Ecology of Witch Hazel (*Hamamelis virginiana*) in the Forest Understory

Scott R. Abella[1], Timothy A. Schetter[2], LaRae A. Sprow[2]

[1]University of Nevada Las Vegas, School of Life Sciences, 4505 S. Maryland Parkway, Las Vegas, NV 89154-4004, U.S.A. and Natural Resource Conservation LLC, 1400 Colorado Street, Boulder City, NV 89005, U.S.A.; [2]Metroparks Toledo, 5100 Central Avenue, Toledo, OH 43615, U.S.A.

Abstract: In northwestern Ohio oak forests, we conducted a series of ecological investigations to advance knowledge of the natural history and conservation needs of witch hazel (*Hamamelis virginiana*), one of several small understory trees serving key ecological roles in eastern North American forests. Dendroecological analyses revealed that trees within witch hazel clones were uneven-aged, indicating that clones continuously recruited new trees rather than all of them originating at the same time. The largest (6.5 cm in diameter at 1.4 m high) and oldest witch hazel tree we recorded was 44 years old, though clones could be older. Spatial pattern analysis indicated that witch hazel trees were clumped at fine scales of 0–4 m, likely reflecting multi-stemmed clonal structure, and at broader scales of 11–20 m in some cases. Witch hazel exhibited minimal resistance to fire, as only 25% of trees 1–6 cm in diameter charred by a low-severity fire survived and only 3 trees/ha (≥ 1 cm in diameter) were alive after two low-severity fires. However, witch hazel cover, via resprouts or seedlings < 1 cm in diameter, persisted after the two fires. On long-term plots in unburned, mature oak forest, witch hazel density declined by 54% between 2002 and 2021, warranting further investigation as to potential reasons or pervasiveness of the trend. In a landscape distributional analysis, witch hazel occurrence was positively correlated with overstory tree canopy cover, decomposing organic layer thickness, and soil organic matter. Witch hazel in tree form was absent from oak forests that had been cleared for cultivation in the 1930s, and the species was a reliable indicator of mature forests at least 80 years old with minimal disturbance. Because conditions generally required to perpetuate oaks (e.g., large canopy gaps and fires) differ from those required by witch hazel (comparatively closed canopies and limited fire), management strategies balancing the needs of both species are likely needed if conserving mixed oak–witch hazel forests is desired over the long term.

Keywords: age structure, fire effects, long-term change, oak forest, Oak Openings region, tree spatial patterns

INTRODUCTION

Temperate deciduous forests, including those in Ohio, often contain shade-tolerant, short-statured tree species in understories (Fajardo et al. 2019). In eastern North America, examples of such species, incapable even when mature of reaching overstories, include common serviceberry (*Amelanchier arborea*), pawpaw (*Asimina triloba*), musclewood (*Carpinus caroliniana*), flowering dogwood (*Cornus florida*), Carolina silverbell (*Halesia carolina*), witch hazel (*Hamamelis virginiana*), Fraser magnolia (*Magnolia fraseri*), and hophornbeam (*Ostrya virginiana*). Belying their small stature, these species can serve large functional roles in forest ecosystems. The small trees can offer fruit, nut, floral, and structural resources to wildlife; influence regeneration of canopy trees; and affect soil nutrient cycling. For example, species such as pawpaw and Fraser magnolia produce large fruits that offer food for frugivorous birds and mammals such as foxes and opossums (Stiles 1980, Willson 1993, Greenberg et al. 2007). Exemplifying providing floral and pollen resources, common serviceberry flowers were visited by bees and other insects in a Michigan forest (Gorchov 1988), and nectar and pollen of witch hazel was utilized by flies and bees in Connecticut (Anderson and Hill 2002). Beaver preferentially cut or cached branches of musclewood in Ohio (Nixon and Ely 1969) and witch hazel in Massachusetts (Busher 1996). Illustrating offering habitat structural resources, Fraser magnolias were preferentially utilized as nest trees by Virginia northern flying squirrels (*Glaucomys sabrinus fuscus*), previously listed under the Endangered Species Act (Menzel et al. 2004). Affecting overstory tree recruitment (likely because of shading and belowground competition), patches of pawpaw contained three times fewer seedlings of overstory tree species in an Ohio forest (Baumer and Runkle 2010). Highlighting influences on forest nutrient cycling, flowering dogwood produces rapidly decomposing leaves enriched in calcium (Borer et al. 2013). Calcium-enriched soil below flowering dogwood trees supported abundant land snails, in turn a source of food and calcium for birds, salamanders, and wild turkeys (Nation 2007).

Here, we focused on advancing ecological knowledge of one of these small-statured tree species, witch hazel. Distribution of this wide-ranging species extends from northern Florida across the eastern U.S. to southern Canada in Nova Scotia, west to eastern Texas including disjunct populations in Mexico, and as far northwest as eastern Iowa and Wisconsin (Wood 1974). Witch hazel inhabits moist to dry sites, often in mature deciduous forests (Davidson 1966, Boerner 1985, Elliott and Vose 2010). Mature witch hazel trees are typically 3–7 m tall, commonly with arching trunks (Wood 1974). In Ohio's 2022 champion tree database, the largest witch hazel tree, which was in Hocking County, was 10 m tall and 14 cm in diameter (ODNR 2022). The species produces yellow to rusty-red flowers from late September to late November, is likely pollinated primarily by flies and bees, and forms a woody capsule fruit (Anderson and Hill 2002). Loss of fruits can result from physiological abortion, damage by caterpillars and a host-specific seed weevil, and consumption by small mammals (De Steven 1982). Surviving fruits open explosively the year after pollination, ejecting up to two seeds per fruit as far as 5 m (Anderson and Hill 2002). Some of the physiologically dormant witch hazel seeds can germinate the spring after autumn dispersal, but many remain dormant until the following year (Barbour and Brinkman 2008). Neither a study in northwestern Ohio nor 29 other studies in eastern North America detected witch hazel in soil seed banks, maybe because its seed banks are limited or germination requirements were unmet using the emergence technique (Abella et al. 2020a). The species is clonal, with clumps of nearby stems typically originating from individual clones, which can reproduce via root suckering (De Steven 1983, Hicks and Hustin 1989). Witch hazel is not among forage most preferred by white-tailed deer, but they will browse it, especially if favored forage is limited (Parker et al. 2020). Witch hazel has long been of ethnobotanical importance to humans, ranging from use of witch hazel infusions as medicines by Native Americans to modern Food and Drug Administration-approved uses in skin care and other applications (Engels and Brinckmann 2017).

Despite the important roles that witch hazel can play in forests, key features related to the ecology and conservation needs of the species remain poorly understood. Several facets of witch hazel ecology with limited information include its age structure, spatial patterns within forests, response to fire, long-term change in abundance, and distribution according to land use history. To examine these uncertainties, we conducted a series of ecological investigations in northwestern Ohio oak forests to assess witch hazel: 1) age structure and stem diameter–age relationships; 2) spatial patterns and size structure; 3) survival and sprouting after prescribed fires; 4) long-term changes in tree density in a 20-year period; and 5) distribution in present forests with varying historical land uses including past cultivation with or without recent fires.

METHODS

Study Area. We performed the study in the 45,000 ha Oak Openings region in Lucas County, northwestern Ohio (Schetter et al. 2013). Based on early 1800s land surveys, this sandy landscape was historically dominated by open oak ecosystems and mesic prairies, all thought to have been partly maintained by frequent fires typically ignited by Native Americans (Brewer and Vankat 2004). The ecosystems were altered through the 1900s via losses to urban and suburban development, clearing for agriculture, and expanded distribution and density of trees in the absence of fires (Schetter et al. 2013). Within the Oak Openings region, our study area was the largest protected area: the 1,737 ha Oak Openings Preserve, managed by Metroparks Toledo (41º33'N, 83º52'W). Contemporary vegetation in the preserve consists of about half oak forest (with primarily black oak [*Quercus velutina*] overstories and secondarily white oak [*Quercus alba*]), with the remainder including conifer plantations, forested wetlands, and managed areas of oak savanna–woodland–prairie kept open through prescribed fires and cutting encroaching trees. Much of the oak forest, long unburned (with the most recent fire perhaps in the 1800s), contains mature oak trees aged 100+ years. Witch hazel, together with the larger-statured red maple (*Acer rubrum*), sassafras (*Sassafras albidum*), and black cherry (*Prunus serotina*), comprise the major understory trees in these mature forests. Most of the remaining oak forest developed in locations that had been under cultivation (as crop fields or pastures) in the 1930s and were thereafter abandoned and acquired by Metroparks Toledo (Abella and Schetter 2021). Soils in the upland oak forests are mapped as Udipsamments of the Oakville and Ottokee series (Stone et al. 1980). The temperate climate, recorded 8 km east of the study area at the Toledo Airport, averages a daily temperature range of -9–0°C in January and 16–29°C in July and 85 cm/year of precipitation (1955–2021 records, Midwestern Regional Climate Center, Champaign, IL).

Age Structure. In July–August 2018 at three sites approximately equally spaced in the preserve in mature oak forest, we randomly selected two witch hazel clumps per site for stem aging. Using a handsaw, we cut all live stems of the clumps as close to ground level as possible (within a few cm) to obtain a cross section 3 cm thick of each stem. We obtained cross sections of 2–3 stems/clump and 14 stems in total. We sanded and cross-dated each sample using a local tree ring chronology calibrated using climate records from the nearby airport weather station. We related stem diameters at a height of 1.4 m (diameter at breast height) to ages at ground level using linear regression.

Within-Site Spatial Patterns. We randomly located three 20 m × 50 m (0.1 ha) plots in mature oak forests containing abundant witch hazel to examine within-site spatial patterns of witch hazel stems. In July–August 2018, we subdivided each plot into 5 m grid cells using measuring tapes and mapped the x, y coordinates of each witch hazel stem (≥ 1 cm in diameter at 1.4 m) to the nearest 0.1 m. We analyzed the data for each plot using correlation length analysis, a point-pattern analytical technique that compares observed frequencies of distances between points to those expected under a random distribution (Cartwright et al. 2011). We used 12 bins of distances for the analysis, executed in PAST 4.06 (Hammer 2022). If observed frequencies of distances exceed the upper 95% confidence limit expected under randomness, points are significantly clumped, compared with anti-clumping below the 95% confidence limit (Cartwright et al. 2011).

Fire Effects. To investigate effects of prescribed fires, we tracked witch hazel stems individually (via mapping them to the nearest 0.1 m using the methods described previously) in two burned and three unburned 20 m × 50 m plots. In July–August 2018, while mapping stems, we recorded the diameter at 1.4 m and status (alive or dead) of each witch hazel stem ≥ 1 cm in diameter at 1.4 m. The two burn plots subsequently received a prescribed fire in April 2019. The dormant-season, low-intensity fire, ignited under weather consisting of 8–24 km/hour winds, 54% relative humidity, and a 9°C temperature, had low flame heights typically < 1 m tall. We re-inventoried witch hazel on plots in August 2020, two years after the initial inventory on burned and unburned plots and two growing seasons post-fire. For the re-inventory, we recorded diameter at 1.4 m for all witch hazel stems with live canopies (including any new recruits into the ≥ 1 cm diameter class) and status of all stems as 1) canopy dead but sprouting around the base of the stem; 2) canopy alive without basal sprouting; or 3) canopy alive with basal sprouting. This classification enabled us to distinguish the functional effects of fires for persistence of live canopies compared with persistence only as sprouts. We recorded the height of sprouts to the nearest 0.1 m in 2020. Additionally, on burned plots in 2020, we recorded the percentage of the stem charred (in 5% increments) from ground level to a height of 1 m and the maximum char height up the stem.

As complete mortality (i.e., dead canopy and no basal sprouting) rarely occurred (only 1 stem died completely of 319 stems in total on the five plots) on either burned or unburned plots, we focused inferential statistical analyses on the burned plots, rather than inferentially comparing burned and unburned plots. Using combined data from burned plots, we compared mean diameter, char percentage, char height, and sprout height between stems with live or dead canopies in 2020 using t tests. We then modeled canopy status (alive or dead) by inputting diameter, char percentage, and char height as predictor variables into a classification tree, a procedure that splits data into increasingly homogeneous subsets (Breiman et al. 1984). We implemented the model in WEKA 3.8 using the J48 algorithm, a minimum of 3 observations per node, and 5-fold cross-validation (Bouckaert et al. 2017).

To further investigate fire effects on witch hazel by examining effects of repeated fires, we randomly located six 20 m × 25 m (0.05 ha) plots in a twice-burned 10 ha mature oak forest site. The site had received prescribed fires in April 2017 and 2018, 4–5 growing seasons before our retrospective sampling in August 2021. Both fires similarly had mostly low flame heights (< 2 m) and were ignited under weather ranging from 8–21 km/hour winds, 41–42% relative humidity, and 19–21°C temperatures. On each plot, we counted witch hazel stems ≥ 1 cm in diameter and categorized aerial cover (0.1, 0.25, 0.5, and 1%; 1% intervals to 10% cover, and 5% intervals to 100%) of witch hazel < 1 cm in diameter.

Long-Term Change. To determine long-term change in witch hazel density, we counted stems (≥ 1 cm in diameter at 1.4 m) in four 20 m × 25 m plots in summer 2002 and again 20 years later, in 2021. The plots were randomly located throughout the preserve in mature oak forests and were 1.3–3.1 km apart. We compared witch hazel diameter distribution between years with the data from the four plots using an Epps-Singleton test in PAST 4.06 (Hammer 2022).

Landscape Distribution across Land Uses and Habitat Factors. We investigated witch hazel landscape-scale distribution across land uses by extracting out and analyzing witch hazel cover from a published dataset (Abella and Schetter 2021). This dataset included witch hazel cover (using the same cover classes earlier described for the twice-burned plots) on 22 0.05 ha plots distributed throughout Oak Openings Preserve and sampled in August 2020. Plots were distributed across sites that had been under cultivation in the 1930s and that were either unburned (n = 8) or burned (n = 6) in 2013 prescribed fires or that had been in oak forest in the 1930s (n = 8). We identified the 1930s land use from air photos. Analysis of property records revealed that sites under cultivation at that time were subsequently acquired by Metroparks Toledo predominantly in the 1940s, then protected and left unmanaged. In addition to witch hazel cover data, each plot also had habitat data including tree canopy cover, lichen and moss cover (totaled to soil biocrust cover), thickness of the soil organic layer (divided into Oi, or fresh litter, and Oea, partially decomposing litter), pH (1:1 soil:H_2O for 0–15 cm mineral soil), and loss-on-ignition (heating at 300°C for 2 hours, 0–15 cm mineral soil) as a surrogate for organic matter (Abella and Schetter 2021). Witch hazel cover varied widely among plots from 0–15%, so to reduce influence of extreme values and to meet statistical assumptions, we used ranked analyses to analyze the data. We compared median witch hazel cover among the three land use categories using a Kruskal-Wallis test followed by sequential, Bonferroni-adjusted, Mann-Whitney pairwise comparisons in PAST 4.06 (Hammer 2022). We related witch hazel cover to habitat variables using Spearman correlation.

RESULTS

Age. The oldest witch hazel stems we aged became established in the mid-1970s and were 44 years old (Fig. 1). Stems we aged were up to the maximum stem diameter (6.5 cm) recorded for the over 500 witch hazel stems in total measured during the study. Stem diameter appears useful to estimate at least general categories of stem age, as stems smaller than 3 cm in diameter were younger than 30 years old and those over 3 cm were older than 30 years. Within clones, stems were uneven-aged, indicating that clones continually recruited new stems, as compared with all or most stems of a clone recruiting at the same time (Fig. 2).

Within-Site Tree Patterns. On three stem-mapped plots, witch hazel was significantly clumped at fine scales ≤ 4 m, corresponding with spatial structure at an individual clone scale with multiple stems of a clone in close proximity (Fig. 3). Clumping significantly stronger than expected by chance was also observed at greater distances of 11 and 14–20 m on two plots.

Fire Effects. Of 319 stems present in 2018 and tracked individually on once-burned and unburned plots, only one stem died completely (i.e., dead canopy and no basal sprouting) between 2018 and 2020. This dead, 1.5 cm diameter stem was on a burned plot but did not have an unusual bole char

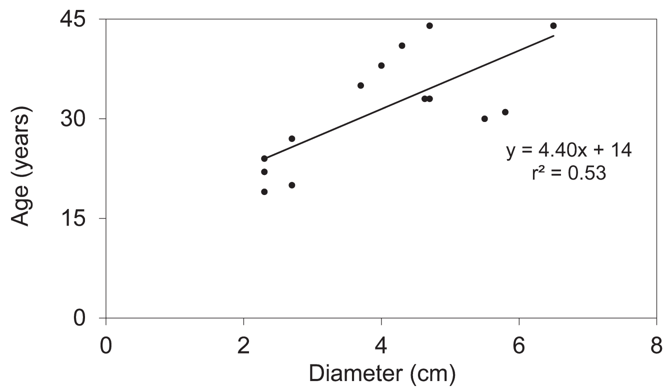

Fig. 1. Relationship of stem diameter (at a height of 1.4 m) with age of witch hazel (*Hamamelis virginiana*) at ground level in oak forests, Oak Openings Preserve, northwestern Ohio.

Fig. 2. Examples of stem ages within witch hazel (*Hamamelis virginiana*) clones in oak forests, Oak Openings Preserve, northwestern Ohio. Stem diameters at 1.4 m range from 1.0-6.5 cm among aged stems in the photos. Photos taken in 2018 (S.R. Abella).

height (0.1 m) or bole scorch area (10%). There were three new stems recruiting between 2018 and 2020 on plots (all of which were on unburned plots), representing a new-recruit density of 6 recruits/ha, or 3 recruits/ha/year on the five plots in total (Table 1). Of 206 stems present on unburned plots in 2018, 19 (9%) had their canopies die, or 32 canopies/ha/year dying. Five of the stems with canopies that died were hit by falling canopy trees and knocked over. However, all 19 of the stems with dead canopies exhibited basal sprouting near the base of the dead stems. Of the 209 total stems present on unburned plots by 2020, 204 (98%) exhibited basal sprouting regardless of whether canopies were alive or dead. Of the 190 stems with live canopies on unburned plots in 2020, 25% had diameters of 1–2 cm, 35% had diameters of 2–3 cm, and 40% had diameters ≥ 3 cm (up to a maximum of 6.5 cm).

In a classification tree modeling whether canopies were alive or dead two years post-fire in 2020 for 106 stems present in 2018 on burned plots, any amount of bole char was associated with a greater chance witch hazel canopies would die (Fig. 4). For stems charred to a height of at least 0.1 m, most (86%) died if their diameter was < 3 cm. If their diameters were ≥ 3 cm, about a third (37%) maintained live canopies two years after fire. Only the largest stems of 4–6 cm displayed more consistent fire resistance, but there were few stems this large. Stems with live canopies were significantly larger and had incurred less charring than those with canopies that died (Table 2). Overall, the model correctly classified the post-fire canopy status of 73% of stems. Misclassification mainly resulted from high variability in canopy survival in mid-sized stems 3–4 cm in diameter. Except for one stem completely dead, 105 of the 106 stems (99%) exhibited basal sprouting regardless of whether the canopy was alive or dead (Fig. 5). The basal sprouts were twice as tall in 2020 if canopies had survived compared to if canopies were dead, but sprouts averaged nearly 20 cm tall even if canopies had died (Table 2). As a result, complete mortality of witch hazel stems within two years after the low-severity fire was nearly non-existent.

On the twice-burned site, only one of the six 20 × 25 m plots had a witch hazel larger than 1 cm in diameter, resulting in only 3 stems/ha. However, plots averaged 3.5 % (SEM = 1.5) cover of witch hazel from basal sprouts and seedlings.

Long-Term Change. In the 20 years between 2002 and 2021, witch hazel stem density declined by an average of 54% (970 to 445 stems/ha) on four long-term plots, with all four plots experiencing declines (Fig. 6). Stem diameter distribution changed significantly, shifting from many to fewer small stems (≥ 1 < 2 cm in diameter) and toward more larger stems (2–6 cm in diameter; Fig. 7). Average stem diameter increased from 1.2 cm (SEM = 0.1) in 2002 to 2.2 cm (SEM = 0.1) in 2021.

Relationship with Landscape Factors and Land Use History. Witch hazel occurrence was associated with mature forests on sites without a history of past cultivation in at least the last 80 years, and its median cover was highest in mature forests (Kruskal-Wallis $\chi 2$ = 7.8, P = 0.005, pairwise comparisons P < 0.016; Table 3). Average witch hazel cover was 100× greater in mature forests that had not been under cultivation in the 1930s compared with sites that had been cultivated. If formerly cultivated sites also received recent (2013) fire, witch hazel was entirely absent. Witch hazel cover was significantly positively correlated with tree canopy cover, thickness of the decomposing soil organic layer (Oea horizon), and soil rich in organic matter.

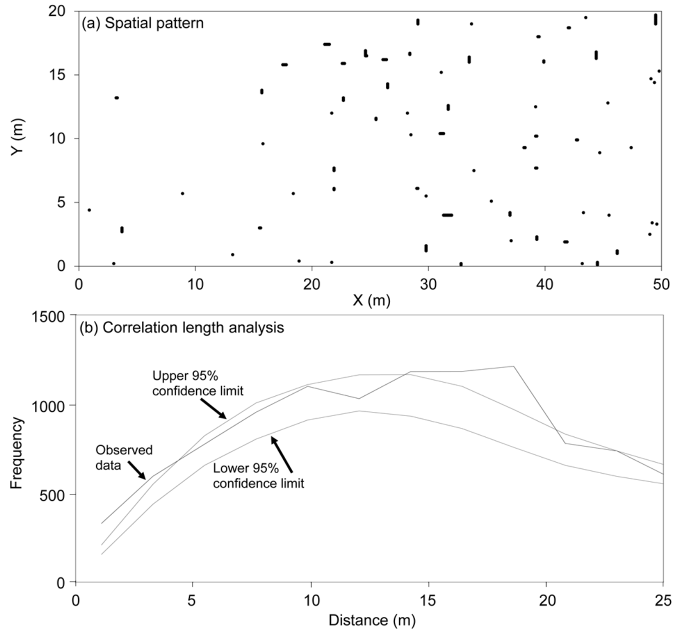

Fig. 3. Within-site spatial patterns of witch hazel (*Hamamelis virginiana*) trees in a representative site (out of three mapped) in oak forests, Oak Openings Preserve, northwestern Ohio. In (b), values above the 95% confidence limit are significantly clumped.

Char height = 0 m **alive, 100%** (9/9 stems)
Char height ≥ 0.1 m
  Diameter < 3 cm **dead, 86%** (44/51 stems)
  Diameter ≥ 3 cm
    Diameter 3-4 cm **dead, 67%** (29/43 stems)
    Diameter > 4 cm **alive, 100%** (3/3 stems)

Fig. 4. Classification tree model for aboveground survival of 106 witch hazel (*Hamamelis virginiana*) trees on burned plots in 2020, two growing seasons after an April 2019 prescribed fire, Oak Openings Preserve, northwestern Ohio. Predictor variables entering the model include height of char up stems and stem diameter at 1.4 m. The predicted outcome (stems with either live or dead canopies) is provided at each division along with the percentage and number of stems correctly classified by model predicted outcomes. All but one of the stems with dead canopies showed resprouting at the base of trunks. Statistics for the classification tree included a Kappa statistic of 0.24, mean absolute error of 0.35, and a root mean squared error of 0.43.

Table 1. (a) Fate of 209 witch hazel (*Hamamelis virginiana*) stems (≥ 1 cm in diameter at 1.4 m) on unburned plots between 2018 and 2020 and (b) diameter distribution of stems with surviving canopies in 2020 in oak forests, Oak Openings Preserve, northwestern Ohio.

(a) Fate of individual stems	
Status in 2020	**Number of stems**
Canopy died after 2018, basal sprouting[1]	19
Canopy alive, no basal sprouting[2]	5
Canopy alive, basal sprouting[3]	185
(b) 2020 diameter distribution of live-canopy stems	
Diameter class (cm)	
≥ 1 < 2	47
≥ 2 < 3	66
≥ 3 < 4	39
≥ 4 < 5	23
≥ 5 < 6	13
6	2

[1]Five of the stems with canopies that died were hit by falling trees and knocked over.
[2]Includes 1 new recruit between 2018 and 2020.
[3]Includes 2 new recruits between 2018 and 2020.

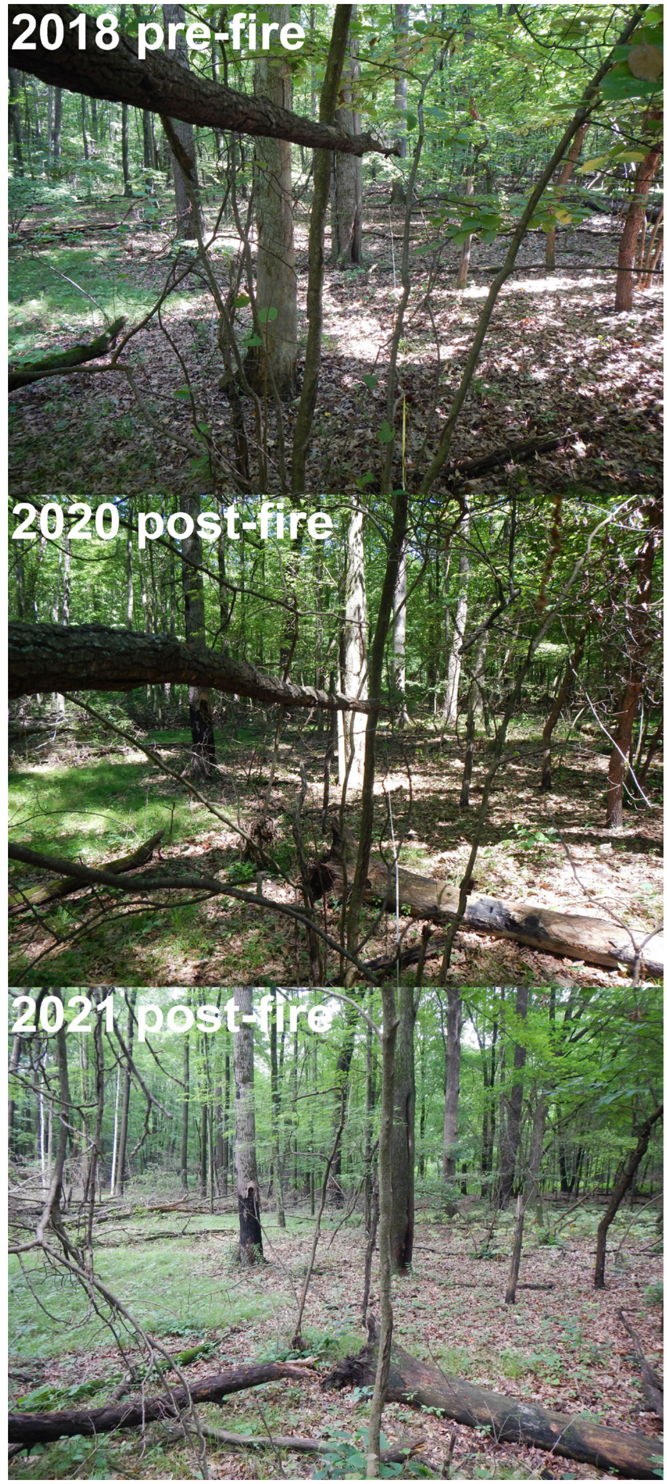

Fig. 5. Top-killing of witch hazel (*Hamamelis virginiana*) and its resprouting after an April 2019 prescribed fire, Oak Openings Preserve, northwestern Ohio. Photos by S.R. Abella.

DISCUSSION

Age. In our modest sample of 14 trees, the oldest witch hazel tree of 44 years was similar to maximum witch hazel tree ages reported in two prior studies: 30 years in oak forests in Michigan (De Steven 1983) and 58 years in New York (Taylor et al. 2017). Given that we found that witch hazel tree diameter was significantly correlated with age and our sampling included the largest-diameter trees (up to 6.5 cm in diameter) we recorded throughout our study landscape and thus likely the oldest, it seems plausible that witch hazel stems may not typically live longer than 30–60 years. Our finding of uneven-aged structure of stems within clones indicates that clones can continuously recruit new stems, compared with all of them becoming established simultaneously, highlighting a question of how much older clones could be than their oldest aboveground stem. A scenario in which witch hazel clones are not much older than their oldest stem could be if clones can only become established once a forest reaches a certain age. Our mature forest sites in which we aged witch hazel contained overstory oaks 120–200 years old (S.R. Abella, unpublished data), and the formerly cultivated sites with forests less than 80 years old did not contain any witch hazel stems ≥ 1 cm in diameter. In mature forests without a history of cultivation, it is possible that many of the clones in our study are not much older than their oldest-aged stems of approximately 44 years and did not become established until after the mid-1900s, once forests had matured without fires since the 1800s. A separate question then could be how long witch hazel clones could be capable of living, which is unclear compared to the documented multi-century or even millennial lifespans of some clonal shrubs and trees (de Witte and Stöcklin 2010).

Tree Spatial Patterns. Clumping at fine scales of ≤ 4 m may be expected from witch hazel's clonal habit and likely represents clusters of clonal stems (De Steven 1983). Clumping at broader scales of 11–20 m could originate from several possibilities, such as seed dispersal from clones. Ballistic ejection from witch hazel fruits results in seeds dispersing up to 5 m from parent stems (Anderson and Hill 2002). If individual clones are approximately 3 m wide and disperse seed 5 m, then two clones from their furthest edges plus a 5 m dispersal distance total 11 m of distance, the lower limit of clumping we observed at broad scales. Clones could also exhibit clumping by becoming established near each other because of favorable microsite conditions, such as overstory canopy gaps (Reader et al. 1995). Hicks and Hustin (1989) found that witch hazel seedling density was not higher in canopy gaps (compared to below canopy trees), but genets produced more ramets in canopy gaps, which would accentuate witch hazel clumping.

Table 2. Statistics for 106 witch hazel (*Hamamelis virginiana*) stems (≥ 1 cm in diameter at 1.4 m) with canopies that survived or died following an April 2019 prescribed fire in an oak forest, Oak Openings Preserve, northwestern Ohio. Stem diameter is at 1.4 m and represents 2018 before the fire. Char height is the maximum height of charring up stems. Percent char area is the amount of char from ground level to a height of 1 m up stems.

	Canopy status			
	Alive (n = 72)	Dead (n = 34)	t-statistic	P-value
	Mean ± SEM			
Diameter (cm)	3.0 ± 0.2	2.5 ± 0.1	2.6	0.011
Char height (m)	0.07 ± 0.01	0.11 ± 0.01	-5.1	< 0.001
Char area (%)	5.3 ± 0.7	9.5 ± 0.5	-4.7	< 0.001
Sprout height (m)	0.35 ± 0.05	0.17 ± 0.01	4.5	< 0.001

Table 3. (a) Frequency and cover of witch hazel (*Hamamelis virginiana*) in 2020 on 22 sites that had differing land uses in the 1930s and that were either burned or unburned in 2013 prescribed fires, Oak Openings Preserve, northwestern Ohio. (b) Spearman correlations of witch hazel cover in 2020 with habitat variables.

(a) *Hamamelis* occurrence across land uses			
	Historical Forest	Cultivated unburned	Cultivated burned
Frequency (%)	75	25	0
Cover (%)	3.03 ± 1.81[1]	0.03 ± 0.02	0 ± 0
(b) Correlations with *Hamamelis* cover			
Correlate	r_s	P	
Canopy cover[2]	0.54	0.009	
Lichen cover	-0.51	0.014	
Moss cover	-0.55	0.008	
Oi thickness	0.36	0.103	
Oea thickness	0.57	0.005	
Loss-on-ignition[3]	0.65	0.001	
pH[3]	-0.53	0.011	

[1]Mean ± SEM.
[2]Overstory and mid-story tree canopy cover, primarily consisting of black oak (*Quercus velutina*) with some white oak (*Quercus alba*), red maple (Acer rubrum), sassafras (*Sassafras albidum*), and black cherry (*Prunus serotina*).
[3]0-15 cm mineral soil.

Fire Response. One low-intensity fire sharply reduced witch hazel tree density, and two low-intensity fires nearly eliminated witch hazel stems ≥ 1 cm in diameter. Cover of witch hazel < 1 cm in diameter, supplied by seedlings and sprouts, persisted, which could eventually grow to tree size. However, witch hazel's growth rate is slow (Hicks and Hustin 1989), so fires more frequent than every few decades may preclude witch hazel from reaching tree size. Our results support prior studies identifying witch hazel as a fire-sensitive tree even at maturity. In the southern Appalachians, density of witch hazel trees ≥ 1 cm in diameter was halved after one fire and was zero after a second fire (Elliott and Vose 2010). In Pennsylvania oak forests, witch hazel cover was 50-90% lower in sites burned 2–4 years prior (Signell and Abrams 2006). Witch hazel relative density was 20 times lower on sites burned 5–51 years earlier in Rhode Island (Brown 1960). Witch hazel's low fire resistance and slow resilience suggests the species follows a fire-avoider strategy, at least regarding persistence as trees (Rowe 1983).

Long-Term Decline in Tree Density. We found that witch hazel tree density declined substantially in undisturbed, unburned forests during 20 years between 2002 and 2021. We discuss three possible reasons. First, declining witch hazel density could represent a combination of losses of clones and self-thinning within clones (Clary and Tiedemann 1986). Second, the decline could relate to browsing by white-tailed deer, limiting witch hazel survival or recruitment. Although witch hazel is not necessarily preferred forage, deer browse witch hazel if more preferred forage is sparse (Parker et al. 2020). In our study area, deer populations increased after the early 2000s up to densities around 20 deer/km^2, before declining to a moderate density averaging 9 deer/km^2 after 2016 when deer began being managed (Abella et al. 2022). Townsend and Meyer (2002) found that witch hazel recovered quickly via sprouting within two years of complete protection from deer herbivory. If decreased witch hazel density in our study was associated with abundant deer, recovery of witch hazel may be delayed given its slow growth and the fact that deer remain present at moderate density. Third, it is possible that climatic events, such as late-spring

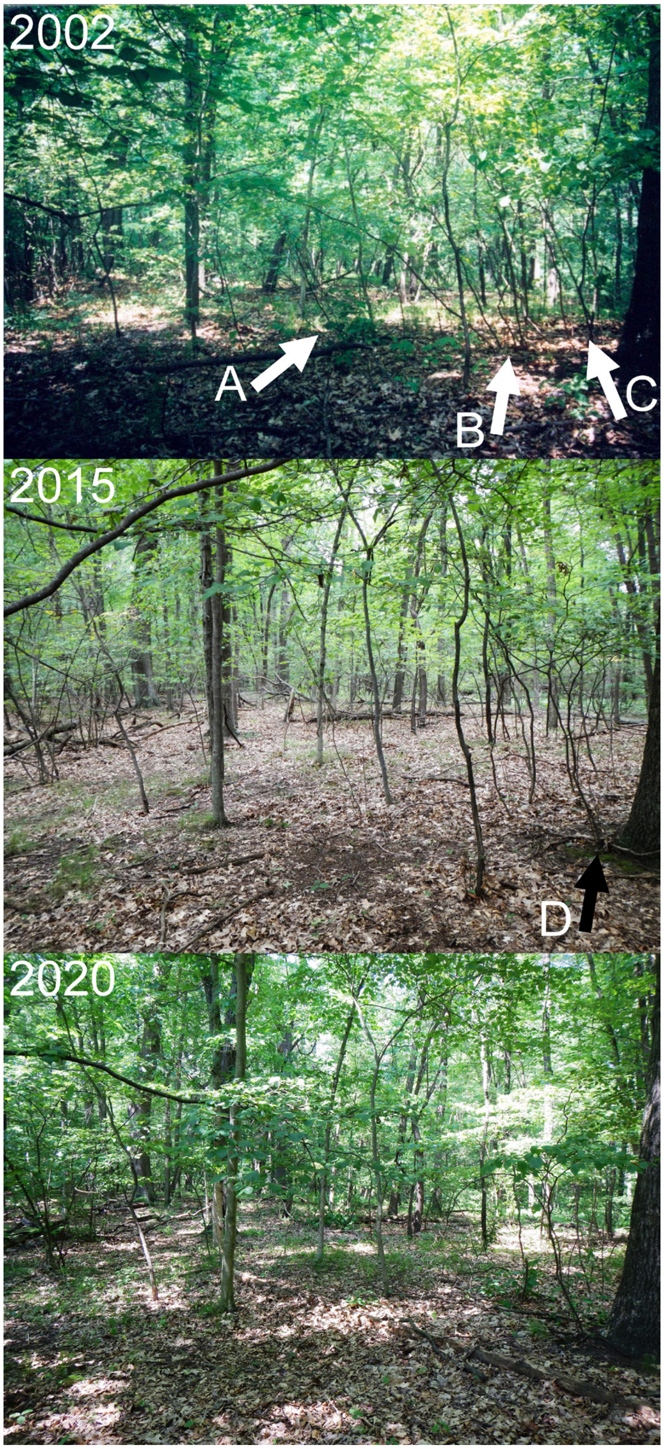

Fig. 6. Reduction in density of witch hazel (*Hamamelis virginiana*) trees in an example plot which experienced a 51% decline in witch hazel density in an oak forest, Oak Openings Preserve, northwestern Ohio. Major witch hazel clumps, likely representing individual clones, shown in the photo in 2002 are labeled as A (decreasing from 3 stems ≥ 1 cm in diameter in 2002 to 1 stem in 2015 and 0 in 2020), B (decreasing from 4 to 3 to 1), and C (decreasing from 2 to 1 and 1). Only one new clone visible in the photo, labeled as D, appeared after 2002 and had one stem ≥ 1 cm in diameter in 2015 that persisted in 2020. Photos by S.R. Abella.

freezes, could relate to witch hazel's decline. For example, in the eastern U.S., 2007 had an atypical combination of an unusually warm March, triggering early plant growth, followed by a severe freeze in April (Gu et al. 2008). This freeze extensively damaged vegetation, and understory trees can be particularly susceptible to such damage if they leaf out early or inhabit lower areas with cold air drainage (Gu et al. 2008).

Landscape Distribution and Land Use History. Across the landscape, witch hazel cover was highest in sites with the most forest cover, thickest soil organic layers, most soil organic matter, and land use history of continuous forest cover since before the 1930s. Witch hazel cover was nearly absent in forests younger than 80 years old and witch hazel trees ≥ 1 cm in diameter were absent. Furthermore, witch hazel cover was also absent in these young forests if fire had occurred within the last seven years. These results support witch hazel's classification as a shade-tolerant species of minimally disturbed, mature forests (Davidson 1966). Witch hazel thus appears to be a reliable indicator of mature forests with minimal disturbance history.

Status of Witch Hazel in Historical and Contemporary Ecosystems and Implications for Conservation. Witch hazel's limited fire resistance and affinity for closed-canopy, mature forests raise questions regarding the species' status in the fire-prone savanna- and woodland-dominated landscape of our study area in the Oak Openings region preceding Euro-American settlement (Brewer and Vankat 2004). It is possible that witch hazel, at least as larger trees, was more restricted in distribution before settlement, perhaps largely inhabiting ravine or riparian forests where fires occurred less frequently (Brewer and Vankat 2004). Witch hazel's occurrence in tree form in upland oak ecosystems could therefore be a more recent phenomenon in the past ≈50–100 years as lack of fire corresponded with conversion of oak savannas and woodlands to forest (Brewer and Vankat 2004). If witch hazel inhabited pre-settlement, frequent-fire oak savannas and woodlands, it may have mainly occurred as seedlings or small sprouts (< 1 cm in diameter), similar to in contemporary burned sites, potentially with seeds being supplied from mature trees in infrequently burned sites. It is also possible that witch hazel could have attained larger sizes in oak woodlands than in savannas. Oak woodlands are thought to have developed in locations partly protected from fire spread (e.g., leeward sides of rivers) or during time periods when fire was less frequent (Brewer and Vankat 2004). Although historical fire frequencies have not been quantified in the region, oak woodlands are thought to have experienced fire at least as frequently as every 1–2 decades and savannas at least every 2–10 years to avoid conversion to forest (Abella et al. 2020b).

In the contemporary landscape, conserving witch hazel while sustaining oak forests could represent a conundrum. We suggest three scenarios, each likely affecting witch hazel

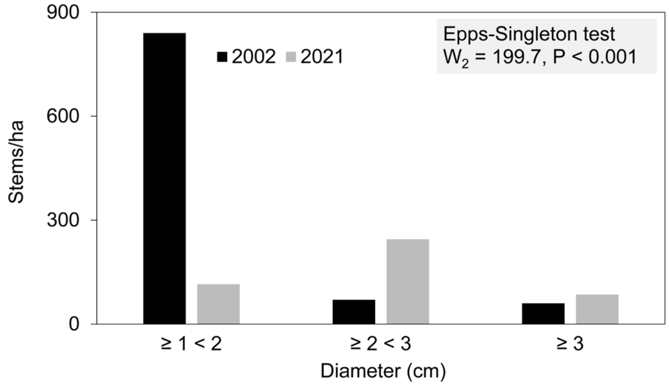

Fig. 7. Comparison of diameter distributions of witch hazel (*Hamamelis virginiana*) trees in 2002 and 2021 in oak forests, Oak Openings Preserve, northwestern Ohio. The Epps-Singleton test revealed that diameter distributions differed significantly between 2002 and 2021.

differently, including ecological restoration to reestablish oak savanna or woodland; management to sustain oak forests; or leaving forests unmanaged. Using tree thinning and prescribed fire to restore savanna and woodland on presently forested sites is a priority in the region owing to the nearly complete loss of these open habitats and their unique biodiversity (Abella et al. 2020b). This restoration scenario is likely to be unfavorable to witch hazel, which may persist only as short sprouts repeatedly top-killed by the frequent fires needed to maintain the open habitats. Sustaining oak forests, to avoid their long-term conversion to mesophytic trees such as red maple, benefits from a combination of periodic fires and creation of canopy gaps sufficiently large (often > 0.1 ha) to support seedling-to-sapling transition of the moderately shade-tolerant oaks (Abrams 1996). These management activities, likely required to maintain oak forest over the long term, would probably reduce or eliminate witch hazel as a small tree, similar to what we observed in the once- and twice-burned sites. An alternative strategy, perhaps still facilitating some oak recruitment, could involve cutting large openings (including removing red maple and trees competing with oak) but not using fire, enabling witch hazel trees to persist in locations below the overstory canopy. Leaving the current oak forests containing witch hazel unmanaged may enable persistence of witch hazel clones indefinitely if clones continue regenerating, though perhaps this regeneration would occur below overstory trees other than oaks in future decades and centuries. A transition from oak to red maple forests would likely be accompanied by reduced habitat quality for birds and wildlife owing to losses of resources including acorns, high-density oak foliage, and the unique morphologies of oaks that offer abundant microhabitats (Rodewald and Abrams 2002). The different requirements for persistence of trees of witch hazel and oaks result in tradeoffs in habitat management strategies and may require customized strategies if conserving both witch hazel and oak is desired.

ACKNOWLEDGMENTS

We thank University of Nevada, Las Vegas, undergraduate students for processing dendroecology samples and Jacob Luna and Lindsay Chiquoine for analyzing the dendroecology samples; Metroparks Toledo personnel for conducting prescribed fires; Annabel Cartwright for sharing insight on correlation length analysis; and Metroparks Toledo and the Ohio Biological Survey for funding the study through a contract and grant to Natural Resource Conservation LLC.

REFERENCES CITED

Abella, S.R., J.L. Hodel, and T.A. Schetter. 2020a. Unusually high-quality soil seed banks in a midwestern U.S. oak savanna region: variation with land use history, habitat restoration, and soil properties. Restoration Ecology 28: 1100–1112.

Abella, S.R., K.S. Menard, T.A. Schetter, L.A. Sprow, and J.F. Jaeger. 2020b. Rapid and transient changes during 20 years of restoration management in savanna-woodland-prairie habitats threatened by woody plant encroachment. Plant Ecology 221: 1201–1217.

Abella, S.R., and T.A. Schetter. 2021. Variation in characteristics and conservation values of plant communities on abandoned agricultural lands with and without fires. Applied Vegetation Science 24: e12629.

Abella, S.R., T.A. Schetter, and T.D. Gallaher. 2022. Rapid increase in sensitive indicator plants concurrent with deer management in an oak forest landscape. Wildlife Society Bulletin 2022: e1377.

Abrams, M.D. 1996. Distribution, historical development and ecophysiological attributes of oak species in the eastern United States. Annals of Forest Science 53: 487–512.

Anderson, G.J., and J.D. Hill. 2002. Many to flower, few to fruit: the reproductive biology of *Hamamelis virginiana* (Hamamelidaceae). American Journal of Botany 89: 67–78.

Barbour, J.R., and K.A. Brinkman. 2008. *Hamamelis* L., witch-hazel, pp. 582–584. *In* Bonner, F.T., and R.P. Karrfalt (eds.). The woody plant seed manual. Agriculture handbook 727. U.S. Department of Agriculture, Forest Service, National Seed Laboratory, Dry Branch, GA.

Baumer, M., and J.R. Runkle. 2010. Tree seedling establishment under the native shrub, *Asimina triloba*. Castanea 75: 421–432.

Boerner, R.E.J. 1985. Foliar nutrient dynamics, growth, and nutrient use efficiency of *Hamamelis virginiana* in three forest microsites. Canadian Journal of Botany 63: 1476–1481.

Borer, C.H., S.G. Sapp, and L.H. Hutchinson. 2013. Flowering dogwood (*Cornus florida* L.) as mediator of calcium cycling: new insights are revealed by analysis of foliar partitioning. Trees 27: 841–849.

Bouckaert, R.R., E. Frank, M. Hall, R. Kirkby, P. Reutemann, A. Seewald, and D. Scuse. 2017. WEKA manual for version 3-8-2. University of Waikato, Hamilton, New Zealand.

Breiman, L., J.H. Friedman, R.A. Olshen, and C.J. Stone.

1984. Classification and regression trees. Wadsworth, Inc., Belmont, CA.

Brewer, L.G, and J.L. Vankat. 2004. Description of the vegetation of the Oak Openings of northwestern Ohio at the time of Euro-American settlement. Ohio Journal of Science 104: 76–85.

Brown, J.H. 1960. The role of fire in altering the species composition of forests in Rhode Island. Ecology 41: 310–316.

Busher, P.E. 1996. Food caching behavior of beavers (*Castor canadensis*): selection and use of woody species. American Midland Naturalist 135: 343–348.

Cartwright, A., J. Moss, and J. Cartwright. 2011. New statistical methods for investigating submarine pockmarks. Computers and Geosciences 37: 1595–1601.

Clary, W.P., and A.R. Tiedemann. 1986. Distribution of biomass within small tree and shrub form *Quercus gambelii* stands. Forest Science 32: 234–242.

Davidson, D.W. 1966. Response of six shrub species to light regimes in two controlled-environment rooms. Bulletin of the Torrey Botanical Club 93: 432–437.

De Steven, D. 1982. Seed production and seed mortality in a temperate forest shrub (witch-hazel, *Hamamelis virginiana*). Journal of Ecology 70: 437–443.

De Steven, D. 1983. Reproductive consequences of insect seed predation in *Hamamelis virginiana*. Ecology 64: 89–98.

de Witte, L.C., and J. Stöcklin. 2010. Longevity of clonal plants: why it matters and how to measure it. Annals of Botany 106: 859–870.

Elliott, K.J., and J.M. Vose. 2010. Short-term effects of prescribed fire on mixed oak forests in the southern Appalachians: vegetation response. Journal of the Torrey Botanical Society 137: 49–66.

Engels, G., and J. Brinckmann. 2017. Witch hazel, *Hamamelis virginiana*, family: Hamamelidaceae. HerbalGram 116: 8–16.

Fajardo, A., E.J.B. McIntire, and M.E. Olson. 2019. When short stature is an asset in trees. Trends in Ecology and Evolution 34: 193–199.

Gorchov, D.L. 1988. Effects of pollen and resources on seed number and other fitness components in *Amelanchier arborea* (Rosaceae: Maloideae). American Journal of Botany 75: 1275–1285.

Greenberg, C.H., D.J. Levey, and D.L. Loftis. 2007. Fruit production in mature and recently regenerated forests of the Appalachians. Journal of Wildlife Management 71: 321–335.

Gu, L., P.J. Hanson, W.M. Post, D.P. Kaiser, B. Yang, R. Nemani, S.G. Pallardy, and T. Meyers. 2008. The 2007 eastern US spring freeze: increased cold damage in a warming world? BioScience 58: 253–262.

Hammer, Ø. 2022. PAST 4.06, paleontological statistics reference manual. University of Oslo, Norway.

Hicks, D.J., and D. Hustin. 1989. Response of *Hamamelis virginiana* L. to canopy gaps in a Pennsylvania oak forest. American Midland Naturalist 121: 200–204.

Menzel, J.M., W.M. Ford, J.W. Edwards, and M.A. Menzel. 2004. Nest tree use by the endangered Virginia northern flying squirrel in the central Appalachian Mountains. American Midland Naturalist 151: 355–368.

Nation, T.H. 2007. The influence of flowering dogwood (*Cornus florida*) on land snail diversity in a southern mixed hardwood forest. American Midland Naturalist 157: 137–148.

Nixon, C.M., and J. Ely. 1969. Foods eaten by a beaver colony in southeast Ohio. Ohio Journal of Science 69: 313–319.

Parker, H.A., J.T. Larkin, D. Heggenstaller, J. Duchamp, M.C. Tyree, C.S. Rushing, E.J. Domoto, and J.L. Larkin. 2020. Evaluating the impacts of white-tailed deer (*Odocoileus virginianus*) browsing on vegetation in fenced and unfenced timber harvests. Forest Ecology and Management 473: 118326.

Reader, R.J., S.P. Bonser, T.E. Duralia, and B.D. Bricker. 1995. Interspecific variation in tree seedling establishment in canopy gaps in relation to tree density. Journal of Vegetation Science 6: 609–614.

Rodewald, A.D., and M.D. Abrams. 2002. Floristics and avian community structure: implications for regional changes in eastern forest composition. Forest Science 48: 267–272.

Rowe, J.S. 1983. Concepts of fire effects on plant individuals and species, pp. 135–154. *In* Wein, R.W., and D.A. MacLean (eds.). The role of fire in northern circumpolar ecosystems. John Wiley and Sons, New York.

Schetter, T.A., T.L. Walters, and K.V. Root. 2013. A multi-scale spatial analysis of native and exotic plant species richness within a mixed-disturbance oak savanna landscape. Environmental Management 52: 581–594.

Signell, S.A., and M.D. Abrams. 2006. Influence of rocky landscape features and fire regime on vegetation dynamics in Appalachian *Quercus* forests. Journal of Vegetation Science 17: 675–684.

Stiles, E.W. 1980. Patterns of fruit presentation and seed dispersal in bird-disseminated woody plants in the eastern deciduous forest. American Naturalist 116: 670–688.

Stone, K.L., E.H. McConoughey, G.D. Bottrell, and D.J. Crowner. 1980. Soil survey of Lucas County, Ohio. U.S. Department of Agriculture, Soil Conservation Service. U.S. Government Printing Office, Washington, D.C.

Taylor, B.N., A.E. Patterson, M. Ajayi, et al. 2017. Growth and physiology of a dominant understory shrub, *Hamamelis virginiana*, following canopy disturbance in a temperature hardwood forest. Canadian Journal of Forest Research 47: 193–202.

Townsend, D.S., and A.D. Meyer. 2002. Rapid recovery of witch hazel (*Hamamelis virginiana* L.) by sprouting, following release from white-tailed deer (*Odocoileus virginianus* Zimm.) browsing. Natural Areas Journal 22: 290–295.

Willson, M.F. 1993. Mammals as seed-dispersed mutualists in North America. Oikos 67: 159–176.

Wood, G.E. 1974. Witch-hazel, *Hamamelis virginiana* L., pp. 154–157. *In* Gill, J.D., and W.M. Healy (compilers). Shrubs and vines for northeastern wildlife. General Technical Report NE-9. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, Upper Darby, PA.