

Canopy-Derived Fuels Drive Patterns of In-Fire Energy Release and Understory Plant Mortality in a Longleaf Pine (*Pinus palustris*) Sandhill in Northwest Florida, USA

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Abstract. Wildland fire radiant energy emission is one of the only measurements of combustion that can be made at high temporal and spatial resolutions. Furthermore, spatially and temporally explicit measurements are critical for making inferences about ecological fire effects. Although the correlation between fire frequency and plant biological diversity in frequently burned coniferous forests is well documented, the ecological mechanisms explaining this relationship remains elusive. Uncovering these mechanisms will require highly resolved, spatially explicit fire data (Loudermilk et al. 2012). Here, we describe our efforts at connecting spatial variability in fuels to fire energy release and fire effects using fine scale (1 cm²) longwave infrared (LWIR) thermal imagery. We expected that the observed variability in fire radiative energy release driven by canopy-derived fuels could be the causal mechanism driving plant mortality, an important component of community dynamics. Analysis of fire radiant energy released in several experimental burns documented a close connection among patterns of fire intensity and plant mortality. Our results also confirmed the significance of cones in driving fine-scale spatial variability of fire intensity. Spatially and temporally resolved data from these techniques show promise to effectively link the combustion environment with postfire processes, remote sensing at larger scales, and wildland fire modeling efforts.

Résumé. L'émission d'énergie rayonnante des feux de forêt est l'une des seules mesures de combustion qui peut être faite à des hautes résolutions temporelles et spatiales. En outre, les mesures qui sont spatialement et temporellement explicites sont essentielles en vue de faire des inférences sur les effets écologiques des feux. Bien que la corrélation entre la fréquence des incendies et la diversité végétale biologique dans les forêts de conifères fréquemment brûlées est bien documentée, les mécanismes écologiques expliquant cette relation restent, mal connus. Pour découvrir ces mécanismes, des données de feu à très haute résolution et spatialement explicite sont nécessaires (Loudermilk et coll. 2012). Nous décrivons ici nos efforts pour relier la variabilité spatiale des combustibles à la libération de l'énergie du feu et aux effets du feu à l'aide de l'imagerie thermique à infrarouge de grande longueur d'onde (LWIR) à une échelle fine (1 cm²). Nous attendions à ce que la variabilité observée dans l'énergie radiative libérée par le feu ait été alimentée par les combustibles issus de la canopée qui pourrait être le mécanisme causal menant à la mortalité des plantes, un élément important de la dynamique communautaire. L'analyse de l'énergie rayonnante des feux libérée dans plusieurs feux expérimentaux a montré un lien étroit entre l'intensité du feu et la mortalité des plantes. Nos résultats ont également confirmé l'importance des cônes comme source de la variabilité spatiale à l'échelle fine de l'intensité du feu. Les données spatialement et temporellement résolues à partir de ces techniques sont prometteuses pour relier efficacement l'environnement de combustion avec les processus post-incendie, la télédétection à plus grande échelle, et les efforts de modélisation des incendies de forêt.

INTRODUCTION

The positive correlation between fire frequency and plant biological diversity in longleaf pine (*Pinus palustris*) and other fre-

quently burned coniferous forests is well known (e.g., (O'Brien 1998; Kirkman and Mitchell 2006), but the ecological mechanisms driving this relationship remain unclear. Johnson and Miyanishi (2001) observed that although "...the processes of combustion and heat transfer lie at the heart of fire ecology," very few studies actually quantify the energy released during

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a wildland fire. The lack of understanding of the mechanisms driving plant community response to fire is partly due to the dearth of fine-scale spatially and temporally explicit measurements of fire behavior (Hiers et al. 2009). Current measurement techniques provide intensity indices and/or point measurements at only coarse or mismatched scales. For example, many studies used pyrometers consisting of temperature-sensitive paints or waxes (Thaxton and Platt 2006; Davies et al. 2010; Brudvig et al. 2012) to characterize fire intensity. These point measurements are, at best, a qualitative index of fire temperature and are heavily influenced by their placement and construction (Iverson et al. 2004; Kennard et al. 2005). Thermocouples have also been extensively used to report fire temperatures, but these measurements are also limited by their construction, placement, and probe energy balance (Yilmaz et al. 2008). Furthermore, although rarely acknowledged, thermocouples generally measure only the convective energy fraction of combustion, but at worse represent a poor index of heat release due to thermal inertia.

These problems associated with qualitative and/or coarse resolution fire behavior measurements have limited progress toward understanding how variation in fire behavior influences fire effects. Recent advances in longwave infrared (LWIR) thermography, however, have allowed the quantitative measurement of LWIR radiant energy emission from surfaces involved in combustion at high temporal and spatial resolutions (Loudermilk et al. 2012; Loudermilk et al. 2014; O'Brien et al. 2016). Such highly resolved spatial and temporal measurements are critical for mechanistically linking fire behavior to antecedent fuel characteristics and postfire effects (Hiers et al. 2009). Highly resolved, fine-scale measurements of LWIR emission are also useful for quantifying accurate patterns of fire spread. For example, Hiers et al. (2009) and Loudermilk et al. (2012) combined LWIR thermography with LiDAR to demonstrate how variation in fuel characteristics ("fuel cells") affected fire behavior but, at the time, only speculated about the link to fire effects. LWIR thermography measurements are especially relevant to fire ecology because the system captures the heating of vegetation, soils, and fuels, and not the energy released by the flames themselves (see O'Brien et al. 2016 for a discussion of the utility of LWIR thermography). Despite this utility, studies relating LWIR emission to fire behavior and plant response are rare (see Wiggers et al. 2013).

In frequently burned ecosystems, fuel consumption is often thorough, with few areas left unburned within a stand. Although much of fire ecology has focused on the effects of heterogeneity represented by burned vs. unburned areas, very few studies have examined spatial patterns of fire behavior within burned areas (Mitchell et al. 2009). Mitchell et al. (2009) posited that canopy-derived fuels such as needles, cones, and other woody fuels are a critical component of "fuel ecology," especially in longleaf pine woodlands. Recent work has illustrated the potential of long-duration smoldering pine cones to affect patterns of plant diversity at fine scales (Fonda and Varner 2004; Wiggers et al.

2013). Wiggers et al. (2013) found that at a plot scale (1m^2) the addition of pine cones was sufficient to reduce cover of wiregrass and kill hard-seeded legumes within the top 2 cm of the soil surface, effectively opening a fine-scale gap within the matrix of understory species and their propagules. They suggested that the localized high-severity fire caused by smoldering cones could be sufficient to open niche space for regeneration of legumes in the continuous vegetation of longleaf pine understory.

Although fire heterogeneity in energy release and subsequent impacts on vegetation driven by canopy-derived fuels is a likely mechanism linking plant diversity and high fire frequency (Mitchell et al. 2009), it is possible to test this mechanistically only through the connection of spatially resolved fire energy release and plant response (Hiers et al. 2009). Whereas Wiggers et al. (2013) observed that pine cones' combustion influenced legume seed germination and mortality, they did not directly measure the energy released by combustion in a spatially explicit manner. Furthermore, other studies (Thaxton and Platt 2006; Gagnon et al. 2015) used experimental fuels loads that were uniform and nonspatially resolved measurement of fire, subject to the limitations of methods described herein.

Here, we describe our efforts at connecting spatial variability in fire energy release to patterns of fuels and fire effects by using LWIR thermal imagery captured at fine scales ($\sim 1\text{ cm}$) to variation in preburn fuel structures at similar ($10\text{ cm} \times 10\text{ cm}$) scales and postburn plant mortality.

Specifically, we hypothesize that canopy-derived fuels (specifically pine cones) significantly increase fire energy release compared to noncanopy-derived fuels, and fire energy release associated with these canopy-derived fuels significantly influences understory plant mortality. This experiment is meant to provide a foundation for further experiments testing whether variability in fire radiative energy release could be a causal mechanism driving plant community assembly rules in these systems. Because high plant diversity exists at very fine scales ($30+$ vascular plant species per m^2) in a relatively homogeneous sandy soil (Lavoie et al. 2014) in these systems, neutral processes (*sensu* Hubbell 2001) would likely drive patterns of diversity seen in the frequently burned study sites. If our hypothesis that localized patches of high-intensity fire driven by an overstory canopy-derived fuel (e.g., pine cones) caused mortality in understory plants, it would lend credence to neutral drivers of plant community dynamics that could be investigated further. We further explore whether spatially and temporally resolved data from these techniques can effectively link the combustion environment with postfire processes and, potentially, remote sensing at larger scales.

METHODS

Study Area

This study was conducted at Eglin Air Force Base during 2014 (Figure 1). Eglin Air Force Base, the former

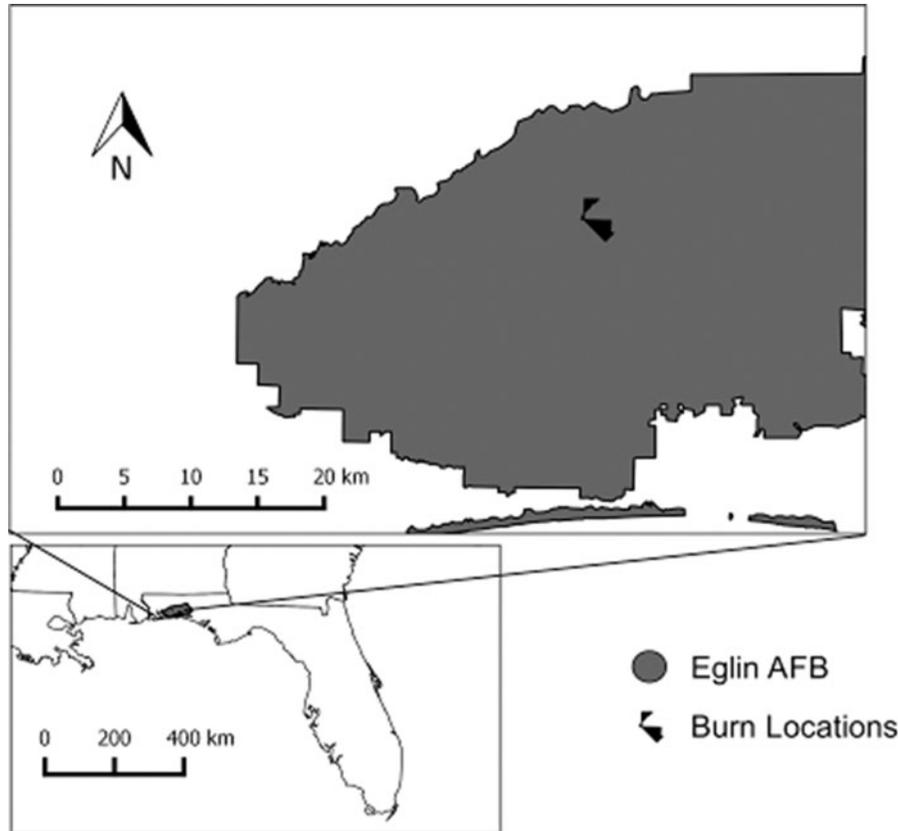


FIG. 1. Fire management unit locations for this study, conducted in sandhill habitat at Eglin Air Force Base, northwest Florida.

Choctawhatchee National Forest, is located in northwest Florida, USA, and has nearly 180,000 ha of longleaf pine forests and over half of the remaining old growth of this forest type (Varner et al. 2000; Holliday 2001). The study sites were within the Southern Pine Hills District of the Coastal Plain Physiographic Province with deep, well-drained, sandy soils. Soils of the study sites were all Typic Quartzipsamments of the Lakeland series with mean depth to water table > 200 cm (Overing et al. 1995). The climate of the area is subtropical, with warm, humid summers and mild winters. Mean annual temperatures in the area are 19.7 °C, with a mean annual precipitation of 1580 mm, concentrated in the months from June to September (Overing et al. 1995). Elevations of the study sites were 52 m to 85 m above sea level, and all sites had the minimal topography typical of longleaf sand hills (Myers 1990). Vegetation was dominated by a longleaf pine overstory with a sparse midstory of various deciduous oaks, e.g., *Quercus laevis* Walter, *Q. margareta* Ashe, *Q. incana* Bartram, *Q. germinata* Small. The understory is highly variable, but dominated by graminoids (*Schizachyrium scoparium* Michx., *Andropogon virginicus* L.), Ericaceous subshrubs (*Gaylussacia dumosa* J. Kenn., *Vaccinium darrowii* Camp), asters (*Pityopsis aspera* Shuttlew, ex Small, *Solidago odora* Aiton), and legumes (*Galactea regularis* L., *Tephrosia virginiana* L.).

Study Design

The data used for this study are part of a larger experiment at Eglin Air Force Base, northwest FL (SERDP project #RC-2243). The part of the study reported here consisted of blocks of 3 plots (1 m × 3 m) established in 3 Eglin AFB fire management units F-18, 137 ha; F-19, 441 ha; and F-22, 474 ha (Figure 2). The study represents a split-plot design. These fire management units were a randomly chosen subset of the reference plots established by Provencher et al. (2001) that were scheduled for burning in 2014. These areas have been burned with an approximately 2-year fire return interval for the last 20 years. The study areas had not burned for approximately 2.5 years (F18, 882 days, F-19, 883 days, and F22, 821 days since last fire). For consistency in fuel influence by canopy structure (O'Brien et al. 2008), the plot location was randomly located with the following constraints: plots were less than 5 m away from a single adult (>10 cm diameter at 1.4 m height) pine, but more than 5 m away from any other adult pine. Each 1-m × 3-m plot was divided into 3 adjacent 1-m × 1-m subplots, each 1-m² subplot was randomly assigned one of 3 cone treatments from which we either removed all cones or randomly distributed 5 or 10 longleaf pine cones to assess the influence of this specific coarse woody debris on fine-scale fire intensity and subsequent plant mortality. The design was constructed to specifically test how

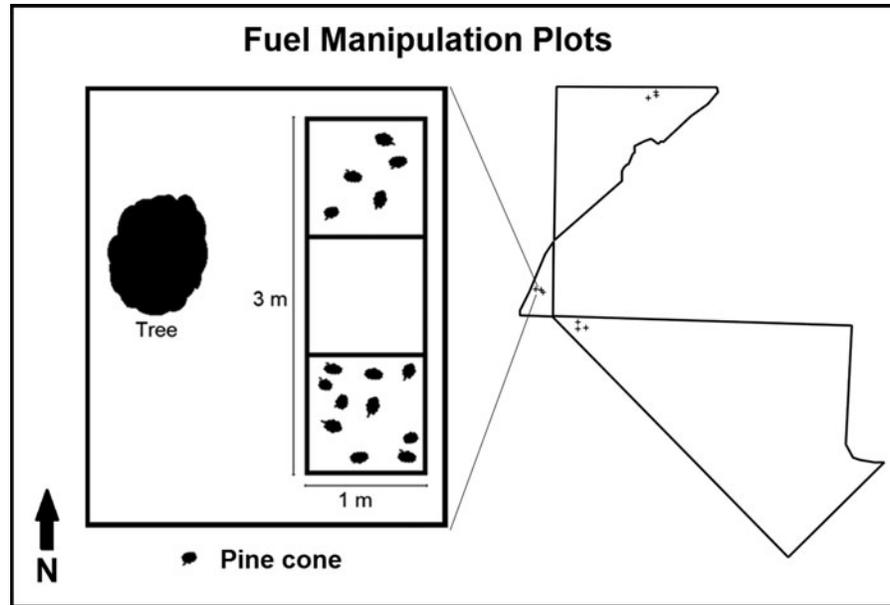


FIG. 2. Layout of individual plots within the burn units. The 1-m \times 1-m subplots for the respective treatments were chosen randomly within each 1-m \times 3-m plot.

variable mortality rates influence plant community dynamics. In this manuscript, however, we report on the impact of fuel-driven variability in fire intensity on plant mortality rates.

Plant Monitoring

All living plants within the 1-m \times 3-m plot area were mapped using a 10-cm- \times -10-cm grid coordinate system. Four 20-cm long, 12-mm diameter stainless steel rods were driven into the soil at the corners of the central 1-m² subplot. A 1-m \times 1-m aluminum frame with guides for removable 3-mm diameter steel pins was then placed on the rods. Pins were installed in the guides and used to create the coordinate grid to map the plants (Figure 3). All plant individuals were recorded by species in Fall 2013 (preburn) and Fall 2014 (postburn). About 80% of cells (10 cm \times 10 cm) with plants had one individual plant. The remaining 20% had 2–4 individuals in each cell. These data were used to estimate mortality within and across cells and plots. Mortality was coded as a binary variable, where an individual plant either died without self-replacement (no resprouting or seed germination within the same cell) or survived within each cell (1 = mortality, 0 = survival).

Fuels, Weather, and Fire

Three experimental burns were conducted on May 23, 24, 25 2014. The 3 burns were 6 ha, 62 ha, and 260 ha in extent. All 3 burns consisted of ground-ignition-prescribed fires as part of regular fire management operations at Eglin AFB. Target fuel moisture and fire weather conditions were monitored up to the test fire to ensure fire behavior would allow for ignition of

pine cones and achieve complete consumption. The fire rate of spread and to a lesser extent, type, varied in the plots (Table 1). The burns were ignited on 3 consecutive days with similar ignition times (approximately 10:00 a.m. CDT). Weather conditions during the burns were comparable: the temperature ranged from 31 °C to 32 °C and relative humidity ranged from 44% to 54%. Although in situ fuel loading was not collected, fuels types within plots were recorded in the 300 grid cells described previously. These data were used to estimate fuel volume and loading



FIG. 3. The 10-cm \times 10-cm grid coordinate system within a 1-m \times 1-m aluminum frame used to create the coordinate grid to map the plants and fuels within our 1-m \times 3-m plots. These are held in place with permanent steel rods driven into the soil at the corners of the frame. As the plants and fuels are mapped, the frame is moved up to the adjacent 1-m \times 1-m treatment.

TABLE 1
Date of ignition, rate of spread, and fire type in the experimental plots

Unit	Plot	Ignition Date	Type	cm s ⁻¹
F-22	1	5/23/14	Head	11.1
	2		Head	9.1
	3		Head	28.2
F-18	4	5/24/14	Head	10.1
	5		Flanking	1.2
	6		Head	3.5
F-19	7	5/25/14	Head	16.7
	8		Head	11.1
	9		Head	4.2

Rate of spread was measured as the time the fire took to travel 1 m perpendicular to the fire front while in a plot. Fire type refers to head fire (fire moving parallel to the wind direction) and flanking fire (fire moving perpendicular to the wind direction).

indirectly using photogrammetry and 3D rendering techniques (see Bright et al. 2016, Rowell et al. in press).

LWIR Measurements

High-resolution LWIR thermography was collected for each plot, using 3 thermal imaging systems from FLIR Inc.: an SC660 and 2 A655SC. Both models of FLIR systems have a focal plane array of 640 × 480 pixels, a spatial resolution of 1.3 mRad, a sensitivity of 0.03 °C and a thermal accuracy of ± 2%. The temperature range selected for data collection during the fires was 300 °C–1,500 °C at a measurement rate of 1 Hz. The imaging systems had a nadir view of the plots by using an 8.2-m tall tripod system (Loudermilk et al. 2014; O'Brien et al. 2016), which positions the camera optics 7.7 m directly above the center of the 1-m × 3-m plots. Having the camera optics 7.7 m above the target resulted in a pixel resolution of ≈ 1 cm².

Image Processing

The initial processing step of the LWIR imagery used the proprietary FLIR Inc. ExaminIR Pro software in which plot boundary coordinates were identified and local conditions specified (emissivity, air temperature, relative humidity, and distance to target) for proper calibration of the image files. The files were then exported as an ASCII array of temperatures in °C with rows and columns representing pixel positions. The identified plot boundary coordinates were used to extract the region of interest and then converted into another ASCII file of 3 columns where x , y , z = pixel row, pixel column, and temperature, respectively, using the Python 2.7 processing language. Temperatures were then converted to degrees Kelvin and the Stefan–Boltzmann equation for a gray body emitter with an emissivity of 0.98, the approximate mean of soils and fuels in the wavelengths

measured by the FLIR instruments (Snyder et al. 1998; López et al. 2012) was used to convert temperatures into fire radiant flux density (FRFD, Wm⁻², O'Brien et al. 2016). The LWIR data was aggregated to the 10-cm × 10-cm scale to be comparable to the scale of the plant demography data. This was accomplished by summing the FRFD in each 10-cm × 10-cm area over time (Figure 4). When integrated over time, FRFD is converted to fire radiative energy density (FRED, J m⁻²).

In order to evaluate the effects of high FRFD on plant mortality, we created a threshold FRED by extracting 18 pine cones (2 from each plot) from the LWIR imagery and integrating the values over time to give fire radiative energy density (FRED, kJ m⁻²) released by cones. A mask consisting of the original perimeter of the cone was created, and all pixels within this mask were extracted and the FRFD and FRED calculated as described above.

Data Analysis

We used a blocked split-plot experimental design to examine the additional energy released by cones compared to background fuels and with an overall experiment-wise Type I error (rejecting a true null hypothesis of no difference) probability of 0.05. Three fire management units were chosen as a stratified random sample of burn units scheduled for prescribed burning in 2014. The 3 individual fire management units were treated as blocks, each having 3 plots (total plots = 9), and cone treatments split within the plots (2 levels of cones versus no cones). A general linear mixed-effect model was run using STATISTICA¹ the cone treatment and burn blocks were fixed effects and the plots were treated as a random effect. We applied a Tukey's HSD post hoc means test with an $\alpha = 0.05$ to the mean cone and plot FRED values. We measured the magnitude and significance of spatial autocorrelation of fire intensity using the Moran's I analysis within the "ape" package (Paradis et al. 2004) in R (R Core Team 2013). To assess the range of spatial correlation and magnitude of spatial variability between the cone density subplots, we modeled the semivariance (spatial autocorrelation function) within treatments using the "geoR" package in R (Ribeiro Jr. and Diggle 2001). For each group of cone-density subplots, an isotropic exponential autocorrelation function (Goovaerts 1997) was fit to the empirical semivariance. All semivariance parameters were the same between groups (lags = 10, lag separation distance = 5 cm, nugget = 0, range ~ 20 cm), except for the sill (sill ~ 900, 11,000, 22,000 for 0, 5, 10 cone densities, respectively).

We assessed the impact of fine-scale fire intensity, i.e., "hot spots" created by burning pine cones, on understory plant mortality patterns on a 10-cm × 10-cm cell-by-cell basis, using a logistic regression with mortality as the dependent variable and FRED as the independent variable. We calculated a binary fire intensity metric by using cone FRED as determined by the

¹Data analysis software system, version 12, StatSoft, Inc., 2013.

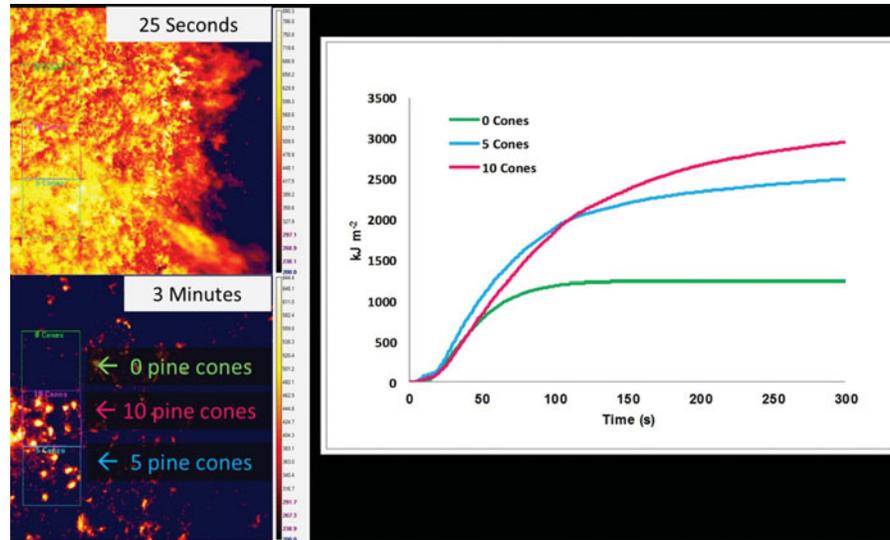


FIG. 4. Fire intensity measured with the LWIR illustrating the difference in cumulative radiative power, i.e., fire radiative energy, in each of the 3, 1-m² areas influenced by the cone density treatments (0, 5, 10). Each 1 m² was placed adjacent to the next frame in a 1-m × 3-m plot with randomly selected treatments. As the fire enters the plots (top image) grasses, shrubs, and leaf litter carry the fire, whereas 3 minutes after the fire, pine cones and other coarse woody debris are still releasing radiant heat above 300 °C.

LWIR imagery (see image processing) as a threshold for a high (1) and low (0) FRED. The mean (standard deviation) FRED of 18 pine cones (2 per plot) was 7,730 (3,154) kJ m⁻². We calculated the threshold value for a high FRED (4,576 kJ m⁻²) as the mean cone FRED minus 1 standard deviation. We used this threshold to separate areas within the plots that were influenced by cones or other woody fuels from areas of sparse fuels or other quick-burning fuels such as grasses and pine litter.

RESULTS

The results from the linear mixed-effect model illustrated that there was a significant difference between FRED among the burn units and cone treatment, but no interaction between burn unit and plots (Table 2, Figure 5). The Tukey's test indicated that the plots in fire management unit F-22 (Figure 5) released significantly more energy ($\mu = 6.19$ MJ, $p < 0.01$) than both F-18 ($\mu = 2.86$ MJ) and F-19 ($\mu = 3.51$ MJ) though these 2 blocks did not differ ($p > 0.05$). The cones had higher FRED

than the background fine fuels ($p < 0.0001$); cones emitted a mean of 7.73 MJ compared to 0.64 MJ emitted by background fine fuels, a 12 times greater energy release.

The Moran's I test illustrated that there was significant spatial autocorrelation for all 3-cone density treatments ($MI = 0.78$, $p < 0.0001$ for all treatments). From the semivariance analysis (Figure 6), we found that the range (distance) of spatial autocorrelation was similar (~ 17 cm) for all cone densities, but the inclusion of more dense fuel at fine scales (pine cones) created significantly higher magnitude of spatial variability (sill). The spatial heterogeneity in fuelbed heights and FRED is apparent at these fine scales (Figure 7), whereas, in this study, 1 woody fuels (pine cones) drove FRED increases (Figures 4 and 5).

In all, 1,317 cells out of a total of 2,700 had plants prior to the experimental burn, of these, 620 were dead in the subsequent census. The logistic regression showed that higher mortality rates occurred in areas of high fire intensity associated with burning cones (Table 3). The odds ratio for the model was 2.78

TABLE 2
Results of split plot mixed linear model ANOVA

Effect	Effect (F/R)	Degrees of Freedom	SS	MS	F	<i>p</i>
Intercept	Fixed	1	315.47	315.47	82.12	>0.001
Block	Fixed	2	37.441	18.721	4.871	0.041
Cones	Fixed	1	226.121	226.121	58.861	>0.001
Plot*Block	Random	6	12.10	2.01	0.525	0.775
Error		8	30.73	3.84		
Total			306.41			

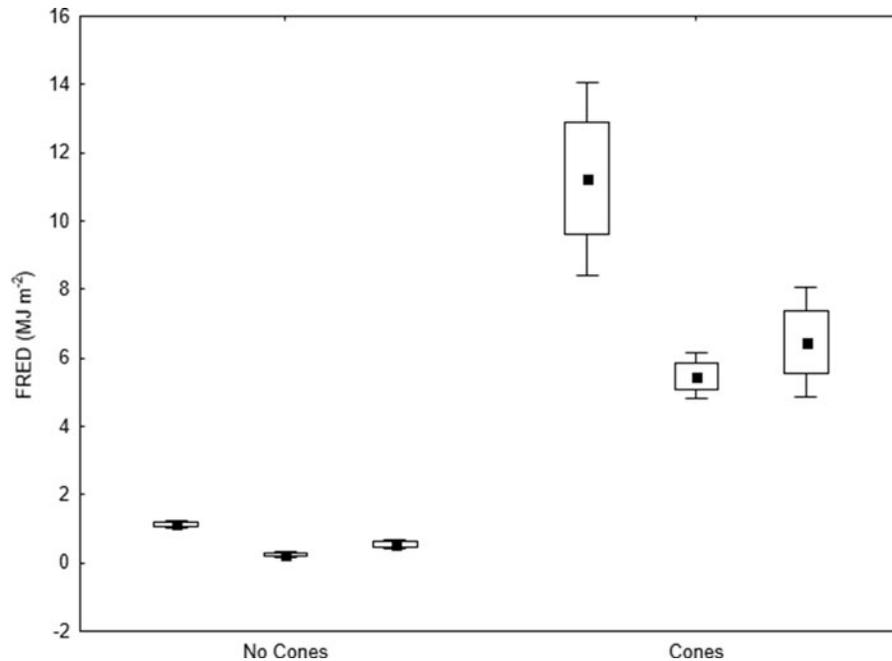


FIG. 5. Box plots of background fuel and cone FRED. Results within the fire management units are arranged in the plot from left to right (F-18, F-19, and F-22) within each cone treatment. The square point represents the mean, the box is standard error, and the whiskers are 1 standard deviation of the subplots.

($p = 0.023$), meaning that plants in cells above the high FRED threshold were 2.78 times more likely to experience mortality than plants in areas with lower FRED.

DISCUSSION

The goal of this study was to examine the spatial heterogeneity of within-fire energy release, its relationship to type of fuel and link this information to fire effects, particularly vascular plant mortality. The heterogeneity in FRED did vary at fine spatial scales; observations of FRED were spatially dependent at less than 17 cm, similar scales to the arrangement of individual herbs and grass clumps consumed in the fire. This scale of variation matches that observed in previous studies (Hiers et al. 2009; Loudermilk et al. 2014). Woody fuels (pine cones) increased the magnitude of spatial variability and also resulted in more than twice the energy release. We were successful in demonstrating that areas with higher FRED were related to woody fuels (i.e., pine cones), and these woody fuels also had a much higher radiative energy density than background fine dead fuels, with cones releasing 12 times more energy (Figure 5). This higher FRED, though very local (<17 cm, Figure 5), resulted in the 2.78 increase in probability of vascular plant mortality within our plots.

Quantifying the spatial pattern of fire-induced mortality is critical for understanding the processes structuring vegetative communities postfire. Alonso et al. (2006) identified 3 requirements of any theoretical attempt for explaining the distribution, abundance, and diversity of species in a biogeographical context

that are fulfilled by ecological neutral theory (Hubbell 2001). First, the random dynamics of species over time must be defined; second, the theory must have a spatial formulation and third, the fates of discrete individuals must be considered, which allows the empirical testing of the theory. The connection of spatial variation in fire energy release driven by stochastic fuel elements to postfire mortality in this study documents a key prerequisite for a neutral model of plant community dynamics in frequently burned longleaf pines: a random agent of mortality. Although we do not explicitly test Hubbell's theory, we provide a spatially explicit formulation that provides a critical first step for further testing.

Although the distribution of cones is certainly not random at larger spatial scales because cone density is linked to tree location and tree locations themselves are likely not random, we argue that at the fine scales relevant to individual plants, the final position of a cone falling from a tree to the ground could be considered random (Figure 8). We can also exploit this correlation by being able to link a fine scale process to landscape scale patterns of tree density (Hudak et al. in press) and episodic cone production common in these systems (Boyer 1998). We recognize that random processes are not the only mechanisms at work in longleaf community dynamics. For example, deterministic processes such as facilitation (Espeleta et al. 2004, Loudermilk et al. in press) and competition (McGuire et al. 2001, Pecot et al. 2007) are well-known elements of community ecology in longleaf woodlands. Nonetheless, these mechanisms also require highly resolved LWIR data to elucidate microsites and

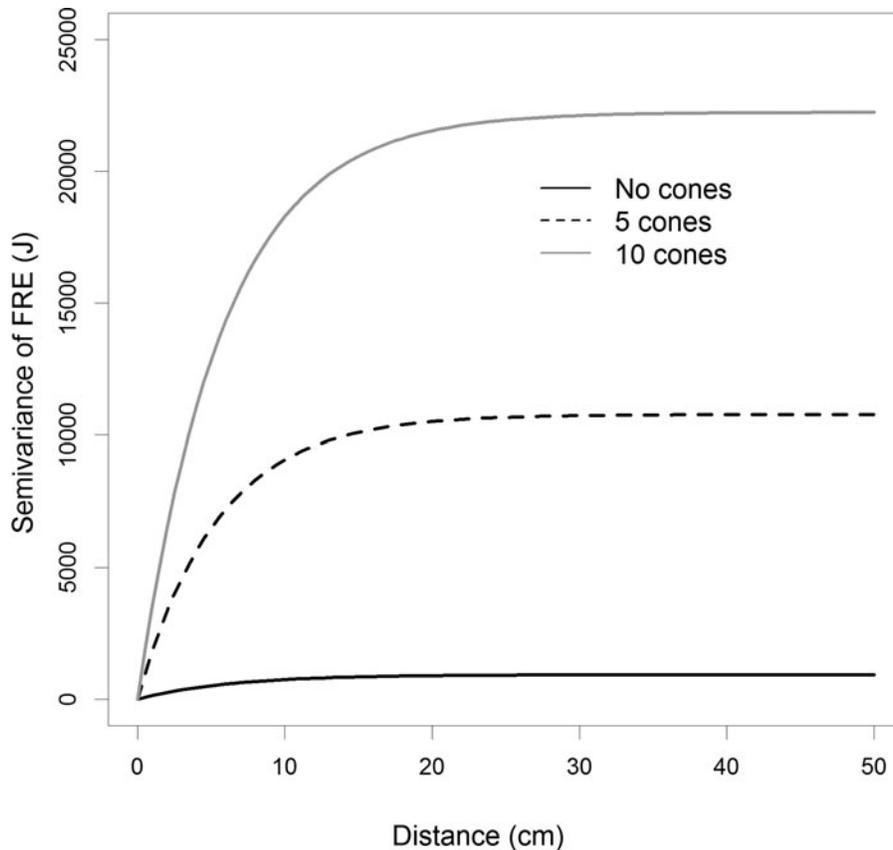


FIG. 6. Semivariance of original LWIR data ($\sim 1 \text{ cm}^2$ resolution images) illustrating the significant spatial autocorrelation in fire radiative energy (FRE) occurring below 17.5 cm for all cone density treatments. This illustrates the effects of cone densities affecting the magnitude of spatial variability (semivariance of FRE).

niche space in frequently burned ecosystems (Loudermilk et al. in press). Competition becomes especially relevant when fire return intervals lengthen or fire is excluded (Wahlenberg 1946; Mitchell et al. 2006). Also, other causes of mortality are likely not random, for example, plant size or stature might affect mortality. Likewise, species-specific regeneration strategies such as vegetative propagation versus reproduction through seed could be important as well and are the subject of ongoing investigation. It is important to note, however, that the majority of species present in longleaf sandhills are perennial and survive most fires. These other mechanisms, notwithstanding, with frequent fire, we argue that the mechanism identified here—mortality driven by fine-scale variation in fire behavior—could prove to be a key component of community assembly among the high diversity understory plant community. Although further analysis of resulting patterns in plant demography will be needed to fully test a neutral model of biodiversity, our results are a critical first step. Nonetheless, these results highlight the critical importance of understanding spatial patterns of within-fire spatial heterogeneity at fine scales when studying ecological fire effects.

There were differences across the fire management units in total FRED, likely driven by management legacies. Unit F-22 had nearly double the FRED of Units F-18 and F-19. F-22 also had been treated with hexazinone herbicide approximately 10 years before the experiment and this could have resulted in higher loading of fine fuels (Addington et al. 2012) and subsequently higher fire intensity. Plots in F-22 also likely burned with higher intensity due to fireline geometry. Two authors (Hornsby and Pokswinski person observations, May 23, 2014) observed 2 head fires that were ignited on either side of the plot and the fireline interactions increased fire intensity as the fire moved across the plot. The higher intensity would have resulted in greater fuel consumption at total higher FRED. Regardless of the differences observed between blocks, the cones still burned with higher intensity within all the fire management units, and were the statistical drivers of plant mortality.

The availability of portable thermal imagers has allowed for the capture of quantitative data on spatial and temporal heat transfer at ecologically relevant scales (O'Brien et al. 2016). This has enabled the mechanistic linkage of fuel structure to fire behavior in ways not possible in the recent past. For example,

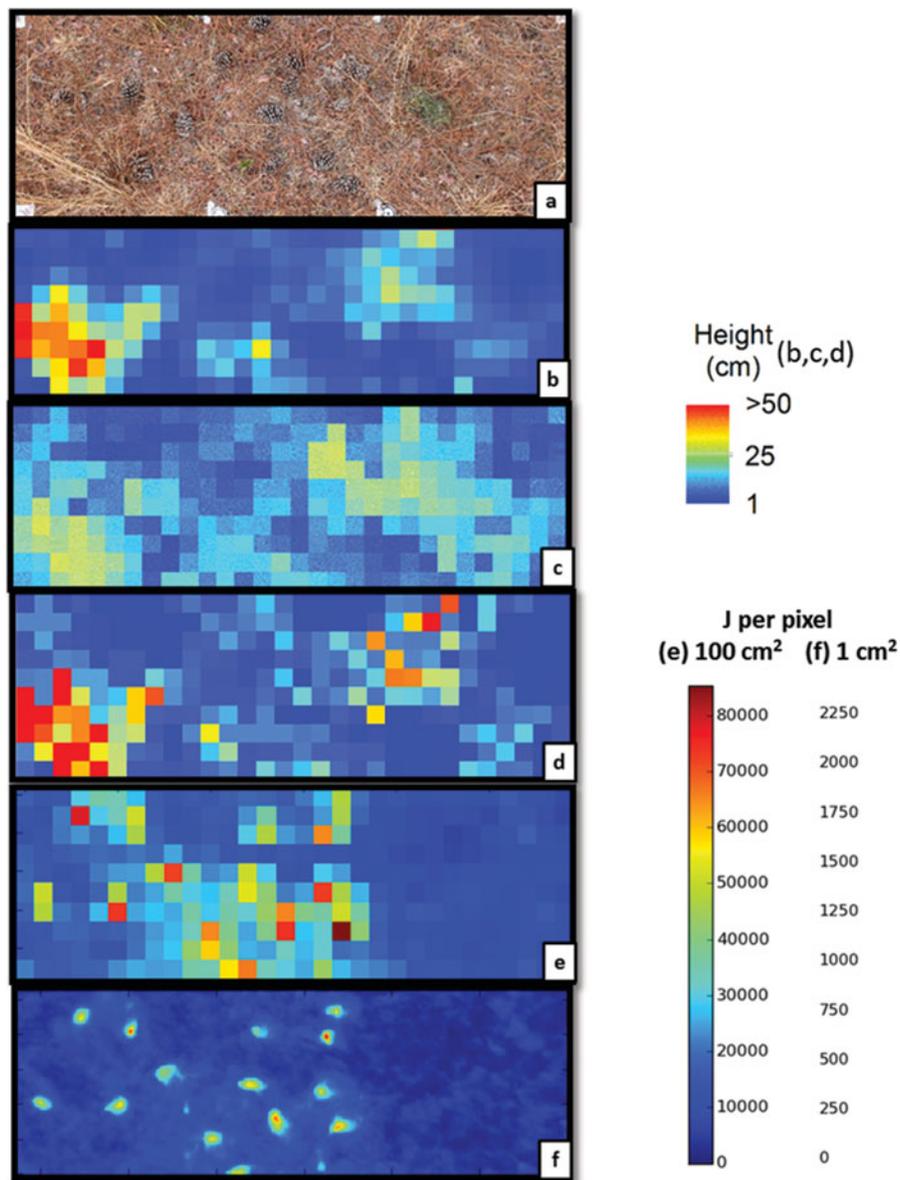


FIG. 7. Illustration of datasets collected at the 10-cm \times 10-cm grid scale or below, (a) a prefire photograph at nadir of the plot, (b) spatial maximum fuelbed heights determined by in situ point-intercept fuel measurements, (c) spatial maximum fuelbed heights determined by photogrammetry heights (Bright et al. 2016), (d) spatial maximum fuelbed heights determined by 3D animation modeling technique (Rowell et al. in press), (e) spatial total fire radiative energy (FRE, J) measured by the LWIR camera, coarsened to the 10-cm \times 10-cm scale, and (f) spatial total FRE measured by the LWIR camera at its original resolution of approximately 1 cm \times 1 cm.

TABLE 3
Results of the logistic regression on plant mortality versus high or low FRED

	D.F.	Wald Statistic	<i>p</i> value	Odds Ratio	Lower 95% CI	Upper 95% CI
High-Low FRED	1	5.101	0.023	2.78	2.34	3.22

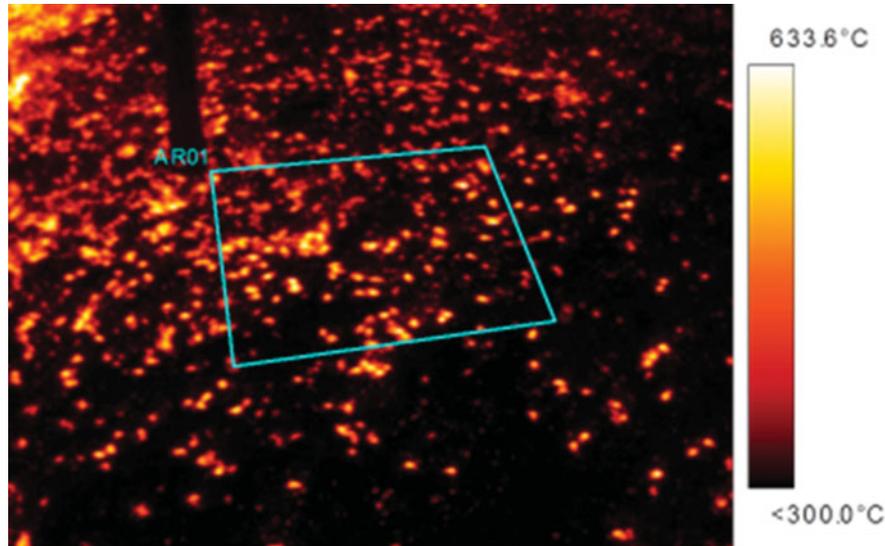


FIG. 8. An oblique LWIR thermal image of a prescribed fire at the Joseph W. Jones Ecological Research Center in Newton, Georgia, in 2008. The blue plot is 4 m on a side. The plot was established under the canopy of a longleaf pine that had produced an asynchronous mast crop of cones that burned much longer than other fuels (seen as higher temperature points in the image). During a masting year, most trees in a stand produce a comparable number of cones illustrating the potential for a large effect on fire behavior of cones after a masting year.

Hiers et al. (2009) and Loudermilk et al. (2009, 2012) were able to link fuel structure to fire behavior at the 0.25 m^2 scale, though they recognized that their analysis would not detect the influence of point-like fuels such as cones. We show here that even finer scale processes related to cones or other compact, high-energy releasing fuels (Figures 4, 6) can have a major impact on plant mortality through fine-scale, long-duration smoldering. Although the technology itself is more than a decade old, the application of thermal imagery to fine-scale fire behavior measurements still represents a new direction for fire ecology (Hiers et al. 2009).

Although the application of this technology deployed here within the fire environment is at fine scales, such spatially and temporally resolved data might prove critical at larger scale fires (10 ha–1,000 ha) (O'Brien et al. 2016). There currently remains a technology gap for such scale to resolve a nadir perspective between airborne and group-based sensors (Hudak et al. 2016, Dickinson et al. 2016). Airborne sensors often produce gaps in data due to turnaround times and operational constraints on airspace around fires (Hudak et al. 2016). UAVs (Kiefer et al. 2012, Zajkowski et al. 2016) offer promise to bridge this spatial scale. Nonetheless, attenuation of LWIR signals by canopies remains a challenge (Hudak et al. 2016, O'Brien et al. 2016), and might require a combination of sensors and platforms across scales to overcome these issues.

LWIR thermal imagery provides high-resolution quantitative measurements of in-fire energy transfer with complete spatial coverage at scales relevant to many ecological processes, such as plant mortality and stem or soil heating. These measurements

are also useful for directly linking spatial fuelbed metrics to fire behavior that should prove useful in better understanding mechanisms driving fire spread.

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