

Could canopy, bark, and leaf litter traits of encroaching non-oak species influence future flammability of upland oak forests?

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ABSTRACT

Shade-tolerant, fire-intolerant tree species are expanding in historically oak-dominated landscapes in the central and eastern U.S. Once established, these species are hypothesized to accelerate their own expansion through canopy, bark, and leaf litter traits that decrease forest flammability, consequently hindering the growth and survival of pyrophytic, shade-intolerant upland oaks (*Quercus* spp.). To better understand how canopy, bark, and leaf litter traits associated with flammability differ between oaks and common competitors, we quantified these traits in an upland oak forest in western Kentucky for four oak species and five non-oak species varying in shade and fire tolerance. Compared to oaks, American beech (*Fagus grandifolia* Ehrh.), red maple (*Acer rubrum* L.), and sugar maple (*A. saccharum* Marshall.) had: (1) wider, deeper canopies, traits associated with shadier, cooler understory conditions and higher fuel moisture; (2) thinner, smoother bark, traits that increase fire susceptibility, yet produce higher stemflow volume and potentially moister fuels near the tree's bole; and (3) leaf litter with a higher specific leaf area and surface area:volume ratio, traits linked to higher fuel bed bulk density and fuel moisture. Hickory (*Carya* spp.) and tulip poplar (*Liriodendron tulipifera* L.) traits were generally similar to that of oaks. Our findings show that non-oak tree competitors commonly found in upland oak forests display canopy, bark, and leaf litter traits often associated with low flammability, but that the number and array of non-flammable traits varies widely by species and sometimes changes with tree size, leading to a gradient of traits and potentially fire dampening abilities. If these species continue to expand, reduced flammability could limit prescribed fire effectiveness in upland oak restoration.

1. Introduction

Across much of the central and eastern U.S., oak-dominated landscapes are shifting species composition to shade-tolerant, fire-intolerant species. Oak (*Quercus* spp.) dominance began at the end of the last glaciation during a period of warming and drying and has persisted in a relatively stable state for the last ~8000–16,000 years (Abrams, 1992; Ballard et al., 2017; Foster et al., 2002). Prior to European settlement, oak woodlands and forests comprised 40–70% of eastern U.S. landscapes, intermixed with pine (*Pinus* spp.), hickory (*Carya* spp.), and American chestnut (*Castanea dentata* Marshall.) (Hanberry and Nowacki, 2016). While mature oak trees still dominate forest overstories, and oak volume continues to increase as these trees grow larger, oak relative density and importance value (IV; the sum of relative frequency, relative density, and relative basal area) are declining, while the inverse is true of shade-tolerant, fire-intolerant species like red maple (*Acer rubrum* L.), sugar maple (*A. saccharum* Marshall.), and

American beech (*Fagus grandifolia* Ehrh.) (Abrams and Downs, 1990; Abrams and Nowacki, 1992; Fei et al., 2011; Fei and Steiner, 2007; Knott et al., 2019; Lorimer, 1984; McDonald et al., 2002). For example, red maple has increased IV in almost every portion of its pre-European 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 and understory classes relative to their proportion in the overstory (Fei et al., 2011; McEwan et al., 2011; Sutherland et al., 2005). This problem is particularly evident in the sapling stage, thus often referred to as the "oak sapling bottleneck" (Clark and Schweitzer, 2019; Nowacki and Abrams, 1992; Palus, 2017).

If oaks fail to recruit into the canopy, this could have negative economic and ecological repercussions (Abrams, 2003). For example, 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). Furthermore, where present, oaks provide

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vital food and habitat resources for wildlife and a shift away from oaks could negatively impact songbird (Fox et al., 2010), black bear (*Ursus americanus*) (McDonald and Fuller, 2005), and white-tailed deer (*Odocoileus virginianus*) populations (McShea and Schwede, 1993). Ecologically, oaks are both “foundation” and “keystone” species (Ellison et al., 2005; Fralish, 2004) that can alter understory microclimate and impact ecosystem-level processes like decomposition, nutrient cycling, and precipitation distribution (Alexander and Arthur, 2014, 2010; Caldwell et al., 2016; Fabio et al., 2009).

Poor oak recruitment likely stems from “multiple interacting ecosystem drivers,” such as climate change (McEwan et al., 2011) and changes in herbivore populations (Rooney and Waller, 2003); however, fire suppression beginning in the 1930s is generally considered the primary cause (Nowacki and Abrams, 2015, 2008). Most upland oaks are disturbance-dependent and historically associated with low-intensity surface fire (Abrams, 2002; Ballard et al., 2017; Gill et al., 2009) due to morphological and physiological adaptations including a moderate intolerance of shade, deep and extensive rooting, vigorous sprouting ability, and hypogaeal germination (Abrams, 2003; Arthur et al., 2012; Brose et al., 2005; Johnson et al., 2009; Royse et al., 2010). Consequently, in the absence of periodic, low-intensity fire, upland oaks often fail to regenerate on all but the most xeric sites within their range, and shade-tolerant (often late-successional), fire-sensitive species are able to establish and outcompete oak especially in the sapling strata (Hutchinson et al., 2008; Lorimer et al., 1994).

Once established, these shade-tolerant species are hypothesized to contribute to mesophication, which is a positive-feedback loop of self-promoting conditions, such as shadier, cooler, and moister understories with higher fuel moisture, lower fuels loads, and dampened flammability, that promote shade-tolerant, fire-sensitive species (i.e., mesophytes) while hindering disturbance-dependent oaks (Nowacki and Abrams, 2008). Thus, the mesophication hypothesis posits that forest compositional changes occur as a function of species traits that influence moisture conditions and forest flammability, rather than only changing light conditions as suggested by traditional successional theory (Clements, 1916). The ability of mesophytes to alter understory conditions and reduce forest flammability may stem from “single-tree influence circles,” where trees strongly influence forest floor conditions and resources beneath their canopies (Boettcher and Kalisz, 1990; Zinke, 1962). For example, Wing (1937) noticed that oak trees in southern Michigan prairies changed the soil color in a way that was noticeable even a century after the trees were gone. 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 understory microclimate. Thus, as mesophytes increase in historically oak-dominated landscapes, 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 historic fire disturbance regime, and upland oak landscapes may shift to mesophytic-dominated stands in which the effectiveness of prescribed fire may be compromised (Nowacki and Abrams, 2008).

The zone of influence of mesophytes may be less flammable due to their canopy, bark, and leaf litter traits that alter understory microclimate and fuel bed conditions (Table 1). For example, increased canopy area of mesophytes may lead to more shaded and cooler understory conditions compared to oaks that could increase leaf litter moisture and reduce flammability (Ray et al., 2010). Leaf litter inputs may also impact flammability. If mesophyte leaf litter lies flatter and has lower leaf area, this could create compact, less aerated fuel beds with reduced flammability (Grootemaat et al., 2017; Scarff and Westoby, 2006). Although some anecdotal information exists regarding differences in these traits among oaks and mesophytes (Nowacki and Abrams, 2008), empirical evidence is just starting to be acquired through research (Alexander and Arthur, 2010; Dickinson et al., 2016; Kreye et al., 2018, 2013). For example, Alexander and Arthur (2010) quantified canopy traits and bark roughness in mesophytes and oaks and discovered that

red maple had higher canopy area and smoother bark when compared to chestnut oak (*Q. montana* Willd.) and scarlet oak (*Q. coccinea* Münchh.) and directed more rainfall down the trunk as stemflow, potentially forming a zone of fire protection near the bole. Kreye et al. (2013) measured leaf litter traits in 17 species and found that red maple, American beech, and tulip poplar (*Liriodendron tulipifera* L.) had thinner leaves with increased surface area:volume (SA:V) ratio and were able to retain more moisture per surface area when compared to white oak. While these studies provide preliminary data to support the mesophication process, especially for red maple, little is known about traits of other non-oak species that are increasing dominance and whether these tree traits are associated with reduced flammability.

The primary objective of this study was to quantify canopy, bark, and leaf litter traits of several upland oaks and co-occurring, non-oak species that encompass a range of sizes (~15–60 cm DBH) to identify species and potential mechanisms that may contribute to or inhibit the mesophication process. We hypothesized that, because co-occurring, non-oak species were often shade-tolerant, late-successional species, they would have increased canopy area, volume, and total canopy leaf area when compared to oaks (Abrams and Kubiske, 1990; Canham et al., 1993). We also expected that the more fire-sensitive mesophytes would have thinner bark when compared to more fire-resistant oak species (Alexander and Arthur, 2010). As non-oak species reach larger size classes, we hypothesized that their canopy traits would become more pronounced when compared to oaks, and thus, this may suggest that their circles of influence would also be larger. Our final hypothesis was that non-oak leaf litter would have traits associated with decreased flammability including smaller, thinner, less curly leaves with increased specific leaf area, surface area to volume ratio, tissue density, and lower lignin concentrations when compared to oak species (Abrams and Kubiske, 1990; Kreye et al., 2013). Identifying the ways in which certain species contribute to changes in forest flammability will help managers determine where prescribed fire may be a useful management tool.

2. Methods

2.1. Study area

This study was conducted at Bernheim Arboretum and Research Forest (hereafter referred to as Bernheim), located in the Western Knobs ecoregion of Kentucky, 40 km south of Louisville (37°55'28" N, 85°39'45" W) where the climate is humid, temperate, and continental. From 1981 to 2010, Bernheim had average growing season (June–August) temperatures of 24.0 °C and dormant season (December–February) temperatures of 2.5 °C (Arguez et al., 2010). Mean annual rainfall was 126 cm, evenly distributed throughout the year, and average annual snowfall was 33 cm (Arguez et al., 2010). Agriculture and logging activities occurred within Bernheim before 1929 but have been absent since this time.

Soils are primarily composed of the Lenberg-Carpenter and Trappist complex. The Lenberg series consists of moderately deep, well-drained silt loam soils formed of acidic clayey shale with slopes ranging from 6 to 45 percent. The Carpenter series consists of deep, well drained loamy soils, formed from weathered shale or limestone and occupies slopes from 2 to 60 percent. The Trappist series is composed of eroded silt loam soils that range in slope from 12 to 30 percent and are well-drained soils formed from weathered acidic shale on ridgetops, side slopes, and benches. Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture. Web Soil Survey. Available online at the following link: <https://websoilsurvey.sc.egov.usda.gov/>. Accessed 09/16/2019.

Forest composition and size class structure was typical of upland oak forests in the central and eastern U.S. experiencing an “oak sapling bottleneck” (Table 2). White oak (52%; 11.2 m² ha⁻¹) and chestnut oak (31%; 6.5 m² ha⁻¹) dominated the overstory (> 20 cm diameter at

Table 1

Canopy, bark, and leaf litter traits and their influence on forest flammability and fire behavior in the context of mesophication.

Trait	Role in flammability	Citation
Canopy		
Canopy area	High canopy area can increase stemflow production and decrease throughfall. These traits may increase fuel moisture near the tree bole	Aboal et al., 1999; Ford and Deans, 1978
Canopy depth	Light intensity decreases with increasing canopy depth, leading to a more shaded understory. A more shaded understory may lead to cooler and moister conditions reducing flammability	Kozłowski and Pallardy, 1997; Tanskanen et al., 2005
Canopy leaf area	High total leaf area creates a shaded understory, which can reduce vapor pressure deficit, fire spread rate, and ignition success. High leaf area can also increase rainfall interception and decrease throughfall, directing more water around tree bases	Ray et al., 2005; Tanskanen et al., 2005; Gómez et al., 2001; Herwitz, 1985
Bark		
Thickness	Thin bark can absorb less water and increase stemflow. Increased stemflow may lead to moister understory conditions and increased fuel moisture. Thin bark also provides less cambium protection during fire	Aboal et al., 1999; Herwitz, 1985; Hengst and Dawson, 1994; Vines, 1968
Roughness	Smooth bark increases stemflow, resulting in more water deposited near the tree bole. As a result, understory fuel moisture may increase near the bole	Aboal et al., 1999; Van Stan and Levina, 2010
Leaf litter		
Thickness	Thin leaves burn with lower maximum temperatures. Leaf thickness negatively correlates with initial moisture content of litter beds	Grootemaat et al., 2017; Kreye et al., 2013
Curling	Flat leaves create less aerated fuel beds, with decreased rate of fire spread and flame height	Grootemaat et al., 2017; Engber and Varner, 2012
Leaf area	Small leaves create a compact litter-bed that is less aerated and burns slowly; small leaves have a longer time to ignition	Scarff and Westoby, 2006; Murray et al., 2013
Specific leaf area	Leaves with a low SLA can ignite slowly and have a lower rate of spread	Grootemaat et al., 2015, 2017; Murray et al., 2013
Leaf tissue density	High tissue density is linked to greater initial litter moisture content of litter beds and slower fire spread rate	Kreye et al., 2013; Grootemaat et al., 2017
Surface area:volume	A high SA:V can increase fuel moisture and decrease susceptibility of ignition	Kreye et al., 2013; Rothermel, 1972
Lignin	Low lignin concentrations are associated with low fuel consumption and increased decomposition rates	Grootemaat et al., 2017; Melillo et al., 1982

Table 2

Forest composition and size class structure of overstory, midstory, saplings, and seedlings measured in 12 fixed radius plots in fall 2016 at Bernheim Arboretum and Research Forest, KY. ⁺ red oaks included black oak (*Q. velutina*), scarlet oak (*Q. coccinea*), and northern red oak (*Q. rubra*). Other species included blackgum (*Nyssa sylvatica*), flowering dogwood (*Cornus florida*), common persimmon (*Diospyros virginiana*), sassafras (*Sassafras albidum*), white ash (*Fraxinus americana*), and winged elm (*Ulmus alata*). Hickory included both pignut (*C. glabra*) and mockernut (*C. tomentosa*).

Common name	Overstory (> 20 cm DBH)		Midstory (10–20 cm DBH)		Saplings (< 10 cm DBH)		Seedlings (< DBH tall)	
	m ² ha ⁻¹	%	m ² ha ⁻¹	%	m ² ha ⁻¹	%	stems ha ⁻¹	%
Non-oaks								
Red maple	0.8	3.7	0.53	21.3	0.166	10.2	14,987	42.0
Sugar maple	0.9	4.1	0.53	21.3	0.310	18.9	66	0.2
Hickory	1.2	5.5	0.25	10.2	0.449	27.5	1459	4.1
American beech	0.0	0.0	0.38	15.1	0.350	21.4	0	0.0
Other*	0.0	0.0	0.07	2.7	0.344	21.0	1459	4.1
Total non-oak	2.8	13.3	1.76	70.7	1.618	98.9	17,971	50.4
Oaks								
White oak	11.2	52.4	0.12	4.7	0.003	0.2	10,743	30.1
Red oak ⁺	0.8	3.7	0.00	0.0	0.014	0.9	4310	12.1
Chestnut oak	6.5	30.7	0.62	24.7	0.001	0.1	2653	7.4
Total oak	18.5	86.7	0.73	29.3	0.018	1.1	17,706	49.6
Total	21.3	100.0	2.50	100.0	1.637	100.0	35,677	100

breast height [DBH]). Non-oaks, mostly red maple, sugar maple, American beech, and hickory (pignut (*C. glabra* (Mill.) Sweet) and mockernut (*C. tomentosa* (Lam.) Nutt.) occupied much (71%; 1.76 m² ha⁻¹) of the midstory (10–20 cm DBH), although chestnut oak represented ~25% (0.62 m² ha⁻¹) of this size class. Oaks were almost non-existent (1%; 0.018 m² ha⁻¹) from the sapling size class (< 10 cm

DBH), which was largely occupied by maple (29%), hickories (28%), American beech (21%), and other species (21%), including black gum (*Nyssa sylvatica* Marshall), flowering dogwood (*Cornus florida* L.), common persimmon (*Diospyros virginiana* L.), sassafras (*Sassafras albidum* (Nutt.) Nees), white ash (*Fraxinus americana* L.), and winged elm (*Ulmus alata* Michx). Oaks and non-oaks were equally represented in the seedling size class (stems < DBH tall); most non-oak seedlings were red maple.

2.2. Canopy and bark traits

We sampled canopy and bark traits from non-oak and oak tree species along a gradient of shade tolerance and fire sensitivity during June/July of 2016 or 2017 (Table 3). Non-oak species represented those expanding 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; Knott et al., 2019), including red maple, sugar maple, American beech, hickory, and

Table 3

Shade tolerance, fire sensitivity at maturity, and total numbers of trees (N) measured for canopy and bark traits of tree species at Bernheim Arboretum and Research Forest, KY (Burns and Honkala, 1990). Hickory included both pignut (*C. glabra*) and mockernut (*C. tomentosa*). Trees ranged in size from 15 to 60 cm DBH.

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

tulip poplar. Upland oak species included those present at Bernheim: white oak, chestnut oak, black oak, and scarlet oak. We originally planned to sample 15 individuals of each species ranging in size from 15 to 60 cm DBH; however, our sampling size ended up ranging from 9 to 20 trees because we initially could not find American beech at the larger end of the size range but added larger individuals later when found. We also realized late in the study that we had mis-identified some scarlet oaks as black oaks and then had to find additional individuals of both species within the desired size range to increase their sample sizes but failed to find 15 of each.

All trees occupied canopy or sub-canopy positions and occurred on ridgetops. Diameter at breast height (1.37 m) was measured with a 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. Total canopy leaf area was estimated by collecting fresh canopy leaves with a slingshot, which were then kept hydrated and transported to the lab. Once in the lab, we measured specific leaf area (SLA) by passing leaves through an Area Meter 3100 (Licor, Lincoln, NE) and dividing this value by the oven-dried weight after leaves were dried at 60 °C for 48 h. SLA values were then multiplied by biomass estimates obtained using allometric equations to calculate total canopy leaf area. For all species except tulip poplar, the allometric equation used was in the form of $\log_{10} \text{biomass} = a + b(\log_{10}(\text{dia}^c))$ (Jenkins et al., 2004). Coefficients a , b , and c were -1.62 , 1.778 , and 1 for red maple (Martin et al., 1998); -2.595 , 2.356 , and 1 for hickory (Martin et al., 1998); 2.066 , 1.8089 , and 1 for American beech (Ribe, 1973); 2.0383 , 1.6701 , and 1 for sugar maple (Ribe, 1973); -1.599 , 1.673 , and 1 for white oak (Martin et al., 1998); and -0.38 , 0.928 , and 1 for scarlet oak (Martin et al., 1998). The allometric equation used for tulip poplar was $\ln \text{biomass} = a + b * \text{dia} + c * (\ln(\text{diam}^d))$, where a , b , c and d were -2.882 , 0 , 1.392 , and 1 , respectively (Sollins et al., 1973). Bark roughness was determined following Alexander and Arthur (2010), where the depth of bark fissures was measured 1.5 m above the ground on four sides of the tree and then averaged. Bark thickness was measured on one randomly selected side of the tree at the top of a ridge using a bark thickness gauge.

2.3. Leaf litter traits

In December 2017, leaf litter traits were measured on fresh leaf litter collected near the trees selected for canopy and bark trait measurements. Leaf litter freshness was determined by judging the visible appearance and texture of leaves. The following measurements were selected because they have previously been linked to flammability metrics (Table 1). 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 described above. 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). Leaf 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. To obtain leaf litter lignin concentrations, we ground and dried 10 g of leaf litter for each species at 60 °C for 48 h before sending to Dairy One Lab (Ithaca, NY) where an Ankom fiber digester (Ankom Technology, Macedon, NY) was used. These measurements were then made on 50 randomly-selected air-dried leaves for each of the nine species.

2.4. Statistical analyses

An analysis of covariance (ANCOVA) was used to determine 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 pooled into a “maple” category when their means and slopes were not significantly different ($P > 0.05$) for canopy and bark traits. Next, linear regressions of tree size vs. the canopy or bark trait were run and tested with 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, SAS, Cary, NC). F -values were computed based on least square means.

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

3. Results

American beech had the largest normalized canopy area, volume, and total canopy leaf area, which on average was 3.3, 6.0, and 2.7 times greater than the oak species, respectively ($P < 0.001$) (Table 4). Although not significantly different from other oaks ($P = 0.50$), black oak canopy area was ~ 2.3 times smaller compared to red maple, sugar maple, and hickory ($P < 0.001$). Canopy depth was similar between most species, although American beech and sugar maple canopy depth was ~ 1.8 times greater compared to hickory, chestnut oak, and white oak ($P < 0.001$ for all comparisons). American beech, maples, and hickory total canopy leaf area was ~ 1.3 times greater when compared to oaks, and tulip poplar had the lowest leaf area ($P < 0.001$ for all comparisons). American beech and the maples had the thinnest and smoothest bark, which was ~ 3.7 times thinner and ~ 5.8 times smoother, respectively, when compared to all other species ($P < 0.001$ 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 ($P < 0.001$ for all comparisons).

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) (Tables 5 and 6; Fig. 1A and B). Canopy area as function of DBH for hickory increased at a rate that was three times faster than that of the other species. With the exception of black oak and scarlet oak, all species had a significant positive linear increase in canopy depth (Tables 5 and 6; Fig. 1C and D) and bark thickness (Tables 5 and 6; Fig. 2A and B) with increasing DBH ($P < 0.05$ for all interactions). American beech and the maples had a significant rate of increase in canopy depth vs. size which was ~ 3.8 times that of oaks ($P < 0.001$). 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 (Tables 5 and 6; Fig. 2C and D) as they became larger,

Table 4

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. Hickory included both pignut (*C. glabra*) and mockernut (*C. tomentosa*). Values are means \pm SE. Different superscript letters indicate significant differences ($P < 0.05$) among leaf litter types for a given parameter. CA = canopy area, BA = basal area, CD = canopy depth, LA = leaf area, SLA = specific leaf area, SA:V = surface area: volume. n.d. = no data. Asterisks denote lignin values taken from Ball et al. (2008) and Washburn and Arthur (2003).

	American beech	Red maple	Sugar maple	Hickory	Tulip poplar	Black oak	Chestnut oak	Scarlet oak	White oak	P value
Canopy traits										
CA:BA ($\text{m}^2 \text{m}^{-2}$)	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	< 0.001
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	< 0.001
LA:BA ($\text{m}^2 \text{m}^{-2}$)	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	< 0.001
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	< 0.001
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	< 0.001
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	< 0.001
SLA ($\text{cm}^2 \text{g}^{-1}$)	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	< 0.001
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	< 0.001
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	< 0.001
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	< 0.001
SA:V ($\text{cm}^2 \text{cm}^{-3}$)	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	< 0.001
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 ^{AB} ± 0.01	< 0.001
Lignin (%)	12.1 ^A ± 0.2	9.5 ^B ± 0.2	10.9 ^C ± 0.2	9.0 ^B ± 0.2	8.6 [*]	19.8 ^D ± 0.2	13.9 ^E ± 0.1	18.7 [*]	11.4 ^C ± 0.2	< 0.001

except for scarlet oak ($P = 0.752$) and white oak ($P = 0.063$). The rate of increase in bark roughness was most pronounced for tulip poplar which was on average ~ 2.5 times greater compared to other species and lowest in American beech, which had a rate near zero.

Black oak leaves were significantly larger, thicker, had increased lignin content and smaller SA:V and tissue density when compared to all other species ($P < 0.001$ for all comparisons) (Table 4). Alternatively, 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 thinner when compared to most oaks. Hickory had relatively small leaves and greater SLA in comparison to the oaks ($P < 0.001$), 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. 3). PC 1 explained 64% 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 (Table 7). Lignin concentration and tissue density were the only factors strongly related to PC 2, accounting for an additional 17% of variation in the data (Table 7). Larger, curlier leaves with lower SLA and greater SA:V had more negative values on PC 1, while smaller, flatter leaves with greater SLA and lower SA:V had more positive values. On PC 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. 3). Red maple, sugar maple, and American beech comprised Cluster 1; tulip poplar, white oak, chestnut oak, and scarlet oak were in Cluster 2; and hickory and black oak grouped by themselves to make up Clusters 3 and 4.

4. Discussion

Our findings show that non-oak tree species commonly found in upland oak forests of the central and eastern U.S. display canopy, bark, and leaf litter traits associated with low flammability (Table 1), but that the number and array of non-flammable traits vary widely by species and sometimes changes with tree size, leading to a gradient of traits and potentially fire dampening abilities. Maples, which have documented increases in IV across the region (Fei and Steiner, 2007; Knott et al., 2019), were characterized by deep canopies that continued to deepen with increasing tree size, a crown architecture prevalent among shade-tolerant species that limits horizontal crown growth once canopies reach higher light levels in dominant overstory positions (Poorter et al., 2003; Niinemets, 2010). American beech, a species commonly found in fire-excluded areas and within the midstory and sapling size classes at Bernheim, had the greatest normalized canopy area, volume, and depth and canopy depth and area that increased with size. All of these traits reflect this species' high shade tolerance, crown plasticity, and consequential capacity to occupy canopy space at both small and large size classes (Pretzsch and Schütze, 2005; Schröter et al., 2012). Hickory had the largest increase in canopy area with increased DBH but a less pronounced increase in canopy depth, which was similar to that of oaks. Hickories are relatively shade-intolerant compared to maples and beech and often concentrate their foliage at the top of their canopy as they grow larger, thereby reducing the amount of vertical canopy layering through self-pruning of lower limbs (Niinemets, 2010). Tulip poplar, the least shade-tolerant of the non-oaks evaluated here, had canopy traits similar to those of oaks. As non-oaks like American beech, maple, and hickory increase in fire-excluded areas, their greater canopy area and/or depth may create more shaded, cooler, and moister understorey conditions that increase fuel moisture and decrease ignition

Table 5

ANCOVA results comparing regression slopes of DBH (15–60 cm) for canopy area, canopy depth, bark thickness, and bark roughness in American beech, maple (sugar and red maple), hickory, tulip poplar, black oak, chestnut oak, scarlet oak, and white oak within Bernheim Arboretum and Research Forest, KY. Hickory included both pignut (*C. glabra*) and mockernut (*C. tomentosa*). Significant interactions ($P < 0.05$) noted in bold; marginally significant values ($P < 0.06$) are in bold and italics; DBH = diameter at breast height.

Source	Canopy area (m ²)			Canopy depth (m)		Bark thickness (cm)		Bark roughness (cm)	
	df	F	P	F	P	F	P	F	P
Species	7	3.83	< 0.001	4.61	< 0.001	26.40	< 0.001	27.78	< 0.001
DBH	1	51.08	< 0.001	26.61	< 0.001	44.81	< 0.001	61.61	< 0.001
Species × DBH	7	3.82	< 0.001	2.35	0.022	2.14	0.046	5.38	< 0.001
<i>Contrasts</i>									
American beech vs. Maple	1	9.84	0.003	7.79	0.194	3.75	0.391	6.61	0.017
American beech vs. Hickory	1	0.03	0.015	18.85	0.013	36.32	0.210	26.11	0.048
American beech vs. Tulip poplar	1	3.61	0.101	10.99	0.024	33.60	0.013	42.30	< 0.001
American beech vs. Black oak	1	8.88	0.646	1.04	0.007	43.40	0.567	55.73	0.017
American beech vs. Chestnut oak	1	8.35	0.458	44.34	0.003	108.72	0.007	116.35	< 0.001
American beech vs. Scarlet oak	1	7.16	0.285	4.45	0.005	30.89	0.868	60.87	0.962
American beech vs. White oak	1	7.50	0.579	26.21	0.010	55.74	0.238	15.17	0.135
Maple vs. Hickory	1	11.18	< 0.001	4.69	0.146	25.79	0.528	11.17	0.995
Maple vs. Tulip poplar	1	0.81	0.415	1.11	0.234	23.05	0.076	24.89	0.001
Maple vs. Black oak	1	1.00	0.124	0.16	0.037	33.29	0.253	39.29	0.433
Maple vs. Chestnut oak	1	0.04	0.058	24.81	0.056	103.95	0.053	99.46	0.129
Maple vs. Scarlet oak	1	0.11	0.433	0.001	0.041	20.94	0.485	43.13	0.128
Maple vs. White oak	1	0.01	0.042	10.13	0.143	43.37	0.647	3.91	0.532
Hickory vs. Tulip poplar	1	4.31	< 0.001	0.79	0.800	0.22	0.637	2.30	0.004
Hickory vs. Black oak	1	9.70	0.026	2.01	0.249	2.95	0.089	13.37	0.474
Hickory vs. Chestnut oak	1	9.41	0.005	7.28	0.777	15.28	< 0.001	34.06	0.192
Hickory vs. Scarlet oak	1	8.01	0.008	2.69	0.392	0.00	0.987	12.70	0.161
Hickory vs. White oak	1	8.48	0.008	1.12	0.928	1.49	0.224	1.17	0.595
Tulip poplar vs. Black oak	1	2.29	0.425	0.82	0.185	4.58	0.019	6.13	0.076
Tulip poplar vs. Chestnut oak	1	0.92	0.379	11.72	0.578	20.99	0.987	17.87	0.074
Tulip poplar vs. Scarlet oak	1	0.97	0.876	0.69	0.286	0.18	0.061	5.04	< 0.001
Tulip poplar vs. White oak	1	0.72	0.308	3.45	0.860	3.10	0.238	6.43	< 0.001
Black oak vs. Chestnut oak	1	0.62	0.924	8.38	0.315	1.83	0.014	0.56	0.725
Black oak vs. Scarlet oak	1	0.37	0.595	0.12	0.679	2.72	0.765	0.17	0.064
Black oak vs. White oak	1	0.73	0.975	3.92	0.215	0.58	0.166	19.48	0.236
Chestnut oak vs. Scarlet oak	1	0.02	0.600	14.88	0.505	13.18	0.051	1.81	0.015
Chestnut oak vs. White oak	1	0.01	0.873	2.43	0.690	7.47	0.205	45.37	0.053
Scarlet oak vs. White oak	1	0.05	0.523	6.10	0.337	1.32	0.335	19.36	0.301

probability and fire susceptibility (Kozłowski and Pallardy, 1997; Ray et al., 2005; Tanskanen et al., 2005). These conditions may also reduce survival of shade-intolerant oak and increase survival of shade-tolerant, fire-sensitive species, further contributing to reduced flammability and the mesophication process (Lorimer, 1984; Nowacki and Abrams, 2008; Walters and Reich, 1996).

We also found that American beech and maples had thinner, smoother bark compared to oaks, hickory, and tulip poplar; these traits are associated with increased susceptibility to fire damage (Pellegri et al., 2017) while forming a zone of fire protection by precipitation funneling via stemflow (Alexander and Arthur, 2010; Levina and Herwitz, 2005; Siegert and Levina, 2014). This finding corroborates other studies (Bova and Dickinson, 2005; Hammond et al., 2015; Hare,

1965; Starker, 1934) and is one of the major rationales behind using repeated prescribed fire as a tool to limit the proliferation of non-oak competitors: oaks have evolved with fire and have thick bark to protect them from fire injury, while species like American beech, red maple, and sugar maple are thin-barked, fire-avoiders, historically being relegated to riparian zones, coves, and other fire-protected areas (Abrams, 1998, 1992; Brose, 2014). Importantly though, these fire-sensitive species exhibited increased bark thickness and roughness with size, a finding similar to that measured in similar species in Ohio (Yausy et al., 2004), suggesting that fire's ability to kill these species will decrease as the fire exclusion period lengthens because the trees will continue to grow bigger with thicker bark. We also found that tulip poplar bark increased in thickness and roughness with increased DBH at

Table 6

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. Hickory included both pignut (*C. glabra*) and mockernut (*C. tomentosa*). * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

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	0.00	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	0.00	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

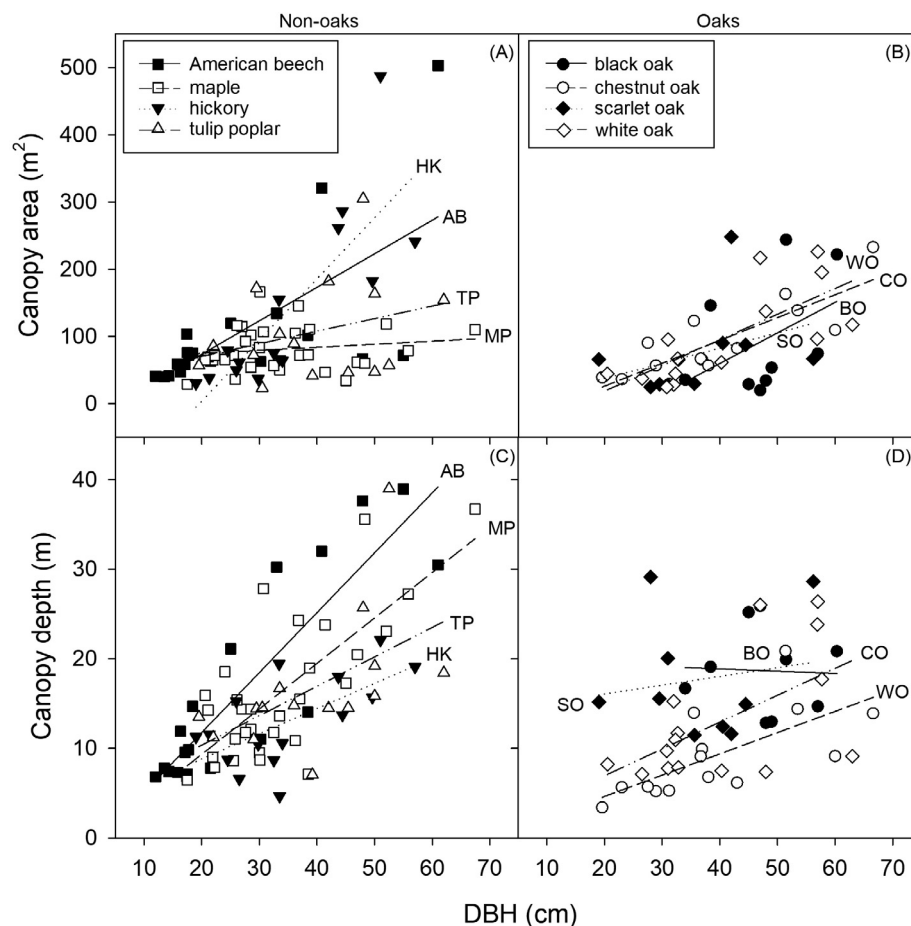


Fig. 1. Non-oak (A) canopy area and (B) depth and oak (C) canopy area and (D) depth as a function of diameter at breast height (DBH). Non-oaks included American beech (AB), maples (MP; red and sugar maple combined), hickory (HK; included both pignut and mockernut), and tulip poplar (TP). Oaks included black oak (BO), chestnut oak (CO), scarlet oak (SO), and white oak (WO), sampled within Bernheim Arboretum and Research Forest, KY.

rates comparable to or faster than oaks. This finding supports previous work indicating that tulip poplar is extremely resistant to fire damage once trees reach a certain size (~7.5 – 10 cm DBH) (Gustafson, 1946; McCarthy, 1933) and that managing this species with fire can be problematic given the fire resistance of adult trees and fire's ability to prepare a favorable seedbed for this species (Burns and Honkala, 1990; Keyser et al., 2019). The link between bark traits and stemflow generation could also be important for protecting non-oak species with thin, smooth bark from fire damage as increased stemflow could lead to higher fuel moisture and fuel discontinuity near the bole of the tree (Alexander and Arthur, 2010).

Leaf litter traits, which play an important role in forest flammability (Engber and Varner, 2012; Parsons et al., 2015; Scarff and Westoby, 2006), varied between species, with non-oak species having less flammable traits than oaks. In general, variations in leaf litter traits between species was mostly explained by leaf thickness and volume and to a lesser degree by SLA and SA:V. Red maple, sugar maple, and American beech leaf litter traits were similar; they were relatively thin and small, with a higher SLA and SA:V than oaks. These leaf litter traits are explained by different life history strategies such as shade-tolerance, browse-tolerance, carbon allocation, growth strategies, and drought tolerance of parent trees (Abrams, 1990; Abrams and Kubiske, 1990; Valladares and Niinemets, 2008). For example, upland oaks tend to have relatively thick leaves as a mechanism to withstand high temperatures and perform evaporative cooling on warm, dry sites (Abrams, 1990), while more shade-tolerant species tend to have thinner leaves with increased SLA, which helps increase light capture efficiency and maximize carbon gain in shady environments (Evans and Poorter, 2001; Jackson, 1967). Leaf traits that American beech, red maple, and sugar maple possess are linked to increased fuel moisture content, a more compact fuel bed, and consequently, decreased rate of fire spread

(Bärlocher, 2005; Engber and Varner, 2012; Kreye et al., 2013). The reduction in flammability may become more pronounced in red maple and sugar maple when coupled with these species' decomposition rates. Maples had the fastest decomposition rates and lost more mass in one year than white oak, chestnut oak, and black oak (Alexander and Arthur, 2014; Babl, 2018), which could reduce fuel loads and further decrease forest flammability (Arthur et al., 2017). The same tendency can be said for wood decomposition (Nowacki and Abrams, 2008), though not studied here.

5. Conclusions

Our findings suggest that tree species in current-day upland oak forests of the central and eastern U.S. often represent a gradient of canopy, bark, and leaf litter traits that act to either promote or dampen forest flammability and that these traits may become more or less pronounced as trees grow larger and ascend into dominant overstory positions. At one end of the gradient are species like American beech, sugar maple, and red maple, which had wide and/or deep canopies with high leaf area and smooth, thin bark, even at larger tree sizes. These traits could create moist zones of reduced flammability immediately beneath the canopies of these trees. These species may also reduce flammability through their leaf litter that can create moister, denser, 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.

Forest succession and mesophication in upland oak forests are complex and dynamic ecosystem processes that we are only beginning to understand. Identifying species that contribute to this process

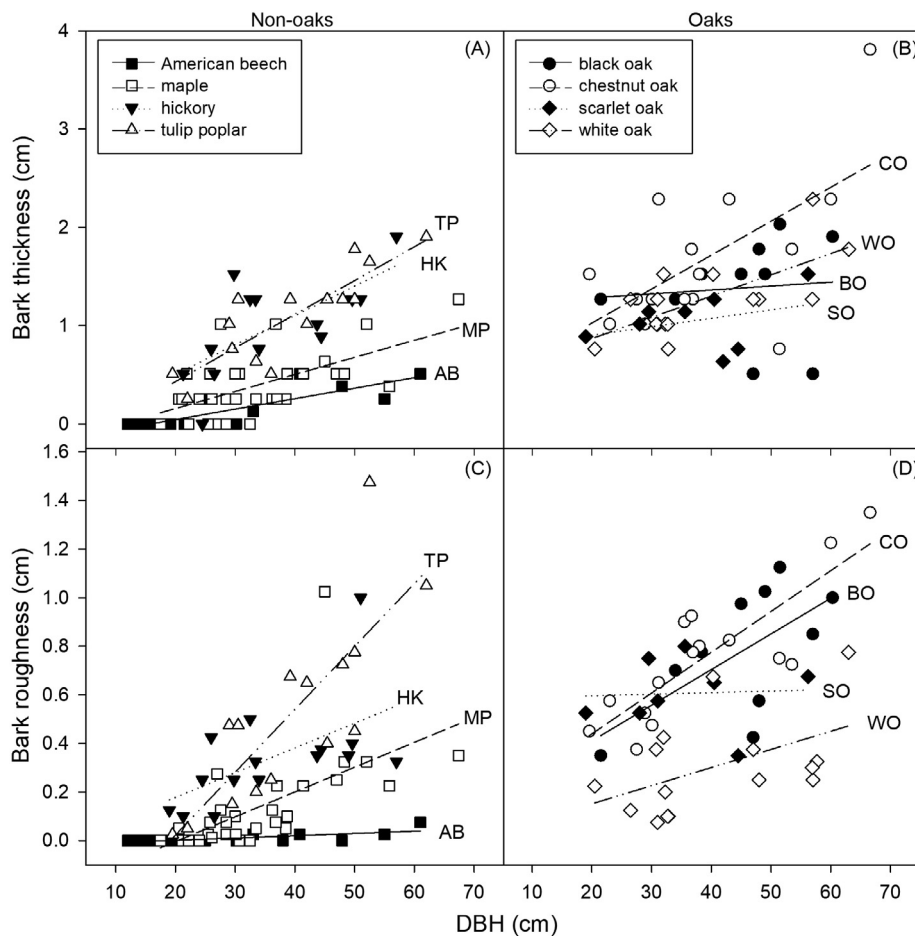


Fig. 2. Non-oak (A) bark thickness and (B) roughness and oak (C) bark thickness and (D) roughness as a function of diameter at breast height (DBH). Non-oaks included American beech (AB), maples (MP; red and sugar maple combined), hickory (HK; included both pignut and mockernut), and tulip poplar (TP). Oaks included black oak (BO), chestnut oak (CO), scarlet oak (SO), and white oak (WO), sampled within Bernheim Arboretum and Research Forest, KY.

mesophication and the mechanisms that reduce flammability and benefit mesophyte proliferation at the expense of oaks could lead to more effective prescribed fire implementation and management for oaks. For example, if managing for upland oak species, it would be beneficial to know the density of mesophytes and their impact on

flammability before conducting a prescribed fire. We focused on the impact individual midstory/overstory species have as they move from subdominant to dominant canopy positions; however, many mesophytes still occupy midstory/sapling size classes, and a high density of these smaller individuals may have disproportionate impacts on

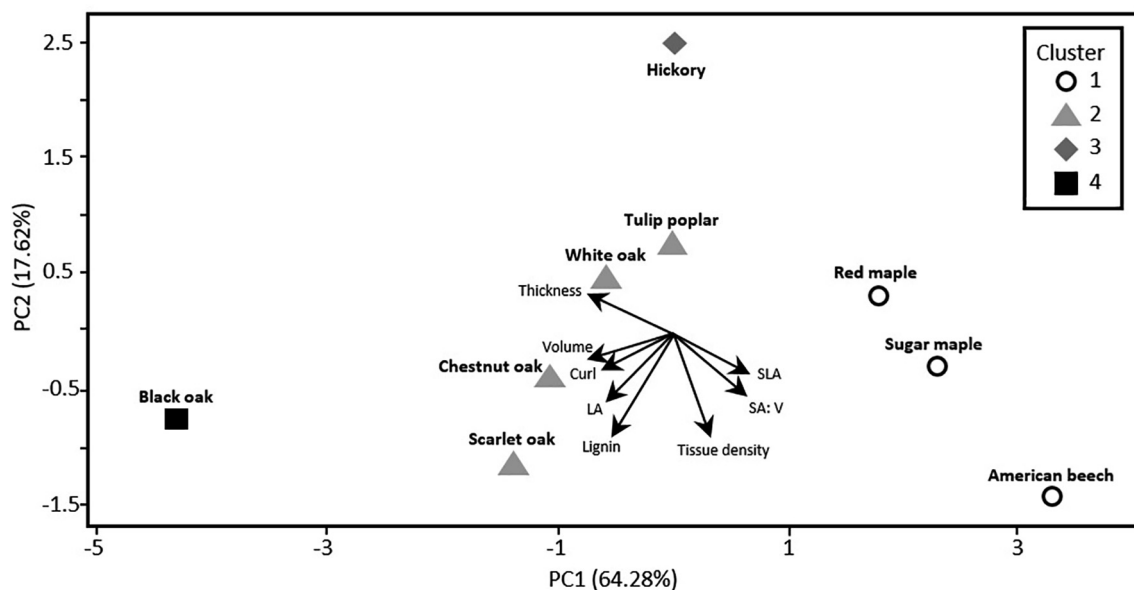


Fig. 3. Principal Components Analysis (PCA) of litter traits for American beech, hickory, red maple, sugar maple, tulip poplar, black oak, chestnut oak, scarlet oak, and white oak. Litter traits include leaf area (LA), specific leaf area (SLA), curl, thickness, volume, surface area: volume (SA:V), tissue density, and lignin. Cluster groups obtained through use of *k*-means cluster analysis.

Table 7

Factor loadings from the principal components analysis (PCA) of leaf litter traits of the American beech, red maple, sugar maple, hickory, tulip poplar, black oak, chestnut oak, scarlet oak, and white oak. SLA = specific leaf area; SA:V = surface area: volume.

Variable	PC 1	PC 2
Leaf area	−0.72	−0.43
SLA	0.87	−0.26
Curl	−0.81	−0.23
Thickness	−0.97	−0.22
Volume	−0.93	−0.17
SA: V	0.86	−0.41
Tissue density	0.46	−0.67
Lignin	−0.69	−0.65
% variance	64.28	17.62

understory conditions that are not observed beneath larger trees. Future studies should explore how midstory trees/saplings contribute to forest flammability through the mesophication process. We also acknowledge that changing climate and its impact on fire behavior could influence the relative success of oaks compared to mesophytes. Climate change predictions vary across the central and eastern U.S., but hotter and drier conditions that promote pyrophytic oaks and more conducive fire weather could slow the mesophication process, while cooler, moister conditions could promote mesophytes and hinder fire disturbances (Nowacki and Abrams, 2015; Vose and Elliott, 2016).

Ultimately the relative contribution of fire-sensitive species to upland oak forests will determine whether forests will proceed along a mesophication pathway with continued fire exclusion, thereby transitioning to a new steady-state characterized by self-reinforcing conditions that promote the mesophication process and an increasing inability to burn. Given the increasing use of prescribed fire as a tool for managing oak landscapes across much of the central and eastern U.S., there is a clear need to quantify the influence of different species on the burn regime because if certain species act to suppress fire, then their increasing dominance on the landscape will eventually lead to an inability to effectively apply prescribed fire. Knowing where the threshold of mesophication occurs could help managers target their fire restoration efforts to stands with traits conducive to flammability and identify stands where non-fire alternatives for restoring oak may be needed.

Author contributions

EB: Designed study, performed research, analyzed data, wrote manuscript; HDA: Assisted with study design, research, and manuscript preparation; CMS: Assisted with study design and manuscript preparation; JLW: Assisted with study design and manuscript preparation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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