



Mesophication of upland oak forests: Implications of species-specific differences in leaf litter decomposition rates and fuelbed composition

E.K. Babl-Plauche^{a,c}, H.D. Alexander^{b,*}, C.M. Siegert^c, J.L. Willis^d, A.I. Berry^e

^a Texas Trees Foundation, 2906 Swiss Ave, Dallas, TX 75201, USA

^b College of Forestry and Wildlife Science, 602 Duncan Dr., Auburn University, Auburn, AL 36832, USA

^c Mississippi State University, College of Forest Resources, Department of Forestry, Box 9680, Mississippi State, MS 39762, USA

^d Southern Research Station, U.S. Forest Service, 521 Devall Drive, Auburn, AL 36849, USA

^e Bernheim Arboretum and Research Forest, 2075 Clermont Rd., Shepherdsville, KY 40110, USA

ARTICLE INFO

Keywords:

Flammability
Lignin
Fire suppression
Red maple
American beech
Hickory

ABSTRACT

Without periodic fire, historically open-canopied, oak-dominated upland woodlands of the central and eastern United States are shifting to closed-canopied forests with increased abundance of shade-tolerant and typically fire-sensitive species. Once established, these encroaching species (i.e., mesophytes) are hypothesized to initiate a positive feedback termed mesophication where mesophytes perpetuate conditions that foster their own proliferation at the expense of oaks (*Quercus* spp.). One potential mechanism of mesophication is reduced fuel loads through faster decomposition rates of mesophyte leaf litter, as leaf litter is the primary fuel in closed canopy forests. To better understand how different tree species impact fuel loads, we compared initial leaf litter chemistry and one-year (2016–2017) decomposition rates of four non-oak species exhibiting increased abundance in the region and/or relatively high sapling/midstory abundance relative to the overstory on our sites (red maple [*Acer rubrum*], sugar maple [*A. saccharum*], American beech [*Fagus grandifolia*], and hickory [*Carya* spp.]) and three oak species (black oak [*Q. velutina*], chestnut oak [*Q. montana*], white oak [*Q. alba*]) in an upland oak forest in north-central Kentucky. We also evaluated fuelbed mass, composition, and bulk density beneath overstory (20–60 cm DBH) individuals of each species following leaf fall in December 2016. Except for American beech (66% mass remaining), we found non-oak leaf litter, especially that of red and sugar maple, decomposed the fastest (45 and 48% mass remaining), and oak leaf litter decomposed the slowest (54–64% mass remaining). Further, although total leaf litter fuel loads in December were similar beneath individuals of different tree species, fuel composition differed. Under non-oak crowns, the proportion of leaf litter from non-oaks was 22–35%, while under oak crowns, the proportion of leaf litter from non-oaks was only 10–12%. This suggests that individual trees of non-oaks are impacting fuel composition beneath their own crowns despite continued oak dominance at the stand scale. Considering differences between species in both leaf litter inputs based on allometric equations and decomposition rates, modeled leaf litter fuel loads in a forest composed entirely of red maple, sugar maple, or *Carya* spp. were ~20% lower than an oak forest after one year of decomposition. While limited to the species examined in this study, these findings confirm that the leaf litter of non-oaks, excluding American beech, decomposes more rapidly than oak and that individual non-oak trees alter fuelbed composition beneath their crowns, suggesting that oak woodlands will become less-flammable with increasing mesophytic dominance.

1. Introduction

Leaf litter in forested ecosystems plays an important role in stand and landscape level processes such as decomposition dynamics and mediating feedbacks between fire and vegetation (Alexander et al., 2021;

Marchal et al., 2020; Mitchell et al., 2009; Schwilk, 2015). For example, shade-tolerant hardwoods 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 (Evans and Poorter, 2001; Jackson, 1967). These traits can increase decomposition rates (Cornelissen et al.,

* Corresponding author.

E-mail address: heather.alexander@auburn.edu (H.D. Alexander).

<https://doi.org/10.1016/j.foreco.2022.120141>

Received 23 November 2021; Received in revised form 28 February 2022; Accepted 2 March 2022

Available online 16 March 2022

0378-1127/© 2022 Elsevier B.V. All rights reserved.

2017; Grootemaat et al., 2015) and contribute to the formation of dense fuelbeds that inhibit fire spread (Cornwell et al., 2015; Scarff and Westoby, 2006). In contrast, hardwood species adapted to high-light environments produce thick leaves with low SLA to enhance water use efficiency (Abrams, 1990; Abrams and Kubiske, 1990). Leaf thickness, which is correlated with leaf curl (i.e., the maximum absolute height of a leaf when positioned on a flat surface) (Kreye et al., 2013), can create a more aerated fuelbed and increased rate of fire spread (Engber and Varner, 2012; Grootemaat et al., 2017; Varner et al., 2015). Differences in leaf litter chemistry may also impact flammability (Varner et al., 2015). For example, high leaf litter lignin:nitrogen (N) and/or carbon (C):N ratios often correlate with slow decomposition rates (Melillo et al., 1982; Taylor et al., 1989), leading to reduced fuel loads (Cornelissen et al., 2017). High leaf litter lignin and N concentrations have also been linked to prolonged smoldering, increased fuel consumption, and shorter flame duration (Grootemaat et al., 2017, 2015). Because of the multitude of ways in which leaf litter can impact important forest functions (e.g., decomposition and fuelbed structure), understanding species-specific controls on these processes may help predict future forest flammability.

Understanding species controls on decomposition rates and fuelbed properties is particularly important in upland oak (*Quercus* spp.) forests of the central and eastern United States. Oaks have dominated the region since warming and drying began following the last glaciation event (8000–16,000 years ago) (Ballard et al., 2017), but they are undergoing pronounced structural and compositional shifts in contemporary landscapes. Open-canopied oak woodlands and savannas with a sparse midstory and a species-rich herbaceous understory are transitioning to dense, closed-canopy forests with a predominantly leaf litter fuelbed and increased representation, especially in the sapling and midstory layers, from shade-tolerant, often fire-sensitive tree species such as maple (*Acer* spp.), American beech (*Fagus grandifolia*), and elm (*Ulmus* spp.) (Alexander et al., 2021; Hanberry et al., 2020b; Nowacki and Abrams, 2008). This shift is most notable in the Central Hardwood Region, where oak importance value (IV; defined as average relative density and relative volume) is declining on ~80% of forested areas (Fei et al., 2011) by about 1.5% per decade (Knott et al., 2019), while non-oak IV is increasing across the range from ~0.10% per decade for *Betula*, *Fraxinus*, and *Nyssa* spp. to ~1.9% per decade for *Acer* spp. (Knott et al., 2019), driven mostly by increases in red maple (Fei and Steiner, 2007).

The marked decrease in upland oak importance, and simultaneous increase in competitors like red maple, is at least partially due to oak recruitment problems stemming from anthropogenic fire exclusion, although other factors like climate change and altered herbivore populations are also likely contributors (Alexander et al., 2021; Hanberry et al., 2020a, 2020b; McEwan et al., 2011). Historically, frequent surface fires were a key disturbance in upland oak woodlands and savannas that helped exclude shade-tolerant, fire-sensitive competitors and kept forest structure relatively open with adequate understory light to facilitate oak regeneration and flammable fuelbeds (Abrams, 1992; Arthur et al., 2012a; Hanberry et al., 2020b; Hanberry and Nowacki, 2016). In the absence of fire, shade-tolerant, fire-sensitive species can establish in upland oak forests and are hypothesized to create a positive feedback termed mesophication whereby encroaching non-oak species (i.e., mesophytes) create shadier, moister, less flammable conditions compared to upland oaks, thereby promoting their own proliferation at oaks' expense (Alexander et al., 2021; Nowacki and Abrams, 2008).

Mesophytes could reduce flammability (i.e., ignition probability, fuel continuity and consumption, fire intensity) by reducing leaf litter fuel loads and/or by changing leaf litter fuel traits to those that are less prone to ignite and carry a fire. Many non-oaks, such as red maple and sugar maple, have leaf litter with a lower lignin:N than co-occurring oaks and faster decomposition rates (Alexander and Arthur, 2014; Ball et al., 2008; Blair and Crossley, 1988; Cromack and Monk, 1975). Faster decomposition rates can reduce leaf litter mass, and consequently, lead to less development of the underlying duff, which is typically a thin layer

(<5 cm deep) comprised of unidentifiable, mostly decomposed leaf litter (generally, referred to as Oe) and humus (Oa) in these systems (Arthur et al., 2017; Stottlemeyer et al., 2009). Because fires in closed-canopy forests typically spread through leaf litter, and to a lesser degree duff (Arthur et al., 2017), any reduction in the litter layer will likely reduce forest floor flammability (Arthur et al., 2017; Brewer and Rogers, 2006; Dickinson et al., 2016). Furthermore, mesophytes may reduce flammability through additions of thin, flat leaf litter to the fuelbed. For example, Kreye et al. (2013) found that red maple leaf litter "cements" together, which could cause compaction of the "fluffy," aerated, and flammable fuelbeds that characterize upland oak forests. Thus, faster decomposition rates and less flammable leaf litter traits of mesophytes likely interact to reduce forest floor flammability (Babl et al., 2020; Kreye et al., 2018, 2013; McDaniel et al., 2021).

A reduction of flammability is problematic because prescribed fire is commonly used throughout the region to restore oak woodlands and savannas and promote oak regeneration (Arthur et al., 2012a; Brose, 2014). Zones of low flammability created by mesophyte leaf litter may act to interrupt fire continuity, protect mesophytes from fire damage, and potentially lessen the overall effectiveness of prescribed fire (Alexander et al., 2021). Decreased effectiveness of prescribed fire may allow for future mesophyte survival which could negatively impact oak regeneration via increased competition. Limited upland oak regeneration and the consequential perpetuation of the mesophication process via the replacement of upland oaks with mesophytic species has cascading consequences on ecosystem function (Ellison et al., 2005; Hanberry and Nowacki, 2016). Oaks are of major importance in maintaining ecosystem diversity, providing a vital mast source, and their replacement has numerous potential negative consequences for wildlife populations (McShea et al., 2007; McShea and Healy, 2002). Oaks are also important for influencing ecosystem-level processes such as nitrogen mineralization and availability in surface soils (Alexander and Arthur, 2014) and water inputs to the forest floor via throughfall and stemflow (Alexander and Arthur, 2010; Siegert et al., 2019), and oaks are likely to be critically important for forest sustainability because of their high resilience to warming climate (Vose and Elliott, 2016). Further, many upland oaks are premier hardwoods of high economic importance as timber (Luppold, 2019). Thus, understanding the biotic feedbacks between trees and fuels and how they vary between upland oaks and mesophytes is critical for predicting the future role of fire in historically oak-dominated landscapes.

The primary objective of this study was to quantify initial leaf litter chemistry, decomposition rates, and fuelbed properties (mass, composition, and bulk density) between several non-oak species, including (red maple, sugar maple, hickory (a combination of pignut (*Carya glabra*) and mockernut (*C. tomentosa*)), and American beech) and upland oaks (black oak [*Q. velutina*], chestnut oak [*Q. montana*] and white oak [*Q. alba*]). The non-oaks, except hickory, have low fire tolerance (Burns and Honkala, 1990) indicating fire exclusion allowed their encroachment into upland oak forests, and they are often considered mesophytes because of their leaf litter, bark, and crown traits (Babl et al., 2020) and lower leaf litter flammability compared to upland oaks (Varner et al., 2021). Hickories, which are often lumped with upland oaks functionally (Knapp et al., 2021), have moderate fire tolerance and flammability compared to upland oaks (McDaniel et al., 2021; Varner et al., 2021), suggesting that hickories may fall somewhere in the middle of the mesophyte-pyrophyte spectrum. Red and sugar maple are increasing dominance in the region (Knott et al., 2019), while American beech and hickories are abundant in sapling and midstory size classes relative to the overstory on our study sites in Kentucky and Mississippi (Alexander et al., 2021; Izbicki et al., 2020). Ultimately, understanding how different species promote or inhibit the mesophication process will help us predict how changes in forest composition and structure associated with fire exclusion impact forest flammability and our ability to restore desired ecosystem services with prescribed fire.

2. Methods

2.1. Study area

This study was conducted in Bernheim Arboretum and Research Forest (hereafter referred to as Bernheim; 37°52' N, 85°35'), located in the Western Knobs ecoregion of Kentucky, USA, 40 km south of Louisville. Bernheim is a 65-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. 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; mean annual rainfall was 126 cm, evenly distributed throughout the year, and average annual snowfall was 33 cm (Arguez et al., 2010). Soils are primarily composed of the Lenberg-Carpenter and Zanesville 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%. The Carpenter series consists of deep, well-drained loamy soils, formed from weathered shale or limestone and occupies slopes from 2% to 60% (Natural Resources Conservation Service, 2001). The Zanesville series is composed of silt-loam soils that are found on ridgetops (United States Department of Agriculture, 2014).

Forest composition and size class structure was typical of upland oak forests in the central and eastern United States experiencing an “oak sapling recruitment bottleneck.” The overstory (>20 cm diameter at breast height [DBH]) was dominated by oak species, including white oak (*Q. alba*; 11.2 m² ha⁻¹, 52%) and chestnut oak (*Q. montana*; 6.5 m² ha⁻¹, 31%). Mostly non-oak species dominated the midstory (10–20 cm DBH), including red maple, sugar maple, American beech, mockernut hickory, and pignut hickory, with a collective basal area of non-oaks of 1.76 m² ha⁻¹ (71%). However, chestnut oak represented a modest proportion of the midstory (0.62 m² ha⁻¹, ~25%). The sapling size class (<10 cm DBH) was primarily occupied by red maple and sugar maple (29%), mockernut and pignut hickory (28%), American beech (21%), and minor components of other shade-tolerant species. Oak species represented <1% of the sapling size class (Babl et al., 2020).

2.2. Leaf litter decomposition

To assess whether leaf litter decomposition rates varied among upland oaks and encroaching non-oaks, we used a traditional decomposition bag study (Bocock and Gilbert, 1957). Throughout the litterfall period during 2016 (November–December), fresh leaf litter from each species (red maple, sugar maple, mockernut and pignut hickory, black oak, chestnut oak, and white oak) was collected bi-weekly by hand from the forest floor across upland oak stands throughout the study area. Because American beech is marcescent, some leaves were removed directly from trees during the same period. We acknowledge that removing leaves, rather than waiting for them to fall, could have impacted leaf litter chemistry and decomposition rates, as marcescence has been hypothesized to be a strategy to increase nutrient resorption prior to leaf fall (Otto and Nilsson, 1981). Yet, explanations of marcescence remain controversial (Karban and Pearse, 2021), and even if marcescence increased nutrient resorption, removing leaves would have impacted only the magnitude, and not the direction, of our findings, as resorption would have created poorer litter quality, and consequently, slower decomposition rates. Fresh leaf litter was returned to the lab, air-dried, homogenized, and 5 g was placed into fine-mesh, 20 × 20-cm plastic decomposition bags, which were tightly sealed and labeled with a unique identification number. Mesh size was 1 × 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 deployed in the forest at a location away from the

bole of overstory (>20 cm DBH) trees, not in a gap, and free of understorey/midstorey plants, to eliminate confounding factors, and thereby, represent a common garden experiment. Bags were placed directly atop the litter layer. One bag per site was retrieved starting at time 1 (spring 2017; 3 months after initial placement), then again at 6, 9, and 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 h and weights recorded to obtain an oven-dry conversion factor, which was applied to the mass of all initial samples. 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. A subsample was then combusted in a muffle furnace at 500 °C for 4 h 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 based on mass loss by using single exponential decay model (Olson, 1963): $M_t / M_0 = \exp(-kt)$, 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. To better understand how initial leaf litter chemistry relates to decomposition rates, C and N concentrations were measured on leaf litter from time 0 from a 5 g subsample that was ground to pass through a 60 mesh sieve, oven dried at 60 °C, and analyzed using elemental combustion (ECS 4010 CHNO-S; Costech, Valencia, California, USA). In addition, lignin concentration for time 0 samples was measured at Dairy One Lab (Ithaca, New York, USA) with an Ankom Fiber Analyzer (ANKOM Technology, Macedon, New York, USA).

2.3. Fuelbed properties

To determine the tree-level impacts of leaf litter production on fuel composition and loads beneath individual tree crowns, we sampled leaf litter and duff layer fuelbed properties (composition, mass, and bulk density) under upland oaks and non-oaks trees along a gradient of shade tolerance and fire sensitivity (see Babl et al., 2020 for details) within Bernheim in December 2016 and January 2017. All trees were embedded in forests dominated by an oak overstory. Tree species sampled included those mentioned above for decomposition rates, excluding black oak, and met the following criteria: (1) not located near a road (>20 m away) or near/within a canopy gap to avoid potential edge effects; (2) had a reasonably clear understorey to target single-tree influences and limit potential confounding effects (<30% non-tree understorey cover); and (3) located on relatively flat areas of the landscape to limit topographic effects on moisture drainage.

The original goal of this study was to sample 15 individual overstory (>20 cm DBH) trees of each species because we expected the most pronounced differences in leaf litter and duff fuels would occur in the understorey of relatively large trees. We found 15 individuals of red maple (min 17.5–max 52.0 cm; mean 31.9 ± 2.3 cm), chestnut oak (min 19.6–max 66.6 cm; mean 40.6 ± 3.4 cm), and white oak (min 20.5–max 63.0 cm; mean 40.6 ± 3.4 cm) that mostly met the size criteria and all other criteria. However, we found only 12 American beech trees that met other criteria but were generally not present in larger size classes (min 12.0–max 21.5 cm; mean 16.7 ± 0.7 cm). We only found 10 sugar maple (min 20.6 – max 38.7 cm; mean 27.8 ± 2.0 cm) and 10 hickories (min 19.0–max 49.6 cm; mean 29.7 ± 2.7 cm) meeting all criteria.

To sample annual litter inputs and the duff layer, two 30 × 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 then harvested and placed in an air-tight plastic bag, and then the same steps were repeated to harvest the duff layer. In the lab, leaf litter was sorted by species, placed in the oven at 60 °C, and dried to a constant weight to determine species-specific contributions to leaf litter mass. Non-duff components (e.g., seeds, bark, twigs) were removed from the duff

layer, and the duff layer was then placed in the oven at 60 °C, and dried to a constant weight to determine duff mass. Bulk density was then calculated by dividing the oven-dried leaf litter or duff mass by the volume occupied by leaf litter or duff.

2.4. Statistical analyses

Differences in litter mass remaining over time between species were analyzed as a two-way Analysis of Variance (ANOVA) with species and time (time 0 removed) and their interaction as main effects in JMP v. 13. Although litter bags were placed at two different sites, we inadvertently did not record site locations for pick up for times 3 and 6, and as a result, we were unable to analyze these times for site effects. However, we do not expect site differences, as pick up times 9 and 12 had no significant site effect ($P = 0.185$) when analyzed with an ANOVA with site as a main effect and percent mass remaining as the response variable. 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.

Differences in initial litter chemistry (lignin, %C, %N, lignin:N, and C:N ratios), total leaf litter and duff mass and bulk density, and percent contribution of each species to the leaf litter fuelbed in December 2016 were compared using a one-way ANOVA with the main effect of species. For tree-level fuelbed variables measured on the north and south sides of trees, values were averaged at the tree level prior to analysis such that the tree served as the replicate. All leaf litter and fuelbed variables were tested for normality (Shapiro-Wilk W Test) and homogeneity of variance (Levene's Test), and those that did not meet these assumptions were transformed using logarithmic or square-root (for percentages) functions to meet model assumptions. When significant main effects or interactions were detected ($P < 0.05$), least squares means were compared via a post-hoc Tukey's HSD 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.

3. Results

Initial leaf litter chemistry varied between non-oaks and oaks, with significant differences among species ($P < 0.001$) for all traits measured (Table 1). Black oak ($50.22 \pm 0.18\%$) litter C concentration significantly exceeded all species except chestnut oak (49.12 ± 0.31) ($P < 0.001$ for all comparisons). Carbon concentrations of all other species were statistically similar ($P > 0.309$ for all comparisons). Black oak also had the highest lignin concentration ($19.77 \pm 0.19\%$; $P < 0.001$ for all comparisons) followed by chestnut oak ($13.90 \pm 0.19\%$), which had higher lignin concentrations than other species ($P < 0.001$ for all comparisons). Lignin concentration in American beech ($12.10 \pm 0.19\%$) and white oak ($11.37 \pm 0.19\%$) were similar ($P = 0.162$) as were lignin concentrations of white oak and sugar maple ($10.87 \pm 0.19\%$; $P = 0.551$). Red maple ($9.50 \pm 0.19\%$) and hickory ($9.00 \pm 0.19\%$) had the lowest lignin concentrations compared to all other species ($P < 0.001$ for all comparisons). Nitrogen concentration was lowest in red maple ($0.73 \pm 0.05\%$) and highest in hickory ($1.32 \pm 0.07\%$), while all other species had N concentrations of $\sim 1.00\%$. Black oak also had the highest lignin:N

N ratio (18.87 ± 0.92 ; $P < 0.001$ for all comparison), while hickory (6.92 ± 0.92) and sugar maple (9.87 ± 0.92) had the lowest lignin:N ratio ($P < 0.001$ for all comparisons). Red maple had the highest leaf litter C:N (67.10 ± 4.56), while hickory had the lowest (35.32 ± 1.79).

Percent leaf litter mass remaining over time was distinct between non-oaks and oaks (Fig. 1). There was a significant main effect of time ($P < 0.001$) and species ($P < 0.001$) on the mass remaining (%), but the interaction between time and species was not significant ($P = 0.789$), indicating that differences between species did not change over time. After the first 3 months, red maple had only 58% of its mass remaining, which was significantly less than all other species ($P < 0.001$). Hickory and sugar maple had $\sim 70\%$ remaining after 3 months, while white oak, chestnut oak, red oak, and American beech had 77–85% of their original mass remaining. Therefore, after 12 months, trends were still similar, with red maple and sugar maple having only 46% of their mass remaining, while black oak and American beech had $\sim 65\%$ of their mass remaining ($P < 0.001$). Except for American beech, decomposition rates based on a single exponential decay model were generally faster in non-oaks compared to oaks (Table 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 ($k = 0.43$).

Total leaf litter and duff mass were similar underneath oaks and non-oaks when sampled soon after leaf fall ($p = 0.807$ and 0.096 ,

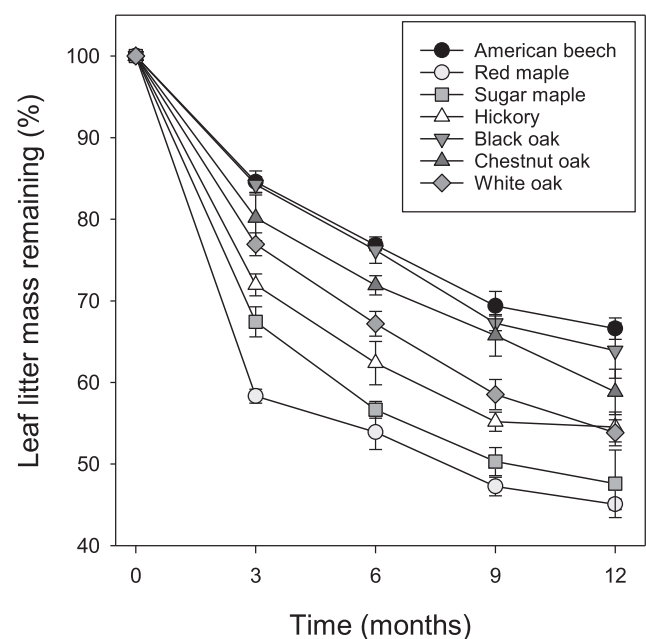


Fig. 1. Mean percentage of mass (\pm SE) remaining of American beech, red maple, sugar maple, hickory, black oak, chestnut oak, and white oak leaf litter from a one-year litter decomposition bag study in Bernheim Arboretum and Research Forest, Kentucky, USA. Hickory included both pignut (*C. glabra*) and mockernut (*C. tomentosa*).

Table 1

Initial leaf litter chemistry for American beech, red maple, sugar maple, hickory, black oak, chestnut oak, and white oak leaf litter collected in December 2016 within Bernheim Arboretum and Research Forest, Kentucky, USA, as part of a 1-year study to assess decomposition rates. Values are means \pm SE. Different letters indicate significant differences ($P < 0.05$) between tree species (i.e., across rows) for a given leaf litter characteristic. C = Carbon, N = Nitrogen. Hickory included both pignut (*C. glabra*) and mockernut (*C. tomentosa*). All variables were significantly different among species at $P < 0.001$.

Litter characteristic	Am. beech	Red maple	Sugar maple	Hickory spp.	Black oak	Chestnut oak	White oak
C (%)	46.04c \pm 0.33	47.51bc \pm 0.65	45.88c \pm 0.72	45.98c \pm 0.34	50.22a \pm 0.18	49.12ab \pm 0.31	46.61c \pm 0.77
Lignin (%)	12.10c \pm 0.10	9.50e \pm 0.06	10.87d \pm 0.26	9.00e \pm 0.06	19.77a \pm 0.26	13.90b \pm 0.10	11.37 cd \pm 0.32
N (%)	1.00bc \pm 0.05	0.73c \pm 0.05	1.13ab \pm 0.08	1.32a \pm 0.07	1.08ab \pm 0.08	1.04ab \pm 0.08	0.89bc \pm 0.07
Lignin:N	12.25b \pm 0.59	13.46b \pm 1.04	9.87bc \pm 0.77	6.92c \pm 0.37	18.87a \pm 1.43	13.72b \pm 0.99	13.17b \pm 0.90
C:N	46.55bc \pm 2.07	67.10a \pm 4.56	41.49bc \pm 2.77	35.32c \pm 1.79	47.94bc \pm 3.65	48.48bc \pm 3.47	53.97ab \pm 3.84

Table 2

Calculated decomposition rates (k values \pm SE) and R^2 values based on single exponential models fitted to each species' leaf litter mass remaining over a one-year period in Bernheim Arboretum and Research Forest, Kentucky, USA. Listed in order of decreasing decomposition rates. All models were significant at $P < 0.05$. Hickory included both pignut (*C. glabra*) and mockernut (*C. tomentosa*).

Tree Species	k value (y^{-1})	R^2
Red maple	0.91 \pm 0.23	0.84
Sugar maple	0.84 \pm 0.15	0.92
Hickory spp.	0.68 \pm 0.13	0.91
White oak	0.65 \pm 0.07	0.97
Chestnut oak	0.53 \pm 0.05	0.97
Black oak	0.47 \pm 0.04	0.98
American beech	0.43 \pm 0.04	0.97

respectively), as were total leaf litter and duff bulk density ($p = 0.148$ and 0.346 , respectively), but non-oak leaf litter contributed a greater proportion of fuelbed mass underneath non-oaks compared to oaks (Table 3). Across tree species, total leaf litter fuelbed mass was ~ 400 g m^{-2} , but $\sim 90\%$ of this mass was contributed by oak litter beneath chestnut and white oaks, with 65–78% of the fuelbed contributed by oak beneath the other species. In addition, non-oak leaf litter contribution to the total fuelbed was consistently higher beneath non-oaks (22–35%) compared to oaks (10–12%). The leaf litter mass of any non-oak species was significantly higher beneath that species than beneath other species ($p < 0.0001$).

4. Discussion

Our results indicate that increased abundance of non-oak species in upland oak forests may alter fuelbed dynamics in several ways that serve to reduce leaf litter fuel loads and increase contribution of leaf litter with traits associated with low flammability. Except for American beech, leaf litter of non-oaks decomposed faster than that of oaks. In addition, although annual total leaf litter mass beneath non-oak and oak overstory

trees was similar, non-oak leaf litter contributed more to the fuelbed beneath non-oaks than beneath oak trees, highlighting that individual trees do have a zone of influence in their understories that likely impacts fuel heterogeneity (Alexander et al., 2021). These findings indicate that fuelbed mass and continuity could decline through species-level variations in decomposition rates and individual tree impacts on understory fuel inputs and flammability traits as certain non-oak species continue to replace oaks throughout the region.

Variations in decomposition rates between upland oaks and non-oaks were likely driven by differences in leaf litter chemistry and morphology (see Babl et al., 2020), with both direct and indirect implications for flammability. Red maple and sugar maple had only 45 and 48% of their leaf litter mass remaining after one year while oaks had 54–64% of their mass remaining, findings similar to those reported in eastern Kentucky, USA (Alexander and Arthur, 2014) and southwestern North Carolina, USA (Blair and Crossley, 1988). Hickory leaf litter mass remaining was 55%, similar to decomposition rates in central Kentucky, USA (Arthur et al., 2012b). Red maple leaf litter had the lowest initial percent N and highest C:N ratio, traits often associated with slow decomposition (Melillo et al., 1982), indicating that red maple's fast decomposition rate may be due to high concentrations of highly labile C, which is consistent with findings in other studies (Alexander and Arthur, 2014; Blair and Crossley, 1988). Notably, red maple leaf litter also dries very slowly compared to oaks (Kreye et al., 2013), which may further accelerate its decomposition rates. Sugar maple and hickory leaf litter had relatively high initial percent N, low percent lignin, and low C:N ratios when compared to other species, characteristics often associated with fast decomposition rates (Cornwell et al., 2008), but also shorter flame durations and decreased fuel consumption (Grootemaat et al., 2017, 2015). These flammability consequences match those measured for sugar maple compared to white, chestnut, and red oak in laboratory trials (Kane et al., 2021), but only shorter flame durations compared to several oaks were found for hickory (Varner et al., 2021). American beech leaf litter chemistry did not exhibit traits associated with slow decomposition rates (e.g., high lignin:N) (Cornwell et al., 2008), yet still exhibited

Table 3

Leaf litter mass, percent leaf litter mass contribution by tree species, bulk density, and duff mass and bulk density in the understory of American beech, red maple, sugar maple, hickory, chestnut oak, white oak, and red oak (black/scarlet/northern red) in December 2016 and January 2017 within Bernheim Arboretum and Research Forest, Kentucky, USA. Values are means \pm SE. Different letters indicate significant differences ($P < 0.05$) between tree species. Hickory included both pignut (*C. glabra*) and mockernut (*C. tomentosa*).

Fuelbed characteristic	American beech	Red maple	Sugar maple	Hickory spp.	Chestnut oak	White oak	P value
<i>Leaf litter</i>							
Total mass (g m^{-2})	377.1 \pm 22.3	410.6 \pm 30.7	412.3 \pm 19.4	409.2 \pm 22.7	410.3 \pm 22.9	434.3 \pm 32.9	0.807
American beech (%)	10.8a \pm 1.0	1.9b \pm 0.7	0.6b \pm 0.4	2.1b \pm 0.6	2.1b \pm 0.7	1.8b \pm 0.5	< 0.001
Red maple (%)	5.6b \pm 1.4	26.5a \pm 3.7	1.6b \pm 0.8	5.5b \pm 1.3	3.7b \pm 1.1	4.0b \pm 1.6	< 0.001
Sugar maple (%)	0.9b \pm 0.4	2.5b \pm 1.0	22.7a \pm 3.1	0.4b \pm 0.3	0.6b \pm 0.3	2.0b \pm 0.9	< 0.001
Hickory spp. (%)	4.4b \pm 2.1	4.0b \pm 1.3	3.9b \pm 1.2	22.3a \pm 2.4	3.1b \pm 1.1	4.5b \pm 1.0	< 0.001
Chestnut oak (%)	20.6b \pm 3.2	16.9b \pm 3.0	28.7ab \pm 5.4	20.9b \pm 3.9	40.6a \pm 3.0	31.6ab \pm 4.2	< 0.001
White oak (%)	44.6 \pm 6.1	33.6 \pm 3.9	31.4 \pm 4.3	27.6 \pm 4.4	35.8 \pm 3.5	41.9 \pm 4.2	0.159
Red oak (%)	13.1 \pm 3.9	14.6 \pm 3.7	11.0 \pm 2.7	21.2 \pm 5.3	14.2 \pm 3.7	14.3 \pm 4.5	0.657
Total oak (%)	78.2ab \pm 2.5	65.1c \pm 4.2	71.2bc \pm 3.7	69.7bc \pm 2.2	90.5a \pm 1.6	87.7a \pm 2.2	< 0.001
Total mesophyte (%)	21.8a \pm 2.5	34.9a \pm 4.2	28.8a \pm 3.7	30.3a \pm 2.2	9.5b \pm 1.6	12.3b \pm 2.2	< 0.001
Bulk density (g cm^{-3})	0.015 \pm 0.003	0.023 \pm 0.006	0.016 \pm 0.002	0.010 \pm 0.001	0.012 \pm 0.001	0.016 \pm 0.002	0.148
<i>Duff</i>							
Mass (g m^{-2})	505.1 \pm 43.3	646.8 \pm 48.7	477.4 \pm 66.4	677.3 \pm 34.5	580.9 \pm 52.1	588.8 \pm 55.7	0.096
Bulk density (g cm^{-3})	0.044 \pm 0.007	0.041 \pm 0.007	0.053 \pm 0.008	0.030 \pm 0.002	0.041 \pm 0.005	0.039 \pm 0.005	0.346

the slowest decomposition rate, with ~66% remaining after one year, similar to findings in northern hardwood forests where this species had 74–87% litter remaining after one year in east-central New York, USA (Elliott et al., 1993). American beech leaf litter may have high levels of structural carbons or tannins, which were not measured here, that make it less palatable to consumers and hinder decomposition. Notably, those leaf litter chemical traits are also inhibitory to surface fire spread (Grootemaat et al., 2017). Yet, American beech leaf litter has moderately high flammability (Varner et al., 2021), further signaling the need to include the drying capacity of the leaf litter, and the moisture environment where the leaf litter is typically found, into flammability assessments. Overall, these findings indicate that decomposition rates vary markedly between non-oaks and oaks and that encroachment by several non-oak species into current-day oak forests could lower flammability through this mechanism (Alexander et al., 2021).

Species-level differences in decomposition rates may be accentuated if variations in microclimatic conditions beneath different tree species are also considered. Our decomposition rate study was conducted as a common garden experiment with relatively uniform understory conditions absent of the influence of any particular tree. However, we commonly observed lower light levels and cooler air temperatures beneath American beech compared to the understory of upland oaks (Babl, 2018), which are environmental conditions that have been shown to influence decomposition rates (Aerts, 1997; Kirschbaum, 1995, 2006). Thus, decomposition rates of American beech leaf litter may be different beneath its own crown. In addition, compositional shifts do not occur independently of structural changes that could impact microclimatic interactions with decomposition rates and fuel loads. Notably, oak savannas or woodlands have substantially lower basal area than closed canopy oak forests, which coincides with reduced leaf litter fuel mass but increased herbaceous fuels, both in more open, higher light, drier environments (Hanberry et al., 2020b) that typically act to slow decomposition rates (Aerts, 1997).

Greater mass of non-oak leaf litter in the understory of non-oaks compared to upland oaks has important implications for forest restoration efforts in the region, as prescribed fire is a primary management tool for reducing mesophyte competition and promoting oak regeneration in the region (Arthur et al., 2012a; Brose, 2014; Dey, 2014; Dey and Hartman, 2005). In addition to often decomposing faster, leaf litter from some non-oaks possess characteristics that are linked to decreased flammability, like being small, flat, and thin (Alexander et al., 2008; Babl et al., 2020; Kane et al., 2021; Kreye et al., 2018; McDaniel et al., 2021) with slow drying rates (Kreye et al., 2013; McDaniel et al., 2021); thus, increased inputs of this litter beneath non-oak trees may lead to a zone of reduced flammability through not only reduced fuel loads, but also from fuelbed compaction and increased moisture holding capacity (Grootemaat et al., 2017; Varner et al., 2015) in addition to other mechanisms like increased stemflow near thin-barked, non-oak trees that could serve as a natural “wet line” to protect these trees from fire (Alexander et al., 2021; Alexander and Arthur, 2010). As these low-flammability zones converge with non-oak encroachment, prescribed fire may be rendered less effective, facilitating encroachment by non-oak advance regeneration (Alexander et al., 2008; Izbicki et al., 2020; Schweitzer et al., 2016), and further contributing to the mesophication positive feedback.

Despite higher non-oak leaf litter contribution beneath non-oaks compared to upland oaks, oak litter still dominated the fuelbed throughout the forest, and fuelbed differences in bulk density were not statistically detectable, suggesting that oak leaf litter still retains the capacity to control flammability trends in current-day stands at Bernheim and in forests elsewhere in which oaks retain overstory dominance but other species dominate the sapling layer and midstory, a common condition throughout the central hardwoods region (Knott et al., 2019). Previous studies have shown that leaf litter drying rates and flammability decline substantially as mesophyte contribution to the fuel bed increases from 33% to 66% (Kreye et al., 2018; McDaniel et al., 2021).

Leaf litter fuelbeds beneath overstory red maple, sugar maple, and hickory, which were embedded in an oak-dominated overstory, were comprised of 29–35% non-oak litter, indicating that these forests still have some time before their flammability capacity is lost. In addition, we collected leaf litter fuels just after leaf fall, and leaf litter may redistribute overtime, especially in areas with substantial topography (Boerner and Kooser, 1989), thereby lessening single tree influences on understory fuel bed composition. Despite a lack of bulk density fuelbed differences underneath non-oaks and oaks at Bernheim, these differences are likely to occur as non-oak contribution to the fuelbed increases. For example, Dickinson et al. (2016) found increased bulk density in maple litter beds when compared to oak, which led to reduced fire spread potential and lower fire intensities. Thus, as non-oak encroachment continues, and overstory oaks die, flammability will likely continue to decline.

Importantly, the net balance of decomposition rates and leaf litter inputs should be considered when trying to understand the potential implications of shifting species composition for fuelbed mass. To illustrate this point, we calculated annual fuel loads in hypothetical monocultures of the different species at the current overstory/midstory basal area at Bernheim (30 m² ha⁻¹) using annual leaf litter inputs obtained from allometric equations (Martin et al., 1998; Ribe, 1973) and mass loss rates determined from our decomposition study (Table 4), fully acknowledging that current-day, oak-dominated forests show a successional trajectory consisting of 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, 2009; Izbicki et al., 2020), and that monocultures do not represent reality. Using these conditions, we found that the mesophytic maples, which are expected to replace oaks in the eastern United States (Amatangelo et al., 2011; Fei and Steiner, 2007; Knott et al., 2019), produce between 18 and 43% less leaf litter fuel mass after one year compared to chestnut or black oak. Hickories, which have similar ecological traits as oaks and historically were common in oak forest landscapes (Knapp et al., 2021), yielded a similar reduction in leaf litter fuel mass, with a projected ~20% decrease after one year compared to chestnut or black oak. In contrast, an American beech monoculture had the highest remaining fuel loads after one year, a product of this species' relatively high leaf litter inputs and slow decomposition rates, averaging 20–56% more fuel when compared to the other species in this study. Our modeled scenario also indicates that shifting dominance among oak species could lead to changes in fuelbed mass, as the white oak monoculture yielded ~33% less fuel after one year compared to black or chestnut oak monocultures. However, it is important to note that other aspects of fuel dynamics beyond fuel loads may counteract these trends. For example, compared to several red oaks, white oak is more fire-tolerant (Mann et al., 2020) with leaf litter that absorbs less water, dries faster, and has more curl (Kreye et al., 2013) and higher flammability (Kane et al., 2021; Varner

Table 4

Calculated mean (±SE) leaf litter inputs (based on allometric equations), outputs (based on our decomposition rates), and net leaf litter fuel loads after one year in a forest entirely composed of American beech, red maple, sugar maple, hickory spp., chestnut oak, black oak, and white oak at the current overstory/midstory basal area at Bernheim Arboretum and Research Forest, Kentucky, USA (30 m² ha⁻¹). Hickory included both pignut (*C. glabra*) and mockernut (*C. tomentosa*).

Species	Leaf litter inputs (kg ha ⁻¹)	Leaf litter outputs (kg ha ⁻¹)	Net leaf litter 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 spp.	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

et al., 2021). In addition, there may be non-additive effects on decomposition rates unaccounted for here such that litter types within mixtures decompose differently than would be predicted by the decomposition rates of litter types in isolation. While we do not expect monocultures to replace mixed-species forests throughout the eastern United States, this exercise demonstrates how the replacement of upland oak by a maple forest could cause pronounced differences in fuelbed mass over time. Furthermore, as illustrated by American beech and white oak, our results show how grouping species at the functional level can lead to erroneous projections of fuelbed dynamics.

5. Conclusions

Our results indicate that inputs of leaf litter from some non-oaks will lead to increased decomposition rates, a higher proportion of non-oak leaf litter beneath non-oak crowns, and a possible reduction of fuel loads across the forest floor, which could lower forest flammability. Among the species examined in this study, red maple and sugar maple have the greatest potential to reduce fuel loads through faster decomposition rates and are expected to expand throughout the central and eastern United States (Amatangelo et al., 2011; Fei and Steiner, 2007; Knott et al., 2019). In contrast, American beech leaf litter decomposed even slower than the oak species and has a high moisture retention capacity (Kreye et al. 2013), indicating that it may not contribute to this particular aspect of the mesophication process, but could lower flammability through other leaf litter traits (Babl et al., 2020). The oak species examined in this study generally produced recalcitrant litter, but black oak and chestnut oak decomposed more slowly than white oak, highlighting the importance of species-level variations even among upland oaks. Quantifying fuel load dynamics is an important part of determining forest flammability (Grootemaat et al., 2017), but fuelbed structure, moisture-holding capacity, and leaf litter chemistry undoubtedly play a role and complicate our understanding of the mesophication process. As forests transition from upland oak to mesophyte dominance, our results as well as other recent field and laboratory studies (Kane et al., 2021; Kreye et al., 2018; McDaniel et al., 2021; Varner et al., 2021), suggest that the ability to implement prescribed fire on the landscape may become increasingly difficult, and future research is needed to understand these complex state shifts. Future studies should explore how decomposition rates, leaf litter chemistry, fuelbed structure, and understory microclimate work in tandem to inhibit or promote flammability and identify how mixtures of different species influence prescribed fire efficacy.

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.

Acknowledgements

We thank Bernheim Arboretum and Research Forest for their logistical support and field work assistance, especially Kelly Vowels, Rick Caldwell, and Christina Casto Teltser. We would also like to acknowledge those all others who helped in the field and lab including: Brian Izbicki, Rachel Arney, Homero Peña, Evie Von Boeckman, Jennifer McDaniel, William Webb, Josh Byers, Harry Mehgart, and Daniel Harrison. We also thank two anonymous reviewers for their valuable input that greatly improved earlier versions of this manuscript. This material is a contribution of the Forest and Wildlife Research Center, Mississippi State University and is based upon work that was supported by the National Institute of Food and Agriculture, U.S. Department of Agriculture, McIntire-Stennis project under accession numbers MISZ-069450 and MISZ-06939. This paper was written and prepared in part by a U.S. Government employee on official time, and therefore it is in the public

domain and not subject to copyright. The findings and conclusions in this publication are those of the author(s) and should not be construed to represent an official USDA, Forest Service, or United States Government determination or policy.

References

- Abrams, M.D., 1992. Fire and the development of oak forests. *Bioscience* 42 (5), 346–353.
- Abrams, M.D., 1990. Adaptations and responses to drought in *Quercus* species of North America. *Tree Physiol.* 7 (1-2-3-4), 227–238.
- Abrams, M.D., Downs, J.A., 1990. Successional replacement of old-growth white oak by mixed mesophytic hardwoods in southwestern Pennsylvania. *Can. J. For. Res.* 20 (12), 1864–1870.
- Abrams, M.D., Kubiske, M.E., 1990. Leaf structural characteristics of 31 hardwood and conifer tree species in central Wisconsin: influence of light regime and shade-tolerance rank. *For. Ecol. Manage.* 31 (4), 245–253.
- Abrams, M.D., Nowacki, G.J., 1992. Historical variation in fire, oak recruitment, and post-logging accelerated succession in central Pennsylvania. *Bull. Torrey Bot. Club* 119 (1), 19. <https://doi.org/10.2307/2996916>.
- Aerts, R., 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. *Oikos* 79 (3), 439. <https://doi.org/10.2307/3546886>.
- Alexander, H.D., Arthur, M.A., 2014. Increasing red maple leaf litter alters decomposition rates and nitrogen cycling in historically oak-dominated forests of the eastern US. *Ecosystems* 17 (8), 1371–1383.
- Alexander, H.D., Arthur, M.A., 2010. Implications of a predicted shift from upland oaks to red maple on forest hydrology and nutrient availability. *Can. J. For. Res.* 40 (4), 716–726.
- Alexander, H.D., Arthur, M.A., Loftis, D.L., Green, S.R., 2008. Survival and growth of upland oak and co-occurring competitor seedlings following single and repeated prescribed fires. *For. Ecol. Manage.* 256 (5), 1021–1030.
- Alexander, H.D., Siegert, C., Brewer, J.S., Kreye, J., Lashley, M.A., McDaniel, J.K., Paulson, A.K., Renninger, H.J., Varner, J.M., 2021. Mesophication of Oak Landscapes: Evidence, Knowledge Gaps, and Future Research. *BioScience* 1–12.
- Amatangelo, K.L., Fulton, M.R., Rogers, D.A., Waller, D.M., 2011. Converging forest community composition along an edaphic gradient threatens landscape-level diversity. *Divers. Distrib.* 17 (2), 201–213.
- Arguez, A., Durre, I., Applequist, S., Squires, M., Vose, R., Yin, X., Bilotta, R., 2010. NOAA's US climate normals (1981–2010). NOAA Natl. Centers Environ. Inform. 10, V5PN93JP.
- Arthur, M.A., Alexander, H.D., Dey, D.C., Schweitzer, C.J., Loftis, D.L., 2012a. Refining the oak-fire hypothesis for management of oak-dominated forests of the eastern United States. *J. Forest.* 110 (5), 257–266.
- Arthur, M.A., Blankenship, B.A., Schörgendorfer, A., Alexander, H.D., 2017. Alterations to the fuel bed after single and repeated prescribed fires in an Appalachian hardwood forest. *For. Ecol. Manage.* 403, 126–136.
- Arthur, M.A., Bray, S.R., Kuchle, C.R., McEwan, R.W., 2012b. The influence of the invasive shrub, *Lonicera maackii*, on leaf decomposition and microbial community dynamics. *Plant Ecol.* 213 (10), 1571–1582.
- Babl, E., Alexander, H.D., Siegert, C.M., Willis, J.L., 2020. Could canopy, bark, and leaf litter traits of encroaching non-oak species influence future flammability of upland oak forests? *For. Ecol. Manage.* 458, 117731. <https://doi.org/10.1016/j.foreco.2019.117731>.
- Babl, E.K., 2018. Could Mesophyte Canopy, Bark, and Leaf Litter Traits Drive Future Flammability of Upland Oak Forests? Mississippi State University, Mississippi State University, MS.
- Ball, B.A., Hunter, M.D., Kominoski, J.S., Swan, C.M., Bradford, M.A., 2008. Consequences of non-random species loss for decomposition dynamics: experimental evidence for additive and non-additive effects. *J. Ecol.* 96 (2), 303–313.
- Ballard, J.P., Horn, S.P., Li, Z.-H., 2017. A 23,000-year microscopic charcoal record from Anderson Pond, Tennessee, USA. *Palynology* 41 (2), 216–229.
- Blair, J.M., Crossley, D.A., 1988. Litter decomposition, nitrogen dynamics and Litter microarthropods in a southern Appalachian hardwood forest 8 years following clearcutting. *J. Appl. Ecol.* 25 (2), 683. <https://doi.org/10.2307/2403854>.
- Bocock, K.L., Gilbert, O.J.W., 1957. The disappearance of leaf litter under different woodland conditions. *Plant Soil* 9 (2), 179–185.
- Boerner, R.E.J., Kooser, J.G., 1989. Leaf litter redistribution among forest patches within an Allegheny Plateau watershed. *Landscape Ecol.* 2 (2), 81–92.
- Brewer, S., Rogers, C., 2006. Relationships between prescribed burning and wildfire occurrence and intensity in pine-hardwood forests in north Mississippi, USA. *Int. J. Wildland Fire* 15 (2), 203. <https://doi.org/10.1071/WF05068>.
- Brose, P.H., 2014. Development of prescribed fire as a silvicultural tool for the upland oak forests of the eastern United States. *J. Forest.* 112 (5), 525–533.
- Burns, R.M., Honkala, B.H., 1990. *Silvics of North America*. United States Department of Agriculture.
- Cornelissen, J.H.C., Grootemaat, S., Verheijen, L.M., Cornwell, W.K., Bodegom, P.M., Wal, R., Aerts, R., 2017. Are litter decomposition and fire linked through plant species traits? *New Phytol.* 216 (3), 653–669.
- Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., Hobbie, S.E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H.M., Santiago, L.S., Wardle, D.A., Wright, I.J., Aerts, R., Allison, S.D., van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T.V., Díaz, S., Garnier, E., Gurvich, D.E., Kazakou, E., Klein, J.A., Read, J., Reich, P.B., Soudzilovskaia, N.A.,

- Vaieretti, M.V., Westoby, M., 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecol. Lett.* 11 (10), 1065–1071.
- Cornwell, W.K., Elvira, A., Kempen, L., Logtestijn, R.S.P., Aptroot, A., Cornelissen, J.H.C., 2015. Flammability across the gymnosperm phylogeny: the importance of litter particle size. *New Phytol.* 206 (2), 672–681.
- Cromack Jr, K., Monk, C.D., 1975. Litter production, decomposition, and nutrient cycling in a mixed hardwood watershed and a white pine watershed. *Mineral Cycling in Southeastern Ecosystems; Proceedings of a Symposium.*
- Dey, D.C., 2014. Sustaining oak forests in eastern North America: regeneration and recruitment, the pillars of sustainability. *Forest Sci.* 60 (5), 926–942.
- Dey, D.C., Hartman, G., 2005. Returning fire to Ozark Highland forest ecosystems: effects on advance regeneration. *For. Ecol. Manage.* 217 (1), 37–53.
- Dickinson, M.B., Hutchinson, T.F., Dietenberger, M., Matt, F., Peters, M.P., Yang, J., 2016. Litter species composition and topographic effects on fuels and modeled fire behavior in an oak-hickory forest in the eastern USA. *PLoS ONE* 11 (8), e0159997. <https://doi.org/10.1371/journal.pone.0159997>.
- Elliott, W.M., Elliott, N.B., Wyman, R.L., 1993. Relative effect of litter and forest type on rate of decomposition. *Am. Midl. Nat.* 129 (1), 87. <https://doi.org/10.2307/2426438>.
- Ellison, A.M., Bank, M.S., Clinton, B.D., Colburn, E.A., Elliott, K., Ford, C.R., Foster, D.R., Kloeppel, B.D., Knoepp, J.D., Lovett, G.M., Mohan, J., Orwig, D.A., Rodenhouse, N. L., Sobczak, W.V., Stinson, K.A., Stone, J.K., Swan, C.M., Thompson, J., Von Holle, B., Webster, J.R., 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Front. Ecol. Environ.* 3 (9), 479–486.
- Engber, E.A., Varner, J.M., 2012. Patterns of flammability of the California oaks: the role of leaf traits. *Can. J. For. Res.* 42 (11), 1965–1975.
- Evans, J., Poorter, H., 2001. Photosynthetic acclimation of plants to growth irradiance: the relative importance of specific leaf area and nitrogen partitioning in maximizing carbon gain. *Plant, Cell Environ.* 24, 755–767.
- Fei, S., Kong, N., Steiner, K.C., Moser, W.K., Steiner, E.B., 2011. Change in oak abundance in the eastern United States from 1980 to 2008. *For. Ecol. Manage.* 262 (8), 1370–1377.
- Fei, S., Steiner, K.C., 2007. Evidence for increasing red maple abundance in the eastern United States. *Forest Sci.* 53, 473–477.
- Grootemaat, S., Wright, I.J., Bodegom, P.M., Cornelissen, J.H.C., Cornwell, W.K., Schweitzer, J., 2015. Burn or rot: leaf traits explain why flammability and decomposability are decoupled across species. *Funct. Ecol.* 29 (11), 1486–1497.
- Grootemaat, S., Wright, I.J., van Bodegom, P.M., Cornelissen, J.H.C., 2017. Scaling up flammability from individual leaves to fuel beds. *Oikos* 126 (10), 1428–1438.
- Hanberry, B.B., Abrams, M.D., Arthur, M.A., Varner, J.M., 2020a. Reviewing fire, climate, deer, and foundation species as drivers of historically open oak and pine forests and transition to closed forests. *Front. Forests Glob. Change* 3, 56.
- Hanberry, B.B., Bragg, D.C., Alexander, H.D., 2020b. Open forest ecosystems: an excluded state. *For. Ecol. Manage.* 472, 118256. <https://doi.org/10.1016/j.foreco.2020.118256>.
- Hanberry, B.B., Nowacki, G.J., 2016. Oaks were the historical foundation genus of the east-central United States. *Quat. Sci. Rev.* 145, 94–103.
- Hart, J.L., Grissino-Mayer, H.D., 2009. Gap-scale disturbance processes in secondary hardwood stands on the Cumberland Plateau, Tennessee, USA. *Plant Ecol.* 201 (1), 131–146.
- Izbicki, B.J., Alexander, H.D., Paulson, A.K., Frey, B.R., McEwan, R.W., Berry, A.I., 2020. Prescribed fire and natural canopy gap disturbances: Impacts on upland oak regeneration. *For. Ecol. Manage.* 465, 118107. <https://doi.org/10.1016/j.foreco.2020.118107>.
- Jackson, L.W.R., 1967. Effect of shade on leaf structure of deciduous tree species. *Ecology* 48, 498–499.
- Kane, J.M., Kreye, J.K., Barajas-Ramirez, R., Varner, J.M., 2021. Litter trait driven dampening of flammability following deciduous forest community shifts in eastern North America. *For. Ecol. Manage.* 489, 119100. <https://doi.org/10.1016/j.foreco.2021.119100>.
- Karban, R., Pearse, I.S., 2021. Loss of branches due to winter storms could favor deciduousness in oaks. *Am. J. Bot.* 108 (11), 2309–2314.
- Kirschbaum, M.U.F., 1995. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. *Soil Biol. Biochem.* 27 (6), 753–760.
- Kirschbaum, M., 2006. The temperature dependence of organic-matter decomposition—still a topic of debate. *Soil Biol. Biochem.* 38 (9), 2510–2518.
- Knapp, L.S., Pile, S., Snell, R., Vickers, L.A., Hutchinson, T., Kabrick, J., Jenkins, M.A., Graham, B., Rebeck, J., 2021. The ‘other’ hardwood: Growth, physiology, and dynamics of hickories in the Central Hardwood Region, USA. *For. Ecol. Manage.* 497, 119513. <https://doi.org/10.1016/j.foreco.2021.119513>.
- Knott, J.A., Desprez, J.M., Oswalt, C.M., Fei, S., 2019. Shifts in forest composition in the eastern United States. *For. Ecol. Manage.* 433, 176–183.
- Kreye, J.K., Varner, J.M., Hamby, G.W., Kane, J.M., 2018. Mesophytic litter dampens flammability in fire-excluded pyrophytic oak-hickory woodlands. *Ecosphere* 9 (1). <https://doi.org/10.1002/ecs2.2018.9.issue-110.1002/ecs2.2078>.
- Kreye, J.K., Varner, J.M., Hiers, J.K., Mola, J., 2013. Toward a mechanism for eastern North American forest mesophication: differential litter drying across 17 species. *Ecol. Appl.* 23 (8), 1976–1986.
- Luppold, W.G., 2019. The oak timber base and market: past, present, and future. e-Gen. Tech. Rep. SRS-237. Asheville, NC: US Department of Agriculture Forest Service, Southern Research Station 237, 25–31.
- Mann, D.P., Wiedenbeck, J.K., Dey, D.C., Saunders, M.R., 2020. Evaluating economic impacts of prescribed fire in the Central Hardwood Region. *Journal of Forestry* 118, 275–288.
- Marchal, J., Cumming, S.G., McIntire, E.J.B., 2020. Turning down the heat: vegetation feedbacks limit fire regime responses to global warming. *Ecosystems* 23 (1), 204–216.
- Martin, J.G., Kloeppel, B.D., Schaefer, T.L., Kimbler, D.L., McNulty, S.G., 1998. Aboveground biomass and nitrogen allocation of ten deciduous southern Appalachian tree species. *Can. J. Forest Res.* 28, 1648–1659.
- McDaniel, J.K., Alexander, H.D., Siegert, C.M., Lashley, M.A., 2021. Shifting tree species composition of upland oak forests alters leaf litter structure, moisture, and flammability. *For. Ecol. Manage.* 482, 118860. <https://doi.org/10.1016/j.foreco.2020.118860>.
- McEwan, R.W., Dyer, J.M., Pederson, N., 2011. Multiple interacting ecosystem drivers: toward an encompassing hypothesis of oak forest dynamics across eastern North America. *Ecography* 34 (2), 244–256.
- McShea, W.J., Healy, W.M., 2002. *Oak Forest Ecosystems: Ecology and Management for Wildlife.* Johns Hopkins University Press.
- McShea, W.J., Healy, W.M., Devers, P., Fearer, T., Koch, F.H., Stauffer, D., Waldon, J., 2007. *Forestry matters: decline of oaks will impact wildlife in hardwood forests.* *J. Wildl. Manage.* 71 (5), 1717–1728.
- Melillo, J.M., Aber, J.D., Muratore, J.F., 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63, 621–626.
- Mitchell, R.J., Hiers, J.K., O'Brien, J., Starr, G., 2009. Ecological forestry in the Southeast: understanding the ecology of fuels. *J. Forest.* 107, 391–397.
- Nowacki, G.J., Abrams, M.D., 2008. The demise of fire and “mesophication” of forests in the eastern United States. *BioScience* 58, 123–138.
- Olson, J.S., 1963. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* 44, 322–331.
- Otto, C., Nilsson, L.M., 1981. Why do beech and oak trees retain leaves until spring? *Oikos* 387–390.
- Ribe, J.H., 1973. *Puckerbrush weight tables.* University of Maine, Life Sciences and Agriculture Experiment Station, Orono, ME.
- Scarff, F.R., Westoby, M., 2006. Leaf litter flammability in some semi-arid Australian woodlands. *Funct. Ecol.* 20 (5), 745–752.
- Schweitzer, C.J., Dey, D.C., Wang, Y., 2016. Hardwood-pine mixedwoods stand dynamics following thinning and prescribed burning. *Fire Ecology* 12 (2), 85–104.
- Schwilk, D.W., 2015. Dimensions of plant flammability. *New Phytol.* 206 (2), 486–488.
- Siegert, C.M., Drotar, N.A., Alexander, H.D., 2019. Spatial and temporal variability of throughfall among oak and co-occurring non-oak tree species in an upland hardwood forest. *Geosciences* 9, 405.
- Stottlemeyer, A.D., Shelburne, V.B., Waldrop, T.A., Rideout-Hanzak, S., Bridges, W.C., 2009. Fuel characterization in the southern Appalachian Mountains: an application of Landscape Ecosystem Classification. *Int. J. Wildland Fire* 18 (4), 423. <https://doi.org/10.1071/WF08017>.
- Taylor, B.R., Parkinson, D., Parsons, W.F., 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. *Ecology* 70, 97–104.
- Varner, J.M., Kane, J.M., Kreye, J.K., Engber, E., 2015. The flammability of forest and woodland litter: a synthesis. *Curr. Forest. Rep.* 1 (2), 91–99.
- Varner, J.M., Kane, J.M., Kreye, J.K., Shearman, T.M., 2021. Litter Flammability of 50 Southeastern North American Tree Species: Evidence for Mesophication Gradients Across Multiple Ecosystems. *Frontiers in Forests and Global Change* 153.
- Vose, J.M., Elliott, K.J., 2016. Oak, fire, and global change in the eastern USA: What might the future hold? *Fire Ecol.* 12 (2), 160–179.