NRC Research Press

ARTICLE

Direct effects of lightning in temperate forests: a review and preliminary survey in a hemlock–hardwood forest of the northern United States

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Abstract: Lightning strikes millions of trees worldwide each year, yet structured lightning damage surveys are relatively rare. Estimates drawn from the literature suggest that lightning directly or indirectly kills up to 4% of large canopy trees in a stand annually. Lightning is a major cause of death for pines in southeastern US forests and for large cacti in some deserts, but its landscape-level effects exclusive of fire at higher latitudes are poorly known. We quantified damage to trees from lightning and other sources in hemlock–hardwood forests of the Huron Mountain Region of Michigan, USA. This region receives ca. 100 cloud-to-ground lightning flashes per year, with most occurring in May to August. We recorded abiotic and biotic damage on 309 trees distributed among nine transects, each >2 km long. None of the transect trees had lightning scars, and we observed only 14 clear cases of lightning damage among thousands of trees examined during associated meander surveys (each ca. 0.5 ha). This damage was more commonly associated with emergent stature (50% of struck trees) and higher rates of biotic damage (50%) than we observed in the 309 transect trees (22% emergent status and 16% incidence of biotic damage). Nearly all (93%) of the lightning damaged trees were conifers, suggesting that either susceptibility to, or response to, lightning strikes has a phylogenetic basis. These preliminary results provide a foundation for comparative studies in other forests. Accurate quantification of lightning-induced tree mortality will improve forest turnover models and facilitate predictions of future forest structure under conditions of increased lightning frequency.

Key words: lightning, forest, Michigan, survey, review.

Résumé : La foudre frappe des millions d'arbres à l'échelle du globe chaque année mais les inventaires structurés des dommages causés par la foudre sont relativement rares. Les estimations tirées de la littérature indiquent que la foudre tue annuellement, directement ou indirectement, jusqu'à 4 % des arbres de l'étage dominant dans les peuplements. La foudre est une cause majeure de mortalité chez les pins dans le sud-est des É.-U. et chez les gros cactus dans certains déserts mais ses effets à l'échelle du paysage, à l'exclusion du feu, aux latitudes plus élevées sont mal connus. Nous avons quantifié les dommages causés aux arbres par la foudre ou d'autres causes dans les prucheraies de la région des montagnes de Huron dans l'État du Michigan, aux É.-U. Cette région reçoit environ 100 éclairs nuage-sol par année, dont la plupart surviennent de mai à août. Nous avons noté les dommages abiotiques et biotiques sur 309 arbres répartis le long de neuf transects, chacun ayant plus de 2 km de long. Aucun des arbres présents dans les transects ne portait de cicatrices de foudre et nous avons observé seulement 14 cas évidents de dommages causés par la foudre parmi les milliers d'arbres examinés durant des inventaires par cheminement associés (chacun ayant env. 0,5 ha). Ces dommages étaient le plus souvent associés à une stature émergente (50 % des arbres frappés) et à des taux plus élevés de dommages biotiques (50 %) que ceux que nous avons observés chez les 309 arbres dans les transects (22 % avaient une stature émergente et 16 % avaient subi des dommages biotiques). Presque tous (93 %) les arbres endommagés par la foudre étaient des conifères, ce qui indique que soit la susceptibilité soit la réaction à la foudre aurait un fondement phylogénétique. Ces résultats préliminaires jettent les bases pour effectuer des études comparatives dans d'autres forêts. La quantification précise de la mortalité des arbres causée par la foudre va améliorer les modèles de renouvellement de la forêt et faciliter les prédictions concernant la structure future de la forêt soumise à une augmentation de la fréquence de la foudre. [Traduit par la Rédaction]

Mots-clés : foudre, forêt, Michigan, inventaire, révision.

Introduction

Lightning is among the most destructive of atmospheric phenomena. Its dramatic but localized effects on natural systems — from killing plants to shattering rocks (Jones and Gilbert 1918; Knight and Grab 2014) — have fascinated and terrified humans throughout history (Bazelyan and Raizer 2000; Rakov and Uman 2003; Bouquegneau and Rakov 2010). Lightning is one of many abiotic agents of tree damage (others include fire, frost cracking, and mechanical injury) that can lead to tree death either directly or indirectly by facilitation of subsequent biotic damage (e.g., beetle invasion, pathogen infection; Franklin et al. 1987). However, unlike other conspicuous disturbances (e.g., drought, wild fire, hurricanes; Lugo and Scatena 1996; Dale et al. 2001), the direct effects of lightning at larger scales (i.e., on forests and other ter-

Received 25 February 2015. Accepted 7 May 2015.

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Can. J. For. Res. **45**: 1258–1268 (2015) dx.doi.org/10.1139/cjfr-2015-0081

restrial ecosystems) rarely are quantified. This is a significant knowledge gap given the near ubiquity of lightning and the expectation that its frequency will increase dramatically with climatic change (Williams 2005; Romps et al. 2014). Here, we review the ecological effects of lightning in forests and provide a preliminary assessment of the distribution of lightning damage relative to other types of tree damage in a northern temperate woodland.

Lightning: an overview

Rakov and Uman (2003) comprehensively reviewed lightning physics and its effects at multiple scales. Other texts provide thorough treatments of subtopics such as protection against lightning damage (Bazelyan and Raizer 2000), lightning interaction with electrical power distribution infrastructure (Darveniza et al. 1967), and effects of lightning on humans and other animals (Andrews et al. 1992). Here we focus on the characteristics of lightning that are relevant to its non-fire ecological effects in forests (also see Komarek 1964; Taylor 1977).

The distribution of lightning frequency varies seasonally and geographically (e.g., Christian et al. 2003; Williams 2005; Price and Asfur 2006). Although lightning can occur in winter (i.e., “thundersnow”; Market et al. 2002), most lightning in the temperate zone is associated with storms during summer months (e.g., Plummer 1912; Mäkelä et al. 2011). Globally, lightning flash frequency is highest at tropical latitudes, where the frequency of intense storms also is relatively high. For example, central Panama (9°N) and the African Congo (1°S) receive ca. 40 and 80 flashes·km^{-2}·year^{-1}, respectively (Christian et al. 2003), which is 10–20 times more than the Huron Mountain region of Michigan, USA (47°N; the focus of this study).

Individual lightning flashes are complex electrical phenomena. The visible, destructive portion of lightning is the “return stroke”, which forms when ascending and descending electrical leaders meet. Lightning flashes vary in intensity and may occur from cloud to ground (CG), ground to cloud (GC), or within and between clouds (intra- and inter-cloud; IC). Whereas IC flashes generally are not ecologically relevant (Price and Rind 1993), a powerful subclass of lightning consisting of especially long-duration return strokes (i.e., continuing current or CC lightning) likely is responsible for shattering trees and igniting forest fires (Brook et al. 1962; Fuquay et al. 1972; Anderson 2002; Mäkelä et al. 2009).

Ecological effects of lightning

Biologists have been fascinated by lightning and its effects on trees for over a century (e.g., Anonymous 1898; Stone 1903). Millions of trees are directly damaged by lightning annually, and lightning scars (the characteristic longitudinal, localized stripe of damage on a struck tree trunk) are often easy to recognize when they occur. However, the biological effects of direct interactions between lightning and trees remain poorly understood and are largely based on anecdotal information (reviewed by Komarek (1964) and Taylor (1977)). Many of these anecdotes note that lightning was not immediately identified as the agent of tree damage or mortality (i.e., lightning scars were absent), suggesting that the direct ecological effects of lightning in forests are significantly underestimated. By contrast, the indirect effects of lightning — especially its role as a source of wild fire — are relatively well known (e.g., Chapman 1950; Taylor 1971, 1974; Platt et al. 1988; Latham and Williams 2001). Lightning is an important source of fire in temperate forests worldwide (e.g., Anderson 2002; Wierzchowski et al. 2002; Larjavaara et al. 2005; Duncan et al. 2010); however, on a global scale, exceedingly few lightning flashes result in fires (Taylor 1977; Paul and Waters 1978; Ruffner and Abrams 1998).

Although ecologists regularly list lightning as an important agent of tree death (e.g., Franklin et al. 1987; McCune et al. 1988; Clark and Clark 1991; Wright et al. 1997; Clark 2007), few have explored the relevance of direct, lightning-caused tree mortality to forest dynamics. Resolving this problem requires accurate counts of lightning-killed trees. Such data exist for very few sites (our search revealed only 15 apart from this study; Table 1) and often lack fundamental information required to accurately estimate landscape-level effects such as the number of CG flashes per hectare. Other key parameters for these estimates include the number of trees in a stand that are damaged by lightning annually, the fraction of trees in a stand that die from lightning damage annually, and stand composition.

One parameter in the above list — the annual rate of mortality attributed to lightning — is of primary interest and requires long-term census data, because trees often are not immediately killed by lightning (Wadsworth 1943; Taylor 1971). Existing long-term data tend to be biased toward pine forests (Table 1), perhaps because lightning damage to a pine tree often occurs as a conspicuous longitudinal scar and thus is easily quantified (Taylor 1977). Regardless, lightning is a particularly important direct agent of pine tree mortality in the southeastern US (Platt et al. 1988; Outcalt 2008), with as much as 90% of strikes leading to tree death (Reynolds 1940; Baker 1973). By contrast, only about half of lightning strikes to hardwood trees result in tree mortality (Baker 1973), although this estimate is based on data from a single Florida pine forest.

Lightning and trees: key hypotheses

The major hypotheses concerning ecological interactions between trees and lightning roughly fall into three categories: location effects, species-level effects, and indirect effects. The two principal location-based hypotheses are (1) that tall trees are struck more often than midcanopy or smaller trees and (2) that trees on ridge tops are struck more often than those in the surrounding lowlands. The physics of lightning suggests that relatively tall, isolated objects are highly susceptible to lightning (Rakov and Uman 2003). Similar patterns are hypothesized to occur in forests; specifically, trees with crowns projecting above the surrounding forest canopy (i.e., “emergent” trees; King and Clark 2011) are expected to receive proportionally more lightning strikes (Plummer 1912; Defandorf 1955; Anderson 1964). However, apart from anecdotes and isolated observations (e.g., Tutin et al. 1996), the only quantitative support for this hypothesis is from pine forests, where lightning damage is most common on larger trees (Reynolds 1940; Wadsworth 1943; Palik and Pederson 1996; Outcalt 2008). Other attempts to test this hypothesis have been inconclusive (Mäkelä et al. 2009), and lightning physicists likely would contend that small differences in crown height are inconsequential relative to the large scale a single lightning stroke (Bazelyan and Raizer 2000).

Similar to the relative tree height hypothesis, the significant elevation difference (i.e., hundreds of metres) between lowlands and ridge tops could lead to higher strike probability for ridge-top trees (Johnson 1966; Minko 1975; Muzika et al. 2015). Again, evidence supporting this hypothesis generally is lacking. The trend for lightning-initiated fires to be most common on the upper portions of montane slopes facing regular storm tracks (Fowler and Asleson 1984; Vankat 1985; Latham and Williams 2001) provides circumstantial support; however, fire-based evidence of lightning distribution and frequency is confounded by many other factors such as local moisture gradients and fuel loads (e.g., Anderson 2002). We suspect that advances in remote sensing of lightning flashes (and CG lightning in particular) such as the National Lightning Detection Network (NLDN; Cummins and Murphy 2009) ultimately will provide the data required to test the ridge-top hypothesis. Such data also will reveal the effects of communications towers (i.e., potential lightning attractors) specifically on peaks, which we suspect modify the landscape-level distribution of CG flashes and thus the spatial characteristics of lightning damage to trees (Yanoviak 2013).

Table 1. Estimated annual mortality rate of large (>30 cm DBH), mature trees in various forests due to lightning.

Location	Community	Method	Variable	Value ($\mathrm{ha}^{-1}\cdot\mathrm{year}^{-1}$)	Annual mortality (%)	Citation
Arizona	Pine forest	15-year tree survey	Trees killed	0.02	0.2	Wadsworth 1943
Arizona	Cactus desert	One-time survey	Cacti killed	0.5–3.2	0.6–4.0	Steenbergh 1972
Arizona	Mixed-conifer forests	14-year survey	Trees killed	0.1–0.9	0.7[ab]	Kane et al. 2014
Florida	Pine forest	10-year tree survey	Trees killed	0.29	1.5[c]	Outcalt 2008
Florida	Pine forest	Multi-year tree survey	Struck trees	0.06	1.5	Baker 1973
Georgia	Pine forest	4-year tree survey	Trees killed	n/a	3.7[a]	Platt et al. 1988
Georgia	Pine forest	5-year tree survey	Trees killed	0.15[d]	0.2	Palik and Pederson 1996
Georgia	Pine forest	One-time tree survey	Struck trees	1.55	4.7[a]	Paul and Waters 1978
Louisiana	Pine forest	5-year tree survey	Trees killed	0.01	<0.1[a]	Chapman 1923
Michigan	Hardwood–hemlock forest	One-time tree survey	Struck trees	0.04	0.7	This study
South Carolina	Pine forest	4-year tree survey	Trees killed	0.13	0.4	Outcalt 2008
South Carolina	Pine forest	3-year wildlife habitat survey	Trees killed	0.15	0.5	Harlow and Guynn 1983
Texas	Pine forest	Thunder days	Lightning strikes	1.12	3.4[a]	Rykiel et al. 1988
Texas	Pine forest	13-year wildlife habitat survey	Trees killed	n/a	0.3[a]	Conner et al. 1991
Australia	Pine forest	15-year survey	Trees killed	0.06	0.2	Minko 1975
Germany	Hardwood forest	Multi-year tree survey	Struck trees	n/a	0.3	Covert 1924

Note: "Annual mortality" estimates assume that 90% of strikes to pine trees and 50% of strikes to hardwoods are lethal (e.g., Baker 1973), and large tree density is 30·ha^{-1} in mature forests (Tyrrell and Crow 1994*b*; Gilliam and Platt 1999). n/a, not applicable.

[a] Calculated based on multiple assumptions described above and in the text.

[b] Although this study spanned 14 years, the estimates provided here were calculated based on 7 years, given the expectation that lightning damage is obscured by beetle damage within that time frame.

[c] For trees at least 30 m tall.

[d] Assumes that lightning causes 50% of mortality for pines with DBH > 20 cm.

The species-effect hypothesis posits that the likelihood of being struck by lightning varies predictably among tree species or plant growth forms (Anonymous 1898; Stone and Chapman 1912; Yanoviak 2013). Proposed mechanisms include differences in electrical conductivity, bark structure, and stem architecture (e.g., Plummer 1912; Gora and Yanoviak 2015). Field observations indicate that oak and pine trees are struck comparatively often and beech trees are struck comparatively infrequently (Shipley 1946; Taylor 1977; Ruffner and Abrams 1998). However, rigorous quantitative support for this hypothesis (i.e., a survey of lightning damage in the context of stand composition) is limited to a single study (Covert 1924). Moreover, an important alternative hypothesis cannot be ignored: all trees in a stand are equally likely to be struck by lightning, but different tree species respond differently to lightning, resulting in observer bias (Plummer 1912; Taylor 1977).

The indirect-effect hypothesis suggests that lightning frequently does not kill trees immediately; mortality of mature trees more often results from secondary damage caused by insect or pathogen infestation of the wound or by catastrophic wildfire. Unlike the ideas summarized above, this hypothesis has relatively good experimental and observational support. Lightning damage to pine trees is especially attractive to bark beetles (e.g., Chapman 1923; Johnson 1966; Schmitz and Taylor 1969; Coulson et al. 1983, 1999), and beetle infestation following lightning strikes is responsible for more than half of all tree mortality in some cases (Reynolds 1940; Conner et al. 1991). Similarly, lightning strikes have been associated with bud rot disease of individual coconut palms and dieback disease of rubber trees in Malaysia (reviewed by Taylor 1971, 1974). Although insect- and pathogen-mediated indirect effects often are spatially limited, their shifting distribution across landscapes and over time is hypothesized to have broader relevance to forest structure and dynamics (Knight 1987; Rykiel et al. 1988). At larger spatial scales, indirect lightning-caused mortality via wildfire is common in some forests (e.g., Taylor 1971, 1974; Latham and Williams 2001; Larjavaara et al. 2005) and has been exacerbated by fire suppression (e.g., Duncan et al. 2010). More information regarding the role of lightning in wildfire ignition is provided elsewhere (e.g., Latham and Williams 2001; Anderson 2002). Regardless of the direct or indirect nature of the mechanisms, accurate quantification of lightning-induced tree mortality will improve forest turnover models (e.g., Franklin et al. 1987; Keane et al. 2001) and facilitate predictions of future forest structure under conditions of increased lightning frequency (Williams 2005; Romps et al. 2014).

Research objectives

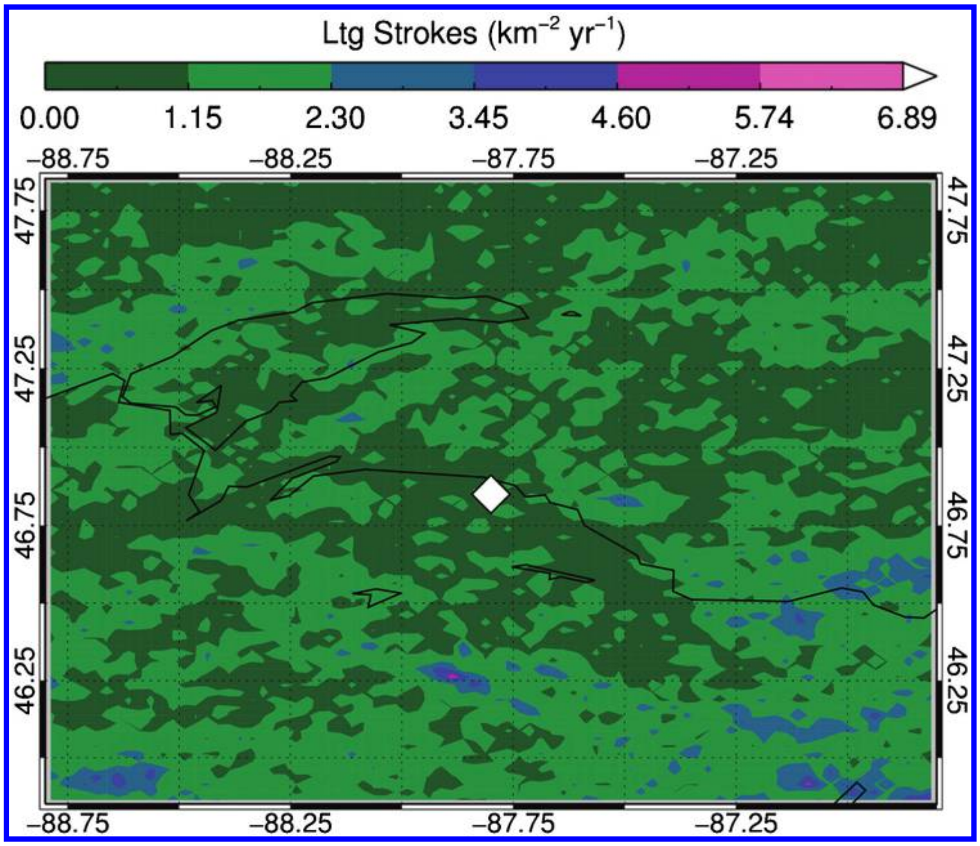
The principal goal of this study was to quantify the common types of damage to trees in an old-growth northern hemlock–hardwood forest of Upper Michigan with an emphasis on damage caused by lightning. A secondary goal was to estimate the annual rate of direct lightning mortality of trees in a variety of temperate forests based on information in the literature. We conducted a preliminary field survey in the Huron Mountain Region to address four predictions regarding the distribution of lightning damage: (*i*) lightning damage is more frequent among emergent trees than trees of average canopy height; (*ii*) lightning damage is more common at higher elevations; (*iii*) lightning damage is unevenly distributed among species; and (*iv*) trees damaged by lightning are more likely to have biotic damage than the surrounding tree community.

Methods

Estimation of lightning-caused tree mortality

We gathered lightning damage and tree mortality data from the literature to estimate annual lightning-caused mortality rates in a variety of temperate forests (Table 1). Relevant papers were obtained via electronic searches (e.g., Google Scholar with terms such as "lightning", "tree", "mortality", and "forest") and by cross-reference. We limited the results to articles written in English, and we excluded papers focusing on tropical forests and mangroves (although lightning is important in these systems; e.g., Anderson 1964; Smith et al. 1994; Magnusson et al. 1996; Zhang et al. 2008). We also excluded studies that did not provide sufficient or appropriate data for use in the estimations described below. These mainly included studies lacking quantitative information concerning the frequency of lightning-caused damage or tree mortality that was not due to fire (e.g., Coulson et al. 1983, 1999; Abdel-Rahman et al. 2014). Likewise, we excluded studies that carefully quantified snags and standing dead trees but could not identify the proportion of those killed by lightning (e.g., Harcombe and Marks 1983; Busing 2005). Ultimately, only 14 studies

Fig. 1. Lightning flash frequency (CG flashes, km⁻²·year⁻¹) for the Huron Mountain Region (white diamond) and surrounding areas based on NDLN data from 2008–2012.



of 141 articles examined met these criteria. Collectively, they provided enough detail to estimate landscape-scale lightning effects at 15 different sites.

Very few forest studies specifically quantified annual mortality due to lightning (e.g., Palik and Pederson 1996; Steenbergh 1972; Outcalt 2008), and inconsistencies in the type and quality of published information required us to base our estimates on three key assumptions derived from the literature. First, we assume that 90% of lightning strikes to pine trees and 50% of strikes to hardwood trees are lethal — if not immediately, then via subsequent insect or pathogen damage (Baker 1973; Reynolds 1940; Outcalt 2008). Second, although no two forests are exactly alike, we assume that old-growth temperate forests have ca. 150 trees per hectare with diameter at breast height (DBH) > 10 cm of which 30 per hectare are large individuals with DBH > 50 cm (e.g., Tyrrell and Crow 1994*b*; Palik and Pederson 1996; Gilliam and Platt 1999). This assumption was necessary as a basis for estimating the density of lightning-damaged trees when stand characteristics were not provided. Third, in most cases, the estimated mortality rates in Table 1 are for the largest trees only (i.e., "canopy" trees with DBH > 30 cm; Busing 2005), as these tend to receive the majority of lethal lightning strikes (e.g., Reynolds 1940; Palik and Pederson 1996; Outcalt 2008).

Study site

We conducted the field portion of this study in a large (80 km²) remnant of an old-growth hemlock–hardwood forest in the Huron Mountain region of the Upper Peninsula of Michigan (46.87°N, 87.88°W; Fig. 1). The Huron Mountain Club and other private landowners (hereafter collectively referred to as HMC) have managed this site since 1889. The HMC is located along the southern shore of Lake Superior and is subject to lacustrine boreal climate; most precipitation occurs as snow. The growing season typically extends from early June to late August, and the winds are predominantly from the west during this period. The bedrock is mainly Precambrian Canadian Shield, and the topography is composed of lakes and low rounded peaks across the landscape. The forests are typical of mesic, deciduous, sub-boreal forests; common trees include eastern hemlock (*Tsuga canadensis* (L.) Carrière), sugar maple (*Acer saccharum* Marshall), red maple (*Acer rubrum* L.), white pine (*Pinus strobus* L.), red pine (*Pinus resinosa* Aiton), red oak (*Quercus rubra* L.), and yellow birch (*Betula alleghaniensis* Britton). Additional details about the region and its forest cover are provided elsewhere (Dorr and Eschman 1970; Simpson et al. 1990; Dickmann and Leefers 2003).

Lightning frequency

Lightning activity in the Great Lakes region of North America is relatively low, with a combined (IC + CG) density of 2–4 flashes·km⁻²·year⁻¹ (Christian et al. 2003). However, strong summer storms do occur in the region, and the lakes significantly influence the local distribution of lightning (Letcher and Steiger 2010). The ratio of IC to CG flashes for Upper Michigan is ca. 2:1 (Boccippio et al. 2001), and the median CG flash density in the region is 1.2 flashes·km⁻²·year⁻¹ (Fig. 1). Consequently, the HMC and adjacent lands receive up to 100 CG strikes per year. Peak lightning activity for the region occurs in July (Fig. 2), and hourly flash frequency tends to be lowest between 0500 and 1100 hours (Fig. 3). These estimates (Figs. 1–3) were calculated from NLDN data for the years 2008–2012, inclusive. NLDN detects 60%–80% of CG lightning strokes with an estimated spatial accuracy of ca. 500 m (Cummins and Murphy 2009).

Tree damage survey

We surveyed trees at nine different locations in the HMC in July–August 2013. Each location was chosen based on the presence

Fig. 2. Average (+SE) monthly CG lightning flash counts for the area represented in Fig. 1 from 2008–2012.

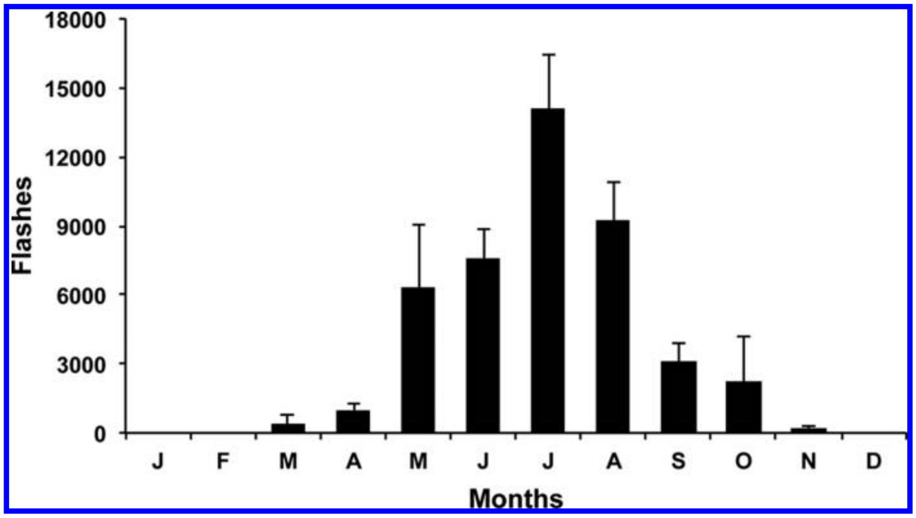
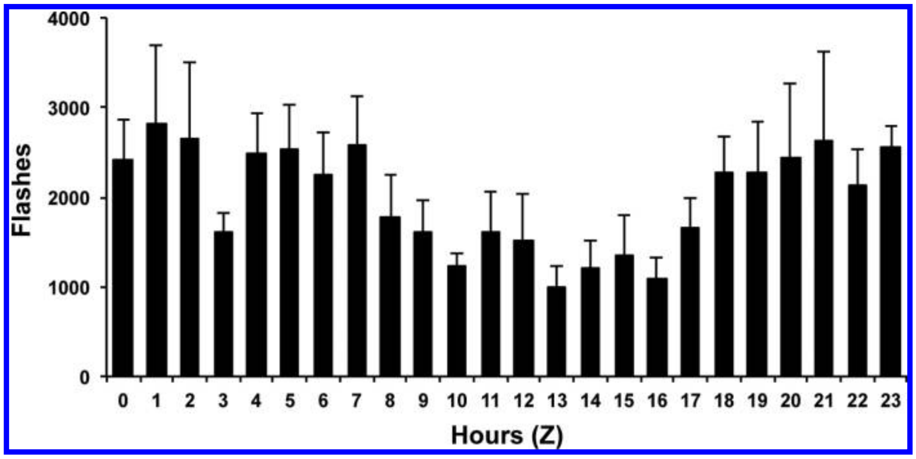


Fig. 3. Average (+SE) hourly CG lightning flash counts for the area represented in Fig. 1 from 2008–2012. Hours are given in Zulu (Z) time; the corresponding local time in the Huron Mountain Region is Z – 5 hours (e.g., Z = 10 corresponds to 0500 hours).



of a road or trail originating at a low elevation and continuing upslope (in six cases, ending on a ridge top). Each trail thus served as a linear transect for tree surveys spanning various forest types and elevations. Five of these transects were on approximately north-facing slopes, three were south-facing, and one was east-facing. At every 100 paces (71.3 ± 2.3 m) along each transect, we randomly chose (by coin flip) a side of the trail and walked 25–50 paces orthogonal to the trail. At the end of each walk, we selected the nearest living canopy tree as a focal tree for the survey (hereafter, "transect tree"). For each transect tree, we recorded its species, height, DBH, slope position (lowland, slope, ridge), trunk damage, tree condition, epicormic shoots (absence or presence), and location. We also noted its canopy status as "canopy" (i.e., approximately as tall as the average forest canopy level) or "emergent" (i.e., crown fully extending above the average canopy level; Clark and Clark 1992). Trees intermediate between these two relative heights were classified as "partially emergent". Finally, we estimated crown dieback (dead branches) as a percentage of the total tree crown volume (Stolte et al. 2002).

Trunk damage on each transect tree was recorded categorically as "biotic" (e.g., putative pathogen infection, insect invasion) or "abiotic" (e.g., frost crack, lightning). All types of bacterial and fungal damage were collectively referred to as "infection". Frost crack was defined as a vertical split of varying length and depth, but with little bark loss (Allen et al. 2010). Lightning damage was defined as a narrow furrow in the trunk bounded by stripped bark running nearly the full height of the tree (Murray 1958; Taylor 1965; Allen et al. 2010; Supplementary Fig. S1[1]). Lightning damage is sometimes inconspicuous or difficult to distinguish from other types of damage (Sharples 1933). To avoid this potential source of bias, we conservatively estimated lightning damage by classifying all longitudinal trunk scars of ambiguous origin as frost crack. The other extreme — explosive destruction of a tree by lightning (e.g., Norbury 1927) — also was not included in our survey due to its relative rarity and our inability to definitively identify lightning as the agent in such cases (Mäkelä et al. 2009). We measured tree condition by subjectively estimating overall tree health (on a scale of 0–10, with 10 being the healthiest) based on the superficial appearance of the crown and trunk (Ferretti 1996). Epicormic shoots (hereafter referred to as "sprouts") were recorded as a potential indicator of tree stress.

Upon completion of data collection from a transect tree, we conducted a 2-min "meander" survey covering ca. 0.5 ha of forest around the tree (similar to the "zig-zag" survey of Conner et al. 1991). Each meander survey consisted of a haphazard walk in a roughly circular area with the transect tree at the center, during

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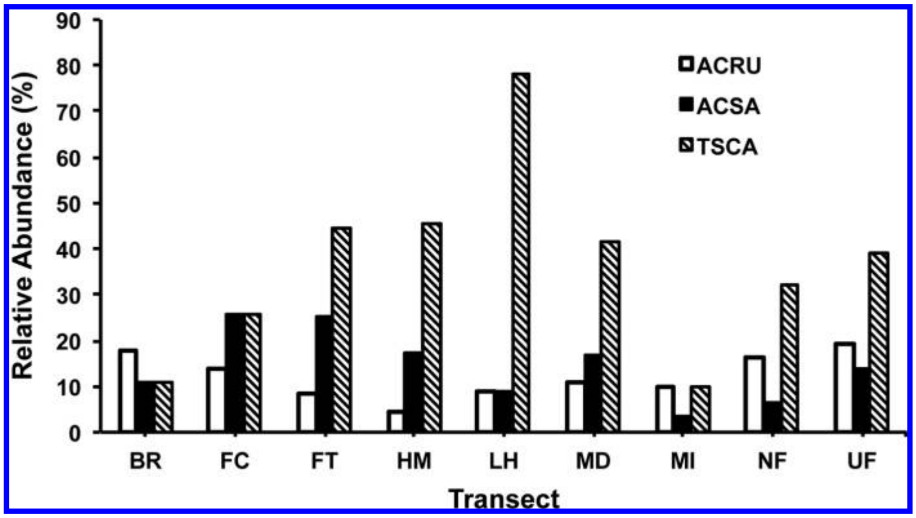
[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2015-0081.

Fig. 4. Abundance of the three most common tree species as a percentage of the total sampled in each transect (ACRU, *Acer rubrum*; ACSA, *Acer saccharum*; TSCA, *Tsuga canadensis*). See Table 2 for transect abbreviations.



which live and dead trees were examined for lightning damage. We only identified trees that had clearly been struck by lightning; consequently, extensive healing or decay may have disqualified some candidate trees. The same protocol used to record transect tree characteristics was applied to lightning-struck trees encountered during meander surveys. We recognize that structured surveys of randomly located plots would generate more robust data for this portion of the study; however, this approach was not possible given time and resource constraints. The meander surveys provided a useful and efficient mechanism for examining a large number of trees at all transect locations.

Quantitative analysis

We calculated focal tree species diversity for each transect using the Shannon index (H'; Magurran 1988) and compared species diversity among slope position categories with ANOVA. We used the Shannon index (instead of species richness) as the focal variable because the number of focal trees differed among transects. Slope position, canopy class, trunk damage, and sprout frequencies were compared using G tests (Sokal and Rohlf 1995). Canopy class and slope position violated test assumptions of minimum expected values, so trees in the partially emergent category were combined with the emergent category for analysis. Conifers do not produce epicormic shoots and were excluded from analyses of sprouts. Crown dieback was grouped into 20 categories, each containing a 5% range of dieback (category 1 = 0%–5%, 2 = 6%–10%, etc.). Trees exhibiting unambiguous lightning damage were too infrequent for parametric analysis, so we used simple descriptive statistics to compare characteristics of lightning-damaged trees encountered in meander surveys with those of the transect trees. All statistical analyses were conducted using the R statistical package ver. 3.1.1 (R Core Team 2014).

Results

Data gathered during our field survey in Michigan showed that tree community composition in the transects was consistent with previous descriptions for the region (Simpson et al. 1990; Dickmann and Leefers 2003). The three species present in all transects were red maple, sugar maple, and hemlock, with hemlock being the most common overall. Collectively, these three species represented >50% of the trees in seven of the nine transects (Fig. 4). Despite some minor compositional differences, tree diversity indices were very similar among transects (Table 2), and average diversity did not differ among slope position classes (ANOVA, $F_{[2,19]} = 0.158$, $p = 0.86$).

Clear evidence of lightning strike damage was rare in the HMC forest. Although nearly one-third of the 309 trees (and half of all maple trees) in the transect surveys had some type of trunk damage (Tables 3 and 4), none of these cases could be attributed to lightning with a high degree of confidence. In general, lowland trees, emergent trees, and hardwoods were more likely to show some kind of damage (Tables 3 and 4). Most biotic damage occurred as bacterial or fungal infections, whereas frost crack was the most common type of abiotic damage (Table 5). The presence of sprouts (a potential indicator of stress) was consistently associated with high levels of crown dieback (Fig. 5).

Biotic damage was twice as common on emergent trees than on canopy trees and six times more common on emergent trees than on partially emergent trees (Table 3). However, these patterns were not statistically significant ($G < 5.38$, $p > 0.07$, in both tests), and we view them as very preliminary, given a sample size of a few hundred trees. Similarly, the relative frequency of canopy and combined emergent and partially emergent trees did not vary with slope position ($G = 3.1$, df = 2, $p = 0.21$). Despite trends for increasing frequency of sprouts (Fig. 6) and decreasing frequency of frost cracking with elevation (Fig. 7), slope position was not associated with sprout presence, biotic damage, abiotic damage, or frost cracking ($G < 4.9$, df ≤ 2, $p > 0.09$, in all tests). Transect trees in poor health (with a combination of extensive crown dieback, low condition score, and sprouts) were rare in our survey.

Although none of the 309 transect trees had lightning damage, we found clear evidence of 14 lightning strikes among the several thousand trees observed during the associated meander surveys (Table 6; Supplementary Fig. S1[1]). Half of these lightning-struck trees were of emergent stature, which is considerably higher than the frequency of emergent trees in the transect surveys (22%; Table 6). Although not statistically significant (and with low statistical power due to the low lightning frequency that is characteristic of the region), this pattern provides correlative support for the prediction that emergent trees are more susceptible to lightning strikes. In contrast, the prediction that lightning damage frequency increases with elevation within the region was not supported. Specifically, there was no association between the occurrence of lightning damage and slope position (Table 6). Likewise, there was no obvious effect of slope aspect; nine of 14 lightning-damaged trees were on north-facing slopes, with the remaining five trees facing east or south, which roughly corresponds to the distribution of transect aspects (Fisher exact test, $p > 0.35$).

The distribution of lightning damage among tree taxa suggests that some tree species are either more likely to be struck or more

Table 2. Transect location (coordinates of the beginning of the transect), average elevation, Shannon diversity (*H*'), and tree species composition.

		Location (degrees)				Relative abundance (%)[a]						
Transect	*N*	Latitude (N)	Longitude (W)	Elevation (m) (range)	*H*'	ACRU	ACSA	BEAL	PISP	QURU	TSCA	Other
BR	28	46.8581	87.8240	286 (220–351)	1.82	17.9	10.7	3.6	32.1	17.9	10.7	7.1
FC	43	46.8574	87.8791	239 (193–265)	1.86	14.0	25.6	16.3	4.7	0	25.6	14.0
FT	36	46.8767	87.8841	258 (207–317)	1.59	8.3	25.0	5.6	8.3	2.8	44.4	5.6
HM	46	46.8862	87.8958	320 (197–466)	1.44	4.3	17.4	0	21.7	10.9	45.7	0
LH	23	46.8834	87.9096	256 (203–312)	0.75	8.7	8.7	4.3	0	0	78.3	0
MD	36	46.8734	87.9349	366 (300–462)	1.68	11.1	16.7	11.1	5.6	8.3	41.7	5.6
MI	30	46.8513	87.8389	289 (245–409)	1.89	10.0	3.3	0	50.0	13.3	10.0	13.3
NF	31	46.8712	87.8960	306 (259–368)	1.57	16.1	6.5	0	32.3	12.9	32.3	0
UF	36	46.8187	87.8532	267 (243–289)	1.32	19.4	13.9	27.8	0	0	38.9	0

Note: "Relative abundance" is the percentage of each species per transect. Species codes: ACRU, *Acer rubrum*; ACSA, *Acer saccharum*; BEAL, *Betula alleghaniensis*; PISP, combined *Pinus strobus* and *Pinus resinosa*; QURU, *Quercus rubra*; TSCA, *Tsuga canadensis*. Transect codes: BR, Breakfast Roll; FC, Fisher Creek; FT, Fortress; HM, Huron Mountain; LH, Lower Huron Mountain; MD, Mount Ida; MI, Mount Ives; NF, Norways/Fortress; UF, Upper Falls.

Table 3. The proportion (%) of trees having abiotic, biotic, or both types of trunk damage in relation to regional topography, status in the local forest profile, and wood type.

			Proportion (%) of trees with trunk damage			
Factor	Level	*N*	Abiotic	Biotic	Both	Total
Relative elevation	Lowland	170	12.9	20.6	7.1	40.6
	Slope	91	12.1	12.1	4.4	28.6
	Ridge	48	6.3	12.5	6.3	25.0
Canopy class	Canopy	241	12.0	17.4	6.2	35.7
	Partially emergent	49	10.2	6.1	6.1	22.4
	Emergent	19	10.5	36.8	5.3	52.6
Tree type	Conifer	163	11.7	12.9	4.3	28.8
	Hardwood	146	11.6	21.2	8.2	41.1

Note: "Total" is the proportion of damaged trees (regardless of damage type) in each category. Data are from 309 trees distributed among nine transects, thus *N* = 309 for each factor.

Table 4. Frequency (%) of trunk damage (biotic, abiotic, both, and total trees with damage) among the six most common tree species in the transect tree survey.

		Frequency (%) of trunk damage			
Species	*N*	Abiotic	Biotic	Both	Total
Red maple (ACRU)	37	8.1	24.3	18.9	51.4
Sugar maple (ACSA)	47	19.1	25.5	6.4	51.1
Yellow birch (BEAL)	25	8.0	16.0	8.0	32.0
White pine (PIST)	44	9.1	20.5	2.3	31.8
Red oak (QURU)	22	9.1	13.6	4.5	27.3
Eastern hemlock (TSCA)	111	13.5	9.9	3.6	27.0
All species pooled	309	11.3	16.2	6.1	32.7

Note: *N* = number of trees of each species. See Table 2 for species codes.

Table 5. The frequency (%) of biotic and abiotic damage among affected individuals in the transect tree survey.

Damage	Damage type	Frequency (%)
Biotic (*N* = 65 trees)	Infection	77
	Insect infestation	15
	Browse	5
	Strangle	3
Abiotic (*N* = 55 trees)	Frost crack	76
	Fire	2
	Miscellaneous, major	13
	Miscellaneous, minor	9

Note: Damage type: infection, bacterial and fungal infection; browse, damage by deer and beavers; strangle, trees growing around each other; miscellaneous, installation of fence wire (minor), snags contacting living trees (major), and unidentifiable sources.

Fig. 5. The frequency (%) of hardwoods with and without sprouts in each crown dieback category. Low dieback values indicate healthier trees (i.e., characterized by low relative abundance of dead branches in a crown).

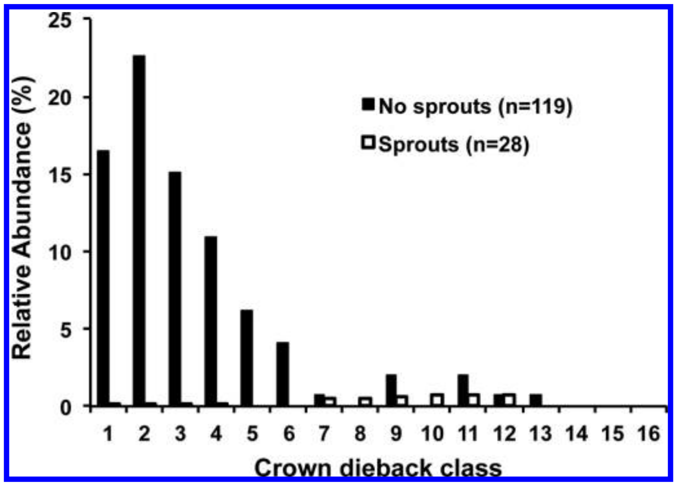
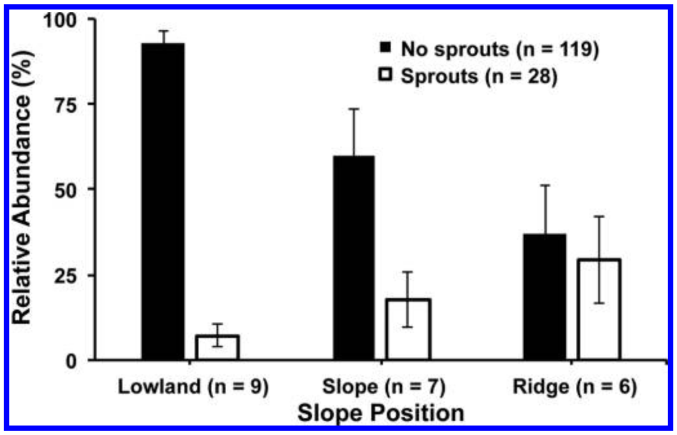


Fig. 6. Average (±SE) frequency of sprouts (epicormic shoots) on trees of differing slope position.



vulnerable to lightning damage than others. Conifers and hardwoods were approximately equally represented in our transect tree survey (Table 2), but >90% of lightning-damaged trees were conifers (Table 6). Within lightning-struck conifers, there was no obvious species bias (white pine, *n* = 5; red pine, *n* = 3; hemlock, *n* = 5).

Fig. 7. Average (±SE) frequency of frost crack and biotic damage on trees of differing slope position.

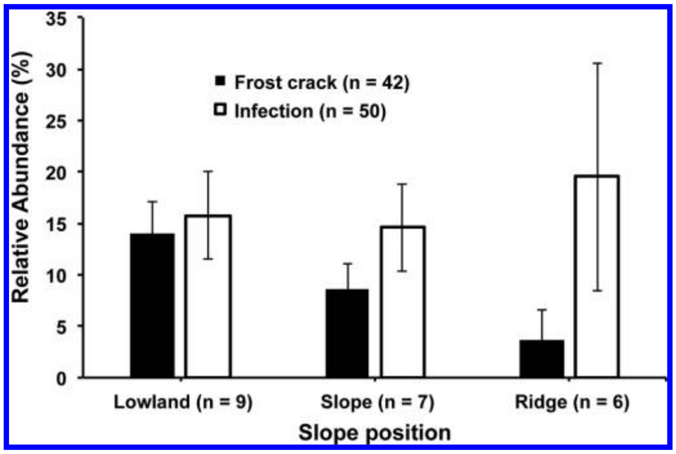


Table 6. Characteristics of lightning damaged trees (*n* = 14) encountered in 309 meander surveys versus trees not struck with lightning observed in 309 corresponding transect surveys.

Characteristic	Lightning-damaged	Not lightning struck
Mean (± SE) elevation (m)	296±17	289±4
Slope position (%)		
Lowland	43	55
Slope	29	29
Ridge	29	16
Biotic damage (%)	50	21
Conifer (%)	93	53
Emergent (%)	50	22

Note: Characteristics: slope position, frequency (%) of trees in each elevation class; biotic damage, fraction of trees exhibiting biotic damage as described in Table 4; conifer, fraction of trees that are coniferous (vs. hardwood); emergent, fraction of trees having emergent or partially emergent stature (vs. canopy).

Half of the lightning-damaged trees also had secondary fungal, bacterial, or insect damage (Table 6). This frequency of biotic damage was more than double the overall frequency of biotic damage observed among transect trees (Table 4) and for conifers alone (13%; Table 3). Although biotic damage was more frequent in emergent trees in the focal survey, less than half of the lightning-struck trees with biotic damage were emergent.

Discussion

Lightning and tree mortality

Numerous forest surveys are conducted around the world each year, but very few systematically record direct lightning damage to trees (Table 1). When lightning damage is specifically quantified, the results often lack the context of tree density or stand composition (Ruffner and Abrams 1998; Mäkelä et al. 2009). Overall, the most informative data regarding direct lightning damage to trees are from pine forests in southern North America (e.g., Outcalt 2008); similar information for northern forests is limited to very few studies (e.g., Covert 1924). Here, we contribute a preliminary assessment of lightning damage to trees in a hemlock–hardwood forest in a region characterized by very low lightning frequency. We examine the results in the context of major hypotheses concerning the distribution of lightning damage and compare the frequency of lightning damage with estimates for other forests.

Our literature review revealed that rates of lightning-caused mortality vary by an order of magnitude within and among sites (from <0.1% to >3.0%; Table 1) and approach 4.7% annually for the largest trees in some pine forests (e.g., Paul and Waters 1978). Similar mortality data from non-pine forests are limited to studies of cactus communities in Arizona and hardwood forests in Germany (Table 1). The former experience up to 4% annual lightning-caused mortality (Steenbergh 1972), whereas lightning mortality rates are 10 times lower in the German forests (Table 1). Even where annual mortality is low, direct damage from lightning can still be an important variable in forest dynamics over longer temporal scales (Johnson 1966; Outcalt 2008). For example, Wadsworth (1943) estimated that lightning ultimately causes one-third of large ponderosa pine mortality in northern Arizona, although annual lightning-associated mortality rates are only ca. 0.2% (Table 1). Similarly, the low lightning mortality rates in mixed-conifer forests of Arizona (Kane et al. 2014) likely are underestimates, given the high potential for secondary beetle damage to obscure lightning damage after just a few years.

The results of our field study provide the first quantitative survey of tree damage and, specifically, direct lightning damage in a sub-boreal forest of the Western Hemisphere. Lightning frequency generally decreases with increasing latitude in North America (Christian et al. 2003) and currently is very low in Upper Michigan. Consequently, the rarity of clear lightning strike damage that we observed was expected and is similar to the results of lightning damage surveys conducted in other northern forests (Ruffner and Abrams 1998; Mäkelä et al. 2009). Results of our survey suggest that lightning damages ca. 0.7% of the largest trees in northern Michigan annually. Although not all lightning damage is lethal, this estimate roughly coincides with the rate of standing dead snag production in old-growth forests of the region (Tyrrell and Crow 1994*a*) and is consistent with lightning-caused mortality rates calculated for other temperate forests (Table 1).

Following the major hypotheses concerning lightning interactions with trees, we expected that the frequency of lightning damage would be conspicuously higher on emergent trees and trees on exposed ridge tops (e.g., Plummer 1912; Muzika et al. 2015). However, only our prediction for the role of emergent status was supported. We cannot generalize based on data from 14 lightning-damaged trees, but some differences between those trees and the transect trees suggest patterns that deserve further exploration. For example, the even distribution of abiotic damage among canopy classes for transect trees suggests that the more frequent lightning damage to emergent trees was a product of their height rather than other factors such as tree age. Similar studies in pine forests also suggest that lightning damage is more common on emergent trees (e.g., Palik and Pederson 1996), but the evidence remains entirely correlative. Regardless, collecting cores from damaged trees (e.g., Kane et al. 2014) would resolve age effects and thus be a useful extension of this project.

Our observation that lightning damage is more common on conifers corresponds with results of similar surveys in mixed temperate forests (e.g., Ruffner and Abrams 1998). We propose three hypotheses to explain this pattern: (1) conifers are struck more often than hardwoods, (2) conifers show lightning damage more conspicuously, or (3) conifers survive longer following a lightning strike. Published anecdotes suggest that physiological and structural characteristics underlie the variability of lightning damage among species (Furtado 1935; Shipley 1946; Orville 1968). However, numerous factors (e.g., tree age, tree health, and characteristics of the lightning flashes) are potentially confounding. The post-hoc nature of our survey did not allow us to differentiate between these three explanations.

Any biotic or abiotic agent that damages living tree tissues is likely to facilitate secondary infection by microbial or insect pathogens. Surveys in southern US forests showed that trees damaged by lightning were significantly more attractive to beetles than trees damaged by other abiotic factors (Coulson et al. (1983, 1999) and Conner et al. (1991) and references therein). Our results suggest a similar pattern in the HMC forest: trees with lightning damage had a higher rate of biotic damage than did the surrounding tree community, and this was not confounded by the higher frequency of lightning damage on emergent trees. Although this trend is supported in the literature, we caution that our data are insufficient to establish a causal relationship between biotic damage and lightning in the HMC.

In summary, the results of our forest survey at least superficially supported three of our four predictions. Specifically, lightning damaged trees were often emergent, conifers showed lightning damage more often than hardwoods, and biotic damage occurred with higher frequency on lightning-struck trees than on trees in the surrounding community. However, we did not find a relationship between lightning damage and elevation across the landscape. Although this intensive tree damage survey is the first of its kind in northern Michigan, our conclusions clearly are limited by the correlative nature of the results, the low incidence of lightning in the region, and the necessarily conservative identification of lightning damaged trees. Nonetheless, studies like this one are uncommon and provide an important first step in evaluating the ecological importance of lightning in eastern deciduous forests.

Obstacles to lightning research

The non-fire ecological effects of lightning on trees remain poorly understood for several reasons, most of which are practical. The most challenging aspect of lightning is its spatial and temporal unpredictability, which presents a formidable obstacle for empirical ecological studies conducted in real time (Komarek 1964; Knight 1987). Direct observations of lightning strikes to trees are characteristically rare and fortuitous (e.g., Furtado 1935; Orville 1968; Tutin et al. 1996). Data from lightning monitoring networks (e.g., Cummins and Murphy 2009) offer a potential solution to this problem by providing approximate locations of probable strikes. However, the spatial resolution of this technology (hundreds of metres) is currently insufficient for practical use in the field (Mäkelä et al. 2009). Consequently, most lightning data are collected via post-hoc forest surveys (Table 1), which are time- and labor-intensive and prone to underestimation (see below) and observer bias (Mäkelä et al. 2009).

A second major obstacle to lightning research in an ecological context is that the effects of lightning on trees are often delayed or inapparent (Taylor 1977). For example, in two cases in which lightning strikes to trees were captured on film (Orville 1968; Mäkelä et al. 2009), subsequent inspection of the trees revealed no evidence of the event. In another study, Furtado (1935) chronicled lethal lightning strikes to three trees in a small area of Singapore. One (*Fagraea fragrans* Roxb.) died immediately and explosively, but the other two (*Ficus variegata* Blume and *Falcataria moluccana* (Miq.) Barneby & Grimes) showed less obvious signs of damage and died over a period of weeks. Taylor (1977) summarized other similar examples. It is unlikely that lightning would be identified as the agent of mortality in these cases, and such trees typically would be classified as "standing dead" in forest surveys (e.g., McCune et al. 1988). This classification obscures potentially important effects of lightning on forest dynamics and its role in increasing snag density.

The third major logistical obstacle to lightning research is that lightning is inherently dangerous and not easily manipulated or replicated for experimental studies. Most lightning strikes to humans and other animals are unpredictable and frequently lethal (Andrews et al. 1992), thus lightning research requires special precautions (Fieux and Hubert 1976). Although it is possible to induce lightning strikes (e.g., by launching rockets trailing copper wires; Newman et al. 1967; Fieux et al. 1975; Uman and Krider 1989), this approach would be very technically challenging and not feasible in many (e.g., protected) forests.

Finally, as a localized, transient, stochastic disturbance, lightning is presumed to have unimportant or immeasurable population-level consequences. The lack of information to address this problem motivated our effort to compile the estimates in Table 1. We and others (Komarek 1964) argue that lightning has been an important selective force in the evolution of trees (and possibly vines; Yanoviak 2013), and we hope that increased awareness of these important data gaps and more careful documentation of lightning-caused mortality will enhance our understanding of its population-level effects.

Acknowledgements

We thank the Huron Mountain Club for allowing us to conduct research on their land. Kerry Woods and the Huron Mountain Wildlife Foundation provided logistical support. Comments from two anonymous reviewers improved the manuscript. This research was supported by grants from the Huron Mountain Wildlife Foundation to S.P.Y. and W.P.C. and the National Science Foundation (grant DEB-1354060 to S.P.Y.).

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