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ARTICLE

# Electrical properties of temperate forest trees: a review and quantitative comparison with vines

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**Abstract:** Trees form the terrestrial interface with the atmosphere in forested regions. The electrical properties of trees may influence their response to atmospheric conditions and potentially lethal phenomena (e.g., lightning). We review the literature describing electrical properties of trees and provide a tabular summary of the methods and goals of each study. We hypothesized that electrical resistivity varies consistently among species and between growth forms. We surveyed resistivity of eight tree and three vine species in Michigan and Kentucky, and we quantified resistivity over a moisture gradient for wood blocks of four tree species. Resistivity varied predictably with stem diameter and differed among species and growth forms. Specifically, resistivity of trees was approximately 200% higher than resistivity of vines, and resistivity of conifers was 135% higher than that of hardwoods. The regional comparison showed no difference in resistivity of red maple (*Acer rubrum* L.) and sugar maple (*Acer saccharum* Marsh.) between Michigan and Kentucky. These results, in combination with interspecific differences observed among wood blocks, suggest that there is a phylogenetic basis for variation in resistivity that reflects differences in anatomy and physiology. Our review and empirical survey provide a framework for studying the ecological effects of lightning in the context of the electrical properties of trees.

*Key words:* lightning, Michigan, resistivity, Kentucky, moisture.

**Résumé :** Dans les régions forestières les arbres constituent l'interface terrestre avec l'atmosphère. Les propriétés électriques des arbres peuvent influencer leur réaction aux conditions atmosphériques et aux phénomènes potentiellement létaux (p. ex. la foudre). Nous avons fait une revue de la littérature qui porte sur les propriétés électriques des arbres et nous présentons un tableau sommaire des méthodes et objectifs de chaque étude. Nous formulons l'hypothèse que la résistivité électrique varie uniformément parmi les espèces et que des facteurs physiologiques ou anatomiques, autres que la teneur en humidité, font partie des mécanismes importants qui sous-tendent ces différences. Nous avons relevé la résistivité de huit espèces d'arbre et de trois espèces de vigne au Michigan et au Kentucky et nous avons quantifié la résistivité de blocs de bois de quatre espèces d'arbre en fonction d'un gradient d'humidité. La résistivité variait de façon significative selon l'espèce et la forme de croissance. Plus particulièrement, la résistivité des arbres était environ 200 % plus élevée que celle de la vigne et la résistivité des conifères était 135 % plus élevée que celle des feuillus. La comparaison entre les régions n'a révélé aucune différence de résistivité chez l'érable rouge (*Acer rubrum* L.) et l'érable à sucre (*Acer saccharum* Marsh.) entre le Michigan et le Kentucky. Ces résultats, combinés aux différences interspécifiques observées parmi les blocs de bois, indiquent que la variation de la résistivité a un fondement phylogénétique qui reflète probablement des différences anatomiques et physiologiques. Notre revue de la littérature et notre relevé empirique fournissent un cadre de travail pour étudier l'écologie de la foudre dans le contexte des propriétés électriques des arbres. [Traduit par la Rédaction]

*Mots-clés :* foudre, Michigan, résistivité, Kentucky, humidité.

## Introduction

Scientific interest in the electrical properties of plants spans more than a century (e.g., Stone 1903). We briefly summarize the literature concerning the biologically relevant electrical characteristics of plants with an emphasis on trees. Although not comprehensive, our review includes the bulk of the available literature written in English and spans the full historical range of the subject. We focus on three subtopics concerning the electrical properties of trees: their physiological or anatomical basis; the effects of tree condition (i.e., the presence of pathogens or decay); and diel, seasonal, and climate-driven variation. Then, the results from a field-based survey of electrical resistivity (Ωm) of temperate tree and vine species are presented. The broader goal of this work is to provide a framework for exploring how the electrical properties of plants affect their response to atmospheric conditions and phenomena, particularly lightning (see, e.g., Stone (1903) and Yanoviak (2013)).

## Electrical properties: variables and methods

The electrical properties of plants generally are measured using the same focal variables that characterize electrical circuits and their components. These include electrical potential, resistance, conductance, impedance, capacitance, and inductance (Table 1). The three variables most commonly measured in trees are potential (the internal current or voltage), resistance (the opposition to direct current between two points and the inverse of conductance), and impedance (the opposition to alternating current between two points; see, e.g., Tattar and Saufley (1973) and Gibert et al. (2006)). By contrast, capacitance and inductance are rarely measured for trees.

Although the suite of electrical variables commonly measured for trees is relatively small, the methodological approaches are diverse and often employ single-use or custom-made equipment (Table 1; Glerum and Krenciglowa 1970; Inaba et al. 1995; Gibert

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**Table 1.** Summary of literature pertaining to the electrical properties of plants, especially trees.

| Electrical property | Location | Species | Focal tissue | Objective or topic | Citation |
|---|---|---|---|---|---|
| Capacitance | Lab | *Salix myrsinifolia* | Root | Root system size | Cao et al. 2011 |
| | Lab | *Cornus sericea* | Stem | Cold injury and acclimation | Evert and Weiser 1971 |
| | Nova Scotia, Canada | *Abies balsamea* | Cambium, trunk | Foliar biomass | MacDougall et al. 1987 |
| | Nova Scotia, Canada | *Abies balsamea* | Cambium | Foliar biomass, spacing, season | Piene et al. 1984*b* |
| | Ontario, Canada | *Populus* sp. | Root | Root biomass | Preston et al. 2004 |
| Conductance | Lab | *Cornus sericea* | Stem | Cold injury and acclimation | Evert and Weiser 1971 |
| Conductivity | Lab | Various | Stem, root, leaf | Plant fluids | Heald 1902 |
| | Various | Various | Various | Literature review | Stiles and Jorgensen 1914 |
| | Lab | Various | Various | Differences among tissues and species | Plummer 1912 |
| Impedance | Lab | *Salix myrsinifolia* | Root | Root system size | Cao et al. 2011 |
| | New Brunswick, Canada | *Picea glauca, Persea americana* | Twigs | Water potential, temperature | Dixon et al. 1978 |
| | Lab | *Cornus sericea* | Stem | Cold injury and acclimation | Evert 1973 |
| | Ontario, Canada | Various | Twig, bark, xylem | Tissues before and after death | Glerum and Krenciglowa 1970 |
| | Hawkes Bay, New Zealand | *Prunus persica* | Fruit | Cells during ripening | Harker and Maindonal 1994 |
| | Okayama, Japan | *Cucumis sativus* | Fruit | Cellular components, ethylene production | Inaba et al. 1995 |
| | Pescia, Italy | *Olea europaea* | Stem, leaf | Seasonal changes in cells | Mancuso 1999 |
| | Lab | Various | Cellulose fibers | Types of pulp fibers; ions | Mason et al. 1950 |
| | Eastern Finland | *Salix viminalis* | Stem | Frost hardening | Repo et al. 1997 |
| | Central Finland | *Betula pendula* | Leaf | Effects of atmospheric gas composition on leaves | Repo et al. 2004 |
| | Lab | *Salix myrsinifolia* | Root | Root growth | Repo et al. 2005 |
| | Turin, Italy | Various | Trunk | Tree decay | Sambuelli et al. 2003 |
| | Lab | *Lotus corniculatus* | Stem | Cold acclimation | Stout 1988 |
| | Maine, USA | *Acer saccharum, Acer rubrum* | Heartwood | Wood decay stages | Tattar and Saufley 1973 |
| | Lab | *Eucalyptus marginata* | Trunk | Mold lesions | Tippett and Barclay 1987 |
| | Nova Scotia, Canada | *Solanum tuberosum* | Tuber | Cold injury | Zhang and Willison 1992 |
| | Lab | *Solanum tuberosum* | Tuber section | Heat injury | Zhang et al. 1993 |
| Polarity | Various | Various | Various | Literature review; growth and regeneration, physiology | Bloch 1943 |
| Potential | Ontario, Canada | *Solanum lycopersicum* | Stem | Stimulation of growth | Black et al. 1971 |
| | Ontario, Canada | *Ulmus americana, Pinus resinosa, Acer saccharum* | Trunk | Daily and seasonal changes | Fensom 1963 |
| | Lab | *Populus nigra* | Trunk, roots | Daily and seasonal changes | Gibert et al. 2006 |
| | Slovakia | *Phaseolus angularis* | Stem | Gravitropism | Imagawa et al. 1991 |
| | Ontario, Canada | *Quercus serris* | Trunk | Annual changes | Koppán et al. 2000 |
| | Lab | *Pseudotsuga menziesii* | Trunk | Radial and longitudinal variation in living and dead sections | Lund 1931 |
| | Brittany, France | *Populus nigra* | Trunk | Vertical, diel, seasonal variation; passing clouds | Le Mouël et al. 2010 |
| | Lab | *Chara vulgaris* | Cell | Vacuole fluid in light and dark | Murdoch and Sinclair 1976 |
| | Various | Various | Wood | Literature review; piezoelectric properties of wood | Ross et al. 2012 |

**Table 1** (*continued*).

| Electrical property | Location | Species | Focal tissue | Objective or topic | Citation |
|---|---|---|---|---|---|
| Resistance | Lab | *Solanum lycopersicum* | Stem | Stimulation of growth | Black et al. 1971 |
| | Lab | *Ulmus americana* | Xylem | Dutch elm disease | Blanchard and Carter 1980 |
| | New England, USA | *Abies balsamea* | Cambium | Growth rate | Blanchard et al. 1983 |
| | Lab | *Salix myrsinifolia* | Root | Root system size | Cao et al. 2011 |
| | Maine, USA | *Acer rubrum* | Phloem | Phloem width | Carter and Blanchard 1978 |
| | Lab | *Lycopersicon esculentum* | Roots | Fungal infections | Caruso et al. 1976 |
| | Montana, USA | *Pinus contorta* | Phloem | Phloem thickness | Cole and Jensen 1979 |
| | Lab | *Chara corallina* | Cell pairs | Properties of plasmodesmata | Côté et al. 1987 |
| | New England, USA | *Abies balsamea, Picea rubens* | Cambium | Spruce budworm infestation | Davis et al. 1980 |
| | Unreported | *Liriodendron tulipifera* | Entire tree | Variation from soil to branch tips | Defandorf 1955 |
| | New Brunswick, Canada | *Picea glauca, Persea americana* | Twigs | Water potential, temperature | Dixon et al. 1978 |
| | Ontario, Canada | *Acer saccharum* | Trunk, branch | Temperature | Fensom 1960 |
| | Ontario, Canada | *Acer saccharum* | Trunk | Daily and seasonal trends | Fensom 1963 |
| | Quebec, Canada | *Abies balsamea, Picea glauca* | Cambium | Tree vigor | Gagnon et al. 1987 |
| | Lab | *Triticum* sp. | Seeds | Moisture content; evaluation of different meters | Hlynka et al. 1949 |
| | Washington D.C., USA | *Pinus strobus* | Cambium | Tree vigor | Kostka and Sherald 1982 |
| | Nova Scotia, Canada | *Abies balsamea* | Cambium, trunk | Foliar biomass | MacDougall et al. 1987 |
| | Massachusetts, USA | *Acer saccharum* | Xylem | Wood decay | Malia and Tattar 1978 |
| | Arizona, USA | *Pinus ponderosa* | Cambium | Tree vigor | McCullough and Wagner 1987 |
| | Lab | *Chara vulgaris* | Cell | Cell components | Murdoch and Sinclair 1976 |
| | Massachusetts, USA | *Acer saccharum* | Cambium | Tree vigor | Newbanks and Tattar 1977 |
| | Lab | *Triticum* sp. | Seeds | Moisture content | Paull and Martens 1949 |
| | Nova Scotia, Canada | *Abies balsamea* | Cambium | Foliar biomass, spacing, season | Piene et al. 1984*b* |
| | Nova Scotia, Canada | *Abies balsamea* | Cambium | Growth, ion content | Piene et al. 1984*a* |
| | Pennsylvania, USA | *Pinus strobus* and various others | Cambium | Decay | Shigo and Shigo 1974 |
| | Vermont, USA | *Acer saccharum* | Cambium | Growth rate | Shortle et al. 1979 |
| | Maine, USA | *Acer rubrum* and various others | Cambium | Decay | Skutt et al. 1972 |
| | New Hampshire, USA | *Abies balsamea* | Cambium | Change per cambial cell | Smith and Blanchard 1984 |
| | New England, USA | *Abies balsamea, Picea rubens* | Trunk | Decay | Smith and Shortle 1988 |
| | New England, USA | *Picea rubens* | Trunk, cambium | Stand vigor | Smith and Ostrofsky 1993 |
| | Wisconsin, USA | *Pseudotsuga menziesii* | Trunk | Moisture | Stamm 1927 |
| | New England, USA | *Ulmus americana, Acer saccharum,* and others | Bark, cambium, heartwood | Electrical tree damage | Stone 1903 |
| | Massachusetts, USA | *Ulmus americana, Acer saccharum, Nicoliana tabacum* | Trunk, stem | Time, temperature, mortality | Stone and Chapman 1912 |
| | Massachusetts, USA | *Castanea dentate, Betula lenta, Betula populifolia* | Trunk cankers | Infection, cankers | Sylvia and Tattar 1978 |
| | Quebec, Canada | *Malus* sp. | New sprouts | Sprout vigor | Taper and Ling 1961 |
| | Quebec, Canada | *Malus robusta* | Bark, wood | Differences among tissues | Taper and Ling 1963 |
| | Maine, USA | *Pinus strobus, Betula populifolia*, and various *Acer* and *Quercus* sp. | Trunk, radial sections | Decay stages; moisture, ions | Tattar et al. 1972 |
| | Maine, USA | *Acer saccharum, Acer rubrum* | Heartwood | Wood decay stages | Tattar and Saufley 1973 |
| | Massachusetts, USA | *Acer saccharum, Acer platanoides* | Cambium, xylem | Fungal infection | Tattar 1976 |
| | Lab | *Eucalyptus marginata* | Trunk | Fungal infection | Tippett and Barclay 1987 |
| | Pennsylvania, USA | *Quercus* sp. | Trunk | Defoliation | Wargo and Skutt 1975 |
| | New Zealand | *Nothofagus fusca* | Trunk, sap | Review of shigometer | Wilson et al. 1982 |

**Table 1** (*concluded*).

| Electrical property | Location | Species | Focal tissue | Objective or topic | Citation |
|---|---|---|---|---|---|
| Resistivity | Europe (various) | Various | Trunk | Internal structure; imaging methods | al Hagrey 2007 |
| | Italy | *Prunus persica*, *Olea europea*, *Quercus suber* | Roots, trunk | Decay detection | al Hagrey 2006 |
| | Rheinsberg, Germany | *Quercus robur* | Trunk | Radial variation, ionic effects | Bieker and Rust 2010 |
| | Italy | Various | Trunk | Decay | Sambuelli et al. 2003 |
| | Lab | *Cocos nucifera* | Fibres | Fiber properties | Satyanarayana et al. 1982 |
| | Kentucky, USA | Various | Cambium | Growth form | Yanoviak 2013 |
| | Kentucky and Michigan, USA | Various | Cambium | Species, region, growth form | This study |

et al. 2006). Resistance was first quantified for trees using a Wheatstone bridge in the early 1900s (Stone 1903), and the "Shigometer" became the device of choice in the 1970s (Shigo and Shigo 1974). More recent methods include impedance tomography and spectroscopy that, among other things, map tree resistivity (the material property associated with resistance) using rings of electrodes (Repo et al. 2005; al Hagrey 2006; Cao et al. 2011). Despite this methodological diversity, all of these devices ultimately measure similar electrical characteristics and generally damage tree tissues via insertion of probes. Some newer approaches include less intrusive (but more costly) technology such as ultrasonic tomography and georadar (Sambuelli et al. 2003; al Hagrey 2007).

## The physiology of electrical properties

The electrical properties of plants arise at the cellular level. Cell and organelle membranes function as microcapacitors; they oppose the flow of electrical current (i.e., high resistance and low conductance) and store electrical energy (i.e., high capacitance; Zhang and Willison 1992; Inaba et al. 1995). By contrast, extracellular and intracellular fluids tend to have low resistance and negligible capacitance (Glerum and Krenciglowa 1970; Zhang and Willison 1992; Inaba et al. 1995). Intracellular connections (e.g., plasmodesmata) allow low-resistance intracellular fluid to flow among cells. As a result, these connections function as electrical bridges between cells, decreasing membrane resistance (Côté et al. 1987).

Differences in cell physiology and structure cause electrical properties to vary among tissues within tree roots and stems. Woody root tissue tends to have higher resistivity than soft root tissue (al Hagrey 2007), and leaves have six times higher resistance than stems (Defandorf 1955). Resistivity also tends to decrease radially from the center of the trunk outward (with some exceptions; Bieker and Rust 2010). In particular, the vascular tissue of tree cambium tends to have lower resistance than the bark and heartwood (Stone 1903), and stem resistance increases after cambial tissue is damaged by girdling (Stone and Chapman 1912). Variation in moisture content causes differences in resistivity among tissues and species (Plummer 1912); however, more recent evidence suggests that other factors are also important (e.g., ion content; Bieker and Rust 2010). It is clear that electrical properties vary among tissues within stem types, leaves differ electrically from stems, and stems differ electrically from roots. However, such patterns remain underexplored and are based on a few species or on individual trees. For example, the only comparative data between roots and stems indicate that both root resistance and stem resistance tend to decrease with higher growth rates (Blanchard et al. 1983; Repo et al. 2005).

Individual trees generate weak internal electrical charges (on the order of mV) that tend to decrease internally and increase externally from the roots to the crown (Lund 1931; Gibert et al. 2006). Tree tissues also generate voltage in response to mechanical stress (i.e., a piezoelectric effect; Ross et al. 2012). Despite their intimate contact with the ground, root voltage differs from that of the surrounding soil, indicating that roots are electrically insulated (Gibert et al. 2006). However, soil moisture, soil composition, and many other variables presumably affect the general applicability of this observation. Apart from piezoelectric effects (Ross et al. 2012), electrical potential within trees primarily originates from sap flow and, therefore, tends to peak during the growing season (Morat et al. 1994; Gibert et al. 2006). Tree voltage can change over short time scales (e.g., minutes) independently from temperature, humidity, and light intensity (Fensom 1963), suggesting that it is the product of physiological and structural processes rather than a passive response to external conditions (Fensom 1963; Gibert et al. 2006). One exception to this mechanism is the observation that stems develop stronger electrical charges when clouds pass overhead (Abbott and Crossley 1982; Le Mouël et al. 2010).

Further evidence for the role of physiology in the maintenance of electrical properties of trees comes from studies of foliar biomass and metabolic activity. Capacitance increases and resistance decreases with increasing foliar biomass in trees (e.g., balsam fir, *Abies balsamea* (L.) Mill.; Piene et al. 1984*b*; MacDougall et al. 1987). Observations from a natural experiment similarly showed that the mean cambial resistance of trees in stands defoliated by herbivores was higher than in healthy stands (Davis et al. 1980). Likewise, the electrical impedance of stems changed after they were boiled in the laboratory, presumably due to damage of cellular components (see, e.g., Glerum and Krenciglowa 1970). In experiments using olive tree cuttings (*Olea europaea* L.), root growth was higher when intracellular leaf resistance was high and intracellular stem resistance was low, suggesting that increased metabolic activity increases resistance (Mancuso 1999). Although the contributions summarized above provide a useful foundation for exploring the effects of sap flow and cellular processes on the electrical properties of trees, general knowledge of this topic remains very poor.

### Effects of disease and decay

The electrical properties of living trees often are modified in predictable ways by pathogens and decay (Smith and Shortle 1988). Resistance, in particular, has been used to assess the wood quality of many commercial timber species (Table 1). Resistance tends to be lower in woody tissues infected by microbes such as *Phytophthora cinnamomi* Rands, *Verticillium dahliae* Kleb., and Dutch elm disease (Tippett and Barclay 1987; Malia and Tattar 1978; Blanchard and Carter 1980). This pattern is so consistent that it is possible to map wood defects and decay in living stems using resistivity alone (Sambuelli et al. 2003).

The mechanism underlying lower resistance in decaying wood likely is the accumulation of moisture and ions in damaged areas of a tree (Tattar et al. 1972). Resistance generally decreases with increasing moisture and ion concentrations in vascular tissue (e.g., Ca, K, Na, and pH; Malia and Tattar 1978; Sylvia and Tattar 1978; Blanchard et al. 1983), and impedance decreases with increasing water potential (Dixon et al. 1978). Although the contributions of specific ions to resistance and other electrical variables remain unclear (Piene et al. 1984*a*), moisture appears to be the most important variable in the resistance–decay relationship (see, e.g., Stamm (1927), Carter and Blanchard (1978), and al Hagrey (2006)). Resistance also decreases with increasing number of cells in a radial file of cambium, suggesting that physical damage to vascular tissue is relevant to the electrical signatures of woody decay (Smith and Blanchard 1984). Collectively, these patterns indicate that changes in electrical properties associated with wood damage or decay are the product of local physiological (i.e., ion and water content) and anatomical (i.e., size and structure) changes in vascular tissue. Although comparative data are few, the magnitude of these changes appears to vary among types of damage and among tree species.

### Temporal and climatic variation

The electrical properties of trees vary on long (seasonal) and short (diel) time scales. Seasonal variation generally is associated with cold tolerance and tree growth rates (Evert and Weiser 1971; Blanchard et al. 1983). However, the patterns of variation differ interspecifically and among tissue types. For example, intracellular resistance increases in *Salix viminalis* L. (Repo et al. 1997) and decreases in the shrub *Cornus sericea* L. (Evert and Weiser 1971) as cold hardiness increases. In olive trees (*O. europaea*), intracellular shoot resistance increases, whereas intracellular leaf resistance decreases during the winter (Mancuso 1999). Resistance is negatively correlated with growth rate during the summer in balsam fir (*A. balsamea*); however, this trend disappears when growth stops during the winter (Blanchard et al. 1983). Diel variation in resistance is associated with temperature and humidity (Stone 1903; Gagnon et al. 1987; MacDougall et al. 1987). Specifically, resistance decreases with short-term increases in humidity and temperature, and the rate of resistance decrease is higher when temperatures are below freezing (Fensom 1963; Dixon et al. 1978). By contrast, electrical potential and capacitance appear to be unaffected by diel changes in temperature, humidity, and light intensity (MacDougall et al. 1987), although the internal electrical potential of trees increases transiently when clouds pass overhead (Le Mouël et al. 2010).

Tree electrical properties also are sensitive to changes in atmospheric composition. Repo et al. (2004) showed that resistance of silver birch (*Betula pendula* Roth) changed with increasing $O_3$ and $CO_2$ concentrations. Specifically, extracellular resistance increased in saplings grown under high (twice the normal amount) $O_3$ conditions, and their intracellular resistance increased when grown under similarly high $CO_2$ conditions. These electrical changes probably resulted from membrane damage and changes in symplastic composition, respectively (Repo et al. 2004).

Collectively, the patterns summarized above suggest that changes in local and regional conditions associated with climatic change (e.g., temperature, precipitation, and atmospheric composition) will be reflected in the electrical properties of trees. Although there is considerable interspecific variation in some parameters, systematic monitoring of tree electrical properties may provide a more tractable and immediate measure of tree responses to climatic change than current methods, which generally require long-term data (e.g., monitoring tree phenology and distribution; Parmesan 2006).

### Broader context and objectives

Our interest in the electrical properties of trees is related to their interaction with lightning. Trees commonly are the ground terminus of lightning strikes because they are approximately $10^{13}$ times more conductive than the surrounding air, and differences in tree resistivity likely influence the path of lightning at a local scale (Defandorf 1955). The hypothesis that resistivity, in particular, affects tree responses to lightning was posed over a century ago (Anonymous 1898; Stone and Chapman 1912) and has been revisited since then (Komarek 1964); however, it remains untested. Some tree species appear to be more attractive to or suffer greater damage from lightning than others (Furtado 1935; Taylor (1977) and references therein), but all evidence is anecdotal. Solving this problem partly requires understanding the physics of lightning attachment to objects on the ground, which remains unclear (Rakov and Uman 2003). Likewise, determining how interspecific differences in tree electrical properties affect their response to lightning (e.g., by conducting electric current while minimizing damaging thermal energy) requires experimentation with lightning-like charges in the laboratory, which is technically very challenging (Wakasa et al. 2012). Regardless, understanding how electrical properties of trees vary within a forest is increasingly important in this context given that cloud-to-ground lightning frequency is predicted to increase in the coming decades (Williams 2005; Romps et al. 2014).

Connecting the electrical properties of trees to their interaction with lightning requires a level of experimentation beyond the scope of this project. However, this review and a structured comparison of tree resistivity (below) provide a framework for advancing research on the ecological effects of lightning (see, e.g., Yanoviak 2013). The basis for our empirical study is the hypothesis that resistivity varies consistently and predictably among species and functional groups of woody plants. Based on the unreplicated measurements of Stone (1903) and our pilot studies (Yanoviak 2013), we expected resistivity to be lower in hardwoods than in conifers and lower in vines than in trees across a similar range of diameters. Likewise, following Stone and Chapman (1912), we predicted that resistivity would be consistent on all sides of a tree trunk. Secondarily, we hypothesized that interspecific differences in resistivity are also revealed in their wood products. Specifically, we expected resistivity of wood to vary consistently among species over an experimental gradient of moisture content.

## Methods

### Study sites

Field work was conducted in forests and wooded parklands at two locations in the continental United States. The first site (hereafter, HMC) consisted of old-growth, subboreal remnant forest in the Upper Peninsula of Michigan along the south shore of Lake Superior (46.87°N, 87.88°W). The HMC forest has been managed since 1889 by the Huron Mountain Club and other private landowners (Simpson et al. 1990). The second site (hereafter, KY) consisted of six urban and suburban woodlands, each >150 ha, near Louisville, Kentucky (38.16°N, 85.79°W).

### Resistivity measurements

Interspecific comparisons using impedance or resistance (the most common focal variables; Table 1) are confounded by measurement-specific parameters (e.g., dimensions of the sample). We focus on resistivity because it accounts for these parameters (al Hagrey 2006). Moreover, resistivity is easily quantified in the field using portable equipment.

To measure the resistivity of a given tree or vine, we inserted two aluminum nails (length, 40 mm; diameter, 3 mm) into vascular tissue of the trunk or stem 1.0–2.0 m above the ground and 30 cm apart along the longitudinal stem axis. We used aluminum nails because they are inexpensive, relatively durable, and readily available. Lab measurements showed that they consistently have very low resistance (0.2 Ω), even when covered with a patina of oxidation. The test leads of a megaohmmeter (DT-6605; Ruby Electronics, Saratoga, California, USA) were secured to the nails, which were lightly abraded to provide clean contact points. Voltage was applied under the auto-ranging function of the meter; therefore, the recording voltage was highly correlated with measured resistance (log transformed; $\rho = 0.99$). We recorded the diameter of the trunk or stem to the nearest 1 mm at the midpoint between the electrodes. We measured the temperature of the plant tissue by inserting a thermocouple (Omega Engineering, Stamford, Connecticut, USA) into each nail hole following resistance measurement.

We measured the resistivity of three different populations (≥10 individuals each) of eight tree and three vine species across a broad range of diameters (vines, 2.5–96 mm; trees, 6–1088 mm) to determine interspecific differences in resistivity. At HMC, we measured at least 40 individuals of each of seven common tree species: red maple (*Acer rubrum* L., $n = 46$), sugar maple (*Acer saccharum* Marsh., $n = 41$), yellow birch (*Betula alleghaniensis* Britton, $n = 40$), eastern hemlock (*Tsuga canadensis* (L.) Carrière, $n = 50$), red oak (*Quercus rubra* L., $n = 50$), red pine (*Pinus resinosa* Aiton, $n = 43$), and white pine (*Pinus strobus* L., $n = 41$). In KY, we surveyed at least 20 individuals of four tree and three vine species: red maple ($n = 31$), sugar maple ($n = 40$), Virginia pine (*Pinus virginiana* Mill., $n = 32$), red oak ($n = 41$), poison ivy (*Toxicodendron radicans* (L.) Kuntze, $n = 29$), grape vine (*Vitis* sp., $n = 35$), and Virginia creeper (*Parthenocissus quinquefolia* (L.) Planch., $n = 22$). We chose these tree and vine species because they are common in the region, and three of the focal tree species are abundant at both sites. Vines are rare in the HMC forest; consequently, all of the vine data used in this study are from the KY site. For a subset of the trees (*A. saccharum*, $n = 11$; *Carya glabra* (Mill.) Sweet, $n = 8$; *Ulmus americana* L., $n = 5$; and *Juglans nigra* L., $n = 6$), we measured resistance separately on the north and south sides of the tree at the same height above the ground. All resistance measurements were taken during peak lightning season (May–October).

Although we did not quantify the moisture content of trees measured in the field portion of this study, we explored the effects of moisture on the resistivity of commercially available wood of *Pinus* sp., *Populus* spp. (poplar and aspen), and *Q. rubra* in the laboratory. We measured nine small blocks (approximately 1 cm × 2 cm × 30 cm) of poplar and seven blocks each of pine, oak, and aspen. We inserted nails (described above) into the wood 20 cm apart and centered at the midpoint of each block to minimize the effect of more rapid drying at the ends. Nails were inserted orthogonal to the wood grain, which ran longitudinally in all blocks. Each block was hydrated to a constant mass by complete immersion in distilled water for six days; then, the blocks were removed from the water, blotted dry, and allowed to air dry in the lab (21 °C, <50% relative humidity). Resistance and mass were measured upon removal from the water and again every 3 h until every block was unable to conduct electric current (i.e., up to 45 h). The blocks were then dried to a constant mass at 60 °C.

### Statistical analysis

All resistance data were converted to resistivity using the equation $\rho = RA/L$, where $R$ = resistance in ohms, $A$ = cross-sectional area of the plant stem or wood block, and $L$ = distance between the measurement leads. We evaluated the importance of temperature and diameter in determining resistivity for each tree and vine species using multiple regression analysis; significant effects were further analyzed with simple linear regression. The temperature of the laboratory was relatively constant (internal temperature of blocks was 20.5 ± 0.2 °C); therefore, we excluded temperature from the wood block analysis. We quantified the moisture content of the wood blocks as the absolute mass of bound water. We used mass of moisture per unit volume rather than percent dry mass, because the former is likely to vary independently from wood density. Differences in the exponential rate of desiccation were compared among species of wood blocks with an analysis of variance (ANOVA), and their resistivity was similarly compared with a mixed linear model using species and moisture mass as main effects.

The mean resistivity of trees and vines was compared among species nested within growth form or tree type (vines vs. trees and hardwoods vs. conifers, respectively) with an analysis of covariance (ANCOVA) and Tukey's honestly significant difference (HSD) post hoc comparisons. Vines were only compared with trees in KY and conifers were only compared with hardwoods in HMC due to the general lack of vines in HMC and the limited number of conifers in the KY dataset. To standardize the effects of sample dimensions, only data for tree stems and branches 10–100 mm in diameter were used for the growth form comparison with vines. Diameter (trees and vines) and mass (wood blocks) were used as covariates in these analyses. We used ANCOVA to test Stone and Chapman's (1912) data comparing resistivity on four different sides of trees (north, south, east, and west), with temperature as the covariate. We also compared mean resistivity on opposite sides of a subset of our focal trees using a nested ANOVA with position (north or south) nested within tree species. Data were log or cube-root transformed before analysis as needed to correct variance heterogeneity and improve normality. We used a Bonferroni-adjusted alpha ($\alpha = 0.0125$) to account for multiplicity in analyses of tree resistivity data. All analyses were conducted with the R statistical package version 3.1.1 (R Core Team 2014).

## Results

Mean resistivity differed consistently among the focal tree species across a large range of diameters (6–1088 mm; Fig. 1; Tables 2 and 3). In KY, the resistivity of red maple was lower than for Virginia pine, sugar maple, and red oak ($F_{[3,139]} = 12.6$, $p < 0.001$; Table 2). At the HMC site, resistivity of red pine was the highest and red maple was the lowest ($F_{[5,310]} = 6.1$, $p < 0.001$; Table 3). More generally, resistivity differed between hardwoods and conifers and between vines and comparably sized tree stems (Tables 3 and 4). Specifically, the mean resistivity of conifers was 135% higher than

**Fig. 1.** Electrical resistivity (Ωm) vs. stem diameter (mm) for selected tree species at the HMC site (red pine, short-dashed line; yellow birch, solid line; and red maple, long-dashed line). The three species in this plot represent the full range of variation among tree species measured at the site. Stem diameters are cube-root transformed.

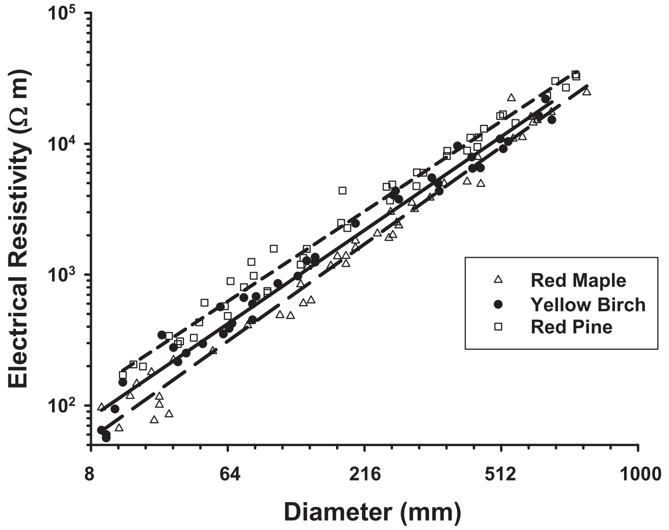


**Table 2.** Mean (±SE) stem diameter and resistivity of the complete dataset for focal tree species at the KY site (in contrast with Table 4, which presents comparative results using a size-constrained subset of the KY tree data).

| Species | *N* | Stem diameter (mm) | Resistivity (Ωm) |
|---|---|---|---|
| Red oak | 41 | 287±40 | 6570±1345a |
| Virginia pine | 32 | 169±30 | 3349±850a |
| Sugar maple | 40 | 176±32 | 2892±724a |
| Red maple | 31 | 136±29 | 1576±738b |

**Note:** Similar lowercase letters indicate means that do not differ based on ANCOVA and Tukey's HSD post hoc tests.

**Table 3.** Mean (±SE) stem diameter and resistivity of the seven focal tree species at the HMC site grouped by wood type.

| Tree type | Species | *N* | Stem diameter (mm) | Resistivity (Ωm) |
|---|---|---|---|---|
| Conifer (pooled: 7168 ± 828*x*) | Red pine | 43 | 272±35 | 7408±1434a |
| | White pine | 41 | 260±41 | 6750±1379ab |
| | Eastern hemlock | 50 | 271±33 | 7304±1480bc |
| Hardwood (pooled: 4448 ± 492*y*) | Yellow birch | 40 | 219±33 | 3883±825bcd |
| | Sugar maple | 41 | 264±37 | 5302±1066cde |
| | Red oak | 50 | 247±30 | 4680±1146de |
| | Red maple | 46 | 245±31 | 4226±918e |

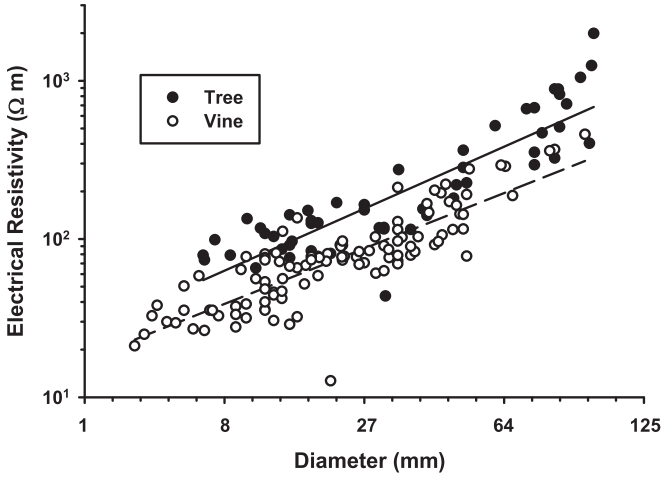
**Note:** Similar lowercase letters indicate means that do not differ based on a nested ANCOVA and Tukey's HSD post hoc tests.

**Table 4.** Mean (±SE) resistivity of three common tree species (limited to stem diameter range = 10–100 mm) and three common vine species at the KY site.

| Growth form | Species | *N* | Resistivity (Ωm) |
|---|---|---|---|
| Trees (pooled: 318 ± 34*x*) | Virginia pine | 15 | 372±61a |
| | Sugar maple | 19 | 449±77a |
| | Red oak | 14 | 246±75a |
| | Red maple | 17 | 184±32b |
| Vines (pooled: 108 ± 9*y*) | Grape vine | 35 | 145±16b |
| | Poison ivy | 29 | 86±12c |
| | Virginia creeper | 22 | 76±5c |

**Note:** Similar lowercase letters indicate means that do not differ based on a nested ANCOVA and Tukey's HSD post hoc tests.

**Fig. 2.** Tree (solid line) and vine (dashed line) electrical resistivity (Ωm) vs. stem diameter (mm) for the KY site. Stem diameters are cube-root transformed. The tree data were limited to stems 10–100 mm in diameter for direct comparison with vines.



hardwoods ($F_{[1,310]} = 64.9$, $p < 0.001$; Table 3), and the mean resistivity of tree stems was approximately 200% higher than vine stems over the same size range ($F_{[1,172]} = 156.5$, $p < 0.001$; Fig. 2; Table 4). Thus, although there is some overlap in mean resistivity among some species in the different groupings, the vines that we surveyed are generally more electrically conductive than trees, and hardwood trees are more conductive than conifers (Tables 3 and 4).

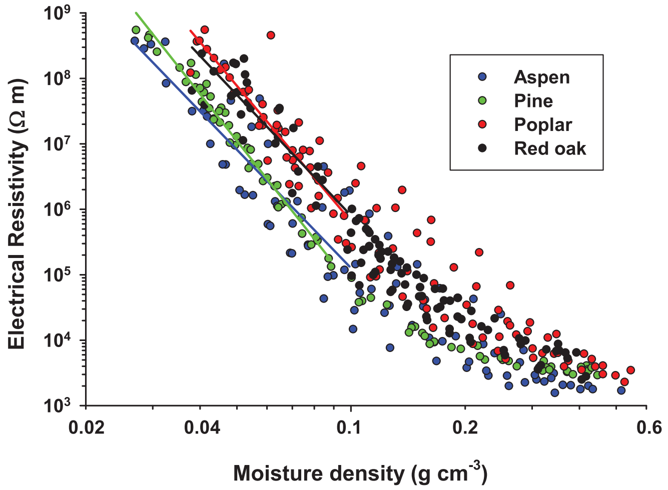
The resistivity of tree and vine species increased with stem diameter at similar rates ($F > 22.2$, $p < 0.001$ in all cases; Figs. 1 and 2). Multiple regression analysis showed that the range of temperatures that we sampled did not affect resistivity for most species ($F < 3.6$, $p > 0.06$). Three species were exceptions to this pattern; however, the significant temperature effect disappeared for all of them in subsequent simple regressions ($F < 0.13$, $p > 0.35$).

The regional comparison of resistivity for the three tree species common to both HMC and KY (sugar maple, red maple, and red oak) produced inconsistent results. When the data were truncated to compare similar ranges of diameter (i.e., a subset of the data used in Tables 2 and 3), the mean resistivities of the maples were marginally similar between sites (sugar maple, $F_{[1,78]} = 1118.6$, $p = 0.035$; red maple, $F_{[1,72]} = 1993.1$, $p = 0.064$; $\alpha = 0.0125$). However, the resistivity of red oak increased with diameter at a higher rate in HMC than in KY; therefore, red oak was not comparable between the regions (ANCOVA interaction $F_{[3,82]} = 1620.2$, $p = 0.002$).

We found no difference in mean resistivity between the north and south sides of trees at the KY site ($F_{[2,52]} = 0.51$, $p = 0.61$). Our analysis of data from Stone and Chapman (1912) showed that resistivity of elm and maple differed on different sides of trees over a 15-day period in April 1907 (elm, $F_{[3,55]} = 8.97$, $p < 0.001$; maple, $F_{[3,71]} = 3.86$; $p = 0.013$). However, the differences were inconsistent between species; the highest resistivity occurred on the north side of maple and the south side of elm. These differences disappeared in data from a 3-month survey (April–June; elm, $F_{[3,35]} = 1.87$, $p > 0.15$; maple, $F_{[3,35]} = 1.62$, $p > 0.20$).

The electrical resistivity of wood blocks decreased with increasing moisture content for all four species measured (Fig. 3). However, the shape of the relationship between resistivity and moisture content differed among species and was inconsistent over the full range of moisture mass. Thus, we limited the statistical analysis to the range of moisture density that was log nor-

**Fig. 3.** Electrical resistivity (Ωm) of wood blocks vs. moisture density (g·cm$^{-3}$). Data are repeated measurements of at least seven blocks (1 cm × 2 cm × 30 cm) for each species over a gradient from saturation to complete desiccation. Fit lines: aspen, blue; pine, green; poplar, red; and red oak, black. Statistical analyses were limited to the linear relationships observed at low levels of moisture content (<0.1 g·cm$^{-3}$). Note that the *y* axis range differs from Figs. 1 and 2.



mally distributed (<0.1 g·cm$^{-3}$; Fig. 3). The rate of resistivity decrease varied differently among species across this range (Fig. 3; interaction: $F_{[3,120]} = 7.38$, $p < 0.001$). The different wood species also dried at different rates ($F_{[3,26]} = 34.84$, $p < 0.001$). The mean (±SE) exponential desiccation rate (from the function $y = bx^k$, where $y$ is resistivity, $x$ is moisture mass, and $k$ is the rate of desiccation) was lowest for red oak (−0.34 ± 0.015), highest for pine (−0.65 ± 0.006), and intermediate for both aspen (−0.50 ± 0.013) and poplar (−0.56 ± 0.031).

## Discussion

Many biological characteristics of trees (e.g., decay, sap flow, and changes in physiology) can be at least partly predicted from their intrinsic electrical properties. This phenomenon has interested biologists for more than a century and is appealing for its practical value. The ability to quickly and accurately characterize the health, growth, or other characteristics of a tree based on a single electrical measurement provides an efficient source of data for scientists and resource managers alike. However, our review shows that the literature on this topic is relatively limited and conceptually scattered. Most studies focus on only a few species or even a single individual and are inconsistent with respect to methodology and focal variables. Consequently, the ability to make generalizations about the electrical properties of trees and their relationship to tree ecology and physiology is significantly hindered by a lack of comparative data.

Despite these problematic knowledge gaps, the available literature points to at least three research directions regarding the electrical properties of trees that seem particularly promising. First, the use of electrical tomography and other advanced technologies to identify disease and decay (see, e.g., al Hagrey 2007) can improve our understanding of the patterns and mechanisms of tree mortality. Second, electrical impedance spectroscopy is facilitating the measurement of otherwise inaccessible or unobservable variables such as root growth or in situ changes in physiology (Repo et al. 2004, 2005). Third, electrical data may provide an efficient and reliable measure of tree responses to changing climatic conditions over shorter time scales than are currently possible with ecological data (Repo et al. 2004). More generally, the role of tree electrical characteristics in the quantification of biological traits and processes is likely to increase in importance as field ecology becomes increasingly electronically based.

The empirical results of this study advance our understanding of the electrical properties of trees and vines by showing that resistivity varies consistently and predictably among different species and growth forms and, therefore, reflects intrinsic physiological and anatomical differences among taxa. The considerably lower resistivity of vines relative to trees likely results from the distinct internal stem architecture and the relatively high water content that is typical of vine stems (Carlquist 1991). This difference provides indirect support for the hypothesis that vines inadvertently protect trees from lightning damage by conducting and distributing the bulk of the current (Yanoviak 2013). Definitive tests of this hypothesis will require carefully controlled field experiments.

Interspecific differences in resistivity among trees likely result from differences in cambium anatomy (Smith and Blanchard 1984) and composition (Bieker and Rust 2010). Although tree resistivity is commonly associated with moisture content (Plummer 1912), the results of our wood block experiment suggest that other aspects of anatomy and physiology also are important to interspecific differences in resistivity. Such differences offer mechanistic support for the hypothesis that responses to lightning are species specific (Covert 1924). For example, the relatively high resistivity of conifers may explain why lightning damage to pines usually is conspicuous and unambiguous compared with some hardwoods (Taylor 1977).

Furthermore, the interspecific differences in resistivity that we observed provide circumstantial support for the hypothesis that some species are more attractive to lightning than others (e.g., Taylor 1977). For example, our results suggest that the more highly conductive tissues of a red maple are more likely to be struck by lightning than a less conductive neighboring red pine if, with all things being equal, the former produces longer ascending electrical leaders (Komarek 1964). For the same reason, red maple is better equipped to conduct electric current during a strike and potentially avoid major damage. Some authors have noted that lightning strikes living trees more often than standing dead wood (e.g., Chapman 1950); the very high resistivities that we observed in the wood blocks relative to live stems (twofold higher for even the most saturated wood blocks) explain this pattern if conductivity indeed plays a role in lightning attachment. Regardless, rigorous tests of these hypotheses will require systematic field observations and experimental evidence (e.g., with triggered lightning, Brook et al. 1961). Lacking such evidence, these conclusions remain speculative.

Regardless of their potential ecological relationship to lightning, the consistent differences in resistivity among tree species and between growth forms suggest that variation in electrical resistivity has a strong phylogenetic component. Results of the regional comparison further support this conclusion, at least for two common maple species. We attribute the inconsistent resistivity–diameter slope in red oaks between sites to habitat differences. Red oaks at the HMC site are relatively short, contorted trees occurring on highly exposed rocky ridges (Simpson et al. 1990), whereas red oaks at the KY site are relatively tall, straight trees embedded in continuous forest canopy on gentle slopes or flat terrain. Identifying the physiological and anatomical mechanisms for the regional difference in red oak resistivity was beyond the scope of this project. However, additional studies focusing on intraspecific variation across geographic gradients (e.g., latitude and elevation) would be useful extensions of this work and are needed to separate local environmental effects from phylogeny as determinants of tree electrical properties.

We also observed a linear increase in resistivity with stem diameter among all our focal species, a trend that is consistent with the results of other studies (Wargo and Skutt 1975). Although it has never been explored, this trend may simply indicate that the cross-sectional area of a trunk increases more quickly than cambial thickness. Regardless, the mechanism underlying this relationship remains unresolved.

Although the electrical resistance of wood and living tree tissues vary with both temperature and moisture content (see, e.g., Plummer (1912), Stone and Chapman (1912), and this study), we focused only on temperature as a covariate for three reasons. First, we assumed that the moisture content of living tree tissues is relatively similar among healthy individuals of a given species within a region and season (i.e., lower intraspecific than interspecific variation at small spatial and temporal scales). Second, we expected temperature to be considerably more variable than the moisture content of living tissue over the short time scale of this study. Finally, temperature was easy to measure nondestructively, which was an important consideration for data collection at protected sites (e.g., HMC). Although the relative moisture content of sapwood can be highly variable within a population (see, e.g., Waring et al. 1979), we expect such variation to be lower in more electrically conductive cambium (Stone 1903) where moisture and ion concentrations are regulated anatomically and physiologically. We cannot fully exclude moisture content as a contributor to the variance in our results, but the consistency of measurements among the three populations sampled for each species suggests that moisture content was not a confounding variable.

In conclusion, we surveyed the literature concerning the electrical properties of trees and other plants and identified trends in resistivity that potentially have broader implications for understanding the distribution of lightning damage in forests. We interpreted the results in the context of lighting susceptibility and damage with caution, as even a 200% difference in resistivity may be overwhelmed by the enormous scale of a typical lightning return stroke. Nonetheless, we suspect that understanding variation in tree electrical properties will become increasingly relevant to predicting changes in forest structure and dynamics under rapidly changing climatic conditions, including increased lightning frequency (Williams 2005; Romps et al. 2014). Other questions that could be useful extensions of this work include the following: how does existing decay or disease affect a tree's susceptibility to or response to lightning?; how do electrical properties influence the manifestation of lightning damage to trees?; and how do the electrical properties of trees vary with soil properties, local environmental conditions, etc.? Many electrical parameters of trees can be measured easily and quickly with relatively inexpensive equipment, therefore, generating the comparative data to answer these types of questions is not prohibitively difficult.

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