# The First 100 Years of Research on Barro Colorado

## Plant and Ecosystem Science

VOLUME 2


*Edited by*

*Helene C. Muller-Landau and S. Joseph Wright*

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*A Smithsonian Contribution to Knowledge*

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**ABSTRACT.** The Barro Colorado Nature Monument in Panama, which includes Barro Colorado Island and nearby mainland peninsulas, supports the best studied tropical forest in the world. This 98-chapter edited volume reviews the history and contributions of research undertaken at this moist tropical forest to advance our understanding of tropical plants and ecosystems. The first section describes the setting, including soils, land use history, forest structure, and plant species composition. Nine additional sections concern plant reproduction and seedling regeneration, plant physiology, plant community ecology, population genetics, interactions with microbes and herbivores, remote sensing, observational ecosystem studies, experimental ecosystem studies, and focal taxa and functional group accounts. The authoritative reviews in this volume provide a foundation for future research in this and other tropical forest sites.

*Cover illustration*: Barro Colorado Island's Árbol Gigante (*Ceiba pentandra*) remains the only single-trunked tree known to have had an average crown diameter greater than 61 m. Robert Van Pelt recorded a height of 49.7 m, a 15-m diameter buttressed base, and an average crown diameter of 61.3 m in 1997. Van Pelt used a Wacom tablet as his canvas and a stylus as his paintbrush to create this orthographic illustration from detailed measurements of the crown, stem, and major branch systems, numerous photos and sketches, and a 2009 LiDAR flight (https://doi.org/10.25573/data.22823111) that captured the shape of the upper crown. Orthographic illustrations provide a completely undistorted view in contrast to the single perspective provided by photographs. The Árbol Gigante collapsed and died in 2013.

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# Ecological Effects of Lightning in a Tropical Forest

*Stephen P. Yanoviak,*[1,2]* *Evan M. Gora,*[1,2] *Cesar Gutierrez,*[2] *Jeffrey C. Burchfield,*[3] *and Phillip M. Bitzer*[3]

**ABSTRACT.** Lightning is a common source of disturbance in many tropical forests, but its effects on tropical plants and forest dynamics remain poorly understood. In 2014, we established a unique lightning monitoring system in the Barro Colorado Nature Monument. Data from 93 strikes showed that lightning is an important agent of mortality for the largest trees in this forest and, on average, each strike kills 5.3 trees within 13 months. Mechanistic models indicate that large trees are most likely to be directly struck, and the probability of subsequent death varies interspecifically. Lightning is responsible for 20.1% of new gap area formed, and 16.1% of woody biomass turnover in this forest annually. Although lightning frequency is relatively high in the BCNM, field observations suggest that the per-strike effects are similar in other tropical forests. This ongoing research is revealing that lightning, although often overlooked, has important ecological effects in tropical forests.

**Keywords:** carbon; disturbance; forest dynamics; gap; monitoring; mortality; Panama

Few natural phenomena combine the power and beauty of lightning, and its destructive effects have frightened and fascinated humans throughout history (Rakov and Uman, 2003; Bouquegneau and Rakov, 2010). Globally, lightning frequency is highest in the tropics (Cecil et al., 2014). Given that lightning kills and damages trees (see reviews by Komarek, 1964; Taylor, 1971), presumably it is an ecologically important agent of disturbance in tropical forests. Until recently, however, most information concerning the effects of lightning on tropical trees has been anecdotal or based on post hoc surveys using unverified diagnostics (e.g., Furtado, 1935; Anderson, 1964; Brünig, 1964; Magnusson et al., 1996; Tutin et al., 1996). For the past decade, we have been working to fill this gap by recording lightning damage to the forest in the Barro Colorado Nature Monument (BCNM), Panama, in real time.

This project essentially began with a fortuitous, close-range observation of a lightning strike to a large *Virola* tree near the water tower on Barro Colorado Island (BCI) by author S.P.Y. in 1996. Careful inspection of the tree and the surrounding forest immediately after the strike revealed no conspicuous damage; there was no scar on the tree's trunk, no fresh vegetation littering the ground, and no evidence of burning apart from the scent of ozone. Months passed before the liana mass in the *Virola* crown appeared dead on the ground, whereas the tree lived and reproduced for 10 more years before eventually falling dead. Although not forgotten, these observations were set aside for about 15 years.

1 Department of Biology, University of Louisville, 139 Life Sciences Building, Louisville, Kentucky 40292, USA.
2 Smithsonian Tropical Research Institute, P.O. Box 0843-03092, Balboa, Ancón, Republic of Panama.
3 Department of Atmospheric and Earth Science, University of Alabama in Huntsville, 301 Sparkman Drive, Huntsville, Alabama 35899, USA.
* Correspondence: steve.yanoviak@louisville.edu
Yanoviak, https://orcid.org/0000-0001-6425-1413
Gora, https://orcid.org/0000-0002-0537-5835
Gutierrez, https://orcid.org/0009-0001-5950-5105
Burchfield, https://orcid.org/0000-0003-2858-053X
Bitzer, https://orcid.org/0000-0002-6665-9778
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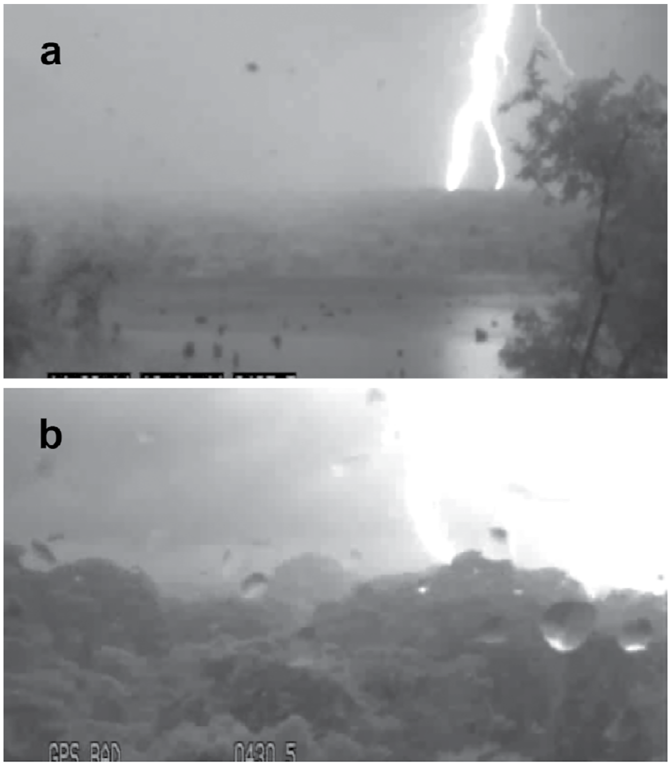


**FIGURE 1.** The first lightning strike located for this project was recorded on August 14, 2014 by a surveillance camera mounted on (**a**) Gigante Peninsula and a second camera on (**b**) the tower at the top of Barro Colorado Island.

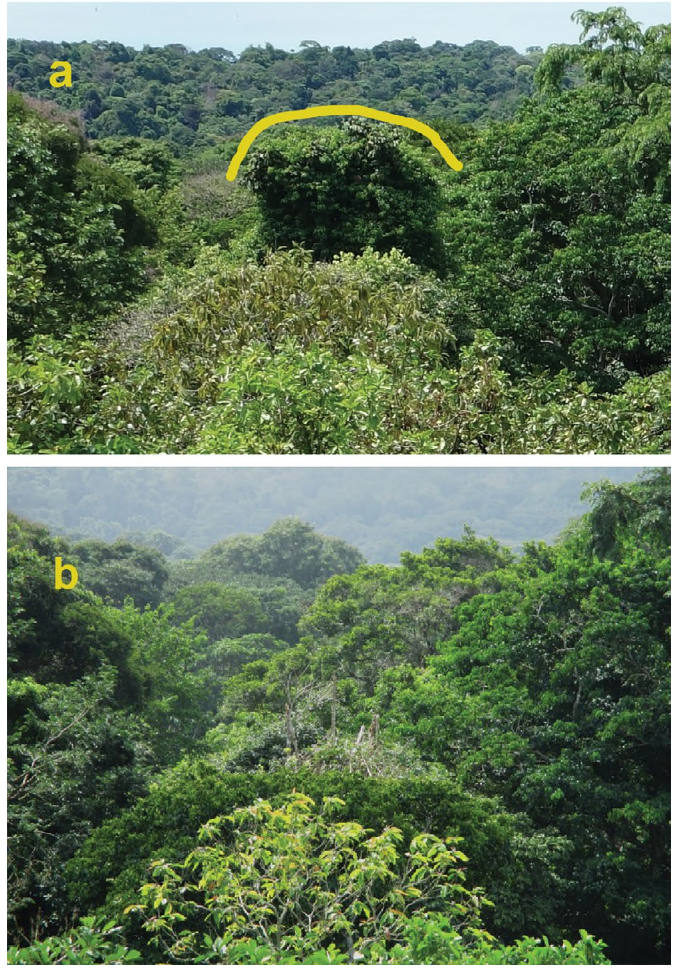


**FIGURE 2.** The damage to a *Sterculia apetala* crown and its resident *Arrabidaea* sp. liana on Barro Colorado Island resulting from the strike shown in Figure 1. The photos were taken from the tower (**a**) before the strike (June 2013) and (**b**) one day after the strike (August 15, 2014). This strike was atypical because it shattered the upper crown of the focal tree but caused no conspicuous damage to neighboring trees.

In 2012, authors S.P.Y. and P.M.B. established a plan to record and experimentally induce lightning strikes in the BCNM with the primary goal of answering three questions: What is the frequency of lightning strikes in the BCI forest? Do tree size, location, or species identity influence tree susceptibility to lightning damage? and Do lianas (woody vines) provide passive lightning protection for trees (Yanoviak, 2013)? Secondarily, we hoped to identify lightning strike sites post hoc using aerial lidar and hyperspectral imagery (with Greg Asner at Arizona State University) and to engineer specialized "lightning-indicator" flagging tape (with Fuquian Yang at the University of Kentucky) that could be wrapped around a tree trunk and left in place indefinitely. The National Science Foundation (NSF) ultimately supported our primary goal, and we recorded our first BCI strike on August 14, 2014 (Fig. 1). That strike was to a *Sterculia apetala* tree and its resident *Arrabidaea* liana (Fig. 2), both of which are alive as of this writing.

Although our efforts to experimentally induce lightning strikes failed, the lightning monitoring system we established on BCI slowly accumulated strike recordings. This system initially consisted of multiple solar-powered surveillance cameras and video recorders mounted on towers previously used for the Automated Radio Telemetry System (ARTS) project on BCI (Kays et al., 2011). J.C.B. developed an algorithm to identify still images of lightning flashes from these videos, which we used to locate lightning strikes in the field if they were captured on two or more cameras (Yanoviak et al., 2017). We—mainly E.M.G. (with additional support from National Geographic, an NSF Graduate Fellowship, and the Smithsonian Tropical Research Institute)—used these images to locate lightning strikes by climbing emergent trees and towers and searching for canopy damage in drone-based imagery. These camera-located strikes represent the first comprehensive sample of lightning strikes in any forest worldwide.

Data accumulated slowly in part because of the spatial and temporal clustering of strikes, multiple years of unusually low storm activity on BCI, the limited spatial coverage of the camera network, and problems associated with operating electronic equipment in a rainforest. But this slow pace gave us time to use observations from known strikes to develop a suite of diagnostics that could be used to reliably identify strike damage post hoc (Yanoviak et al., 2017) and allowed E.M.G. to develop the field protocols and quantitative framework necessary for measuring and modeling the ecological effects of lightning.

Continued funding from NSF allowed us to expand and improve the camera network and to add field change meters (sensors that locate and measure lightning strikes using their electromagnetic waves; Bitzer et al., 2013; Yanoviak et al., 2017) to the recording system. By the end of 2019, we had located and surveyed 93 strike sites in the BCNM forest. This represents the most comprehensive evaluation of the ecological effects of verified lightning strikes in any tropical forest, and it would not have been possible without the effort of C.G. in data collection, data management, and maintenance of the monitoring system. Survey data from those 93 strikes (and subsets thereof) enabled us to answer a variety of questions concerning the ecological effects of lightning in tropical forests. Here, we focus on three of these questions: (1) How does lightning affect trees in the BCNM? (2) What factors affect the probability that any given tree will be killed by lightning? and (3) What are the ecosystem-level effects of lightning in tropical forests?

## HOW DOES LIGHTNING AFFECT TREES IN THE BCNM?

Examination of 2,195 lightning-damaged trees distributed among the 93 strikes showed that on average, a single strike damages 23.6 trees (95% CI: 20.2–27.6), of which 5.3 trees (CI: 3.9–7.1) die within about 1 year (Gora et al., 2021). None of these trees exhibited lightning scars or fires. Although many heavily damaged trees eventually die from their injuries, many also recover (Richards et al., 2022), and more than 25% of directly struck trees exhibit minimal damage and survive for many years (Yanoviak et al., 2020). Our dataset includes one case of a single *Dipteryx oleifera* tree being directly struck twice (once in June 2016 and again in July 2019), yet as of this writing, that tree is still alive and apparently healthy.

At the beginning of this project, our expectation (and that of our critics) was that the contributions of lightning to tree mortality would be small compared with other sources of disturbance (e.g., wind, drought) in the BCNM forest. Thus, we were surprised when the data showed that lightning is the single-most-important cause of death for large trees in this forest. Specifically, by combining data on lightning strike frequency per area with data on mortality per strike, and comparing with long-term mortality rates from the 50-ha plot, we showed that lightning accounts for 40–50% of the mortality of trees >60 cm in diameter (Yanoviak et al., 2020). Although we initially focused on trees, more comprehensive vegetation surveys showed that tree associates, especially lianas and herbaceous climbers, also experience high mortality as a result of lightning strikes, whereas the epiphytes in the crowns of struck trees generally survive unless their host tree dies (Gora et al., 2021).

Surveys of beetle exit holes on tree trunks showed much higher infestation rates for lightning-struck trees than for trees in control sites (Parlato et al., 2020), suggesting that lightning-damaged trees are an important resource for xylophagous beetles in tropical forests. This study also showed that the amount of beetle damage increased with the amount of crown damage observed in the tree (Parlato et al., 2020). However, the relationship between beetle infestations and the fate of lightning-struck tropical trees remains unknown.

## WHAT FACTORS AFFECT THE PROBABILITY THAT ANY GIVEN TREE WILL BE KILLED BY LIGHTNING?

The answer to this question is undoubtedly a combination of many factors, including exposure, tree species identity, tree architecture, liana infestation, and secondary attack by insects and pathogens (Yanoviak, 2013; Yanoviak et al., 2015). Determining the likelihood that any given tree is killed by lightning requires first understanding the likelihood that it will be struck and then the likelihood that it survives the strike (e.g., Mäkelä et al., 2009).

The factors influencing the likelihood that a tree will be struck by lightning are somewhat intuitive. Empirically supported, mechanistic models based on data from this project show that the likelihood of being directly struck increases with increasing tree crown area and height, and the likelihood of secondary damage increases with tree size (Gora et al., 2020b). Whether or not tree electrical properties influence the likelihood that some tree species are struck by lightning is unknown, although such interspecific differences were hypothesized more than two hundred years ago (Maxwell, 1793).

Centuries of observations show that not all trees die from direct lightning strikes. Models suggest that the damage caused by a strike (through heating energy) depends on the electrical resistivity of tree tissues (e.g., Gora and Yanoviak, 2015), the size of the tree, and the presence of lianas, such that larger trees and trees with lianas experience less heating and thus less damage than smaller or liana-free trees (Gora et al., 2017). Data gathered in this research program provide the best evidence to date for interspecific differences in the likelihood that a tree will die following a direct strike (Gora et al., 2020b; Richards et al., 2022). For example, individuals of *Dipteryx oleifera*, *Hura crepitans*, and *Pouteria reticulata* have lower-than-expected probability of death following lightning damage (Richards et al., 2022).

## WHAT ARE THE ECOSYSTEM-LEVEL EFFECTS OF LIGHTNING IN TROPICAL FORESTS?

Answering this question requires measuring the ecological effects of individual lightning strikes and upscaling to the landscape. By mapping the distribution of dead and damaged trees in known strike sites on BCI, we estimated that the average strike creates a canopy gap of 304 $m^2$ (CI: 198–454 $m^2$) and causes 7.36 Mg (CI: 5.36–9.65 Mg) of woody biomass turnover. We further estimated that, on average, lightning creates canopy gaps equaling 0.39% (CI: 0.25–0.58%) of total forest area each year and is thus responsible for 20.1% (CI: 14.4–27.0%) of annual gap area formation in this forest (Gora et al., 2021). Likewise, we estimate that lightning is cumulatively responsible for 16.1% of woody biomass turnover on BCI (Gora et al., 2021). Given that spatial variation in tropical forest carbon stocks is better explained by variation in woody biomass turnover than productivity (Johnson et al., 2016), lightning likely is a major factor limiting the carbon storage capacity of the BCI forest.

Our efforts to understand the ecological effects of lightning in tropical forests initially focused on the BCNM for logistical reasons. Coincidentally, although not a lightning hot spot (Albrecht et al., 2016), central Panama also has relatively high lightning frequency. Specifically, BCI receives an estimated 12.7 cloud-to-ground lightning flashes $km^{-2}$ $yr^{-1}$, or about 190 strikes annually (Yanoviak et al., 2020), placing it in the upper quartile of lightning frequency for tropical ecosystems (Gora et al., 2020a). It is possible that nitrogen oxide ($NO_x$) and other emissions from ship traffic in the Panama Canal have artificially elevated lightning frequency in this region over the past century (Heitz et al., 2011; Thornton et al., 2017), but we lack historical lightning frequency data for comparison.

Despite relatively high lightning frequency in the BCNM, our observations in an Amazonian forest (Gora and Yanoviak, 2020) and similar observations elsewhere (Furtado, 1935; Anderson, 1964; Magnusson et al., 1996) suggest that the effects of individual lightning strikes in Panama are generalizable to other tropical forests (Gora et al., 2020a). This conclusion was supported by an analysis of the associations between spatial variation in lightning frequency and variation in tropical forest structure and dynamics (Gora et al., 2020a). Specifically, tropical forests that experience more lightning strikes have fewer large trees per hectare, higher rates of woody biomass turnover, and less total aboveground biomass across Africa, Asia, and the Americas (Gora et al., 2020a). However, accurately accounting for the effects of lightning in forests and other major tropical landcover types (e.g., savannas) will require more case studies documenting mortality rates per strike, in combination with better large-scale distribution data on lightning frequency.

In conclusion, the lightning recording system we established on BCI (Yanoviak et al., 2017) is providing an unprecedented evaluation of the ecological effects of lightning in tropical forests. Indeed, it is increasingly clear that lightning plays an important role in shaping the structure and dynamics of this forest, and that role is likely to increase given expected changes in lightning frequency in a warmer climate (e.g., Romps et al., 2014). The results of this ongoing work are generating many questions that could be answered by taking a closer look at ecological processes occurring within lightning gaps and by expanding the recording system to include a larger range of forests and forest types. Such questions include: How are lightning-caused forest gaps ecologically different from other types of disturbance? Are lightning-damaged trees a keystone resource that shapes beetle diversity in tropical forests? How does the damage caused by a lightning strike vary among tree species, forest types, and forest ages? Is there a relationship between lightning characteristics (flash intensity and duration) and the number of trees killed? We are continuing to explore these and related questions in the BCNM and look forward to documenting the ecological effects of lightning in tropical forests for decades to come.

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