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Could Mesophyte Canopy, Bark, and Leaf Litter Traits Drive Future Flammability of Upland Oak Forests?

Emily Kathleen Babl

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Could mesophyte canopy, bark, and leaf litter traits drive future flammability of upland
oak forests?

By

Emily Kathleen Babl

A Thesis
Submitted to the Faculty of
Mississippi State University
in Partial Fulfillment of the Requirements
for the Degree of Master of Science
in Forestry
in the College of Forest Resources

Mississippi State, Mississippi

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2018

Could mesophyte canopy, bark, and leaf litter traits drive future flammability of upland
oak forests?

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In the absence of canopy-opening disturbances, upland oak forests in the eastern United States are shifting to shade-tolerant, fire-sensitive tree species (i.e. mesophytes) via a hypothesized positive feedback loop of less flammable, self-promoting conditions, termed mesophication. To evaluate species-specific impacts on mesophication, I quantified canopy, bark, and leaf litter traits of five hypothesized mesophytes [red maple (*Acer rubrum*), sugar maple (*A. saccharum*), American beech (*Fagus grandifolia*), hickory (*Carya* spp.), and tulip poplar (*Liriodendron tulipifera*)] and four upland oaks [black oak (*Quercus velutina*), chestnut oak (*Q. montana*), scarlet oak (*Q. coccinea*), and white oak (*Q. alba*)] in central Kentucky. Red maple, sugar maple, and American beech had increased canopy depth with stem size, smoother bark, and small, thin leaves when compared to oaks. My findings suggest that some mesophytes, such as red maple, sugar maple, and American beech, may decrease future forest flammability by reducing understory light and increasing fuel moisture.

DEDICATION

To all the women in science that have come before me and paved the path I travel down, this journey would not have been possible with you.

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CHAPTER I
SPECIES-SPECIFIC MECHANISMS OF MESOPHICATION AND IMPACTS ON
UNDERSTORY ENVIRONMENT

Introduction

Upland oak (*Quercus* spp.) forests across the eastern U.S. are shifting dominance due to the encroachment of shade-tolerant, fire-sensitive species (i.e. mesophytes; Abrams, 1998, 1992). Prior to this shift, oak forests were in a relatively stable state for the last ~8,000 years (Foster et al., 2002; Abrams, 1992) and comprised 40-70% of eastern U.S. pre-settlement upland forests, with pine (*Pinus* spp.), hickory (*Carya* spp.), and American chestnut (*Castanea dentata* Marshall.) as codominant species (Hanberry and Nowacki, 2016). Beginning in 1980, evidence of decreased oak recruitment and increased importance value (IV; mean relative density and mean relative dominance) of mesophytes in the eastern U.S. was widespread (Abrams and Downs, 1990; Abrams and Nowacki, 1992; Fei et al., 2011; Fei and Steiner, 2007; Lorimer, 1984; McDonald et al., 2002). For example, red maple (*Acer rubrum* L.) has increased IV in almost every portion of its historical range, likely due to this species' low resource requirements and generalist life history strategy (Abrams, 1998; Fei and Steiner, 2007). Furthermore, upland oak species are underrepresented in the midstory size class (2-10 cm DBH) relative to their proportion in the overstory, suggesting problems in their regeneration (Fei et al., 2011; McEwan et al., 2011).

The failure of upland oaks to regenerate likely stems from “multiple interacting ecosystem drivers,” such as climate change and herbivory; however, anthropogenic fire suppression beginning in the 1930s is generally considered the main cause (McEwan et al., 2011; Nowacki and Abrams, 2015). Most upland oaks are disturbance-dependent and pre-historically associated with fire (Abrams, 2002; Prentice et al., 1991) due to morphological and physiological adaptations including a moderately high light requirement, deep and extensive rooting, vigorous re-sprouting ability, and hypogeal germination (Abrams, 2003; Arthur et al., 2012; Brose et al., 2005; Johnson et al., 2009). Consequently, in the absence of periodic, canopy-opening disturbances, mesophytes are able to establish in upland oak forests and outcompete oak, especially in the sapling stage (Lorimer et al., 1994). Once established, mesophytes are hypothesized to contribute to a positive-feedback loop of self-promoting conditions, such as shaded, cool, and humid understories with lower fuels loads and dampened flammability, termed mesophication (Nowacki and Abrams, 2008).

Mesophication may negatively impact eastern U.S. forests both economically and ecologically should oaks fail to recruit to the overstory (Abrams, 2003). For example, oaks provide vital food and habitat resources for wildlife in eastern U.S. deciduous forests and a shift to a maple forest type could negatively impact songbird communities (Fox et al., 2010), black bears (*Ursus americanus*; McDonald and Fuller, 2005), and white-tailed deer (*Odocoileus virginianus*) populations (McShea and Schwede, 1993). Furthermore, the wood of white oak (*Q. alba* L.) contains properties that make it impervious to water and thus ideal for flooring, furniture, and barrel making (Abrams, 2003). Ecologically, oaks are both “foundation” and “keystone” species that can alter

microclimate conditions and impact important ecosystem-level processes including decomposition and nutrient cycling (Ellison et al., 2005; Fralish, 2004). The spatial distribution of water and nutrient inputs via precipitation is partially controlled by species composition (Crockford and Richardson, 2000), and conversion of upland oak stands to mesophytes could cause a change of resource distribution across the forest floor (Alexander and Arthur, 2014, 2010; Caldwell et al., 2016; Fabio et al., 2009). For example, during a rainfall event mesophytes may direct more rainfall down their trunks in the form of stemflow, which, coupled with their leaf litter that has high moisture retention and slow dry-down time, may increase fuel moisture several days post-rainfall (Alexander and Arthur, 2010; Kreye et al., 2013). Therefore, alteration of forest hydrology may effectively alter forest flammability by decreasing and interrupting fire spread, intensity, and continuity, and prescribed fire, which is commonly used in oak regeneration, may become ineffective (Brose et al., 2005; Kreye et al., 2013).

The ability of mesophytes to reduce forest flammability may stem from “single-tree influence circles,” where single overstory trees strongly influence forest floor conditions and resources beneath their canopies (Boettcher and Kalisz, 1990; Zinke, 1962). Zinke (1962) refers to the idea that the forest landscape is a mosaic of forest floor conditions representative of the tree species present and the impacts of species-specific traits on microclimate conditions. Thus, it is hypothesized that as mesophyte representation increases in historically oak-dominated forests, the proportion of the forest floor impacted by their canopies’ will increase. If these zones of influence have low flammability, then mesophytes may effectively alter the fire disturbance regime, and

upland oak forests may shift to mesophytic hardwood-dominated stand in which fire is an ineffective management tool (Nowacki and Abrams, 2008).

The influence circles of mesophytes may be less flammable due to canopy, bark, and leaf litter traits that alter understory conditions, fuel bed moisture, and fuel bed structure (Table 1.1). Although some anecdotal information exists regarding mesophyte traits (Nowacki and Abrams, 2008) and pathways for succession, there are few studies that quantify mesophyte and oak traits (Alexander and Arthur, 2010; Kreye et al., 2013). For example, Alexander and Arthur (2010) is one of the only studies that has quantified canopy traits and bark roughness in mesophytes and oaks and discovered that red maple had increased canopy area and smoother bark when compared to chestnut oak and scarlet oak. Kreye et al. (2013) measured leaf litter traits in 17 species and found that red maple, American beech, and tulip poplar had thinner leaves with increased surface area: volume (SA:V) and were able to retain more moisture when compared to white oak. These studies provide preliminary data to support the mesophication process, but a knowledge gap exists surrounding whether mesophyte traits become more or less pronounced as they reach overstory positions.

The primary objective of this study was to quantify canopy, bark, and leaf litter traits of hypothesized mesophytes (hereafter referred to as mesophytes) and oaks that encompass a range of sizes and identify species that may be mesophication “promoters” or “inhibitors.” A secondary objective was to quantify understory temperature, light intensity, and fuel moisture between mesophytes and oaks. I hypothesized that because mesophytes are shade-tolerant, late successional species, they would have increased canopy area, canopy volume, and leaf area when compared to oaks (Abrams and

Kubiske, 1990; Canham et al., 1993), which would reduce understory light and air circulation. Decreased radiation and air circulation beneath shade-tolerant species may lower air and fuel temperatures and cause an increase in relative humidity, and therefore, reduce evaporation rates and increase fuel moisture (Nauertz et al., 2004; Siegert and Levia 2011). I also expected fire-sensitive mesophytes to have thinner, smoother bark when compared to more fire-resistant oaks (Alexander and Arthur, 2010), which could cause increased fuel moisture at their bole following rainfall events. As mesophytes reached larger size classes, I expected that their canopy traits would have significant linear increases when compared to oaks and thus, their circles of influence would also increase. My final hypothesis was that mesophyte leaf litter would have traits associated with decreased flammability including smaller, thinner, less curly leaves with increased specific leaf area, surface area to volume, tissue density, and lower lignin concentrations (Abrams and Kubiske, 1990; Kreye et al., 2013). These leaf litter traits may directly impact flammability by causing quickly decomposing, more densely packed, and less aerated fuel beds that could retain more moisture and diminish litter flammability (Kreye et al., 2018, 2013a; Melillo et al., 1982). Identifying the ways in which certain species contribute to mesophication will allow us to further understand this complex successional process and help determine when fire may or may not be a useful management tool.

Table 1.1 Tree traits and forest flammability

	Role in flammability	Citation
Canopy trait		
Area	Greater canopy area can lead to increased stemflow production and decreased throughfall	Aboal et al., 1999; Ford and Deans 1978
Depth	Light intensity decreases with increasing canopy depth, which will lead to a more shaded understory; Increased depth can also lead to decreased ignition success	Kozlowski and Pallardy 1997; Tanskanen et al., 2005
Leaf area	High leaf area can cause a more shaded understory, which can reduce vapor pressure deficit, fire spread rate, and ignition success; Increased leaf area can also lead to increased rainfall interception and decreased throughfall	Ray et al., 2005; Tanskanen et al., 2005; Gomez et al., 2000; Herwitz 1985
Bark trait		
Thickness	Thick bark can absorb more water and decrease stemflow; Thick bark protects cambium from fire	Aboal et al., 1999; Herwitz 1985; Hengst and Dawson 1994; Vines 1968
Roughness	Increased bark roughness leads to decreased stemflow	Aboal et al., 1999; Van Stan and Levia 2010
Leaf litter trait		
Thickness	Thicker leaves burn with higher maximum temperatures. Leaf thickness negatively correlates with initial moisture content of litter beds	Grootemaat et al., 2017; Kreye et al., 2013
Curling	Curlier leaves create more aerated fuel beds, increased rate of spread, and flame height	Grootemaat et al., 2017; Varner and Engber 2012
Leaf area	Large leaves create open litter-bed structure that is more ventilated and will burn more rapidly; large leaves have shorter time to ignition	Scarff and Westoby 2006; Murray et al., 2013
Specific leaf area	Leaves with increased SLA can ignite more quickly and have increased rate of spread	Grootemaat et al., 2015; Murray et al., 2013; Grootemaat et al., 2017
Leaf tissue density	Increased tissue density linked to greater initial litter moisture content of litter beds and slower fire spread rate	Kreye 2013; Grootemaat et al., 2017
Surface area: volume	Increased SA:V can lead to increased fuel moisture and is negatively correlated with time to ignition	Kreye et al., 2013; Gill and Moore 1996
Lignin	Increased lignin concentrations associated with greater fuel consumption and slow decomposition rates	Grootemaat et al., 2017; Melillo et al., 1982

Canopy, bark, and leaf litter traits of mature trees (>10 cm DBH) and their role in forest flammability

Methods

Study area

This study was conducted within Bernheim Arboretum and Research Forest (hereafter referred to as Bernheim), located in Kentucky's Western Knobs ecoregion, 40 km south of Louisville (37°52' N, 85°35) where the climate is humid, temperate, and continental. From 1981-2010, Bernheim had average growing season (JJA) temperatures of 24.0 °C and dormant season (DJF) temperatures of 2.5 °C (NOAA, 2018). Mean annual rainfall was 126 cm, evenly distributed throughout the year, and average annual snowfall was 33 cm (U.S. climate data, 2018). Agriculture and logging activities occurred within Bernheim before 1929, and there has been no prescribed burning since this time (A. Berry, personal communication).

Soils are primarily composed of the Lenberg-Carpenter and Zanesville complex. The Lenberg complex consists of moderately deep, well-drained silt loam soils formed of acidic clayey shale with slopes ranging from 6 to 45 percent. Carpenter series consists of deep, well drained loamy soils, formed from weathered shale or limestone and occupies slopes from 2 to 60 percent (USDA, 2001). Zanesville series is composed of silt-loam soils that are found on ridgetops (USDA, 2014). Forest overstory (>10 cm diameter at breast height [DBH]) basal area is dominated by chestnut oak (25%), scarlet oak and black oak (19%), and white oak (39%), and collectively contribute 23.89 m² ha⁻¹ of basal area. The midstory (2-10 cm DBH) basal area is primarily composed of hickory (35%; majority *Carya glabra* Mill), American beech (27%), sugar maple (24%), and red maple (13%) and make up 1.28 m² ha⁻¹, while oaks only make up ~1.5% of the midstory basal

area. Seedlings within Bernheim (<2 cm DBH) are dominated by red maple (42%), white oak (30%), scarlet oak and black oak (12%).

Tree selection

To test my hypotheses, species were chosen that occupy different levels of shade tolerance and fire sensitivity (Table 1.2) and represent tree species that have a documented increase in areas previously occupied by upland oaks (Abrams, 2003; Abrams et al., 1995; Abrams and Nowacki, 1992; Brewer, 2015; Fei and Steiner, 2007; Hart and Grissino-Mayer, 2008). I chose to focus on trees in the overstory position because differences in canopy/bark traits between species would most likely be more pronounced in bigger trees. Hypothesized mesophytes include: red maple, sugar maple (*A. saccharum* Marshall.), American beech (*Fagus grandifolia* Ehrh.), hickory (*Carya* spp.), and tulip poplar (*Liriodendron tulipifera* L.). Upland oak species include: white oak, chestnut oak (*Q. montana* Willd.), black oak (*Q. velutina* Lam.), and scarlet oak (*Q. coccinea* Münchh.). Although the original goal of this study was to focus on dominant overstory trees (20-60 cm DBH), the absence of some mesophytes (American beech and sugar maple) in these larger size classes led us to select individuals occupying co-dominant overstory positions (10-20 cm DBH). Canopy and bark traits were measured on ~15 individuals per species in the growing season of 2016 or 2017 (Table 1.2). Understory microclimate measurements, including light intensity, air temperature, and instantaneous soil moisture measurements were measured on the species listed above, excluding tulip poplar, black oak, and scarlet oak. Trees selected for microclimate measurements were located at three non-contiguous stands within Bernheim [Ashlock

Hollow (AH), Yoe's Road (YR), and Wilson Creek (WC)] and each site included ~5 trees per species.

Canopy and bark traits

Diameter at breast height (1.37 m) was measured with DBH tape, and tree height and crown depths were measured using a clinometer (Suunto, Vantaa, Finland). Crown width was measured in the four cardinal directions under each tree by walking out the width of the crown, measuring the distance to the tree bole, and adding in trunk radius. Crown area was calculated by taking the average of the four widths to estimate the area of a circle. Leaf area was estimated by collecting fresh canopy leaves with a slingshot, these leaves were kept hydrated and then transported back to the lab. Once in the lab, I measured specific leaf area (SLA) by passing leaves through an Area Meter 3100 (Licor, Lincoln, NE) and dividing this value by their oven-dried weight. SLA values were then multiplied by biomass estimates, which were obtained via allometric equations from Martin et al. (1998) and Ribe (1973) to calculate total canopy leaf area. Bark roughness was determined following Alexander and Arthur (2010), where the mean depth of bark fissures was measured 1.5 m above the ground on four sides of the tree. Bark thickness was measured on one randomly selected side of the tree using a standard bark thickness gauge.

Leaf litter traits

Measurements were made on fresh leaf litter collected from Bernheim immediately following leaf fall in December 2017. Leaf litter was determined to be fresh by judging the visible appearance and texture of leaves. The following measurements

were made on 50 randomly selected air-dried leaves for each of the nine species (same as listed above). Leaf curl was quantified as the maximum height of a leaf horizontally oriented on a flat surface (Kreye et al., 2013). Surface area was calculated by use of an area meter, as stated above. Specific leaf area (SLA) was calculated as the leaf area divided by the air-dried mass (conditions it would be burned in; Grootemaat et al., 2015). Thickness was measured with digital calipers (Traceable Products, Webster, TX) to the nearest 0.01 mm at the mid-vein and leaf-edge locations after the leaf was bisected perpendicular to the main vein, and these two values were then averaged for each leaf (Kreye et al., 2013). Volume (V) was calculated as average leaf thickness multiplied by the one-sided surface area (SA) and SA:V was calculated by dividing the surface area by the volume. Tissue density was calculated by dividing the air-dried leaf weight by the volume. Leaf litter lignin concentrations were measured at Dairy One lab (Ithaca, NY) and determined using an Ankom fiber digester (Ankom Technology, Macedon, NY).

Understory microclimate

I assessed mesophyte and oak impacts on understory light, air temperature, soil moisture, and soil temperature through instantaneous and continuous measurements. All measurements were made under trees that met the following criteria: (1) trees could not be located in proximity to a road (> 20 m away) or near/within a canopy gap to avoid potential edge effects; (2) trees had a reasonably clear understory to target single-tree influences and limit confounding effects (<30% cover); (3) trees were established on relatively flat landscape to avoid effects on understory conditions due to variable drainage. In spring 2017, HOBO pendant sensors (Onset Computer Corporation, Bourne, MA), which recorded light intensity and air temperature, were installed mid-canopy

(horizontal distance from stem) ~0.3 m above the forest floor under three of the largest trees per species. iButtons (Maxim Integrated, San Jose, CA) were installed under the same trees and measured temperature at the soil surface/leaf litter interface at the mid-canopy position and tree bole. Permanent soil moisture sensors (EC5 soil moisture smart sensor, Onset, Bourne, MA) were also installed in spring 2017. Due to financial limitations, two soil moisture sensors were placed under the three largest trees of red maple and chestnut oak, at the bole and mid-canopy. Larger trees were selected because stemflow increases with tree diameter (Levia et al., 2010), and species impacts would be more notable under large individuals. I placed soil moisture sensors under red maple and chestnut oak as any potential differences would be magnified due to dissimilar canopy and bark traits (Alexander and Arthur 2010). All loggers recorded measurements every four hrs.

Instantaneous fuel moisture measurements were made following three discrete precipitation events in June 2017 (at least ~6 hrs after end of rainfall). Measurements were taken from 09:00-12:00 hr at one site per rainfall event to help minimize any effects due to changes in environmental conditions. Instantaneous fuel moisture measurements were taken with a FieldScout TDR 300 moisture meter (Spectrum Technologies, Aurora, IL) in the top 3.5-cm of the litter/organic layer at the bole and mid-canopy locations in each of the four cardinal directions. To account for the mineral soil calibrated probe and measurements taken in leaf litter, I collected 13 litter/soil samples that ranged from 2.1-23.8% volumetric water content as recorded by the probe. I then used the dimensions of the sample along with wet and dry weights to calculate the bulk density and gravimetric soil moisture, which were used to calculate true volumetric soil moisture (VSM). An

exponential relationship was found between the probe VSM and actual VSM, and the equation was applied to correct all field measurements.

Statistical analyses

An analysis of covariance (ANCOVA) was used to understand how tree size might impact species-specific differences in canopy and bark traits. In this analysis, the independent variable was individual tree species plotted with their DBH vs. canopy or bark trait as the dependent variable. Red maple and sugar maple were then pooled into a “Maples” category as their means and slopes were not significantly different ($P > 0.05$) for all canopy and bark traits. Next, linear regressions were run after the maple species were grouped, and I used an ANCOVA to test for interactions between size (DBH) and each specified trait. When an interaction was significant, a post-hoc Student’s t-test was used to determine differences among slopes (JMP v. 13). F-values were computed based on least square means.

I compared tree and litter traits between different species by using an analysis of variance (ANOVA; JMP V. 13). Because of the large variation in size of trees sampled, canopy and bark traits were normalized to each tree’s corresponding DBH or basal area by dividing the trait by tree size. For all significant interactions ($P < 0.05$), least square means were compared via a post-hoc Student’s t-test to determine differences among means at $\alpha = 0.05$. To further explore which traits drive variability between species and the multicollinearity nature of litter traits (e.g., SLA is calculated based on leaf area) all eight leaf litter measurements for the species were combined using principal components analysis (PCA). PCA scores were generated using standardized (mean = 0 and SD = 1) values for each litter characteristic. Number of principal components retained for leaf

litter traits were based eigenvalues, and those ≥ 1 were kept (Kaiser, 1960). To quantify and better visualize similarities between species based on leaf traits, I used k-means cluster analysis to partition species into four defined groups.

Understory light intensity and air temperature were analyzed by using a one-way ANOVA with species as independent variable. A two-way ANOVA was used to compare the soil surface temperature and instantaneous soil moisture, with location (bole vs. mid-canopy) and species as the independent variables. Continuous soil moisture measurements were analyzed with the following steps: First, I used Kentucky Mesonet hourly precipitation summaries to identify rainfall events between June and September 2017 that were relatively small (< 0.40 cm), medium (1.25-2.0 cm), or large (> 2.50 cm). Next, I chose three events per rain event size class, making sure events were discrete and several days of no rain occurred before them. For each rain event, the 24 hrs post-rainfall soil moistures were averaged for each species. Finally, I compared the average values within each event size with a two-way ANOVA, with location (midpoint or bole) and species (red maple or chestnut oak) as the independent variables. Results only include location if significant interactions occurred ($P < 0.05$).

Table 1.2 Shade tolerance and fire sensitivity ranking

Species	Shade tolerance	Fire sensitivity	N
American beech*	Very tolerant	Very sensitive	20
Red maple*	Tolerant	Sensitive	15
Sugar maple*	Tolerant	Sensitive	15
White oak	Intermediate-tolerant	Moderately tolerant	15
Hickory*	Intermediate-intolerant	Moderately tolerant	15
Black oak	Intermediate	Moderately tolerant	10
Chestnut oak	Intermediate	Tolerant	15
Scarlet oak	Intermediate	Low- moderately tolerant	9
Tulip poplar*	Intolerant	Tolerant	15

Shade tolerance ranking, tree fire sensitivity, and total numbers of trees (N) measured for canopy and bark traits of mature (>10 cm DBH) mesophyte* and oak tree species at Bernheim Arboretum and Research Forest, KY (Burns and Honkala, 1990).

Results

Normalized canopy and bark traits differed between some mesophytes and oaks (Table 1.3). When compared to oaks, American beech had the largest normalized canopy area, volume, and leaf area, which on average was 3.3x, 6x, and 2.7x greater, respectively ($P < 0.0001$). Although not significantly different from other oaks ($P = 0.5035$), black oak canopy area was ~ 2.3x smaller compared to red maple, sugar maple, and hickory ($P < 0.0001$). Canopy depth was similar between most species, although American beech and sugar maple canopy depth was ~1.8x greater compared to hickory, chestnut oak, and white oak ($P = 0.0002$ for all comparisons). American beech, red maple, sugar maple, and hickory leaf area was ~1.3x greater when compared to oaks, and tulip poplar had the lowest leaf area. American beech, red maple, and sugar maple had the thinnest and smoothest bark, which was ~3.7x thinner and ~5.8x smoother, respectively, when compared to all other species ($P < 0.0001$ for all comparisons). Black oak, scarlet oak, and chestnut oak had the roughest bark, while chestnut oak also had the thickest bark when compared to all other species ($P < 0.0001$ for all comparisons).

Table 1.3 Canopy, bark, and leaf litter traits

	American beech	Red maple	Sugar Maple	Hickory	Tulip Poplar	Black oak	Chestnut oak	Scarlet oak	White oak	P value
Canopy traits										
CA:BA(m ² m ⁻²)	2142.9 ^A ± 154.4	1147.8 ^B ± 178.2	1095.6 ^B ± 178.2	1225.2 ^B ± 178.2	1039.9 ^{BC} ± 178.2	507.2 ^C ± 218.3	748.4 ^{BC} ± 178.2	790.3 ^{BC} ± 230.1	730.2 ^{BC} ± 178.2	< 0.0001
CD: DBH (m m ⁻¹)	65.4 ^A ± 7.5	41.0 ^{BCD} ± 4.1	55.9 ^{AB} ± 3.6	38.6 ^{CD} ± 3.6	43.9 ^{BCD} ± 3.9	40.2 ^{BCD} ± 4.2	31.9 ^D ± 9.0	52.9 ^{ABC} ± 8.7	32.5 ^D ± 3.1	0.0002
LA: BA (m ² m ⁻²)	3836.9 ^A ± 56.5	2643.9 ^B ± 65.2	2707.9 ^B ± 65.2	2198.7 ^C ± 63.2	924.7 ^F ± 50.3	n.d.	1685.3 ^D ± 65.2	1235.8 ^E ± 151.0	1388.7 ^E ± 65.2	< 0.0001
Bark traits										
Thickness: DBH (cm cm ⁻¹)	0.003 ^A ± 0.003	0.010 ^{AB} ± 0.003	0.013 ^B ± 0.003	0.025 ^C ± 0.003	0.027 ^{CD} ± 0.003	0.033 ^{CD} ± 0.003	0.045 ^E ± 0.003	0.031 ^{CD} ± 0.003	0.034 ^D ± 0.003	< 0.0001
Roughness: DBH (cm cm ⁻¹)	0.000 ^A ± 0.001	0.004 ^B ± 0.001	0.003 ^{AB} ± 0.001	0.009 ^{CD} ± 0.001	0.012 ^D ± 0.001	0.017 ^E ± 0.002	0.020 ^E ± 0.001	0.017 ^E ± 0.002	0.008 ^C ± 0.001	< 0.0001
Leaf litter traits										
LA (cm ²)	45.1 ^{AB} ± 2.4	36.3 ^{CD} ± 2.0	35.0 ^D ± 2.0	28.4 ^E ± 2.1	51.2 ^A 9± 2.9	82.7 ^F ± 3.8	71.4 ^G ± 4.3	43.4 ^{BC} ± 2.0	47.3 ^{AB} ± 2.5	< 0.0001
SLA (cm ² g ⁻¹)	281.1 ^A ± 12.0	164.1 ^B ± 4.8	221.4 ^C ± 8.9	138.4 ^D ± 6.5	109.0 ^E ± 2.0	82.9 ^F ± 2.1	108.4 ^E ± 3.2	94.3 ^{EF} ± 1.8	93.7 ^{EF} ± 2.8	< 0.0001
Curl (cm)	1.7 ^A ± 0.1	1.9 ^A ± 0.1	2.3 ^B ± 0.1	2.4 ^B ± 0.1	2.3 ^B ± 0.2	3.7 ^C ± 0.1	2.2 ^B ± 0.1	3.8 ^C ± 0.2	2.5 ^B ± 0.1	< 0.0001
Thickness (mm)	0.05 ^A ± 0.00	0.08 ^B ± 0.00	0.06 ^C ± 0.00	0.14 ^D ± 0.01	0.12 ^E ± 0.00	0.20 ^F ± 0.01	0.13 ^E ± 0.00	0.13 ^E ± 0.00	0.14 ^D ± 0.00	< 0.0001
Volume (cm ³)	0.24 ^A ± 0.02	0.29 ^A ± 0.02	0.22 ^A ± 0.02	0.42 ^B ± 0.04	0.65 ^C ± 0.05	1.60 ^D ± 0.07	0.90 ^E ± 0.06	0.59 ^C ± 0.04	0.68 ^C ± 0.04	< 0.0001
SA:V (cm ² cm ⁻³)	238.2 ^A ± 15.6	131.0 ^B ± 4.0	171.7 ^C ± 7.3	75.2 ^D ± 2.7	83.9 ^D ± 2.3	53.3 ^E ± 1.8	83.8 ^D ± 3.0	78.5 ^D ± 2.3	72.7 ^D ± 1.8	< 0.0001
Tissue density (g cm ⁻³)	0.84 ^A ± 0.04	0.81 ^{AB} ± 0.02	0.79 ^{AB} ± 0.02	0.57 ^C ± 0.02	0.77 ^B ± 0.02	0.65 ^D ± 0.02	0.77 ^B ± 0.01	0.84 ^A ± 0.02	0.79 ^B ± 0.01	< 0.0001
Lignin (%)	12.1 ^A ± 0.2	9.5 ^B ± 0.2	10.9 ^C ± 0.2	9.0 ^B ± 0.2	8.58 [*] ± 0.2	19.8 ^D ± 0.2	13.9 ^E ± 0.1	18.7 [*] ± 0.2	11.4 ^C ± 0.2	< 0.0001

Canopy, bark, and leaf litter traits for American beech, red maple, sugar maple, hickory, tulip poplar, black oak, chestnut oak, scarlet oak, and white oak, sampled on 15-60 cm DBH trees within Bernheim Forest and Arboretum, KY

Changes in canopy area, canopy depth, bark thickness, and bark roughness as a function of tree size varied among species (Tables 1.4 and 1.5; Fig 1.1 and 1.2). All species showed a positive linear increase in canopy area with increasing DBH, although this trend was only significant for American beech, hickory, chestnut oak, and white oak ($P < 0.01$ for all interactions). Canopy area as function of DBH for hickory increased at a rate $\sim 3x$ that of the other species. All species had a significant positive linear increase in canopy depth and bark thickness with increasing DBH ($P < 0.05$ for all interactions), except for black oak and scarlet oak, which could be due to low replication. American beech and maple had a significant rate of increase in canopy depth vs. size which was $\sim 3.8x$ that of the oaks ($P < 0.0001$). American beech and scarlet oak had the smallest rate of increase in bark thickness as a function of size while this was greatest in hickory, tulip poplar, and chestnut oak. All species had significant linear increases in bark roughness as they became larger, except for scarlet oak ($P = 0.7522$) and white oak ($P = 0.0632$). The rate of increase in bark roughness was most pronounced for tulip poplar which was on average $\sim 2.5x$ greater when compared to the other species and lowest in American beech, whose rate of increase was close to zero.

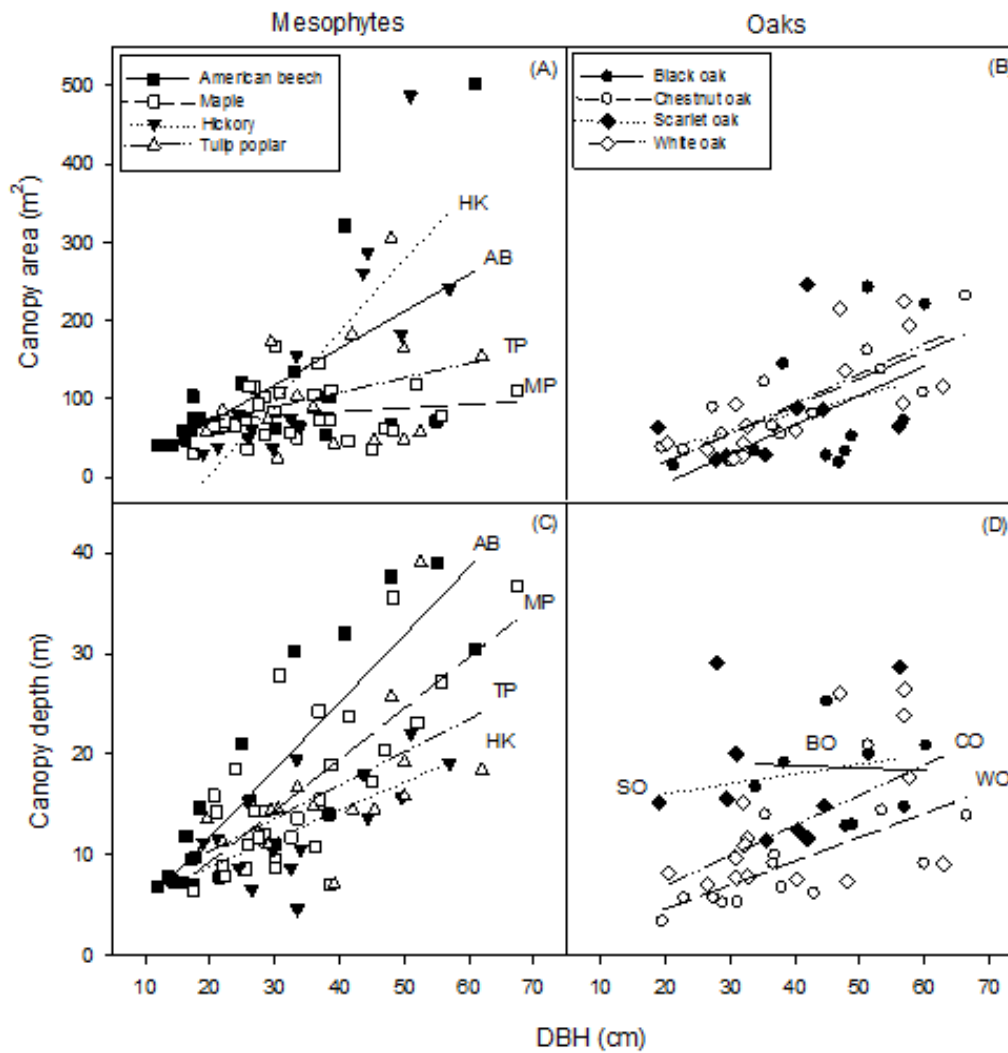


Figure 1.1 Regressions of tree size and canopy traits

Regression of diameter at breast height (DBH) for (A) canopy area of mesophytes, (B) canopy area of oaks, (C) canopy depth of mesophytes, and (D) canopy depth of oaks sampled within Bernheim Arboretum and Research Forest, KY.

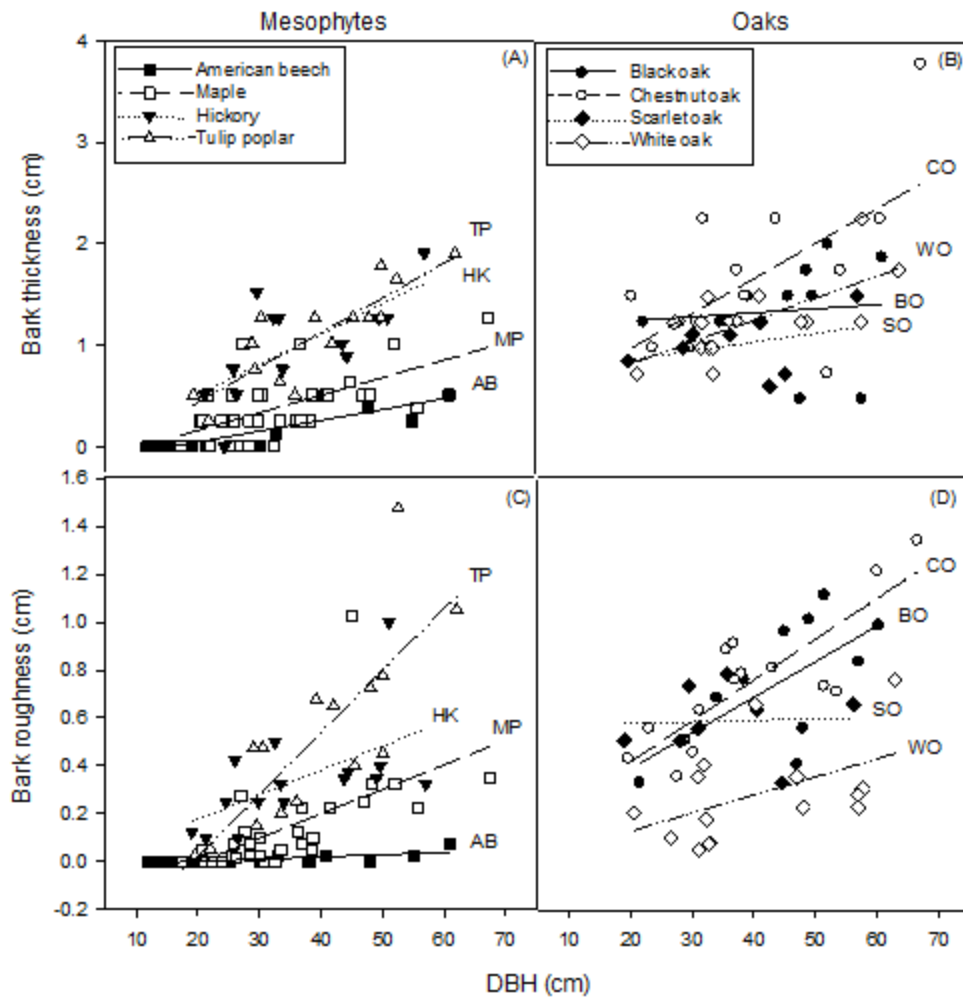


Figure 1.2 Regressions of tree size and bark traits

Regression of diameter at breast height (DBH) for (A) canopy area of mesophytes, (B) canopy area of oaks, (C) canopy depth of mesophytes, and (D) canopy depth of oaks sampled within Bernheim Arboretum and Research Forest, KY.

Table 1.4 Canopy and bark analysis of covariance results

Source	Canopy area (m ²)			Canopy depth (m)			Bark thickness (cm)			Bark roughness (cm)		
	d	F	P	F	P	P	F	P	F	P	P	
Species	7	3.83	0.0009	4.61	< 0.0001	< 0.0001	26.40	< 0.0001	27.78	< 0.0001	< 0.0001	
DBH	1	51.08	< 0.0001	26.61	< 0.0001	< 0.0001	44.81	< 0.0001	61.61	< 0.0001	< 0.0001	
Species x DBH	7	3.82	0.0009	2.35	0.0224	0.0455	2.14	0.0455	5.38	< 0.0001	< 0.0001	
Contrasts												
American beech vs. Maple	1	9.84	0.0033	7.79	0.1941	0.3905	3.75	0.3905	6.61	0.0165	0.0165	
American beech vs. Hickory	1	0.031	0.0149	18.85	0.0128	0.2095	36.32	0.2095	26.11	0.0479	0.0479	
American beech vs. Tulip poplar	1	3.61	0.1007	10.99	0.0244	0.0133	33.60	0.0133	42.30	< 0.0001	< 0.0001	
American beech vs. Black oak	1	8.88	0.6460	1.04	0.0067	0.5673	43.40	0.5673	55.73	0.0168	0.0168	
American beech vs. Chestnut oak	1	8.35	0.4575	44.34	0.0025	0.0072	108.72	0.0072	116.35	0.0003	0.0003	
American beech vs. Scarlet oak	1	7.16	0.2851	4.45	0.0047	0.8676	30.89	0.8676	60.87	0.9616	0.9616	
American beech vs. White oak	1	7.50	0.5787	26.21	0.0097	0.2377	55.74	0.2377	15.17	0.1349	0.1349	
Maple vs. Hickory	1	11.18	< 0.0001	4.69	0.1462	0.5280	25.79	0.5280	11.17	0.9950	0.9950	
Maple vs. Tulip poplar	1	0.81	0.4150	1.11	0.2339	0.0756	23.05	0.0756	24.89	0.0010	0.0010	
Maple vs. Black oak	1	1.00	0.1241	0.16	0.0365	0.2529	33.29	0.2529	39.29	0.4333	0.4333	
Maple vs. Chestnut oak	1	0.04	0.0582	24.81	0.0562	0.0532	103.95	0.0532	99.46	0.1286	0.1286	
Maple vs. Scarlet oak	1	0.11	0.4325	0.001	0.0410	0.4847	20.94	0.4847	43.13	0.1279	0.1279	
Maple vs. White oak	1	0.009	0.0418	10.13	0.1426	0.6470	43.37	0.6470	3.91	0.5316	0.5316	
Hickory vs. Tulip poplar	1	4.31	0.0006	0.79	0.8002	0.6366	0.22	0.6366	2.30	0.0039	0.0039	
Hickory vs. Black oak	1	9.70	0.0259	2.01	0.2490	0.0889	2.95	0.0889	13.37	0.4737	0.4737	
Hickory vs. Chestnut oak	1	9.41	0.0046	7.28	0.7774	0.0002	15.28	0.0002	34.06	0.1916	0.1916	
Hickory vs. Scarlet oak	1	8.01	0.0079	2.69	0.3923	0.9869	0.0003	0.9869	12.70	0.1613	0.1613	
Hickory vs. White oak	1	8.48	0.0077	1.12	0.9276	0.2241	1.49	0.2241	1.17	0.5954	0.5954	
Tulip poplar vs. Black oak	1	2.29	0.4245	0.82	0.1854	0.0192	4.58	0.0192	6.13	0.0760	0.0760	
Tulip poplar vs. Chestnut oak	1	0.92	0.3792	11.72	0.5776	0.9867	20.99	0.9867	17.87	0.0737	0.0737	
Tulip poplar vs. Scarlet oak	1	0.97	0.8758	0.69	0.2860	0.0609	0.18	0.0609	5.04	0.0003	0.0003	
Tulip poplar vs. White oak	1	0.72	0.3083	3.45	0.8600	0.2377	3.10	0.2377	6.43	0.0004	0.0004	
Black oak vs. Chestnut oak	1	0.62	0.9243	8.38	0.3152	0.0143	1.83	0.0143	0.56	0.7248	0.7248	
Black oak vs. Scarlet oak	1	0.37	0.5950	0.12	0.6786	0.7653	2.72	0.7653	0.17	0.0643	0.0643	
Black oak vs. White oak	1	0.73	0.9745	3.92	0.2154	0.1662	0.58	0.1662	19.48	0.2359	0.2359	
Chestnut oak vs. Scarlet oak	1	0.02	0.5995	14.88	0.5050	0.0509	13.18	0.0509	1.81	0.0149	0.0149	
Chestnut oak vs. White oak	1	0.009	0.8730	2.43	0.6896	0.2049	7.47	0.2049	45.37	0.0533	0.0533	
Scarlet oak vs. White oak	1	0.05	0.5228	6.10	0.3370	0.3353	1.32	0.3353	19.36	0.3012	0.3012	

Analysis of covariance results comparing the regression slopes of DBH (15-60 cm) for canopy area, canopy volume, bark thickness, and bark roughness in American beech, maple (sugar maple and red maple), hickory, tulip poplar, black oak, chestnut oak, scarlet oak, and white oak within Bernheim Arboretum and Research Forest, KY. Significant interactions ($P < 0.05$) noted in bold

Table 1.5 Canopy and bark parameter estimates, regression coefficients, and significance of linear models

Species	Canopy area (m ²)			Canopy depth (m)			Bark thickness (cm)			Bark roughness (cm)		
	Int	Slope	R ²	Int	Slope	R ²	Int	Slope	R ²	Int	Slope	R ²
American beech	-24.29	4.71	0.39**	-1.60	0.67	0.88***	-0.17	0.01	0.74***	-0.02	0.001	0.56**
Maple	65.54	0.46	0.03	-0.82	0.51	0.55***	-0.19	0.02	0.37**	-0.21	0.01	0.35**
Hickory	-178.50	9.11	0.66**	3.19	0.28	0.40**	-0.10	0.03	0.47**	-0.03	0.01	0.32*
Tulip poplar	33.04	1.87	0.09	3.80	0.33	0.29*	-0.26	0.03	0.73***	-0.49	0.03	0.64**
Black oak	-81.89	3.74	0.25	19.87	-0.03	0.91	1.203	0.004	0.01	0.12	0.01	0.40*
Chestnut oak	-49.62	3.53	0.69**	-0.11	0.24	0.46**	0.34	0.03	0.38*	0.10	0.02	0.71***
Scarlet oak	-7.83	2.26	0.12	14.12	0.10	0.02	0.73	0.01	0.12	0.58	0.00	0.00
White oak	-57.59	3.82	0.56**	0.95	0.30	0.32*	0.44	0.02	0.48**	0.00	0.01	0.24

Parameter estimates, regression coefficient, and significance of linear models for American beech, maple (red maple and sugar maple), hickory, tulip poplar, black oak, chestnut oak, scarlet oak, and white oak for canopy area, canopy volume, bark thickness, and bark roughness on 15-60 cm DBH trees within Bernheim Arboretum and Research Forest, KY. *P < 0.05, ** P < 0.01, *** P < 0.001

Leaf traits of the nine species encompassed a wide range of foliar characteristics (Table 1.3). Black oak leaves were significantly larger, thicker, had increased lignin content and smaller SA:V and tissue density when compared to all other species ($P < 0.0001$ for all comparisons). At the other end of the spectrum, American beech leaf litter was significantly thinner, lower in SLA, and greater in SA:V when compared to other species ($P < 0.001$ for all comparisons). Although not as pronounced as American beech, red maple and sugar maple had lower leaf area, higher SLA, and were relatively thin when compared to most oaks. Hickory had relatively small leaves and greater SLA in comparison to the oaks ($P < 0.0001$) but leaves were significantly thicker and curlier when compared to American beech and red maple.

The PCA of litter traits explained 82% of the variation in the data set with the first two principal components (Fig. 1.3). Axis 1 explained 64.28% of the variation between species, with leaf thickness and volume closely related to the axis and SLA and SA:V related to a lesser extent. Lignin concentration and tissue density were the only factors strongly related to axis 2, accounting for an additional 17.62% of variation in the data. Large, curled leaves with lower SLA and greater SA:V have more negative values on axis 1, while small, flat leaves with greater SLA and lower SA:V had more positive values. On axis 2, leaves with greater lignin and tissue density had more negative values, while those with lower lignin concentration and tissue density had more positive values. The *k*-means cluster analysis divided the species into four distinct groups based on litter characteristics (Fig. 1.3). Red maple, sugar maple, and American beech comprised cluster

one, tulip poplar, white oak, chestnut oak, and scarlet in in cluster two while hickory and black oak grouped by themselves to make up clusters 3 and 4.

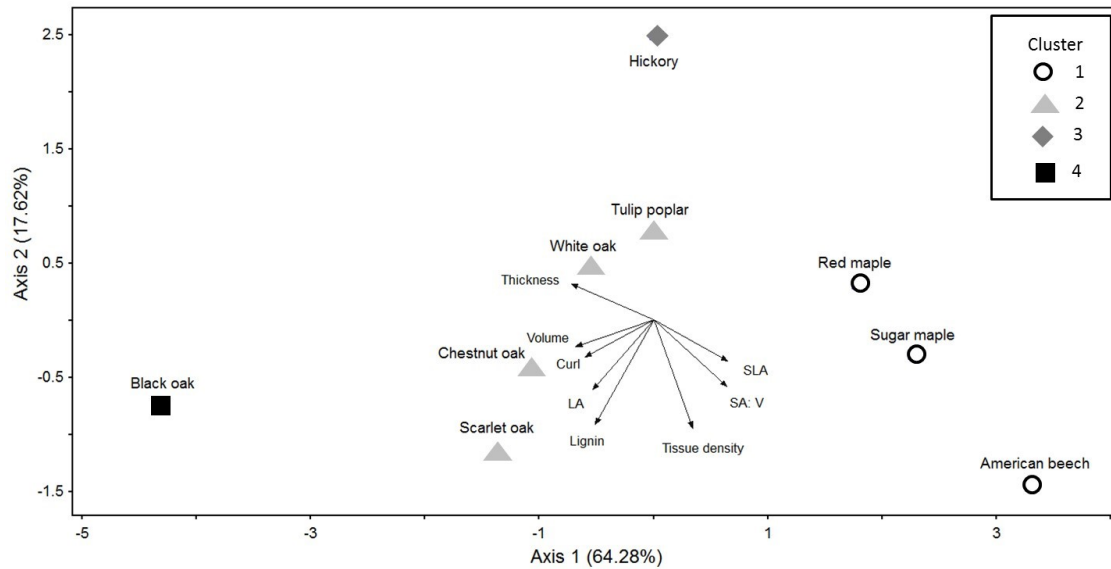


Figure 1.3 Leaf litter traits principal components analysis

Principal Components Analysis (PCA) of litter traits for mesophytes and oaks. Litter traits include leaf area (LA), specific leaf area (SLA), curl, thickness, volume, surface area: volume (SA:V), tissue density, and lignin. Cluster groups obtained through use of *k*-means cluster analysis.

Light intensity, air temperature, and soil surface temperature varied between species (Table 1.6). Light intensity was 30% lower under American beech when compared to all other species, and was surprisingly 24% higher under red maple. Sugar maple and white oak had light intensities that were 13% lower when compared to chestnut oak, but light intensity beneath other species were similar. Differences in air temperature and soil surface temperature mirrored light intensity trends. American beech and sugar maple had significantly lower air temperature (~23.79 °C), while red maple

and chestnut oak had the warmest understories (~ 24.44 °C; $P < 0.0001$ for both comparisons). Soil surface temperature at the bole of American beech and sugar maple was significantly lower when compared to other species and the soil surface temperature under red maple had the highest temperature ($P < 0.0001$ for both comparisons).

Table 1.6 Understory light intensity, air temperature, and soil surface temperature

Environmental variable	American beech	Red maple	Sugar maple	Hickory	Chestnut Oak	White Oak	P value
Light intensity (Lumens m ⁻²)	3401.40 ^A ±13.86	5783.45 ^B ±14.01	4394.26 ^C ±13.81	4801.35 ^{CD} ±13.83	5058.29 ^D ±15.11	4426.88 ^C ±13.77	< 0.0001
Air temperature (C°)	23.63 ^A ±0.13	24.46 ^B ±0.13	23.95 ^{AC} ±0.13	24.03 ^C ±0.13	24.42 ^{BD} ±0.14	24.07 ^{CD} ±0.13	< 0.0001
Soil surface temperature (C°)	Bole 20.94 ^A ± 0.06	Bole 21.53 ^B ±0.08	Bole 20.99 ^A ± 0.06	Bole 21.56 ^B ±0.07	Bole 21.80 ^C ±0.08	Bole 21.22 ^D ±0.07	< 0.0001
	Mid 21.41 ^{AB} ±0.09	Mid 22.06 ^C ±0.10	Mid 21.44 ^{AB} ± 0.07	Mid 21.38 ^B ±0.07	Mid 21.72 ^D ±0.07	Mid 21.59 ^{BD} ± 0.06	

Average light intensity, air temperature, and soil surface temperature at mid-canopy position (mid) and bole position in the understory of American beech, red maple, sugar maple, hickory, chestnut oak and white oak trees located within Bernheim Arboretum and Research Forest, KY. Values are means ± SE. Different superscript letters indicate significant differences (p < 0.05) among leaf litter types for a given parameter. Bole and mid-canopy comparisons made independently between species.

Continuous soil moisture measurements made 24 hrs following a rainfall event were not significantly different between chestnut oak and red maple for small ($P = 0.82$), medium ($P = 0.93$), or large rainfall ($P = 0.16$) events (Table 1.7). Instantaneous fuel moisture measurements varied between species in some post-rainfall measurements, although location (midpoint vs. bole) was not significant ($P > 0.05$) for any event (Table 1.8). In the absence of rainfall (6/6/2017), American beech, sugar maple, and hickory had significantly higher fuel moisture when compared to chestnut oak and white oak ($P = 0.0003$). Three days post-rainfall for the event on 6/15, there were also significant differences between species: hickory had the highest fuel moisture, followed by American beech and red maple, and white oak fuel was the driest ($P < 0.0001$). After the rainfall event on 6/19, hickory had the driest fuels, but soil moisture between all other species was similar ($P = 0.0002$). Other significant results occurred the day after the rainfall event on 6/23, when the fuels under sugar maple and chestnut oak were moister in comparison to white oak, red maple, and American beech ($P = 0.0002$). After the same event and two days post rainfall, sugar maple still had significantly increased fuel moisture when compared to all other species ($P < 0.0001$).

Table 1.7 Continuous understory soil moisture measurements

Rain event size (avg. rainfall)	Volumetric soil moisture $m^3 m^{-3}$		
	Red maple	Chestnut oak	<i>P</i> value
Small (0.31 cm)	0.118 ± 0.014	0.114 ± 0.011	0.82
Medium (1.4 cm)	0.185 ± 0.014	0.185 ± 0.012	0.93
Large (5.8 cm)	0.222 ± 0.011	0.244 ± 0.009	0.16

Average understory volumetric soil moisture measurements in the 24 hrs. following small, medium, and large rainfall events that occurred during June-September 2017 for red maple and chestnut oak within Bernheim Arboretum and Research Forest, KY.

Values are means ± SE

Table 1.8 Instantaneous understory fuel moisture measurements

Rainfall date	Rainfall amount (cm)	Location	Hrs. since rainfall	Volumetric fuel moisture m ³ m ⁻³							P value
				Beech	Red maple	Sugar maple	Hickory	Chestnut oak	White oak		
6/6	0.58	All sites	120	0.033 ^{ABC} ±0.002	0.031 ^{BCD} ±0.002	0.038 ^A ±0.002	0.036 ^{AB} ±0.002	0.030 ^{CD} ±0.002	0.029 ^D ±0.002	0.0003	
6/15	1.51	YR	4	0.080 ±0.008	0.076 ±0.008	0.083 ±0.009	0.0833 ±0.012	0.060 ±0.010	0.060 ±0.008	0.0981	
6/18 - 6/19	1.29	WC	4	0.071 ±0.006	0.066 ±0.006	n.d.	0.050 ±0.005	0.067 ±0.006	0.064 ±0.006	0.0613	
6/23	4.38	AH	10	0.041 ^A ±0.002	0.043 ^A ±0.003	n.d.	0.026 ^B ±0.003	0.035 ^A ±0.003	0.035 ^A ±0.003	0.0002	
			52	0.034 ±0.002	0.030 ±0.002	n.d.	0.026 ±0.002	0.030 ±0.002	0.029 ±0.002	0.0506	
			58	0.075 ^A ±0.016	0.095 ^A ±0.01	0.143 ^B ±0.01	0.118 ^{AB} ±0.016	0.122 ^B ±0.010	0.085 ^A ±0.010	0.0002	
			58	0.041 ^{AB} ±0.007	0.041 ^B ±0.004	0.076 ^C ±0.004	0.057 ^A ±0.007	0.047 ^{AB} ±0.004	0.041 ^{AB} ±0.004	< 0.0001	

Average volumetric fuel moisture in the understory of American beech, red maple, sugar maple, hickory, chestnut oak, and white oak following rainfall events during June 2017 at three sites [Yoe's road (YR), Wilson's creek (WC), and Ashlock hollow (AH)] within Bernheim Arboretum and Research Forest, KY. Values are means ± SE. Different superscript letters indicate significant differences ($p < 0.05$) among leaf litter types for a given parameter. n.d. = no data. Significant values noted in bold

Discussion

Some overstory tree species showed a positive correlation between canopy traits and stem size, signifying the potential for large, light-limiting zones of influence to occur beneath these trees as they increase in size. Maples did not have a significant linear increase in canopy area as a function of DBH; rather, canopy area increased until 30-40 cm DBH before leveling off while canopy depth significantly increased. This may be caused a growth strategy that is prevalent among shade tolerant species, which allows maples to have wider spreading crowns that stop horizontal growth and extend vertically once they reach higher light levels in dominant overstory positions (Lourens Poorter et al., 2003; Niinemets, 2010). Consequently, maples may have narrower zones of influence than I originally hypothesized, and this zone could have reduced light transmittance (Canham et al., 1993), although my findings do not support this. Hickory had the most significant increase in canopy area with increased DBH when compared to almost every species, but less a pronounced increase in canopy depth, which was similar of oaks growth patterns. Hickory, which is relatively more shade-intolerant than maples, can shift their foliage to the top of their canopy and limit the amount of vertical canopy layers in order to avoid shelf-shading lower limbs (Niinemets 2010), which may be why I found that hickory did not reduce understory light intensity. American beech was unique in that it was the only species to have significantly greater normalized canopy area, volume, and depth, likely due to its high shade tolerance, crown plasticity, and the consequential capacity to occupy canopy space at small and large size classes (Pretzsch and Schütze, 2005; Schröter et al., 2012). Greater canopy area and depth likely led to reduced light levels and temperatures I found in the understory, which may lower the vapor pressure

deficit and consequently decrease ignition probability and fire susceptibility in these influence zones (Kozlowski and Pallardy, 1997; Ray et al., 2005; Tanskanen et al., 2005). Lower understory light levels beneath American beech may also lead to reduced survival of shade intolerant oak and increased survival of shade tolerant conspecifics, further promoting the mesophication process (Lorimer, 1984; Walters and Reich, 1996).

My findings were consistent with the well-established concept that bark thickness increases with stem size, but differences in the bark allocation rates were species dependent (Hoffmann et al., 2003). Overall, American beech and maples had thinner and smoother bark when compared to other species sampled in this study but did not experience a significant increase in thickness or roughness with DBH. A study conducted on silver maple (*A. saccharinum* L.) yielded similar results showing the trees to have thin bark when saplings with a slow rate of bark thickening as the tree ages (Hengst and Dawson, 1994). Thin, smooth bark may be a mechanism of mesophication through alteration of precipitation distribution. Although not directly investigated in this study, there is substantial evidence that smooth-barked trees produce larger stemflow inputs than co-occurring rough-barked species, which could increase understory soil moisture post-rainfall and protect mesophytes from surface fires (Alexander and Arthur, 2010; Siegert and Levia, 2014; Levia and Herwitz, 2005). Chestnut oak, tulip poplar, and hickory experienced a large increase in bark thickness and roughness as DBH increased, which is likely a fire adaptation (Pellegrini et al., 2017), and extreme fire resistance is noted in mature tulip poplar (McCarthy, 1933). Not only can thick, rough bark decrease stemflow and cause less water to be deposited in the immediate zone surrounding its bole (Levia et al., 2010), thick bark may also provide increased cambium insulation and

protection from fire (Pausas, 2015). Increased bark thickness may lead to increased survival during a fire, which could be problematic when trying to increase light levels and decrease competition for oak by removal of overstory trees (Harmon, 1984).

American beech had the lowest understory light intensity compared to all other species and understory air and litter temperatures that were cooler compared to oaks. Similar results were found in a study conducted in a northern hardwood forest, where the understory of American beech had the lowest percent of photosynthetically active radiation (PAR) when compared to red maple, sugar maple, and northern red oak (*Q. rubra* L.; Canham 1994). The reduction of light transmittance under American beech is likely a product of increased leaf area and canopy depth, which allows less light to reach the forest floor (Abrams and Kubiske 1990; Kozlowski and Pallardy 1997). Because light and air temperatures are linked, a decrease in radiation will lead to cooler understory temperatures during the growing season (Barkman, 1992). Differences between other species understory environmental variables were not as pronounced, although red maple surprisingly had the highest understory light intensity and litter layer temperature at the canopy midpoint. Increased radiation and subsequent increase in the soil surface temperature found under red maple may be caused by this species high susceptibility to ice damage, which has been documented across the eastern U.S. and specifically within Bernheim (Duguay et al., 2001; Vowels, 2012). Ice damage can cause limb breakage and crown loss and an *Acer-Fagus* forest that experienced ice damage had understory photosynthetic photon flux density increase 4-5x at 0.3 to 4 m aboveground (Beaudet et al., 2007). Although some variability in understory conditions between species existed, I recognize that light in forest understories is not the function of single canopy tree, and

although I targeted large overstory individuals with relatively clear understories (<30% cover) some light interception by small plants/shrubs likely occurred (Canham et al., 1994).

Instantaneous and continuous fuel and soil measurements yielded few significant differences between species and no differences between bole and midpoint locations. Lack of distinction between fuel moisture and soil moisture under various species and at different understory locations may be due to several methodological errors. Soil moisture loggers, which measured volumetric water content in the mineral soil, lacked adequate replication due to unforeseen complications with animals, and limited measurement capacity per species (red maple and chestnut oak) is not sufficient when soil moisture variability across the forest is high (Cosh et al., 2004). Fuel moisture following rainfall events varied between some species but these differences had no logical pattern that could be attributed solely to canopy or bark traits of the overstory tree. These instantaneous measurements had no across site replication and the sample size per species within a single location was low, with an average five individuals. In addition, fuel moisture measurements were corrected for being taken in the litter layer vs. the mineral soil but litter depths have a high range (0-9 cm) across Bernheim. Consequently, the probe, which was 3.81 cm long, would sometimes be fully or partially inserted into mineral soil, which has very different water holding capacity than litter and could lead to inaccurate reading (Cosby et al., 1984; Hudson, 1994). Lack of variation in soil moisture between species may also be attributed to the effect of several small-scale factors, such as vegetation present in midstory/understory and preferential pathways of stemflow, which may have not been detected by sensors (Voigt, 1960).

Conclusions

Instead of dividing species into exclusive oak and mesophyte categories, it may be more appropriate to think of species that contribute to mesophication along a gradient that accounts for canopy, bark, and litter traits (Fig. 1.4). Furthermore, as mesophytes ascend into dominant overstory positions in eastern forests, their canopy and bark traits are subject to change, which may impact forest flammability. In this study, American beech may be most likely to contribute to mesophication due to increased canopy area, depth, and leaf area that are projected to keep increasing with DBH and relatively smooth and thin bark, even at larger tree sizes. These traits could then create large moist zones of reduced flammability on the forest floor as American beech reaches dominant overstory positions, although this species has slow leaf litter decomposition, which may lead to an accumulation of leaf litter overtime. As maple species reach larger size classes (>40 cm DBH), they may contribute to mesophication less through alteration of understory microclimate conditions and more through their leaf litter that can create moist, dense, and less flammable fuel beds in their understory. Hickory and tulip poplar should not contribute to mesophication to the extent in which American beech and maple species do, but may not actively create flammable conditions because of less pyrophytic leaf litter in comparison to oak leaf litter.

Mesophication is a relatively new term (2008), and we are only beginning to understand this complex successional process that is occurring in the eastern United States. Identifying species that contribute to this process and the mechanisms used to reduce flammability and benefit their proliferation could lead to more effective prescribed fire implementation. This study focused on the impact individual overstory

species have as they move from subdominant to dominant canopy positions, but the majority of mesophytes still occupy midstory/sapling stages in eastern U.S. forests. Therefore, future studies should explore how midstory trees/saplings contribute to mesophication, since these trees may have disproportionate impacts on understory conditions that were not observed in overstory trees. In conclusion, this study documented the ways in which certain species may or may not contribute to the mesophication process through the alteration of forest flammability and provides preliminary data to assess species-specific understory impacts.

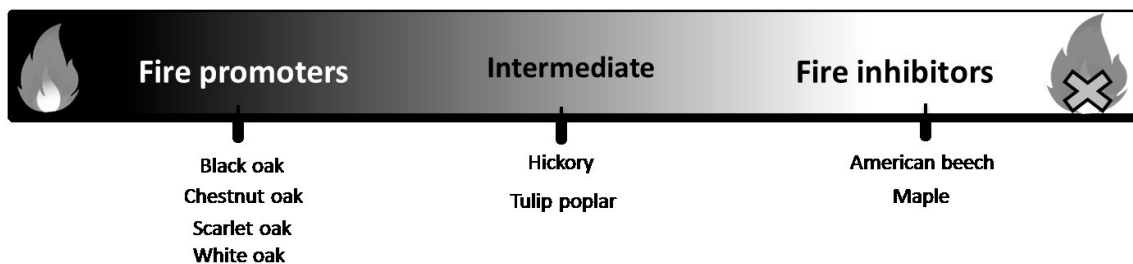


Figure 1.4 Species conceptual flammability ranking

Ranking of species that possess canopy, bark, and leaf litter traits that will either promote or inhibit fire based on findings in this study and documented implications

CHAPTER II

MESOPHICATION OF UPLAND OAK FORESTS: THE ROLE OF SPECIES-SPECIFIC DIFFERENCES IN LEAF LITTER DECOMPOSITION AND FUEL BED STRUCTURE

Introduction

Leaf litter in forested ecosystems plays an important role in stand level processes such as decomposition dynamics and mediating feedbacks between fire and vegetation (Whelan 1995; Mitchell et al., 2009; Schwilk 2015). Deciduous hardwoods produce leaves with varying morphological and chemical adaptations to different environmental conditions, and once senesced, leaves can then impact ecosystem-level processes like forest flammability (Mutch 1970; Prescott 2002; Engber and Varner 2012). For example, shade-tolerant tree species generally have thin leaves with high specific leaf area (SLA) and surface area:volume ratio (SA:V) to maximize light capture in low-light environments (Jackson 1967; Evans and Poorter 2001). These traits can lead to increased decomposition rates (Swift et al., 1979) and the formation of a dense fuel bed that inhibits fire spread (Scarff and Westoby 2006; Cornwell et al., 2015). In contrast, broadleaf species adapted to xeric environments with high light produce thick leaves to enhance water use efficiency (Abrams 1990), which can then lead to decreased SLA, a more aerated fuel bed, and increased rate of fire spread (Grootemaat et al., 2017). Differences in leaf litter chemistry may also directly impact flammability; for example, litter with

high lignin content and low nitrogen (N) content are linked to slower decomposition rates (Melillo et al., 1982; Taylor et al., 1989), increased fuel consumption, and longer flame duration (Grootemaat et al., 2015). Because the myriad of ways in which leaf litter can impact important forest functions (e.g., decomposition and fuel bed structure), understanding species-specific controls on these processes may help predict future forest flammability.

Understanding species controls on decomposition rates and fuel bed properties is especially important in upland oak forests of the eastern United States. While these forests have been oak-dominated for 8,000 years, they are undergoing a pronounced compositional shift to fire-sensitive, shade-tolerant species (i.e. mesophytes; Abrams 1992; Foster et al., 2002; Nowacki and Abrams 2008). This is most notable in the Central Hardwood Region, where oak importance value (IV; average relative density and relative volume) is declining, while mesophyte IV, in particular red maple (*Acer rubrum* L.), is increasing (Fei and Steiner 2007; Fei et al., 2011).

The marked decrease in upland oak IV, and simultaneous increase in competitors like red maple, is likely due to oak regeneration problems stemming from anthropogenic fire suppression (McEwan et al., 2011). Historically, fire was a key disturbance in upland oak forests that kept light conditions relatively open for shade-intolerant oak and helped exclude fire-sensitive competitors (Abrams 1992; Delcourt and Delcourt 1997). In the absence of fire, shade-tolerant mesophytes are able to establish in upland oak forests and are hypothesized to create a positive feedback-loop of self-promoting conditions (Nowacki and Abrams 2008). This feedback-loop is termed mesophication and posits that

the presence of mesophytes creates more cool, damp, and less flammable conditions, further reducing the influence of fire (Nowacki and Abrams 2008).

One way that mesophytes could reduce flammability (i.e. ignition probability, fuel continuity, intensity, consumption) is through alteration of leaf litter fuel loads and/or the structure of those fuels. Mesophytes, such as red maple and sugar maple (*A. saccharum* Marshall), can have leaf litter with lower lignin:N than co-occurring oaks and a consequent increase in decomposition rates (Cromack and Monk 1975; Blair and Crossley 1988; Ball et al., 2008; Alexander and Arthur 2014). Increased decomposition rates can lead to a reduction in leaf litter, and because fires often spread by consuming the litter layer, any reduction in the organic layer will inevitably reduce forest floor flammability (Arthur et al., 2015; Brewer and Rogers 2006). Furthermore, shade-tolerant mesophytes may reduce flammability through additions of thin, flat leaf litter (Babl et al., In preparation; Kreye et al., 2013), which can cause compaction of the “fluffy,” aerated, and flammable fuel beds that are characteristic of upland oak forests (Scarff and Westoby 2006). Increased bulk density (or compaction) of fuel beds under mesophytes’ canopies can cause decreased aeration and increased fuel moisture, further yielding a reduction in forest floor flammability (Kreye et al., 2013, 2018; Dickinson et al., 2016).

Reduction of flammability is problematic because prescribed fire is frequently used in upland oak regeneration efforts in the eastern U.S. (Brose and Van Lear 1998; Brose et al., 2005, 2013) to reduce canopy cover and decrease competition (Abrams 1992; Lorimer et al., 1994). Zones of reduced flammability created by leaf litter of fire-sensitive mesophytes may protect themselves from fire damage, interrupt fire continuity, and potentially lessen the overall effectiveness of prescribed fire. A reduction in the

effectiveness of prescribed fire may allow for future mesophyte survival which could negatively impact oak survival via increased competition.

Lack of upland oak regeneration and the consequential perpetuation of the mesophication process (survival of mesophytes) are detrimental because oaks are foundation and keystone species in the eastern U.S. (Fralish 2004; Hanberry and Nowacki 2016). Oaks are of major importance in maintaining ecosystem diversity, providing a vital mast source, and controlling ecosystem-level processes such as decomposition and nutrient cycling (Fralish 2004; Ellison et al., 2005) and their replacement can have cascading effects on wildlife populations and forest hydrology (Rodewald and Abrams 2002; Alexander and Arthur 2010). For example, a study conducted in a xerophytic oak stand in the Southern Appalachians that underwent mesophication had an 18% reduction in water yield, which overtime can lead to large changes in water supply and negatively impact human and wildlife interests (Caldwell et al., 2016).

The primary objective of this study was to quantify decomposition rates, leaf litter chemistry, and fuel bed properties (loads and bulk density of leaf litter and duff layer) between hypothesized mesophytes [red maple, sugar maple, hickory (*Carya* spp.), and American beech (*Fagus grandifolia* Ehrh.)] and upland oaks [black oak (*Q. velutina* Lam.), chestnut oak (*Q. montana* Willd.) and white oak (*Q. alba* L.)]. Because mesophication is a relatively new term, many assumptions classifying mesophytes as “less flammable” are based on anecdotal accounts which lack supporting empirical data (Nowacki and Abrams 2008). To understand which species may promote or inhibit the mesophication process, I selected hypothesized mesophytes that have increased

dominance in areas previously occupied by upland oaks within the eastern U.S. For example, red maple, sugar maple, and American beech have experienced notable increases in abundance on historically oak-dominated landscapes in the eastern U.S. (Abrams and Nowacki 1992; Abrams et al., 1995; Abrams 2003; Fei and Steiner 2007; Hart and Grissino-Mayer 2008; Izbicki et al., In preparation). There is also evidence of increasing levels of mockernut hickory (*C. tomentosa* Lam.) in parts of the southern U.S. where oak is declining (Brewer 2015), warranting further investigation of this species. Understanding decomposition and fuel bed dynamics of these hypothesized mesophytes is necessary to help predict cascading effects on forest flammability and implications for increased mesophyte survival.

Methods

Site description

This study was conducted in Bernheim Arboretum and Research Forest (hereafter referred to as Bernheim; 37°52' N, 85°35'), located ~40 km south of Louisville in western Kentucky. Bernheim is a 57 km² second-growth (80-100 year old) hardwood forest dominated by upland oaks. Fire has been excluded from the upland oak stands within Bernheim since the cessation of agriculture and logging activities in 1929 (A. Berry, Bernheim Arboretum & Research Forest, 2016, Personal communication). The climate is humid, temperate, and continental. From 1981-2010, Bernheim has average growing season (JJA) temperatures of 24.0 °C and dormant season (DJF) temperatures of 2.5 °C (NOAA). Mean annual rainfall is 126 cm, evenly distributed throughout the year and average annual snowfall is 33 cm (NOAA). Soils are primarily of the Lenberg-Carpenter and Zanesville complex. Lenberg-Carpenter complex is found on side slopes that usually

range from 20 to 40 percent, is well-drained with silty loam topsoil and formed from weathered shale (NRCS). The Zanesville complex, usually located on ridgetops, has 6 to 12 percent slopes, is moderately well drained with a silty loam topsoil, and parent material of siltstone and shale (NRCS).

Forest overstories (>10 cm diameter at breast height [DBH]) are dominated by chestnut oak (25%), scarlet oak and black oak (19%), and white oak (39%), and collectively make up 23.89 m² hectare⁻¹ of basal area. Midstory (2-10 cm DBH) is primarily composed of hickory (*Carya spp*; 35%), American beech (27%), sugar maple (24%), and red maple (13%), which collectively comprise 1.28 m² hectare⁻¹, while oaks only make up ~1.5% of the midstory size class. Seedlings within Bernheim (<2 cm DBH) are dominated by red maple (42%), white oak (30%), scarlet oak (*Q. coccinea* Münchh.) and black oak (12%).

Leaf litter decomposition

To assess whether leaf litter decomposition rates vary among mesophytes and upland oaks, I used a traditional decomposition bag study (Bocock and Gilbert 1957). Throughout litterfall during 2016, fresh leaf litter from each species (red maple, sugar maple, hickory, black oak, chestnut oak, and white oak) was collected by hand, bi-weekly across upland oak stands throughout the study area. Because American beech is marcescent, leaves were removed directly from trees during the same time period. Fresh litter was returned to the lab, air-dried, and 5 g was placed into fine-mesh decomposition bags. Mesh size was 1 x 2 mm, which was large enough to not impede soil fauna and microbial entry (Melillo et al., 1982). Bags were returned to two non-contiguous ridge-top sites in December 2016 (2 sites, 7 species, 3 replicates, 4 pick-ups, for a total of 168

bags). Bags were set up in the forest at a location that was away from the bole of large trees, not in a gap, and free of understory/midstory plants, to eliminate confounding factors and represent a common garden experiment. One bag per site was picked up starting at time 1 (spring 2017), then again at 3, 6, 9, 12 months (winter 2017) afterwards. Time 0 samples had 5 g of air-dried litter weighed and placed into a Ziplock bag, returned to the lab and oven-dried at 60 °C for 48 hr and weights recorded to obtain an oven-dry conversion factor. After removal from the field, original leaf litter contents from each bag were returned to the lab, cleaned of external debris and invertebrates, oven-dried at 60 °C for 48 h, and weighed to determine mass loss. A subsample was then combusted in muffle furnace at 500 °C for 4 hr to account for possible mineral soil contamination. The air-dried to oven-dried weights for time 0 samples were used to calculate decomposition rates for each retrieval date by using single exponential decay model (Olson 1963):

$$M_t/M_0 = \exp^{(-kt)} \quad (2.1)$$

where M_0 is the absolute dry weight of litter remaining at time 0, M_t is the absolute dry weight of litter remaining at time t , t is the time in the field (in years), k is the decomposition rate constant. C and N were measured by grinding a 5 g subsample of leaf litter at time 0 and after each pick-up date and running in an Elemental Combustion Analyzer (ECS CHNO-S; Costech, Valencia, CA). Lignin (time 0 only) was measured at Dairy One Lab (Ithaca, NY) with an Ankom Fiber Analyzer (ANKOM Technology, Macedon, NY). For each sample date, the percent of C and N remaining in relation to initial values were calculated using the following formula:

$$\%C \text{ (or N) remaining: } ((C_{t1} * \text{mass}_{t1}) / (C_{t0} * \text{mass}_{t0})) \times 100 \quad (2.2)$$

where C_{t0} and C_{t1} are the proportion of C in litter sample at time 0 and on a given sampling date, and $mass_{t0}$ and $mass_{t1}$ are the dry weights of the litter sample at those times.

Fuel bed properties

To identify if single trees have reduced zones of flammability in their understory, fuel beds, which included the litter layer (annual leaf fall) and duff layer (decomposed, unidentifiable organic matter), were sampled for mass and bulk density under upland oak and mesophytes within Bernheim in December 2016 and January 2017. Tree species sampled in this study include those mentioned above, excluding black oak, and met the following criteria: (1) trees encompassed a size gradient from 20-60 cm DBH, because most notable differences would occur in the understory of mature overstory trees due to larger zones of influence; (2) trees were not located near the road (> 20 m away) or near/within a canopy gap to avoid potential edge effects; (3) trees had a reasonably clear understory to target single-tree influences and limit confounding effects (<30% cover); (4) trees sat relatively flat on the landscape to avoid effects on understory conditions due to variable drainage. The original goal of this study was to sample 15 overstory trees per species along the selected size gradient, but due to some mesophytes, such as American beech and sugar maple, not being present in larger size classes, these species had several trees selected that ranged from 10-20 cm DBH.

To sample annual litter inputs and the duff layer, two 30 x 30-cm quadrats were placed mid-canopy in the north and south cardinal directions under each tree in December 2016 (just following leaf fall). In the center of each quadrat, leaf litter depth was measured with a ruler after gently inserting a knife into this layer. The leaf litter

layer was harvested and placed in an air-tight plastic bag, and then the same steps repeated to harvest the duff layer. In the lab, leaf litter was sorted by species and all components (twigs, fruit, bark) were placed in the oven at 60 °C and dried to a constant weight. Litter was weighed to determine species-specific contributions to leaf litter mass, with non-litter components (twigs, fruit, bark) removed from this layer and duff layer. Non-litter components were removed from both layers to minimize variation that may not be attributed to species-specific zones of influence. Bulk density was then calculated by dividing the oven-dried leaf litter or duff mass by the volume the litter or duff occupied.

Statistical analyses

Differences in litter mass remaining, C and N remaining, and C:N ratios between species were analyzed as a two-way ANOVA with species and time (time 0 removed) and their interaction as fixed effects in JMP v. 13. Although litter bags were placed at two different sites, I inadvertently did not record site locations for pick up for times 3 and 6 and as a result was unable to analyze these times for site effects. However, I do not expect site differences because of similar soil acidity (~4 pH) and overstory composition ($30 \text{ m}^2 \text{ ha}^{-1}$). In addition, pick up times 6 and 9 had no significant site effect ($P= 0.1850$) when analyzed with an ANOVA with site as a fixed effect and percent mass remaining as the response variable. Differences in initial litter chemistry (lignin, %C, %N, lignin:N, and C:N ratios) were compared using a one-way ANOVA with the fixed effect of species. Decay constants, R^2 and P-values for the single exponential models were calculated by fitting the model to raw data for percent mass remaining using SigmaPlot v. 12.3.

All variables were tested for normality and homogeneity of variance and those that did not meet these assumptions were transformed using logarithmic or square-root functions. For significant interactions ($P < 0.05$), least squares means were compared via a post-hoc Student's T test to determine differences among means at $\alpha = 0.05$. Reported P values were computed on transformed data, but means and standard errors are presented on untransformed data.

To see if there were differences in the amount of fuel or bulk density under mesophytes and oaks, a one-way ANOVA was used with the fixed effect of tree species and response variable of leaf litter, duff, or bulk density. Because fuel loads were collected in December and most prescribed burning in oak forests occurs in late dormant season (Ryan et al., 2013), and lightning ignited fires historically occurred in June (Komarek 1964), leaf litter inputs from forest floor blocks were multiplied by the average percent mass loss after 3 months (March) and 6 months (June) for each species. These results were then analyzed using a two-way ANOVA with the fixed effects of species group (mesophyte or oak) and time and the response variable as percent leaf litter.

To calculate projected net fuel loads that would remain for each species after one year, the following steps were taken: First, average leaf biomass (kg) per unit basal area (m^2) for each species was obtained with allometric equations from Martin et al. (1998) and Ribe (1973). For this step, DBH for all sampled species was put into the allometric equation which produced leaf biomass; this value was then divided by the corresponding tree's basal area before being averaged for the entire species. Next, I multiplied these averaged values by the current midstory/overstory basal area within Bernheim ($30 m^2 ha^{-1}$

¹) to calculate average leaf litter inputs (kg ha^{-1}) per species. Leaf litter outputs were calculated by multiplying leaf litter inputs by percent mass loss in one year for each species. Finally, annual fuel loads were calculated by subtracting leaf litter outputs from inputs.

Results

Initial chemistry varied between mesophytes and oaks (Table 2.1). Black oak and chestnut oak had the highest carbon concentration ($50.22 \pm 0.18\%$ and $49.12 \pm 0.31\%$, respectively), while other species were similar ($P = 0.2923$). Black oak had the highest lignin concentration ($19.77 \pm 0.19\%$), followed by chestnut oak ($13.90 \pm 0.19\%$) then American beech ($12.10 \pm 0.19\%$; $P < 0.0001$ for all comparisons). Lignin concentration in white oak ($11.37 \pm 0.19\%$) and sugar maple ($10.87 \pm 0.19\%$) were similar ($P = 0.2906$), while red maple ($9.50 \pm 0.19\%$) and hickory ($9.00 \pm 0.19\%$) both had the lowest lignin concentration ($P < 0.0001$ for both comparisons). Nitrogen concentration was lowest in red maple ($0.73 \pm 0.05\%$) and white oak leaf litter ($0.89 \pm 0.07\%$; $P < 0.0001$ for both comparisons) and highest in sugar maple ($1.13 \pm 0.08\%$) and hickory ($1.32 \pm 0.07\%$; $P < 0.0001$ for both comparisons) litter, while all other species were similar ($P = 0.2790$). Lignin:N ratio followed a similar trend; black oak had the significantly highest lignin:N concentration (18.87 ± 0.92 ; $P < 0.0001$), while hickory (6.92 ± 0.92) and sugar maple (9.87 ± 0.92) had the lowest lignin:N concentration ($P < 0.0001$ for both comparisons). Leaf litter C:N was similar between most species ($P = 0.1391$), although it was significantly highest in red maple (67.10 ± 4.56) litter and lowest in hickory (35.32 ± 1.79 ; $P < 0.0001$ for both comparisons).

Table 2.1 Initial leaf litter chemistry

Litter characteristic	American Beech	Red maple	Sugar maple	Hickory	Black oak	Chestnut oak	White oak	<i>P</i> value
C (%)	46.04 ^{AB} ±0.33	47.51 ^A ±0.65	45.88 ^B ± 0.72	45.98 ^B ± 0.34	50.22 ^C ± 0.18	49.12 ^C ± 0.31	46.61 ^{AB} ± 0.77	< 0.0001
Lignin (%)	12.10 ^A ±0.19	9.50 ^B ±0.19	10.87 ^C ±0.19	9.00 ^B ±0.19	19.77 ^D ±0.19	13.90 ^E ±0.19	11.37 ^C ±0.19	< 0.0001
N (%)	1.00 ^{AB} ± 0.05	0.73 ^C ± 0.05	1.13 ^{BD} ± 0.08	1.32 ^D ± 0.07	1.08 ^{AB} ± 0.08	1.04 ^{AB} ± 0.08	0.89 ^{AC} ± 0.07	< 0.0001
Lignin: N	12.25 ^{AB} ± 0.92	13.46 ^A ±0.92	9.87 ^B ± 0.92	6.92 ^C ± 0.92	18.87 ^D ± 0.92	13.72 ^A ± 0.92	13.17 ^A ± 0.92	< 0.0001
C:N	46.55 ^{AB} ± 2.07	67.10 ^C ± 4.56	41.49 ^{AD} ± 2.77	35.32 ^D ± 1.79	47.94 ^{AB} ± 3.65	48.48 ^{AB} ± 3.47	53.97 ^B ± 3.84	< 0.0001

Initial chemistry for American beech, red maple, sugar maple, hickory, black oak, chestnut oak, and white oak leaf litter collected within Bernheim Arboretum and Research Forest, KY. Values are means ± SE. Different subscript letters indicated significant differences among leaf litter types (i.e. across rows) for a given parameter. C = Carbon, N = Nitrogen

Percent mass remaining was distinct between some mesophytes and oaks (Fig. 2.1A), and percent C remaining mirrored these trends (Fig. 2.1B). Red maple lost ~42% of its mass within the first three months, which was significantly more than all the other species ($P < 0.0001$). Hickory and sugar maple experienced the next greatest mass loss after three months, with only ~70% remaining, while white oak, chestnut oak, red oak, and beech only lost 15-23% of their original mass. There was a significant effect of time ($P < 0.0001$) and species ($P < 0.0001$) on the mass remaining (%) but the effect of species by time was not significant (0.7890), indicating that differences between species did not change over time. Therefore, after 12 months, trends were still similar, with red maple and sugar maple having lost 54% of their mass, while red oak and American beech only lost ~35% ($P < 0.0001$). Decomposition rates based on a single exponential decay model were generally faster in mesophytes, with the exception of American beech, when compared to oaks (Table 2.2). Red maple had the fastest decomposition rate ($k = 0.91$)

followed by sugar maple ($k = 0.84$), hickory ($k = 0.68$), white oak ($k = 0.65$), chestnut oak ($k = 0.53$), black oak ($k = 0.47$) and American beech ($k = 0.43$).

All species experienced a decrease in percent N remaining within the first 6 months before immobilization began to occur and percent N began to increase (Fig. 2.1C). After 12 months, there were no significant differences in the N remaining between species ($P = 0.1271$). In general, the C:N ratio decreased with time for all species and was significantly lower after 12 months ($P < 0.0001$; Fig. 2.1D). Initial C:N was significantly highest in red maple when compared to other species ($P < 0.0001$; 67.10 ± 3.30), while hickory had the lowest C:N ratio (35.3 ± 1.79). After 12 months, C:N was similar in most species but was significantly lower in sugar maple and hickory ($P < 0.0001$).

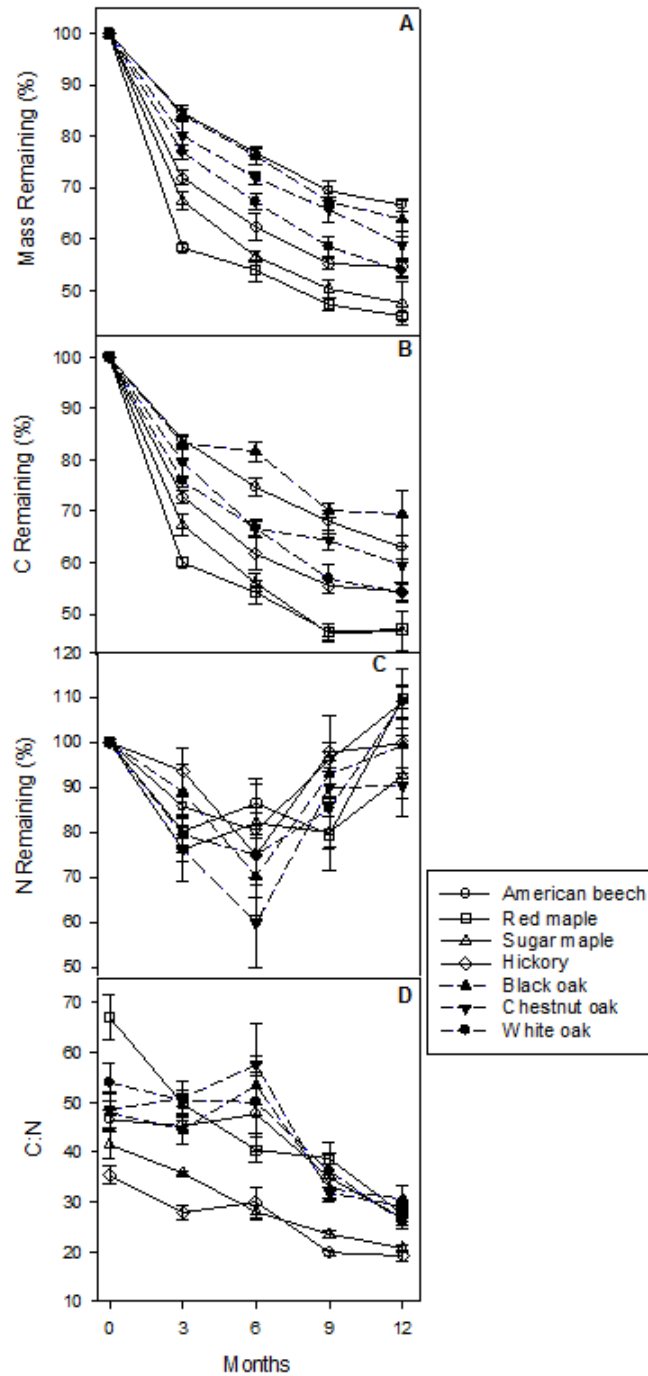


Figure 2.1 Mass remaining, nitrogen, carbon, and carbon: nitrogen

Remaining mass (A), nitrogen (B), carbon (C), and carbon: nitrogen (C:N) ratio (D) of American beech, red maple, sugar maple, hickory, black oak, chestnut oak, and white oak from a one-year litter decomposition bag study in Bernheim Arboretum and Research Forest, KY.

Table 2.2 Decomposition rates

Litter Type	k value (y^{-1})	R^2	P value
Red maple	0.91 ± 0.23	0.84	0.0284
Sugar maple	0.84 ± 0.15	0.92	0.0107
Hickory	0.68 ± 0.13	0.91	0.0124
White oak	0.65 ± 0.07	0.97	0.0023
Chestnut oak	0.53 ± 0.05	0.97	0.0023
Black oak	0.47 ± 0.04	0.98	0.0010
American beech	0.43 ± 0.04	0.97	0.0021

Calculated decomposition rates (k values \pm SE) based on single exponential models fitted to each species mass remaining over a one-year period and “goodness-of-fit” results for the model.

Fuel bed properties (annual leaf litter inputs and duff) were similar between oaks and mesophytes, although the composition of leaf litter inputs varied between some species (Table 2.3 and 2.4). Annual leaf litter inputs (kg m^{-2}) beneath mesophytes and oaks were not significantly different at the time of sampling (December/January; $P = 0.7440$) or when decomposition rates were applied to calculate leaf litter loads in the spring (March; $P = 0.6297$) or summer (June; $P = 0.6348$; Table 2.3). Oak dominated the litter pools at all three times, but interestingly, there was a significantly lower percentage of oak litter ($P=0.0002$) found under the canopies of mesophytes ($\sim 18\%$ reduction). The percent of mesophyte and oak leaf litter that composed fuel beds did not change in March or June when compared to December/January ($P = 0.0789$). Leaf litter bulk density ($P = 0.1625$),

duff bulk density ($P = 0.2811$), or duff loads ($P = 0.6450$) were not significantly different between species (Table 2.4).

Table 2.3 Measured and calculated leaf litter layer mass

Overstory tree species	December/January			March			June		
	Mesophyte kg m ⁻²	Oak kg m ⁻²	Total kg m ⁻²	Mesophyte kg m ⁻²	Oak kg m ⁻²	Total kg m ⁻²	Mesophyte kg m ⁻²	Oak kg m ⁻²	Total kg m ⁻²
American beech	0.08 ^A ± 0.01	0.30 ^A ± 0.02	0.38 ± 0.03	0.06 ^A ± 0.01	0.24 ^A ± 0.02	0.30 ± 0.02	0.054 ^A ± 0.01	0.21 ^A ± 0.01	0.26 ± 0.02
Red maple	0.13 ^B ± 0.01	0.28 ^A ± 0.03	0.41 ± 0.02	0.08 ^A ± 0.01	0.22 ^A ± 0.02	0.30 ± 0.02	0.075 ^B ± 0.01	0.20 ^A ± 0.019	0.27 ± 0.02
Sugar maple	0.11 ^{AB} ± 0.01	0.30 ^A ± 0.02	0.40 ± 0.02	0.07 ^{AB} ± 0.01	0.23 ^A ± 0.01	0.31 ± 0.02	0.062 ^{AB} ± 0.01	0.21 ^A ± 0.01	0.27 ± 0.01
Hickory	0.12 ^B ± 0.01	0.29 ^A ± 0.01	0.41 ± 0.02	0.08 ^B ± 0.01	0.23 ^A ± 0.01	0.32 ± 0.02	0.076 ^B ± 0.01	0.20 ^A ± 0.01	0.28 ± 0.01
Chestnut oak	0.04 ^C ± 0.01	0.37 ^B ± 0.02	0.41 ± 0.02	0.028 ^C ± 0.00	0.29 ^B ± 0.01	0.32 ± 0.02	0.024 ^C ± 0.00	0.26 ^B ± 0.01	0.28 ± 0.01
White oak	0.05 ^C ± 0.01	0.38 ^B ± 0.02	0.43 ± 0.02	0.036 ^C ± 0.01	0.30 ^B ± 0.02	0.32 ± 0.02	0.032 ^C ± 0.01	0.27 ^B ± 0.02	0.30 ± 0.02

Measured and calculated annual litter layer mass from the understory of American beech, red maple, sugar maple, hickories, chestnut oak, and white oak within Bernheim Arboretum and Research Forest, KY. Winter leaf litter was collected in December 2016 and January 2017 while spring and summer leaf litter amounts were calculated by multiplying winter leaf litter by each species' respective decomposition rates. Values are means ± SE. Different subscript letters indicate significant differences among leaf litter types (i.e. down columns) for a given parameter.

Table 2.4 Leaf litter bulk density, duff bulk density, and amount of duff

	American beech	Red maple	Sugar maple	Hickory	Chestnut oak	White oak	<i>P</i> value
Litter bulk density kg m ⁻³	15.53 ± 3.00	21.54 ± 6.22	18.56 ± 3.49	9.80 ± 0.73	11.42 ± 1.09	15.31 ± 1.70	0.1625
Duff bulk density kg m ⁻³	44.27 ± 6.46	39.40 ± 7.06	56.00 ± 8.55	34.64 ± 4.04	41.52 ± 5.29	37.94 ± 4.39	0.2811
Duff weight kg m ⁻²	58.20 ± 5.32	54.15 ± 5.68	46.28 ± 4.76	49.63 ± 4.48	53.67 ± 3.72	50.62 ± 4.06	0.6450

Leaf litter bulk density, duff bulk density, and the amount of duff in the understory of American beech, red maple, sugar maple, hickory, chestnut oak, and white oak in December 2016 and January 2017 within Bernheim Arboretum and Research Forest, KY. Values are means ± SE.

Discussion

My findings suggest that increased abundance of some mesophytes may lead to increased decomposition rates in upland oak forests and decreased fuel loads, although the magnitude of these impacts are species-specific. Leaf litter inputs occur annually and differences in decomposition rates within the subsequent year could dramatically alter fuel loads (Table 2.5). Currently, at Bernheim, oak leaf litter dominates the organic layer, reflecting overstory composition (80% oak), but as the forest composition shifts to mesophytic species, fuel loads will likely decline. For example, red maple's dominance in the eastern U.S. has been termed "inevitable" (Fei and Steiner 2007), and a forest composed entirely of red maple at the current basal area ($30 \text{ m}^2 \text{ ha}^{-1}$) would yield an ~18% reduction in leaf litter after one year when compared to a forest comprised of chestnut oak or black oak. Surprisingly, hickory, which are often categorized together with oaks, will yield similar reductions, with a projected ~20% decrease in fuel loads after one year when compared to chestnut oak or black oak. In contrast, an American beech forest would have the highest remaining fuel loads after one year, a product of this species' increased leaf litter inputs and slow decomposition rates, which would have an average of 20-56% more fuel when compared to the other species in this study. Across oak species, there was substantial variability; a white oak forest would yield a ~33% reduction in fuel loads after one year when compared to a forest entirely occupied by black oak or chestnut oak. Increased decomposition and reduction in leaf litter will likely lead to more pronounced differences in fuel bed mass over time, and a forest occupied by maple or hickory may disproportionately reduce flammability when compared to an upland oak dominated forest.

Table 2.5 Projected net fuel loads

Species	Leaf litter inputs (kg ha ⁻¹)	Leaf litter outputs (kg ha ⁻¹)	Net fuel loads (kg ha ⁻¹)
American beech	4524.7 ± 92.7	1511.2 ± 30.9	3013.4 ± 61.7
Red maple	4287.4 ± 67.9	2358.1 ± 37.3	1929.3 ± 30.5
Sugar maple	2778.2 ± 86.2	1455.8 ± 45.2	1322.4 ± 41.0
Hickory	3434.3 ± 101.0	1561.0 ± 45.9	1873.4 ± 55.1
Chestnut oak	3935.6 ± 75.9	1613.2 ± 31.1	2321.4 ± 44.8
Black oak	3745.0 ± 457.5	1348.2 ± 164.7	2396.8 ± 292.8
White oak	2930.0 ± 82.6	1347.7 ± 38.0	1578.0 ± 44.6

Projected leaf litter inputs, outputs, and net fuel loads after one year in a forest entirely composed of American beech, red maple, sugar maple, hickory, chestnut oak, black oak, and white oak at a basal area of 30 m² ha⁻¹. Leaf litter inputs were calculated by obtaining average foliar biomass per unit basal area (kg m⁻²) for each species and multiplying this number by the current overstory/midstory basal area at Bernheim (30 m² ha⁻¹). Next, leaf litter outputs were obtained by multiplying inputs by the average percent mass lost after one year of decomposition for each species. Finally, net fuel loads were calculated by subtracting outputs from inputs. Values are means ± SE.

Although my calculations indicate that changes in species dominance may alter fuel loads, this study was conducted as a common garden experiment (i.e., not under the canopy of any particular tree/species) and does not account for how understory microclimate conditions may alter decomposition rates. For example, the understory of American beech has reduced light levels and air temperatures when compared to the understory of upland oaks (Babl et al. 2018, In preparation), which may inhibit or promote decomposition rates (Kirschbaum 1995; Aerts 1997). Another uncertainty to my calculations is that although I projected fuel loads based on single species, compositional shifts are unlikely to be dominated entirely by a single species. Across the Central Hardwoods region, oak-dominated sites show a successional trajectory that will be

dominated by a mixture of species such as red maple, sugar maple, and American beech (Abrams and Downs 1990; Abrams and Nowacki 1992; Hart and Grissino-Mayer 2008). If multiple mesophytes increase dominance simultaneously, there may be non-additive effects on decomposition rates such that the combination of different leaf litter types leads to different decomposition rates than would be predicted if the litter types decomposed separately. However, one study that mimicked increased red maple dominance in oak stands found “additive effects” of leaf litter decomposition rates when scarlet oak, chestnut oak, and red maple leaf litter decomposed together (Alexander and Arthur 2014). Therefore, my projections could capture a realistic estimation of how fuel loads may be altered in the presence of mesophytes.

My findings also suggest that as mesophytes increase dominance, higher proportions of mesophytic leaf litter will be located in their understory compared to oak understory. These findings are also true for spring and summer fuel bed projections, and my results indicate there will be no significant differences in the composition of fuel beds (% oak vs. % mesophyte) in the winter vs. spring or summer. Leaf litter from some mesophytes possess characteristics that are linked to decreased flammability, like being small, flat, and thin (Babl et al., In preparation) and having slower drying rates (Kreye et al., 2013); thus, increased inputs of mesophyte litter to their understory may lead to a zone of reduced flammability through compaction of the fuel bed and increased moisture holding capacity (Varner et al., 2015; Grootemaat et al., 2017). Although there are not currently differences in leaf litter bulk density under mesophytes and oaks within Bernheim, a reflection of overstory oak dominance and similar leaf litter inputs, Dickinson et al., (2016) found increased bulk density in maple litter beds when compared

to oak, which led to reduced fire spread potential and fire intensities. These implications indicate that increased bulk density and a more moist fuel bed in mesophytes' understories could create a zone of reduced flammability to protect them from surface fires.

Initial leaf litter chemistry varied between species, which can directly and indirectly provide implications for forest flammability. Sugar maple and hickory had "high quality" leaf litter, with greater initial percent N, and less lignin and lower C:N ratio when compared to other species. Not only can this high quality leaf litter lead to increased decomposition rates and a reduction of fuel, but greater percent N and less lignin have been linked to shorter flame durations and decreased fuel consumption (Grootemaat et al. 2015, 2017). American beech leaf litter had C:N and lignin:N ratios that were not particularly high (46.55 and 12.25, respectively) in comparison to other oaks or mesophytes in this study, but still had one of the slowest rates of decomposition ($k = 0.43$). A slow decomposition rate within the first year and little change in C:N ratio within the first three months indicate that American beech leaf litter may have increased structural carbons or tannins that make it less palatable to consumers (Anderson 1973), and could also cause decreased rate of spread in a surface fire (Grootemaat et al. 2017). Furthermore, red maple leaf litter had the fastest decomposition rate but the lowest initial %N, largest lignin:N ratio, and the highest C:N ratio, which rapidly decreased in the first three months. These characteristics suggest that red maple's fast decomposition is due to highly labile C, which is consistent with findings in other studies (Blair and Crossley 1988; Alexander and Arthur 2014) and suggests that rapid decomposition and consequent reduction of fuel loads may be a mechanism used to decrease flammability.

Conclusions

My findings suggest that inputs of leaf litter from some mesophytes will lead to increased decomposition rates, a possible reduction of fuel across the forest floor, and provide implications for decreased flammability. Although I group species into “mesophyte” and “oak” categories, my results are in accordance with Babl et al. (In preparation), which recognizes that a species’ ability to impact flammability should be considered on an individual basis versus a generalized group. For example, the most extreme mesophytes in terms of potential to reduce fuels within one year would be red maple or sugar maple, followed by hickories and then American beech. Within oaks, white oak would be more likely to reduce fuel loads when compared to chestnut oak or black oak. Understanding fuel loads is an important part of determining forest flammability (Grootemaat et al. 2017), but fuel bed structure, moisture-holding capacity, and leaf litter chemistry undoubtedly play a role and complicate our understanding of the mesophication process. As forests begin to shift from upland oak to mesophytes, the ability to implement fire on the landscape may become increasingly difficult, and future research is needed to understand these complex successional dynamics. Future studies should explore how decomposition, leaf litter chemistry, and fuel bed structure may work in tandem to inhibit or promote flammability and try to identify which mesophytes influence flammability, and the amount of forest they must occupy to potentially alter forest stand dynamics and diminish the effects of fire.

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