Contrasting the influence of overstory tree species identity on microclimate, fuels, and tree regeneration in a longleaf pine forest

by

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Abstract

Fire-dependent ecosystems worldwide are facing a significant threat from anthropogenic activities, particularly land use changes and decades of fire exclusion. These alterations have led to a transformation in once open canopy landscapes, to closed canopies with mid-story dominated by shade-tolerant trees and leaf litter fuels. Consequently, the understory becomes wetter and cooler, with a higher accumulation of leaf litter on the fuel bed due to the encroachment of shade-tolerant and fire-sensitive species. To understand the impact of these species on the understory, we conducted a study and experiment focusing on tree microclimate, fuel loads, and tree regeneration in a longleaf pine forest located at the Jones Center at Ichauway in Georgia, USA. Our study revealed that encroaching species have distinct influences on microclimate, fuel loads, and moisture retention, which could affect flammability. By understanding these effects, we can better comprehend the dynamics of the understory and its potential for flammability.

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Table of Contents

Abstract 2

Acknowledgments 3

List of Figures 6

List of Tables 7

List of Abbreviations 8

Chapter 1. Effects of pyrophytic and mesophytic overstory trees on microclimate, fuel loads, and tree regeneration 9

- **Abstract** 9
- **Introduction** 11
- **Methods** 14
  - **Study Area** 14
  - **Study Design** 15
  - **Statistical Analysis** 21
- **Results** 22
- **Discussion** 29
- **Conclusion** 32
- **References** 34

Chapter 2. Influence of overstory pyrophytic and mesophytic trees on fuel moisture retention 44

- **Abstract** 44
- **Introduction** 46
- **Methods** 49
  - **Study Area** 49
  - **Experimental Design** 50
  - **Fuel Moisture Measurements** 52
  - **Microclimate Measurements** 55
  - **Fuel Traits Measurements** 58
  - **Statistical Analysis** 59
- **Results** 59
  - **Microclimate** 59
  - **Fuel Moisture** 60
  - **Fuel Traits** 64

Discussion 65
Conclusion 67
References 69
Appendices 77

List of Figures

Figure 1. Sampling design indicating canopy cover, microclimate, fuel composition and loads, and tree regeneration measurements beneath each functional tree group. 17
Figure 2. Microclimate sensors. A. Microcontroller (Particle Boron, Particle Industries, Inc., San Francisco CA). B. Microcontroller in rain shield settled on the tree bark. C. Air temperature (VEML 7770) and relative humidity (SHT31) sensors radiation shield. 19
Figure 3. Box plot with standard error of vapor pressure deficit (VPD) (kPa) mean of gap, pyrophytic pine, mesophytic oak, and pyrophytic oak at 11:00 (A) and 17:00 (B) 23
Figure 4. Box plot with standard error of temperature (°C) mean of gap, pyrophytic pine, mesophytic oak, and pyrophytic oak at 11:00 (A) and 17:00 (B). 24
Figure 5. Box plot with standard error of light intensity (μmol m^{-2} s^{-1}) mean of gap, pyrophytic pine, mesophytic oak, and pyrophytic oak at 11:00 (A) and 17:00 (B). 24
Figure 6. Mean ± SE woody debris load (kg/m^2) of 10 h and 100 h across functional groups (gaps, pyrophytic pine, mesophytic oak, and pyrophytic oak). 27
Figure 7. Mean ± SE tree regeneration density (individuals/m^2) of pyrophytic pine, pyrophytic oak, mesophytic oak, and other trees across functional groups (pyrophytic pine, mesophytic oak, and pyrophytic oak). 29
Figure 8. A) Jones Center at Ichauway located in Georgia, USA; B) Experiment plot at the Jones Center at Ichauway; C) Study area showing locations of 15 individual trees and 5 gaps organized into five blocks. 51
Figure 9. A) 60 soaked litter bags were placed under 20 plots following the bole to the edge of the crown. B) After 48 hours at 60 °C, 15 g of leaf litter and 50 g of woody debris were weighed C) Fuels were placed in mesh bags, soaked in water for 24 hours, drained, and re-weighed and placed under each tree. 54
Figure 10. Litter and fine woody debris moisture experiment arrangement with mesophytic oak, pyrophytic oak, and pyrophytic longleaf pine mesh bags under tree crown. 54
Figure 11. Microclimate sensors. A) Microclimate sensors positioned under the tree canopy. B) Microcontroller (Particle Boron, Particle Industries, Inc., San Francisco CA). C) Microcontroller in rain shield settled on the tree bark. D) Air temperature (VEML 7770) and relative humidity (SHT31) sensors radiation shield. Sensors were placed in duplicate for measurement redundancy. 56
Figure 12. Box and whisker plots of initial moisture content (%) across leaf litter functional group (pyrophytic pine, mesophytic oak, and pyrophytic oak), where individual points are outliers and groups different letters are significantly different ($p < 0.05$) as determined by post hoc Tukey's Honest Significant Difference test. 61
Figure 13. Box and whisker plots of initial moisture content (%) across woody debris functional group (pyrophytic pine, mesophytic oak, and pyrophytic oak), where individual points are outliers and groups different letters are significantly different ($p < 0.05$) as determined by post hoc Tukey's Honest Significant Difference test. 63

List of Tables

Table 1. Tree species chosen for the zone of influence characterization in a pine-oak woodland, Newton, Georgia, USA by species name, common name, shade tolerance, fire tolerance, and functional group. ... 16
Table 2. Means and ± SE of crown area (m^2), crown volume (m^3) and canopy cover (%) beneath pyrophytic pine, pyrophytic oak and mesophytic oak trees in a pine-oak woodland, Newton, Georgia, USA. Values with different letters are significantly different ($p < 0.05$) as determined by a post-hoc Tukey's Honest Significant Difference test. ... 22
Table 3. Mean fuel loads (g/m^2) and their relative proportion (%) (± standard error) of individual fuel types (grasses, herbaceous plants, woody plants, pyrophytic pine litter, pyrophytic oak litter, herbaceous and shrub leaf litter (others), and other material and in gaps and beneath pyrophytic pine, pyrophytic oak and mesophytic oak trees. Values with different letters are significantly different ($p < 0.05$) as determined by post hoc Tukey's Honest Significant Difference test. ... 26
Table 4. Woody tree found beneath individual trees and categorized by functional group in a longleaf pine-oak woodland, Georgia, USA. ... 28
Table 5. Tree species chosen for fuel moisture loss experiment in a pine-oak woodland, Newton, Georgia, USA by scientific and common name, shade tolerance, fire tolerance, and functional group ... 51
Table 6. Temperature (°C) and relative humidity (mean, daily minimum, daily maximum) over the experiment days in a pine-oak woodland, Newton, Georgia, USA. ... 52
Table 7. Vapor Pressure Deficit (kPa) (mean (± standard error)) along the day beneath different overstory functional groups (gap, pyrophytic pine, pyrophytic oak, and mesophytic oak). ... 60
Table 8. Drying response time (mean (± standard error)) in hours measured of litter functional group (pyrophytic pine, pyrophytic oak, and mesophytic oak) and overstory functional group (gap, pyrophytic pine, pyrophytic oak, and mesophytic oak). Values with different letters are significantly different ($p < 0.05$) as determined by post hoc Tukey's Honest Significant Difference test. ... 62
Table 9. Drying response time (mean (± standard error)) in hours measured of woody debris functional group (pyrophytic pine, pyrophytic oak, and mesophytic oak) and overstory functional group (gap, pyrophytic pine, pyrophytic oak, and mesophytic oak). Values with different letters are significantly different ($p < 0.05$) as determined by post hoc Tukey's Honest Significant Difference test. ... 64
Table 10. Means and standard error (shown in parenthesis) of leaf traits (curl, thickness, SLA, and volume) and woody debris density of different functional groups (pyrophytic pine, pyrophytic oak, mesophytic oak), followed by ANOVA p-values. Values with different letters are significantly different as determined by Tukey's Honest Significant Difference test. ... 65

List of Abbreviations

ANOVA	Analysis of variance
DBH	Diameter at breast height
G	Gap plots
M	Mesophytic oak
P	Pyrophytic pine
PPFD	Photosynthetic photon flux density
PO	Pyrophytic oak
SLA	Specific leaf area
VPD	Vapor pressure deficit
U.S. or USA	United States of America

Chapter 1. Effects of pyrophytic and mesophytic overstory trees on microclimate, fuel loads, and tree regeneration

Abstract

Decades of intentional fire exclusion have modified the structure and composition of many forest systems across the globe, including upland pine (*Pinus* spp.) and oak (*Quercus* spp.) forests of the eastern U.S. In the absence of frequent, low-intensity fires, historically open-canopy forests with a biodiverse and highly flammable herbaceous understory can transition to closed-canopy forests with a dense midstory of shade-tolerant, often fire-sensitive and/or opportunistic tree species (i.e., mesophytes) with fuel beds dominated by leaf litter. This transition can create a self-reinforcing, positive feedback loop known as mesophication, whereby conditions become increasingly favorable for mesophytic species at the expense of fire-adapted (i.e., pyrophytic) species. Research on mechanisms of mesophication typically emphasizes differences in leaf litter flammability among tree species along a mesophyte-to-pyrophyte gradient. However, there is a lack of information on how individual overstory trees, once established, may contribute to differences in fuel bed conditions beneath their crowns in ways that further reinforce mesophication, at least within their zones of influence. The primary goal of this study is to understand how individual pyrophytic and mesophytic overstory tree species impact understory microclimate, fuel characteristics, and seedling regeneration within a longleaf pine forest, where frequent fires have been restored but many encroaching mesophytes remain. We hypothesized that mesophytic trees have zones of influence that create cooler, wetter, and shadier microclimate than pyrophytic trees, and consequently, higher mesophytic regeneration. To test this hypothesis, we selected 45 individual overstory trees (DBH > 20 cm), 15 each from three functional groups (pyrophytic pine, pyrophytic oak, and mesophytic oak) and distributed across three sites in pine–oak woodlands in southwestern GA, USA. For each tree, we characterized tree crown traits (canopy cover, crown area, crown volume), 10-day microclimate (vapor pressure deficit (VPD), air temperature, light intensity), and fuel types and loads (leaf litter, ground layer vegetation, and woody debris) during the dormant season (February 2023), when prescribed fires are often ignited. During the growing season (July 2022), we characterized the density and composition of regenerating trees. We found that compared to pyrophytic pines and oaks, mesophytic oaks had higher canopy cover (68.1 ± 4.1%) and crown area (84.4 ± 10.6 m^2), lower light intensity (119.2 ± 8.9 µmol m^{-2} s^{-1}), temperature (19.5 ± 0.81 ºC), and VPD (0.93 ± 0.08 kPa) at 11:00, but no difference in crown volume. Pyrophytic pine, pyrophytic oaks, and mesophytic oaks had the highest amount of their respective leaf litter beneath their own crown. Despite these differences in microclimate and fuel loads beneath mesophytic and pyrophytic trees, there were no differences in functional group regeneration beneath overstory functional groups. However, we found that mesophytic oaks had ~ 4 and 2.9 times more other trees regeneration than pyrophytic pine (2.7 ± 0.8 individuals/m^2) and pyrophytic oak (5.7 ± 1.7 individuals/m^2) respectively. This study demonstrates that overstory trees create zones of influence beneath them that differentially impact microclimate conditions and fuel characteristics depending on their functional group regardless of the restoration of frequent fire across the broader landscape in which they exist. This individual tree effect on microclimate and fuels could create heterogeneity in fire behavior with important implications for flammability beneath different trees the continued encroachment of mesophytic species, especially in landscapes with higher densities of mesophytic overstory trees. We believe that this study can help future microclimate and fuel modeling to improve intensity and ignition of prescribed fires.

Introduction

Fire is a critical natural disturbance in many forest ecosystems across the globe, including grasslands in Brazil, shrublands in Australia and taiga forests in north America and Russia (Kelly *et al.* 2020). In longleaf pine (*Pinus palustris* L.) and upland oak (*Quercus* spp.) systems in eastern United States, periodic, low-intensity surface fires support the persistence of many fire-dependent plants and animals (Wright and Bailey 1982; Nowacki and Abrams 2008; Babl *et al.* 2020; Alexander *et al.* 2021), contributing to high biodiversity (Hanberry *et al.* 2020). However, anthropogenic activities, especially land use changes and decades of intentional fire exclusion, are threatening these pyrophytic ecosystems (Nuzzo 1986). Most notably, changes in land use and enactment of fire suppression policies in the 1920s changed fire frequency of these landscapes, eventually modifying their structure and composition from open forests with a flammable, herbaceous-dominated understory to closed-canopy forests with a dense midstory and leaf litter fuel beds (Nowacki and Abrams 2008; Arthur *et al.* 2012; Hanberry *et al.* 2020; Alexander *et al.* 2021). Closed canopies and increasing contribution of leaf litter fuels of encroaching species can hinder fire spread through increased decomposition rates and higher fuel bed compaction due to thin, flat, and small leaves (Varner *et al.* 2016; Babl *et al.* 2020; McDaniel *et al.* 2021; Babl-Plauche *et al.* 2022). These fire-suppressing traits can create a self-reinforcing, positive feedback loop known as mesophication that further increases the abundance of fire-sensitive and/or opportunistic species (i.e., mesophytes) while hindering pyrophytic species.

While often considered at the landscape or stand scale, this self-reinforcing process of mesophication may occur at the scale of the individual tree. Individual trees have a zone of influence beneath them that runs from the bole to the edge of the crown and beyond (Zinke

1962). The environmental characteristics beneath trees may be driven by individual tree crown, bark, and leaf litter traits (Alexander et al. 2021; Babl et al. 2020), leading to unique biotic (e.g. tree regeneration and litter) and abiotic (e.g. relative humidity, soil moisture, air temperature) characteristics beneath different species. For example, many mesophytic species have dense crowns (Alexander et al. 2010; Babl et al. 2020), which can decrease solar radiation and air temperature beneath them, leading to increased fuel moisture and reduced fuel flammability (Nowacki and Abrams 2008; Kreye *et al.* 2013, 2018, 2020). Shady conditions can favor regeneration of shade-tolerant, often fire-sensitive species over pyrophytic tree species, which are often shade-intolerant (McDonald *et al.* 2002; Parker and Dey 2008; Arthur *et al.* 2012; Iverson *et al.* 2017; Alexander *et al.* 2021). Many mesophytes also have thinner and smoother bark compared to pyrophytic species (Alexander and Arthur 2010; Babl *et al.* 2020), as having a thick and rough bark is typically an adaptation to persisting in fire-prone landscapes (Hammond *et al.* 2015; Varner *et al.* 2016). Thin, smooth bark tends to funnel high volumes of nutrient- and carbon-rich precipitation to soils in a zone near the bole (Tonello *et al.* 2020), which could create a firebreak near the tree and serve as a fire suppressing mechanism (Alexander and Arthur 2010). Leaf litter composition, size, and structure are also important to predict fire behavior and effects. For example, beneath adult longleaf pines, needles form low bulk density fuel beds combined with high leaf terpene concentrations lead to high fire intensity (Ormeño *et al.* 2009) that can suppress establishment of pines and hardwoods (Brockway and W. Outcalt 1998; Whelan *et al.* 2021). Upland oaks, which have relatively large leaves with high curl tend to hold less water than encroaching mesophytes (Kreye *et al.* 2018; McDaniel *et al.* 2021), favoring increased oxygen flow and litter flammability (Schwilk and Caprio 2011; Cornwell *et al.* 2015). In contrast, some mesophytic hardwoods have smaller, compact leaves with lower air circulation, leading to a moist fuel bed with low oxygen flow (Varner *et al.* 2016). Thus, the set of individual trees, their specific traits, and their overlapping zones of influence can create major changes in environmental conditions (Boettcher and Kalisz 1990) that may ultimately coalesce to impact tree regeneration, fire behavior, and forest flammability.

Encroachment of mesophytic trees into pyrophytic environments such as pine and oak savannas and woodlands is an increasing concern due to the important economic and ecological roles of fire-dependent ecosystems (Hanberry *et al.* 2018; Bragg *et al.* 2020; Abrams *et al.* 2021). Understanding how mesophytic trees alter tree regeneration and forest flammability is critical for avoiding the loss of important species and conserving these significant ecosystems and their ecosystem services they provide. Thus, the primary objective of this study was to understand how individual pyrophyte and mesophyte trees create varying zones of influence that impact microclimate conditions, fuel characteristics, and tree regeneration, using a longleaf pine oak woodland in southwestern Georgia, USA as a study site, where frequent low-intensity fire has been restored to this forest for more than 30 years, yet many overstory trees of mesophytic oaks (e.g., water oak and live oak) remain. We hypothesized that pyrophytic pines and oaks would have a more open crown than mesophytic oaks, resulting in greater light penetration to their understory (Battaglia *et al.* 2003), and a drier and warmer zone of influence. We also hypothesized that pyrophytic individuals would facilitate an understory environment consisting mainly of herbaceous vegetation with pyrophytic leaf litter, a relatively low amount of woody debris, and greater regeneration of pyrophytic tree seedlings. For mesophytic oaks, we hypothesized that their closed crowns would lead to a comparatively cooler and wetter understory environment, with higher mesophytic regeneration and leaf litter, and higher amounts of woody debris. Ultimately, this research could help guide a better understanding of vegetation-fire feedback in a spatially explicit manner for improving ecological understanding, management, and restoration of historically open forests maintained by frequent, low-intensity surface fires.

Methods

Study Area

Research was conducted at the Jones Center at Ichauway Research Center (31.2201°N, 84.4792°W) located in southwest Georgia, USA. The Jones Center consists of 11,740 ha of forest, comprised of mostly upland woodlands dominated by longleaf pine (Holland *et al.* 2019). The property has a long history of fire management extending to the 1920s; much of the property has been managed with frequent (~ every 2 year), low-intensity prescribed fire since at least 1991 (Rutledge and McIntyre 2022), typically in the dormant season between February and April.

The study area is classified as humid subtropical, with daily temperature average of 27 ºC during summer (May – August) and 11 ºC during winter (November-February) (Gaya *et al.* 2023) and mean precipitation of 1310 mm equally distributed throughout the year (Golladay *et al.* 2021). The region consists of karst topography, with sandy acid soil, containing Entisols and deep Utisols (Jacqmain *et al.* 1999). The history of frequent fire results in open pine woodlands with a bilayer structure composed primarily of longleaf pine overstory and herbaceous understory of wiregrass (*Aristida stricta* Michx) and bluestem (*Andropogon* spp.) (Gaya *et al.* 2023). However, some pyrophytic oaks such as sand post oak (*Quercus margaretta* Ashe), turkey oak (*Quercus laevis* Walt.), and southern red oak (*Quercus falcata* Michx.) and mesophytic oaks such as southern live oak (*Quercus virginiana* Mill.) and laurel oak (*Quercus laurifolia* Michx) are also present. The proximity and coexistence of pyrophytic longleaf pine, pyrophytic oaks, and mesophytic oaks provides an ideal setting for testing hypotheses of how established adults alter microenvironments driving mesophication.

Study Design

We selected trees to characterize understory microclimate, fuel loading and composition, and tree regeneration within three sites at the Jones Center. Sites were located ~10 km apart and were last burned in 2021. In each of the three sites, we established five blocks located ~ 15 m away from each other. In each block, we selected one tree from each of three fire tolerance functional groups (pyrophytic pine, pyrophytic oak, and mesophytic oak; Table 1) and a "gap" area devoid of tree cover (28 m^2 area circular plots) for comparison. The trees chosen were at least 10 cm diameter at breast height (DBH), and trees within a block were similar in size (within 10 cm DBH), at least 10 m from a road or trail, 5 m from another individual tree, and in a dominant canopy position. In total, we selected 15 trees and 5 gap areas in each site, for a total of 45 individual trees and 15 gap areas. Trees were chosen by their shade tolerance and fire tolerance in literature, where pyrophytic pines were shade-intolerant and fire-tolerant longleaf pine trees; pyrophytic oaks were shade-intolerant and fire-tolerant oak trees and mesophytic oaks shade-tolerant and fire-intolerant oak trees (Table 1).

Table 1. Tree species chosen for the zone of influence characterization in a pine-oak woodland, Newton, Georgia, USA by species name, common name, shade tolerance, fire tolerance, and functional group.

Tree species	**Common name**	**Shade tolerance**	**Fire tolerance**	**Functional group**
Quercus laurifolia Michx	Laurel oak	Tolerant[1]	Intolerant[3]	Mesophytic oak[1]
Quercus virginiana Mill.	Southern live oak	Tolerant[1]	Intolerant[1]	Mesophytic oak[1]
Quercus falcata Michx	Southern red oak	Intolerant[1]	Tolerant[1]	Pyrophytic oak[7]
Quercus margaretta Ashe	Sand post oak	Intolerant[1]	Tolerant[4]	Pyrophytic oak[4]
Quercus laevis Walt.	Turkey oak	Intolerant[1]	Tolerant[5]	Pyrophytic oak[5]
Pinus palustris L.	Longleaf pine	Intolerant[2]	Tolerant[6]	Pyrophytic pine[6]

Note: (Burns and Honkala 1994[1]; Loudermilk *et al.* 2011[2]; McReynolds and Hebb 1990[3]; Hannon *et al.* 2020[4]; Carey 1992[5]; McCune 1988[6]; Kreye *et al.* 2018[7])

Beneath each tree and in each gap area, we conducted measurements of crown traits, fuel composition and loads, and regeneration. In the northwest site, we also characterized microclimate variables; only one site was used due to a limited number of microclimate stations. Beneath each tree, we established a transect extending from the bole of the tree to the edge of the crown (Figure 1). Along this transect, we mounted microclimate stations (northwest site only), and we measured fuel loading and composition at mid-crown on the north and south sides beneath each tree. We measured woody debris along the transect from the bole to the edge of the crown, and measured tree regeneration in a fixed radius plot of 2 meters beneath the trees.

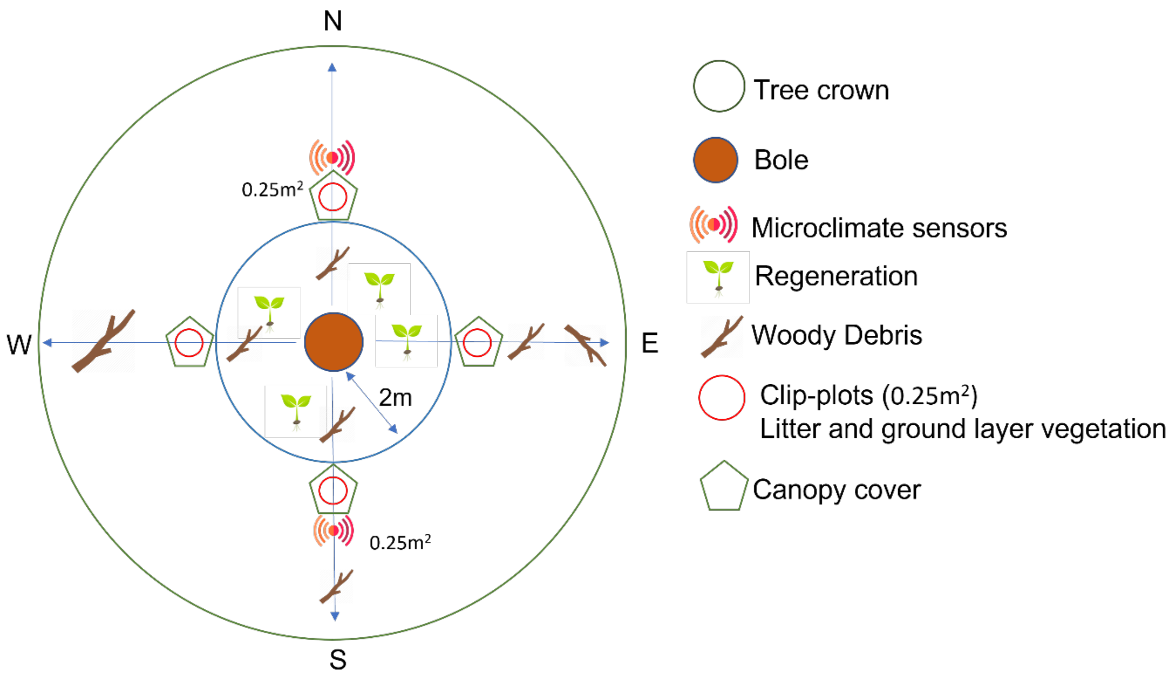

Figure 1. Sampling design indicating canopy cover, microclimate, fuel composition and loads, and tree regeneration measurements beneath each functional tree group.

Crown Traits and Microclimate

We estimated crown area (m^2) and volume (m^3) of each tree using a laser rangefinder to measure the crown diameter across the dripline along major and minor axes, and crown depth (length of the top to the bottom of the crown). Next, we calculated crown volume based on the volume of an elliptical cylinder (Alexander and Arthur 2010), as shown in the equation below:

$$(1)\ \ V = \pi \times R_1 \times R_2 \times depth$$

Where V is crown volume (m^3), R_1 is radius of the major axis (m), R_2 is the radius of the minor axis (m), and depth is crown depth (m). To determine the canopy cover (%) beneath each tree, we used a spherical densiometer, where we took one measurement at each four cardinal directions at middle crown, facing the end of the crown. We averaged all four measurements.

For microclimate conditions (i.e., air temperature (ºC), relative humidity (%), and light intensity (µmol m^{-2} s^{-1})), we used two microclimate stations (Cannon *et al.* 2017) positioned 50 cm aboveground on wooden stakes in the north and south directions of the tree under the crown (Figure 2). Stations measured air temperature and relative humidity using an SHT31 sensor housed in a miniature radiation shield (Cannon *et al.* 2017) and measured total light intensity using a VEML 7770 lux sensor. All sensors obtained measurements every 15 minutes for 10 days in the dormant season (February 2023), during which prescribed fires are often applied. We used microclimate data between February 7th and 17th, at 11:00, as a proxy for typical ignition times, and 17:00, to understand the microclimate at the end of the day.

All sensors were wired to open-source microcontrollers (Particle Boron, Particle Industries, Inc., San Francisco CA). The Boron microprocessor uploaded the data using onboard cellular data capabilities and custom firmware to Google Sheets (Cannon *et al.* 2017). To protect the humidity and solar radiation sensors (SHT31), a miniature radiation shield printed on PRUSA MK3 3D printer (Prusa Research) was constructed using polyethylene terephthalate glycol (PETG) filament and we encased the loggers in a protective enclosure (HOBO CASE 4X; Onset Computer Corp., Bourne, MA).

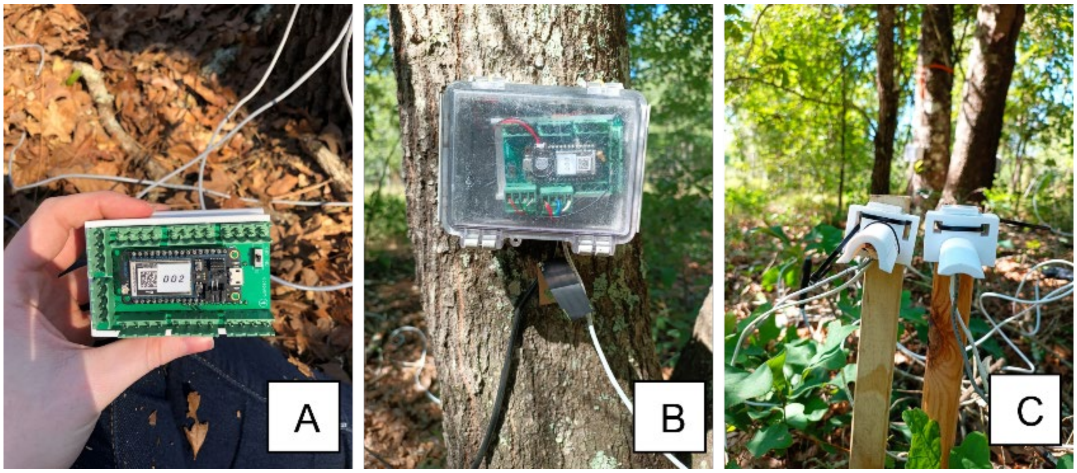

Figure 2. Microclimate sensors. A. Microcontroller (Particle Boron, Particle Industries, Inc., San Francisco CA). B. Microcontroller in rain shield settled on the tree bark. C. Air temperature (VEML 7770) and relative humidity (SHT31) sensors radiation shield.

With data collected by the microclimate sensors, we transformed the light incidence from lux to photosynthetic photon flux density (PPFD), by multiplying by the sunlight factor (0.0185) (Singh *et al.* 2020). We also calculated vapor pressure deficit (VPD), which is an important measurement in climate studies and fire models (Anderson 1936; Sedano and Randerson 2014). VPD is an indicator of the atmosphere's capacity to draw moisture from the surrounding vegetation, consequently indicating changes in moisture levels of live plants and fuels, and susceptibility to wildfires (Seager *et al.* 2015). VPD is defined as the difference between the actual vapor in the atmosphere and the vapor holding capacity for a given temperature (Anderson 1936; Sedano and Randerson 2014). VPD is easily calculated by relative humidity and air temperature and explains variance in flammability and moisture content better than other variables, such as air temperature, relative humidity and wind speed (Castellví *et al.* 1996; Pechony and Shindell 2009; Seager *et al.* 2015). We calculated VPD of each tree's understory using the following Magnus-Tetens equation (Bonan 2015):

$$(2)\ VPD = (100 - RH) \times (610.7 \times 10^{\frac{7.5\,T}{237.3+T}})$$

Where VPD is vapor pressure deficit (kPa), T is understory air temperature (◦C), 610.7 is the scaling factor to convert the result in Pascal unit, 237.3 is a constant reference to determine the rate of change in temperature in the vapor pressure curve, and RH is the understory relative humidity (%).

Fuel Composition and Loads

To characterize fuel beds beneath individual trees, we installed two 0.25-m^2 circular subplots mid-crown to the north and south of the bole beneath each tree. Within these plots, we harvested all herbaceous and woody ground layer vegetation and leaf litter. The harvested material was dried in oven for 48 hours at 60 ^{o}C and separated into grasses; live herbaceous; live woody plants; pyrophytic pine leaf litter; pyrophytic oak leaf litter; mesophytic oak leaf litter; herbaceous leaf litter; and shrubs leaf litter. All dried and classified fuels were weighed to the nearest 0.01 g.

For coarse and fine woody debris, we used the adapted planar intercept method (Brown 1974), in which four transects in cardinal directions followed the bole to the edge of the crown. Woody debris were counted by 1 and 10 h (0.1 – 2.3 cm), 100 h (2.5 – 7.6 cm) and 1000 h (over 7.6 cm) diameter following the cardinal transects. Woody debris of 1 hour diameter were counted when easily visualized to avoid disturbance on understory and included in the 10 h category. Plot density of woody debris (kg/ m^2) of each category was calculated using the Brown (1974) formula.

Tree Regeneration

In July 2022, we measured the density (individuals/m^2) and composition of regenerating trees (< 1.50 m tall) within fixed radius plot of 2 meters extending from the tree bole to the edge of the crown in a north-south direction. Regenerating trees were classified as pyrophytic pine (longleaf pine), pyrophytic oak (shade-intolerant and fire tolerant oaks), mesophytic oak (shade-tolerant and fire-intolerant oaks), and tree others.

Statistical Analysis

We used R- 4.2.2 (R Core Team, 2022) for all statistical analysis. Prior to analysis, we tested homogeneity and normality using Levene's and Shapiro-Wilk Tests, respectively, on crown area, crown volume, canopy cover, temperature, VPD, light intensity fuel loads, and tree regeneration. When there were violations of assumptions, we transformed the variable using a logarithmic transformation, but we reported back-transformed means and standard errors for ease of interpretation. We used a linear mixed effects model to determine if there were differences in crown area, crown volume, canopy cover and fuel loads among functional groups. To control variability in conditions among groups of trees, blocks were considered a random effect. A linear mixed effects model was also used to determine differences on morning (1100) and afternoon (1700) temperature, VPD, and light intensity, among overstory functional groups. We did an average of the every 15 minutes measurements per chosen period (1100 and 1700). Dates were considered a random effect, to account for diurnal weather variability. We also used a linear effect model with tree blocks as random effect, and a two-way ANOVA testing interaction between overstory functional group and understory regeneration group. For significant results ($p < 0.05$) on crown area, crown volume, canopy cover, morning and afternoon air temperature, morning and afternoon VPD, morning and afternoon light intensity, fuel loads, and trees regeneration, we conducted a post hoc Tukey's Honest Significant Difference test.

Results

Crown Traits and Microclimate

Overall, we found that pyrophytic pines had the lowest crown area ($p = 0.0441$), but crown volume was similar among the species ($p = 0.5742$) (Table 2). For crown area, just pyrophytic pines and mesophytic oaks were statistically different from each other, where mesophytic oaks had 1.9 higher crown area compared to pyrophytic pines ($p = 0.0298$). Canopy cover was also significantly different between functional groups ($p < 0.0001$), where pyrophytic pines had the lowest canopy cover, followed by pyrophytic oak and mesophytic oaks. Mesophytic oaks had approximately 1.6 higher canopy cover than pyrophytic pines ($p = 0.0004$).

Table 2. Means and ± SE of crown area (m^2), crown volume (m^3) and canopy cover (%) beneath pyrophytic pine, pyrophytic oak and mesophytic oak trees in a pine-oak woodland, Newton, Georgia, USA. Values with different letters are significantly different ($p < 0.05$) as determined by a post-hoc Tukey's Honest Significant Difference test.

	Pyrophytic pine	Pyrophytic oak	Mesophytic oak	P-value
Crown area (m^2)	65.6 (11.1)^{a}	81.7 (13.3)^{ab}	84.4 (10.6)^{bc}	0.0441
Crown volume (m^3)	107.8 (14.7)^{a}	92.7(10.4)^{a}	105.6(13.1)^{a}	0.5742
Canopy cover (%)	42.2 (4.3)^{a}	46.1 (4.7)^{ab}	68.1 (4.1)^{c}	< 0.0001

Our results showed that functional groups did not have distinct microclimate conditions related to VPD in the afternoon (17:00), but they did differ morning VPD (11:00), temperature, and light availability. We found statistical differences in VPD at 11:00, where gap and pyrophytic pines were the only functional groups different from each other ($p = 0.0254$). The understory beneath pyrophytic pines had ~1.2 higher VPD compared to gap areas (1.1 ± 0.1 kPa and 0.9 ± 0.1 kPa, respectively) (Figure 3). We did not find differences in VPD at 17:00 ($p = 0.5694$) among functional groups. For temperature at 11:00, pyrophytic pine was the only group with statistical differences among other groups ($p < 0.0001$), with ~1.1 higher temperature than gaps, pyrophytic oaks, and mesophytic oaks (20.4 ± 0.9 ºC) (Figure 4). We found differences for temperature at 17:00 among groups, where pyrophytic oaks had ~1.1 higher temperature (20.2 ± 0.7 ºC) compared to pyrophytic pines and mesophytic oaks ($p = 0.0089$). We found statistical differences in light intensity ($p < 0.0001$) among groups (Figure 5). At 11:00, pyrophytic pines had the highest light intensity mean (201.7 ± 14.5 µmol m^{-2} s^{-1}), which was similar to gap areas. By contrast, mesophytic oaks had the lowest light intensity at 11:00 (119.2 ± 8.9 µmol m^{-2} s^{-1}), 1.7 times lower than pyrophytic pines. For light intensity at 17:00, all groups were similar from each other, with exception of gap and pyrophytic oak ($p < 0.0001$). Mesophytic oaks again had ~1.3 times lower light intensity compared to the other groups with a mean of 26.1 ± 1.8 µmol m^{-2} s^{-1} ($p = 0.9998$).

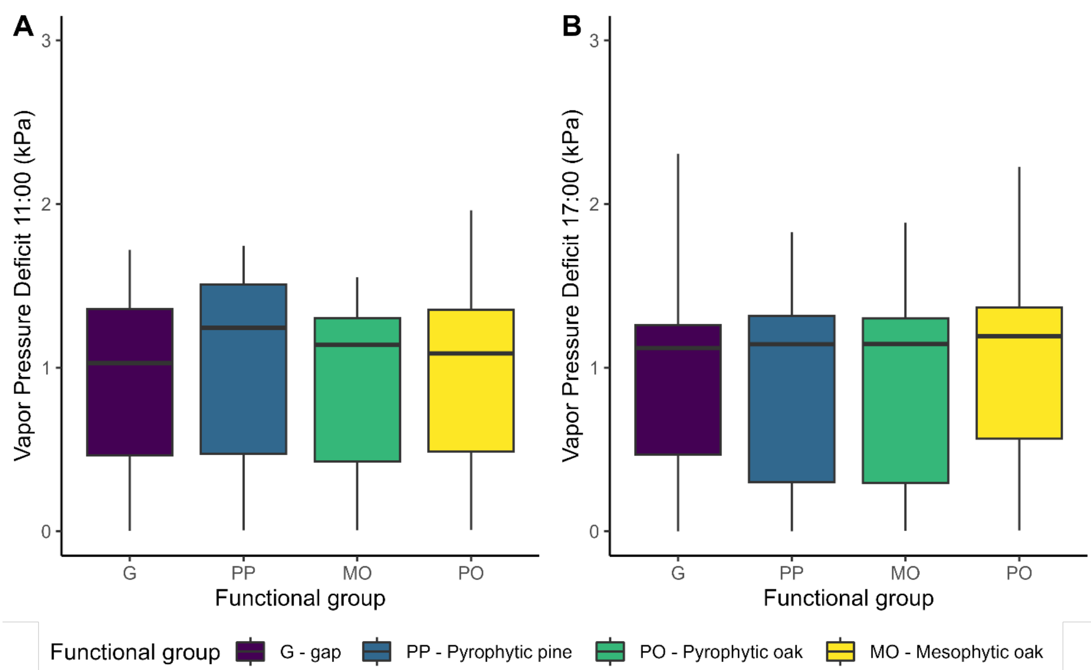

Figure 3. Box plot with standard error of vapor pressure deficit (VPD) (kPa) mean of gap, pyrophytic pine, mesophytic oak, and pyrophytic oak at 11:00 (A) and 17:00 (B)

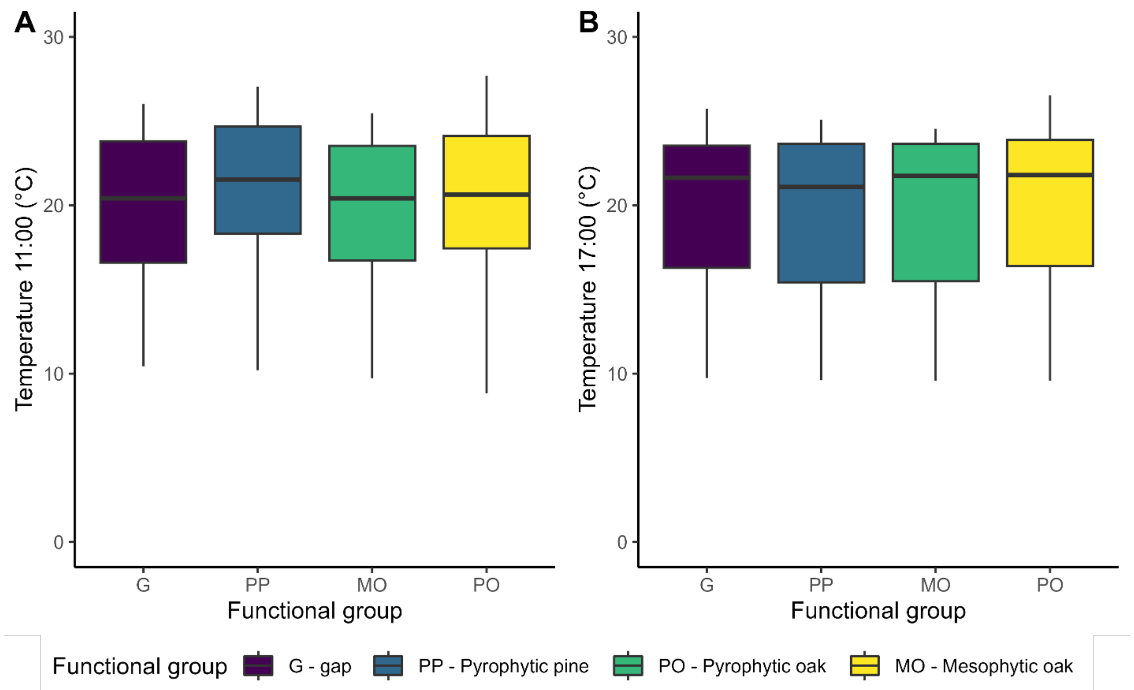

Figure 4. Box plot with standard error of temperature (ºC) mean of gap, pyrophytic pine, mesophytic oak, and pyrophytic oak at 11:00 (A) and 17:00 (B).

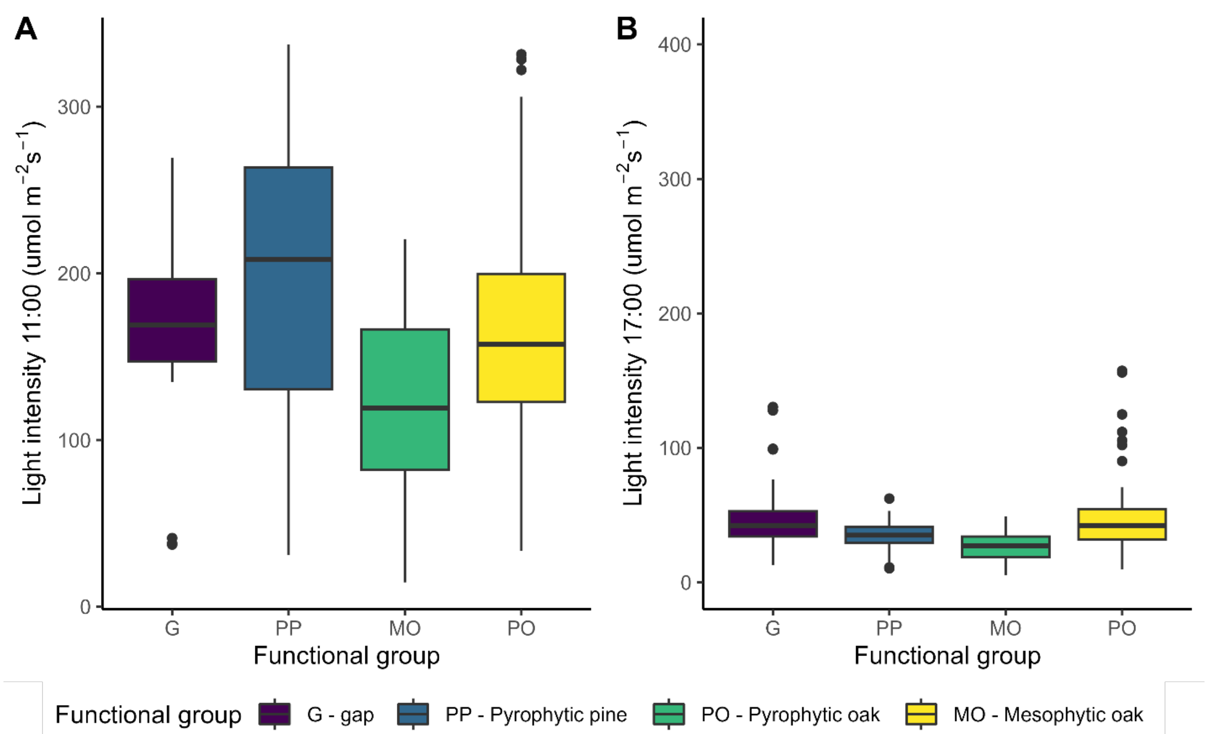

Figure 5. Box plot with standard error of light intensity (µmol m^{-2} s^{-1}) mean of gap, pyrophytic pine, mesophytic oak, and pyrophytic oak at 11:00 (A) and 17:00 (B).

Fuel Composition and Loads

As we expected, fuel load varied among functional groups (Table 3). We found statistical differences in grasses ($p < 0.0001$), where pyrophytic pines and gaps had similar mean grass loading ($p = 0.9900$), with approximately 2.1 times higher load compared to pyrophytic oaks and mesophytic oaks. Pyrophytic oaks and mesophytic oaks did not differ in grass loading between them ($p = 0.9855$) We did not find differences among herbaceous plants and functional groups ($p = 0.9766$). For woody plants, gap plots had 4.2 times lower loading than pyrophytic oaks and mesophytic oaks functional groups ($p = 0.0202$), not presenting differences in woody plants compared to pyrophytic pine ($p = 0.3790$). Other materials category was excluded from further analysis due to zero-inflated data, not passing of 15% of relative proportion among functional groups.

Overall, leaf litter load was highest for the functional group matching the overstory tree (Table 3). For pine leaf litter, pyrophytic pines had the highest mean load ($p < 0.0001$), while gaps, pyrophytic oaks and mesophytic oaks were not statistically different from each other. Pyrophytic oaks had ~2.4 times more pyrophytic oak leaf litter than mesophytic oaks ($p < 0.0001$). Low pyrophytic oak leaf litter load was found in gap, and pyrophytic pines which did not statistically differ ($p = 0.4871$). Mesophytic oak group had ~3.5 and 14.5 times more mesophytic oak leaf litter than pyrophytic oak and pyrophytic pine, respectively ($p < 0.0001$) whereas gaps and pyrophytic oaks had the lowest load mean ($p = 0.9621$). Other leaf litter category was excluded from the analysis due to zero-inflated data, having less than 3% of relative proportion among functional groups.

Table 3. Mean fuel loads (g/m^2) and their relative proportion (%) (± standard error) of individual fuel types (grasses, herbaceous plants, woody plants, pyrophytic pine litter, pyrophytic oak litter, herbaceous and shrub leaf litter (others), and other material and in gaps and beneath pyrophytic pine, pyrophytic oak and mesophytic oak trees. Values with different letters are significantly different ($p < 0.05$) as determined by post hoc Tukey's Honest Significant Difference test.

	Gap		Pyrophytic pine		Pyrophytic oak		Mesophytic oak	
Fuel types	Fuel load (g/m^2)	Relative proportion (%)	Fuel load (g/m^2)	Relative proportion (%)	Fuel load (g/m^2)	Relative proportion (%)	Fuel load (g/m^2)	Relative proportion (%)
Grasses	128.9 (23.3)^{a}	42.8	150.4 (23.4)^{ab}	27.6	70.5 (16.0)^{c}	14.3	69.9 (12.8)^{cd}	17.0
Herbaceous plants	12.9 (3.1)^{a}	4.3	11.30 (2.9)^{a}	2.1	14.9 (3.8)^{a}	3.0	13.91 (3.5)^{a}	3.4
Woody plants	4.3 (3.1)^{a}	1.4	17.46 (2.9)^{ab}	3.2	17.2 (3.8)^{bc}	3.5	16.0 (3.5)^{bcd}	3.9
Pyrophytic pine litter	106.9 (15.2)^{a}	35.5	279.78 (24.3)^{b}	51.3	171.4 (23.3)^{c}	34.7	116.5 (17.6)^{acd}	28.3
Pyrophytic oak litter	15.1 (4.1)^{a}	5.0	22.27 (4.0)^{ab}	4.1	147.8 (16.2)^{c}	29.9	61.50 (14.6)^{d}	14.9
Mesophytic oak litter	6.9 (2.1)^{a}	2.3	4.18 (1.0)^{ab}	1.6	17.3 (5.3)^{c}	2.3	60.47 (12.1)^{d}	2.7
Others litter	-	1.6	8.81 (2.0)^{ab}	1.6	-	2.3	-	2.7
Other materials	-	6.9	50.72 (19.1)^{ab}	9.3	-	8.5	-	15.0
Total	301.2	100	544.9	100	493.1	100	411.1	100

Woody fuels also differed among functional groups, particularly among 1-10- and 100-hour fuels. (figure 6). For 10 h woody fuels, mesophytic oaks had ~10.4 times more 10h woody fuel compared to gaps ($p = 0.0049$), where gaps averaged 0.09 kg/m^2 ± 0.04, which was significantly lower than the other groups ($p = 0.0025$). Considering 100 h woody fuels, gaps had 33.3 times fewer woody fuels than the other functional groups. Gaps had the lowest mean (0.03 ± 0.03 kg/m^2), and mesophytic oaks had the highest load (1.00 ± 0.35 kg/m^2) ($p < 0.0001$). Zero-inflated data obtained from 1000-hour fuel sampling suggests that Brown's transect method (1974) may not sufficiently capture variability observed in 1000-hour fuels located in the relatively small areas beneath trees. Thus, we opted to exclude them from subsequent analyses.

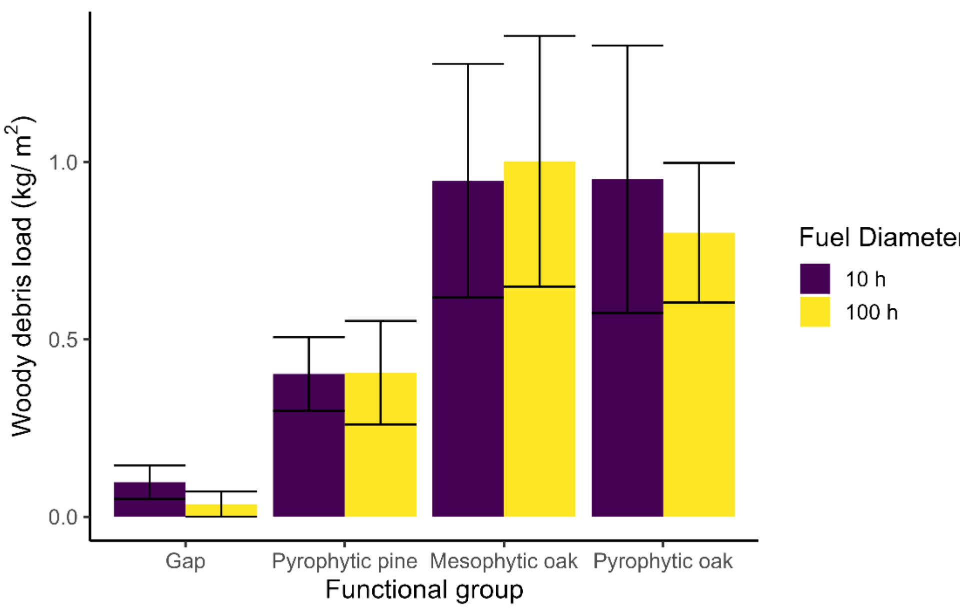

Figure 6. Mean ± SE woody debris load (kg/m^2) of 10 h and 100 h across functional groups (gaps, pyrophytic pine, mesophytic oak, and pyrophytic oak).

Tree Regeneration

Overall, we found differences in regeneration density among overstory treatments (Table 4). There were no statistical differences among regeneration density of pyrophytic pine (p =

0.3437), pyrophytic oak (p = 0.4614), and mesophytic oak (p = 0.0793) (Figure 7). For other tree categories we found that mesophytic oaks had ~4.1 and 1.9 times higher regeneration density than pyrophytic pine and mesophytic oak respectively (p = 0.0139). For total density, we also found that mesophytic oaks had the highest density, with ~1.5 and 1.1 higher density than pyrophytic pine and pyrophytic oak respectively (p=0.0122). Interaction between overstory and understory regeneration functional group was not statistically significant (p = 2989).

Table 4. Woody tree found beneath individual trees and categorized by functional group in a longleaf pine-oak woodland, Georgia, USA.

Species	Functional group
Pinus palustris	Pyrophytic pine
Quercus falcata	Pyrophytic oak
Quercus laevis	Pyrophytic oak
Quercus margaretta	Pyrophytic oak
Quercus nigra	Pyrophytic oak
Quercus stellata	Pyrophytic oak
Quercus geminata	Mesophytic oak
Quercus laurifolia	Mesophytic oak
Quercus virginiana	Mesophytic oak
Pinus taeda	Other trees
Prunus serotina	Other trees
Sassafras albidum	Other trees
Aesculus spp.	Other trees
Diospyros virginiana	Other trees
Asimina triloba	Other trees

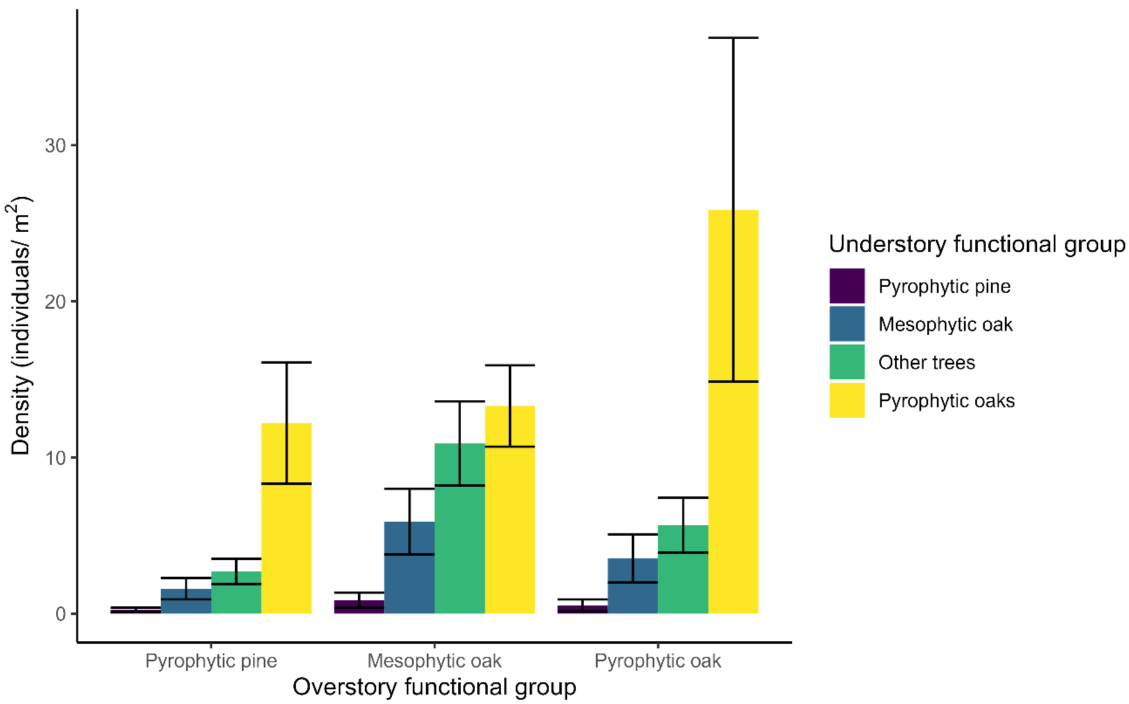

Figure 7. Mean ± SE tree regeneration density (individuals/m^2) of pyrophytic pine, pyrophytic oak, mesophytic oak, and other trees across functional groups (pyrophytic pine, mesophytic oak, and pyrophytic oak).

Discussion

This study demonstrates that overstory trees create zones of influence beneath them that differentially impact microclimate conditions and fuel characteristics depending on their functional group. Crown area and canopy cover were higher beneath mesophytic oaks compared to pyrophytic pines and oaks, leading to 20-40% lower incident light, air temperature, and VPD beneath mesophytic oaks, specially at 11:00, when many prescribed fires at this site are ignited. The mesophytic oaks sampled here are shade-tolerant (Burns and Honkala 1994), and shade-tolerant species typically have high leaf area, which creates a denser crown (Alexander and Arthur 2010; Babl *et al*. 2020) with low understory light (Canham *et al.* 1994) which can decrease understory VPD by lowering temperature and raising relative humidity. VPD is a variable commonly used to predict flammability due to its ability to explain moisture extraction from surface vegetation by atmosphere (Costa and Sandberg 2004; Shearman and Varner 2021), and studies have shown that higher VPD is related to higher flammability (Williams *et al.* 2013; Williams *et al.* 2014; Seager *et al.* 2015; Burton *et al.* 2023). Thus, the lower VPD at the morning period under mesophytes, compared to higher VPD beneath pyrophytes, also found on Chapter 2, could hinder ignition in mixed forests, potentially affecting mesophytic encroachment.

As we expected, we found differences in grass loading among functional groups, which can be related to light incidence and flammability. Pyrophytic pines, which presented the highest light incidence, also had ~ 2.1 times more grasses than mesophytic oaks. Besides their shade intolerance (Maynard and Brewer 2013), grasses are highly flammable (Pausas *et al.* 2017) and benefit from frequent fire by opening canopy, removing surrounding biomass and stimulating new growth and flowering (Everson *et al.* 1988; Caturla *et al.* 2000; Gagnon *et al.* 2010; Pausas *et al.* 2017). Higher grass fuel loads could potentially increase flammability. This combination of grasses and pine needles perched atop them is commonly cited a reason why tree regeneration is relatively low beneath individual longleaf pine trees (Johnson *et al.* 2021).

As hypothesized, leaf litter loading beneath overstory trees was dominated by litter from its own functional group, but with presence of other functional groups. While unsurprising, this finding can be a problem, due to the accumulation of mesophytic leaf litter in a pyrophytic landscape with mesophytic encroachment. Mesophytic leaf litter tends to increase fuel moisture due to their specific leaf area and compaction, hindering flammability (Alexander and Arthur 2010; McDaniel *et al.* 2021), which could favor more mesophytic species. Furthermore, areas with more pyrophytic pines, producing more pyrophytic pine needles with rich terpenes (Ormeño *et al.* 2009), and pyrophytic oaks, with aerated fuel bed, enhance fire ignition and rate of spread (Kreye *et al.* 2014) increasing the chances of killing encroaching species in fire dependent landscapes. These findings highlight the importance of mixed litter beds (Kreye *et al.* 2013, 2018b; McDaniel *et al.* 2021) and in situ studies of mixed litter beds as our Chapter 2

Contrary to our hypothesis, there were no differences in herbaceous and woody vegetation in fuel loads between pyrophytic pines, pyrophytic oaks, and mesophytic oaks and it may be explained due to data collection on dormant season. Perennial herbs and woody plants tend to be dormant in autumn, winter and early spring (Haines and Johnson 1975; Hutchinson 2005), which could have affected our herbaceous and woody plant load. Our results imply that burning in the dormant season may help increase native plant diversity (Kral *et al.* 2018) due to higher flammability, burning more dormant season grasses (Shay *et al.* 2001) with lower herbaceous and woody vegetation. However, more studies are needed comparing differences in herbaceous and woody vegetation beneath different functional group trees in different seasons.

Although differences in total woody fuel loading between functional groups were relatively small, they did differ in their fuel composition. Mesophytic oaks and pyrophytic oaks had woody debris fuel loads compared to pyrophytic longleaf pine and gap areas, a trend also found in another study, where oaks had high woody debris loads (MacMillan 1988). These differences between oaks and pine could affect the woody fuel moisture retention, and consequently flammability, in mixed forests. As found on Chapter 2, mesophytic oak woody debris tends to absorb less water due to their lower rugosity and higher density (Costa and Sandberg 2004; Shearman and Varner 2021); however, they tend to dry slower compared to pyrophytic pines and oaks which could hinder fuel bed flammability, especially after rain events.

Contrary to our hypothesis, there were no statistical differences in understory functional group regeneration density between overstory functional groups, which can be explained by frequent fire on all three sites and for being a mixed forest. Frequent fires can decrease woody cover and increase herbaceous and grass vegetation on mixed pine and oak forest (Nuzzo *et al.* 1996; Arthur *et al.* 1998; Hutchinson 2005; Holzmueller *et al.* 2009). However, we observed subtle differences between pyrophytic oaks and mesophytic oaks in terms of their regeneration, which can be attributed to their zones of influence. Pyrophytic oaks, characterized in this chapter by a medium canopy cover and abundant sunlight reaching the understory, exhibited a higher rate of self-regeneration. This phenomenon can be attributed to their moderate shade tolerance and the favorable conditions provided by the open canopy and higher light incidence. On the other hand, mesophytic oaks, with a dense canopy cover and limited light penetration to the understory, appeared to have established a zone of influence conducive to their own regeneration. The process of mesophytic oak regeneration may be a problem in pyrophytic landscapes, as the encroachment of mesophytic regeneration by old mesophytic oaks, likely from fire suppression from the beginning of 20th century could occur even in landscapes with reintroduction of fire.

Conclusion

Overall, this work supports our initial hypothesis related to mesophication, where pyrophytic and mesophytic trees can create zones of influences affecting understory conditions and flammability. Our study reinforces the idea that crown traits, such as crown area and canopy cover, can affect microclimate and may have an important role in flammability and encroachment of mesophytic species. Thus, for future microclimate modeling research, it is important to consider additional variables beyond relative humidity and temperature. For instance, vapor pressure deficit (VPD) is a crucial factor linked to fire behavior and surface evapotranspiration, besides temperature and relative humidity, and likely plays a large role in fire ignition, yet VPD is not considered as much such as temperature and relative humidity (Castellví *et al.* 1996; Pechony and Shindell 2009; Sedano and Randerson 2014; Seager *et al.* 2015).

Further research is needed to explore the impacts of pyrophytes and mesophytes on fuel loads. Our study showed that pyrophytes and mesophytes can have different leaf litter loads beneath them besides their own functional group, and woody debris load can differ between pyrophytic pines and oaks. This information can change the fire management in mixed forests, and how intensity and ignition can be applied in these forests, depending on the overstory composition and burn objectives. Mixed forests are common worldwide due to fire exclusion, and it is crucial to explore more mixed fuel loads in different pyrophytic landscapes with different mesophytic and pyrophytic species (Cabrera *et al.* 2023).

Additionally, expanding our knowledge on regeneration processes within these ecosystems is crucial. While there is existing research on regeneration and its response to prescribed fires or thinning practices, there is still a knowledge gap concerning the specific effects of pyrophytic and mesophytic tree species on regeneration at a smaller scale. Further studies are needed to investigate how different species within these categories influence regeneration dynamics. It is also important to conduct such studies in various ecosystems across the United States and globally to account for regional variations. By examining regeneration patterns and responses to different pyrophytic and mesophytic tree species, we can enhance our understanding of ecosystem dynamics and management practices, hindering loss of biodiversity.

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Chapter 2. Influence of overstory pyrophytic and mesophytic trees on fuel moisture retention

Abstract

Following decades of fire exclusion, pyrophytic oak and pine landscapes across the central and eastern U.S. are shifting to closed-canopy forests with a dense midstory occupied by shade-tolerant, often fire-sensitive species (i.e., mesophytes). As mesophytic species encroach into historically pyrophytic landscapes, changes in crown traits and groundlayer microclimate may alter fuel bed drying rates, ultimately affecting fire behavior during both prescribed burns and wildfires. To better understand how overstory trees of different functional groups impact fuel bed drying rates, we investigated fuel drying dynamics beneath overstories of pyrophytic pine (*Pinus palustris*), pyrophytic oak (*Quercus margaretta* and *Quercus laevis*), and mesophytic oak (*Quercus laurifolia)* in a longleaf pine-mixed oak woodland in Newton, Georgia, USA during summer 2022. We implemented a fuel bed drying experiment, where 60 fully-hydrated bags with either leaf litter or fine woody fuels of different pyrophytic and mesophytic species were placed under five overstory individuals of each tree and in nearby gap areas early in the morning and weighed every two hours for 10 hours, and this was repeated for 5 days. We also measured relative humidity and air temperature and determined vapor pressure deficit (VPD) beneath each tree and measured leaf litter (curling, thickness, specific leaf area, volume) and wood (density) traits. We found that pyrophytic pine and oak leaf litter dried ~1.8x faster than mesophytic leaf litter (3.5, 4.4, and 6.4 hours, respectively), independent of the overstory. In addition, both leaf litter and woody fuels dried faster under pyrophytic pine and oaks compared to mesophytic oaks. For woody debris fuel groups, there were no statistical differences in drying rates between pyrophytic and mesophytic groups. Vapor pressure deficit beneath pyrophytic pines and in gaps

was ~1.4x higher than VPD beneath pyrophytic and mesophytic oaks during the afternoon (13:00 and 17:00). Thus, fuels beneath pyrophytic pines and oaks lose moisture faster than those beneath mesophytic oaks, likely due to VPD, and fuel morphology, which could affect flammability and the continued encroachment of mesophytic species. This study highlights how fine-scale differences in VPD and fuel drying dynamics occurs in mixed forests. Understanding drying rates can inform spatially explicit and mechanistic models of fire behavior, inform conceptual frameworks to classify species in pyrophytic and mesophytic species, and better define prescribed burning windows based on stand composition. Ultimately better understanding feedbacks among vegetation, fire behavior, and fire effects can help future prescribed burns to hinder mesophytic species encroaching on pyrophytic ecosystems, preventing loss of flora and wildlife biodiversity.

Introduction

Historically, many upland oak (*Quercus* spp.) and pine (*Pinus* spp.) woodlands and savannas in the central and eastern United States were maintained with frequent, low-intensity surface fires (Frost 1998) that promoted pyrophytic tree species, open forest structure, and a diverse, highly flammable herbaceous understory (Hanberry *et al.* 2014, 2020). However, due to land use changes and 20th century fire exclusion, these historically open forests are shifting to closed-canopy forests dominated by a dense midstory of shade-tolerant, often fire-sensitive tree species (i.e., mesophytes) and sparse understory with a leaf litter fuelbed (Nuzzo 1986; Abrams 1992; Nowacki and Abrams 2008; McEwan *et al.* 2011; Stambaugh *et al.* 2015; Hanberry *et al.* 2018, 2020). The mesophication hypothesis posits that the transition from pyrophytic trees to increased dominance of mesophytic species creates a shaded understory that reduces flammability, regeneration of pyrophytic species, and understory plant diversity due to increased shade, higher relative humidity, lower air temperature, and moister fuels (Alexander *et al.* 2021). Much research has focused on understanding leaf litter flammability traits of encroaching species in laboratory settings (Babl *et al.* 2020; Kane *et al.* 2022; Varner *et al.* 2022; Kreye *et al.* 2023), but far less attention has focused on how encroaching trees may alter fuel dynamics and fire behavior *in situ* (McDaniel *et al.* 2021; Cabrera *et al.* 2023).

Leaf litter is considered a fundamental driver of flammability and is the primary fuel consumed in a prescribed fire in closed canopy forests (Cornwell *et al.* 2015; Burton *et al.* 2021; Kane *et al.* 2022). Differences in properties of leaf litter between species such as moisture dynamics, fuel bed arrangement, and flammability are likely to occur due to variations in leaf morphology (Varner *et al.* 2015). For example, leaf size and shape influence both fire intensity and moisture retention (Schwilk and Caprio 2011; Kreye *et al.* 2013; Cornwell *et al.* 2015;

McDaniel *et al.* 2021). Leaves with high leaf area and curl, often as a pyrophytic characteristic, tend to hold less water, creating an aerated fuel bed and increasing flammability (Schwilk and Caprio 2011; Kreye *et al.* 2013; Cornwell *et al.* 2015; McDaniel *et al.* 2021). In contrast, small, flat leaves, often a mesophytic characteristic, create more compact fuel beds that retain moisture with low evaporation rates and decreased flammability (Schwilk and Caprio 2011; Engber and Varner 2012; Cornwell *et al.* 2015). Therefore, high moisture retention of smaller, flatter leaves associated with mesophytes (Cornwell *et al.* 2015) may be an essential factor in modifying the flammability of pyrophytic ecosystems (Rothermel 1993).

Fine woody debris, defined as fallen and dead woody materials with diameter ≤1 cm and length <10 cm (Yan *et al.* 2006), may differ between pyrophytic and mesophytic species in ways that influence fire behavior. Thicker and fresher wood materials have a lower chance of ignition and combustion, due to their lower surface area relative to their mass (Sullivan *et al.* 2018). In contrast, smaller dead fuels from fallen branches have a greater influence on fire behavior because of their higher surface area relative to their mass (Sullivan et al. 2018, Rothermel 1993). Fire-adapted trees typically have thicker bark, preventing mortality in frequent fire ecosystems (Pausas 2015; Charles-Dominique *et al.* 2017; Shearman and Varner 2021). Pyrophytic trees may therefore deposit thicker woody debris and alter flammability. Although woody debris from fallen branches can significantly contribute to flammability, there is little information on how the moisture retention and drying rates of woody debris vary among pyrophytic and encroaching species.

Fuel bed moisture dynamics may also vary between mesophytic and pyrophytic species due to differences in exposure to solar radiation and microclimate conditions. Pyrophytic species tend to have more open canopies, allowing more precipitation, but higher solar incidence which increases the drying rate of fuel materials, consequently affecting fuel flammability (Biddulph and Kellman 1998; Tanskanen *et al.* 2006). Despite that canopy cover decreases precipitation in the understory, reduced solar radiation and ventilation reduces fuel moisture loss due to reduced evaporation (Raynor 1971; Kunkel 2001; Tanskanen *et al.* 2006). While the dense canopies of mesophytic species reduce the amount of precipitation received by the fuel bed (Alexander and Arthur 2010; Siegert *et al.* 2019), the high percentage of canopy cover simultaneously reduces evaporation rates through lower levels of light incidence and reduced wind speeds (Kreye *et al.* 2018; Babl *et al.* 2020; Alexander *et al.* 2021). As a result, the fuel beds beneath mesophytic species are typically cooler and more humid than their pyrophytic counterparts (Kreye *et al.* 2018; Babl *et al.* 2020; Alexander *et al.* 2021).

The primary goal of this study is to test whether mesophytic species alter fuel dynamics and fire behavior through both microclimate conditions and leaf litter and woody debris traits. To achieve this goal, we characterized moisture dynamics in leaf litter and woody debris of pyrophytes, mesophytes and associated leaf litter and woody debris traits under various canopy conditions. We expected that moisture loss in longleaf pine and pyrophytic oak leaf litter and woody debris would be rapid, because of low leaf surface area, the lack of a compacted fuel bed and lower density of woody debris (Hoffmann and Solbrig 2003; Lawes *et al.* 2011). In contrast we expected that mesophytic leaf litter and woody debris would lose water slower compared to pyrophytes because of their small, flat, and thin leaves, compacting the fuel bed (Schwilk and Caprio 2011; Cornwell *et al.* 2015) and thinner (Varner *et al.* 2016) and denser woody debris, creating moisture retention.

In addition to leaf litter and woody debris traits, we expected that microclimate conditions would differ among overstory tree groups and indirectly influence the drying rates of fuel. We expected that fuels under pyrophytic pines and pyrophytic oaks would dry faster because of their open canopy allowing direct light to penetrate to the understory (Battaglia *et al.* 2003), increasing the surface temperature and evaporation. By contrast, for mesophytic oaks, we hypothesized that the fuels would have a lower rate of moisture loss compared to pyrophytic oaks and pines due to the higher percentage of canopy cover and cooler and more humid understory of mesophytic trees (Nowacki and Abrams 2008; Kreye *et al.* 2013).

Knowing the relationship between understory microclimate, solar incidence, and fuel moisture in prescribed burns leads to safer planning and the execution of management objectives (Kreye *et al.* 2014). However, there is insufficient data to fully understand how the gradual loss of moisture in the fuel bed is affected by sunlight under mesophytic and pyrophytic tree species, which affects fire ignition, prescribed burns, and wildfires.

Methods

Study Area

This study was conducted at the Jones Center at Ichauway 31.2201°N, 84.4792°W, in Newton, Georgia, United States, which is comprised of 11,740 ha of forest dominated by longleaf pine (*Pinus palustris* L.) (Holland *et al.* 2019), and wiregrass (*Aristida stricta* Michx) (Gaya *et al.* 2023). The property also contains mesophytic (*Quercus virginiana* Mill., *Quercus laurifolia* Michx) and pyrophytic (*Quercus margaretta* Ashe, *Quercus laevis* Walt., *Quercus falcata* Michx.) oaks. Management using fire has been implemented since the 1920s and occurred approximately every two years typically during the late dormant season and early growing season (Rutledge and McIntyre 2022). Soils at the site include sandy acidic soil, including Entisols and deep Utisols (Jacqmain *et al.* 1999). Classified as a humid subtropical area, temperatures at the site range from -10 ºC to 39 ºC during the year (Golladay *et al.* 2021), with daily temperature of 27 ºC average between May and August, and 11 ºC average between November and February (Gaya *et al.* 2023) and 1310 mm of precipitation throughout the year (Golladay *et al.* 2021).

Experimental Design

We selected a study area that was dominated by longleaf pine but containing numerous pyrophytic and mesophytic oaks, last burned in 2021. We established 20 plots that varied in overstory cover including 15 plots with individual trees, and five plots containing gaps with no overstory cover. The individual trees were stratified across three functional groups depending of shade and fire tolerance: Pyrophytic pine (shade-intolerant and fire-tolerant), Pyrophytic oak (shade-intolerant and fire-tolerant), and Mesophytic oak (shade-tolerant and fire-intolerant) (Table 4). One tree from each functional group along with one gap comprised a study block. Individual trees within blocks varied in size by no more than 10 cm diameter at breast height (DBH), and all trees met the following criteria: > 10 m from a road or trail, > 5 m from another tree individual, and no overlapping crown with another tree (Figure 7).

Table 5. Tree species chosen for fuel moisture loss experiment in a pine-oak woodland, Newton, Georgia, USA by scientific and common name, shade tolerance, fire tolerance, and functional group .

Tree species	Common name	Shade tolerance	Fire tolerance	Functional group
Quercus laurifolia Michx	Laurel oak	Tolerant[1]	Intolerant[3]	Mesophytic oak[1]
Quercus margaretta Ashe	Sand post oak	Intolerant[1]	Tolerant[4]	Pyrophytic oak[4]
Quercus incana Roxb	Bluejack	Tolerant [1]	Tolerant[1]	Mesophytic oak
Quercus laevis Walt.	Turkey oak	Intolerant[1]	Tolerant[5]	Pyrophytic oak[5]
Pinus palustris L.	Longleaf pine	Intolerant[2]	Tolerant[6]	Pyrophytic pine[6]

Note: Species information from: (Burns and Honkala 1994[1]; Loudermilk et al. 2011[2]; McReynolds and Hebb 1990[3]; Hannon et al. 2020[4]; Carey 1992[5]; McCune 1988[6])

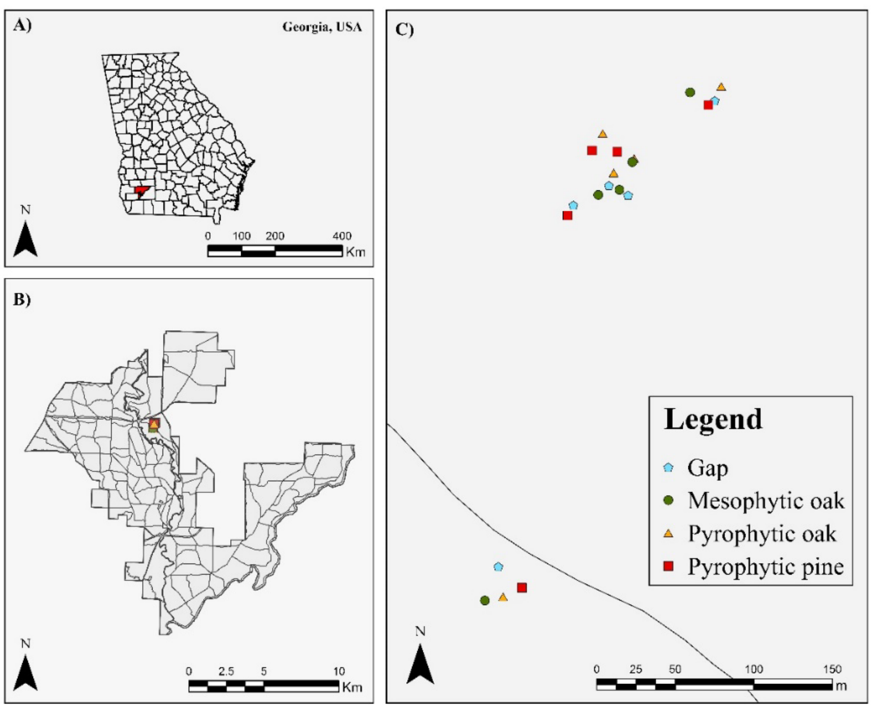

Figure 8. A) Jones Center at Ichauway located in Georgia, USA; B) Experiment plot at the Jones Center at Ichauway; C) Study area showing locations of 15 individual trees and 5 gaps organized into five blocks.

Fuel Moisture Measurements

To understand the moisture dynamics of leaf litter and woody debris under mesophytic oaks, pyrophytic oaks, and pyrophytic pines, we placed 60 mesh bags (30 cm x 30 cm) under each tree and in gaps plots along a transect extending from the bole to the end of the crown in the growing season (June 2022) when prescribed fires are often applied. Of the 60 bags, 30 had leaf litter, and the other 30 had fine woody debris. The experiment was performed over five days, one block each day with temperatures ranging between 16 ºC to 44 ºC and relative humidities ranging from 22% to 100%, over the day (Table 6) and little cloud coverage.

Table 6. Temperature (°C) and relative humidity (mean, daily minimum, daily maximum) over the experiment days in a pine-oak woodland, Newton, Georgia, USA.

	Experiment days (2022)				
	Jun1	Jun 7	Jun 10	June 15	June 21
Temperature (ºC)					
Mean	32.9	32.3	31.7	33.7	35.2
Daily Minimum	16.8	18.4	20.4	22.2	19.2
Daily Maximum	42.8	40.5	40.4	42.2	44.2
Relative humidity (%)					
Mean	55.9	60.2	58.1	62.1	48.5
Daily Minimum	30.1	32.5	31.7	38.2	22.8
Daily Maximum	99.2	100	99.2	100	99.6

During summer 2022, immediately outside the study area, we collected leaf litter and woody debris of the observed dominant species: laurel oak (*Quercus laurifolia*), sand post oak (*Quercus margaretta)*, and longleaf pine (*Pinus palustris*) to represent mesophytic oaks, pyrophytic oaks, and pyrophytic pines, respectively. We collected litter by hand from the understory, gathering leaves with no sign of decomposition from the understory. For woody debris, we collected live branches on the trees of 10 hour (diameter between 0.6 - 2.3 cm), for each functional group to avoid material decomposition and to standardize results.

We followed methods by Kreye et al. (2013) and McDaniel et al. (2021) to hydrate collected fuels. Briefly, we dried litter and fine woody debris in an oven for 48 hours at 60 ºC. After drying the materials, we weighed 15 g of leaf litter and 50 g of woody debris (Figure 9B) and carefully placed them in separate mesh bags. The bags were immersed in water for 24 hours then removed and drained for 1 hour in trays with drainage holes. After draining, materials within the bag were removed, reweighed (Figure 9C and 9D), and returned to the bag to avoid fuel compression. In the field, the bags were placed in each plot as shown in Figures 9A and 10. We placed 60 bags beneath each tree, following the bole to the edge of the crown, 30 bags to the north and 30 bags to the south. At 2-hour intervals, we randomly withdrew one bag of each leaf litter and fine woody functional group on each side of the tree for weighing, starting at 09:00 and ending at 17:00 each day of the experiment.

Figure 9. A) 60 soaked litter bags were placed under 20 plots following the bole to the edge of the crown. B) After 48 hours at 60 °C, 15 g of leaf litter and 50 g of woody debris were weighed C) Fuels were placed in mesh bags, soaked in water for 24 hours, drained, and re-weighed and placed under each tree.

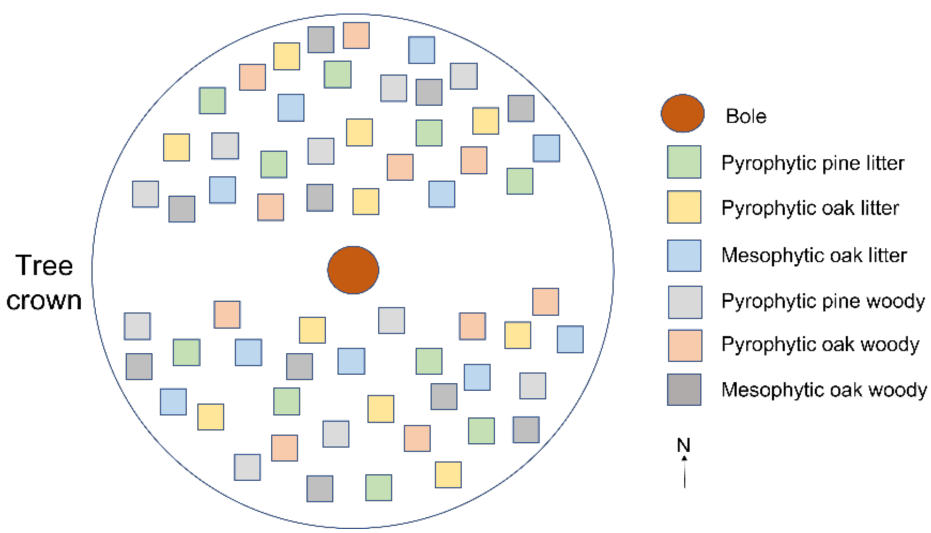

Figure 10. Litter and fine woody debris moisture experiment arrangement with mesophytic oak, pyrophytic oak, and pyrophytic longleaf pine mesh bags under tree crown.

To understand the fuel moisture loss process among functional groups, we used the Byram (1963) time lag concept model. The model describes fuel moisture response by calculating relative moisture content (%), which is defined as portion of moisture that remains evaporable at a particular moment during the desorption process and calculated by the following equations (Kreye *et al.* 2012, 2013; McDaniel *et al.* 2021):

$$(1)\ Mt = \frac{(Mass_t - Mass_{od})}{(Mass_{od})}$$

Where M_t is the fuel moisture at time t (%), $Mass_t$ is the fuel mass at time t , and $Mass_{od}$ is the oven-dry mass of the fuel.

$$(2)\ Et = \frac{(M_t - M_f)}{(M_i - M_f)}$$

Where E_t is the relative moisture content (%), M_t is moisture content at time t (%), M_f is moisture content at oven-dry (%), and M_i is initial moisture content (%).

Due to combination of physical and chemical process and a decay pattern, the time lag theory explains that relative moisture content can be characterized by response time (τ) (Nelson 1969), which can be described as the duration needed for 63.2% overall moisture change to take place during the adsorption or desorption process (Kreye *et al.* 2012). Response time (hours) is mathematically represented by the following equation:

$$(3)\ \frac{d}{dt}(lnEt) = \frac{-1}{\tau}$$

Microclimate Measurements

To better understand the relationship between moisture loss with air temperature and relative humidity, we measured microclimate conditions during fuel drying experiments. We placed two microclimate stations that measured temperature and relative humidity at each plot. Air temperature was measured by a VEML 7770 sensor and relative humidity by a SHT31 sensor housed in a miniature radiation shield printed on PRUSA MK3 3D printer (Prusa Research), using polyethylene terephthalate glycol acid (PETG) filament (Cannon *et al.* 2022). Sensors were placed 100 cm above herbaceous vegetation in the north and south directions of the tree under the mid crown **(**Figure 11)**.** The radiation shields were positioned facing north and south and measurements were collected every 15 minutes throughout the experiment (from 7:00 to 17:00 each day).

Figure 11. Microclimate sensors. A) Microclimate sensors positioned under the tree canopy. B) Microcontroller (Particle Boron, Particle Industries, Inc., San Francisco CA). C) Microcontroller in rain shield settled on the tree bark. D) Air temperature (VEML 7770) and relative humidity (SHT31) sensors radiation shield. Sensors were placed in duplicate for measurement redundancy.

The SHT31 sensors were connected to an accessible microcontroller (Particle Boron, Particle Industries, Inc., San Francisco CA). The data were uploaded using onboard cellular data capabilities and custom firmware to Google Sheets by the Boron microprocessor (Cannon *et al.* 2022). The data loggers were protected using cable ties in a HOBO CASE-4X protective enclosure (Onset Computer Corp., Bourne, MA).

To understand how tree functional groups influence microclimate conditions, we calculated vapor pressure deficit (VPD). Defined as the difference between the actual vapor content present in the atmosphere and the vapor content that could exist at a given temperature, VPD has been elucidated by many researchers (Anderson 1936; Sedano and Randerson 2014). VPD serves as a valuable indicator of the atmosphere's ability to extract moisture from the vegetation, reflecting changes in forest moisture levels and the associated vulnerability to wildfires (Seager *et al.* 2015). VPD calculation involves relative humidity and temperature and explains variances in flammability and moisture content more effectively than the variables that comprise it like temperature, relative humidity, and wind (Castellví *et al.* 1996; Pechony and Shindell 2009; Seager *et al.* 2015). To calculate the understory VPD (kPa), we used the following equation (Bonan 2008):

$$(4) VPD = (100 - RH) \times (610.7 \times 10^{\frac{7.5\,T}{237.3+T}})$$

Where VPD is vapor pressure deficit (kPa), RH is understory relative humidity, T is understory air temperature (°C), 610.7 is a factor to transform the result in Pascals, and 237.3 is a constant to establish the change in a vapor pressure curve.

Fuel Traits Measurements

To test the hypothesis that leaf traits differ among species, we used the methods in McDaniel et al. (2021) using 50 samples from this moisture experiment of laurel oak, sand post oak and longleaf pine after being oven dried for 48h at 60 ºC. For leaf litter, we measured leaf perimeter and surface area of each leaf using a HP ScanJet Pro 2500f1 scanner and ImageJ software (1.53t) (McDaniel *et al.* 2021). As a proxy for leaf curling, we measured leaf height at the highest height point of the leaf laid horizontally to the nearest 1 mm (McDaniel *et al.* 2021). Using a caliper, we measured leaf thickness to the nearest 1 mm in two ways depending on the species. For oaks, we cut the leaves in half from base to apex and measured the midvein and margin (McDaniel et al. 2021), and for longleaf pine, we measured the three individual needles in the middle and calculated an average. To obtain the specific leaf area (SLA), we weighed the leaf and divided its value by the one-sided surface area obtained by the scan.

For woody debris characteristics we measured fuel volume and density. We weighed the oven-dried mass to the nearest 0.01g and measured the length and diameter to the nearest 1 mm) in 50 individual fuel particles for each species. To determine the volume of woody debris, we used the following equation:

$$(6)\ \mathrm{V} = \pi R^2 \times \mathrm{L}$$

Where V is the volume, R is the radius, and L is the length of the woody material. We also calculated density as:

$$(7)\ D = \frac{M}{V}$$

Where D is density of the material, M is the oven-dried mass, and V is volume calculated before.

Statistical Analysis

For all statistical analyses we used R- 4.2.2 (R Core Team, 2022). Data was tested for homogeneity using Levene's Test and normality using Shapiro-Wilk Test, and log transformed when assumptions were violated. Means and standard errors are presented back-transformed values. To determine differences in VPD among overstory functional groups, we ran a linear mixed effect model. The model used an average of the four VPD measurements per period of time. We also included experimental block and date as random effects. Functional groups were the predictor variable and VPD at the five interval times were the response variables. To determine if there were differences in response time and initial moisture content on leaf litter, woody debris, and overstory between functional groups, we used a linear mixed effects model, where experimental block and date were included as random effects. The overstory and litter and woody debris functional groups and their interaction were the predictor variables, and response time and initial moisture were the response variables. An ANOVA was used to test how fuel traits differed among functional groups with fuel measurements (leaf curling, leaf thickness, SLA, leaf volume, woody density) as a response variable. For significant results ($p < 0.05$), we conducted a post hoc Tukey's Honest Significant Difference test to evaluate individual differences among functional groups.

Results

Microclimate

Overall, we found that VPD varied with time, and was usually greatest in gap and beneath pyrophytic pine compared to pyrophytic and mesophytic oak microsites. Across the five days, VPD tended to increase beneath all functional groups between 9:00 and 15:00 (Appendices). At 9:00, gaps and mesophytic oaks had similar VPD means, where mesophytic oaks had ~1.3 and 1.7 times higher VPD than pyrophytic pine and oak, respectively ($p < 0.0001$) (Table 7). At 11:00, pyrophytic oaks had the lowest VPD compared to the other functional groups, with ~1.4 times lower VPD than gaps ($p < 0.0001$). Among functional groups, gaps and pyrophytic oaks had the highest VPD at 13:00, where pyrophytic pine had ~1.3 and ~1.2 times higher mean VPD than pyrophytic and mesophytic oaks ($p < 0.0001$). At 15:00, pyrophytic oaks and mesophytic oaks had similar VPD, ~1.4 times lower than gaps and pyrophytic pines ($p < 0.0001$). At the end of the experiment, at 17:00, pyrophytic oaks had the lowest VPD, ~1.3 and 1.2 times lower than that of pyrophytic pine and mesophytic oaks, respectively ($p < 0.0001$).

Table 7. Vapor Pressure Deficit (kPa) (mean (± standard error)) along the day beneath different overstory functional groups (gap, pyrophytic pine, pyrophytic oak, and mesophytic oak).

	Vapor Pressure Deficit (VPD) (kPa)			
	Functional group			
Time	Gap	Pyrophytic pine	Pyrophytic oak	Mesophytic oak
9:00	1.22 (0.13)	0.83 (0.08)	0.64 (0.08)	1.08 (0.11)
11:00	2.66 (0.13)	2.52 (0.19)	1.87 (0.10)	2.35 (0.16)
13:00	4.13 (0.20)	3.25 (0.19)	2.49 (0.12)	2.70 (0.21)
15:00	4.26 (0.20)	4.34 (0.25)	3.10 (0.17)	3.42 (0.25)
17:00	3.57 (0.32)	3.40 (0.15)	2.59 (0.16)	3.41 (0.31)

Fuel Moisture

Leaf Litter

As expected, initial moisture content differed among all leaf litter functional groups ($p < 0.0001$). Pyrophytic pines had the lowest initial moisture content (145.5 ± 3.2%), followed by mesophytic oaks (185.8 ± 7.8%), then pyrophytic oaks (223.8 ± 7.8%). Pyrophytic oaks retained ~1.5 times more initial moisture than pyrophytic pine ($p < 0.0001$) (Figure 12).

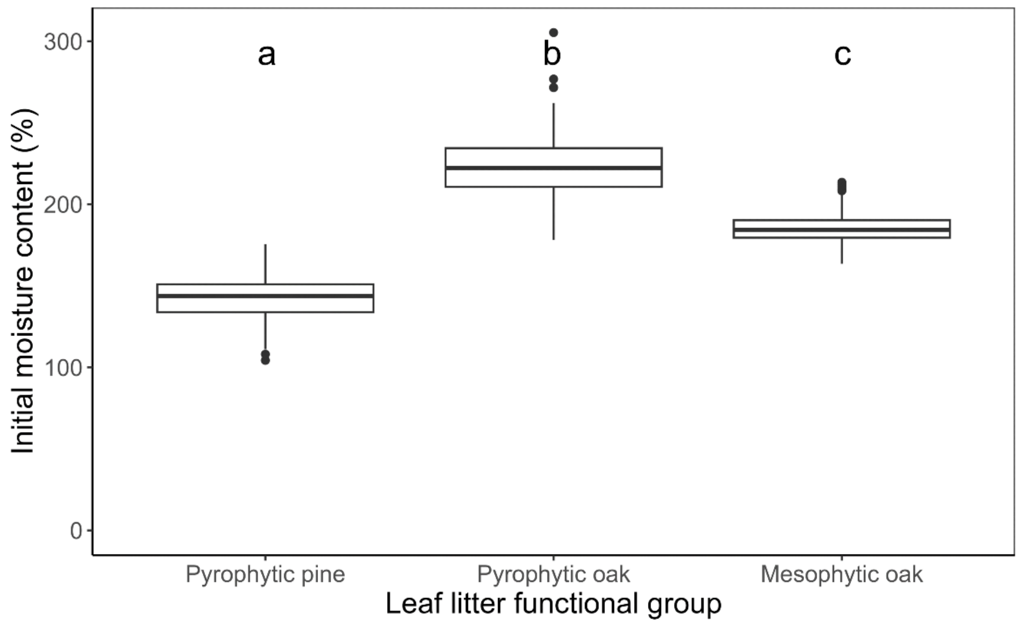

Figure 12. Box and whisker plots of initial moisture content (%) across leaf litter functional group (pyrophytic pine, mesophytic oak, and pyrophytic oak), where individual points are outliers and groups different letters are significantly different ($p < 0.05$) as determined by post hoc Tukey's Honest Significant Difference test.

Drying response times between leaf litter functional groups were significantly different ($p = 0.0002$) (Table 8), with pyrophytic pine litter drying ~1.8 times slower than that of mesophytic oaks. Drying response time also varied among litter placed beneath different overstory functional groups ($p < 0.0001$). Leaf litter within gaps dried the fastest, ~2.2 times faster than litter of mesophytic oaks. We did not find a significant interaction between litter identity and overstory identity ($p = 0.5505$).

Table 8. Drying response time (mean (± standard error)) in hours measured of litter functional group (pyrophytic pine, pyrophytic oak, and mesophytic oak) and overstory functional group (gap, pyrophytic pine, pyrophytic oak, and mesophytic oak). Values with different letters are significantly different ($p < 0.05$) as determined by post hoc Tukey's Honest Significant Difference test.

	Response time (hours)
Litter functional group	
Pyrophytic pine	3.53 (0.36)[a]
Pyrophytic oak	4.35 (0.60)[ab]
Mesophytic oak	6.39 (0.69)[c]
Overstory functional group	
Gap	2.94 (0.34)[a]
Pyrophytic pine	3.69 (0.39)[ab]
Pyrophytic oak	5.80 (0.71)[bc]
Mesophytic oak	6.60 (0.89)[cd]

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Woody Debris

Mean initial moisture content of woody debris significantly differed among functional groups ($p < 0.0001$) (Figure 13) but not different among overstory functional groups and response time ($p = 0.7372$) or their interaction ($p = 0.8856$) (Table 9). Pyrophytic pines had the highest initial moisture content (54.9 ± 1.7%) followed by pyrophytic oaks (51.1 ± 0.7%), then mesophytic oaks (29.8 ± 0.7%) ($p < 0.0001$), which held ~1.8 times less moisture than pyrophytic pines. Response time differed among woody debris placed beneath different overstory functional groups ($p = 0.0046$). Gaps had the fastest drying response time, followed by pyrophytic pine, pyrophytic oak, and mesophytic oak. Woody material beneath mesophytic oaks dried ~1.3 times slower than that beneath pyrophytic pines.

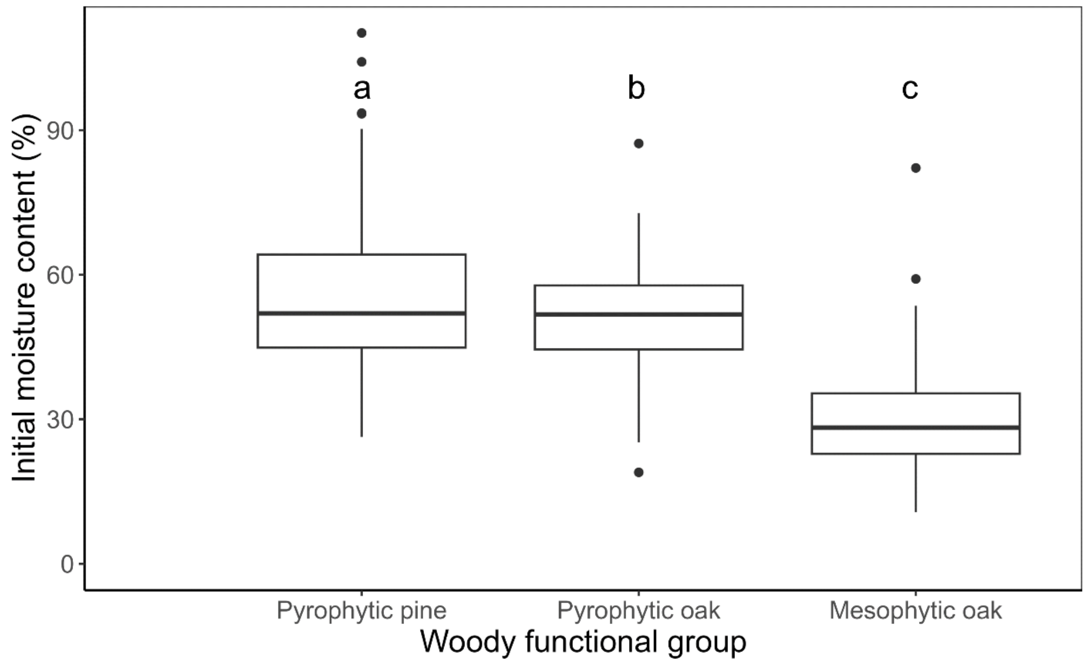

Figure 13. Box and whisker plots of initial moisture content (%) across woody debris functional group (pyrophytic pine, mesophytic oak, and pyrophytic oak), where individual points are outliers and groups different letters are significantly different ($p < 0.05$) as determined by post hoc Tukey's Honest Significant Difference test.

Table 9. Drying response time (mean (± standard error)) in hours measured of woody debris functional group (pyrophytic pine, pyrophytic oak, and mesophytic oak) and overstory functional group (gap, pyrophytic pine, pyrophytic oak, and mesophytic oak). Values with different letters are significantly different ($p < 0.05$) as determined by post hoc Tukey's Honest Significant Difference test.

	Response time (hours)
Woody debris functional group	
Pyrophytic pine	7.26 (0.77)[a]
Pyrophytic oak	7.24 (0.51)[a]
Mesophytic oak	7.90 (1.05)[a]
Overstory functional group	
Gap	5.18 (0.31)[a]
Pyrophytic pine	6.83 (0.99)[ab]
Pyrophytic oak	9.00 (0.90)[b]
Mesophytic oak	9.08 (0.75)[b]

Fuel Traits

Overall, pyrophytic pines, pyrophytic oaks, and mesophytic oaks differed significantly among leaf litter curliness, thickness, SLA, and volume, and wood density ($p < 0.0001$ for all comparisons) (Table 10). Pyrophytic oaks had the highest curl ($p < 0.0001$), and pyrophytic pines and mesophytic oaks were similar ($p = 0.0539$). Pyrophytic pines were ~2.3 and 1.9 times thicker than mesophytic and pyrophytic oaks, respectively ($p < 0.0001$). Pyrophytic pines had the lowest SLA ($p < 0.0001$), but pyrophytic oaks and mesophytic oaks were not significantly different from each other ($p = 0.1631$). Pyrophytic oaks had the highest volume, with ~2.9 and 1.5 times higher volume than mesophytic oaks and pyrophytic pines, respectively ($p < 0.0001$). For density of woody debris, all functional groups were significantly different from each other ($p < 0.0001$). Mesophytic oaks had the highest wood density, being ~1.5 times and 1.2 times denser than pyrophytic pines and pyrophytic oaks, respectively ($p < 0.0001$).

Table 10. Means and standard error (shown in parenthesis) of leaf traits (curl, thickness, SLA, and volume) and woody debris density of different functional groups (pyrophytic pine, pyrophytic oak, mesophytic oak), followed by ANOVA p-values. Values with different letters are significantly different as determined by Tukey's Honest Significant Difference test.

Fuel traits	Pyrophytic pine	Pyrophytic oak	Mesophytic oak	P-value
Leaf curl (cm)	0.79 (0.05)[a]	1.36 (0.09)[b]	0.52 (0.06)[a]	<0.0001
Leaf thickness (cm)	0.62 (0.01)[a]	0.32 (0.007)[b]	0.27 (0.007)[c]	<0.0001
Leaf SLA (cm^2g^{-1})	30.79 (0.68)[a]	95.14 (4.95)[b]	108.76 (7.61)[b]	<0.0001
Leaf Volume (cm^3)	5.89 (0.20)[a]	8.71 (0.72)[b]	2.96 (0.19)[c]	<0.0001
Wood Density (g/cm^3)	0.59 (0.01)[a]	0.81 (0.02)[b]	0.95 (0.02)[c]	<0.0001

Discussion

This work supports the hypothesis that both species fuel identity and overstory functional group influence fuel drying characteristics. The results also help to classify species not often studied in fuel moisture experiments (*Quercus margaretta* and *Quercus laurifolia*) into the commonly uses framework of pyrophytes and mesophytes. As expected, we found that the functional group determined initial moisture content of litter, litter drying time, and several leaf litter traits. As in other studies, we found that pyrophytic species have higher initial moisture content and lose moisture faster compared to mesophytic species (Kreye *et al.* 2013, 2018; McDaniel *et al.* 2021). This trend can be related to leaf curliness, and specific leaf area, which differed among litter functional groups. Pyrophytic pines and pyrophytic oaks had the highest curl, which can create a less compacted fuel bed, favoring the loss of moisture (Schwilk and Caprio 2011; Kreye *et al.* 2013; Cornwell *et al.* 2015; McDaniel *et al.* 2021). The more compacted, less curly, and higher specific leaf area of mesophytic oaks, could create a flat and unventilated fuel bed, hampering loss of moisture (Schwilk and Caprio 2011; Cornwell *et al.* 2015; McDaniel *et al.* 2021), and consequently flammability on pyrophytic ecosystems.

Most research focuses on species differences in leaf litter, but species identity of woody debris may also affect drying characteristics of fuel beds. We found that the initial moisture content of woody debris from pyrophytic species was higher than mesophytic oaks. The lower density (Costa and Sandberg 2004) and higher rugosity (Shearman and Varner 2021) of pyrophytic woody debris may allow these fuel components to absorb more moisture. We did not find statistical differences between functional groups and drying response on woody debris as expected. Newer branches can affect flammability due to their lower surface area relative to their mass (Sullivan *et al.* 2018). In order to control fuel particle size, we dried live material with no decay which can alter fuel drying properties (Zhao *et al.* 2018). However, we found small differences, where mesophytic oaks had a ~1.1 times higher response time, compared to pyrophytic pines and oaks. Woody debris from pyrophytic species could absorb more water after a rain due to their density, hindering flammability, due to higher energy to heat-up before ignition and lower flaming temperature (Babrauskas 2006; Cornwell *et al.* 2009; Hyde *et al.* 2011), but they would dry faster than mesophytic oaks.

Notably, the results support that overstory consideration may be important in fuel moisture behavior. As shown in Chapter 1, crown area and canopy cover can affect light intensity, affecting surface fuel temperature and relative humidity, consequently affecting VPD and loss of moisture. We found that VPD differed among overstory functional groups altered the drying rates of fuel beneath them. Drying times beneath mesophytic oaks trees were higher compared to gaps, pyrophytic pines, and pyrophytic oaks for leaf litter and woody debris. This could be explained by canopy density due to specific leaf area and differences in VPD between functional groups. Mesophytic species, which are shade tolerant, tend to have higher specific leaf area, as shown in this work, creating a higher crown density, decreasing light incidence (Canham *et al.* 1994; Nowacki and Abrams 2008; Alexander and Arthur 2010; Babl *et al.* 2020). This trait can alter VPD understory, increasing humidity, decreasing wind speed and consequently increasing fuel moisture (Siegert and Levia 2011; Kreye *et al.* 2018) and hampering flammability.

Conclusion

This study aimed to understand how microclimate conditions of mesophytic and pyrophytic species could alter fire behavior by fuel moisture dynamics. As expected, denser crowns from mesophytic species may create lower solar irradiance understory, decreasing VPD, response time of fuels, and consequently flammability (Canham *et al.* 1994; Biddulph and Kellman 1998; Tanskanen *et al.* 2006). Also, leaf litter and woody debris dried in distinctive patterns, potentially due to their morphological characteristics. The lower moisture loss in mesophytic leaf litter could decrease flammability and reinforce mesophytic encroachment (Alexander et al. 2021; Cornwell et al. 2015; Rothermel 1993). The higher initial moisture content in pyrophytic pines and oaks woody debris, probably due to their density and rugosity (Costa and Sandberg 2004; Shearman and Varner 2021), could affect flammability in a mixed woodland. However, our study showed that pyrophytic species can lose moisture faster compared to mesophytic oaks, increasing their flammability capacity along the day, which could help to decide better timing for prescribed burnings.

This study helps future research and management to classify some species in pyrophytic and mesophytic species. For the first time, laurel oak (*Quercus laurifolia*) was implemented into a moisture drying experiment and had similar results as mesophytic species (low understory VPD and higher response time due to crown density and fuel morphology). Also, sand post oak (*Quercus margaretta*), considered as a pyrophytic species, was used in Kreye et al. (2013);

however in this study, the species was used for the first time in an overstory and fuel drying experiment. The intermediate crown density, affecting VPD, and fuel drying rates of sand post oak, confirmed the species as pyrophytic. Thus, more studies are needed using laurel oak and sand post oak, especially on overstory and woody debris experiments.

The use of VPD in this study also reinforced the importance of this variable in fuel moisture modeling and future wildfires. Vapor pressure deficit is calculated by temperature and relative humidity and can explain better the evapotranspiration, directly impacting fire ignition. However, VPD is still not common in daily prescribed burns and wildfire predictions.

The transformation of open canopy savannas into closed canopy forests is a significant concern for scientists, landowners, and agencies. The encroachment of mesophytic species in these areas leads to a loss of biodiversity and wildlife habitat. Therefore, this study aims to contribute to the future modeling and management of these previously open pyrophytic ecosystems. By understanding the impact of the overstory on fuel moisture and subsequent flammability, this research will facilitate more effective implementation of prescribed fires for improved management strategies.

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Appendices

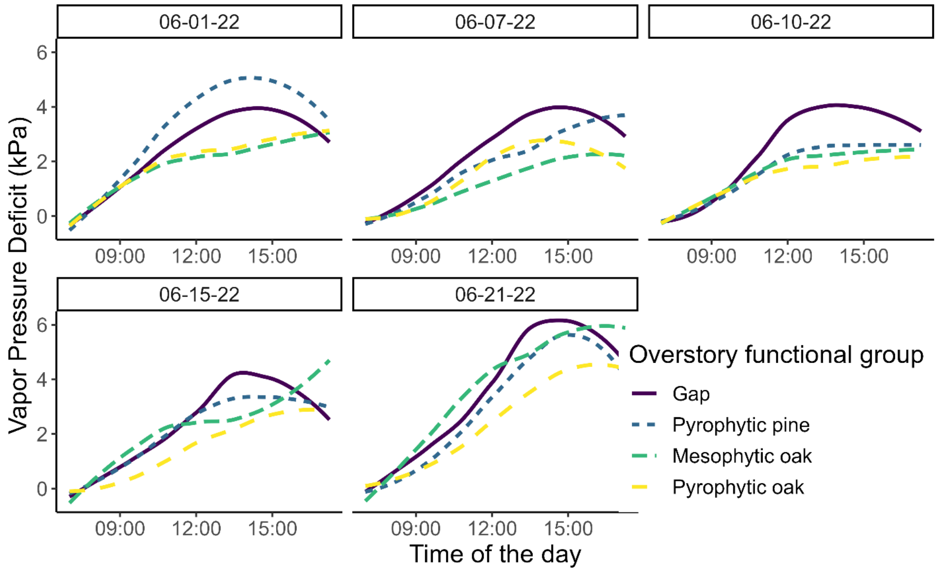

Figure 1. Vapor Pressure Deficit (kPa) patterns throughout the day of overstory functional groups (gaps, pyrophytic pines, mesophytic oaks, and pyrophytic oaks) for different days of experiment.

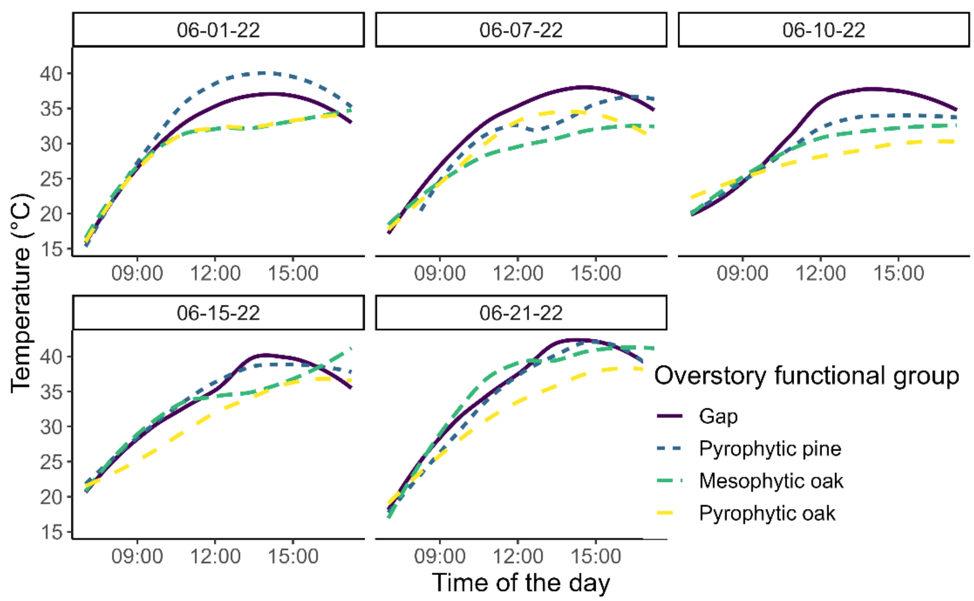

Figure 2. Temperature (°C) patterns throughout the day of overstory functional groups (gap plots, pyrophytic pines, mesophytic oaks, and pyrophytic oaks) for different days of experiment.

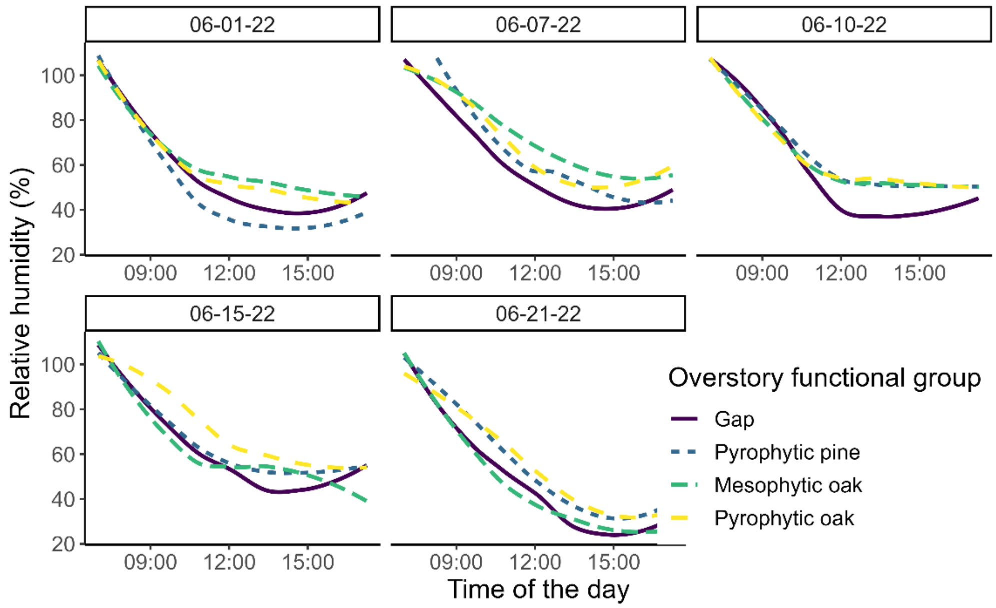

Figure 3. Relative humidity (%) patterns throughout the day of overstory functional groups (gap plots, pyrophytic pines, mesophytic oaks, and pyrophytic oaks) for different days of experiment.

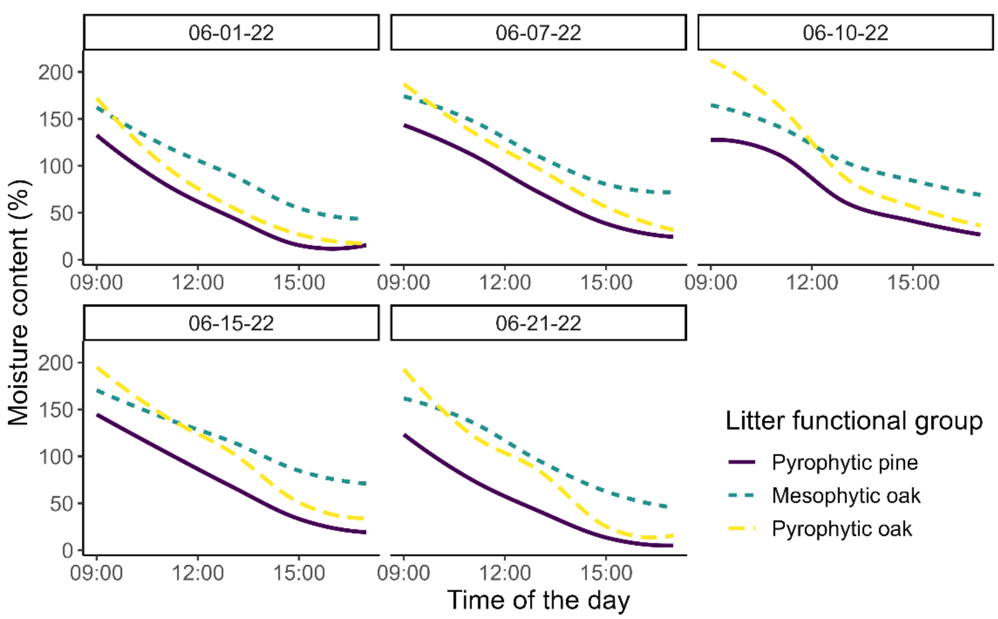

Figure 4. Moisture content (%) pattern by time of the day of leaf litter functional groups (pyrophytic pine, mesophytic oak, and pyrophytic oak) for different days.

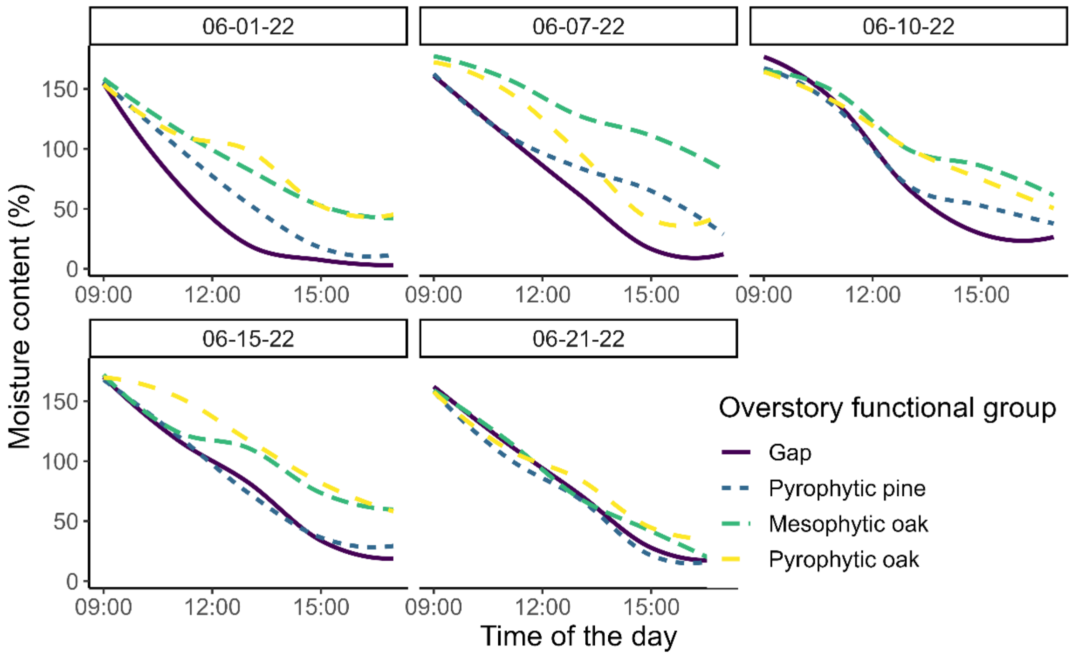

Figure 5. Moisture content (%) of leaf litter pattern by time of the day of overstory functional groups (gap, pyrophytic pine, mesophytic oak, and pyrophytic oak) for different days.

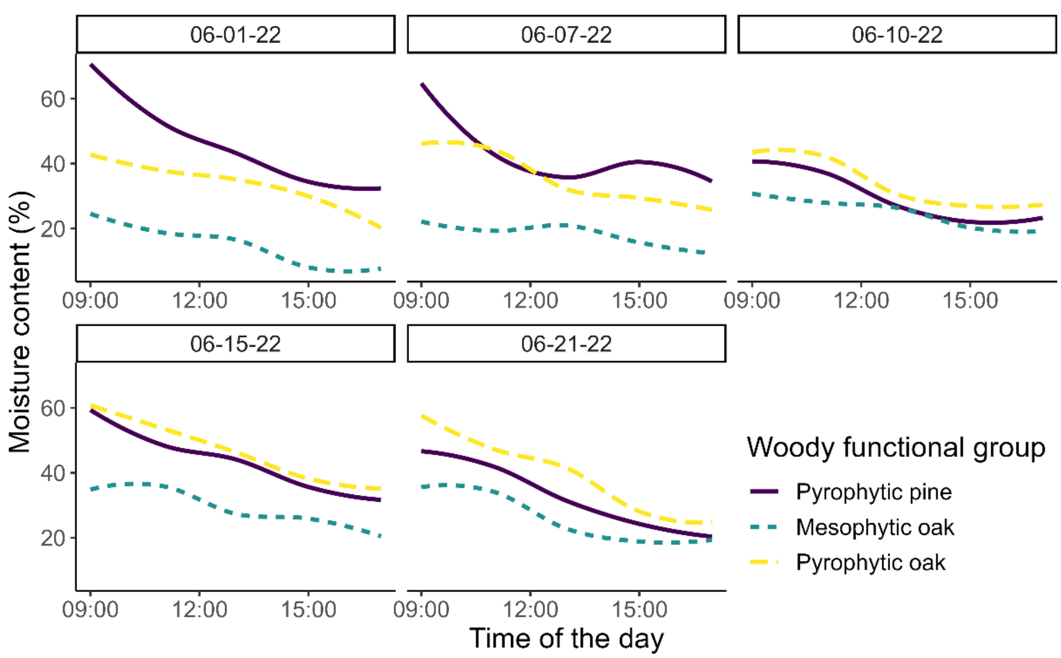

Figure 6. Moisture content (%) pattern by time of the day of woody debris functional groups (pyrophytic pine, mesophytic oak, and pyrophytic oak) for different days.

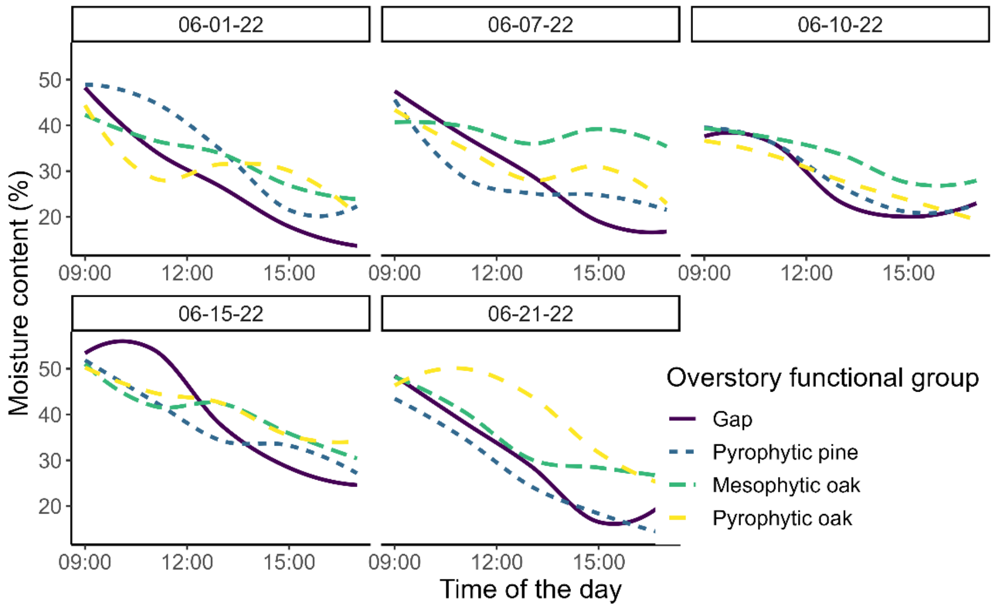

Figure 7. Moisture content (%) of woody debris by time of the day for four overstory functional groups (gap, pyrophytic pine, mesophytic oak, and pyrophytic oak).