A comparison of witness tree and contemporary compositions for old-growth forests at Savage Mountain, Maryland, and secondary forests of the northern Allegheny Mountains1

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A comparison of witness tree and contemporary compositions for old-growth forests at Savage Mountain, Maryland, and secondary forests of the northern Allegheny Mountains[1]

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Abstract. We used historical and contemporary survey data to assess the dynamics in two old-growth forests at Savage Mountain, Maryland, *versus* secondary forests from the surrounding landscape of the northern Allegheny Mountain Plateau (AMP). This is the first published compilation of witness trees from western Maryland. The old-growth forests on Savage Mountain, Maryland, are presently dominated by mixed oak (*Quercus* spp. L.; 42%), red maple (*Acer rubrum* L.), and black birch (*Betula lenta* L.). Witness trees (1620–1825) from Savage Mountain were dominated by mixed oak (55%), hickory (*Carya* spp.; 18%), and chestnut (*Castanea dentata* (Marsh.) Borkh.; 10%), and lacked red maple and black birch. The witness trees of the AMP in Pennsylvania were dominated by mixed oak (41%), pine (*Pinus* spp. L.; 12%), maple (11%), chestnut (10%), and hickory (6%). Currently the AMP is dominated by mixed oak (25%), red maple (25%), and black cherry (*Prunus serotina* Ehrh.; 11%). The old-growth stands on Savage Mountain are similar to its witness trees in regard to oak species and have greater oak dominance than the AMP secondary forests. This suggests that old-growth retains more oak compared with cut-over forests. However, old-growth on Savage Mountain has a higher density of red maple and black birch when compared to the AMP. Our research illustrates differences in forest dynamics and oak dominance between old-growth and second-growth forests that have important implications for the sustainability of native forests.

Key words: Allegheny Mountains, fire, oak forests, red maple, succession

Witness trees are an important direct source of quantitative data based on surveys conducted in the period 1600–1900. Land surveyors marked and recorded witness (*e.g.*, warrant, bearing, corner) trees to identify property corners and boundaries during the early European settlement of the eastern United States (Lutz 1930, Bourdo 1956). The original land surveys along the Appalachian Mountains and coastal regions from Maine to Georgia were primarily conducted using metes and bounds of property boundaries, which eventually developed into a more regular and systematic land partitioning following the Northwest Ordinance of 1785. These data can be used in conjunction with contemporary surveys of old-growth forests and palaeoecological analysis to assess the composition of forests prior to European settlement (Lutz 1930, Bourdo 1956, Abrams and Downs 1990, Abrams and Ruffner 1995, Delcourt *et al*. 1998, Ruffner and Abrams 1998, Black and Abrams 2001, Foster *et al*. 2002). Despite certain biases and inconsistencies, witness tree data remain an important resource in historical ecological studies and reveal consistent species patterns that accord with other lines of evidence, such as historical accounts (Bourdo 1956, Hanberry *et al*. 2020, Hanberry 2021).

Witness trees have been helpful in quantifying large-scale changes in tree composition over time. When witness tree data are compared with modern-day forests, researchers can assess how and why they have changed over several centuries or more. Applications include impacts of Native American land use and subsequent European settlement and land-clearing activities as well as helping map historic fire patterns and landscape flammability (Abrams 2010, Thomas-Van Gundy *et al*. 2015, Hanberry *et al*. 2018).

Witness tree data have been compiled and analyzed for much of the northern half of the eastern United States (Cogbill 2000). One exception to this is the state of Maryland, where only one witness tree paper from the Eastern Shore has been published (Briand and Folkoff 2019). No

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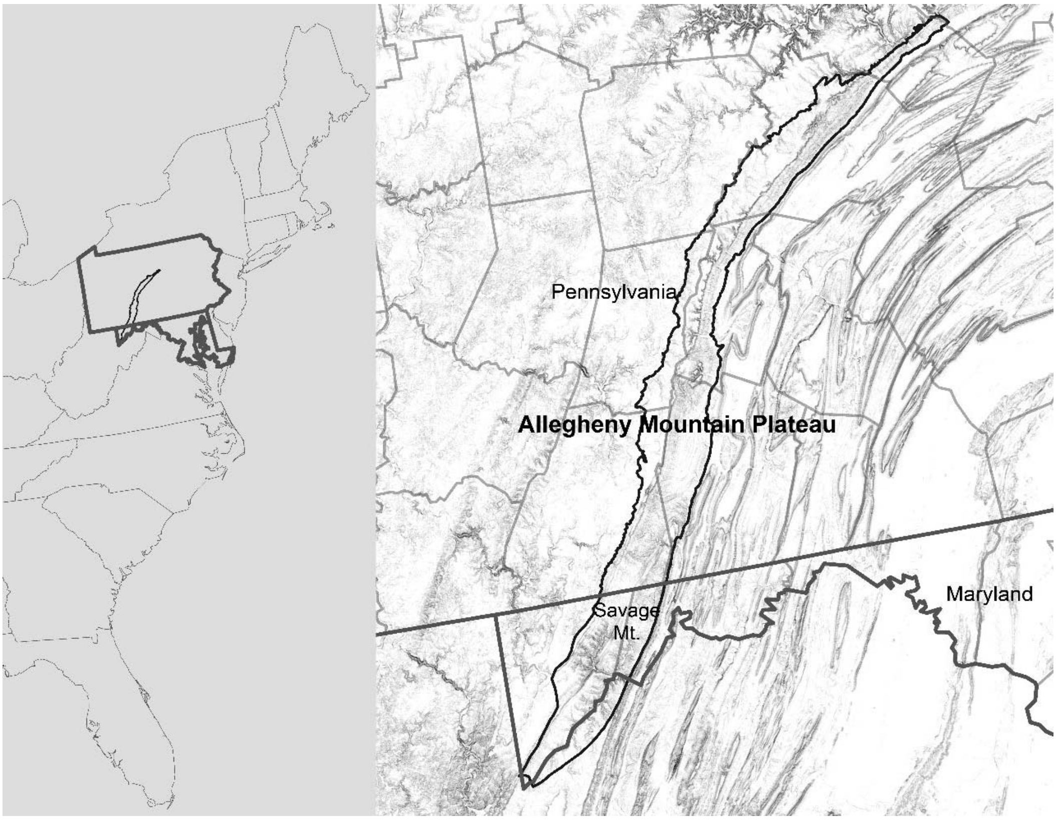

Fig. 1. The Allegheny Mountain Plateau ecological subsection in Pennsylvania and Maryland, which contains Savage Mountain.

witness tree data have been compiled for the mountainous regions of western Maryland and none exist on historical databases, such as PalEON (http://paleonproject.org/). Western Maryland contains a well-documented old-growth forest on Savage Mountain, which was the location of a fire history and dendroecological study spanning four centuries (Shumway *et al*. 2001). Savage Mountain extends into southwestern Pennsylvania, where historical witness tree records are more accessible. Our purposes for this study are as follows:

(a) Evaluate the contemporary composition of two old-growth forests on Savage Mountain, Maryland, and Forest Inventory and Analysis (FIA) records for the Allegheny Mountain Plateau (AMP) in Maryland and Pennsylvania (Fig. 1).
(b) Compile the witness tree data for Savage Mountain, Maryland, and the AMP in Pennsylvania.
(c) Compare and contrast witness tree and contemporary forest composition for old-growth *versus* secondary forests across the regional landscape.

Study Area and Methods. The Allegheny Mountains represent the high-eastern margin (subsection) of the Allegheny Plateau running southwesterly from north central Pennsylvania to southeastern West Virginia (Fig. 1). Fenneman (1938) reported the subsection as a mixture of mildly folded ridges in anti-, mono-, and synclinal structures separated by dendritically eroded cuesta uplands. Our specific study area is located on Big Savage Mountain in Garrett and Allegany counties, Maryland, running northward into Somerset and Bedford counties, Pennsylvania (39°30′–40°00′N, 79°15′–78°45′W). It is located on the southern terminus of Big Savage Mountain in the Savage River State Forest in the Allegheny Mountain section of the Appalachian Plateau.

Elevation ranges from about 600 to 670 m. This ridgeline area is characterized by extensive sandstone outcroppings and many areas constitute periglacial scree-talus slopes (Fenneman 1938). Although the area was not glaciated, these rock outcrops constitute periglacial screes. Soils belong to the DeKalb-Gilpin-Cookport association, which are very stony, acidic soils derived largely in residuum from sandstone. Ericaceous shrubs dominate the ground layers on such sites. The Allegheny Mountains have a wet and cool climate, with approximately 98 cm of precipitation per year with about 20% falling as snow, an annual average temperature of 7 °C to 11 °C, an average annual maximum temperature of 14 °C to 17 °C, an average annual minimum temperature of 2 °C to 3 °C, and a growing season of 126 to 155 days in the study area (Cleland *et al*. 1997, Thomas-Van Gundy 2014).

Braun (1950) related the highly varied forest cover of this subsection to the complex erosional surfaces driven by soil and parent material types and ages. Overall, she mapped the larger area as mixed-mesophytic forest but specifically identified localized communities dominated strongly by mixed oak on upper slopes and ridgetops of western Maryland. Survey records indicate that the area was not settled until 1789 (Schlosnagle 1978), and therefore, we designated pre-1780 as the presettlement period. The area appears free of historical logging activity and was acquired as a Maryland State Forest in 1929.

Witness Trees. Early survey notes for Savage Mountain, including northeast Garrett and western Allegany counties, Maryland, were obtained from the Maryland Hall of Records. Maryland counties are not divided into townships but use municipalities instead. The witness tree data were compiled for surveys recorded from 1774 to 1796. Several tracts were initially patented in 1774 and then 50-acre (20 ha) parcels were surveyed as military lots and recorded in 1796. A total of 321 witness trees were recorded, and relative abundance calculated by species. Recorded trees are ≥ 8 cm diameter at breast height (DBH).

For the Pennsylvania side of the AMP ecological subsection, we determined historical percentage of composition of tree genera surveyed during Euro-American settlement (circa 1620–1825) estimated for an 8-km grid (PalEON project, Paciorek *et al*. 2016). Recorded trees are ≥ 8 cm DBH. Grids help resolve the issue of using the irregular metes and bounds surveys. However, historical tree surveys typically contain many more trees than contemporary national surveys. The gridded witness tree data are to genus only.

Old-growth Forest Surveys at Savage Mountain, Maryland. Twenty sampling plots were randomly located along transects in each of the two old-growth forest interiors (Coleman Hollow and South Savage Mountain) of approximately 35 ha each. A 400-m^2 circular plot was used at each sampling point to inventory all tree species ≥ 8 cm DBH. Species and diameter were recorded for all "in" trees. For each forest, tree data were used to calculate a relative importance value from the average of the relative frequency, relative density, and relative dominance (basal area).

Current Forest Surveys of the Allegheny Mountain Plateau. For the entirety of the AMP ecological subsection in Maryland and Pennsylvania, we used 128 United States Department of Agriculture Forest Service FIA survey plots during the most recent inventories of 2009 to 2015 (FIA 2021, Bechtold and Patterson 2005) to quantify current forest composition. We selected all records for trees ≥ 8 cm DBH, and we accounted for the difference between survey plot area for trees ≥ 12.7 cm DBH and trees ≤ 12.7 cm DBH by expanding the number of trees ≤ 12.7 cm by the plot area ratio (*i.e.*, 12.45 m) The FIA plots typically occur every 2,500 ha, and thus, FIA surveys provide landscape-scale estimates.

Results. The Coleman Hollow old-growth forest at Savage Mountain, Maryland, is presently dominated by *Acer rubrum* L. (red maple) with an importance value of 24.3%, followed by *Quercus montana* Willd. (chestnut oak), *Quercus alba* L. (white oak), *Quercus rubra* L. (red oak), and *Quercus velutina* Lam. (black oak) (Table 1). South Savage Mountain is dominated by chestnut oak (20.4% importance), followed by *Betula lenta* L. (black birch), red oak, red maple, black oak, and white oak. A comparison of forest surveys at Savage Mountain with present-day FIA data for the AMP reveals a higher importance of oak at Savage Mountain, 41.8% *versus* 25.5% in the AMP (Table 2). This is mainly due to the dominance of chestnut oak at Savage Mountain. Black birch and red maple have a higher combined importance at Savage Mountain *versus* AMP (50.1% and 31.3%, respectively). In contrast,

Table 1. Relative stand density (RDN), dominance (RBA), frequency (RFQ), and importance value (RIV) by species, stand totals, and number of plots encountered for Coleman Hollow and South Savage forests at Savage Mountain in western Maryland. Other species included ironwood *Carpinus caroliniana* Walter, *Acer pensylvanicum* L., and *Amelanchier laevis* Wiegand.

	Coleman Hollow				South Savage			
Species	RDN (stems ha^{-1})	RBA (m^2 ha^{-1})	RFQ (no. of plots)	RIV (%)	RDN (stems ha^{-1})	RBA (m^2 ha^{-1})	RFQ (no. of plots)	RIV (%)
Quercus alba	12.2	31.1	15.8	19.7	3.8	9.4	5.9	6.4
Q. montana	22.3	28.1	19.7	23.4	11.0	33.4	16.7	20.4
Q. rubra	8.5	18.2	14.5	13.7	14.8	19.4	16.7	17.0
Q. velutina	5.3	12.5	9.2	9.0	6.2	18.6	8.3	11.0
Acer rubrum	41.5	6.4	25.0	24.3	23.9	7.5	19.0	16.8
Betula lenta	5.3	2.4	6.6	4.8	29.2	9.1	16.7	18.3
Carya spp.	1.1	1.0	2.6	1.6	1.9	0.4	3.6	2.0
Sassafras albidum	3.2	0.3	5.3	2.9	5.7	1.3	6.0	4.3
Other	0.5	0.04	1.3	0.6	3.3	0.8	7.1	3.8
Total	472.2	39.3	76		525.0	44.0	84	

AMP has a higher density of *Prunus serotina* (black cherry) and *Pinus* (pine).

Witness trees at Savage Mountain were dominated by white oak (26.5%), followed by *Carya* spp. (hickory), black oak, chestnut oak, and *Castanea dentata* (chestnut) (Table 2). Witness tree data in the AMP of Pennsylvania were dominated by oak (41.2%), followed by pine, maple, and chestnut (Table 2). The main differences in witness trees between Savage Mountain and the AMP were the greater presence of pine and maple in the AMP in Pennsylvania.

A comparison of witness trees with contemporary surveys indicated the loss of chestnut, oak, and hickory in both study areas. Oak averaged 55% and 41% in the witness tree record of Savage Mountain and the AMP, respectively, *versus* 42% and 21% present-day. Hickory declined from 17% to 2% at Savage Mountain. In contrast, maple increased from 0.3% to 32% and black birch from 0% to 18% at Savage Mountain, while *Nyssa sylvatica* Marshall (blackgum) and black cherry increased from 0% to 2% and 10%, respectively, in the AMP.

Table 2. Relative density of witness trees and contemporary survey data for Savage Mountain, Maryland, and the Allegheny Mountain Plateau/M221Bf (AMP) in western Maryland and Pennsylvania. Witness tree data for the AMP are to genus only and do not contain data for Maryland.

	Witness trees (%)		Contemporary (%)	
Species	Savage Mountain, MD	AMP, PA	Savage Mountain, MD	AMP, PA and MD
Quercus alba	26.5		7.8	3.0
Q. montana	11.0		16.4	6.1
Q. velutina	11.8		5.8	0.9
Q. rubra	5.2		11.8	9.3
Quercus		41.2		
Pinus		12.4		3.3
Carya	17.6	5.7	1.5	1.6
Castanea dentata	10.3	10.4		
Acer rubrum			32.2	25.3
Acer		10.7		
Betula lenta		1.8	17.9	6.9
Prunus serotina		0.4		10.6
Sassafras albidum			4.5	3.4
Nyssa sylvatica		0.3		2.0
Others*	17.6	17.1	2.1	27.6
No. of trees	321	3,888	498	2,848

* Other species mainly include *Fraxinus americana*, *Robinia pseudoacacia*, *Picea abies*, *Quercus coccinea*, *Ostrya virginiana*, *Tsuga canadensis*, *Betula alleghaniensis*, *Fagus grandifolia*, and *Magnolia acuminata*.

Discussion. Loss of fire-tolerant oaks and increase in red maple and other mesophytes, from pre-European settlement to the present day, in this study corresponds with similar trends throughout most of the eastern United States (Nowacki and Abrams 2008, Thompson et al. 2013). Given current management and ecological conditions the loss of pyrogenic trees (*e.g*., oak, hickory, pine) and continued expansion of later successional tree species (*e.g*., red maple) is nearly ubiquitous (Abrams 1998, Fei and Steiner 2007). Periodic burning prior to and catastrophic land clearing and fires after European settlement were arguably key factors promoting oak-hickory and limiting mesophytic species in eastern forest stands (Shumway *et al*. 2001, Aldrich *et al*. 2009, Howard *et al*. 2021). This changed after fire suppression in the early 20th century, which facilitated the increase in mesophytic and later-successional, shade-tolerant trees (Abrams 2010, Hanberry *et al*. 2020). The clear-cut and catastrophic-fire era also resulted in the deconiferization of northeastern forests; thus the loss of pine in our AMP study area (Whitney 1990, 1994; Nowacki and Abrams 2015; Abrams and Nowacki 2016).

Another mesophytic species, black birch, increased from pre-European settlement to the present day. Black birch has also increased across its range, perhaps corresponding to the demise of chestnut from the blight and hemlock (*Tsuga* canadensis (L.) Carrière) due to the hemlock woolly adelgid (*Adelges tsugae* Annand; Shumway *et al*. 2001, Orwig and Foster 1998). Black birch is also highly competitive on north-facing upper slopes and ridges (Nowacki and Abrams 1992) and is benefitting from oak decline on a wide range of sites. Repeated gypsy moth defoliation and eventual death of overstory oaks has also promoted black birch (Kegg 1971, Hix *et al*. 1980). However, the low shade tolerance and competitive ability of black birch may limit future increases in eastern forests (Leak 1958). The AMP saw a slight increase in shade-tolerant blackgum, from limited presence to 2% of all trees, which will likely continue to slowly increase in eastern forests (Abrams 2007). A large increase in blackgum in the 1930s coincided with fire suppression at Catoctin Mountain in north-central Maryland (Howard et al. 2021). Blackgum is unique in the combination of being both shade-tolerant and resistant to fire from its thick bark and sprouting ability, including root suckers. Thus, it can maintain itself in pyrogenic and nonpyrogenic forests, despite its inherently slow growth and fecundity (Abrams 2007). The large post-logging increase in the disturbance-oriented black cherry in the AMP is consistent with previous studies, although this trend may be reversed due to its diminished establishment, growth, and survival in recent decades (Nowacki and Abrams 1992, Royo *et al*. 2021).

Our previous research at Savage Mountain reported a very frequent pre-European and early European settlement fire return interval of approximately 8 yr (Shumway *et al*. 2001). Pine trees on Catoctin Mountain, Maryland, had a mean fire interval of 5.47 yr between 1702 and 1951 (Howard *et al*. 2021). Prior to European settlement, burning of the forest understory was a common and long-term practice of Native Americans, including at Savage Mountain, as evidenced by archaeological and anthropological records and artifacts, accounts of early settlers, and paleoecological charcoal and fire scar studies (Day 1953, Abrams 1992, Whitney 1994, Foster *et al*. 2002, Abrams *et al*. 2022). In northeastern oak forests, Native American burning facilitated travel, improved visibility in the forest, increased browse for game, increased berry and mast production, and cleared and maintained land for agricultural fields, as well as improved hunting, plus other uses (Patterson and Sassaman 1988, Williams 2004, Abrams and Nowacki 2008). The high frequency of surface burning perpetuated oak and hickory, as well as pine, all of which are particularly well adapted to reproduce and grow in high light conditions. Characteristics of oaks and hickories that allow them to be so well adapted to fire and other disturbances are thick bark, resprouting ability, high root:shoot ratios of growth, and the ability to compartmentalize wounds (Lorimer 1985, Abrams 1996). These characteristics apply to most eastern pine species, although sprouting is uncommon.

The contemporary survey data from the old-growth forests on Savage Mountain are more similar to the witness tree record in regard to oak species, but less similar in regard to red maple and black birch, when compared with the regional AMP data. The AMP also has lower oak dominance in present-day forests than that on Savage Mountain, which may be explained by the extensive cutting of forests throughout the AMP. Large increases in red maple and black birch on

Savage Mountain may be explained by the chestnut blight and suppression of fire after 1940 (Shumway *et al*. 2001). However, old-growth and second-growth stands on xeric sites in the Ridge and Valley Province of central Pennsylvania and western Maryland have resisted mesophytic species invasion (Nowacki and Abrams 1992, Heeter *et al*. 2019).

Following the extirpation of Native Americans in the eastern United States, European settlement brought on intensive land clearing and exploitation that started in the late 1700s, peaked between 1870 and 1930, and moved from east to west (Ruffner and Abrams 1998, 2002; Stambaugh *et al*. 2018). Prior to 1850, extensive logging on the Allegheny Plateau was typically limited to small sawmills in most towns where white pine was highly favored and areas of charcoal iron production (Whitney 1990, 1994; MacCleery 1992). The increasing demands for timber led to the large-scale commercialization of the forest industry by the middle of the 19th century, including steam-powered saws and railroad logging. Logging escalated, leading to the height of the clear-cut era from 1850 to 1920. The original forests were extensively cut on nearly all but the most difficult sites. In addition, a large loss of forest area to land clearing (agriculture) occurred during this period across most eastern states (Whitney 1994). Areas left in old-growth forests totaled less than 0.5%. The "Great Cutover" produced extensive stump-lands covered in logging debris (slash), which resulted in catastrophic wildfires, which, in extent and intensity were not experienced in the original forest (Pyne 1984). Extensive cutting of forests, the charcoal iron industry, mining, and catastrophic wildfires in the early history of European settlement apparently maintained or elevated fire levels and pyrogenic vegetation in most locations of the eastern United States (Abrams 2010). Exceptions to this are the loss of chestnut in the early 1900s from chestnut blight and the loss of conifer species (deconiferization) due to their inability to compete with hardwoods that can sprout after logging and fire (pitch pine, *Pinus rigida* Mill., being the exception). Nonetheless, catastrophic wildfires ushered in the fire suppression (Smokey Bear) era in the United States starting in the 1930s (Nowacki and Abrams 2008, Abrams 2010). Fires in the eastern United States became very infrequent and highly localized after the 1930s.

One of the most dramatic changes that has occurred in forests of eastern North America during the 20th century is the increase in red maple, as evidenced in this and other studies (Abrams 1998, Nowacki and Abrams 2015). Red maple has become nearly ubiquitous across most sites, which is in stark contrast to the rather limited distribution of red maple reported in pre-European settlement forests (Abrams and Ruffner 1995). The increase in red maple is thought to be related, at least in part, to the exclusion of fire in most forests, particularly those dominated by oak and pine, and its being avoided by loggers during the major clear-cut era from 1870 to 1930. The increase in red maple and other shade-tolerant, nonpyrogenic species is resulting in the "mesophication" of eastern forests (Nowacki and Abrams 2008). This results in cooling, dampening, and reduced flammability of the ground layer in many eastern oak forests, increasing the difficulty of using prescribed fire. Low- to moderate-intensity understory fire is needed for the long-term sustainability of most eastern oak and pine forests because it is effective in eliminating fire-sensitive, shade-tolerant, mesophytic trees species, while creating the proper light and forest floor conditions for oak seedlings (and other pyrophiles) to regenerate and recruit into the canopy (Brose 2014, Hanberry et al. 2020).

The results of this study help confirm that AMP forests have changed from pyrogenic to more mesophytic conditions following the fire suppression policies of the Smokey Bear era and, perhaps, accelerated succession from extensive forest cutting and the chestnut blight (Keever 1953, Abrams and Downs 1990, Abrams and Nowacki 1992, Fei *et al*. 2005). This has led to a decline of several historically dominant trees in the AMP and throughout much of the eastern United States, as well as the increase in other tree species that limit the sustainability of eastern oak-hickory-pine forests. This study also demonstrates important differences in the long-term dynamics of old-growth *versus* second-growth forests in the region, with old-growth forests maintaining a greater oak component, as well as the value of comparing witness tree and contemporary survey data.

Literature Cited

Abrams, M. D. 1992. Fire and the development of oak forests. Bioscience 42: 346–353.

Abrams, M. D. 1996. Distribution, historical development and ecophysiological attributes of oak species in the eastern United States. Annales des Sciences Forestieres 53: 487–512.

Abrams, M. D. 1998. The red maple paradox. BioScience 48: 355–364.

Abrams, M. D. 2007. Tales from the blackgum: A consummate subordinate tree. BioScience 54: 347–359.

Abrams, M. D. 2010. Native Americans, Smokey Bear and the rise and fall of eastern oak forests. Penn State Environmental Law Review 18(2): 141–154.

Abrams, M. D. and J. A. Downs. 1990. Successional replacement of old-growth white oak by mixed-mesophytic hardwood species in southwestern Pennsylvania. Canadian Journal of Forest Research 20: 1864–1870.

Abrams, M. D. and G. J. Nowacki. 1992. Historical variation in fire, oak recruitment, and post-logging accelerated succession in Pennsylvania. Bulletin of the Torrey Botanical Club 119: 19–28.

Abrams, M. D. and G. J. Nowacki. 2008. Native Americans as active and passive promoters of mast and fruit trees in the eastern USA. Holocene 18: 1123–1137.

Abrams, M. D. and G. J. Nowacki. 2016. An interdisciplinary approach to better assess global change impacts and drought vulnerability on forest dynamics. Tree Physiology 36: 421–427.

Abrams, M. D. and C. M. Ruffner. 1995. Physiographic analysis of witness tree distribution (1765–1798) and present forest cover through north central Pennsylvania. Canadian Journal of Forest Research 25(4): 659–668.

Abrams, M. D., G. Nowacki, and B. Hanberry. 2022. Oak forests and woodlands as indigenous landscapes in the eastern United States. Journal of the Torrey Botanical Society 149: 101–121.

Aldrich, S. R., C. W. Lafon, H. D. Grissino-Mayer, G. G. DeWeese, and J. A. Hoss. 2009. Three centuries of fire in montane pine-oak stands on a temperate forest landscape. Applied Vegetation Science 13: 36–46.

Bechtold, W. A. and P. L. Patterson. 2005. The enhanced forest inventory and analysis program-national sampling design and estimation procedures. General Technical Report SRS-80. United States Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC. 85 pp.

Black, B. A. and M. D. Abrams. 2001. Influences of physiography, surveyor bias, and Native American catchments on witness tree distribution in southeastern Pennsylvania. Ecology 82: 2574–2586.

Bourdo, E. A., Jr. 1956. A review of the General Land Office survey and of its use in quantitative studies of former forests. Ecology 37: 754–768.

Braun, E. L. 1950. Deciduous Forests of Eastern North America. Blakiston, Philadelphia, PA. 610 pp.

Briand, C. H. and M. E. Folkoff. 2019. Integrating multiple sources to reconstruct the pre- and early postcolonial forests of the Chesapeake: 1588–1838. Human Ecology 47: 27–38. doi.org/10.1007/s10745-019-0058-7.

Brose, P. H. 2014. Development of prescribed fire as a silvicultural tool for the upland oak forests of the eastern United States. Journal of Forestry 112: 525–533.

Cleland, D. T., P. E. Avers, W. H. McNab, M. E. Jensen, R. G. Bailey, T. King, and W. E. Russell. 1997. National hierarchical framework of ecological units, pp. 181–200. *In* M. S. Boyce and A. Haney, eds. Ecosystem Management: Applications for Sustainable Forest and Wildlife Resources. Yale University Press, New Haven, CT.

Cogbill, C. V. 2000. Vegetation of the presettlement forests of northern New England and New York. Rhodora 102: 250–276.

Day, G. M. 1953. The Indian as an ecological factor. Ecology 34: 329–346.

Delcourt, P. A. H. R. Delcourt, C. R. Ison, W. E. Sharp, and K. J. Gremillion. 1998. Prehistoric human use of fire, the eastern agricultural complex, and Appalachian oak-chestnut forests: Paleoecology of Cliff Palace Pond, Kentucky. American Antiquity 63: 263–278.

Fei, S. and K. C. Steiner. 2007. Evidence for increasing red maple abundance in the eastern United States. Forest Science 53: 473–477. doi.org/10.1093/forestscience/53.4.473.

Fei, S., P. J. Gould, K. C. Steiner, J. C. Finley, and M. E. McDill. 2005. Forest regeneration composition and development in upland, mixed-oak forests. Tree Physiology 25: 1495–1500.

Fenneman, N. M. 1938. Physiography of the Eastern United States. McGraw-Hill, New York, NY. 714 pp.

[FIA] Forest Inventory and Analysis. 2021. FIA DataMart. https://apps.fs.usda.gov/fia/datamart/datamart.html. Retrieved February 8, 2021.

Foster, D. R., S. Clayden, D. A. Orwig, B. Hall, and S. Barry. 2002. Oak, chestnut and fire: Climatic and cultural controls of long-term forest dynamics in New England, USA. Journal of Biogeography 39: 1359–1379.

Hanberry, B. B. 2021. Timing of tree density increases, influence of climate change, and a land use proxy for tree density increases in the eastern United States. Land 10: 1121.

Hanberry, B. B., D. C. Bragg, and T. F. Hutchinson. 2018. A reconceptualization of open oak and pine ecosystems of eastern North America using a forest structure spectrum. Ecosphere 9(10): p.e02431.

Hanberry, B. B., M. D. Abrams, M. A. Arthur, and J. M. Varner. 2020. Reviewing fire, climate, deer, and foundation species as drivers of historically open oak and pine forests and transition to closed forests. Frontiers in Forest Global Change 3:56. doi.org/10.3389/ffgc.2020.00056.

Heeter, K. J., S. L. Brosiand, and G. L. Brewer. 2019. Dendroecological analysis of xeric, upland, *Quercus*-dominated old-growth forest within the Ridge and Valley Province of Maryland, USA. Natural Areas Journal 39: 319–332.

Hix, D. M., D. E. Fosbroke, R. R. Hicks, and K. W. Gottschalk. 1980. Development of regeneration following gypsy moth defoliation of Appalachian Plateau and Ridge and Valley hardwood stands. pp. 347–359. *In* Proceedings, 8th Central Hardwoods Forest Conference, March 4–6, 1991, University Park, PA. General Technical Report NE-148. United States

Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Radnor, PA.

Howard, L. F., G. D. Cahalan, K. Ehleben, B. A. Muhammad, H. Halza, and S. DeLeon. 2021. Fire history and dendroecology of Catoctin Mountain, Maryland, USA, with newspaper corroboration. Fire Ecology 17:8. doi.org/10.1186/s42408-021-00096-2.

Keever, C. 1953. Present composition of some stands of the former oak-chestnut forest in the southern Blue Ridge Mountains. Ecology 34: 44–45.

Kegg, J. D. 1971. The impact of gypsy moth: Repeated defoliation of oak in New Jersey. Journal of Forestry 69: 852–854.

Leak, W. B. 1958. Silvical characteristics of sweet birch (*Betula lenta*). Station Paper NE-113. United States Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Upper Darby, PA. 14 pp.

Lorimer, C. G. 1985. The role of fire in the perpetuation of oak forests, pp. 8–25. *In* J. E. Johnson, ed. Proceedings, Challenges in Oak Management and Utilization, March 28–29, 1985, Madison, WI. Cooperative Extension Service, University of Wisconsin, Madison, WI. 161 pp.

Lutz, H. J. 1930. Original forest composition in northwestern Pennsylvania as indicated by early land survey notes. Journal of Forestry 28: 1098–1103.

MacCleery, D. W. 1992. American Forests: A History of Resilience and Recovery. Forest History Society, Durham, NC. 71 pp.

Nowacki, G. J. and M. D. Abrams. 1992. Community, edaphic, and historical analysis of mixed-oak forests in the Ridge and Valley Province of central Pennsylvania. Canadian Journal of Forest Research 22: 790–800.

Nowacki, G. J. and M. D. Abrams. 2008. Demise of fire and mesophication of eastern U.S. forests. BioScience 58: 123–138.

Nowacki, G. J. and M. D. Abrams. 2015. Is climate an important driver of post-European vegetation change in the eastern U.S.? Global Change Biology 21: 314–334.

Orwig, D. A. and Foster, D. R. 1998. Forest response to the introduced hemlock woolly adelgid in southern New England, USA. Journal of the Torrey Botanical Society 125: 60–73.

Paciorek, C., S. Goring, A. Thurman, C. Cogbill, J. Williams, D. Mladenoff, J. Peters, J. Zhu, and J. McLachlan. 2016. Settlement-era gridded tree composition, northeastern US: Level 2 ver 0. Environmental Data Initiative. doi.org/10.6073/pasta/8544e091b64db26fdbbbafd0699fa4f9. Retrieved February 13, 2021.

Patterson, W. A. III and K. E. Sassaman. 1988. Indian fires in the prehistory of New England. pp. 107–135. *In* G. P. Nicholas, ed. Holocene Human Ecology in Northeastern North America. Plenum Publishing, New York, NY.

Pyne, S. J. 1984. Introduction to Wildland Fire. Wiley, New York, NY. 808 pp.

Royo, A. A., L. A. Vickers, R. P. Long, T. E. Ristau, S. H. Stoleson, and S. L. Stout. 2021. The forest of unintended consequences: Anthropogenic actions trigger the rise and fall of black cherry. BioScience 71: 683–696.

Ruffner, C. M. and M. D. Abrams. 1998. Relating land-use history and climate to the dendroecology of a 326-year-old *Quercus prinus* talus slope forest. Canadian Journal of Forest Research 28: 347–358.

Ruffner, C. M. and M. D. Abrams. 2002. Dendrochronological investigation of disturbance history for a Native American site in northwestern Pennsylvania. Journal of the Torrey Botanical Society 129: 251–260.

Schlosnagle, S. 1978. Garrett County: A History of Maryland's Tableland. Garrett County Historical Society, Oakland, MD. 389 pp.

Shumway, D. L., M. D. Abrams, and C. M. Ruffner. 2001. A 400-year history of fire in an old-growth oak forest in western Maryland, USA. Canadian Journal of Forest Research 31: 1437–1443.

Stambaugh, M. C., J. M. Marschall, E. R. Abadir, B. C. Jones, P. H. Brose, D. C. Dey, and R. P. Guyette. 2018. Wave of fire: An anthropogenic signal in historical fire regimes across central Pennsylvania, USA. Ecosphere 9(5): e02222.10.1002/ecs2.2222.

Thomas-Van Gundy, M. A., G. J. Nowacki, and C. V. Cogbill. 2015. Mapping pyrophilic percentages across the northeastern United States using witness trees, with focus on four national forests. General Technical Report NRS-145. United States Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA. 26 pp.

Thomas-Van Gundy, M., J. Rentch, M. B. Adams, and W. Carson. 2014. Reversing legacy effects in the understory of an oak-dominated forest. Canadian Journal of Forest Research 44: 350–364. doi.org/10.1139/cjfr-2013-0375.

Thompson, J. R., D. N. Carpenter, C. V. Cogbill, and D. R. Foster. 2013. Four centuries of change in northeastern United States forests. PLoS ONE 8(9): e72540. doi.org/10.1371/journal.pone.0072540.

Whitney, G. G. 1990. The history and status of the hemlock-hardwood forests of the Allegheny Plateau. Journal of Ecology 78: 443–458.

Whitney, G. G. 1994. From Coastal Wilderness to Fruited Plain: A History of Environmental Change in Temperate North America from 1500 to the Present. Cambridge University Press, Cambridge, UK. 488 pp.

Williams, G. W. 2004. American Indian fire use in the arid west. Fire Management Today 64(3): 10–14.