Chapter 15
Shock Value: Are Lianas Natural Lightning Rods?

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Keywords Canopy • Electrical resistivity • Mortality • Trees • Tropical forest • Vines

Bullet Points

1. Lightning is commonly listed as a source of tropical tree mortality, but lightning effects on trees are often inconspicuous and are rarely quantified.
2. Lianas presumably are struck by lightning at least as often as trees but are more likely to be killed due to their small stem diameters.
3. The relatively low electrical resistivity of liana stems suggests that they are a source of lightning protection for trees.
4. Quantifying lightning-caused tree and liana mortality is critical to understanding current and future forest dynamics.

Summary

Forest canopies are principal contact points for lightning, which may be increasing in frequency due to climatic change. Although lightning is commonly listed as a source of tree mortality, many strikes are nonlethal, and lightning damage to tropical trees often is inconspicuous. Lianas are a major component of lowland tropical forest canopies but have been overlooked in the context of lightning. This chapter summarizes two hypotheses regarding liana–lightning interactions. First, lightning is an important agent of liana mortality. Lianas comprise a large fraction of upper canopy area but have relatively small stem diameters. Consequently, the probability that a liana will be struck is high relative to the likelihood it will survive the damage.

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M. Lowman et al. (eds.), *Treetops at Risk: Challenges of Global Canopy Ecology and Conservation*, DOI 10.1007/978-1-4614-7161-5_15,

Second, lianas provide natural lightning protection for trees. The anatomy of liana stems should impart relatively low electrical resistivity. Preliminary data show that this is true for temperate woody vines compared to live tissues of similar-sized tree branches. If this is a widespread phenomenon, lianas may protect trees by being more attractive to incoming lightning or by bearing the bulk of the electrical current when lightning strikes a host tree. Support for these hypotheses could explain relatively high liana turnover rates. Resolving the importance of climate-driven sources of mortality like lightning is essential for understanding future tropical forest dynamics.

1 Introduction

1.1 Lightning Basics

Lightning is among the most powerful and awe-inspiring environmental phenomena on earth. It is prominent in human cultural history and relatively well understood scientifically (Rakov and Uman 2007). Individual lightning strokes vary in intensity and may occur from cloud to ground (CG), ground to cloud (GC), or within and between clouds (intra/inter-cloud; IC). The visible electrical discharge (the "return stroke" formed when ascending and descending leaders meet) is both hot (ca. 30,000 °C) and powerful (ca. 30,000A) and is the component of lightning that causes significant structural and biological damage (Fig. 15.1). Whereas the basic physics of lightning is relatively well understood (Rakov and Uman 2007), the ecology of lightning remains poorly studied.

Lightning frequency varies seasonally and geographically, but flash density generally is highest in the tropics (e.g., Williams 2005; Price 2009). For example, central Panama receives ca. 40 lightning flashes km^{-2} $year^{-1}$, with peak flash rates occurring between mid-July and mid-August (1995–2012 satellite data courtesy of Phillip Bitzer, University of Alabama in Huntsville). Under current climatic conditions, ca. 25 % of those flashes are potentially damaging to trees (as CG or GC lightning; Boccippio et al. 2001). Consequently, the forest on a 15 km^2 site in Panama (e.g., Barro Colorado Island) receives ca. 150 strikes per year. This number is expected to increase over the next few decades due to climate change. Specifically, for each 1 °C increase in average surface temperature (or [CO_2] doubling), lightning frequency may increase by at least 10 %, with some estimates exceeding 50 % (Williams 2005; Price 2009).

1.2 Lightning (Sometimes) Kills Trees

Widespread tree mortality shapes forest structure at the landscape scale via climate-driven catastrophic disturbance (e.g., fire, hurricanes; Lugo and Scatena 1996). Localized agents of tree mortality also affect forest structure (Lugo and Scatena

Fig. 15.1 Lightning damage to a mature *Tabebuia guayacan* in Panama. The upper trunk 10–15 m above the ground was deeply cracked and partially stripped of bark (*left image*), whereas the lower trunk within 3 m of the ground showed only exit wounds (*right image*). This intense strike caused group mortality (Magnusson et al. 1996)—almost all trees and shrubs within ca. 5 m of the focal tree also were killed. The strike occurred in late May 2012, ca. 2 weeks before the photo was taken. Coincidentally, this tree was one of the tallest within an 80 × 80 m research plot from which all lianas had been removed (Photo credits: S. P. Yanoviak)

1996), but most have only indirect links to climate (e.g., pollution, pathogens). Lightning is an exception. Lightning damages millions of trees worldwide each year (Taylor 1974). It is consistently listed as a source of tree mortality in the ecological literature and is hypothesized to be the main cause of death for the largest and oldest rainforest trees (Anderson 1964; Fig. 15.1). However, evidence for the latter is mostly circumstantial (Magnusson et al. 1996), and observations in temperate forests and tropical plantations show that trees often are not killed by lightning strikes (Taylor 1974).

Some lightning-struck trees exhibit no obvious physical damage (e.g., Furtado 1935), although they may be physiologically compromised or rendered more attractive to pathogens and herbivores (Taylor 1974). Thus, it is likely that lightning damage is frequently undocumented or misclassified by tropical ecologists; by default, the bulk of lightning-caused tree mortality is included in the ecologically ambiguous "standing dead" category. Even nonlethal lightning strikes ultimately affect tree fitness and forest turnover rates; thus, accurate quantification of lightning-induced mortality will improve forest dynamics models and facilitate predictions of future forest structure under conditions of increased lightning frequency.

1.3 Lightning (Always) Kills Lianas

Discussions of the ecological effects of lightning invariably focus on trees. However, lianas (woody vines) are major components of tropical forests (Schnitzer and Bongers 2002), and their abundance in the canopy makes them vulnerable to lightning damage. Liana–lightning interactions have been completely overlooked in the context of forest dynamics, yet both lianas and lightning will shape the ecology of tropical forests over the next century (Williams 2005; Schnitzer and Bongers 2011). Two hypotheses regarding liana–lightning interactions in tropical forests provide a point of entry for field research on this topic: (1) lightning is a significant source of mortality for lianas relative to trees and (2) liana stems act as natural lightning rods that inadvertently protect their host trees.

At least three aspects of the liana growth form suggest that lightning-caused mortality is relatively greater for lianas than for trees. First, individual lianas have disproportionately high lightning exposure relative to their basal area; their leaves are distributed like carpets in the uppermost forest canopy (Putz 1984). Collectively, lianas constitute a large proportion of highly exposed foliage in the canopy, and this fraction peaks (to > 30 %) during the wet season (Avalos and Mulkey 1999) when lightning frequency is also at a maximum. Moreover, liana tendrils commonly emerge above other canopy foliage (SY, pers. obs.), providing numerous origination points for ascending electrical leaders. Second, the small diameters and soft tissues of liana stems (Carlquist 1991) are unlikely to withstand the damage caused by lightning. The radius of a lightning return stroke ranges ca. 1–12 cm (Rakov and Uman 2007), which encompasses the diameters of most liana stems (Hegarty and Caballé 1991). Finally, the internal architecture and relatively high water-holding capacity of liana stems (Carlquist 1991) likely result in higher electrical conductivity than tree tissues. Although the process of lightning formation from specific ascending leaders is not completely resolved (Rakov and Uman 2007), more conductive substrates (e.g., liana stems) presumably generate stronger (more highly charged) or longer leaders, thereby increasing the local probability of a strike. The general characteristics of lianas suggest that they are especially susceptible to lightning-caused mortality, and lightning is likely to be a major contributor to the higher turnover rates observed for lianas relative to trees (Phillips et al. 2005).

1.4 Lianas (Maybe) Protect Trees

Lianas depend on trees for support. This close physical association is generally viewed as mechanical parasitism (Schnitzer and Bongers 2002), but it may also protect trees against lightning damage. A key assumption of this hypothesis is that liana stems have lower electrical resistivity than tree branches of similar diameter. No comparative resistivity data are currently available for tropical plants, but preliminary surveys in temperate forests support this assumption (Fig. 15.2). Such a difference in resistivity could protect trees via two mechanisms. First, as mentioned

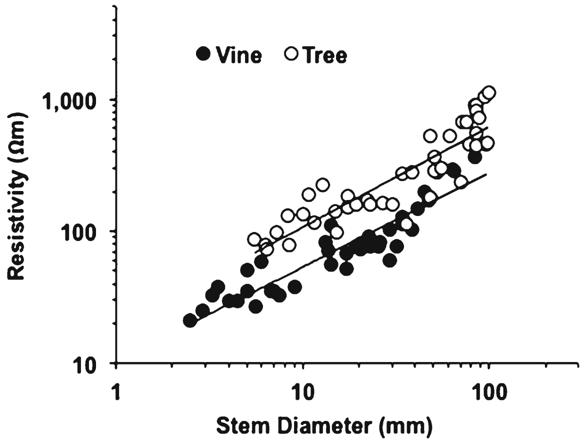

Fig. 15.2 Electrical resistivity of woody vines and tree branches up to 100 mm in diameter in temperate forests around Louisville, Kentucky. Data were recorded in October 2012

above, differential propagation of strike leaders could reduce the probability that a tree will be struck when lianas are present. Second, the bulk of the current in a lightning return stroke is distributed to the most conductive substrates (Rakov and Uman 2007). Thus, even if lightning initially strikes a tree crown, most of the charge (and damage) is likely to be borne by attached lianas. Although purely speculative, these mechanisms are not outside the realm of possibility.

Differential lightning conduction by lianas potentially explains why clear evidence of non-catastrophic (CG) strikes is uncommon among trees in tropical forests. Lianas provide a distributed network of low-resistance stems that effectively conduct the electrical current away from trees and to the ground. This phenomenon could be very common but completely unnoticed. Damage to an individual liana (including death) is likely to be inconspicuous to the ground-based observer in dense forest for various reasons. Liana stems are often very abundant in the understory, and changes in individual stems are easily overlooked. Liana foliage tends to be broadly and thinly distributed in the canopy; thus, leaf litter from a dead individual is unlikely to be conspicuously clumped when it lands on the ground. Moreover, leaves of many liana species do not fall until months after the stem is dead (SY, pers. obs.). Finally, the leaves and understory stems of lianas are often widely separated, such that the leaf litter from a dead individual may be tens of meters from its base. Whereas even low-intensity lightning damage is often conspicuous in temperate forests (e.g., Taylor 1974), the characteristic growth form of lianas may mask similar damage in tropical forests.

1.5 Electrical Properties of Lianas Versus Trees

To explore how electrical resistivity varies among different species and growth forms, my students and I used a megohmmeter to measure the electrical resistivity of living tissues of 43 vine stems (5–100 mm diameter) and 42 similarly sized branches of canopy trees in temperate oak–hickory forests around Louisville. Focal vine species were *Toxicodendron radicans*, *Parthenocissus quinquefolia*, and *Vitis aestivalis*, and focal trees were *Acer saccharum*, *Carya glabra*, *Juglans nigra*, *Quercus rubra*, and *Ulmus americana*. The average (± SE) resistivity of vine stems (167 ± 17.9 Ωm) was significantly lower than the resistivity of tree branches over the same size range (281 ± 18.1 Ωm; ANCOVA $F_{1,82} = 89.2$, $P < 0.0001$; Fig. 15.2), suggesting that vines would carry the bulk of the current from a lightning strike in the crown of their host trees. Resistivity differed among species of trees ($F_{4,36} = 2.84$, $P = 0.038$) and vines ($F_{2,39} = 5.43$, $P = 0.008$), and the range of resistivity values overlapped slightly (Fig. 15.2), suggesting that not all woody vine species are potentially protective of all tree species.

2 Research Needs

Research on the ecological effects of lightning poses many logistical challenges. Principal among these is accurate quantification of the role of lightning in forest dynamics. In particular, documenting nonlethal, inconspicuous strikes on individual trees requires continuous recording of strike activity in forests at smaller spatial scales than are currently possible via triangulation of electromagnetic signals. However, the rapid pace of technological advances in electronics and satellite monitoring capability may soon overcome this hurdle.

Apart from the hypotheses presented here, a number of basic questions remain to be answered regarding the ecology of lightning. First, are the tallest (i.e., emergent) trees in a forest most likely to be struck, as hypothesized by Anderson (1964)? As intuitive as the answer may seem, height differences among trees in continuous forest may be too small to be relevant at the scale of a typical lightning stroke, and evidence from temperate forests is inconclusive (Mäkelä et al. 2009). Second, are some tree species resistant to lightning strikes (Furtado 1935; Anderson 1964)? Lightning has been a selective force throughout the evolution of terrestrial life. Whereas no tree is expected to survive rare, intense (e.g., GC) lightning (Fig. 15.1), it is reasonable to suspect that some canopy tree species have anatomical or physiological traits that minimize damage from lower-intensity (e.g., CG) strikes, which are the most common. Finally, what is the effect of artificial lightning attractors on forest dynamics? Recent growth in wireless telecommunications and hydrocarbon drilling has led to a dramatic increase in the number of towers within forests, even in relatively remote locations. Such towers generally extend well above the surrounding forest canopy and function as lightning attractors (Rakov and Uman 2007), potentially changing local forest dynamics. Ironically, the canopy cranes that have been constructed around the world to study forest ecology should similarly disrupt natural strike frequencies.

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