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Review

Reassessment of the Use of Fire as a Management Tool in Deciduous Forests of Eastern North America

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Abstract: *Prescribed burning is increasingly being used in the deciduous forests of eastern North America. Recent work suggests that historical fire frequency has been overestimated east of the prairie–woodland transition zone, and its introduction could potentially reduce forest herb and shrub diversity. Fire-history recreations derived from sedimentary charcoal, tree fire scars, and estimates of Native American burning suggest point-return times ranging from 5–10 years to centuries and millennia. Actual return times were probably longer because such records suffer from selective sampling, small sample sizes, and a probable publication bias toward frequent fire. Archeological evidence shows the environmental effect of fire could be severe in the immediate neighborhood of a Native American village. Population density appears to have been low through most of the Holocene, however, and villages were strongly clustered at a regional scale. Thus, it appears that the majority of forests of the eastern United States were little affected by burning before European settlement. Use of prescribed burning assumes that most forest species are tolerant of fire and that burning will have only a minimal effect on diversity. However, common adaptations such as serotiny, epicormic sprouting, resprouting from rhizomes, and smoke-cued germination are unknown across most of the deciduous region. Experimental studies of burning show vegetation responses similar to other forms of disturbance that remove stems and litter and do not necessarily imply adaptation to fire. The general lack of adaptation could potentially cause a reduction in diversity if burning were introduced. These observations suggest a need for a fine-grained examination of fire history with systematic sampling in which all subregions, landscape positions, and community types are represented. Responses to burning need to be examined in noncommercial and nonwoody species in rigorous manipulative experiments. Until such information is available, it seems prudent to limit the use of prescribed burning east of the prairie–woodland transition zone.*

Keywords: adaptation, charcoal, fire scar, Native American, oak, vegetation history

Reevaluación del Uso de Fuego como Herramienta de Manejo en Bosques Deciduos de América del Norte

Resumen: *La quema planeada cada vez se usa más en el bosque deciduo del este de Norteamérica. Sin embargo, trabajos recientes sugieren que la frecuencia histórica de los fuegos se ha sobrestimado al este de la zona de transición entre la pradera y el bosque, y su introducción podría reducir la diversidad de hierbas y arbustos del bosque. Recreaciones históricas del fuego derivadas de carbón sedimentario, cicatrices de fuego en los árboles y estimaciones de quemas por los nativos americanos, sugieren tiempos de regreso al punto que van desde 5–10 años hasta siglos y milenios. Los tiempos de retorno actuales probablemente fueron más largos porque tales registros sufren de muestreo selectivo, tamaño pequeño de las muestras y un sesgo probable de publicación hacia el fuego frecuente. Evidencias arqueológicas muestran que los efectos ambientales del fuego pueden ser severos en la vecindad inmediata de una aldea nativa americana. Sin embargo parece que la densidad de población fue baja a lo largo de casi todo el Holoceno y las aldeas estuvieron agrupadas en una escala regional. Por esto, parece que la mayoría de los bosques del este de los Estados Unidos estuvo poco afectada por las quemas antes del establecimiento europeo. El uso de quemas planeadas asume que la mayoría de las especies del bosque son tolerantes al fuego y que la quema tendrá un efecto mínimo sobre la diversidad. Sin embargo, adaptaciones comunes como la serotinia, los brotes epicórmicos, el rebrote de rizomas y la germinación iniciada por humo no existen en casi toda la región decidua. Los estudios experimentales de la quema muestran respuestas de la vegetación que consisten en la

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remoción de tallos y basura: éstas son similares a las respuestas a otras formas de perturbación y no implican necesariamente la adaptación al fuego. La carencia general de adaptación puede causar una reducción en la diversidad si se introduce la quema. Estas observaciones sugieren la necesidad de una revisión cuidadosa de quemas históricas con muestreos sistemáticos en los que estén representadas todas las subregiones, posiciones de paisaje y tipos de comunidad. Las respuestas a la quema necesitan ser revisadas en especies no comerciales y no leñosas en experimentos con manipulación rigurosa. Hasta que tal información esté disponible, parece prudente limitar el uso de quemas planeadas al este de la zona de transición entre pradera y bosque.

Palabras Clave: adaptación, carbón, cicatriz de fuego, historia de vegetación, nativo americano, roble

Introduction

Fire occurs in every forest ecosystem eventually and is widely recognized as an important factor in determining the structure and composition in many plant communities. However, the historical cycle of fire has been interrupted by recent human activity, and intentional burning by land managers is often necessary to maintain biological diversity (Pyne 1982). Since approximately 1980, use of prescribed burning as a management tool has increased steadily in North American ecosystems, including deciduous forests of the eastern United States. Burning in the deciduous forest is based on the assumptions that surface fire was historically a regular and frequent event, occurring every 5–15 years over most of the region before European settlement (Shumway et al. 2001; Lafon et al. 2005); that the presence of fire-resistant *Quercus* and *Carya* (oak and hickory) spp. indicates a history of fire at individual sites (Abrams 1992; Brose et al. 2001); and that the rest of the forest community is resilient to fire because intolerant species have been removed by repeated exposure (Hutchinson et al. 2005). Widespread and frequent burning is considered necessary by some researchers to protect biological diversity in the absence of historical levels of fire (Brose et al. 2001; Abrams 2005) and to maintain soil microbial activity and nutrient availability (Boerner et al. 2008).

Recent field studies and an alternative reading of the fire-history literature call the extent of presettlement fire into question, casting doubt on the use of burning as a management tool. It now seems possible that fires were relatively uncommon at a regional scale, most fires were restricted to a small section of the landscape, most deciduous forest species are not fire tolerant, and intentional burning has the potential to profoundly alter species' composition over large areas. These possibilities are of particular concern because of the broad subcontinental scale at which management agencies are experimenting with burning (Melvin 2012) and the even broader application advocated by some researchers (e.g., Brose et al. 2001; Abrams 2005). Most forest lands in the eastern United States are privately owned and, thus, less likely to be burned for management purposes. However, the oldest, least disturbed, and least fragmented forests tend to be in public ownership, potentially concentrating burning in the sites of highest conservation value. Because a policy based on overestimated fire frequency could potentially cause great loss of diversity, the case for frequent burning needs to be reexamined. This paper considered the assumptions underlying the use of fire as a management tool in deciduous forests of eastern North America. I raise questions about the regularity of fire as a disturbance process, sampling methods used to reconstruct fire history, and responses of plant species to burning in deciduous forests. The goal is to stimulate discussion about the nature and effects of fire in deciduous forest ecosystems and to highlight gaps in current understanding. It was not my intention to provide a comprehensive review of fire ecology or the environmental history of fire.

The paper focuses on the mesic-moist region of eastern North America dominated by broadleaved tree species, an area covering approximately 1.4 million km^2. The region corresponds roughly to 7 forest zones recognized by Braun (1950): oak–hickory (interior highlands), mixed mesophytic, western mesophytic, oak–chestnut, maple–basswood, and beech–maple, and the Allegheny and southern New England sections of the Northern Hardwood zone. For convenience, I refer to the region as the mesic deciduous forest (MDF). It is important to distinguish the MDF from the xeric oak–savanna communities of the prairie–woodland transition zone (predominantly west of 90°W but extending eastward in Illinois), which have a clear and well-documented dependence on frequent fire (e.g., Anderson & Schwegman 1991; Guyette et al. 2002). The MDF also does not include the mixed conifer forests of northern New England and the northern Great Lakes States, which have their own distinctive fire dynamics (e.g., Frissell 1973; Baker 1989), or the pine-dominated communities of the Outer Coastal Plain, although deciduous forests of the Inner Coastal Plain and Piedmont provinces are included. Within the MDF, neither geologically defined barrens (e.g., cedar glades, serpentine barrens, oak openings) nor oak–pine ridge-top forests of the Appalachian Mountains are included. These embedded forest types are distinct communities with a high natural fire frequency that is easily traceable to the microclimatic and edaphic peculiarities of their respective sites. As such, they are qualitatively different from the majority of the forests in the eastern United States.

Fire History

In the early 21st century fire is uncommon in the MDF, and the fires that do occur are usually not of natural origin. In forests of the Ohio River Valley (approximately 39°N, 82°W) only 1% of fires occurring between 1926 and 1977 appear to have ignited naturally, presumably by lightning (Yaussy & Sutherland 1994). Most fires in the southern and central Appalachian Mountains were anthropogenic in the mid to late 20th century; natural ignition accounted for only 5–18% of wildfires on federal lands (Barden & Woods 1974; Lafon et al. 2005). Expressed as point frequencies, these data suggest that natural fire-return intervals have been very long: approximately 500–4000 and 6140 years, respectively. If natural ignition has always been as uncommon as it is today, then most presettlement fires were probably set by humans.

Frequent mention in the historical record leaves no doubt that Native Americans intentionally burned eastern forests for a variety of reasons at the time of European contact (Day 1953; Fowler & Konopik 2007). Although it is clear that fire was widely used, such accounts are notoriously vague about fire size and frequency. Indirect evidence is provided by early descriptions of forests with open understories (e.g., Rose 1794; Heckewelder 1819) consistent with a history of frequent burning. Many accounts describe treeless "prairies" or "meadows," presumably maintained by Native American burning, in regions that currently support deciduous forest (Pyne 1982; Brown 2000). Although such observations establish a convincing link between humans and fire, they are potentially misleading because they come from the relatively brief period of initial European contact—a period of massive social and demographic upheaval in Native American cultures.

Archeology provides a temporal dimension, potentially shedding light on burning practices up to 3000 years before European contact. Before approximately 1000 AD, a scarcity of dated village sites suggests the human population of eastern North America was relatively small (Munoz et al. 2010). In the absence of other forms of evidence, maize can be used as a proxy to gauge the environmental impact of this culture. Starch and phytolith microfossils suggest maize cultivation was present but infrequent in the northeastern United States between 300 BC and 1000 AD (Hart & Lovis 2013), probably planted in small ephemeral plots by nomadic bands of farmer–foragers. There is little direct evidence of fire from this period, but frequent observations of burning in the Contact period suggest that these earlier groups also used fire to shape their environment, including clearing land for garden plots. Shifting location would have diffused the long-term environmental effect over a large area (K. A. Jordan; J. P. Hart, personal communication). At any particular place in the forest, burning would have been infrequent in proportion to the low human population size.

A major transition took place between 1000 and 1200 AD when the frequency of fixed location villages increased abruptly in the East; possibly, this transition was related to the introduction of intensive maize agriculture (Hart & Lovis 2013). In the upper Delaware Valley (approximately 41.5°N, 75°W), for example, reorientation to maize cultivation between 900 and 1500 coincided with a 172% increase in the number of villages (Stinchcomb et al. 2011). Population increase corresponded with greatly increased sedimentation in the Delaware River floodplain. Increased sedimentation implies extensive forest clearance upstream. At a site in eastern West Virginia, stable isotope ratios in sediments and cave deposits correspond with charcoal and artifact concentrations at the surface, suggesting local forest clearance between 1200 and 1500 AD (Springer et al. 2010). At both sites, fire was probably used to create and maintain the forest openings.

Such studies document a moderate or severe effect of burning at individual sites, but the scale and uniformity of burning remain doubtful, in large part because the spatial ecology of Native American populations is not well understood. If villagers burned to clear garden plots, control undergrowth, improve browse for game, enrich the soil, or similar purposes it seems reasonable that such activity would be concentrated within easy walking distance. Contact-period accounts (summarized in Russell 1983 and Williams 1989) describe activities localized around villages at distances reflecting the effort involved. Garden plots were typically <1 km from an established village, whereas burning and fuelwood collection took place within 4–5 km, and most foraging and hunting occurred within a radius of 6–8 km. Native Americans had little means of controlling fires, but topographic variation provides abundant natural firebreaks in many parts of the MDF (personal observation). It seems unlikely that fire would spread far from villages if it were not encouraged with further ignition. Thus, proximity to village sites provides an estimate of the frequency of burning. Concentrated burning activity is consistent with the abundance of sedimentary charcoal around village sites in southern Ontario (Munoz & Gajewksi 2010) and the correspondence of fire-tolerant tree species and village sites on the Allegheny Plateau (Black et al. 2006).

Large sections of eastern North America appear to have supported very few villages and must have escaped village-centered burning activity. In New England, villages were preferentially located along the coast and the banks of principal rivers at the time of European contact; population density was low elsewhere (Cook 1976; Parshall & Foster 2002). Village sites in the Late Woodland period were similarly clustered along estuaries in southern New Jersey (Pagoulatos 1992). Little grass pollen was observed in samples from nearby northern New Jersey, however, suggesting that Native Americans cleared or burned no more than a minor proportion of the landscape (Russell 1980). Meta-analysis of Late Woodland archeological data indicates regional concentrations of population along the New England coast and estuaries of New York, New Jersey, Delaware, Maryland, and Virginia. Concentrations also appeared in the southern Appalachian Mountains and Tennessee Valley (approximately 36°N, 84°W), around the eastern Great Lakes, and intermittently along the floodplains of major rivers (Milner & Chaplin 2010). As few as 50 km from these areas, population densities were probably much lower (estimated at <0.3 people/km^2) and large areas remained unoccupied. Even in relatively populated areas village sites were usually separated by at least 10–30 km (Milner & Chaplin 2010), a distance perhaps determined by social interactions, landform, or resource availability. Assuming that environmental effects, including those of fire, were concentrated within walking distance of villages, a considerable amount of land remained unburned.

These generalizations are based largely on population size and distribution estimates in the most recent period before European arrival. As such, estimates of environmental impact have been strongly influenced by the major population expansion of the Late Woodland period. As few as 50–500 years earlier, a substantially smaller population would have had a much less severe, more diffuse effect on the environment. Indeed, nucleated villages did not develop in New England until shortly before Europeans arrived (Hart & Lovis 2013). It follows from both temporal and spatial evidence that large areas, perhaps the majority of the MDF, probably experienced very low levels of burning throughout most of the Holocene. Eyewitness accounts of burning at the time of European contact should probably not be interpreted as evidence that fire was frequent or widespread before European settlement.

Sedimentary Evidence of Fire

Fire history can also be documented with physical evidence, including charcoal preserved in sediments in ponds and bogs. Such records have been used to detect impressively ancient fire events (e.g., White 1953; Winkler 1982) and they provide compelling evidence of Native American burning at some sites (e.g., Delcourt & Delcourt 1997; Delcourt et al. 1998). At a regional scale, charcoal:pollen ratios indicate that fires were relatively common in densely populated coastal sites in southern New England, but almost nonexistent in the sparsely populated mountains of western Massachusetts and central Maine (Patterson & Sassman 1988). The spatial and temporal variability shown in such studies suggests fire was a local phenomenon rather than a general feature of eastern forests. However, the number of spatially explicit studies is small. In most cases, the lack of particle-size data makes it impossible to pinpoint individual fires.

Fine-textured charcoal (5- to 10-μm diameter) appears at low concentrations in virtually all sediment cores in eastern North America (J. R. Marlon, personal communication), presumably reflecting cumulative deposition of particles from many individual fires distributed over a large area. In most samples, it is difficult to determine fire frequency because layers are not distinct and dating is only possible on a scale of decades or centuries. In an attempt to separate individual fire events from background levels of deposition, Clark and Royall (1996) measured sedimentary charcoal at 9 sites between Maine and Minnesota. Concentrations that were statistically distinct from the background level (implying fire near the sampling point) were only observed at the westernmost (driest) site. It is telling that background levels in the period of active fire suppression (i.e., the 20th century) were equivalent to levels over the previous 1000–2000 years at most sites. The implication is that fire was no more common in Northern Hardwood forests in the prehistoric period than it is today. A similar study at 4 sites in the lower Hudson Valley used coarse-particle deposition to distinguish individual fire events from background levels of deposition (Robinson et al. 2005). Although individual charcoal layers were not dated, fires appeared to have occurred only once, twice, never, and 9 times over the course of 10,000–12,000 years, equivalent to point-return times of 1,000–10,000 years.

A recent review of archeological, palynological, and charcoal studies suggests expansion of the human population in the Late Woodland period caused a generally higher frequency of burning throughout the northeast United States (Fesenmyer & Christensen 2010; Munoz et al. 2010). Alternatively there is some evidence that fire frequency was controlled by global climate change. Coarse-charcoal deposition at a site in the Hudson estuary (Pederson et al. 2005) appears to correspond to the Medieval Warm Period (approximately 800–1300 AD) rather than to local periods of agricultural activity.

Sediment records often suffer from the problem of undersampling. Because fire is inherently patchy at a landscape scale and particle-size data can only detect fire occurrence in a small area (Clark 1988; Ohlson & Tryterud 2000), studies with few sample points are strongly affected by stochastic events. Unfortunately substantial effort is required to collect particle-size information, and individual studies commonly report data from fewer than 5 sediment cores. At the subcontinental scale, sedimentary records are not available in many areas because geomorphology does not favor the formation of bogs and ponds (clearly evident as large blank spaces on maps in Williams et al. 2001). The few studies conducted south of the Northern Hardwood zone are strongly clustered in 2 small areas in the southern Appalachian Mountains (Hart & Buchanan 2012). Although suggestive in their respective study areas, they do not allow generalization across the eastern United States. These weaknesses do not necessarily discredit charcoal as an index of presettlement fire, but it is premature to conclude that fire was frequent and widespread throughout the MDF.

Dendrochronology and Fire

On a shorter time scale, the postsettlement history of fire can be reconstructed with great precision from scars corresponding to annual growth rings in trees. It appears that fire returned at regular intervals at sites in Arkansas, Kentucky, Missouri, Indiana, Kansas, Illinois, New Jersey, and Ohio (Table 1), and must have played an important role in structuring the respective forest communities. Fire-scar evidence has some serious weaknesses, however, which cast doubt on the generalization of fire to the MDF as a whole. To examine sampling methods, I selected 14 studies unsystematically on the basis of citation frequency (mean = 38 cites/paper; Table 1). Collectively, the results of these studies suggest the existence of several problems.

Forested landscapes have not been thoroughly examined. Most published studies have been done in a small subset of possible landscape positions, including dry ridge tops, geologically defined barrens (e.g., cedar glades, serpentine barrens, oak openings), steep slopes, and well-drained dune systems. Nine of the 14 studies fell into one of these categories. Because fire occurrence is strongly affected by landform and soil texture, such sites are likely to have atypical fire regimes (sampled communities were often intentionally selected for high fire frequency). Generalization of frequent fire to all landscape positions is not justified.

Studies have not been representative at a continental scale. Eight of the 14 studies were done in the prairie transition zone on the western edge of the MDF. Six described their sites as "prairie" or "savanna"—community types that are known to have frequent natural fires. Study locations are strongly clustered (4 are from a small area in Missouri), and large regions have received no attention at all. Few studies have been done in Braun's (1950) Appalachian oak, oak–chestnut, or mixed mesophytic regions, making generalization difficult across the whole MDF (Hart & Buchanan 2012).

Few stands have been sampled. Fire reconstructions are usually based on a relatively small number of stands within a study area. Eight of the 14 studies used only a single stand, and only 2 studies used >10. Because fire is patchy at the stand scale, results from any single stand may substantially over- or underestimate the regional frequency of fire.

Fire-scar records are not very long. Although sample sizes in the 20th century allow reconstruction of stand history with a degree of certainty, records become progressively less dependable in the 19th century as the number of trees in older age classes declines due to natural mortality. Only 5 of the 14 studies included at least 10 trees dating back to 1850, and 4 of these studies came from a single study area (i.e., southwestern and central Missouri). Thus, results from before the 20th century may be strongly influenced by stochastic events, and cannot be assumed to accurately reflect fire history.

Probably the greatest weakness in the use of fire-scar records as evidence for the occurrence of fire lies in the handling of negative results. Understandably, trees without fire scars would not be of interest in a study seeking to measure fire interval; few studies mention trees without scars (10 of the 14 studies report only results from scarred trees). It is questionable whether a study reporting mainly unscarred trees would be publishable at all, implying a publishing bias toward scarring. Selective reporting could potentially skew fire-history reconstructions to a high frequency of fires.

Distribution of Fire-Adapted Species

A low historical fire frequency is consistent with the lack of fire adaptations in the MDF flora. Evolution has produced a wide variety of adaptations to fire, including insulating bark (e.g., Bauer et al. 2010), serotinous cones (Johnson & Gutsell 1993), epicormic sprouting (Hanson & North 2006), resprouting from rhizome buds and root suckers (Matlack et al. 1993*a*; McGee et al. 1995; Matlack 1997), germination cued by combustion products (Keeley & Fotheringham 1998), nonlinear seedling growth (bolting) (Wahlenberg 1946), a germination requirement for brightly lit mineral soil (Harvey et al. 1980), and basal sprouting (Schier 1983). These adaptations allow fire-adapted floras to resprout vigorously, often within weeks of a fire, with no long-term compositional or structural changes. Frequently burned communities, such as the longleaf pine (*Pinus palustris*) savanna of the southeastern United States, the chaparral of southern California, and the *Xanthorrhea–Banksia* scrubland of southwestern Australia, are easily recognizable by the frequency and abundance of such adaptations. If fire has been common in the MDF on a scale of centuries or millennia, fire adaptations ought to be evident even if fire has been suppressed in recent decades. The modern MDF flora would presumably show a high tolerance of fire, and prescribed burning would cause no major compositional changes (Brose et al. 2001).

The MDF flora generally does not display adaptations to fire, and burned sites do not revegetate with noticeable speed or vigor. Despite the growth of many forest herbs and shrubs from persistent tubers or rhizomes, these species do not resprout quickly after fire (Glasgow & Matlack 2007*a*). Epicormic sprouting is unknown in the MDF, and serotiny occurs only in isolated *Pinus* spp. populations on dry ridge tops in the Appalachian Mountains (Barden 1979). The lack of such adaptations

Table 1. Locations and sampling methods used in 14 widely cited fire-scar studies.

Authors	*Community*	*Region*[a]	*Elevation (m)*	*Number of stands*	*Number of trees (species)*	*Landscape position*	*Trees without scars*	*Range of dates examined (≥10 trees)*[b]
Harmon (1982)	pine/oak forest	Great Smokey NP	260–940[c]	26[d]	43, *P. rigida, P. echinata*	NA	no scars in 78% of ravines	<1856–1982 (NA)
Shumway et al. (2001)	mixed oak	Western MD	600–670	1	20, *Q. alba, Q. prinus*	south-facing slope	no scars in 1/20 trees	1580–1986 (1690)
Shuler & McClain (2003)	red oak/red pine; xeric	Pendleton Co., WV	1224	1	17, *Q. rubra*	mountain crest	no scars in 4 of 17 trees	1846–2002 (1890)
Cutter & Guyette (1994)	oak/hickory; xeric	N Central MO	ca. 300	1	24, *Q. stellata*	ridge top	NA	1734–1991 (1740)
Sutherland (1997)	second growth mixed oak	Vinton Co., OH	280–320	1	14 oaks (12 *Q. velutina*)	north-facing slope	only scarred trees used	1850–1997 (1865)
Buell et al. (1954)	oak/hickory; mixed mesic	Millstone, NJ	22	1	1 *Q. alba*	level?	only scarred tree used	1627–1950 (1 tree)
Henderson & Long (1984)	wooded dunes; xeric, nutrient poor	Northwest IN	190	2	38, *Q. velutina, Q. alba*	lakeshore dunes	only scarred trees used	1890–1980 (1890?)
Guyette & McGuiness (1982)	grassy openings in oak/hickory forest	Southwest MO	240–440	1	21, *Juniperus, virginiana*	steep slopes, rock outcrops	only scarred trees used	1496–1980 (1698)
Abrams (1985)	corridor forest in prairie matrix; xeric & mesic	Northeast KS (Konza)	330–350	3	19 *Q. macrocarpa, Q. muhlenbergii*	stream corridors and ravines	all examined were scarred	1858–1984 (1897)
Guyette & Cutter (1991)	oak savanna; shallow soils	S central MO	370	4	43, *Q. stellata, P. echinata, J. virginiana*	steep slopes	all examined were scarred	1490–1990 (1720)
McClain et al. (2010)	till plains (oak wood land, 1/3 prairie)	Hamilton Co., IL	140	1	36, *Q. stellata*	“gently rolling”	only scarred trees used	1770–1996 (1859)
Cole & Taylor (1991)	dune prairie or oak savanna	Northwest IN	200–250	1	24, *Q. velutina*	dune-swale complex	all examined were scarred	1890–1991 (NA)
McEwan et al. (2007)	mixed mesophytic	Eastern KY & Southeast OH	240–320	9	225; pred. *Q. alba, Q. prinus*	upper slopes of low ridges	only scarred trees used	1850–2000 (1855)
Guyette et al. (2002)	oak/pine wood-land; prairie Ecotone	Southwest MO	140–410	27	257; ~ 10/site; *P. echinata*	steep slopes	only scarred trees used	1600–2000 (1680)

[a] *NP, national park; Co., county; WV, West Virginia; MD, Maryland; MO, Missouri; OH, Ohio; NJ, New Jersey; IN, Indiana; KS, Kansas; IL, Illinois; KY, Kentucky; Q,* Quercus*; P,* Pinus*; N, north; S, south; pred., predominantly; NA, information not available.*
[b] *The year after which sample size was at least 10 trees is shown in parentheses.*
[c] *Most sites <610 m.*
[d] *1–2 trees per stand.*

militates against a long-term history of fire. Species known to be tolerant of fire in other ecosystems are occasionally found in the MDF, but their presence does not necessarily indicate a history of fire. *Quercus marilandica* and *Quercus stellata*, which occur in both the MDF and the fire-shaped forests of the Atlantic Coastal Plain, are tolerant by virtue of insulating bark, resistance to scarring, and the ability to resprout from root crowns (Lorimer 1985). Ericaceous shrubs, including black huckleberry (*Gaylussacia baccata*), lowbush blueberry (*Vaccinium vacillans*), and wintergreen (*Gaultheria procumbens*), appear to be adapted to survive fire on the Coastal Plain by resprouting from large meristem reserves on buried rhizomes (Matlack et al. 1993*b*; Elliott et al. 1999) and occasionally show such behavior after fire in the MDF (Vandermast et al. 2004). Most co-occurring species lack these traits, however, demonstrating that survival is possible in the MDF without fire adaptations. Because distributions of many MDF species are effectively static on the time scale of human land use (Cain et al. 1998; Matlack 2005), one can assume that the current distribution of nonadapted species indicates a generally low frequency of presettlement fire. It seems unlikely that nonadapted species have colonized large areas following 20th century fire suppression. Oaks and ericaceous shrubs should probably be regarded as opportunistic in the MDF because they appear in infrequently burned communities, where their fire adaptations are superfluous.

Potential Effects of Burning

My treatment of fire history, above, is predicated on the idea that modern forest management should be consistent with historical precedent, following the logic that if fire had a positive effect in the past one could safely assume that its continued use will have beneficial effects today. Alternatively it can be argued that a particular management method should be adopted because it achieves desirable results, irrespective of its history. A chainsaw, for example, is a useful management tool despite the fact that it has no evolutionary history in the MDF. By analogy, prescribed burning should be judged on its practical effectiveness; it should not be disqualified because doubt is cast on the historical role of fire. It follows that prescribed burning may legitimately be used in the MDF as long as it has no negative effects. The long-term effects of burning are unclear, however. Little is known about the specific effect of fire on populations of most MDF species—previous research has focused on commercial tree species to the exclusion of herbs, shrubs, soils, and animals. Scale of examination has often been inappropriate to questions of fire response. For example, stand-scale studies are inescapably vague in their conclusions because they fail to capture plant-scale heterogeneity within the burned areas.

Generalizing from the small number of whole-community studies, it appears that because fire removes plant stems and litter it favors weedy species and those with protected basal meristems. Fire in the MDF is commonly followed by increases in the frequency of grasses, light-requiring summer forbs, seed-banking species, and tree seedlings (Nuzzo et al. 1996; Hutchinson et al. 2005; Glasgow & Matlack 2007*a*). Collectively, the vegetational response to fire is similar to the response following any physical disruption of the forest floor and does not necessarily imply adaptation to tolerate fire (Glasgow & Matlack 2007*a*). Herbaceous species respond to fire individualistically. Many MDF species have been observed to decline in frequency following fire, as would be expected in a flora with no evolutionary history of burning (Nuzzo et al. 1996; Vandermast et al. 2004). Other studies show no effect of fire on herb or shrub cover or a site-specific effect in which fire appears to cause both increased and decreased herb cover (Franklin et al. 2003; Elliott & Vose 2010). Heating appears to stimulate seed germination in a few native perennial herbs, but not in others (Emery et al. 2011). Fire often leads to increased cover of nonnative species, a finding that suggests fire creates opportunities for invasion (e.g., Glasgow & Matlack 2007*b*; Mandle et al. 2011). Many of the vegetational effects described in these studies were not large, perhaps because they report the effect of only a single fire; repeated burning is likely to have stronger effects (Buell & Cantlon 1953). Other growth forms have been largely overlooked (but see Wiley 2012).

On the basis of these observations, what would be the cumulative effect of introducing fire over large areas? In removing aboveground stems fire is similar to herbivory. Deer (*Odocoileus virginianus*) browsing has resulted in a near-complete shift in forest vegetation to graminoids and ferns (species with protected basal meristems) over large areas in western Pennsylvania and northern Wisconsin (Rooney 2001). By analogy, it is reasonable to expect widespread prescribed burning to increase the prominence of graminoids and ferns and substantially reduce species with exposed meristems. With introduction of fire, the MDF could potentially come to resemble the fire-shaped, grass-dominated forests of western North America (e.g., Laughlin & Fule 2008; Coop et al. 2010).

It has been suggested that fire favors oak regeneration by discouraging maples, which competitively suppress oaks (Abrams 1992). I will not attempt to review the extensive literature on oak regeneration except to say that evidence for the fire dependence of oaks remains equivocal. Although some experimental studies show an increase in *Quercus* spp. growth or density in response to fires (e.g., Brose & Van Lear 1998), others show no such effect (Wendell & Smith 1986; McGee et al. 1995; Schuler & McClain 2003; Blankenship & Arthur 2006). Regeneration may depend on the timing and frequency of fire and its interaction with other forms of disturbance

(Hutchinson et al. 2012). If burning does affect oak regeneration, it seems safe to conclude that the ecological mechanism involves complex interactions rather than simple causation. Alternatively, oak regeneration may be controlled by nonfire factors, potentially including patterns of historical land use, climate change, and fluctuations in herbivore populations (McEwan et al. 2011). Considering the poor understanding of oak regeneration at present, it seems premature to prescribe fire for the purpose of oak management.

Research Needs

At present the most parsimonious model of fire in the MDF involves a high historical fire frequency in geologically defined barrens microsites and in the immediate neighborhood of Native American villages, possibly with a severe local effect, but very low fire frequency in the areas of forest between such sites. In this scenario, a consistently low frequency of fire has allowed communities of fire-intolerant plant species to thrive on a scale of centuries or millennia over most of the MDF. The model should be regarded as tentative, however, because it is based on very few actual studies of fire history and vegetation response. Before widespread burning is adopted, there is a pressing need for research targeted to specific gaps in our understanding of fire in the MDF.

Coarse-fragment charcoal data need to be collected uniformly over the entire MDF to allow robust generalization about regional frequencies of fire. This would require locating suitable bogs and ponds in unsampled areas, a difficult task in regions where geomorphology does not favor formation of wetlands. In the absence of wetlands, it would be worth examining forest soils for presence and amount of charcoal (e.g., Hart et al. 2008; Fesenmyer & Christensen 2010). Soils have the great advantages of being available over the entire MDF, quick to collect, and inexpensive to assay.

As with charcoal records, tree-scar data need to be collected in a fine-grained, regular pattern across the entire MDF to produce unbiased estimates of fire frequency. Within regions sampling should be stratified by landscape position, elevation, and soil character. In contrast to most published studies, which concentrate intensive effort on a small number of trees in a small area, it may be profitable to examine more superficially the large number of trees cut for nonscientific purposes.

Data showing the absence of fire scars or charcoal layers must be accorded the same scientific value as the presence of such indicators. Absence must be recorded systematically and published in the same ecological journals that would present any other fire-history study.

Experimental studies are needed to test the effects of fire on all members of the MDF community including herbs, shrubs, soil organisms, and animal species. Small-plot studies have the great advantage of allowing the intensity and uniformity of fire to be controlled, and plots can be replicated extensively, allowing environmental heterogeneity to be characterized. Experimental burns need to be repeated at regular intervals, so they approximate the proposed frequency of management burning and, ideally, continue over at least 4–5 burn cycles.

Historical records of fire are often vague and incomplete and, thus, have limited potential for recreating fire history. Poor record keeping continues today, notwithstanding the scientific and management interest in fire ecology. All parties using prescribed burning for management or research purposes should be encouraged to keep detailed records of fire extent, intensity, prefire vegetation, and date. High spatial resolution requires use of geographic positioning systems.

Finally, there is a need to evaluate the effectiveness of knowledge transfer among researchers, managers, and fire crews on the ground. Research-based recommendations do not always translate into practice by land managers. Conversely researchers do not always recognize the practical limitations managers face.

When these gaps in understanding have been filled and evidence of the long-term, whole-community effect of fire is available, responsible decisions can be made about the use of managed burning in the MDF. Until then, it seems prudent to limit burning in forests of the eastern United States to specific sites and landscape positions that have an obvious natural propensity to fire.

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