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Overstory and fuel traits drive moisture dynamics of mesophytic and pyrophytic leaf litter and 10-h woody debris fuels in a mixed longleaf pine-hardwood woodland

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Abstract

Background Following decades of fire exclusion, many open pine and oak forests across the central and eastern US are shifting to closed-canopy forests that are increasingly dominated by shade-tolerant, fire-sensitive species (i.e., mesophytes). As mesophytes encroach into historically pyrophytic landscapes, changes in crown traits and understory microclimate may interact with fine fuel traits to influence fuel moisture retention, and ultimately, fire behavior. To better understand potential interactions among overstory trees and underlying fine fuels that occur during mesophyte encroachment, we measured in situ drying rates of leaf litter and 10-h woody debris of three functional groups (pyrophytic pine, pyrophytic oak, and mesophytic oak) in gaps and beneath overstory trees of each functional group within a longleaf pine-mixed oak woodland along with crown (area, volume, cover), leaf litter (curling, thickness, specific leaf area, volume), and woody debris (density) traits of each functional group and understory microclimate (vapor pressure deficit (VPD)).

Results We found that leaf litter from pyrophytic and mesophytic oaks had higher initial moisture content than pyrophytic pines, but pyrophytic pine and pyrophytic oak leaf litter dried 1.5 times faster than that of mesophytic oaks, likely due to their greater leaf curl, thickness, and volume. Initial moisture content of mesophytic oak woody fuels was lower than that of pyrophytic pine and pyrophytic oak, potentially because of higher wood density, but there were no differences in fuel drying rates. Regardless of fuel functional type, leaf litter and woody fuels dried 1.5 times faster in gaps and underneath pyrophytic pine compared to mesophytic oaks, likely due to the more open conditions in these areas. Notably overstory functional group and time of the day interacted to influence VPD, with VPD increasing throughout the day for all groups, but more so for gaps and beneath pyrophytic pines than either oak functional group.

Conclusions Thus, fuel and crown traits differentially impacted understory microclimate and leaf litter and 10-h woody debris drying rates, leading to slower drying of fuels of encroaching mesophytes compared to pyrophytic pines and oaks, which could lead to reduced forest flammability, and consequently, the continued encroachment of mesophytic species into fire-dependent pine and oak forests.

Keywords Mesophication, Pyrophytes, Fuel moisture, Overstory, Vapor pressure deficit, Leaf litter, Woody debris

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Resumen

Antecedentes Luego de décadas de exclusión del fuego, muchos bosques abiertos de pino y de robles a lo largo del centro y este de los EEUU, están transformándose en bosques con doseles cerrados que están siendo dominados de manera creciente por especies tolerantes a la sombra y sensibles a los fuegos (i.e. mesófitas). A medida que estas mesófitas invaden paisajes históricamente pirófilos, cambios en las características de los doseles y del microclima en el sotobosque pueden interactuar con las características de los combustibles finos e influenciar la retención de humedad, y finalmente, el comportamiento del fuego. Para entender mejor las interacciones potenciales que ocurren durante la invasión de mesófitas entre los árboles dominantes del dosel y los combustibles finos superficiales del sotobosque, medimos in situ las tasas de desecamiento del mantillo de hojas y los restos leñosos (combustibles de 10 h) en tres grupos funcionales (pinos pirófilos, robles pirófilos y robles mesófilos), en claros de bosque y debajo del dosel arbóreo de cada grupo funcional dentro de un bosque mixto de pino de hoja larga y robles, midiendo también las características de los doseles (área, volumen, cobertura), del mantillo de hojas (enrulado, grosor, área específica de las hojas, volumen) y las características de los restos leñosos (densidad) de cada grupo funcional y del microclima (déficit de vapor de difusión, VPD) de sus respectivos sotobosques.

Resultados Encontramos que el mantillo de hojas de los robles pirófilos y mesófilos tenían mayor contenido de humedad que los pinos pirófilos, aunque el mantillo de hojas de los pinos pirófilos y robles pirófilos se secaba 1,5 veces más rápido que el de los robles mesófilos, probablemente debido a que tenían un mayor enrulado de las hojas y mayor grosor y volumen. La humedad inicial de los combustibles leñosos de los robles mesófilos fue más baja que aquella de los pinos y robles pirófilos, potencialmente debido a su mayor densidad, pero no hubo diferencias en su tasa de secado. Independientemente del tipo funcional del combustible, mantillo de hojas y leñosos de 10 h se secaron más rápidamente en claros y debajo de pinos pirófilos en comparación con robles mesófilos, muy probablemente debido a las condiciones más abiertas en esos lugares. Notablemente, el grupo funcional de combustibles representado por los doseles, y la hora del día interactuaron para influenciar el VPD, incrementándolo durante todo el día para todos los grupos, aunque mucho más en los claros y debajo de los pinos pirófilos que en cualquier otro grupo funcional de los robles.

Conclusiones Las características de los combustibles y de los doseles, entonces, impactaron diferencialmente en el microclima del sotobosque, y en el matillo de hojarasca y en los combustibles leñosos de 10 h, en sus tasa de desecamiento, llevando a una disminución de la tasa de secado en los tipos de invasores mesófílos comparada con los pinos y robles pirófilos. Esto puede llevar a una reducción en la inflamabilidad del bosque, y consecuentemente, a una continua invasion de especies mesofítiicas en bosques de pinos y robles dependientes del fuego.

Background

Historically, many pine (*Pinus* spp.) and upland oak (*Quercus* spp.) woodlands and savannas in the central and eastern United States were maintained with frequent, low-intensity surface fires 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 fire exclusion, many open forests are shifting to closed-canopy forests increasingly dominated by shade-tolerant, fire-sensitive tree species (i.e., mesophytes) and a sparse understory with a leaf litter fuel bed (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 (i.e., the capacity of biomass to burn, to start, and sustain fire (Pausas et al. 2017)), regeneration of pyrophytic species, and understory plant diversity due to increased shade, higher relative humidity, lower air temperature, and high moisture fuels (Alexander et al. 2021). Much research has focused on understanding leaf litter traits and flammability in laboratory settings (Babl et al. 2020; Kane et al. 2022; Varner et al. 2022; Kreye et al. 2023). However, traits of overstory trees may alter fuel dynamics through their influence on understory microclimate, but potential overstory-fuel interactions in situ have received far less attention (McDaniel et al. 2021; Cabrera et al. 2023).

Leaf litter is a fundamental driver of flammability in closed-canopy forests (Cornwell et al. 2015; Burton et al. 2021; Kane et al. 2022). Differences in leaf morphology and chemistry among species drive fuel moisture and fuel bed arrangement, which then impact flammability (Varner et al. 2015). For example, leaf size and shape influence moisture retention and fire intensity (Kreye et al. 2013; Cornwell et al. 2015; McDaniel et al. 2021). Many pyrophytic species have high specific leaf area (SLA), lower surface area to volume ratios (SA:V) and they tend to hold less water, contributing to an aerated and flammable fuel bed (Schwilk and Caprio 2011; Kreye et al. 2013; Cornwell et al. 2015; McDaniel et al. 2021). In contrast, many mesophytic species have small, flat leaves, which contribute to compact, moist fuel beds with low flammability (Schwilk and Caprio 2011; Engber and Varner 2012; Cornwell et al. 2015). 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 1994).

Fine woody debris, defined as fallen and dead woody materials with diameter ≤ 10 cm (Yan et al. 2006), also may differ between pyrophytic and mesophytic species in ways that influence fire behavior. Fire-adaptive trees typically have thick, rugose bark, with low density (Shearman et al. 2023; Siegert et al. 2023), traits which limit damage and mortality in frequent-fire ecosystems (Brando et al. 2012). However, these characteristics could affect water retention and flammability. For example, low-density wood with more exposed pore spaces and a higher SA:V ratio tends to absorb more moisture, but these traits also promote faster drying rates (Eckstein et al. 1979; Pulido-Novicio et al. 2001; Zhang and You 2013), which could have variable impacts on flammability depending on woody debris exposure to precipitation and solar irradiation. 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 mesophytic species.

Although fuel traits alone can lead to differences in fuel drying dynamics among mesophytic and pyrophytic species, far less is known about how tree crown traits can further magnify differences due their impacts on understory microclimate. Pyrophytic species tend to have more open crowns than mesophytic species (Babl et al. 2020; Alexander et al. 2021), allowing more precipitation to pass through to the forest floor as throughfall (Alexander and Arthur 2010; Siegert et al. 2019). Open crowns also increase the amount of solar heating which increases fuel drying rates and decreases fuel moisture due to higher evaporation rates, leading to higher flammability (Kreye et al. 2018, 2020). As a result, fuel beds beneath mesophytic species may be cooler and more humid than their pyrophytic counterparts, leading to lower flammability (Kreye et al. 2018; Babl et al. 2020; Alexander et al. 2021).

The primary objective of this study was to determine whether leaf litter and fine woody debris traits interact with overstory traits to impact fuel drying rates. To address this objective, we examined the moisture dynamics within leaf litter and fine woody debris of pyrophytic and mesophytic individuals across diverse crown conditions in a longleaf pine-oak woodland in southwestern Georgia, USA, which has been subject to regular, low-intensity surface fires for over a century to restore this site to its historical open forest structure and composition. Despite this restoration effort, numerous mesophytic oaks, such as water oak (*Quercus nigra* L.) and live oak (*Quercus virginiana* Mill), persist in the ecosystem, contributing to increased mesophytic recruitment and posing challenges to fire management. We hypothesized that fuel moisture loss in pyrophytic pines and pyrophytic oaks would be fastest due to traits that promote either lower moisture absorption (e.g., low specific leaf area or SA:V and high woody density) or faster drying (e.g., high SA:V and low wood density) (Hoffmann and Solbrig 2003; Lawes et al. 2011), and more open crowns compared to mesophytic oaks (Battaglia et al. 2003). In contrast, we expected that mesophytic leaf litter and woody debris would exhibit slower drying rates due to traits which promote moisture retention (Schwilk and Caprio 2011; Cornwell et al. 2015). Additionally, we expected mesophytes to have more crown area, and thus, cooler, more humid understory conditions (Nowacki and Abrams 2008; Kreye et al. 2013), contributing to less pronounced daily variations in understory vapor pressure deficit (VPD) and slower fuel drying rates. Knowing the relationship between fuel traits, understory microclimate, and fuel moisture prior to and during prescribed burns can lead to better predictions of fire behavior and effects and contribute to planning and the achievement of management objectives with prescribed fire (Kreye et al. 2014).

Methods

Study area

This study was conducted at the Jones Center at Ichauway (31.2201°, − 84.4792°), in southwest Georgia, USA, which is comprised of 11,740 ha of woodland dominated by longleaf pine (*Pinus palustris* L.) (Holland et al. 2019) with a wiregrass (*Aristida stricta* Michx.) understory (Gaya et al. 2023), but also containing a mixture of both mesophytic (*Quercus virginiana* Mill., *Quercus laurifolia* Michx.) and pyrophytic (*Quercus margaretta* Ashe, *Quercus laevis* Walt., *Quercus falcata* Michx.) oaks. Thus, the site is well-suited for testing hypotheses related to mechanisms of mesophication. With some interruptions, the property has been managed with prescribed fire since the 1920s, with fires in recent decades typically occurring during the late dormant season and early growing season (Rutledge and McIntyre 2022). Soils at the site are sandy acidic, including Entisols and deep Utisols (Jacqmain et al. 1999). Classified as a humid, subtropical area, annual temperatures at the site range from − 10 to 39 °C (Golladay et al. 2021), with average daily temperature of 27 °C between May and August and 11 °C between November and February (Gaya et al. 2023), and 1310 mm of precipitation throughout the year (Golladay et al. 2021).

Experimental design

We focused our research within an ~ 120 ha burn unit (last burned in 2021) dominated by longleaf pine but containing numerous overstory (> 20 cm diameter at breast height (DBH)) pyrophytic and mesophytic oaks. Within this unit, we established five blocks, each containing one tree from each of three overstory functional groups based on shade and/or fire tolerance: pyrophytic pine (shade-intolerant, fire-tolerant), pyrophytic oak (shade-intolerant, fire-tolerant), and mesophytic oak (shade-tolerant, fire-intolerant) (Table 1), along with one "gap" area devoid of tree cover (28-m^2 area open circular plots) for comparison. Individual species selected for each functional group varied slightly depending on availability within each block (Table 1). Individual trees within blocks ranged from 20 to 30 cm DBH, and all trees were > 10 m from a road or trail, > 5 m from another tree, and without crown overlap with other trees.

Fuel moisture measurements

To understand the moisture dynamics of leaf litter and 10-h woody fuels beneath overstory trees of pyrophytic pines, pyrophytic oaks, and mesophytic oaks, we implemented a fuel bed drying experiment. The experiment was performed over 5 days during June 2022, with one block sampled each day. Over these 5 days, there was minimal cloud cover (fair to partly cloudy). The air temperature ranged from 16 to 44 °C, and relative humidity ranged from 22 to 100%.

During summer 2022, immediately outside the study site, we collected leaf litter and 10-h woody fuel of the observed dominant species: longleaf pine, sand post oak, and laurel oak to represent pyrophytic pines, pyrophytic oaks, and mesophytic oaks, respectively. We collected leaf litter by hand from the forest floor, gathering leaves with no sign of decomposition. For woody fuel, we collected live branches representing 10-h fuels (diameter between 0.6 and 2.3 cm), which is a common diameter size of woody debris observed beneath all functional groups. We collected the woody material using clippers from trees of each functional group to avoid decomposition impacts on findings and to standardize material used.

We followed methods by Kreye et al. (2013) and McDaniel et al. (2021) to hydrate collected fuels. Briefly, we dried leaf litter and woody fuels in an oven for 48 h at 60 °C. After drying the materials, we weighed 15 g of leaf litter and 50 g of woody debris (Fig. 1B) and carefully placed them in separate, labeled mesh bags (30 cm × 30 cm), which were constructed of charcoal fiberglass screen with a mesh size of ~ 1 mm. The bags were immersed in water for 24 h then drained for 1 h. After draining, materials within the bag were removed, reweighed (Fig. 1C and D), and returned to the bag to avoid fuel compression. Bags were placed in each plot as shown in Fig. 1D. We placed the 60 labeled bags beneath each tree on top of the leaf litter-duff interface — 30 bags to the north and 30 bags to the south — stratified from the bole to the edge of the crown. On each day, the bags were deployed at 0700 and retrieved at 2-h intervals ending at 1700. At each 2-h interval, we randomly withdrew one bag of each leaf litter and fine woody functional group on each side of the tree for reweighing.

To understand fuel moisture loss among overstory and litter functional groups, we used a time lag concept model (Byram 1963). The model describes fuel moisture response by calculating relative moisture content (%), defined as the portion of moisture that remains evaporable at a particular moment during the desorption process

Table 1 Tree species chosen for fuel bed drying experiment in a pine-oak woodland, Newton, Georgia, USA, by scientific and common name, number of individuals, shade tolerance, fire tolerance, and functional group

Overstory functional group and tree species	Common name	Number of individuals	Shade tolerance	Fire tolerance
Pyrophytic pine				
Pinus palustris L	Longleaf pine	5	Intolerant[1]	Tolerant[3]
Pyrophytic oak				
Quercus laevis Walt	Turkey oak	1	Intolerant[2]	Tolerant[4]
Quercus margaretta Ashe	Sand post oak	4	Intolerant[2]	Tolerant[5]
Mesophytic oak				
Quercus laurifolia Michx	Laurel oak	4	Tolerant[2]	Intolerant[2]
Quercus incana Roxb	Bluejack	1	Tolerant [2]	Tolerant[1]

Note: Loudermilk et al. (2011)[1], Burns and Honkala (1990)[2], McCune (1988)[3], Carey (1992)[4], Hannon et al. (2020)[5]

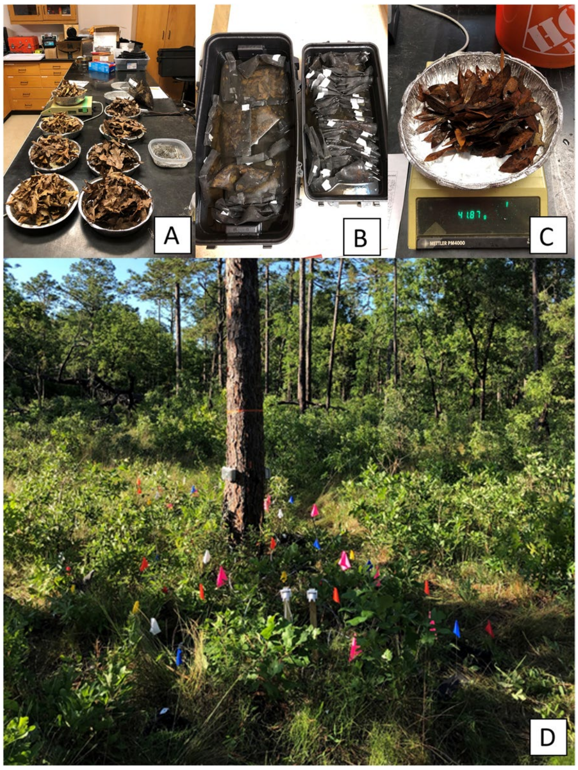

Fig. 1 **A** Oven-dried leaf litter and woody debris were weighed. **B** Water-saturated fuels were placed in mesh bags, drained, and **C** weighed before **D** placing underneath each tree or in a gap

and calculated by the following equations (Kreye et al. 2012, 2013; McDaniel et al. 2021):

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

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

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

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 a combination of physical and chemical processes 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 a 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, where $\frac{d}{dt}$ represents the derivative of the natural logarithm of relative moisture content.

$$\frac{d}{dt}(\ln E_t) = \frac{-1}{\tau} \tag{3}$$

Crown traits

We determined the crown area (m^2) and volume (m^3) for each tree by using a laser rangefinder (LaserTech, TruPulse® 360°R) to measure the crown diameter along the major and minor axes, extending across the dripline. Additionally, we assessed crown length, which represents the length from the top to the bottom of the crown. We calculated crown volume as the volume of an elliptical cylinder:

$$V = \pi \times R_1 \times R_2 \times length \tag{4}$$

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 *length* is crown length (m). To calculate canopy cover percentage beneath each tree, we used a spherical densiometer, averaging measurements taken at four mid-crown locations located in the four cardinal directions facing away from the tree bole.

Microclimate measurements

To better understand the relationship between moisture loss with air temperature and relative humidity beneath different overstory functional groups, we measured microclimate conditions during fuel drying experiments using two microclimate stations placed beneath each tree and in the center of a gap. We measured air temperature and relative humidity using an 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 linked to an open access datalogging system (Cannon et al. 2022). We placed sensors 100 cm above herbaceous vegetation in the north and south directions of the tree under the mid crown and 3 m from mid-point for gap areas and recorded temperature and relative humidity every 15 min throughout the experiment (from 0700 to 1800 each day).

To understand how overstory functional groups and gaps influence microclimate conditions, we calculated vapor pressure deficit (VPD). VPD can explain variance in flammability and fuel moisture content more effectively than the individual variables that comprise it like temperature and relative humidity (Castellví et al. 1996; Pechony and Shindell 2009; Seager et al. 2015). We calculated understory VPD (kPa) using the following equation (Bonan 2015):

$$VPD = (100 - RH) \times (610.7 \times 10^{\frac{7.5T}{237.3+T}}) \quad (5)$$

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 kPa, and 237.3 is a constant to convert Celsius to Kelvin.

Fuel traits

To test the hypothesis that leaf traits differ among functional groups, we used the methods in McDaniel et al. (2021), using 50 samples each of leaf litter and 10-h fuels from three species (longleaf pine, sand post oak, and laurel oak), one from each functional group, as described above for the moisture experiment. For longleaf pine, a leaf was considered the three needles attached to the fascicle. We oven dried samples for 48 h at 60 °C. For leaf litter, we measured leaf perimeter and surface area of each leaf using a high-resolution optical scanner and image measurement software (Image J, version 1.53t) (McDaniel et al. 2021). As a proxy for leaf curling, we measured leaf height at the highest 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 0.10 mm in two ways depending on the species. For longleaf pine, we measured the three individual needles in the middle and calculated an average, and for oaks, we cut the leaves in half from base to apex and measured the thickness of the midvein and margin and averaged them (McDaniel et al. 2021). To obtain the specific leaf area (SLA), we divided the one-sided surface area obtained by the scan by oven-dry leaf mass. For leaf volume, we multiplied the one-sided surface area by its thickness. For surface area (SA) to volume (V) ratio, we divided the total surface area by volume. Total surface area was calculated by multiplying the one-sided surface area by two to obtain double-sided (i.e., total) surface area for the oaks and by 3.14 (i.e., pi) for the pines (Grace 1987).

For woody debris, we measured wood density using dry mass and volume. We weighed the oven-dried mass to the nearest 0.01 g and measured the length and diameter at the middle of each woody debris piece to the nearest 1 mm. To determine the volume of woody debris, we used the following equation:

$$V = \pi R^2 \times L \quad (6)$$

where V is the volume (cm^3), R is the radius (cm), and L is the length of the woody material (cm). We calculated density as:

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

where D is density of the material ($g\ cm^{-3}$), M is the oven-dried mass (g), and V is volume calculated as above. For SA:V of woody material, we used the following formulas:

$$SA = 2\pi R \times L^2 + 2\pi R \times L \quad (8)$$

$$SA : V = \frac{SA}{V} \quad (9)$$

where *SA* is surface area, *R* is radius of the woody material, and *SA:V* is surface volume area ratio of the woody material.

Statistical analysis

We performed all statistical analyses using R-4.2.2 (R Core Team, 2022). We visually inspected the residuals of the models to assess for homogeneity and normality. When assumptions were violated, we used a log transformation on the response variable, but present means and standard errors as back-transformed values. We used linear mixed-effect models to assess differences in initial moisture content, drying response time, and VPD among functional groups, with experimental block and date included as random effects. We modeled initial moisture content and drying response time as a function of overstory functional group, and leaf litter/woody debris functional group, and their interaction as predictor variables. To examine the impact of overstory functional group and hour of the day on VPD, average VPD (average of four measurements taken at 15-min intervals during a 1-h period, either 0900–1000, 1100–1200, 1300–1400, 1500–1600, or 1700–1800, then averaged over the 5-day sampling period) was the response variable and overstory functional group, hour of the day, and their interaction were the predictor variables. An ANOVA was utilized to examine differences in each crown, leaf litter, or woody debris trait among functional groups. For significant results ($P < 0.05$), we conducted post hoc Tukey's honest significant difference tests to evaluate individual differences.

Results

Fuel moisture

Initial moisture content and drying rates differed among leaf litter and overstory functional groups, but we found no significant interaction between leaf litter functional group and overstory functional group ($P = 0.555$). 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%) ($P \leq 0.001$) (Fig. 2A). Drying response times differed among leaf litter functional groups, with pyrophytic pine

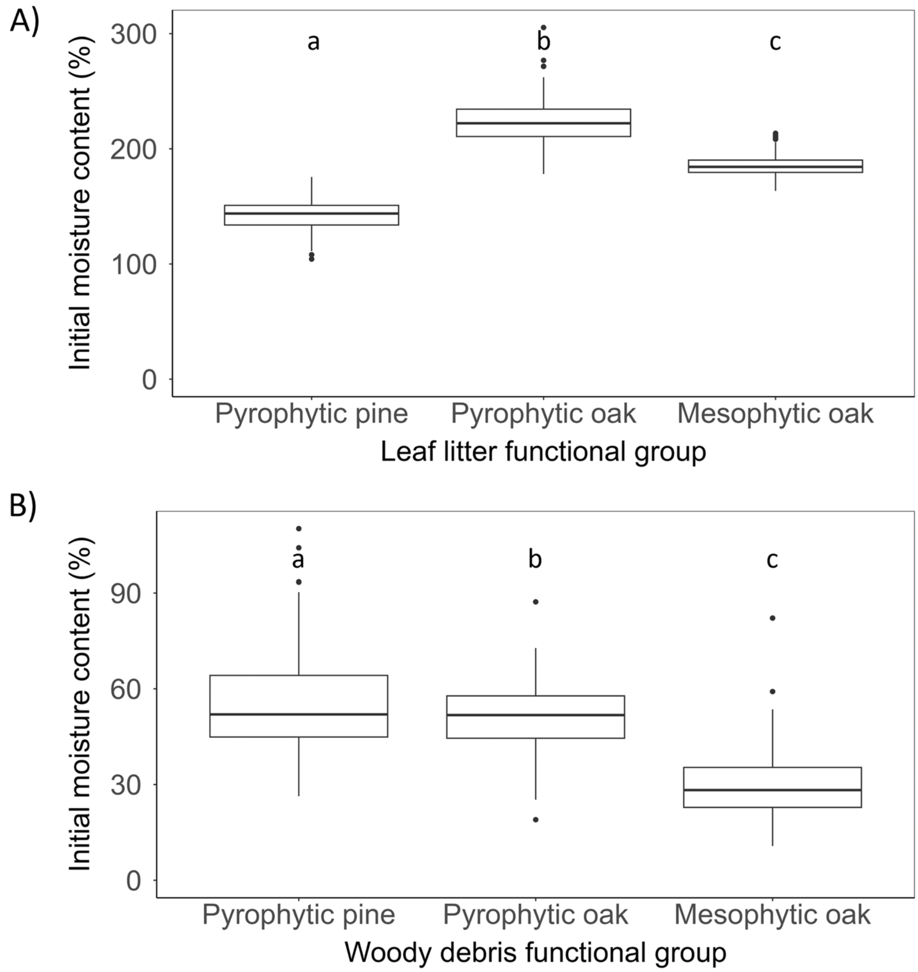

Fig. 2 Initial moisture content (%) across leaf litter (**A**) and 10-h woody debris (**B**) functional group (pyrophytic pine, mesophytic oak, and pyrophytic oak). Letters denote significant differences ($P \leq 0.05$) as determined by post hoc Tukey's honest significant difference test

litter having 1.8 times faster response times than mesophytic oaks ($P \leq 0.001$) (Fig. 3A). Drying response time also varied among leaf litter placed beneath different overstory functional groups ($P \leq 0.001$). Leaf litter within gaps dried the fastest, 2.2 times faster than litter beneath mesophytic oaks (Fig. 3B).

Differences in woody debris moisture dynamics depended on differences in initial moisture content and overstory functional group, but response time did not differ with the identity of woody debris species ($P = 0.737$) (Fig. 3C) or their interaction ($P = 0.886$). Woody debris from 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%) ($P \leq 0.001$) (Fig. 2B). Response time differed among woody debris placed beneath different overstory functional groups ($P = 0.005$) (Fig. 3D). Woody debris in gaps had the fastest drying response times followed by those placed under pyrophytic pines, pyrophytic oaks, and mesophytic oaks. Woody debris beneath mesophytic oaks dried 1.3 times slower than beneath pyrophytic pines, but the result was not statistically different ($P = 0.254$).

Overstory functional groups differed in crown area and canopy cover, while crown volume remained consistent across these groups (Table 2). Specifically, pyrophytic pines exhibited the smallest crown area, followed by pyrophytic and mesophytic oaks ($P = 0.033$). A similar pattern was found for canopy cover ($P \leq 0.001$), with mesophytic oaks displaying the greatest cover (78.1%). There were no statistically significant differences in crown volume among the functional groups ($P = 0.157$).

Overstory functional group and time of day interacted to influence VPD ($P = 0.004$). Overall, VPD increased during the day until 1500 and decreased at 1700. VPD was generally similar among groups at 0900, 1100, and 1700, where pyrophytic oaks were the only functional group statistically different from the other overstory

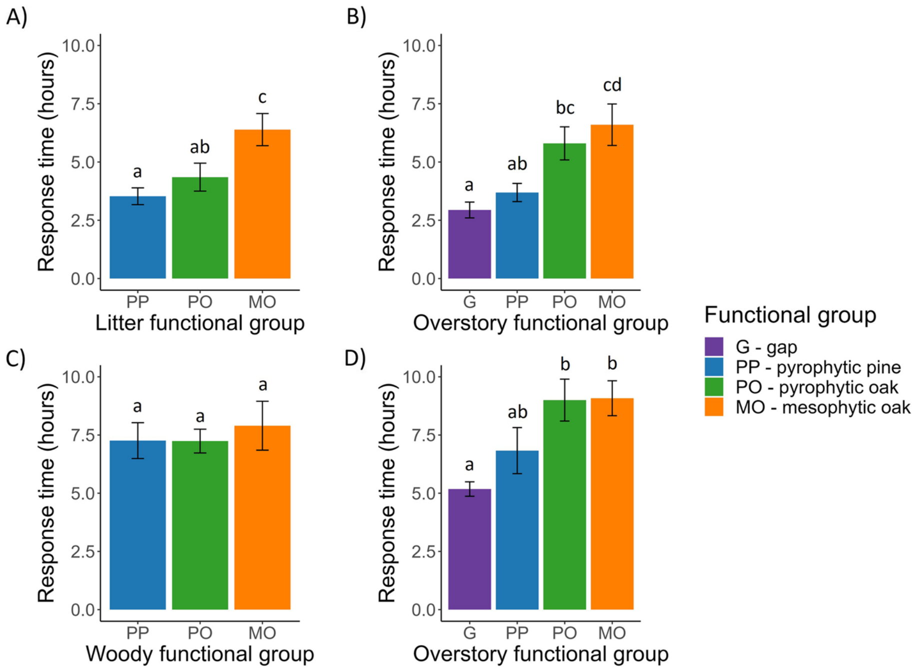

Fig. 3 Drying response time (mean (± SE)) of **A** leaf litter functional groups; **B** leaf litter beneath different overstory functional groups; **C** 10-h woody debris functional groups; **D** 10-h woody debris beneath different overstory functional groups. Letters denote significant differences ($P \leq 0.05$) as determined by post hoc Tukey's honest significant difference test

Table 2 Mean crown area, crown volume, and canopy cover beneath pyrophytic pine, pyrophytic oak, and mesophytic oak trees ($n = 5$/functional group) in a pine-oak woodland, Newton, Georgia, USA. Values in parentheses are standard errors of the mean. Values with different letters are significantly different ($P \leq 0.05$) among overstory functional groups as determined by a post hoc Tukey's honest significant difference test

Crown trait	Overstory functional group			*P* value
	Pyrophytic pine	Pyrophytic oak	Mesophytic oak	
Crown area (m^2)	28.0 (6.5)[a]	44.3 (11.0)[ab]	66.4 (8.8)[bc]	0.033
Crown volume (m^3)	62.7 (11.8)	64.8 (11.2)	104.0 (22.2)	0.157
Canopy cover (%)	28.0 (3.7)[a]	40.0 (6.3)[ab]	78.1 (9.2)[c]	≤ 0.001

functional groups ($P \leq 0.05$). VPD diverged between 1300 and 1500, with highest values in gaps and beneath pyrophytic pines compared to beneath pyrophytic oaks and mesophytic oaks (Fig. 4). At 1300, all functional groups were statistically different, with the exception of pyrophytic oak and mesophytic oak ($P = 0.933$). At 1500, gaps and beneath pyrophytic pines had higher VPD ($P = 0.998$), compared to pyrophytic oaks and mesophytic oaks ($P = 0.483$).

Pyrophytic pines, pyrophytic oaks, and mesophytic oaks differed significantly among leaf litter and woody fuel traits ($P \leq 0.001$ for all comparisons) (Table 3). Pyrophytic pines had the longest perimeter, with 5.0 and 10.3 times higher mean than pyrophytic oak and mesophytic oak, respectively. Pyrophytic oaks had the highest curl ($P \leq 0.001$), and pyrophytic pines and mesophytic oaks were similar ($P = 0.054$). Pyrophytic pines were 2.3 and 1.9 times thicker than mesophytic and pyrophytic oaks, respectively ($P \leq 0.001$). Pyrophytic pines had the lowest SLA ($P \leq 0.001$), but pyrophytic oaks and mesophytic oaks were not significantly different from each other ($P = 0.163$). Pyrophytic oaks had the highest volume, with 2.9 and 1.5 times larger volume than mesophytic oaks and pyrophytic pines, respectively ($P \leq 0.001$). Mesophytic oaks had the highest leaf SA:V ratio ($P \leq 0.001$), presenting 2.32 and 1.1 higher mean than pyrophytic pine and pyrophytic oak, respectively. For density of woody debris, all functional groups were significantly different from each other

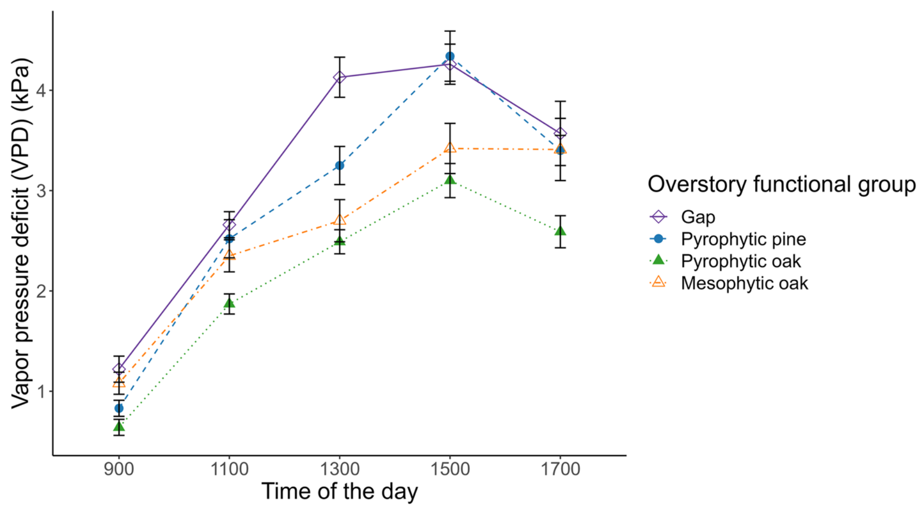

Fig. 4 Vapor pressure deficit (kPa) (mean (± SE)) throughout the day beneath different overstory functional groups (gap, pyrophytic pine, pyrophytic oak, and mesophytic oak)

Table 3 Leaf traits (perimeter, curl, thickness, specific leaf area (SLA), volume, surface area, and surface area to volume ratio (SA:V)) and 10-h woody debris density, SA:V, and diameter of different functional groups (pyrophytic pine, pyrophytic oak, mesophytic oak). Values in parentheses are standard errors of the mean. Values with different letters are significantly different ($P \leq 0.05$) among functional groups as determined by Tukey's honest significant difference test

Fuel traits	Pyrophytic pine	Pyrophytic oak	Mesophytic oak	*P* value
Leaf perimeter (cm)	176.67 (3.02)[a]	33.39 (1.33)[b]	17.14 (0.41)[c]	≤ 0.001
Leaf curl (cm)	0.79 (0.05)[a]	1.36 (0.09)[b]	0.52 (0.06)[a]	≤ 0.001
Leaf thickness (mm)	0.62 (0.01)[a]	0.32 (0.007)[b]	0.27 (0.007)[c]	≤ 0.001
Leaf SLA ($cm^2 g^{-1}$)	30.79 (0.68)[a]	95.14 (4.95)[b]	108.76 (7.61)[b]	≤ 0.001
Leaf surface area (cm^2)	9.46 (0.20)[a]	26.69 (1.81)[b]	10.65 (0.45)[a]	≤ 0.001
Leaf volume (cm^3)	0.59 (0.02)[a]	0.87 (0.07)[b]	0.30 (0.02)[c]	≤ 0.001
Leaf SA:V ($cm^2 cm^{-3}$)	51.7 (1.0)[a]	65.1 (1.6)[b]	76.5 (2.0)[c]	≤ 0.001
Wood density ($g cm^{-3}$)	0.59 (0.01)[a]	0.81 (0.02)[b]	0.95 (0.02)[c]	≤ 0.001
Wood SA:V ($cm^2 cm^{-3}$)	2.14 (0.00)[a]	2.09 (0.00)[b]	2.08 (0.00)[b]	≤ 0.001
Wood diameter (cm)	1.38 (0.03)[a]	1.25 (0.05)[a]	0.93 (0.05)[b]	≤ 0.001

($P \leq 0.001$). Mesophytic oaks had the highest wood density, being 1.5 times and 1.2 times denser than pyrophytic pines and pyrophytic oaks, respectively ($P \leq 0.001$). For woody SA:V ratio, pyrophytic pines had the highest mean compared to pyrophytic oaks and mesophytic oaks ($P \leq 0.001$).

Discussion

This work supports the hypothesis that the functional group identity of both leaf litter/woody debris and overstory trees influences fuel drying rates. Studies often categorize maples (*Acer* spp.), sweetgum (*Liquidambar styraciflua* L.), white oak (*Quercus alba* L.), shortleaf pine (*Pinus echinata* Mill), etc., across a mesophytic and pyrophytic spectrum (Kreye et al. 2013; Babl et al. 2020; McDaniel et al. 2021; Varner et al. 2015). Our results classify species not often studied in fuel moisture experiments (*Quercus margaretta* and *Quercus laurifolia*) into this commonly used framework. As expected, functional group determined the initial moisture content of leaf litter, leaf litter drying time, and several leaf litter traits. Pyrophytic pines had the lowest initial moisture content with the fastest drying rates, and although pyrophytic oaks had the highest initial moisture content, they dried faster than the mesophytic oaks. The relatively slow drying rates of mesophytic litter were similar to those of other mesophytes described in previous studies, including American beech (*Fagus grandifolia*) and winged elm (*Ulmus alata*) (Kreye et al. 2018; McDaniel et al. 2021). These trends can be related to leaf curl and SLA, which differed among leaf 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 lower curl and higher SLA of mesophytic oaks likely create a compact, less ventilated fuel bed that hampers moisture loss and flammability (Schwilk and Caprio 2011; Cornwell et al. 2015; McDaniel et al. 2021). However, there is a possibility that additional traits, not included in this study, may have influenced fuel drying characteristics. Just as leaf litter chemistry can impact flammability (e.g., lignin, %C, %N, lignin:N, and C:N ratios) (Babl-Plauche et al. 2022), chemistry could similarly play a role in moisture adsorption/absorption and retention (Berry and Roderick 2005; Alam et al. 2020).

Although most research focuses on flammability traits that differ among mesophytic and pyrophytic leaf litter, our findings also suggest that woody debris wetting and drying characteristics differ among functional groups. We found that the initial moisture content of 10-h woody debris of pyrophytic species was higher than that of mesophytic oaks. The lower density (Anderson 1970, Costa and Sandberg 2004, Van Altena et al. 2012) and higher SA:V ratio of pyrophytic woody debris may allow these fuel components to absorb more moisture but with faster drying rates (Pulido-Novicio et al. 2001; Zhang and You 2013), especially beneath the more open crowns of these species, thereby creating a flammable fuel bed compared to mesophytic oaks. However, we did not find statistical differences between woody debris functional groups and drying response time. This could be due in part to our use of newly clipped branches. To control fuel particle size, we dried live material with no decay, which can alter fuel drying properties (Zhao et al. 2018). Compared to older branches, newer branches have lower surface area relative to their mass (Sullivan et al. 2018), which could affect moisture absorption and retention. Nonetheless, we found small differences, where mesophytic oaks had a 10% faster drying response time compared to pyrophytic pines and pyrophytic oaks. Woody debris from pyrophytic species could absorb more water after a rain due to their lower density, which could hinder fuel bed flammability, due to higher energy to heat-up before ignition and lower flaming temperature (Babrauskas 2006; Hyde et al. 2011), but the impact would be temporary, as they would dry faster than mesophytic oaks. Stage of decay is also likely important for influencing moisture retention, and thus, flammability. As wood decays, density tends to decline (Mori et al. 2014), but rates of decay likely vary between understories of mesophytes and pyrophytes due to differences in microclimatic conditions (Eldhuset et al. 2017), such as those found here. Wood may decompose faster in the cooler, moister conditions found beneath mesophytes compared to pyrophytes, which may lead to a higher abundance of woody fuels of lower density, but lower VPD beneath the crown might offset faster moisture losses typically associated with lower wood density. In contrast, low density woody fuels beneath pine may decay slower due to the drier understory conditions, but their initially lower wood density combined with higher VPD would render these fuels more susceptible to ignition, and consequently, more prone to burning (Freschet et al. 2012; Fraver et al. 2013). These insights contribute to a more comprehensive understanding of how woody debris characteristics could impact moisture absorption and drying rates.

Notably, we found that fuel moisture dynamics were determined not just by the innate characteristics of the fuels themselves, but also by the overstory under which they occurred. Crown area and canopy cover play a crucial role in influencing light penetration to the forest floor, relative humidity in the understory, and surface fuel temperature (Viney 1991; Matthews 2014; Pickering et al. 2021). This, in turn, has a significant impact on VPD and subsequent moisture loss. Pyrophytic and mesophytic oaks had the highest crown area and canopy cover. This can be attributed to their higher leaf area, which results in reduced light incidence beneath them (Canham et al. 1994; Alexander and Arthur 2010; Babl et al. 2020). These factors could have influenced our VPD results, particularly at 1300 and 1500, which coincided with the peak light incidence of the day and the common timing for prescribed burns. The combination of a higher crown cover, reduced light, and increased humidity beneath oaks during these times may have led to reduced fuel moisture loss beneath pyrophytic and mesophytic oaks (Siegert and Levia 2011; Kreye et al. 2018). The distinctive crown area and cover, light incidence created by leaf characteristics of pyrophytic pines, pyrophytic oaks, and mesophytic oaks, potentially played a key role in VPD outcomes, particularly during peak light exposure fuel moisture loss. These findings imply that fuel drying dynamics are spatially complex, corresponding to microclimate conditions created by trees, and the fuel dispersal from trees. Considering spatially complex patterns can contribute understanding highly variable fire behavior where fuels and tree patterns vary (Blaydes et al. 2023).

The current study has its own set of limitations that need consideration. In this study, we focused on a limited number of species for classification along the mesophyte to pyrophyte spectrum (longleaf pine, turkey oak, sand post oak, laurel oak, bluejack). However, it is crucial to note that trends may vary based on the selected species (Burton et al. 2021; Popović et al. 2021), leading to variations in crown and fuel traits, which in turn influence fuel moisture retention and loss (Varner et al. 2015; Kreye et al. 2013). Additionally, we acknowledge that results may vary in different types of forests. The study site, with over 100 years of frequent fire history (Rutledge and McIntyre 2022), exhibits a blend of pyrophytic and mesophytic species, and an open canopy structure dominated by longleaf pine (Holland et al. 2019) and wiregrass (Gaya et al. 2023). This setting differs from sites with long-term fire exclusion that have a closed-canopy structure (Peterson and Reich 2008; Hanberry et al. 2020). Such variations could have diverse effects on shade conditions beneath trees, particularly with a dense midstory (Hanberry et al. 2018). Furthermore, in fire-excluded forests, there tends to be a greater density of smaller-diameter mesophytes compared to larger mesophytes, such as those studied here (Hanberry et al. 2018). Our study focused on mature trees with a diameter > 20 cm DBH, spaced at least 5 m apart from other trees. Smaller diameter mesophytic trees may differ from overstory mesophytes in terms of understory, structure, and fuel type and their effects in fuel moisture. Future studies should consider a broader range of species and tree sizes in different forest structures to determine fuel dynamics and their role in fuel moisture.

Conclusion

Crowns of mesophytic oaks compared to those of pyrophytic longleaf pine and oaks reduce solar irradiance in the understory, decrease VPD, and decrease the drying response time of leaf litter and fine woody debris fuels (Canham et al. 1994; Biddulph and Kellman 1998; Tanskanen et al. 2006). Depending on functional group identity, both leaf litter and woody debris dried in distinctive patterns, potentially due to their morphological characteristics. The slower moisture loss in mesophytic leaf litter could decrease flammability and reinforce mesophyte encroachment. The higher initial moisture content and faster rate of moisture loss in 10-h woody debris fuels of pyrophytic pines and oaks compared to mesophytic oaks were likely due to increased air exposure because of their lower wood density (Costa and Sandberg 2004, Shearman and Varner 2021) and higher wood SA:V ratio (Eckstein et al. 1979), traits that may influence flammability within mixed woodlands. However, similar to other studies using different species (Kreye et al. 2013; McDaniel et al. 2021), our study showed that pyrophytic species can lose moisture faster compared to mesophytic oaks, potentially increasing their flammability capacity throughout the day, which could help to determine optimal timing for prescribed burnings.

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 (He et al. 2019; Reilly et al. 2022). Therefore, this study aims to contribute to the future modeling and management of these previously open structure pyrophytic ecosystems. New high-resolution models of fire behavior and fuels are being used to make predictions about fire behavior and effects and inform management of fire-frequent systems (Linn et al. 2005, Blaydes et al. 2023, Sancez-Lopez et al. 2023). Understanding how tree composition, crown traits, fuel properties, and temporal dynamics affect fuel moisture loss can provide parameterization to represent spatially and temporarily dynamic fuel conditions. This research will facilitate more effective and assertive implementation of prescribed fires for improved management strategies of pine and mixed woodlands.

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Authors' contributions

LGL: conceptual framework, managed research data, formal analysis, investigation, methodological framework, writing: original draft, review, and editing. HDA: conceptual framework, managed research data, supervision, project administration, funding acquisition, investigation, methodological framework, writing: original draft, review, and editing. JBC: conceptual framework, managed research data, supervision, project administration, funding acquisition, investigation, methodological framework, writing: original draft, review, and editing. MJA: conceptual framework, methodological framework, writing: review and editing.

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Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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