EFFECTS OF CANOPY STRUCTURE ON WATER CYCLING: IMPLICATIONS FOR CHANGING FOREST COMPOSITION

**Courtney M. Siegert, Katy E. Limpert, Natasha A. Drotar, Mercedes L. Siegle-Gaither,
Madeline Burton, J. Andrew Lowery, and Heather D. Alexander**

Abstract—In upland oak (*Quercus* spp.) forests of the Eastern United States, shade-intolerant, fire-tolerant oaks are being replaced by shade-tolerant, fire-sensitive species due to changes in forest management and fire regimes. In these mixed-species forests, rainwater redistribution by the forest canopy is determined by tree species traits as well as canopy position. To better understand how shifting forest composition could impact rainwater partitioning, we quantified differences in canopy structure and the resultant net flux of water to forest soils in a series of experiments across the Southeastern United States. Non-oak species had denser canopies than oaks and intercepted more rainwater, reducing throughfall by more than 15 percent. Conversely, stemflow water inputs were more than four times greater beneath non-oaks, which had smoother bark compared to rougher-bark oaks. This study demonstrates the link between aboveground tree structure and interspecific water fluxes. It supports the hypothesis that a shift in forest composition could influence future ecosystem function in southeastern upland oak forests.

INTRODUCTION

Upland oak (*Quercus* spp.) forests in the Eastern United States have been undergoing a shift in composition due to changes in forest management (Abrams 2003). The suppression of the natural fire regime is a driving factor that has led to the proliferation of fire-sensitive species in the understory and midstory that are out-competing fire-tolerant oak species (Nowacki and Abrams 2008)often increasing fire occurrence (e.g., in northern hardwoods. These species, broadly termed "mesophytes," create an understory environment with cooler, damper, and more shaded conditions. This environment in turn is more suitable for survival and succession of mesophytes and less suitable for oak regeneration (Palus and others 2018).

Hypothesized mesophytes, such as red maple (*Acer rubrum*), hickories (*Carya glabra* and *C. ovata*), and winged elm (*Ulmus alata*), tend to be shade-tolerant and exhibit a suite of physical characteristics that may divert more water to soils surrounding these individuals. For example, smooth-bark mesophytes divert more water to stemflow than co-occurring oak species (Alexander and Arthur 2010, Barbier and others 2009). Mesophytes may also have smoother leaf surfaces, which help shed rainwater, thus reducing canopy interception and increasing throughfall to the forest floor (Pypker and others 2005).

Current restoration efforts use prescribed fire to increase light availability to oak seedlings (Fan and others 2012, Vander Yacht and others 2019) under the assumption that dense, mesophytic subcanopy layers are the principal force inhibiting oak regeneration. However, the redistribution of water resources (Alexander and Arthur 2010), leading to changes in moisture and flammability by mesophytes (Dickinson and others 2016, Kreye and others 2013), may be just as important based on preliminary findings and the limited success of restoration activities to date (Arthur and others 2015, Keyser and others 2019). As such, the objectives of this study were to determine how canopy structure influences canopy water partitioning and subsequent soil moisture availability.

MATERIALS AND METHODS

Study Sites

This study summarized findings from two upland oak stands in Mississippi: Sessums Natural Area and Spirit Hill Farm. Sessums Natural Area was located in

---

Author information: Courtney M. Siegert, Associate Professor, Department of Forestry, Mississippi State University, Mississippi State, MS 39762; Katy E. Limpert, Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Burwood, Australia, 3125; Natasha A. Drotar, Department of Forestry, Mississippi State University, Mississippi State, MS 39762; Mercedes L. Siegle-Gaither, Forester, Colorado State Forest Service, Pagosa Springs, CO 81147; Madeline Burton, Department of Forestry, Mississippi State University, Mississippi State, MS 39762; J. Andrew Lowery, Department of Forestry, Mississippi State University, Mississippi State, MS 39762; and Heather D. Alexander, Associate Professor, Mississippi State University, Mississippi State, MS 39762.

Citation for proceedings: Bragg, Don C.; Koerth, Nancy E.; Holley, A. Gordon, eds. 2020. Proceedings of the 20th Biennial Southern Silvicultural Research Conference. e–Gen. Tech. Rep. SRS–253. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southern Research Station. 338 p.

Starkville, MS (33.4247 N, 88.7607 W) and Spirit Hill Farm was located southwest of Holly Springs, MS (34.6661 N, 89.7004 W). Both stands were considered oak-hickory forests with similar basal areas and stem densities, although the specific species distribution was slightly different (table 1). All hickory species were grouped together and termed "hickory," all oak species from the Section *Quercus* were termed "white oaks," and all oak species from the Section *Lobatae* were termed "red oaks."

Measurements

At both sites, a mixture of oak and non-oak species were selected for measurements. Species were selected based on their contrasting physical characteristics (e.g., canopy structure, bark morphology) in different canopy positions (e.g., overstory and midstory). At Sessums Natural Area, 18 trees (3 individuals across 6 species: *C. glabra, C. ovata, Q. alba, Q. falcate, Q. pagoda,* and *Q. stellata)* were monitored from September 2014 through November 2017. At Spirit Hill Farm, 81 trees (9 individuals across 4 species in the overstory: *A. rubrum, C. glabra, Q. alba,* and *Q. stellata;* 9 individuals across 5 species in the midstory: *A. rubrum, C. glabra, Q. alba, Q. stellata,* and *U. alata*) were monitored from October 2017 through November 2018.

Tree structural characteristics including canopy area, basal area, bark thickness, and bark roughness were measured for all study trees and standardized for tree size. Leaf water storage capacity under calm and windy conditions was determined over three replicate leaves of each species using the water displacement method (Llorens and Gallart 2000). Briefly, leaves were weighed, submerged in water, and then weighed again to determine the change in mass (i.e., water retention) on a per unit area basis. Windy conditions were created by shaking each leaf three times after submersion in water prior to weighing. *In situ* study trees were outfitted with stemflow collars constructed from 2.5-cm-inner-

Table 1—Stand conditions at the study sites

Feature	Sessums Natural Area	Spirit Hill Farm
Basal area (m^2 ha^{-1})	Overstory: 33.6 Midstory: 3.4	Overstory: 17.6 Midstory: 4.4
Density (stems ha^{-1})	Overstory: 207 Midstory: 1,636	Overstory: 123 Midstory: 2,608
Dominant oak species		
White oak section	Post oak White oak	Post oak
Red oak section	Cherrybark oak Shumard oak	Southern red oak
Dominant non-oak species	Pignut hickory Shagbark hickory White ash Winged elm	Blackgum Pignut hickory Sweetgum Winged elm
Soil series[a]	Kipling silt loam	Providence silt loam
Precipitation (mm)[b]	1,402	1,460
Temperature (°C)[b]	6.8 (DJF) to 26.6 (JJA)	7.9 (DJF) to 15.1 (JJA)

Blackgum = *Nyssa sylvatica* Marsh., cherrybark oak = *Quercus pagoda* Raf., pignut hickory = *Carya glabra* P. Mil., post oak = *Q. stellata* Wangenh., shagbark hickory = *C. ovata* Mil., Shumard oak = *Q. shumardii* Buck., southern red oak = *Q. falcata* Michx., sweetgum = *Liquidambar styraciflua* L., white ash (*Fraxinus americana* L., white oak (*Q. alba* L., winged elm (*Ulmus alata* Michx.

[a] USDA NRCS (2015).

[b] National Centers for Environmental Information (Arguez and others 2010).

DJF = December, January, February; JJA = June, July, August.

diameter polyethylene tubing cut longitudinally and sealed around the trunk of each tree above the girdling and inoculation site with aluminum nails and silicone caulk. Collars drained into 20-L polyethylene bins and stemflow volume was measured manually. Funneling ratio (FR) is a measure of the contribution of outlying canopy areas to stemflow generation (Herwitz 1986) and was calculated as

$$FR = \frac{SF}{\left(P_g \times BA\right)} \quad (1)$$

where

FR is the funneling ratio, SF is stemflow volume, P_g is gross rainfall as a depth equivalent, and BA is the basal area of the tree.

When FR is greater than 1, the outlying canopy is contributing to additional stemflow production beyond what would be expected by the basal area occupied by the tree trunk alone. Throughfall collectors were constructed from 3.8-L polyethylene collectors fitted with a 12.5-cm-diameter funnel and placed underneath individual tree crowns. Soil moisture was measured at three distances from tree boles (0.5 m, 1.0 m, 1.5 m) and at three depths (3.0 cm, 7.0 cm, 12.0 cm) (FieldScout 150 TDR probe).

Data Analysis

Canopy structural traits and leaf water storage capacity data were normally distributed, thus differences in sample means were tested using analysis of variance. In the overstory, red maple was omitted from statistical analysis due to limited sampling pool (red maple were infrequent in the overstory). Stemflow and throughfall data were not normally distributed, so a generalized linear model was used to determine differences in these variables among species. These tests were performed using the lme4 package (Bates and others 2014) in R version 3.5.1 (R Core Team 2018). Principal components analysis (PCA) was performed on field-measured variables using the prcomp function in R. Principal components with eigenvalues greater than or equal to 1 were retained following the Kaiser criterion.

RESULTS

Tree Structural Traits

In the midstory, oaks had rougher and thicker bark compared to non-oak species (fig. 1a, b) while non-oaks had greater canopy area per unit basal area (fig. 1c). White oak leaves held more water per unit leaf area than non-oaks under calm conditions, but no differences between species were evident during windy (shaken) conditions (fig. 1d).

Canopy Hydrology

In the overstory, hickories and red oaks generated the largest percent stemflow, which was 5.1 and 3.8 times greater than white oaks, respectively (table 2). Overstory hickories were also the most efficient at generating stemflow, with FR values more than two times greater than oaks. In the midstory, all species partitioned approximately the same amount of rainfall into stemflow, although red maple and winged elm were more efficient in stemflow generation relative to their size with FR values of 23.4 and 15.2, respectively (table 2). Over a 1-year period, this is equivalent to an additional 3,000 L m^{-2} of stemflow around overstory hickories and an additional 30,000 L m^{-2} of stemflow around midstory red maple compared to oak species. The order of magnitude difference in midstory stemflow generation can be attributed to the extremely high FR, with all midstory trees being more efficient at generating stemflow over a given basal area (table 2). For throughfall, there were no differences in the percent throughfall partitioning in the overstory ($p = 0.411$), while midstory throughfall under midstory winged elm was more than 10 percent less than under red oaks (table 2).

Principal Components Analysis

Principal components analysis was used to visualize the relationships between tree structural characteristics, canopy hydrology, and soil moisture. In the midstory, two principal components explained 87 percent of the variation (table 3). The distribution of variables across PC1 separated species with large crowns and high funneling ratios (red maple) from species with high throughfall partitioning, rougher bark, and high soil moisture near the tree bole (red oaks). The distribution of variables across PC2 separated species with thick bark (white oaks) and high soil moisture at the crown edge (hickories and winged elm). With regards to non-oak species influence on water availability, red maple was associated with the greatest stemflow partitioning and funneling ratios while hickory was associated with higher soil moisture (fig. 2).

In the overstory, two principal components explained 90 percent of the variation (table 3). The distribution of variables across PC1 separated species with high throughfall partitioning and rough and thick bark (red oaks) from species with high soil moisture, especially at the crown edge (red maple). PC2 separated species with high stemflow partitioning and funneling ratios (hickories) from species with high leaf water storage capacities (white oaks). In the overstory, hickories were correlated with the greater stemflow production while red maples were correlated with higher soil moisture, opposite of the trends observed in the midstory for these species (fig. 2).

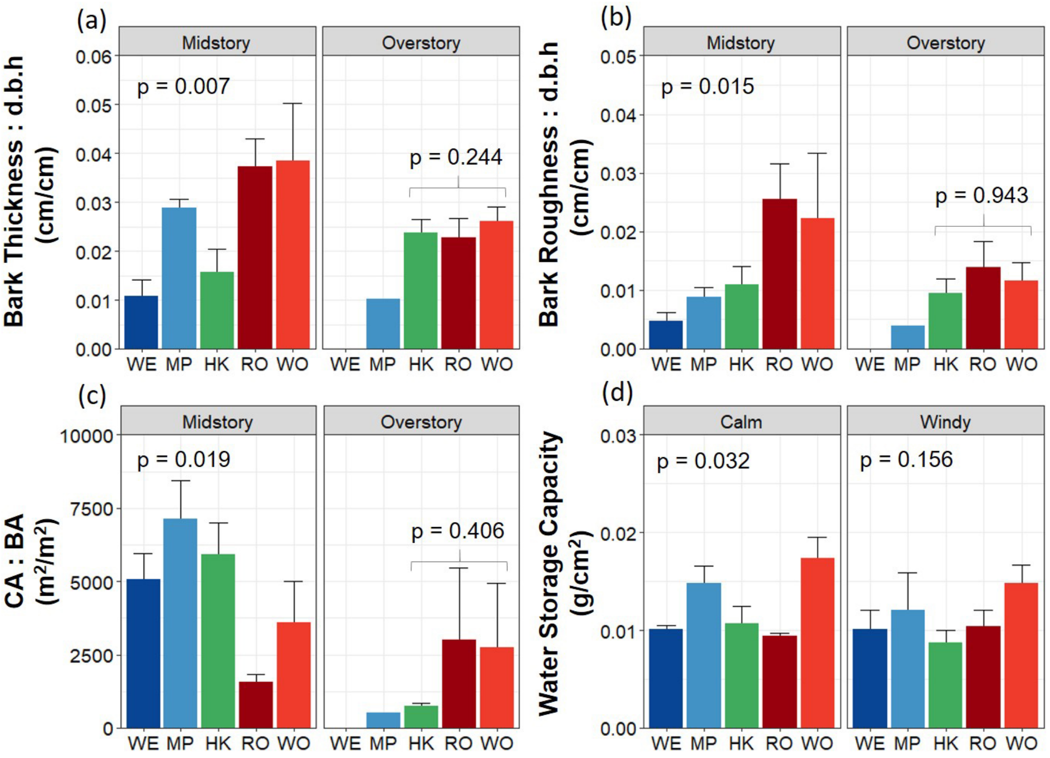

Figure 1—Barplot with standard errors for midstory and overstory tree characteristics including (a) bark thickness standardized to diameter at breast height (d.b.h.), (b) bark roughness standardized to d.b.h., (c) canopy area (CA) standardized to basal area (BA), and (d) leaf water storage capacity under calm and windy (shaken) conditions. WE = winged elm, MP = red maple, HK = hickory, RO = red oak, WO = white oak.

Table 2—Mean canopy hydrology fluxes with standard errors for overstory and midstory species

Fluxes	Red maple	Hickory	Winged elm	Red oaks	White oaks
Overstory					
Stemflow (%)	0.35 ± 0.05 b	0.81 ± 0.08 a	-	0.61 ± 0.05 a	0.16 ± 0.01 c
Stemflow (FR)	0.95 ± 0.14 bc	2.45 ± 0.16 a	-	1.62 ± 0.11 b	0.87 ± 0.07 c
Throughfall (%)	77.0 ± 1.37 a	79.4 ± 0.79 a	-	80.0 ± 0.77 a	79.1 ± 0.98 a
Midstory					
Stemflow (%)	0.42 ± 0.04 a	0.32 ± 0.02 a	0.27 ± 0.04 a	0.22 ± 0.03 a	0.35 ± 0.06 a
Stemflow (FR)	23.37 ± 2.64 a	7.10 ± 0.50 b	15.15 ± 3.55 ab	3.32 ± 0.55 b	6.94 ± 1.38 b
Throughfall (%)	78.3 ± 1.53 ab	79.1 ± 2.60 ab	75.9 ± 1.52 b	86.3 ± 3.41 a	80.4 ± 1.61 ab

FR = funneling ratio.

Winged elm were not observed in the overstory.

Means in a row followed by the same letter are not statistically different.

Table 3—Eigenvector loadings from principal components analysis

	Midstory		Overstory	
Variable	PC1	PC2	PC1	PC2
Variance explained (%)	63.95	22.99	56.76	34.07
Canopy area:basal area	-0.39	0.06	0.23	0.33
Bark thickness:d.b.h.	0.22	-0.57	0.36	0.18
Bark roughness:d.b.h.	0.36	-0.35	0.36	0.15
Stemflow (%)	-0.32	-0.40	0.19	-0.45
Funneling ratio	-0.37	-0.05	0.24	-0.39
Throughfall (%)	0.38	-0.17	0.40	0.02
VWC @ bole	0.36	-0.01	-0.21	0.40
VWC @ mid-canopy	0.32	0.22	-0.14	0.49
VWC @ edge	0.24	0.55	-0.40	0.02
Leaf water storage – calm	-	-	-0.36	-0.18
Leaf water storage – windy	-	-	-0.28	-0.24

d.b.h. = diameter at breast height, VWC = volumetric water content.

Leaf water storage experiments were only performed on leaves from overstory trees.

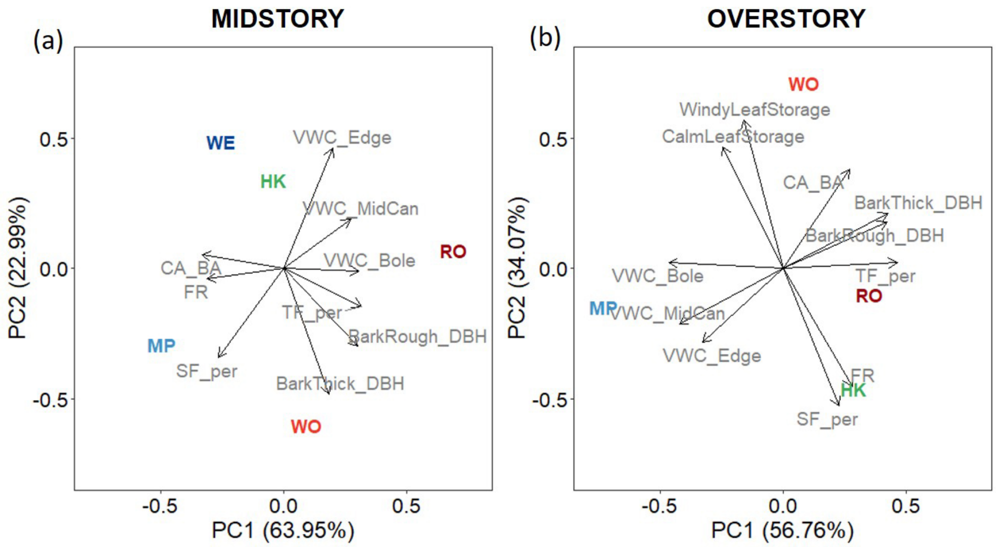

Figure 2—Principal components analysis of midstory and overstory tree traits, water partitioning, and soil moisture where CA_BA is canopy area per basal area; FR is funneling ratio, SF_per is percent stemflow partitioning, TF_per is percent throughfall partitioning, VWC_Bole is volumetric water content at tree bole, VWC_MidCan is volumetric water content at the mid-canopy, VWC_Edge is volumetric water content at the canopy edge, BarkRough_DBH is bark roughness standardized for d.b.h., BarkThick_DBH is bark thickness standardized for d.b.h., CalmLeafStorage is leaf water storage capacity under calm conditions, and WindyLeafStorage is leaf water storage capacity under windy (shaken) conditions. WE = winged elm, MP = red maple, HK = hickory, RO = red oak, WO = white oak.

DISCUSSION

Non-oak species including red maple, hickory, and winged elm have physical characteristics that facilitate mesic conditions in upland oak forests. These mesophytes have thinner and smoother bark compared to oak species, which enhances stemflow generation and consequently greater distribution of water in the vicinity of tree stems. Smoother bark provides uninterrupted flowpaths for stemflow (McGee and others 2019, Siegert and Levia 2014), in conjunction with thinner bark, which has lower water storage capacity (Levia and Herwitz 2005, Van Stan and others 2016). In contrast, the canopy area of mesophytes was greater than that of oak species, especially in the midstory. As such, denser mesophyte crowns will provide additional foliar surfaces for canopy interception, which serves to limit throughfall partitioning (Vrugt and others 2003). However, denser crowns may also reduce light availability to the forest floor, which simultaneously limits survival of shade-intolerant oaks (Larsen and Johnson 1998) and reduces forest floor evaporation.

The trade-off between increased stemflow and decreased throughfall underneath mesophyte crowns appears to favor wetter soil moisture conditions, but the strength of this response is not consistent across species. Instead, the net effect on soil moisture is likely determined by physical traits that change with tree size and canopy position. Our results suggest that even though red maple is capable of generating more stemflow in the midstory, hickory and winged elm are correlated with wetter soil conditions. In the overstory, the opposite is true. Hickories generated the greatest quantities of stemflow while red maple were correlated with the wettest soils. However, there is a caveat to the findings of this study: soil moisture is not the same as fuelbed moisture. It is likely that the same physical traits that lead to higher soil moisture will also maintain high moisture levels in the fuelbed, but there are suite of other characteristics that are important in fuelbed moisture retention (bulk density, specific leaf area, depth, etc.) (Dickinson and others 2016, Varner and others 2015). As such, this study provides preliminary mechanisms in which species-specific aboveground structures alter the forest floor underneath individual tree crowns.

CONCLUSIONS

In this study, we empirically demonstrated the link between aboveground tree architecture and the effects on the redistribution of rainwater to the forest floor. This relationship highlights another pathway in the complex process of mesophication through which non-oak species are creating stand-level conditions unsuitable for natural oak regeneration.

ACKNOWLEDGMENTS

This material is based upon work that is supported by the National Institution of Food and Agriculture, U.S. Department of Agriculture, McIntire Stennis capacity grant # MISZ-032100. Any opinions, findings, conclusions, or recommendations expressed in this publication are those of the author(s) and do not necessarily reflect the view of the U.S. Department of Agriculture.

LITERATURE CITED

Abrams, M. D. 2003. Where has all the white oak gone? BioScience. 53: 927–939.

Alexander, H. D.; Arthur, M. A. 2010. Implications of a predicted shift from upland oaks to red maple on forest hydrology and nutrient availability. Canadian Journal of Forest Research. 726: 716–726.

Arguez, A.; Durre, I.; Applequist, S. [and others]. 2010. NOAA's U.S. climate normals (1981-2010). NOAA National Centers for Environmental Information. https://data.nodc.noaa.gov/cgi-bin/iso?id=gov.noaa.ncdc:C00824#

Arthur, M.A.; Blankenship, B.A.; Schörgendorfer, A. [and others]. 2015. Changes in stand structure and tree vigor with repeated prescribed fire in an Appalachian hardwood forest. Forest Ecology and Management. 340: 46–61.

Barbier, S.; Balandier, P.; Gosselin, F. 2009. Influence of several tree traits on rainfall partitioning in temperate and boreal forests: a review. Annals of Forest Science. 66: 602–602.

Bates, D.; Mächler, M.; Bolker, B.; Walker, S. 2014. lme4: linear mixed-effects models using Eigen and S4. R package version 1.1-7.

Dickinson, M.B.; Hutchinson, T.F.; Dietenberger, M. [and others]. 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. 30 p.

Fan, Z.; Ma, Z.; Dey, D.C.; Roberts, S.D. 2012. Response of advance reproduction of oaks and associated species to repeated prescribed fires in upland oak-hickory forests, Missouri. Forest Ecology and Management. 266: 160–169.

Herwitz, S.R. 1986. Infiltration-excess caused by stemflow in a cyclone-prone tropical rainforest. Earth Surface Processes and Landforms. 11: 401–412.

Keyser, T.L.; Greenberg, C.H.; McNab, W.H. 2019. Season of burn effects on vegetation structure and composition in oak-dominated Appalachian hardwood forests. Forest Ecology and Management. 433: 441–452.

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. Ecological Applications. 23: 1976–1986.

Larsen, D.R.; Johnson, P.S. 1998. Linking the ecology of natural oak regeneration to silviculture. Forest Ecology and Management. 106: 1–7.

Levia, D.F.; Herwitz, S.R. 2005. Interspecific variation of bark water storage capacity of three deciduous tree species in relation to stemflow yield and solute flux to forest soils. Catena. 64: 117–137.

Llorens, P.; Gallart, F. 2000. A simplified method for forest water storage capacity measurement. Journal of Hydrology. 240: 131–144.

McGee, G.G.; Cardon, M.E.; Kiernan, D.H. 2019. Variation in *Acer saccharum* Marshall (sugar maple) bark and stemflow characteristics: implications for epiphytic bryophyte communities. Northeastern Naturalist. 26: 214.

Nowacki, G.J.; Abrams, M.D. 2008. The demise of fire and “mesophication” of forests in the eastern United States. BioScience. 58: 123-138.

Palus, J.D.; Goebel, P.C.; Hix, D.M.; Matthews, S.N. 2018. Structural and compositional shifts in forests undergoing mesophication in the Wayne National Forest, southeastern Ohio. Forest Ecology and Management. 430: 413–420.

Pypker, T.G.; Bond, B.J.; Link, T.E. [and others]. 2005. The importance of canopy structure in controlling the interception loss of rainfall: examples from a young and an old-growth Douglas-fir forest. Agricultural and Forest Meteorology. 130: 113–129.

R Core Team. 2018. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org/.

Siegert, C.M.; Levia, D.F. 2014. Seasonal and meteorological effects on differential stemflow funneling ratios for two deciduous tree species. Journal of Hydrology. 519: 446–454.

U.S. Department of Agriculture, Natural Resources Conservation Service [USDA NRCS]. 2015. Web soil survey. https://websoilsurvey.sc.egov.usda.gov/App/HomePage.htm.

Van Stan, J.T.; Lewis, E.S.; Hildebrandt, A. [and others]. 2016. Impact of interacting bark structure and rainfall conditions on stemflow variability in a temperate beech-oak forest, central Germany. Hydrological Sciences Journal. 61: 2071–2083.

Vander Yacht, A.L.; Keyser, P.D.; Barrioz, S.A. [and others]. 2019. Reversing mesophication effects on understory woody vegetation in mid-southern oak forests. Forest Science. 65: 289–303.

Varner, J.M.; Kane, J.M.; Kreye, J.K.; Engber, E. 2015. The flammability of forest and woodland litter: a synthesis. Current Forestry Reports. 1: 91–99.

Vrugt, J.A.; Dekker, S.C.; Bouten, W. 2003. Identification of rainfall interception model parameters from measurements of throughfall and forest canopy storage. Water Resources Research. 39: 1251.