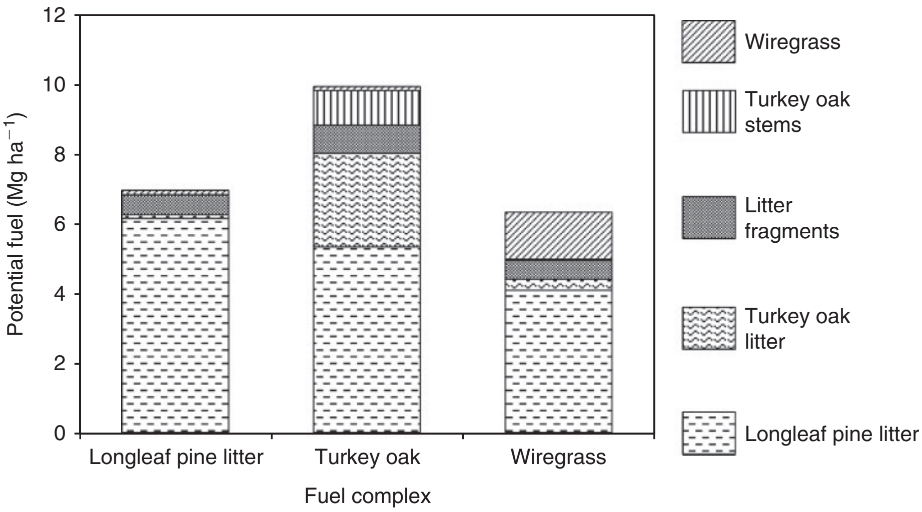

Fig. 2. Potential available fuel weight (Mg ha^{-1}) of fuel components in three fuel complexes in longleaf pine xeric sandhills.

We compared moisture content among fine fuel and litter samples using a mixed model ANOVA in Proc Mixed, including collection date and time as a random effect.

To determine which fuel parameters were significant predictors of peak TCP temperature, duration of burn and total net heat flux, we used stepwise multiple linear regressions in Proc Reg. A significance level of 0.05 was used for variables to enter and to stay in the model. Residual plots were used to determine appropriate data transformations.

Results

Potential fuel weight varied from 4.2 to 15.6 Mg ha^{-1} in our plots. We found significant differences in mean potential fuel weight among fuel complexes, with turkey oak plots containing greater fuel loads (9.9 Mg ha^{-1}) than longleaf pine litter (7.0 Mg ha^{-1}) or wiregrass (6.3 Mg ha^{-1}) plots (Table 2). For the individual fuel components, differences among fuel complexes were significant for consumed turkey oak stems ($P = 0.020$) and wiregrass ($P < 0.001$) (Fig. 2). The weight of wiregrass in wiregrass plots was 10 times greater than that in longleaf pine litter or turkey oak plots, whereas the available weight of turkey oak stems was several orders of magnitude greater in turkey oak plots than either longleaf pine litter or wiregrass plots. The mean total standing turkey oak stem weight was more than three times the mean consumed turkey oak stem weight (Table 2). However, the majority of the potential fuel weight was made up of litter, not live and dead standing vegetation. Longleaf pine litter was the largest component, comprising between 2.0 and 11.4 Mg ha^{-1} in plots, but mean weights did not vary significantly among fuel complexes ($P = 0.074$) (Fig. 2). The mean weight of turkey oak litter varied significantly among fuel complexes ($P = 0.001$), with over 2.5 Mg ha^{-1} in turkey oak plots, compared to less than 0.5 Mg ha^{-1} in longleaf pine litter or wiregrass plots (Fig. 2). Litter fragments comprised ~10% of the overall fuel weight, and their weight did not vary significantly among fuel complexes ($P = 0.520$) (Fig. 2). These differences in fuel components verified our fuel complex designations. For example, the turkey oak plots had the most turkey oak stems and litter and the wiregrass plots had the highest wiregrass weights.

Pre-burn litter depth varied among fuel complexes (Table 2), being 50 and 75% greater in wiregrass and turkey oak plots than longleaf pine litter plots respectively. Litter and fuelbed bulk densities also varied among fuel complexes (Table 2); longleaf pine litter plots had denser litter and fuelbeds than either turkey oak or wiregrass plots. Post-burn litter depth did not vary among fuel complexes, with only a few percent of the original litter depth remaining after burns, regardless of fuel complex (Table 2).

Fuel moisture content varied among the fine fuels sampled ($P < 0.001$) (Fig. 3). Turkey oak twigs had significantly higher fuel moisture content than the other fuels sampled. Wiregrass had significantly higher moisture content than longleaf pine needle litter ($P = 0.050$), but did not significantly vary from turkey oak leaf litter ($P = 0.085$).

Peak TCP temperature, did not vary among fuel complexes, and mean values ranged from 294 to 376°C (Table 3). Duration of burn above 60°C varied among fuel complexes, though duration of burn above ambient temperature did not (Table 3). The residence time above 60°C was significantly shorter in wiregrass plots (4.1 min) than in turkey oak plots (5.7 min) ($P = 0.004$) and marginally longer in longleaf pine litter plots (5.2 min) than in wiregrass plots ($P = 0.056$). Differences in total net heat flux were significantly different among all fuel complexes ($P < 0.001$) (Table 3). Mean total net heat flux was ~37% higher in turkey oak than wiregrass plots, and 24% higher in turkey oak than longleaf pine litter plots. The total net heat flux that occurred above 60°C was significantly higher in turkey oak plots than either longleaf pine litter or wiregrass plots ($P = 0.011$ and 0.001 respectively), but there was no significant difference between longleaf pine litter and wiregrass plots ($P = 0.111$) (Table 3).

We found that only one fuel component, the weight of litter fragments, was a significant predictor of peak TCP temperature, duration of burn above ambient temperature and total net heat flux (Fig. 4). There was a positive relationship between the log of litter fragment weight and all three measures of fire behaviour, but little of the variability in any measure was explained (peak TCP temperature: $R^2 = 0.181$, duration of burn: $R^2 = 0.294$, total net heat flux: $R^2 = 0.263$). No other fuel components were significant in these models at $\alpha = 0.05$.

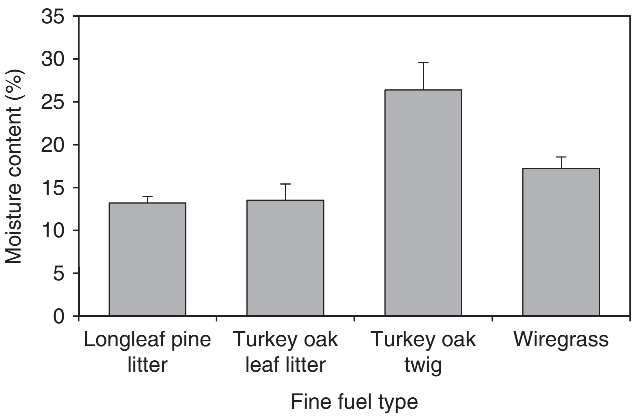

Fig. 3. Mean fuel moisture content of four fine (<0.64-cm diameter) fuels in longleaf pine xeric sandhills, observed over several days.

Discussion

The dominant fuels we measured and the fuel complexes they create, differed in the fire behaviour they produced. Longleaf pine needle litter has high flammability based on its burning characteristics (Fonda 2001) and the highest energy content noted among several species sampled in the xeric sandhills (Wenk 2009). Moisture content of longleaf pine needle litter is more complex than the individual value we presented, and is dependent on both arrangement and loading. Non-horizontal needles dry more quickly than horizontal needles, but the drying rate of horizontal needles is also dependent on fuel load (Nelson and Hiers 2008). We can describe the longleaf pine litter plots as having flammable fuels of high energy content, but a slow desorption rate. Turkey oak leaf litter burns with high intensity (Kane *et al*. 2008) and has nearly as high an energy content as longleaf pine needle litter (Wenk 2009). The turkey oak plots had the highest available fuel weights. In addition, some longleaf pine litter perches vertically on turkey oak litter owing to the curled turkey oak leaves. As a result, turkey oak plots likely support a drier litterbed of high-energy fuels that are capable of burning with high intensity. Wiregrass has lower energy content than either turkey oak leaf litter or longleaf pine needle litter (Hough 1969; Wenk 2009). Wiregrass plots had potential fuel weights similar to longleaf pine litter plots. However, the perched longleaf pine needle litter in wiregrass plots was likely drier, owing to its orientation.

We observed distinct differences in fire behaviour among the three naturally occurring fuel complexes identified in this study. The residence time above 60°C lasted longest where fuel loads were high (turkey oak plots) or the fuelbed bulk density was high (longleaf pine litter plots), and was of shorter duration where there was a well aerated fuelbed created by the combination of

Table 3. A summary of fire behaviour measurements recorded in longleaf pine xeric sandhills with thermocouple probes (TCPs)
Means are shown for each fuel complex (longleaf pine litter, turkey oak and wiregrass) followed by the (s.e.) of the mean. Means followed by the same superscript letter are not significantly different

Fuel measurement	Longleaf pine litter	Turkey oak	Wiregrass	*F*-value	*P*-value
Peak TCP temperature (°C)	294 (34.9)	376 (20.3)	321 (20.2)	1.93	0.188
Duration > ambient temperature (min)	15.0 (1.08)	15.8 (1.27)	13.3 (1.66)	2.64	0.112
Duration >60°C (min)	5.2 (0.54)^{ab}	5.7 (0.61)^{a}	4.1 (0.29)^{b}	6.26	0.014
Total net heat flux > ambient temperature (s × °C)	48 326 (4992)^{b}	59 739 (3830)^{a}	41 976 (3609)^{c}	26.4	<0.001
Total net heat flux >60°C (s × °C)	28 938 (4761)^{b}	39 898 (3023)^{a}	25 389 (2682)^{b}	11.42	0.002

wiregrass and longleaf pine needles (wiregrass plots). Total net heat flux values reflected the energy content of the fuels and the weight of the fuels consumed. Highest fuel weights were consumed in the turkey oak plots, which had the highest total net heat flux. Though fuel weights were similar in both the longleaf pine litter and wiregrass plots, the fuels in the longleaf pine litter plots had higher energy content per weight than those in the wiregrass plots, and accordingly, total net heat flux was higher in the longleaf pine litter plots.

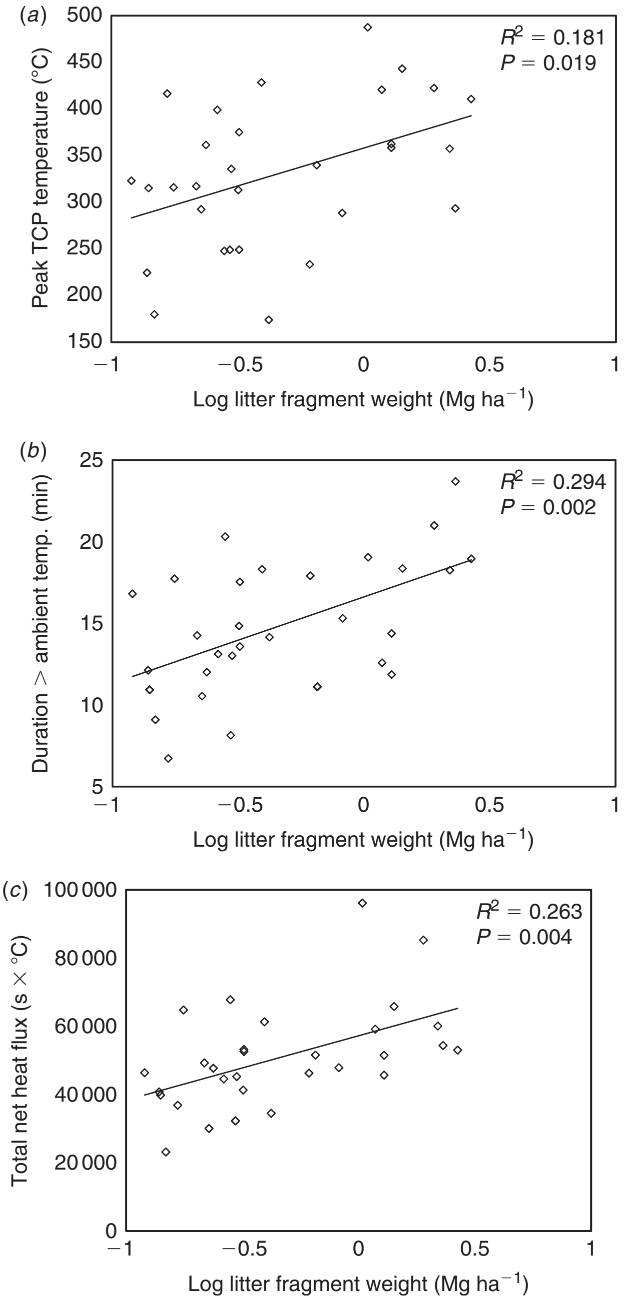

Fig. 4. Relationship between the weight of litter fragments and (*a*) peak thermocouple probe (TCP) temperature, (*b*) duration above ambient temperature and (*c*) total net heat flux during prescribed burns on longleaf pine xeric sandhill sites without duff.

Other studies have noted decreased flammability of turkey oak litter and lower temperature burns near turkey oaks as compared to longleaf pines (Williamson and Black 1981; Rebertus *et al.* 1989*b*). In both those studies, though, a pine canopy was not present in the vicinity of the oaks. The higher total net heat flux and longer burn duration we saw in turkey oak plots suggest that the interaction of turkey oak litter and longleaf pine litter created areas of increased fire intensity. Turkey oak has been identified as a fire facilitator (Kane *et al.* 2008), and the combination of fuels we observed may affect fire behaviour differently than either of the two fuels would independent of the other. Turkey oak leaf litter curls and packs loosely (indicated by the low fuelbed bulk density). In addition, turkey oak litter and stems catch longleaf pine needles in a perched position. Nelson and Hiers (2008) showed that needles perched at 45 and 90° angles had increased drying rates as compared to horizontal needle litter, suggesting that needle litter would dry faster in the turkey oak than in the longleaf pine litter plots. The perched nature of longleaf pine needle litter in wiregrass plants (indicated by the low fuelbed bulk density in wiregrass plots), and the interaction of these two fuels, has been more frequently discussed (Williamson and Black 1981; Rebertus *et al.* 1989*b*; Hendricks *et al.* 2002) than the interaction of hardwood and pine litter. However, the shrub and perched pine litter fuel type is frequently encountered in the longleaf pine ecosystem (Hiers *et al.* 2009) and the interaction of these fuels demands additional study considering that the highest levels of fire intensity we observed were on these sites. We studied longleaf pine stands with turkey oak, a pyric oak species (Kane *et al.* 2008), but in other parts of the longleaf pine ecosystem, the invasion of several oak species is a concern (Gilliam and Platt 1999; Provencher *et al.* 2001*a*, 2001*b*). Fire impeding oak species (e.g. *Quercus hemiphaerica*, *Q. incana*, *Q. nigra* and *Q. virginiana* (Kane *et al.* 2008)) may interact in different ways with longleaf pine litter, creating various types of fire behaviour.

Previously, Hiers *et al.* (2009) found the highest mean fire temperature in areas dominated by flat pine litter. Our results indicated the opposite (i.e. longleaf pine litter plots had the lowest peak TCP temperature). TCPs were placed at equal heights in all plots, but litter depth was significantly lower in longleaf pine litter plots. As a result, peak TCP temperature in longleaf pine litter plots (and, e.g. duration and total net heat flux) may be a lower index of actual values than it was in turkey oak or wiregrass plots (where the fuel being consumed was closer to the TCP). In fact, longleaf pine litter plots may have experienced a significantly longer duration of burn than wiregrass plots, though we found only marginal significance.

The range of potential fuel weight we measured was on the low end of that documented in other parts of the longleaf pine ecosystem (Kennard *et al.* 2005; Thaxton and Platt 2006). The upland xeric sandhills are one of the most nutrient-poor and water-stressed regions in the longleaf pine ecosystem, with sparse understorey vegetation (Peet and Allard 1993; Peet 2006) and low annual net primary productivity for both herbaceous and woody species (Mitchell *et al.* 1999). Fire temperatures and intensities may also be significantly lower in this part of the longleaf pine ecosystem. On another site in the longleaf pine sandhills region, maximum fire temperature was recorded ~300°C at ground level (using temperature-sensitive paints)

(Lippincott 2000), comparable to our observations (294–376°C) at 25 cm above ground. On a Coastal Plain longleaf pine site, fire temperatures up to 700°C were observed (using digital infrared thermography) (Hiers *et al*. 2009). We believe that although the peak temperatures observed in our study may be underestimates owing to sampling methods, they also reflect the lower fuel loads in the xeric sandhills compared to the Coastal Plain.

The fire parameters combining time and temperature variables showed more significant differences among fuel complexes than peak temperature did. Molina and Llinares (2001) found similar results in their study in a Spanish shrubland, suggesting that measures related to time and temperature (burn duration and the area under the time–temperature curve) are more useful than maximum temperature when comparing fuel complexes and their effects on fire behaviour. In addition, measurements that integrate time and temperature minimise the effects caused by the heating and cooling lag times of thick thermocouples (Kennard *et al*. 2005; Bova and Dickinson 2008).

In other longleaf pine stands, peak fire temperature was found to be spatially dependent at scales of 27–157 m (Kennard and Outcalt 2006) and 12–55 m (Estes 2006). The mean distance between plots of different fuel types within a stand in our study was only 27 m, suggesting that variation in fire temperature may not reflect the spatial variation in fuels we observed at the same scale. In Coastal Plain forests, Estes (2006) found no relationship between shrub cover and maximum fire temperature, and in Florida sandhills and Midwestern prairies, Gibson *et al.* (1990) found that fire temperatures were more homogenous in areas not burned for several years than in those burned annually. Because our study sites had last burned either 4 or 5 years before the study, and variation in shrub cover constituted a significant component of fuel heterogeneity, circumstances may not have been ideal for detecting differences in fire temperature. Differences in fire temperature do occur at the stem and plant level, but without more detailed measurements of fire temperature using digital infrared thermography (Hiers *et al*. 2009), identifying differences in fire temperatures at such fine scales is difficult.

Duff accumulation and consumption can help predict burn duration in the longleaf pine ecosystem (Varner *et al*. 2007). Our study sites lacked duff owing to the xeric conditions and short fire-return intervals. Litter fragments (i.e. fine litter particles) comprised the layer between the mineral soil and the easily identifiable, larger litter particles. Given a longer fire-return interval or a less-well drained site, these litter fragments would form a duff layer. Therefore, it was not surprising to find that the weight of litter fragments was a significant predictor of peak TCP temperature, burn duration and total net heat flux at our study sites.

Fuel complexes that create a longer residence time of high burn temperatures (such as turkey oak-dominated sites) may have the potential to heat the upper soil to higher temperatures, increasing injury to plants and soil organisms. Wiregrass withstands fires by sprouting back from the plant crown at ground level after burns. In other bunchgrass plants, the plant crowns heat slowly during fire. Even after several minutes of a high temperature burn, the temperature in the crown peaked at just 50°C, and the temperature of the soil under the plant rose only slightly (Robberecht and Defossé 1995). It is unknown what flame temperature and residence time are required to cause mortality of wiregrass plants, and fire effects may be dependent on plant age and time since last fire. Observations of widespread wiregrass survival in the months following burns suggest that most wiregrass plants survived the fires on our study sites, though few plants were located in areas of dense turkey oak cover.

Litter fragment weight only accounted for a small amount of the variability in TCP temperature, burn duration and total net heat flux, and we did not find a significant effect of other fuel components on fire parameters. In addition to fuel, fire behaviour is also affected by topography and weather (Rothermel 1983). We studied just the effects of fuels on fire behaviour, without seeking to describe all factors affecting fire behaviour and intensity, as other studies before have done in longleaf pine ecosystem fuel types (Hough and Albini 1978; Nelson and Adkins 1986).

Prescribed fire is used at Carolina Sandhills NWR to accomplish several land management goals. The heterogeneity in fuel distribution did not hinder fuel consumption, and turkey oak stems were largely top killed, suggesting that the prescribed fires documented in our study achieved several management objectives (including fuel reduction and hardwood control). We studied stands with heterogeneous understorey vegetation, but stands with a more homogeneous understorey (e.g. dense turkey oak cover, or little or no understorey vegetation throughout a stand) may burn differently than these stands. Our results suggest stands dominated by a turkey oak shrub layer burn with higher fire intensity than those dominated by wiregrass. However, additional work is necessary to know if a reduction in the heterogeneity of understorey vegetation within a longleaf pine stand will limit the range of fire conditions and the scale at which they occur across a stand.

We showed that within-stand variation in understorey vegetation (and associated fuels) created distinct areas of fire behaviour across stands with comparable overstorey influences. This study contributes to the growing discussion on the role of small-scale heterogeneity in fuels and fire in fire-adapted ecosystems (Knapp and Keeley 2006; Thaxton and Platt 2006; O'Brien *et al*. 2008; Rocca 2009). Given the high herbaceous diversity of south-eastern USA longleaf pine forests (Walker and Peet 1983), they could serve as strong models for future research evaluating the role of fuel heterogeneity and the diversity of fire behaviour and effects. This fuel and fire variability may help sustain the diverse plant communities found in the longleaf pine ecosystem (Mitchell *et al*. 2006, 2009) and other diverse, fire-prone ecosystems (Menges and Hawkes 1998; Rocca 2009). Fuel and fire variability created by the pre-fire vegetation may also select for continued dominance of species that tolerate or even prosper in certain conditions (Rebertus *et al.* 1989*a*). Monitoring differences in post-fire regeneration and recruitment are necessary steps to determine the effects of fuelbed heterogeneity on the long-term outcomes for fire-prone plant communities.

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