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Multivariate roles of litter traits on moisture and flammability of temperate northeastern North American tree species

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Abstract

Background Tree litter is the primary fuel affecting surface fire behavior in most fire-prone forest and woodland ecosystems in northeastern North America. Fire exclusion and land use changes have dramatically altered fire regimes in many of these ecosystems, shifting toward species that reinforce the continued diminution of fire. Comparative litter flammability studies provide a useful approach to identify the corresponding leaf and litter bed traits that drive the positive feedback termed "mesophication" in these ecosystems.

Results In this study, we measured laboratory flammability and moisture characteristics of leaf litter from 17 common tree species in temperate forests of northeastern North America. Principal components analysis of flammability and moisture data resulted in species separating along a pyrophyte-to-mesophyte gradient. Pyrophytic *Quercus* litter was the most flammable of all species, and *Pinus* litter dried the most rapidly and flamed for the longest duration. The remaining mesophytic species grouped into either a high moisture retention-poor burning cluster (*Acer rubrum*, *Betula alleghaniensis*, *Nyssa sylvatica*, *Carya glabra*, *C. tomentosa*) or an intermediate flammability cluster (*Acer saccharum*, *C. ovata*, *Tilia americana*). Several litter traits were associated with multivariate factors. Leaf length, density, curling, surface area-to-volume, and litter bed bulk density were associated with the factor comprising saturation moisture content, flaming time, and consumption. Specific leaf area was related to moisture time-lag and flame height. Litter bed packing ratio was most related to smoldering duration.

Conclusions Interspecific variability in leaf and litter bed traits explained substantial differences in moisture dynamics and flammability among the species examined. These findings extend our understanding of litter traits' influence on the combustion environment and affirm the potential effects of pyrophytic and mesophytic tree species on contemporary fire regimes in northeastern North American forests.

Keywords Fire regimes, Fuel, Leaf traits, Litter, Mesophication, Moisture dynamics, Quercus, Time-lag

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Resumen

Antecedentes La hojarasca de los árboles (i.e. broza) es el combustible primario que afecta el comportamiento de fuegos superficiales en la mayoría de los bosques proclives al fuego y ecosistemas boscosos del noreste de América del Norte. La exclusión del fuego y cambios en el uso de la tierra alteró dramáticamente los regímenes de fuego en muchos de esos ecosistemas, sesgándolos hacia la proliferación de especies que refuerzan la continua disminución de los incendios. El estudio comparativo de la inflamabilidad de esta broza provee de una aproximación útil para identificar las características correspondientes a hojas y camas de broza que conducen a una retroalimentación positiva llamada "mesificación" de esos ecosistemas.

Resultados En este estudio, medimos en laboratorio la inflamabilidad y humedades características de la broza proveniente de hojas de 17 especies de árboles comunes de bosques templados del noreste de Norte América. El análisis de componentes principales de datos de inflamabilidad y de humedad resultó en una separación de especies a lo largo de un gradiente de pirofítico a mesofítico. La broza pirofítica de Quercus (robles) fue la más inflamable de todas las especies y la broza de pinos fue la que se secó más rápidamente y cuya llama se mantuvo viva por más tiempo. Las especies mesofíticas remanentes se agruparon en clústeres con una alta retención de humedad y un pobre quemado (*Acer rubrum*, *Betula alleghaniensis*, *Nyssa sylvatica*, *Carya glabra*, *C. tomentosa*), o en un clúster de inflamabilidad intermedia (*Acer saccharum*, *C. ovata*, *Tilia americana*). Las diversas características de la broza fueron asociados con factores multivariados. El largo de las hojas, su densidad, enrollamiento, relación superficie del área-volumen y la densidad aparente de la broza fueron asociados con los factores que comprendieron el contenido de humedad de saturación, el tiempo de presencia de llama, y el consumo. La relación de compactación de la broza fue más relacionada con la duración del ardido sin llama (fuego de rescoldo).

Conclusiones La variabilidad interespecífica en las características de las hojas y la cama de broza explicaron diferencias substanciales en la dinámica de la humedad e inflamabilidad de las especies examinadas. Estos resultados extienden nuestro conocimiento sobre la influencia de las características de la broza en el entorno de la combustión y afirma los efectos potenciales de las especies de árboles pirofíticos y mesofíticos en los regímenes de fuego contemporáneos de Norte América.

Background

Fire is widely recognized as an important ecological process across many terrestrial ecosystems. Interactions among fuels, vegetation, and weather influence fire behavior and subsequently affect plant community composition (Ellair and Platt 2013; Archibald et al. 2018). Anthropogenic alteration of historically fire-prone ecosystems can result in positive feedbacks that modify fire regimes through hastening or dampening fire (e.g., Nowacki and Abrams 2008; Coppoletta et al. 2016; Tepley et al. 2018). In forested ecosystems, structure and composition impact the forest floor environment, including the composition and quantity of surface fuels. The role of these factors on potential fire behavior and effects in fire-prone landscapes may subsequently correspond to changes in vegetation patterns. Such feedbacks may be critical in the resilience and stability of fire-dependent ecosystems. In many cases, the influx of shade-tolerant, fire-sensitive tree species into formerly pyrogenic landscapes has increased stand density and altered litter composition with subsequent reductions in potential fire behavior (Engber et al. 2011; Keyser et al. 2017; Alexander et al. 2021).

Senesced leaves, or "litter," is a major component of the surface fuel layer and a strong driver of fire behavior in many woodland and forest ecosystems. Litter flammability varies widely among species reflecting leaf and litter bed trait differences (Varner et al. 2015; Cornwell et al. 2015; Burton et al. 2020; Popović et al. 2021). Species with physical leaf traits such as greater leaf size, longer leaf perimeter, and significant leaf curl tend to be more flammable (Engber and Varner 2012). These traits also affect litter bed attributes, such as bulk density and packing ratio that contribute to variation in litter flammability through its influence on the permeation of oxygen and heat transfer effectiveness during burning (Rothermel 1972; Scarff and Westoby 2006; Burton et al. 2020). Leaf and litter bed traits can also influence moisture dynamics (i.e., moisture retention and drying rates) and, subsequently, litter flammability (Kreye et al. 2013, 2018b; Kane et al. 2021). In spite of recent advances in our understanding of litter flammability, few studies have examined the trait-based factors that affect both the moisture dynamics and flammability of litter.

In addition to fuel and meteorological conditions, fuel moisture is a primary factor influencing fire behavior

(Matthews 2014). Fuels that adsorb and retain moisture strongly dampen fire behavior (Rothermel 1972), and species are known to vary widely in their ability to gain and lose moisture based on interspecific variation in leaf morphology and litter bed structure (Kreye et al. 2013). In humid environments where precipitation is common during the fire season, e.g., eastern North America (Schroeder and Buck 1970), impacts of species composition on litter moisture dynamics may be more pronounced given the importance of post-rain drying and diel fluctuations (Kreye et al. 2018a). Understanding how surface fuel characteristics and microclimate interact to influence flammability would help elucidate ecological feedbacks in fire-dependent ecosystems as well as identify the potential mechanisms of shifting vegetation composition resulting from long-term fire exclusion.

The long-term exclusion of fire has led to significant changes in species composition and landscape vegetation patterns across much of North America. In northeastern temperate forests, timber extraction in the nineteenth century and fire exclusion throughout the twentieth and early twenty-first centuries have been implicated in widespread and dramatic changes in forest composition. In many instances, the prolonged absence of fire has facilitated the spread of fire-sensitive or mesophytic tree species (e.g., *Acer rubrum* L.) into formerly fire-prone landscapes composed primarily of pyrophytic tree species (Nowacki and Abrams 2008; Alexander et al. 2021). The mechanisms of this positive feedback process termed “mesophication” likely include forest densification (Nowacki and Abrams 2008), increased stem flow by mesophytic species (Alexander and Arthur 2010), enhanced litter moisture retention (Kreye et al. 2013), and the incorporation of species with less flammable litter (Kreye et al. 2018b).

The objectives of this study were to determine the influence of leaf and litter bed traits on the moisture dynamics and flammability of 17 tree species. The northeastern region of North America is an ideal location for this study, given its high tree diversity and the marked contrast between its historic and contemporary fire regimes (Guyette et al. 2012; Stambaugh et al. 2015; Marschall et al. 2019). We hypothesized that differences in litter moisture dynamics and flammability among species would reflect distinct groupings based on possible fire adaptations and historical forest composition under more frequent fires. We also hypothesized that the differences in litter moisture dynamics and flammability would correspond to leaf and litter bed traits. If supported, our findings will provide important insights into the drivers of litter moisture dynamics and flammability that can improve our understanding of fire-vegetation feedbacks and changes with implications toward forest and woodland management.

Methods

Litter collection

We collected fallen leaf litter of 17 native tree species representing temperate forests of northeastern North America in spring 2019 from central Pennsylvania (Center County) and southern New Jersey (Burlington County), USA, for flammability experiments. Species collected included white oak (*Quercus alba* L.), scarlet oak (*Q. coccinea* Münchh.), chestnut oak (*Q. montana* Willd.), northern red oak (*Q. rubra* L.), black oak (*Q. velutina* Lam.), pignut hickory (*Carya glabra* Mill.), shagbark hickory (*C. ovata* (Mill.) K. Koch), mockernut hickory (*C. tomentosa* (Lam.) Nutt.), shortleaf pine (*Pinus echinata* Mill.), pitch pine (*P. rigida* Mill.), eastern white pine (*P. strobus* L.), Virginia pine (*P. virginiana* Mill.), red maple (*Acer rubrum* L.), sugar maple (*A. saccharum* Marshall), yellow birch (*Betula alleghaniensis* Britton), blackgum (*Nyssa sylvatica* Marshall), and American basswood (*Tilia americana* L.). All litter (O_i horizon) collected was recently cast with no visible signs of decomposition. For each species, seven trees were randomly selected (only four trees were selected for *Carya glabra*), and ~ 20 g of litter was collected from the forest floor beneath the crown. All collected litter was bagged in the field and transported to the nearby laboratory where we air-dried the samples in paper bags before shipping the samples to the Cal Poly Humboldt Wildland Fire Laboratory (Arcata, CA, USA) for experiments.

Litter traits

We measured leaf litter characteristics of each of the 17 tree species; leaflets were measured for compound leaved species (*Carya* spp.) given they were detached when collected from the forest floor. We removed seven individual leaves at random for each species and measured leaf mass, leaf length, thickness, surface area, volume, and leaf curl (as in Engber and Varner 2012). Individual leaf dry mass (g) was measured using a digital scale, leaf edge thickness (mm) was measured using electronic calipers, and curl depth (mm) was measured as the maximum height of a horizontally oriented dry leaf above a flat surface. For broadleaf species, sample leaves were then wetted and flattened between two heavy flat surfaces and allowed to dry. Afterward, leaf samples were scanned, and blade length (mm) and area (cm^2) were measured using the WinFOLIA image processing software (Regent Instruments, Quebec, Canada). Leaf volume (cm^3) was calculated by multiplying leaf thickness by the surface area of one side. The surface area-to-volume ratio (cm^{-1}) was calculated by dividing the leaf surface area by volume. For pine species, the needle surface area and volume were calculated based on geometric assumptions for *Pinus* (Johnson 1984). Leaf density (g cm^{-3}) was calculated by dividing leaf dry mass by leaf volume. The specific leaf area (SLA; $\text{cm}^2\ \text{g}^{-1}$) of all samples was calculated by dividing the one-sided leaf area by leaf dry mass.

Litter bed traits were also examined as a factor influencing moisture characteristics and flammability. We calculated litter bed bulk density (g cm^{-3}) by dividing the litter bed mass by burn area (20 × 20 cm) and measured litter bed depth (see the "Burning experiments" section for more detail). We also estimated the packing ratio (unitless) for each litter bed by dividing bulk density (g cm^{-3}) by leaf density (g cm^{-3}).

Drying experiments

We oven-dried all litter samples at 40 °C for 24 h. From our dry samples, we placed seven (four in the case of *C. glabra*) 15-g litter samples for each species in aluminum pans and submerged them in water for 24 h to ensure maximum absorption. Litter samples were subsequently drained, lightly agitated to remove surface water, and placed in pre-weighed 24 × 24 × 4 cm square aluminum drying pan with 36 holes (5 mm diameter) spaced 25 mm apart on the bottom of the pan (as in Kreye et al. 2013). All litter bed samples were allowed to dry under controlled temperature (24 °C, *s.e.* = 0.1 °C) and relative humidity (54%, *s.e.* = 0.6) in a 3 × 3 × 4 m drying chamber. We elevated each pan by 1 cm using wooden slats situated on tables within the drying chamber to allow excess water to drain away from the litter. We weighed litter beds prior to placement in the drying chamber to get the saturation moisture content (%, dry weight basis) and weighed periodically (see below) over a 120-h drying period when the moisture content of all litter beds stabilized over at least two measurements, indicating that equilibrium moisture content had been reached (Kreye et al. 2013). We weighed the litter beds every 2 h for the first 12 h, every 4 h from 12 to 24 h, every 8 h from 24 to 48 h, and then every 12 h from 48 to 120 h as moisture loss rates slowed. We calculated the gravimetric moisture content (%) for each litter bed at each weighing period ([wet weight − dry weight/dry weight] × 100) and subsequently converted these values to relative moisture content (E) based on Eq. 1 (Byram 1963, Fosberg et al. 1970).

$$E = \left(m_t - m_f\right)/\left(m_i - m_f\right) \tag{1}$$

where m_t is the moisture content at time t, m_f is the final moisture content, and m_i is the initial or saturation moisture content.

Drying response time-lag (τ) for each litter bed was calculated using piecewise regression with the *segmented* package (Muggeo 2008) in R (R Development Core Team 2022). Response time represents the time a fuel particle or fuelbed takes to reach 63% of the equilibrium moisture content ($E = 0.368$). Longer response times indicate fuels that lose and gain moisture slower than fuels with shorter response times. Litter moisture loss approximately follows a negative exponential drying model (Nelson 2001); however, deviations from this expectation have been noted (Anderson et al. 1978, Van Wagner 1979). Our initial inspection of the drying rate data indicated that the negative exponential model fit assumption was inadequate to generate a linear equation between time and the natural log of relative moisture content (E). Thus, we separated the data into two linear sections: initial and final time-lags (Nelson and Hiers, 2008) based on the calculated breakpoint determined by the piecewise regression. Response time (i.e., time-lag; τ) for each litter bed was calculated algebraically using the slope of the regression equation of the linear relationship between time and log E for the initial time-lag (Eq. 2).

$$\tau = \frac{\log E}{\text{slope}} \tag{2}$$

Burning experiments

We conducted litter flammability experiments for each species using well-established burn trial methods (Fonda 2001; Kane et al. 2008). Each 15-g litter bed ($n = 7$ per species except $n = 4$ for *C. glabra*) was evenly distributed within the interior 20 × 20 cm portion of a 35 × 35 cm grid of xylene-soaked cotton strings laid out on a stainless-steel platform. A 2.75 × 2.75 m fume hood above the platform generated a constant draw of 15 to 20 cm s^{-1}, though we detected no airflow at the litter bed surface. Laboratory conditions over the duration of burning trials ranged from 21.3 to 26.0 °C ($\bar{x} = 23.1$ °C, *s.e.* = 0.1 °C) and 51 to 70% relative humidity ($\bar{x} = 56\%$, *s.e.* = 0.3%) with no differences across any species ($P > 0.05$). To account for potential differences in bulk density among litter beds, litter depth measurements were taken at four locations (7 cm diagonally from the corners) prior to ignition and averaged for subsequent analyses. Xylene-soaked strings were ignited along the perimeter of the array to uniformly ignite the litter beds. For each burn, we measured maximum flame height (cm), flaming time (s), smoldering time (s), and consumption (%) as in Kane et al. (2021). Maximum flame height was determined using a graduated ruler located behind the litter beds. Flaming time was recorded from the time of litter ignition to the cessation of flaming. Smoldering time was the duration from the end of flaming to the cessation of visible glowing combustion, observed under darkened conditions. These established methods have been used to conduct similar flammability experiments with tree species' litter from other regions (Varner et al. 2015).

Data analysis

All analyses were completed in the R environment (R Development Core Team 2022). Because some litter moisture dynamics and flammability metrics were correlated, we conducted a principal components analysis (PCA) to visualize the multivariate comparisons among species. We included the four flammability metrics (maximum flame height, flaming time, smoldering time, and consumption) and two moisture metrics (saturation moisture content and time-lag) in the principal components analysis using the *prcomp* function to generate axis scores for comparison with litter traits. All variables were scaled based on unit variance prior to analysis. We selected the number of PCA axes that explained at least 80% of the total variation in the dataset and where factor eigenvalues were ≥ 1 (Afifi et al. 2004; Abdi et al. 2010). Thus, the retained PCA axes represent moisture dynamics and flammability indices. For each axis, we report the highest correlation value (r) and direction (+ or −) with each moisture or flammability metric. Subsequently, we compared the relationship between leaf and litter bed traits and moisture/flammability scores using the *envfit* function in the vegan package (Oksanen et al. 2017) and report all significant relationships ($\alpha = 0.05$) based on 999 permutations. Following multivariate analysis, we conducted a k-means cluster analysis to group species with similar litter moisture dynamics and flammability. The number of clusters was determined based on the "elbow method" or examining the inflection point (i.e., bend) of the within-cluster sums of square curve with an increasing number of clusters generated using the *fvis_nbclust* function in the factorextra package.

Results

Litter traits

Leaf and litter bed traits varied widely across the 17 tree species examined (Table 1). Leaf length ranged from 5.4 to 17.1 cm with *Pinus* and *Acer* spp. the shortest, while *C. glabra*, *C. tomentosa*, and *Q. rubra* had the longest leaves. The leaf area ranged from 3.6 to 6.8 cm^2 in *Pinus* species and was much larger in broadleaf species ranging from 30.5 cm^2 in *N. sylvatica* to 86.8 cm^2 in *Tilia americana*. Dry leaf mass ranged from 0.20 to 0.68 g with *N. sylvatica* and *A. saccharum* having the lightest leaves and *T. americana* and *Q. rubra* the heaviest. Leaf curl ranged from as little as 5 mm in *B. alleghaniensis* to 33 mm in *C. tomentosa* leaflets. The surface area-to-volume ratio ranged from 24.8 cm^{-1} in *Q. montana* to 77.0 cm^{-1} in *P. virginiana*. The specific leaf area varied from 79 to 470 cm^2 g^{-1}. Fuelbed traits also varied considerably among species, with bulk density ranging from 0.006 to 0.03 g cm^{-3} and packing ratio ranging from 0.02 to 0.09 across the 17 species.

Table 1 Leaf and litter bed traits of 17 common northeastern North American tree species

Species	Mass (g)	Length (cm)	Curl (mm)	Density (g cm^{-3})	SA:V (cm^{-1})	SLA (cm^2 g^{-1})	Bulk density (g cm^{-3})	Packing ratio
Acer rubrum	0.41 (0.03)	8.6 (0.5)	10.4 (2.1)	0.42 (0.07)	42.1 (1.7)	117 (19)	0.008 (0.0003)	0.021 (0.003)
Acer saccharum	0.26 (0.04)	7.3 (0.4)	16.7 (2.1)	0.32 (0.06)	47.6 (2.6)	186 (35)	0.007 (0.0009)	0.024 (0.003)
Betula alleghaniensis	0.11 (0.02)	10.2 (0.4)	5.0 (0.9)	0.15 (0.02)	68.3 (3.4)	470 (46)	0.012 (0.0025)	0.088 (0.022)
Carya glabr	0.44 (0.03)	14.5 (1.9)	21.4 (5.2)	0.48 (0.09)	45.4 (2.5)	132 (36)	0.007 (0.0004)	0.027 (0.007)
Carya ovata	0.42 (0.04)	13.0 (0.8)	25.6 (2.2)	0.48 (0.08)	39.7 (2.4)	103 (20)	0.007 (0.0006)	0.020 (0.006)
Carya tomentosa	0.53 (0.04)	15.4 (1.5)	33.0 (3.0)	0.23 (0.05)	33.1 (6.8)	147 (24)	0.006 (0.0006)	0.045 (0.020)
Nyssa sylvatica	0.20 (0.02)	9.7 (0.5)	17.1 (0.7)	0.26 (0.04)	38.4 (2.6)	165 (25)	0.011 (0.0011)	0.044 (0.004)
Pinus echinata	0.04 (0.004)	7.9 (0.4)	0.4 (0.05)	0.51 (0.04)	63.2 (5.3)	124 (9)	0.023 (0.0034)	0.045 (0.008)
Pinus rigida	0.09 (0.01)	9.8 (0.9)	0.7 (0.1)	0.57 (0.03)	44.8 (2.8)	79 (3)	0.027 (0.0049)	0.049 (0.010)
Pinus strobus	0.03 (0.003)	8.4 (0.2)	0.4 (0.04)	0.32 (0.05)	62.4 (7.0)	202 (16)	0.015 (0.0022)	0.055 (0.012)
Pinus virginiana	0.02 (0.003)	5.4 (0.3)	0.3 (0.03)	0.49 (0.03)	77.0 (11.2)	153 (14)	0.033 (0.0071)	0.067 (0.010)
Quercus alba	0.47 (0.09)	13.5 (1.0)	27.4 (6.5)	0.33 (0.08)	32.0 (1.6)	144 (36)	0.006 (0.0004)	0.029 (0.007)
Quercus coccinea	0.36 (0.06)	11.7 (0.7)	31.4 (5.8)	0.26 (0.05)	31.4 (1.6)	145 (20)	0.007 (0.0015)	0.034 (0.009)
Quercus montana	0.53 (0.05)	13.6 (0.7)	23.0 (2.3)	0.27 (0.05)	24.8 (2.8)	103 (10)	0.009 (0.0010)	0.037 (0.005)
Quercus rubra	0.60 (0.06)	14.9 (0.6)	19.4 (4.1)	0.29 (0.03)	32.6 (1.6)	116 (9)	0.006 (0.0005)	0.022 (0.002)
Quercus velutina	0.52 (0.07)	14.0 (0.7)	6.0 (0.7)	0.25 (0.04)	28.9 (1.5)	130 (15)	0.006 (0.0006)	0.030 (0.007)
Tilia americana	0.68 (0.07)	11.0 (0.5)	22.6 (3.0)	0.35 (0.05)	43.4 (4.1)	132 (11)	0.010 (0.0009)	0.035 (0.008)

Numbers in parentheses are standard error of the mean

Leaf characteristics for *Carya* species were conducted with leaflets since they were often detached in litter beds

SA:V surface area-to-volume ratio, *SLA* specific leaf area

Table 2 Moisture dynamics and flammability variables of 17 common northeastern North American tree species

Species	Cluster	Time-lag (h)	SMC (%)	Flame height (cm)	Flame time (s)	Smolder time (s)	Consumption (%)
Acer rubrum	4	14 (2.3)	380 (18.8)	60 (4.6)	47 (1.7)	249 (29.0)	84 (1.1)
Acer saccharum	3	10 (0.6)	335 (10.5)	65 (1.9)	32 (2.6)	170 (25.4)	82 (0.6)
Betula alleghaniensis	4	18 (1.7)	413 (17.9)	57 (7.3)	60 (6.2)	294 (30.6)	88 (0.7)
Carya glabra	4	22 (4.1)	428 (14.9)	59 (3.3)	43 (6.7)	186 (37.4)	82 (0.8)
Carya ovata	3	9 (1.0)	353 (9.0)	69 (4.2)	46 (1.8)	114 (11.1)	89 (0.5)
Carya tomentosa	4	16 (2.6)	461 (22.4)	73 (4.7)	45 (4.5)	158 (19.9)	87 (0.8)
Nyssa sylvatica	4	17 (1.5)	379 (7.4)	59 (2.7)	56 (6.0)	256 (29.6)	88 (1.6)
Pinus echinata	1	7 (0.5)	169 (4.3)	48 (5.4)	120 (14.7)	127 (17.3)	80 (1.4)
Pinus rigida	1	8 (0.5)	161 (8.8)	60 (3.5)	104 (8.8)	172 (15.1)	85 (1.3)
Pinus strobus	1	10 (0.4)	219 (8.4)	45 (2.2)	109 (3.6)	170 (15.8)	66 (1.4)
Pinus virginiana	1	9 (0.5)	229 (12.5)	31 (1.4)	98 (7.6)	143 (8.6)	67 (1.1)
Quercus alba	2	7 (0.6)	258 (4.9)	74 (3.4)	43 (3.8)	201 (18.5)	87 (0.5)
Quercus coccinea	2	10 (1.2)	293 (8.3)	76 (4.7)	38 (2.9)	220 (20.4)	89 (1.4)
Quercus montana	2	10 (0.9)	269 (4.6)	64 (2.9)	41 (1.3)	302 (33.3)	90 (1.5)
Quercus rubra	2	12 (2.0)	265 (13.1)	68 (5.1)	46 (2.4)	292 (26.1)	91 (1.3)
Quercus velutina	2	14 (2.9)	274 (8.5)	76 (2.2)	61 (12.5)	205 (28.0)	92 (0.5)
Tilia americana	3	11 (2.5)	300 (16.3)	51 (4.2)	54 (3.2)	173 (18.5)	81 (1.2)

Numbers in parentheses are standard error of the mean

Cluster assignment was based on a *k*-means cluster analysis

SMC saturation moisture content

Drying experiments

Moisture dynamics varied across the 17 tree species' litter with *Q. alba* and *P. echinata* drying the fastest (Table 2). *Q. alba* and *P. echinata* time-lag averaged 7 h, with the three other *Pinus* species drying nearly as fast (*P. rigida* = 8 h, *P. virginiana* = 9 h, and *P. strobus* = 10 h). Litter time-lag ranged as long as 22 h in *C. glabra*. The amount of water adsorbed by species' litter as a proportion of litter dry weight (saturation moisture content) ranged from 161 to 461%. The *Pinus* species adsorbed the least amount of water (ranging from 161 to 221%). *C. tomentosa*, *Betula alleghaniensis*, *C. glabra*, *A. rubrum*, *Nyssa sylvatica*, and *C. ovata* adsorbed the most water, in that order, with each species exceeding 300% saturation moisture content.

Burning experiments

The four flammability metrics during the burning of oven-dry leaf litter varied widely across species. Flame heights ranged from 31 cm in *P. virginiana* to 76 cm in both *Q. velutina* and *Q. coccinea* (Table 2). Flaming time was longest in *P. echinata* (121 s) and shortest in *Acer saccharum*, which flamed for only 32 s. All four of the *Pinus* species flamed for the longest (98 to 121 s). Smoldering time ranged from 114 s in *C. ovata* litter to 302 s in *Q. montana*. Consumption ranged from as little as 66% during the burning of *P. strobus* to as high as 92% of *Q. velutina* litter.

Multivariate analysis

Combining litter flammability and moisture metrics using PCA resulted in three factors accounting for 82% of the variability in the dataset (Fig. 1). Factor 1 (Flam 1) accounted for 44% of variability, with an eigenvalue of 1.6, and included flame time (r = -0.49), consumption (r = 0.47), and saturation moisture content (r = 0.45). Factor 2 (Flam 2) explained an additional 21% of the variability, with an eigenvalue of 1.1, and was primarily composed of maximum flame height (r = -0.48) and time-lag (r = 0.63). Factor 3 (Flam 3) explained 16% of the variability, with an eigenvalue of 1.0, and was strongly associated with smoldering time (r = -0.93).

Many of the leaf and litter bed traits were associated with moisture and flammability factors (Fig. 2). Factor 1 (Flam 1) was associated with the most leaf traits including curl (r = 0.34), length (r = 0.34), surface area-to-volume (r = -0.36), leaf density (r = -0.19), and litter bed bulk density (r = -0.40). The specific leaf area was the trait most associated with factor 2 (Flam 2, r = 0.13). Factor 3 (Flam 3), most related to smoldering duration, was best associated with packing ratio (r = -0.14).

Using cluster analysis with both moisture dynamics and flammability metrics, the 17 species grouped into four clusters that reflected the pyrophyte-mesophyte gradient (Table 2). All *Pinus* species were in a single pyrophytic group (cluster 1) with the shortest time-lag and lowest saturation moisture content, but with

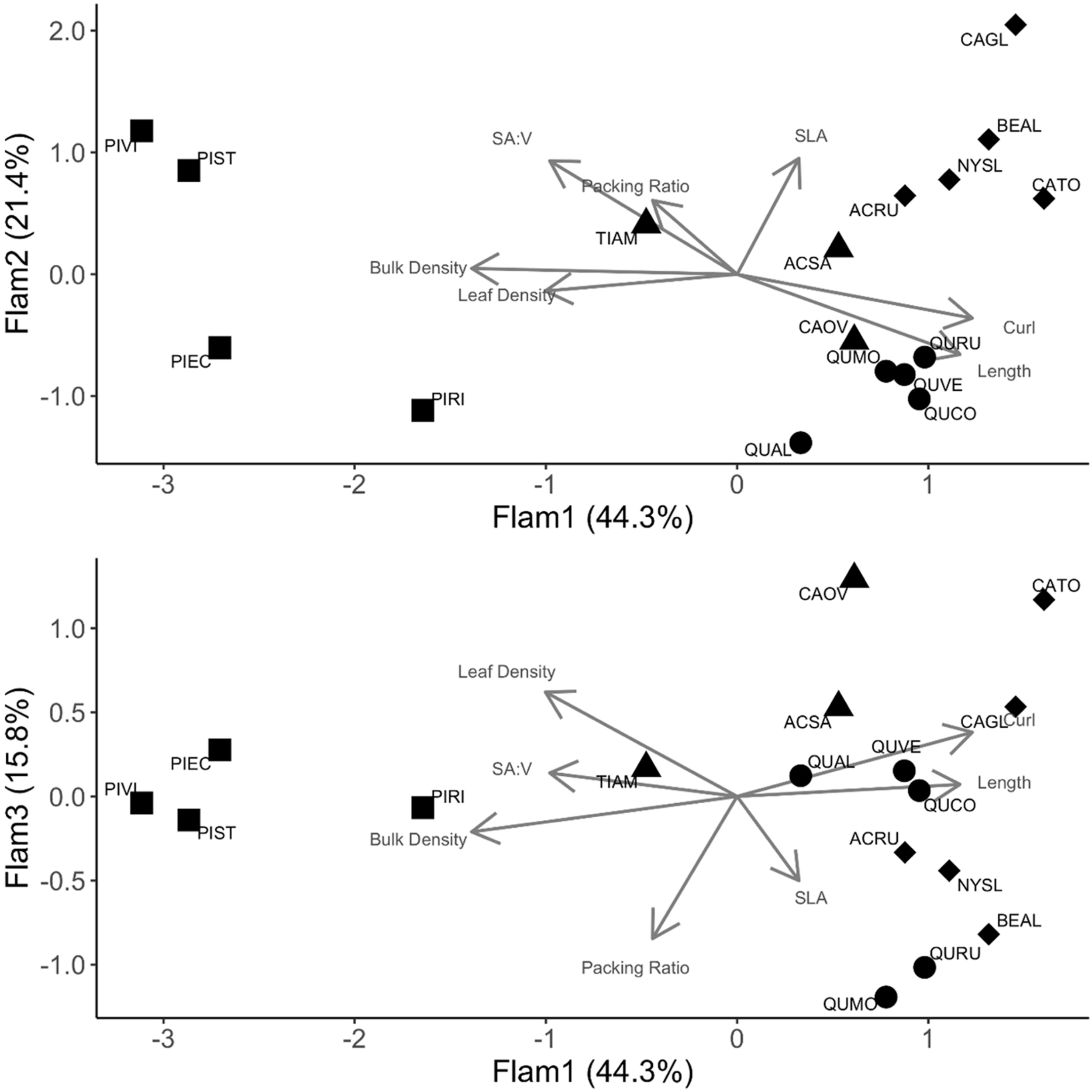

Fig. 1 Species positions along three litter moisture and flammability axes based on principal components analysis (PCA). The first PCA factor (Flam1) explained 44.3% of the variation and was negatively associated with flaming time ($r = -0.49$) and positively associated with consumption ($r = 0.47$) and saturation moisture content ($r = 0.45$). The second PCA axis (Flam2) explained 21.4% of the variation and was negatively associated with maximum flame height ($r = -0.48$) and positively associated with time-lag ($r = 0.63$). The third flammability axis explained 15.8% and was negatively associated with smoldering time ($r = -0.93$). Shared symbol shapes reflect species classified in the same cluster based on a *k*-means cluster analysis. The gray join plots refer to the relative strength and direction of significant relationships ($\alpha = 0.05$) between litter traits and moisture/flammability scores. SA:V, surface area-to-volume ratio; SLA, specific leaf area

shorter flame lengths, longer flame times, and poorer consumption. The second pyrophytic group (cluster 2) comprised all *Quercus* species which adsorbed slightly more water than *Pinus* and had intermediate time-lags but burned with rapid flaming and taller maximum flame heights. *C. ovata*, *Tilia americana*, and *A. saccharum* made up a mesophytic group (cluster 3) with intermediate fire-dampening characteristics and more extensive smoldering. *A. rubrum*, *Betula alleghaniensis*, *Nyssa sylvatica*, *C. glabra*, and *C. tomentosa* were

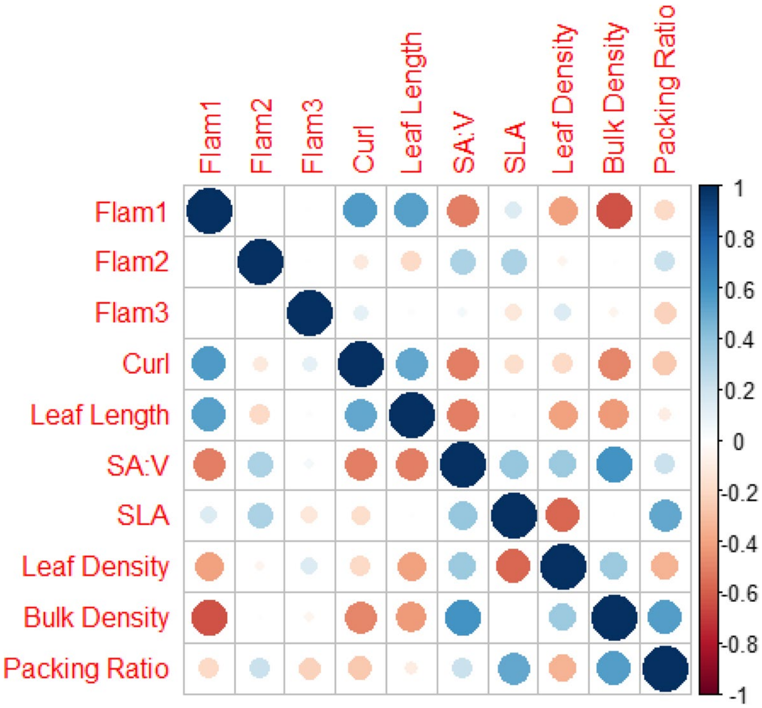

Fig. 2 Correlation matrix of PCA factors from multivariate analysis of leaf litter flammability and moisture dynamics metrics with measured leaf and litter bed traits. SA:V, surface area-to-volume ratio; SLA. specific leaf area

in the least flammable mesophytic group (cluster 4) that had high moisture adsorption (saturation moisture contents exceeded 330%), slow drying rates (all had time-lags > 15 h), and moderate flame heights and flame times.

Discussion

Our findings clearly demonstrate the variation in litter flammability among common northeastern North American temperate tree species. Distinctions between so-called "mesophytes" and "pyrophytes" were evident when considering both moisture dynamics and flammability across the 17 species. Most of our results were confirmatory and consistent with other regional litter flammability studies. Oaks were highly flammable across all species. *Q. alba*, a widely dispersed species in eastern North America, was a clear pyrophyte based on its rapid drying and high flammability, as has been found by others (Kane et al. 2021; McDaniel et al. 2021; Varner et al. 2021). The role of fire in northeastern North American oak ecosystems has been well established (Brose et al. 2014), and long-term fire exclusion has been implicated in the loss of oaks, particularly *Q. alba*, in the region (Abrams 2003; Nowacki and Abrams 2008). Increases in fire-sensitive mesophytic species pose challenges to oak restoration where burning is being applied (Arthur et al. 2012; Kane et al. 2021). The generic-level contribution of *Quercus* to the flammability of these pyrophytic ecosystems should be considered as an important ecological component.

Unlike previous studies that found distinct variation in litter flammability among species within the genera *Pinus* spp. (Varner et al. 2022) and *Quercus* spp. (Kane et al. 2008; Engber and Varner 2012), our species were relatively tightly clustered according to genus. This finding likely reflects the wider phylogenetic range across the 17 species we examined and relatively few species from within the *Pinus* and *Quercus* genera, compared to other studies. Interspecific variability of flammability within genera may also be more important in other regions, e.g., western and southeastern North America, where fire sensitivity varies more widely across species, particularly in the diverse *Quercus* genus (Kane et al. 2008; Kreye et al. 2013; Engber and Varner 2012).

While *Pinus* species burned somewhat poorly in our study, with lower flame heights and less consumption, their duration of flaming was longer than other species. The *Pinus* species absorbed significantly less moisture and dried rapidly compared to other species, highlighting their greater potential to burn under wetter climates, typical in the northeast region. Even though *Pinus* species grouped together in our cluster analysis, *P. rigida* and *P. echinata*, both known to tolerate fire (Delcourt and Delcourt 1997; Marschall et al. 2016), burned with taller flame heights and greater consumption than *P. virginiana* or *P. strobus*. Flammability among the *Pinus* genus varies widely (Cornwell et al. 2015; Varner et al. 2022), and the results here highlight that moisture dynamics may be a critical component to understanding the potential role of *Pinus* litter in the pyrophytic pine and pine-oak ecosystems.

Consistent with our expectations, we found that *A. rubrum*, *Betula alleghaniensis*, *Nyssa sylvatica*, and two of the *Carya* species (*C. glabra* and *C. tomentosa*) were clustered as strong mesophytes with lower flammability and greater moisture retention. *A. rubrum* is commonly implicated as a strong mesophyte throughout eastern North America (Nowacki and Abrams 2008; Kreye et al. 2013; Kane et al. 2021; McDaniel et al. 2021). Similarly, a prior study examining flammability in southeastern US species has identified *Nyssa sylvatica* as being a strong mesophyte (Varner et al. 2021). The inclusion of *Betula alleghaniensis* as a strong mesophyte confirmed our expectations, but our study is the first to report this finding. We were somewhat surprised that *A. saccharum* was not as strong of a mesophyte given its propensity to establish in the absence of fire in some northeastern forests and woodlands (e.g., Nowacki and Abrams 2008). However, *A. saccharum* retained less moisture and dried faster than *A. rubrum*. There remains a debate over the flammability and ecological roles of *Carya* spp. in eastern North American woodlands and forests (Pile-Knapp et al. 2021; Varner et al. 2021). Our data suggest that they function more as a mesophyte, but the clear dichotomy between these two coarse categories is likely more nuanced for this genus and other species (Keeley and Zedler 1998; Varner et al. 2021).

Leaf and litter bed traits were strongly associated with moisture dynamics and flammability of common northeastern tree species. In particular, litter bed bulk density was a major factor explaining the variation in litter flammability in the species examined. Consistent with other findings (Scarff and Westoby 2006; Engber and Varner 2012; Burton et al. 2020), species with longer leaves and greater curling resulted in more porous litter beds that resulted in rapid flaming and increased consumption. In the second flammability dimension, variation in specific leaf area among species was most strongly associated with differences in maximum flame length and time-lag. Somewhat similarly, Burton et al. (2020) found that specific leaf area was associated with flame spread rate and flame duration through its influence on bulk density. Kreye et al. (2013) found that multiple leaf traits were associated with saturation moisture content (surface area: volume, leaf thickness) and time-lag (curling, length, width, and mass). Our analysis determined SLA to be the litter trait most strongly associated with variation in time-lag. Given the propensity for litter flammability to be interactively impacted by both flammability and moisture dynamics (e.g., Kreye et al. 2018a, b; Kane et al. 2021), it is necessary to determine which leaf and litter bed properties best characterize direct and indirect influences on each. Future research focused on a larger suite of species, with varying traits and depth within taxonomically related species, will assist the development of more rigorous trait-flammability relationships.

Variations in litter flammability and species groupings observed here demonstrate the importance of litter composition on fire potential and may elucidate the role of species composition on past, present, and future fire regimes in northeastern North America. Interactive effects of land use change and fire exclusion have resulted in significant changes in forest composition that likely precipitated a dampening mechanism for mesophication. Fire history studies in the region (Shumway et al. 2001; Stambaugh et al. 2018; Abadir et al. 2019; Marschall et al. 2016, 2019, 2022) suggest that fire was frequent and pyrophytic species likely promoted frequent fire to their benefit (as in Stevens et al. 2020). With the loss of pyrophytic species, fire-sensitive mesophytic species are becoming increasingly dominant (Abrams and Downs 1990; Abrams and Nowacki 1992). Given their propensity to dampen flammability, mesophytes are likely to further alter these fire regimes (Kreye et al. 2018a, b; Kane et al. 2021) and reinforce the positive mesophication feedbacks in the region (Nowacki and Abrams 2008; Alexander et al. 2021).

We examined 17 dominant or codominant tree species across temperate northeastern North America, but the region is highly diverse and many important species were not included in this study. Red pine (*P. resinosa* Aiton) is a major overstory tree across the region, southern Canada, and the Great Lakes. Using identical burning methods (but not drying), Varner et al. (2022) found that *P. resinosa* was highly flammable, likely corresponding to our most flammable cluster. Unpublished data (Cigan, Varner, and Kreye) also reveal that *P. resinosa* dries rapidly, reinforcing the pattern we observed in the other pines. American chestnut (*Castanea dentata* (Marshall) Borkh.), functionally extinct but formerly dominant across much of the region, burns with high flammability and dries in an intermediate fashion (Kane et al. 2019; Kane et al. 2020), likely positioning *C. dentata* with the pines or at the most flammable end of the oaks. The region is diverse, so other common species, e.g., *Betula lenta* L., *Prunus serotina* Ehrh., *Fagus grandifolia* Ehrh., *Populus tremuloides* Michx., and other *Quercus* spp. (among others) warrant inclusion in future work. Species formerly common, but currently becoming rare due to pest and disease impacts, e.g., *Fraxinus* spp. and

Tsuga canadensis (L.) Carrière, could also be examined to consider changing impacts on local fire potential (Varner et al. 2017).

Our experiments focused on burning dry litter and measuring the most dominant environmental control, moisture dynamics. As mentioned before, the majority of species we analyzed followed our hypotheses and broader patterns of changes in species composition and structure across the region. A few species diverged from these patterns, most notably *A. saccharum* and *T. americana*. These two species are widely considered classic mesophytes and anecdotally dampen fire spread and intensity. Two additional factors, the effects of shade and differential decomposition rates, may better clarify how these species affect fire regimes. Future work that ties in the ability of these species to cast deep shade, decreasing incoming solar radiation, and slowing drying may better elucidate their role in the fire environment (Kreye et al. 2020). Recent work highlights how decomposition can both decrease litter depths (increasing bulk density; Dickinson et al. 2016) and decrease litter fuel mass (Babl-Plauche et al. 2022), diminishing flammability. The species we measured here and past flammability experiments have mostly overlooked this phenomenon, potentially inflating the flammability of many species. Clearly, more work is needed to tie together field observations with lab experiments and more broadly to understand how species and their differential traits function in past, present, and future fire regimes.

The modification of fire regimes and other global changes have altered fire-vegetation interactions with profound effects on many ecosystems in this region and others (Nowacki and Abrams 2008; Stambaugh et al. 2015). A dramatic shift toward more mesic and fire-sensitive tree species composition has been well established through much of northeastern North America (e.g., Fei and Steiner 2009; Nowacki and Abrams 2008; Knott et al. 2019; Kane et al. 2020) with potentially important impacts on the subsequent fire environment. We demonstrated trait-mediated variation of litter moisture dynamics and flammability that support the incidence of mesophication following major vegetation shifts in deciduous woodlands and forests of northeastern North America. Incidents of forest mesophication resulting from long-term fire exclusion are also being recognized in other temperate regions of the world, e.g., Europe (Spînu et al. 2020). Shifts in vegetation resulting from altered fire regimes and subsequent impacts on the fire-vegetation environment should be examined more broadly to better understand if this is a global phenomenon.

Conclusions

The findings of this study reveal wide variation in leaf litter flammability across 17 common tree species found in temperate northeastern North American forests and woodlands. Species grouped into flammability categories that highlight a spectrum in both flammability and moisture retention. *Quercus* (oak) species were the most flammable among all species and dried quickly, whereas *Pinus* (pine) litter did not burn as intensely, but absorbed very little moisture and dried the fastest, and sustained combustion for long periods. A suite of mesophytic species, including *Acer rubrum*, *Betula alleghaniensis*, *Carya glabra*, *C. tomentosa*, and *Nyssa sylvatica* burned poorly and showed substantial moisture retention. Interspecific variability in leaf and litter bed traits explained substantial differences in both moisture dynamics and flammability among the species examined. Physical trait relationships with flammability indices provide evidence of a potential mechanistic control of tree species composition on surface fire behavior. Our findings extend our understanding of litter traits' influence on the combustion environment and affirm the potential effects of pyrophytic and mesophytic tree species on contemporary fire regimes in temperate forests of northeastern North America.

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Authors' contributions

JKK and JMK designed the study and interpreted the results. JKK wrote the first draft of the paper. JMK led the experimental burning and contributed to the writing. JMV interpreted the results and contributed to the writing. The authors read and approved the final manuscript.

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Availability of data and materials

All data are available from the authors.

Declarations

Ethics approval and consent to participate

This study did not involve human participants, tissue, or data.

Consent for publication

All figures and tables were created by the authors, and all authors give their consent to publish.

Competing interests

The authors declare that they have no competing interests.

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