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Cone and fruit impacts on understory flammability depend on traits and forest floor coverage

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Abstract

Background Understory flammability is affected by abscised plant tissue. Extensive research has shown how interspecific differences in leaf litter traits affect flammability; however, leaves represent only one component of the litter layer. Cones and fruit are also common constituents of the forest floor, yet surprisingly little is known about how flammability is affected by their presence. In this study, we ask how flammability is affected by cones and fruit trait differences, coverage differences, and varying species and coverage combinations. To address these questions, we compared cone and fruit morphological and chemical traits among longleaf pine, loblolly pine, shortleaf pine, sweetgum, post oak, and water oak. We also used burn trials to compare fire behavior of single and mixed-species treatments at three coverage levels (10% of plot area (low), 30% (medium), and 50% (high)) integrated within a common mixed-litter layer under field conditions in central Alabama, USA.

Results Like other plant tissues, cone/fruit dry matter, carbon, and lignin content promote fuel consumption and flame height, while nitrogen suppresses flammability. Single-species treatments produced distinct patterns in fire behavior, with longleaf pine cones consistently showing higher percent fuel consumption, flame height, and maximum smoldering temperature than sweetgum capsular heads. Mixed-species treatment results were less consistent; however, at high coverage, a representative upland three-way mixture (longleaf pine + sweetgum + post oak) showed significantly greater fuel consumption and flame height relative to a bottomland three-way mixture (loblolly pine + sweetgum + water oak) at high coverage. Medium cone/fruit coverage maximized flammability in most single and multi-species treatments and produced non-additive fuel consumption in mixtures containing longleaf pine and sweetgum.

Conclusion Our results confirm that individual species' cone and fruit flammability often parallels that of litter. Fire behavior in mixture is generally driven by the most flammable constituent species, but this result changes with cone and fruit coverage. Collectively, these results indicate that cones/fruit identity and coverage play an important role in understory flammability and should be integrated into fire behavior modeling efforts in monocultures and mixtures.

Keywords Fire behavior, Mesophication, Mixed fuelbeds, Southeastern forests, Longleaf pine

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Resumen

Antecedentes La inflamabilidad del sotobosque está afectada por los tejidos vegetales muertos que se desprenden de las plantas. Extensas Investigaciones mostraron cuánto las diferencias interespecíficas en las características de la broza de las hojas afectan la inflamabilidad; desde luego, las hojas solo representan un componente del mantillo o broza superficial. Los conos y frutos son también constituyentes del piso forestal, y aun así es sorprendentemente poco lo que se conoce sobre cómo la inflamabilidad es afectada por su presencia. En este estudio, nos preguntamos cómo la inflamabilidad es afectada por las diferentes características de conos y frutos, su cobertura, la variación entre especies y las combinaciones entre coberturas. Para responder a esas preguntas, comparamos las características químicas y morfológicas de conos y frutos entre pino de hoja larga, pino taeda, liquidámbar, roble encino, y roble de agua. Usamos también tratamientos de quema para comparar el comportamiento del fuego en tratamientos simples o mixtos en tres niveles de cobertura (10% del área de la parcela, bajo), 30%, (medio), y 50% (alto), integrados dentro de un estrato mixto de broza bajo condiciones de campo en el centro de Alabama, EEUU.

Resultados Como cualquier otro tejido vegetal, los conos/frutos, materia orgánica, carbono y contenido de lignina promueven el consumo de combustible y la longitud de llama, mientras que el nitrógeno suprime la inflamabilidad. Los tratamientos con una sola especie producen distintos patrones de comportamiento del fuego, con los conos del pino de hoja larga mostrando consistentemente un porcentaje más alto de consumo de combustible, de longitud de llama, y máximo calor latente que las cabezas de las cápsulas del liquidámbar. Los resultados de los tratamientos con especies mixtas fueron menos consistentes; desde luego, a coberturas altas, una mezcla representativa de las tres especies de altura (pino de hoja larga + liquidámbar + roble encino), mostró un consumo más significativo y longitud de llama más alto que las especies que crecen en tierras más bajas (pino taeda + liquidámbar + roble de agua) a altas coberturas. La cobertura media de conos y frutos maximizaron la inflamabilidad en la mayoría de los tratamientos de especies individuales y multi-especies, y produjeron el consumo de combustibles de manera no aditiva en mezclas que contenían pino de hoja larga y liquidámbar.

Conclusiones Nuestros resultados confirman que la inflamabilidad individual de conos y frutos de cada especie es frecuentemente similar a aquella de la broza. El comportamiento del fuego en mezclas es conducido generalmente por la especie constitutiva más inflamable, aunque estos resultados cambian con la cobertura de conos y frutos. Colectivamente, estos resultados indican que la identidad de conos/frutos y su cobertura juega un rol importante en la inflamabilidad del sotobosque y debe ser integrada en los esfuerzos del modelado del comportamiento del fuego en monoculturas y también en mezclas de especies.

Background

A primary way that trees affect their environment is through contributing abscised biomass to the forest floor. Abscessed leaves, bark, and fine woody debris provide organic material that supports nutrient cycling and influences understory flammability (Scarff and Westoby 2006; Hobbie 2015). Decaying coarse wood provides an important habitat for amphibians and reptiles (Owens et al. 2008) and favorable germination sites for light-seeded species (Marx and Walters 2008; Bolton and D'Amato 2011); dispersed seed is an important food resource for various vertebrate and invertebrate communities (Perkins and Conner 2004; Willis et al. 2021). However, the effects of organic material input can also be species-dependent, as interspecific differences in abscessed material quantity and quality can affect forest floor processes (Cornelissen et al. 2017; Lyu et al. 2019). Hence, changes in forest demographics can impact ecological function.

Forests throughout North America are undergoing structural and compositional changes (Nowacki and Abrams 2008; Alexander et al. 2021; Ducey et al. 2023). Prior to European settlement, much of the central and southeastern USA was maintained in an open structural condition by the regular occurrence of surface fire (Hanberry et al. 2020; Rother et al. 2020; Abrams et al. 2021; Rother et al. 2022). Forest composition was dominated by species such as longleaf pine (*Pinus palustris* Mill.), shortleaf pine (*P. echinata* L.), and upland oak (*Quercus* spp.) that are adapted to persist in a frequent, low-intensity surface fire regime (Frost 1993; Chapman et al. 2006; Hanberry et al. 2018). Moreover, these species helped promote fire reoccurrence through the combined effects of their open crowns and flammable litter (Mitchell et al. 2006; Sharma et al. 2012; Alexander et al. 2021). However, decades of fire exclusion enabled the encroachment of fire-sensitive species (e.g, sweetgum (*Liquidambar styraciflua* L.), loblolly pine (*P. taeda* L.), and water oak (Q. *nigra* L.)), transforming open bilayer woodlands into multi-layered, dense, closed canopy forests (i.e., mesophication) (Gilliam and Platt 1999; Surrette et al. 2008; Hanberry 2021). The structural transformation from woodland to closed-canopy forest has negatively affected understory flammability, as increased canopy cover reduces light penetration to the forest floor (Canham et al. 1999), constrains herbaceous fuel development (Brewer 2015), and promotes understory humidity and fine fuel moisture retention (Siegert and Levia 2011; Kreye et al. 2018; Scavotto et al. 2024).

In addition to the structural changes caused by fire exclusion, encroaching species contribute organic material to the fuelbed of degraded woodlands. Most studies examining encroachment from a flammability perspective have focused on the effect of encroaching species' litter on fuelbed dynamics (e.g., Varner et al. 2021). Encroaching species' litter generally decomposes faster than historically prevalent species such as oak (Alexander and Arthur 2014; Babl-Plauche et al. 2022). The leaves of encroaching species are also typically smaller, thinner, and less curly, than those of fire-adapted species and thus increase fuelbed bulk density (Dickinson et al. 2016; Grootemaat et al. 2017; Babl et al. 2020). Moreover, encroaching species' litter absorbs and holds moisture longer than fire-adapted species (Kreye et al. 2013a; McDaniel et al. 2021). Indeed, single-species burning experiments conducted in the laboratory or under field conditions have confirmed that encroaching species' litter is less flammable than that of upland oak or pine species (Kane et al. 2008; Mola et al. 2014; Dickinson et al. 2016; Kreye et al. 2018; McDaniel et al. 2021; Varner et al. 2021). Limited research into mixed species fuelbeds also indicates that flammability decreases as the proportion of encroaching species' litter increases (Kreye et al. 2018; McDaniel et al. 2021; Cabrera et al. 2023). However, certain species may disproportionately affect fire behavior creating non-additive mixture effects (i.e., flammability cannot be predicted by the average effects of the component species) (De Magalhães and Schwilk 2012; Blauw et al. 2015). While it is suspected that particle size influences non-additive fire effects (Zhao et al. 2016), much remains unknown about the mechanisms driving flammability in mixed fuelbeds.

Another understudied component of flammability is the contribution of abscessed cones and fruit. Traditional methods of estimating fuels aggregate litter, cones, and fruit together and consider the latter entities to be generic fuels (Brown 1982). In the lone study examining interspecific differences in cone flammability, Fonda and Varner (2004), under laboratory conditions, reported distinct differences in fire behavior among conifers with different life history strategies. Specifically, conifers adapted to resist fire produced greater maximum flame length, smoldered for longer, and were more fully combusted than species adapted to avoid fire. Similarly, Kreye et al. (2013a) reported that plots containing longleaf pine cones were far more likely to ignite the duff layer than plots lacking cones. However, no studies have examined interspecific differences in cone and fruit flammability under field conditions in mixed litter fuelbeds, at varying densities within mixed litter fuelbeds, or in mixed litter and fruit fuelbeds at varying densities. Furthermore, no studies have examined the burning characteristics of abscessed fruits of any upland oak or encroaching species under any conditions. While studies examining the flammability of cones and fruit are limited, certain functional traits have been consistently linked with increased flammability in other plant tissues. For example, leaf dry matter content improves all aspects of flammability (Cornelissen et al. 2003; Grootemaat et al. 2015; Alam et al. 2020). In contrast, lignin and nitrogen show weak or inconsistent effects on fire intensity and flaming duration. (Fernandes 2013; Alam et al. 2020). Thus, the flammability of cones and fruit may be linked to a broader life history strategy or may diverge as a function of morphological differences, which have been shown to have a stronger influence on certain flammability characteristics than chemical composition (Grootemaat et al. 2015).

To improve the existing body of knowledge on mixed species fuelbed flammability, we established an experiment examining the combined effects of cone/fruit type (pine cones, sweetgum capsular heads, and acorns (Fig. 1)) and coverage (10, 30, 50%), under different scenarios (single-species, two-species mixtures, three-species mixtures), when added to a standardized mixed-species litter bed. Specifically, we aimed to answer whether (1) cone/fruit chemistry and morphology differ among species; (2) cone/fruit chemistry and morphology influence flammability; (3) individual cones/fruits promote or inhibit flammability; (4) cone/fruit flammability changes with increasing coverage; and (5) mixing cones and fruit together at varying densities will produce

Fig. 1 From left to right, cones/fruits of longleaf pine, loblolly pine, shortleaf pine, sweetgum, water oak, and post oak

non-additive fire effects. We anticipate that (1) flammability will increase with cone/fruit dry mass and lignin content; (2) southern pine cones will be more flammable than sweetgum capsular heads or acorns; (3) flammability will increase consistently with cone/fruit coverage in single-species plots; and (4) non-additive fire behavior will occur in mixtures containing longleaf pine rather than loblolly pine. Answering these questions will improve our mechanistic understanding of understory flammability and will provide valuable data for fire modeling efforts.

Methods

Study site

This study occurred within a 2.1-ha management unit at the Mary Olive Thomas Demonstration Forest (MOTDF) in Auburn, Lee County, Alabama, USA (32.578 N, 85.423 W). The mean annual low temperature is 11.7 °C and the annual high temperature is 23.3 °C, with 1340 mm average annual precipitation (US Climate Data, weather station location 32.609, − 85.480; data from 1981 to 2010). Site elevation is approximately 206 m (Google Earth Pro Version 7.3). Soil types are primarily Pacolet sandy loam (49.3% at 1–6% slope; 47.5% at 6–10% slope) and Pacolet and Toccoa sandy loam (3.2%; 0–2% slope) (Soil Survey Staff, n.d.). Minimal topography exists on site.

Our research site was a naturally regenerated pine-oak mixture that has had no active management since the property was acquired by the Alabama Cooperative Extension System and Auburn University, College of Forestry, Wildlife and Environment in 1983. Prior to being acquired by the university, the site was high-graded in the 1970s. The canopy layer consisted of scattered large-diameter pines (*P. taeda*, *P. echinata*), upland oaks (*Q. alba* L., *Q. falcata* Ell.), and encroaching hardwoods (Q. *nigra*, *L. styraciflua*). Basal area averaged 14 m^2 ha^{-1} and was dominated by hardwood species (92%).

Experimental design

Our study examined 11 fuelbed treatments: seven treatments at three coverage levels, three treatments at one level, and a litter only control (Table 1). Plot coverages were 10% (0.4-m^2) (low), 30% (1.2-m^2) (medium), and 50% (2-m^2) (high) of the plot area (Fig. 2). Species-specific estimates of cone/fruit density within southeastern mixed stands are currently unknown, and likely variable over time due to the differing reproductive strategies of the constituent species. Thus, our experimental coverage levels serve as coarse points of comparison and are not directly linked to the fecundity of any species.

Acorn additions were based on previous estimates of ~ 100 acorns m^{-2} for white oaks (seedfall rates for the species studied here were not available) during a heavy seedfall year (Greenberg 2021). Species mixtures were designed to represent a common upland forest community (e.g., longleaf pine + sweetgum + post oak (*Q. stellata* Wangenh.) and bottomland forest community (e.g., loblolly pine + sweetgum + water oak). Each treatment was replicated three times (*n* = 74), except for the longleaf pine + sweetgum 50% treatment (*n* = 2) (Table 1) Material shortages of cones/fruits precluded testing all possible treatment combinations. We determined how many cones/fruits of each species were needed to create each treatment by first determining the average area of each cone/fruit type (based on a subsampling of 20

Table 1 The number of replicates for each single-species and mixed-species treatment at each coverage level

Fuel bed treatments	Number of replicates			
	0% coverage (control)	10% coverage (low)	30% coverage (medium)	50% coverage (high)
Single species				
Longleaf pine	0	3	3	3
Shortleaf pine	0	0	3	0
Loblolly pine	0	3	3	3
Post oak	0	3	0	0
Water oak	0	3	0	0
Sweetgum	0	3	3	3
Control	3	0	0	0
Mixed species				
Longleaf pine + sweetgum	0	3	3	2
Loblolly pine + sweetgum	0	3	3	3
Longleaf pine +sweetgum + post oak	0	3	3	3
Loblolly pine + sweetgum + water oak	0	3	3	3

Fig. 2 Images of single-species longleaf pine 50% (high) coverage plot pre-fire (**A**), during fire (**B**), and post-fire (**C**)

individuals of each species), then dividing the plot area to be covered by each species by its average cone/fruit area. This approach produced common levels of plot coverage, but resulted in varying initial mass among treatments due to interspecific differences in bulk density (Table S1). We opted for this approach because the cover can be more easily visually estimated in fuel measurement protocols compared to mass.

Beginning in winter 2023, we established 74 4-m^2 plots. All plots were located at least 5-m apart and separated by fire breaks to maintain independence. Prior to treatment additions, plots were cleared leaving only a thin organic layer (~ 1 cm thick). We then added 400 g each of air-dried longleaf pine needles, loblolly pine needles, water oak leaves, southern red oak (*Q. falcata*) leaves, and sweetgum leaves, to each plot (total of 2 kg air dry leaf litter plot^{-1}, or 500 g air dry leaf litter m^{-2}). This initial litter load was based on previous measurements of litterfall at sites in the region (Nation et al. 2021). Leaf litter composition was based on common pine-hardwood mixture combinations throughout the region. Sweetgum, southern red oak, and water oak leaves were obtained by collecting freshly senesced foliage in the winter of 2023 from local sources, while loblolly pine and longleaf pine straw were purchased from a local vendor (Southeast Straw, Opelika, Alabama). All litter was thoroughly mixed within the plot during application to create a representative mixedwoods fuelbed. Leaf litter was allowed to settle on plots for ~ 1 month before treatment application. Plots were then randomly assigned to a treatment. Each treatment was implemented by hand-dispersing the cones/fruits evenly across the plot on top of the baseline litter. Longleaf and shortleaf pine cones were collected from a Georgia Forestry Commission seed extractory facility (Cochran, Georgia). Loblolly pine cones and sweetgum capsular heads were obtained through a combination of local collection of freshly senesced material and purchase from the Louisiana Forest Seed Company (Lecompte, Louisiana). Post and water oak acorns were purchased from the Louisiana Forest Seed Company. Although some integration of organic material occurred, cones/fruit generally sat above the litter (Fig. 2). All cones and sweetgum capsular heads were added approximately 1-week prior to burning to equilibrate with ambient environmental conditions. Acorns were added on the day of burning to prevent granivory.

Experimental burns

Plots were burned on March 14, 15, and 16, 2023, starting at ~ 1100 and ending at ~ 1600. The Keetch-Byram Drought Index (KBDI) on the days of burn was ~115 (Fire Weather Intelligence Portal; https://products.climate.ncsu.edu/fwip/). The last days of precipitation prior to burning were March 11 and 12, when 2.59 cm fell (NOAA National Centers for Environmental Information Auburn, AL, USA station; https://www.ncei.noaa.gov/cdo-web/datasets/GHCND/locations/ZIP:36832/detail). Prior to burning each plot, we measured fire weather (ambient temperature, relative humidity, wind speed, wind direction) using a Kestrel 3000 pocket weather meter (Kestrel Instruments, Neilsen-Kellerman Company, Boothwyn, PA, USA).

Plots were ignited with a drip torch with a 3:2 diesel-to-gasoline fuel mix with the intention of starting a head fire. Wind conditions were light and occasionally variable throughout the 3-day burn window (Table S2).

A stopwatch was started upon ignition. The fire progressed until the flame self-extinguished or all fuel was consumed. During the burn, we visually estimated flame height every 30 s using a nearby meter stick for reference. For consistency, flame height was measured by the same person at each reading. We measured the rate of spread (ROS) as the time the flame front took to reach two distances within the plot (1 m and 2 m from the ignition point). Upon flame extinction, the total flame duration (time from ignition to complete flame extinction) was recorded.

Plots in which smoldering was measured were all burned on March 16th. We measured smoldering temperature at 2-min intervals for 10-min post-flame extinction with a FLIR E6-XT thermal imaging camera (FLIR Systems, Boston, MA, USA). Images were taken from a 4-m height on a ladder located approximately 3 m from the plot. The E6-XT records temperatures in 43,200 pixels per image (240 × 180 pixels) from a temperature range of − 20 °C to 550 °C ± 2 °C at a sensitivity of 0.06 °C. Thermal images were obtained at a frequency of 9 Hz. The E6-XT estimates temperatures from emitted radiation at wavelengths between 7.5 and 13 µm. All measurements were adjusted for air temperature, distance from plot, and relative humidity. Emissivity was set at 0.96 in all images. Due to logistical constraints, smoldering measurements were limited to longleaf pine, loblolly pine, shortleaf pine, and sweetgum in single-species fuelbeds at medium coverage.

To determine fuel consumption, we collected all residual leaf litter, cones, and fruit from the plots with shovels and placed it in garbage bags, transported the bags to our nearby laboratory, dried the residual fuel at 60 °C for 72 h, sieved the material through a 1-mm mesh to remove any dirt or ash, separated fuel by type (litter, pine cones, sweetgum capsular heads, acorns) and weighed each fuel type to the nearest gram to determine total residual fuel mass.

Fruit/cone morphology and chemistry

Morphological characteristics were determined on 12 randomly selected cones/fruits of each species obtained from the same populations used in the burn trials. Weight, moisture, and dry matter content were determined by taking an initial weight of the air-dried samples, drying at 60 °C for 72 h, and reweighing the samples. Volume calculations varied based on cone/fruit shape. Sweetgum, post oak, and water oak fruit volumes were calculated as a sphere. In contrast, longleaf, loblolly, and shortleaf pine cone volumes were calculated as a prolate spheroid. Bulk density was then calculated by dividing dry mass by volume. Percent lignin, carbon, and nitrogen were determined on three samples per species. Each sample contained seven randomly selected cones/fruits that were crushed and fully homogenized. Percent lignin was determined by digesting samples for 3 h in sulfuric acid (72%) at ambient temperature in an ANKOM Daisy Incubator (ANKOM Technology, Macedon, NY). Sample carbon and total nitrogen were determined through combustion using a CN928 Macro Determinator (LECO Corporation, Saint Joseph, MI). All chemical analyses were conducted at Dairy One Forage Testing Laboratory (Ithaca, NY).

Statistical analyses

Fire behavior models

To analyze the effect of within-coverage treatment on fire behavior variables, we used a series of linear mixed-effect models. Fire behavior response variables modeled included (1) percent of the fuel consumed, (2) flame height (cm), (3) ROS (m s^{-1}), and (4) total flaming time (s). Percent of fuel consumed was the oven-dried fuel mass (litter, cones, and fruit) in plots after burning (g) divided by the initial, oven-dried fuel mass applied to plots (g). Fixed effects included either single-species or mixed-species treatments (Table 1). The random effect was a variable that included date (March 14, 15, 16) and time of day (early (before noon), mid (12:01–2:30 PM), late (2:30–4:30 PM)) when the burns took place to control for between and within day variability. Control plots (leaf litter only) were included in all sets of models. Within a given coverage (low, medium, high), analyses were conducted separately within single-species treatments and mixed-species treatments. Thus, the analysis included a total of six linear mixed models for each fire behavior variable. Data were log-transformed as needed to meet statistical assumptions as determined by visual assumption of diagnostic plots generated using the check_model function in the performance package in R (Lüdecke et al. 2021), and Levene's test for homogeneity of variance. Models were fit using the lme4 package in R (Bates et al. 2015). The significance of pairwise estimated marginal means comparisons was determined using a Kenward-Roger degrees-of-freedom method and a Tukey multiplicity adjustment in the emmeans R package (Length 2023).

Principal component analysis

Principal component analysis (PCA) was used to understand the combined effects of treatment on several fire behavior characteristics. PCAs were conducted within coverage levels and independently for single-species and mixed-species treatments, resulting in six PCAs. Fire behavior variables included were those listed in the *fire behavior models* methods. Data were centered and scaled such that the mean of each variable was 0 with a standard deviation of 1. Singular value decomposition of centered and scaled data matrix was used to compute PCAs with the prcomp R function. The package factoextra was used to extract variable contributions to PCs and loading values (Kassambara and Mundt 2022). PCA biplots were visualized using the ggbiplot R package (Vu 2011).

Morphological and chemical traits

One-way ANOVAs with Tukey Honest Significant Differences tests were used to determine differences in mean cone/fruit traits among species. Plot fire behavior characteristics including percent consumption and flame height were regressed against species dry matter content (g), as well as percent lignin, nitrogen, and carbon across all coverages. Flame height was log-transformed to meet statistical assumptions of linear models.

Additivity

We assessed non-additivity in eight mixed-species treatments, including six two-species mixtures and two three-species mixtures (Table 3). Species mixtures for which we did not have individual species plots at the same coverage were omitted, as we were not able to calculate an expected flammability for those treatments. We compared the observed fuel consumption values of mixed-species treatments to expected consumption values based on the performance of each constituent species in single- species plots. Expected consumption was first calculated without any weighting adjustment using the following formula:

Expected fuel consumption = [observed fuel consumption of fuel A + observed fuel consumption of fuel B]/2

We then calculated a weight-adjusted expected consumption value to correct for initial mass differences between the constituent species in mixture using the following formula:

Expected fuel consumption = [mass fraction of fuel A * consumption of fuel A] + [mass fraction of fuel B * consumption of fuel B]

Effect sizes were then calculated using the following formula (Zhao et al. 2019):

[observed % consumption − expected % consumption]/ expected % consumption

T-tests were used to detect differences in mean observed % consumption and expected % consumption, both unweighted and mass-weighted.

Smoldering

To understand the effect of species differences on smoldering temperature over time, a linear mixed effects model was fitted with maximum temperature (°C) as the response variable modeled as a function of fixed effects (species, time, and their interaction), with plot as a random effect. A Kenward-Roger degrees-of-freedom method with a Tukey method of *p*-value adjustment for comparing a family of four estimates was used for pairwise comparisons of estimated marginal means at each time using the emmeans package (Length 2023).

Results

Morphological (air dry weight, volume, bulk density) and chemical/moisture (% dry matter, % moisture, % lignin, % nitrogen (N), % carbon (C), and C:N ratio) traits differed consistently among certain species (Table 2). Longleaf pine cones had a significantly higher dry weight, volume, and C:N ratio than all other cones/fruits; however, its cones contained less lignin than any other pine species. Acorns consistently featured significantly less volume than pine cones, regardless of species, but had the highest bulk density among all cones/fruit. Post oak acorns held statistically more moisture and less dry matter than any other cone/fruit, while sweetgum capsular heads statistically held the lowest amount of moisture and the

Table 2 Mean (SE) cone and fruit morphological and chemical traits. Different letters represent statistically significant ($p < 0.05$) trait differences

Trait	Longleaf pine	Shortleaf pine	Loblolly pine	Post oak	Water oak	Sweetgum
Air dry weight (g)	69.7^{a} (2.0)	6.5^{c} (2.0)	15.9^{b} (2.0)	1.2^{c} (2.0)	1.2^{c} (2.0)	2.6^{c} (2.0)
Moisture (%)	7.6^{bc} (0.4)	8.1^{bc} (0.4)	8.0^{bc} (0.4)	19.9^{a} (0.4)	9.4^{b} (0.4)	7.1^{c} (0.4)
Dry matter (%)	92.4^{ab} (0.04)	91.9^{ab} (0.4)	92.0^{ab} (0.4)	80.1^{c} (0.4)	90.6^{b} (0.4)	92.9^{a} (0.4)
Volume (cm^3)	457.8^{a} (13.4)	82.0^{b} (13.4)	95.4^{b} (13.4)	0.9^{c} (13.4)	1.0^{c} (13.4)	12.5^{c} (13.4)
Bulk density (gcm^{-3})	0.2^{b} (< 0.1)	0.1^{b} (< 0.1)	0.2^{b} (< 0.1)	1.5^{a} (< 0.1)	1.3^{a} (< 0.1)	0.1^{b} (< 0.1)
Lignin (%)	23.6^{b} (1.0)	32.2^{a} (1.0)	34.2^{a} (1.0)	6.4^{d} (1.0)	14.2^{c} (1.0)	13.5^{c} (1.0)
Total N (%)	0.2^{e} (< 0.1)	0.4^{d} (< 0.1)	0.3^{d} (< 0.1)	0.9^{a} (< 0.1)	0.7^{b} (< 0.1)	0.6^{c} (< 0.1)
C (%)	54.4^{b} (0.2)	53.9^{bc} (0.2)	53.2^{c} (0.2)	50.3^{e} (0.2)	56.2^{a} (0.2)	51.5^{d} (0.2)
C:N	224.2^{a} (4.0)	134.6^{c} (4.0)	161.6^{b} (4.0)	56.8^{e} (4.0)	79.8^{d} (4.0)	83.5^{d} (4.0)

highest amount of dry matter. There were no statistical differences among pine species in cone moisture content, dry matter content, or bulk density.

Cone/fruit morphology (% dry matter) and chemistry (% lignin, carbon, and nitrogen) influenced fuel consumption and flame height (Fig. 3). Fuel consumption increased with increasing cone/fruit dry matter, lignin, and C content. In contrast, consumption declined with increasing cone/fruit N content. Log-transformed flame height similarly increased with % dry matter, % lignin, and % C, and decreased with % N.

Burning single-species treatments produced distinct patterns in fire behavior (Table S3). Longleaf pine cones consistently showed higher consumption and flame height than sweetgum capsular heads. Additionally, sweetgum capsular heads smoldered at a significantly lower maximum temperature than the cones of each pine species at every 2-min interval (Fig. 4). There were no differences in maximum smoldering temperature among southern pine species (Fig. 4). There was little difference, however, in either ROS or flame duration among cones/fruit in single species treatments (Table S3). Principal component analyses (PCAs) showed that fuel consumption and flame height tended to load onto one axis, while fire behavior variables related to time — flame duration and ROS — tended to load onto another (Fig. 5; Table S4). There was little differentiation among treatments at low coverage (Fig. 5); however, clear differentiation occurred at medium and high coverage for single-species treatments (Fig. 5).

Mixed-species treatments also had a significant effect on fire behavior, particularly at high coverage; however, the results were less consistent than single-species treatments (Table S 3). At high coverage, the bottomland three-way treatment (loblolly/sweetgum/water oak) had significantly lower consumption and flame height than the upland three-way (longleaf/sweetgum/post oak) treatment (Table S3). There were no statistical differences in ROS or flame duration among mixed species treatments at high coverage; however, at medium coverage, the bottomland three-way treatment flame duration was significantly lower than other mixture treatments (Table S3). In PCA analyses, mixed-species treatments were largely overlapping across coverage levels (Fig. 5; Table S4).

Mixing cones and fruit at varying coverages produced inconsistent, non-additive trends in fuel consumption (Table 3). At low coverage, mixing longleaf pine cones

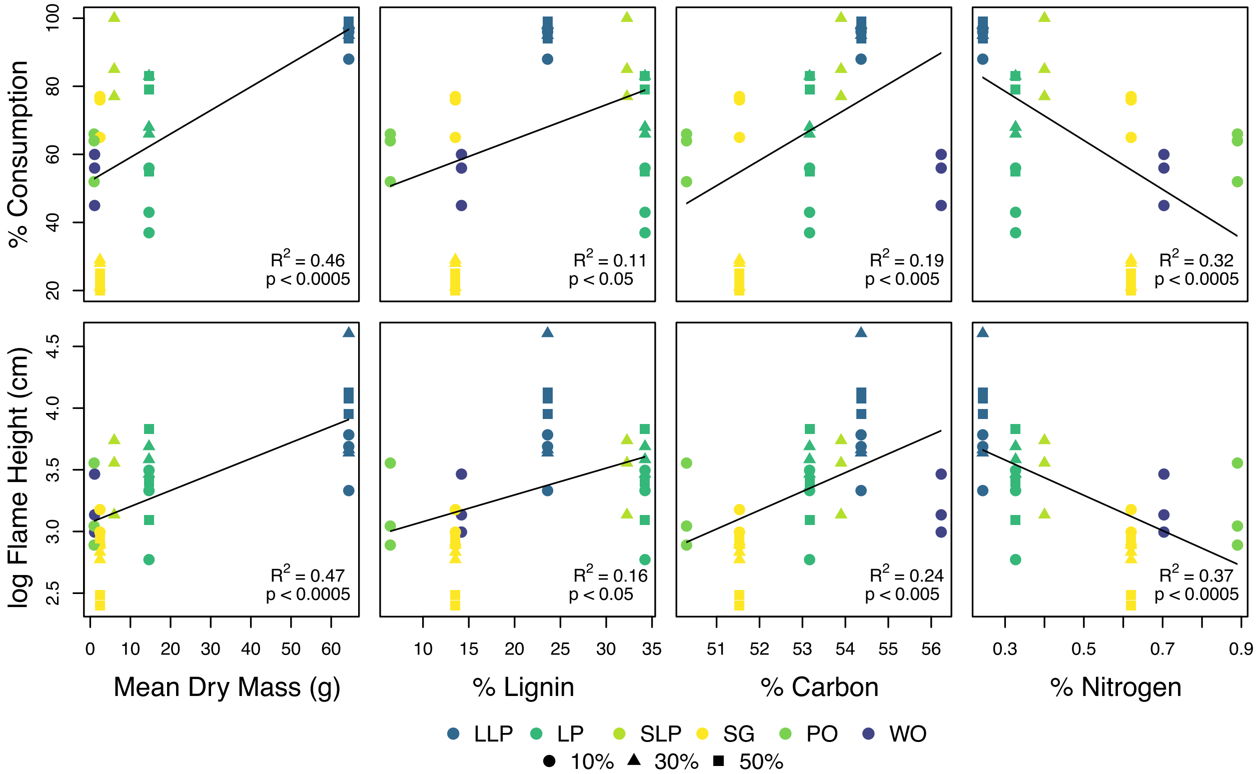

Fig. 3 Fire behavior (% consumption and flame height) as a function of morphological (dry mass) and chemical (percentage lignin, carbon, and nitrogen) traits. All linear regressions were significant ($p < 0.05$). Colors represent species: LLP, longleaf pine; LP, loblolly pine; SLP, shortleaf pine; SG, sweetgum; PO, post oak; WO, water oak, and shapes represent coverage levels

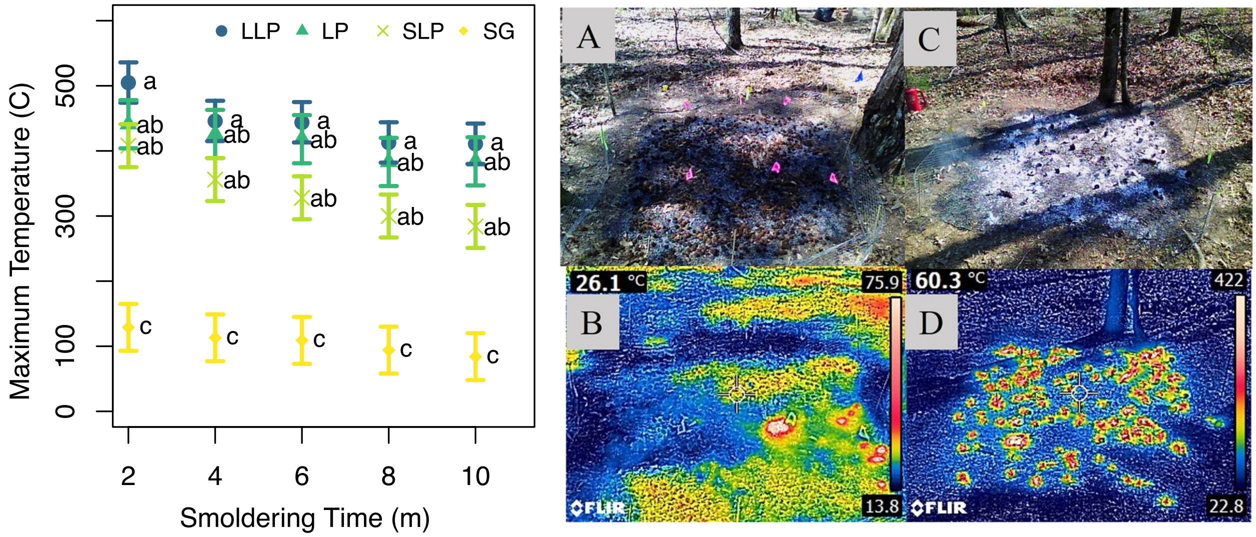

Fig. 4 Left: Species maximum smoldering temperature (mean ± SE) over time (LLP, longleaf pine; LP, loblolly pine; SLP, shortleaf pine; SG, sweetgum). Right: Sweetgum plot photo (**A**) and thermal image (**B**) at 10 min post flame extinction; Longleaf plot photo (**C**) and thermal image (**D**) at 10 min post flame extinction

and sweetgum capsular heads created a significant, non-additive reduction in fuel consumption regardless of mass weighting adjustment. Increasing longleaf pine/sweetgum density to medium coverage created a statistically significant, non-additive positive effect on fuel consumption irrespective of weighting adjustment. Further increasing longleaf pine/sweetgum coverage to the high-level reduced fuel consumption compared to medium coverage; however, this result was not statistically significant and the overall effect on fuel consumption switched from positive (unweighted) to negative (weighted) based on how expected consumption was calculated (Table 3). Mixing loblolly pine cones and sweetgum capsular heads had a similar disjointed effect on fuel consumption, but produced no statistically detectable results.

Discussion

Drivers of cone/fruit flammability

Cone/fruit morphological and chemical traits exerted varying influence on flame height and fuel consumption. Consistent with studies examining shoot flammability, dry matter content had a strong positive effect on flame height and fuel consumption (Cornelissen et al. 2003; Pérez-Harguindeguy et al. 2013; Alam et al. 2020). Dry matter content reflects high tissue mass per volume, which has been linked to increased ignitability, fire intensity, flame duration, and fuel consumption (Dimitrakopoulos and Papaioannou 2001; Cowan and Ackerly 2010; Alam et al. 2020). Thus, it was not surprising that cone/fruit dry matter had a strong positive influence on flammability.

Lignin content was another factor that improved fuel consumption and flame height. Although lignin is known to reduce fuel combustibility during pyrolysis (Scarff et al. 2012; Grootemaat et al. 2015), lignin increases fire temperature and duration post-ignition (Fernandez 2013). Indeed, lignin content has been found to improve fuel consumption and promote overall shoot flammability (Grootemaat et al. 2017; Alam et al. 2020). Similar to lignin, N has been shown to reduce combustibility at the pyrolysis stage and can also inhibit fire duration (Green 1996; Scarff et al. 2012; Grootemaat et al. 2015). Our results demonstrate that cone/fruit N content can also reduce fuel consumption and flame height. The opposing effects of lignin and N on fuel consumption likely reflect the high energy content of lignin that can be accessed post-ignition (McKendry 2002). Collectively, our results indicate that cones/fruits possessing high dry matter and lignin content promote several aspects of flammability.

Single-species flammability

Single-species treatments produced distinct patterns in fire behavior. In general, the addition of longleaf pine cones promoted flammability, compared to the control, while the addition of sweetgum capsular heads suppressed fire. Clear examples of this trend occurred at the highest coverage (50%), where longleaf cones produced twice the maximum flame height compared to the control, and four times that of sweetgum capsular heads. Moreover, at medium coverage (30%), the longleaf cone maximum smoldering temperature was consistently ~ 400 °C hotter than sweetgum. As previously discussed,

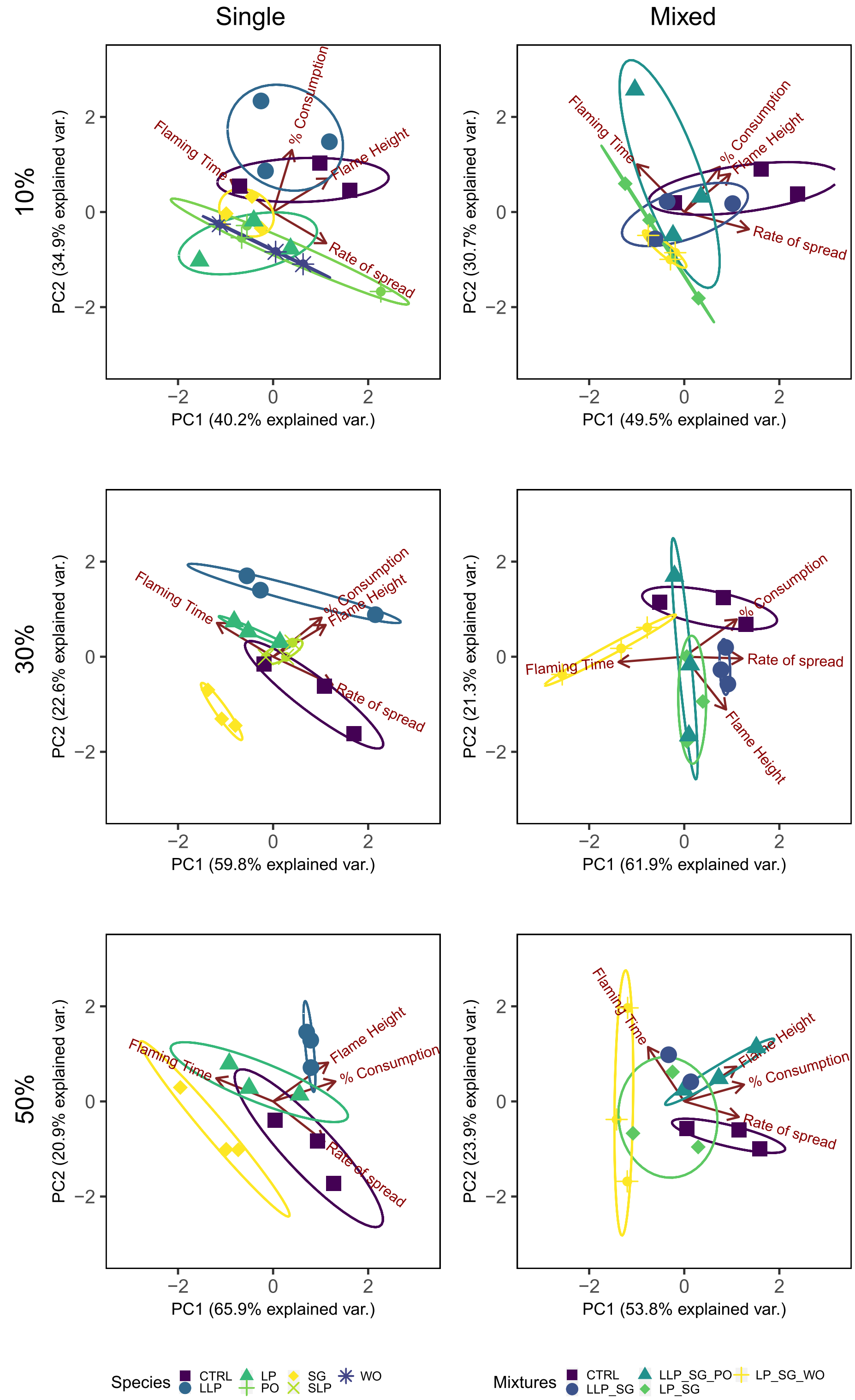

Fig. 5 Principal component analysis (PCA) biplots of fire behavior variables flaming time, rate of spread, flame height, and percent consumption for single- and mixed-species treatments at low (10%), medium (30%), and high (50%) coverage. Points represent individual plots, and arrows represent variable contributions to principal components. Point shape and color represent plot treatment. CTRL, control; LLP, longleaf pine; LP, loblolly pine; PO, post oak; SG, sweetgum; SLP, shortleaf pine; WO, water oak. Cones and fruit were not added to the control treatment

Table 3 Additivity of mixed-species flammability analysis results. Both unweighted and mass-weighted expected consumption, *t*-test results, and effect sizes are shown. LLP, longleaf pine; LP, loblolly pine; SG, sweetgum; PO, post oak; WO, water oak

Treatment	Mean observed % cons. (SE)	Unwtd. exp. % cons.	Unwtd. *t*-test	Unwtd. mean effect size	Mass-wtd. Exp. % cons.	Mass-wtd. *t*-test	Mass-wtd. mean effect size
LLP+SG 10%	75.67 (1.45)	83.120	$t = 5.2$ **$p < 0.05$**	– 9.02	87.31	$t = 8.0$ **$p < 0.05$**	– 13.34
LLP+SG 30%	95.67 (0.9)	61.500	$t = -38.7$ **$p < 0.005$**	55.56	75.41	$t = -23.0$ **$p < 0.005$**	26.87
LLP+SG 50%	72.5 (1.5)	59.833	$t = -8.4$ $p = 0.07$	21.17	74.50	$t = 1.3$ $p > 0.1$	– 2.68
LP+SG 10%	56.67 (8.7)	59.000	$t = 0.3$ $p > 0.1$	– 3.95	56.36	$t = 0.04$ $p > 0.1$	0.54
LP+SG 30%	75.67 (6.98)	49.167	$t = -4$ $p = 0.06$	53.90	53.53	$t = -3.2$ $p = 0.09$	41.34
LP+SG 50%	60 (15.6)	47.333	$t = -0.8$ $p > 0.1$	26.76	52.05	$t = -0.5$ $p > 0.1$	15.27
LLP+SG+PO 10%	66 (6.5)	75.667	$t = 1.5$ $p > 0.1$	– 12.78	82.19	$t = 2.5$ $p > 0.1$	– 19.69
LLP+SG+WO 10%	49 (2.6)	57.222	$t = 3.1$ $p = 0.09$	– 14.37	55.55	$t = 2.5$ $p > 0.1$	– 11.79

much of this difference could derive from the disparity in dry mass and lignin content between species. Sweetgum capsular heads are also largely enclosed, hollow spheres, which potentially simultaneously limit fuel packing and ventilation and promote water absorption and retention. Overall, our results correspond with other studies recognizing longleaf pine litter and cones as important drivers of understory flammability. (Mitchell et al. 2009; Kreye et al. 2013b; Dell et al. 2017; Varner et al. 2021). Our results also demonstrate that capsular head abscission is another mechanism through which sweetgum suppresses understory flammability.

Loblolly pine is another species that has become prolific in the contemporary forest landscape (Hanberry 2013). However, unlike sweetgum, the effects of loblolly cones on flammability are difficult to discern. For example, transitioning from low-to-medium cone coverage improved fuel consumption, flame height, and ROS. Loblolly cone maximum smoldering temperature was also comparable to longleaf pine, potentially reflecting similarities in cone lignin content (Alam et al. 2020). Nevertheless, plots receiving loblolly cone additions were less flammable than the control at low coverage, and indistinguishable at medium-to-high coverage suggesting that loblolly cones neither strongly inhibit nor promote flammability. Part of this complicated pattern could be related to initial fuel loading differences among treatments. Due to its intermediate cone size, single-species loblolly pine fuelbeds contained less fuel than longleaf pine (– 21–32%) but more fuel than sweetgum (+ 24–32%) at a given coverage level.

Fuel quantity contributes to several elements of flammability, as it directly affects energy release (Byram 1959; Rothermel 1972; Simpson et al. 2016). Morphological factors may also have limited loblolly cone flammability. Loblolly cones have smaller scales, are slower to open under warming conditions, and have less pore space between scales when open to support fuel bed ventilation compared to longleaf pine (Personal observation). We suspect these cone attributes may be analogous to foliar traits, such as leaf size and curl, that affect fuel bed packing (Scarff and Westoby 2006; Santoni et al. 2014; Burton et al. 2021).

Less evidence exists to assess the flammability of shortleaf pine cones and the oak acorns, as each species was only evaluated at one cover level. However, based on measured chemical and morphological traits, our results suggest that shortleaf cones are comparable to loblolly pine in flammability, while post and water oak acorns align more closely with fire-inhibiting species such as sweetgum. Like loblolly pine, shortleaf cones had intermediate dry matter content, high lignin, and low N and moisture content, which generally promote flammability (Grootemaat et al. 2015; Alam 2020). In contrast, the acorns of both oak species were low in dry matter content and high in bulk density, N content, and, for post oak, moisture content, which negatively affect several aspects of flammability (Sullivan et al. 2012; Grootemaat 2015; Burton et al. 2021). Thus, we suspect the flammability trends observed from shortleaf pine, post oak, and water oak, in the single-level burning trials, would maintain their general direction but vary in strength based on the degree of cone/fruit cover. Nevertheless, the importance of acorns for understory flammability may be limited to mast years, as they may be too scattered or predated to influence flammability in non-mast years. It should also be recognized that the timing and placement of acorns in the fuelbed were not fully representative of natural stand dynamics.

One particularly surprising result from our study was the lack of differentiation in fire duration and ROS among species given their chemical and morphological differences. Part of this result may be related to the limited range of bulk densities encountered in this study, as bulk density is a strong driver of flame duration and rate of spread (Burton et al. 2021). Wind conditions during the experiment were consistently light and occasionally variable in direction. Consequently, we do not suspect that wind strongly affected fire behavior.

Mixed-species flammability

Flammability in mixed-species fuelbeds is generally thought to be controlled by the most flammable constituent species (De Magalhães and Schwilk 2012; van Altena et al. 2012). In contrast, fuel consumption is thought to be controlled by the least consumable species in mixture (Della Rocca et al. 2018). The combined results of our single- and mixed-species treatments support the former view, as mixtures containing longleaf pine cones consistently consumed more fuel and had taller flames than mixtures containing loblolly pine. Specific examples of this trend were evident at high coverage, where the upland three-way mixtures featuring longleaf pine statistically differed from the bottomland three-way mixture containing loblolly pine. While post oak and water oak may also have contributed to this result, given that both oak species had similar suppressing effects on fire in the monospecific burns, we attribute this result primarily to the difference in cone flammability. Longleaf pine also produced a stronger non-additive increase in fuel consumption than loblolly pine in two-way mixtures with sweetgum at medium coverage. Identifying the mechanism underlying this pattern is beyond the scope of this study; however, we suspect the combination of pore space between scales and rigidity of longleaf pine cones likely reduced fuelbed bulk density helping promote ignitability, combustibility, and non-additive fuel consumption. Indeed, elevated fuelbed bulk density has been suggested as a cause for negative non-additive fire behavior (Zhao et al. 2016 and 2019).

One important caveat to our results is the assumption of equal fruit coverage within mixtures. In most years, longleaf pine produces less than 50 cones per tree (Chen and Willis 2023). Thus, even in a mixed stand with heavy longleaf pine representation, longleaf cones will likely be underrepresented in most years. In contrast, loblolly pine produces good seed crops every 2 years, while sweetgum produces fair crops annually and bumper crops every 3 years (Kormanik 1990; Cain and Shelton 2001). Consequently, future studies should focus on cone/fruit proportions determined as a function of species fecundity and reproductive timing to generate more realistic cone/fruit mixtures.

Another interesting pattern was observed with changes in cone/fruit coverage. With few exceptions, fuel consumption and flame height increased from low-to-medium coverage, but decreased from medium-to-high coverage. This trend was found across mixture treatments suggesting that changes in fuelbed structure wrought by increasing cone/fruit density altered flammability independent of mixture identity. At low density, flammability is likely driven by the litter layer and only slightly augmented by the dispersed cones/fruit. Fuelbed bulk density is unlikely to be strongly affected by cones/fruit at low density. At medium density, cones/fruit may be sufficiently aggregated to supersede leaf litter effects, but dispersed enough to avoid reaching an undetermined fuelbed bulk density threshold that inhibits flammability. Lines: At high density, we suspect the aggregated cones/fruit reduced fuelbed porosity, potentially increasing moisture retention and dampening flammability. Increased moisture retention could also indirectly affect flammability by inhibiting pine cone openness; thereby further reducing fuelbed porosity and limiting ignition points (Harlow et al. 1964).

If true, this would account for the consistent decline in flammability as cone/fruit coverage increased from medium to high. Thus, at least for this group of mixture treatments, fuelbeds with cones/fruit covering approximately 30% of the forest floor represent the optimal conditions for flammability.

Conclusions

Our study demonstrated that cone/fruit production affects understory flammability, which is integral to the maintenance of open-forest structures. Southern pine species produced cones that had high lignin and dry matter content and were generally flammable. Among this group, longleaf pine demonstrated the highest flammability likely due to the comparatively high dry matter content and open structure of its cones. In contrast, the fruits of sweetgum, water oak, and post oak were low in dry matter and lignin content, high in nitrogen content, and generally dampened flammability. When burned together, mixtures featuring longleaf pine as the conifer component were generally more flammable than those containing loblolly pine at medium and high cover.

Collectively, these findings have important implications for restoring fire-suppressed woodlands in the southeastern USA. Specifically, our results confirm that longleaf pine cones play an important part in maintaining understory flammability and can offset the presence of sweetgum fruit if found in equal abundance at 30–50% coverage. Loblolly pine cones can play a similar role in offsetting the dampening effects of sweetgum fruit, but to a lesser extent compared to longleaf pine. However, in most years, loblolly pine cones will be more numerous than those of longleaf pine, which may compensate for lower flammability. Future studies examining fruit flammability should explore how changes in fruit proportionality and degree of decomposition affect flammability in mixture.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-024-00281-z.

Supplementary Material 1: Table S1. Oven dry weight of litter, cones, fruit, and total fuel in each fuelbed treatment. LLP = longleaf pine; LP = loblolly pine; SLP = shortleaf pine; SG = sweetgum; PO = post oak; WO = water oak.

Supplementary Material 2: Table S2. Mean (SD) fire weather parameters throughout the experiment.

Supplementary Material 3: Table S3. Predicted mean (SE) fire behavior as a function of single-species fuelbed treatment. F and *p*-values represent ANOVA results, and distinct letters represent statistically significant differences in fire behavior values. LLP = longleaf pine; LP = loblolly pine; SLP = shortleaf pine; SG = sweetgum; PO = post oak; WO = water oak; CTRL = litter-only control.

Supplementary Material 4: Table S4. Results from principal component analyses. Left shows factor loadings and right shows factor contributions to principal components.

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Authors' contributions

JLW and HDA conceptualized the experiment and methods. JLW, TFM, and HDA implemented the experiment, analyzed data, wrote the original draft, and edited the manuscript.

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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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