

Mesophytic litter dampens flammability in fire-excluded pyrophytic oak–hickory woodlands

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Abstract. Fire exclusion in eastern North American *Quercus*–*Carya* woodlands has resulted in overstory compositional changes, linked to altered fuel composition, structure, and ultimately, altered fire regimes. These compositional changes have been implicated in a dampening effect on fire behavior in formerly fire-prone ecosystems, the positive feedback termed “mesophication.” Several proposed mechanisms are likely involved in this process; however, few have been examined. We evaluated the potential mechanism of dampened forest floor flammability through changes in litter composition in a southeastern U.S. oak–hickory forest undergoing mesophication. Laboratory drying and burning experiments revealed that increasing the relative contribution of litter from fire-sensitive mesophytic tree species (*Liquidambar styraciflua*, *Ulmus alata*, and *Cornus florida*) increased moisture retention and diminished litter flammability. Litterbeds composed of $\geq 66\%$ mesophyte litter gained the most moisture following fuelbed saturation and were consistently wetter than pyrophyte litter following 12 and 24 h of drying. Flammability metrics decreased with increasing contribution of mesophyte litter with reductions most pronounced under more moist conditions. Under dry conditions, where litter moisture did not differ across compositional treatments, mesophyte litter was less flammable than fuelbeds that contained any pyrophyte litter. The combined effects of moisture retention and less flammable litter reveal an important synergistic impact that may result with increased dominance of fire-sensitive mesophytic species. Restoration efforts in long-unburned eastern hardwood forests may require altering stand composition to limit mesophytic litter input or developing burn prescriptions that intensify surface fire behavior in less flammable fuels.

Key words: ecological stability; ecosystem restoration; fire behavior; flammability; mesophication; oak–hickory forests; prescribed fire; pyrophytic.

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INTRODUCTION

Historically fire-prone oak–hickory (*Quercus*–*Carya* spp.) savannas, woodlands, and forests of eastern North America have undergone major shifts in forest structure and composition due to legacies of land-use change and fire exclusion (Abrams 1992, Brewer 2001, Nowacki and Abrams 2008, Hanberry et al. 2012, Dickinson et al. 2016). Presettlement oak–hickory savannas

and woodlands were widespread and dominant in this region largely as a result of frequent fires ignited by lightning and Native Americans (Abrams 1992, Nowacki and Abrams 2008, Stambaugh et al. 2015, Varner et al. 2016). Fire exclusion has generally led to encroachment and eventual replacement by many tree species that were rare in historically fire-prone forests (Abrams 1992, Brewer 2001, Nowacki and Abrams 2008).

Increased establishment and dominance of fire-sensitive and often shade-tolerant tree species has been implicated in the positive feedback termed “mesophication” in many formerly fire-prone ecosystems of eastern North America (Nowacki and Abrams 2008, Hanberry et al. 2012, Kreye et al. 2013). The ecological consequences of mesophication are wide-ranging, but of primary importance are the changes to vegetation structure and species composition given their influence on many other ecosystem components, processes, and functions (Tilman et al. 1997, Alexander and Arthur 2010). For instance, structural changes including increased tree density and subsequent canopy closure can reduce herbaceous diversity (Fralish 2004) and subsequently diminish wildlife habitat (Harper 2007). In addition, sheltering of surface fuels from the drying elements of solar insolation increases moisture conditions at the forest floor (Byram and Jemison 1943, Nowacki and Abrams 2008). Increased surface fuel moisture resulting from altered stand structure is expected to reduce forest floor flammability, creating a potential positive feedback which promotes further encroachment, survival, and dominance by less flammable, fire-sensitive species (mesophytes; Nowacki and Abrams 2008, Kreye et al. 2013).

Fire–vegetation feedbacks of mesophication are not limited to changes in stand structure, but might also be driven by resulting shifts in fuelbed composition, such as changes in leaf litter composition or the disappearance of grasses in former oak savannas and woodlands (Veldman et al. 2013, Brewer 2015). Grasses can be a flammable fuel component in savannas and woodlands, when present; however, leaf litter is a primary carrier of fire in long-unburned oak–hickory uplands (Brewer and Rogers 2006). Therefore, changes in fuelbed composition (i.e., fallen foliar litter) due to increasing dominance of mesophytes may play a key role in the dampening of forest flammability (Kane et al. 2008, Kreye et al. 2013). Litter of mesophytes gains more moisture, through absorption or adsorption processes, and retains moisture longer than litter cast from the fire-resistant species (pyrophytes) they replace (Kreye et al. 2013). Furthermore, comparative studies of litter flammability have shown that fire-sensitive species are often less flammable (burning with reduced flame heights, diminished fuel consumption) than fire-resistant species, even within the same genus (e.g.,

Fonda 2001, Kane et al. 2008, Engber and Varner 2012). Given that mesophytes have been hypothesized to increase forest floor moisture (Nowacki and Abrams 2008) and produce less flammable litter, their impacts on the intensity, frequency, and extent of fire in fire-dependent ecosystems may have significant ecological consequences.

Restoration of ecosystems in which fire has been excluded ultimately requires the reintroduction of fire, so understanding the impacts of altered forest composition on fire behavior is of critical importance. Efforts to restore historic fire regimes in many oak–hickory forests have been hampered by altered fire behavior and subdued effects (i.e., minimal mortality of fire-sensitive tree species; McEwan et al. 2011). Diminished fire behavior and effects in these ecosystems have been hypothesized to be driven by the greater moisture retaining ability (Kreye et al. 2013) and the low flammability (Kane et al. 2008) of litter from fire-sensitive mesophytic species. The combined effects of moisture retention and flammability, however, have not been examined. Moreover, these effects have not been examined across mixtures of litter composed of mesophytic vs. pyrophytic species to evaluate the relative impact mesophytic litter has on flammability. Such work would enhance our understanding of the mechanisms of mesophication and provide land managers with insight into thresholds of mesophytic encroachment where fuel composition may hinder forest floor flammability and restoration efforts in these formerly fire-prone ecosystems.

The goal of this research was to examine the influence of mesophication and resultant fuelbed compositional changes on forest floor flammability in a historically fire-prone oak–hickory upland in northern Mississippi, USA. Our specific objectives were to vary the proportion of mesophytes relative to several pyrophytic *Quercus* and *Carya* species to quantify the effects of litter composition on moisture loss and flammability metrics. We hypothesized (1) that litterbeds composed of increasing proportions of mesophytic species would retain more moisture vs. pyrophyte-dominated litterbeds following soaking and drying and (2) that mesophyte-dominated litter mixtures would burn with dampened flammability (lower intensity, consumability, and greater sustainability; Varner et al. 2015) compared to pyrophyte-dominated litter. Results from our study will have direct

implications for oak–hickory woodlands, but may more widely apply to other fire-prone regions that have shifted dominance toward mesophytic species.

MATERIALS AND METHODS

Study site and species

Litter was collected in an oak–hickory forest at Strawberry Plains Audubon Center in the loess plains of north-central Mississippi, USA. The area is characterized by gently rolling hills with moderate soil fertility typical of the southeastern Coastal Plain. Soils at the study site include a mixture of Providence silt loam and Cahaba sandy loam (Morris 1981, Brewer 2015). Fire was excluded from this site for several decades, and fire-sensitive mesophytic tree species had developed in the midstory (Brewer 2001). The overstory consisted of several oak species (*Quercus falcata* Michx., *Quercus stellata* Wangenh., *Quercus alba* L., *Quercus coccinea* Muenchh., and *Quercus velutina* Lam.), two hickories (*Carya tomentosa* (Poir.) Nutt. and *Carya glabra* Mill.), and a mid-story that included fire-sensitive species (*Liquidambar styraciflua* L., *Ulmus alata* Michx., *Nyssa sylvatica* Marsh., *Cornus florida* L., *Prunus serotina* Ehrh., and *Acer rubrum* L.) locally absent in the presettlement overstory, but common in the region (Brewer 2001). Climate in the study area consists of long hot summers and short cool winters (average summer high 32°C, average winter low 0°C) with >50% of annual precipitation, which averages 1270 mm, occurring between April and September (Morris 1981).

Litter collection and burning experiments

In December 2016, we collected recently cast litter (Oi horizon, no significant signs of decomposition) from across the site. We collected

approximately 40 g of litter from eight locations surrounding the bases of 24 randomly selected dominant oaks at 0, 45, 90, 135, 180, 225, 270, and 315° azimuths as well as at eight locations beyond their dripline, along the same azimuths, to ensure capture of other species' (*Carya* spp. and mesophytes) litter. Litter samples were bagged, oven-dried, sorted by species, and weighed.

We used the collected litter to create sixty fuelbeds (~15 g each) comprised of four different relative contributions of mesophytic and pyrophytic litter (0%, 33%, 66%, and 100% mesophytes; by weight; Table 1). This design represented a gradient of increasing dominance by mesophytic tree litter vs. pyrophytes. For all fuelbeds, pyrophyte litter was composed of equal contributions of *Q. stellata*, *Q. falcata*, *Q. alba*, *Q. coccinea*, *Q. velutina*, and *Carya* spp. The mesophyte litter was comprised of litter from three species most represented in the litter collected: *L. styraciflua*, *U. alata*, and *C. florida*, with each of these three species contributing different amounts of litter per fuelbed based on their relative abundance by mass (Table 1). There was not enough litter from the remaining mesophyte species (*N. sylvatica*, *A. rubrum*, and *P. serotina*) to be included in experiments.

Litterbeds were burned in a 4 × 3 experimental design. Each of the fifteen fuelbeds within the four litter-composition treatments was randomly assigned to one of three moisture treatments: wet, moderate, and dry. All litter was oven-dried at 60°C and then allowed to equilibrate under controlled laboratory conditions (24–28°C, 40–50% relative humidity) prior to experiments. Moisture treatments were established through defined drying times, allowing moisture desorption to vary across litter compositions (Kreye et al. 2013). For wet and moderate moisture treatments, litter was soaked in a water bath for 24 h to reach saturation moisture content (SMC),

Table 1. Fuelbed mass by species for laboratory burning experiments conducted to observe the influence of litter composition on flammability at Strawberry Plains Audubon Center, Mississippi, USA.

Mesophyte litter %	Pyrophytes						Mesophytes		
	<i>Quercus stellata</i> g	<i>Quercus falcata</i> g	<i>Quercus alba</i> g	<i>Quercus coccinea</i> g	<i>Quercus velutina</i> g	<i>Carya</i> spp. g	<i>Liquidambar styraciflua</i> g	<i>Ulmus alata</i> g	<i>Cornus florida</i> g
0	2.50	2.50	2.50	2.50	2.50	2.50	0.00	0.00	0.00
33	1.67	1.67	1.67	1.67	1.67	1.67	1.50	3.00	0.50
66	0.83	0.83	0.83	0.83	0.83	0.83	3.00	6.00	1.00
100	0.00	0.00	0.00	0.00	0.00	0.00	4.50	9.00	1.50

as conducted by Kreye et al. (2013), and then allowed to dry for 12 h for the wet moisture treatment and 24 h for the moderate treatment under the same laboratory conditions above. The dry moisture treatment consisted of litterbeds at equilibrium moisture content (EMC; constant moisture content attained following prolonged exposure to stable atmospheric conditions; Blackmarr 1971) in the laboratory, with litter moistures expected to be similar across all compositional litter mixes thus allowing the ability to compare the exclusive effect of litter composition on flammability. Each litterbed, across all fuel moisture treatments, was weighed prior to ignition to determine gravimetric moisture content [(ignition wet weight – oven-dry weight)/oven-dry weight] at the time of burning.

Litterbeds were burned using standard methods of Kane et al. (2008) within the same combustion laboratory (Humboldt State University Wildland Fire Science Laboratory, Arcata, California, USA). Litter was placed on an array of xylene-soaked cotton string laid out in a 35 × 35 cm grid. Litterbeds were carefully transferred from drying pans to the burn platform and were approximately 20 × 20 cm. To account for potential differences in bulk density, litter depth measurements were taken at four locations (~7 cm from the corners diagonally into the litterbed) prior to ignition and averaged for subsequent analysis. Xylene-soaked strings were then ignited around the perimeter of the array that uniformly ignited the litterbeds. Laboratory conditions during burns ranged from 19.3° to 22.6°C ($\bar{x}$ = 21.1, SD = 0.8) and 45% to 55% relative humidity ($\bar{x}$ = 50, SD = 3) with no differences across any treatments ($P > 0.05$).

For each burn, we measured maximum flame height (cm), flaming time (s), smoldering time (s), and consumption (%; as in Kane et al. 2008, Engber and Varner 2012). Because these flammability metrics are typically correlated (Engber and Varner 2012), we conducted a principal components analysis (PCA) to combine correlated metrics into PCA factors. Factor scores were then compared across moisture and litter-composition treatments using general linear modeling (GLM) testing for both main effects and their interactions. Assumptions of homoscedasticity and normality of residuals were tested using the modified Levene test and Shapiro-Wilk test, respectively. Since we

allowed for variability in moisture contents across our drying treatments, an expected outcome of differential moisture desorption (Kreye et al. 2013), we also conducted a GLM analysis of covariance to evaluate whether flammability metrics differed across litter composition after accounting for moisture content. Post hoc multiple comparisons of means were conducted using the Tukey-Kramer test (Sokal and Rohlf 1995) for all GLM analyses. All analyses were performed in NCSS version 9 (NCSS, Kaysville, Utah, USA).

RESULTS

In accordance with our first hypothesis, litterbeds composed of increasing proportions of mesophytic species retained more moisture compared to pyrophyte-dominated litterbeds. Saturation moisture content, following 24 h of water soaking, differed across litter composition ($P < 0.001$) with all litter mixtures differing from each other (Fig. 1; drying time = 0). Saturation moisture contents increased with increasing

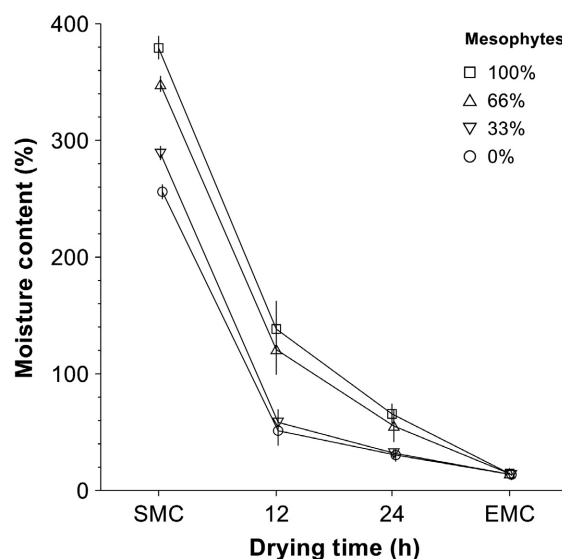


Fig. 1. Moisture contents of litterbeds comprised of varying proportions of mesophytic (shown as a percentage) vs. pyrophytic species during laboratory burning across three different moisture treatments. Litterbeds were initially soaked to saturation moisture contents (SMCs) and then allowed to dry for either 12 h (wet treatments) or 24 h (moderate treatments) before burning. Litterbeds at equilibrium moisture content (EMC) were also burned.

proportions of mesophytes, averaging 256% (SE = 6), 289% (SE = 6), 348% (SE = 7), and 379% (SE = 10) for litterbeds comprised of 0%, 33%, 66%, and 100% mesophytic species, respectively. Fuel moisture content at the time of burning differed across moisture treatments ($P < 0.001$) and litter compositions ($P < 0.001$), but with a significant interaction between these main effects ($P = 0.006$), as expected. Litterbeds were wettest following 12 h of drying, moderately moist following 24 h of drying, and driest at EMC across all litter compositions (Fig. 1). Moisture contents differed across litter compositions at the higher moisture contents, following 12 and 24 h of drying, but not at EMC. As at time 0, moisture content was greater in litterbeds comprised of increasing percentages of mesophytic species after both 12 and 24 h of drying (Table 2, Fig. 1). Litterbed depths ranged from 3.6 to 8.3 cm and averaged 5.6 cm (SD = 0.9). Differences in depth were found across litter composition ($P = 0.036$); however, post hoc differences were not detected (Table 2). Litterbed depth did not differ across moisture treatments ($P = 0.349$).

Flammability metrics varied across moisture and composition treatments (Table 2). Correlations between flammability metrics were apparent and

supported combining metrics. The strongest correlation was between flame height and consumption ($r = 0.85$; Table 3). Flame height was positively correlated with smolder time ($r = 0.41$), but was negatively, although weakly, correlated with flame time. Smolder time and consumption were also positively correlated ($r = 0.50$). Combining correlated flammability metrics using PCA resulted in two factors explaining 81% of the variability in the dataset, with eigenvalues of 2.24 and 0.99 for Factor 1 and Factor 2, respectively. Factor 1 explained 56% of the dataset and was positively related to flame height, smoldering time, and litter consumption, with factor loadings of 0.91, 0.71, and 0.91, respectively. Factor 2 explained an additional 25% of the dataset and was positively related to flame time, with a factor loading of 0.96.

We confirmed our second hypothesis that litterbeds with increasing proportions of mesophytic species were less flammable than litterbeds composed of primarily pyrophytic species. The combined flammability metrics included in PCA Factor 1 (flame height, smolder time, consumption) differed across both moisture treatments and compositions ($P < 0.001$ for both), but with marginal evidence of an interaction ($P = 0.053$) using a general linear model (Fig. 2). The two composition

Table 2. Mean values of litterbed characteristics, individual flammability metrics, and PCA factor scores of correlated flammability metrics combined across moisture and composition treatments of litter flammability experimental burns.

Treatment	FMC %	Litter depth cm	Flame height† cm	Flame time s	Smolder time s	Consumption %	PCA Factor 1‡ Unitless	PCA Factor 2§ Unitless
12-h drying								
100%	138 (24)	4.9 (0.4)	17 (4)	62 (15)	64 (11)	13 (3)	-2.03 (0.21)	0.02
66%	121 (21)	5.7 (0.2)	27 (4)	48 (2)	170 (34)	30 (8)	-1.03 (0.32)	-0.78
33%	59 (11)	5.1 (0.2)	43 (5)	50 (4)	225 (28)	55 (7)	-0.07 (0.25)	-0.37
0%	52 (14)	6.7 (0.3)	52 (6)	50 (4)	236 (32)	64 (9)	0.32 (0.34)	-0.19
24-h drying								
100%	66 (9)	5.4 (0.4)	27 (2)	64 (7)	143 (16)	47 (5)	-0.97 (0.18)	0.47
66%	55 (14)	5.4 (0.2)	43 (7)	55 (7)	275 (81)	58 (10)	0.09 (0.46)	-0.02
33%	32 (4)	5.7 (0.3)	56 (6)	47 (3)	210 (8)	77 (3)	0.54 (0.14)	-0.25
0%	30 (5)	5.3 (0.5)	56 (5)	50 (9)	200 (16)	76 (6)	0.48 (0.24)	-0.07
EMC								
100%	14 (1)	5.8 (0.4)	44 (2)	66 (3)	217 (16)	76 (2)	0.12 (0.05)	0.97
66%	14 (0)	5.9 (0.3)	57 (7)	53 (3)	246 (52)	81 (3)	0.70 (0.14)	0.20
33%	14 (1)	5.2 (0.5)	61 (4)	54 (3)	276 (29)	84 (1)	0.94 (0.14)	0.28
0%	13 (0)	6.5 (0.6)	60 (6)	45 (2)	229 (36)	88 (1)	0.90 (0.11)	-0.27

Notes: Values in parentheses are standard error. FMC, Fuel moisture content; EMC, equilibrium moisture content; PCA, principal components analysis.

† Maximum flame height.

‡ Factor 1 is comprised primarily of flame height, smolder time, and consumption.

§ Factor 2 is comprised primarily of flame time.

Table 3. Correlation matrix between measured flammability metrics during burning of litterbeds comprised of different combinations of pyrophytic and mesophytic species.

Flammability metric	Flame height	Flame time	Smolder time	Consumption
Flame height				
Flame time	-0.23			
Smolder time	0.41	-0.16		
Consumption	0.85	-0.03	0.50	

treatments with the least mesophytic litter (0% and 33%) did not differ in flammability Factor 1, but litterbeds with 66% mesophytic litter were lower than both 0% and 33% mesophytic litterbeds. Litterbeds comprised of 100% mesophytes had the lowest in flame heights, smolder time, and consumption of all treatments. Principal components analysis Factor 2 (flame time) did not differ across moisture ($P = 0.151$) or composition ($P = 0.206$) treatments. When the moisture content of each litterbed was used as a covariate ($P < 0.001$), instead of evaluating moisture treatment as a main factor,

flammability Factor 1 differed across composition treatments ($P < 0.001$), but only litterbeds comprised of 100% mesophytes were lower than the other three mixtures according to the Tukey-Kramer test (Fig. 3).

DISCUSSION

Results here highlight the capacity for litter from mesophytic trees to gain more moisture, retain moisture longer, and diminish overall flammability. Changes in overstory composition resulting from encroachment by fire-sensitive mesophytes into pyrophytic *Quercus-Carya* woodlands may dampen fire behavior through incorporation of less flammable or fire-impeding litter. In conjunction with direct and indirect influences of altered forest structure (e.g., increases in density and basal area, greater shade and decline of shade-intolerant herbaceous species, and inhibition of below-canopy winds), the impacts of shifting species composition on these once fire-prone ecosystems may result in losses of ecological function (Nowacki and Abrams 2008, Stambaugh et al. 2015).

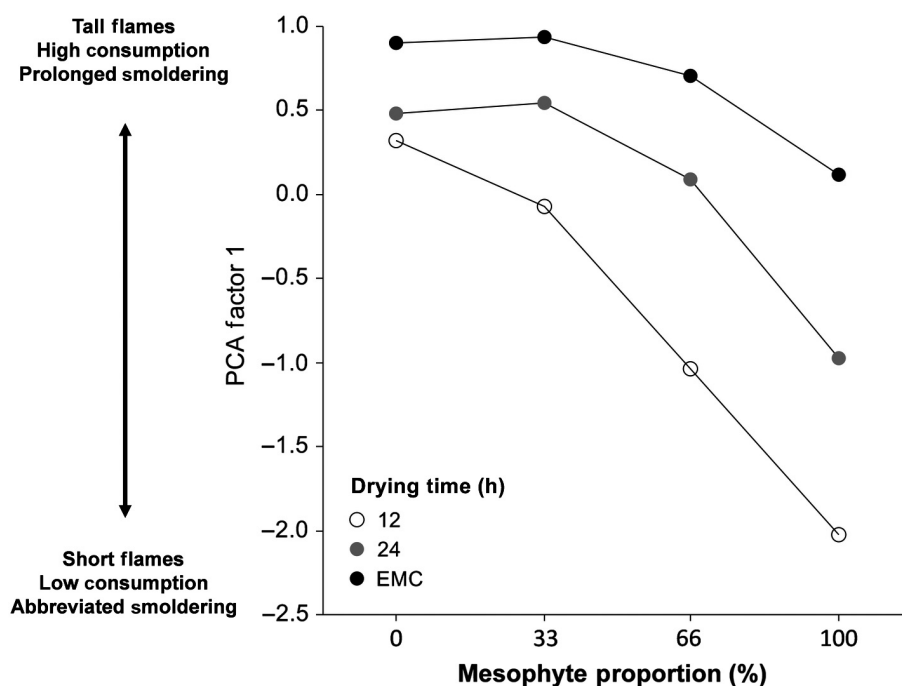


Fig. 2. Flammability metrics (flame height, smolder time, consumption) combined through principal components analysis (PCA) across different litter compositions with varying amounts of mesophytic species (0%, 33%, 66%, 100%) after 12 and 24 h of drying, following saturation, and at equilibrium moisture contents.

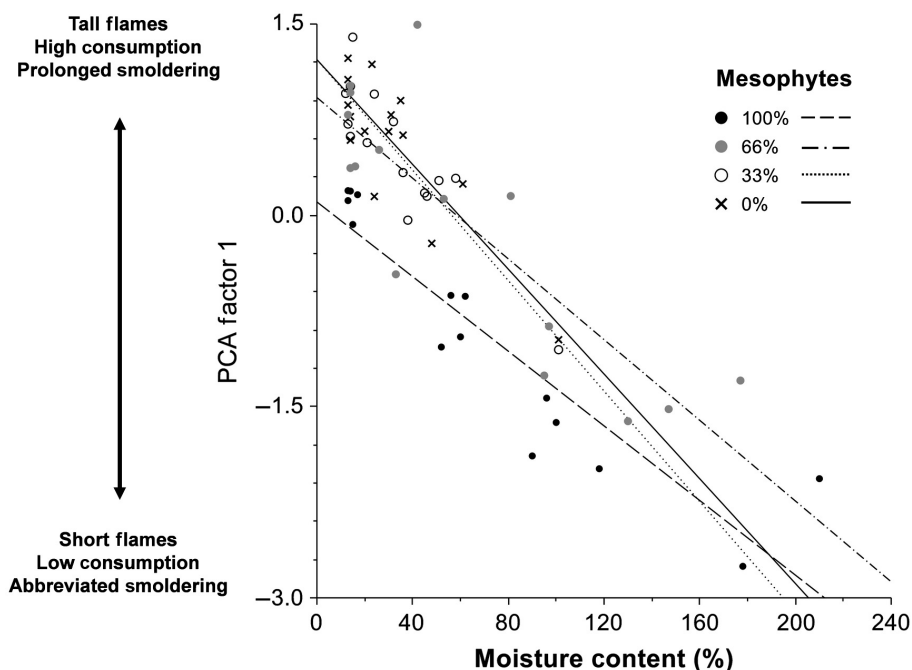


Fig. 3. Flammability metrics (flame height, smolder time, consumption) combined through principal components analysis (PCA) of different litter compositions with varying amounts of mesophytic species (0%, 33%, 66%, 100%) as a function of litterbed moisture contents at the time of laboratory burning.

The influence of litter from the mesophytes *Liquidambar styraciflua*, *Ulmus alata*, and *Cornus florida* on both fuelbed moisture retention and diminished flammability was demonstrated in these experiments. Leaf-level characteristics (e.g., thickness, surface area:volume, size, leaf curling) and fuelbed characteristics (e.g., depth, bulk density) are likely drivers of moisture dynamics (Kreye et al. 2013) and flammability (Engber and Varner 2012). Significant impacts, however, were most pronounced in litterbeds with $\geq 66\%$ mesophytic litter. While recent research has shown that fire-sensitive species' litter is prone to moisture retention (Kreye et al. 2013) and dampening of litter flammability (Kane et al. 2008, Mola et al. 2014), we found that substantial increases in mesophytic litter were required to cause major impacts on flammability. Pyrophytic litter may disproportionately enhance flammability in a non-additive manner (Magalhães and Schwilk 2012). These results suggest that changes in litter composition may not be problematic until later stages of mesophication in these forests. Restoration efforts may still be most effective in early stages of mesophytic encroachment when

pyrophytic litter still provides sufficient litterbed flammability to topkill encroaching mesophytes. Success, however, may depend on the mesophytic species that are present (Kreye et al. 2013), the cover and dominance of remnant pyrophytic grasses and forbs, and perhaps the impacts of overstory and midstory forest structure to microclimate (e.g., higher relative humidity, lower wind speeds, less solar insulation; Lee 1978).

Differences in litterbed depths were minor in this study, but trended toward shallower depths when mesophytes were dominant. Since mesophyte-dominant litterbeds soaked up significantly more moisture at SMC, differences may have translated to wetter fuelbeds following 12- and 24-h dry times regardless of moisture loss rate. When comparing dry litterbeds, however, pure mesophytic litterbeds were significantly less flammable than litterbeds that included pyrophytic *Quercus* and *Carya* species, highlighting that these mesophytes were less flammable regardless of moisture content.

Liquidambar styraciflua is a common fire-sensitive species of the southeastern United States and was

the primary mesophyte in this study. Although found extensively in mesic sites, *L. styraciflua* readily establishes in many fire-excluded pyrophytic *Pinus* and *Quercus* forests (Waldrop et al. 1987, Brewer 2001, Surrrette et al. 2008) and can be difficult to control due to prolific sprouting and suckering following topkill (Waldrop et al. 1987). Given widespread establishment of *L. styraciflua* in fire-excluded uplands in the southeastern United States, its dampening effect on flammability and sprouting ability highlights challenges to restoring fire to *Quercus*–*Carya* woodlands in the region. Aside from *L. styraciflua*, *U. alata* and *Cornus florida* contributed the remainder of the mesophytic litter in our study. These two shade-tolerant species are typically represented as midstory trees with smaller stature than the canopy dominant *L. styraciflua*. Their collective importance has increased locally (Brewer 2001) and more broadly in their wide native ranges. Beyond their dampening effect on flammability, their midstory role filters remaining sunlight and further diminishes subcanopy winds, two factors that may stall moisture loss and diminish local flammability. Unlike *L. styraciflua*, these species do not dominate local forests, but their strong relative effects on flammability illustrated here suggest that targeted removal of these species and others that diminish flammability (e.g., *Acer* species; Kreye et al. 2013) may be effective restoration strategies.

Mesophication of oak–hickory forests may also create challenges for restoring herbaceous fuels. In the transition from woodland or savanna to forest, the relative abundance shifts from herbaceous to litter fuels with a corresponding decline in surface fire intensity (Engber et al. 2011, Trauernicht et al. 2012). High residual canopy closure at this Strawberry Plains site has been associated with poor survival of native warm-season grasses (Maynard and Brewer 2013), dominant surface fuels that are very flammable in oak–hickory woodlands. A restoration challenge is synchronous restoration of both groundcover herbaceous diversity and flammable surface fuels required for successful reintroduction of fire. The inhibitory effects of mesophytic trees via shading, litter inputs, and occupation of growing space hinder this trajectory.

In addition to the impacts observed in these sites, mesophication has been implicated as a widespread phenomenon in other historically

pyrophytic ecosystems across eastern North America. One widespread mesophytic species that has gained significant attention as an invader of fire-excluded sites is *Acer rubrum* (Abrams 1998, Gilbert et al. 2003, Nowacki and Abrams 2008, Alexander and Arthur 2010, Kreye et al. 2013). *Acer rubrum* was present in our study sites, but was a somewhat rare midstory species. In a comparison among 17 southeastern tree species examined, *A. rubrum* litter had a substantially greater capacity to absorb and retain moisture than all others (Kreye et al. 2013). Future research that includes other mesophytes, such as *A. rubrum*, *Acer saccharum*, *Nyssa sylvatica*, *Prunus serotina*, *Tsuga canadensis*, *Liriodendron tulipifera*, and others that can be locally dominant (Nowacki and Abrams 2008, Hanberry et al. 2012), may help identify thresholds of invasion that can be used in prioritizing restoration and management treatments based on their impacts on flammability and fire effects as ecological functions.

Restoration of pyrophytic *Quercus* woodlands and forests will likely require additional treatments where fire-sensitive mesophytic species are well established. Harvesting or girdling mesophytic species prior to reintroducing fire would hasten the removal of mesophytic litter inputs and also promote surface litter drying via losses of shade. The removal of mesophytic species could restore surface fuels that promote higher intensity fire capable of generating desired understory diversity and restoring other ecological components, processes, and functions (Maynard and Brewer 2013, 2015, Ryan et al. 2013). Further evaluations of forest floor moisture dynamics and flammability in fire-excluded *Quercus* forests and the efficacy of restoration treatments are needed to verify laboratory results and evaluate stand-scale effects. The impacts of mesophication and the restoration challenges it presents are of considerable concern in the eastern United States and likely many other regions where long-term fire exclusion and invasion of mesophytic species has occurred.

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