United States Department of Agriculture

Interactions Between Weather-Related Disturbance and Forest Insects and Diseases in the Southern United States

James T. Vogt, Kamal J.K. Gandhi, Don C. Bragg, Rabiu Olatinwo, and Kier D. Klepzig

Forest Service Southern Research Station General Technical Report SRS–255 August 2020

The Authors:

James T. Vogt is a Supervisory Biological Scientist, U.S. Department of Agriculture Forest Service, Southern Research Station, 320 E. Green Street, Athens, GA 30602-1530.

Kamal J.K. Gandhi is a Professor of Forest Entomology and Director of Southern Pine Health Research Cooperative, University of Georgia, D.B. Warnell School of Forestry and Natural Resources, 180 E. Green Street, Athens, GA 30602-2152.

Don C. Bragg is a Project Leader and Research Forester, U.S. Department of Agriculture Forest Service, Southern Research Station, P.O. Box 3516 UAM, Monticello, AR 71656.

Rabiu Olatinwo is a Research Pathologist, U.S. Department of Agriculture Forest Service, Southern Research Station, 2500 Shreveport Highway, Pineville, LA 71360-4046.

Kier D. Klepzig is a Research Entomologist and the Director of The Jones Center at Ichauway, 3988 Jones Center Drive, Newton, GA 39870.

Cover photo: A gap in a longleaf pine woodland created during Hurricane Michael in 2018. Photo by James Guldin, USDA Forest Service, Southern Research Station.

Disclaimer

August 2020

Southern Research Station
200 W.T. Weaver Blvd.
Asheville, NC 28804

www.srs.fs.usda.gov

Interactions Between Weather-Related Disturbance and Forest Insects and Diseases in the Southern United States

James T. Vogt, Kamal J.K. Gandhi, Don C. Bragg, Rabiu Olatinwo, and Kier D. Klepzig

ABSTRACT

Forests in the Southern United States experience a wide variety of weather-related disturbances, from small-scale events which have management implications for one or a few landowners to major hurricanes impacting many ownerships across multiple States. The immediate impacts of catastrophic weather disturbance are obvious—trees are killed, stressed, or damaged due to wind, flooding, ice, hail, or some combination of events. How forests respond to disturbance depends on several factors such as forest types and attributes, ecoregion, local pressure from invasive plants, preexisting infestations of pests and pathogens, prior disturbance events, and other variables which interact in complex ways, influencing successional dynamics and management decisions. In this review, we synthesize the major weather perturbations affecting the forests of the Southern United States and current state of the knowledge surrounding interactions between these events, forest pests, and forest diseases. We present a compilation of non-quantitative observations between 1955 and 2018 from annual U.S. Department of Agriculture Forest Service "Major Forest Insect and Disease Conditions in the United States" reports describing where insects or diseases were found on trees that were stressed by weather disturbances. Two conceptual models are presented, one describing changes in forest structure and composition, and a generalized model of herbivorous pest population fluctuations following different severity levels of disturbance. Finally, we propose 11 questions that require additional research to better inform sustainable forest management decisions in preparation for and in response to catastrophic weather events.

Keywords: Flooding, forest pathogens, forest pests, ice storms, post-disturbance management, post-disturbance recovery, windstorms.

https://doi.org/10.2737/SRS-GTR-255

Contents

INTRODUCTION

Forests of the Southern United States (fig. 1), hereafter "the South," are among the most productive and intensively managed in the world. While containing only about 2.5 percent of global forest area, southern forests—sometimes referred to as the Nation's "wood basket"—account for 12 percent of the world's industrial roundwood production, including 8.5 percent of sawnwood and 22 percent of pulpwood (FAO 2018, Howard and Liang 2019, Oswalt and others 2019). Long dominated by conifers, this region also has the highest timber removal rates and most planted (versus naturally regenerated) timberland in the United States (Oswalt and others 2019). Indeed, over half of the South's softwood area is classified as planted, with > 70 percent being loblolly/shortleaf (*Pinus taeda*/*P. echinata*) forest type. Eighty-five percent of planted pine area is in loblolly pine, with most of the balance in slash pine (*P. elliottii*) (Oswalt and others 2019). This is significant, as planted and natural-origin stands differ greatly in their management intensity, forest structural characteristics, species composition, stocking, tree age, response to disturbance, and other factors. For example, pine plantations have much greater silvicultural inputs and fewer tree species, and are typically managed on much shorter rotations than natural pine and pine-hardwood stands. Hardwood-dominated forests in the South are mostly of natural origin, are important contributors to hunting and recreation activities, produce high-value lumber and some pulpwood, and are increasingly being utilized for pellet production (Oswalt and others 2019).

Regardless of stand origin or composition, weather-related natural disturbances pose a significant threat to southern forests. While these disturbances alter stand dynamics and succession and serve many other important ecological functions (for example, Bragg and others 2003, Curry and others 2008, Everham and Brokaw 1996, Holzmueller and others 2012), the consequence of most importance to most landowners is a reduction in and degradation of their merchantable timber. For example, severe wind events can impact large areas of forest, killing trees by breaking or uprooting them

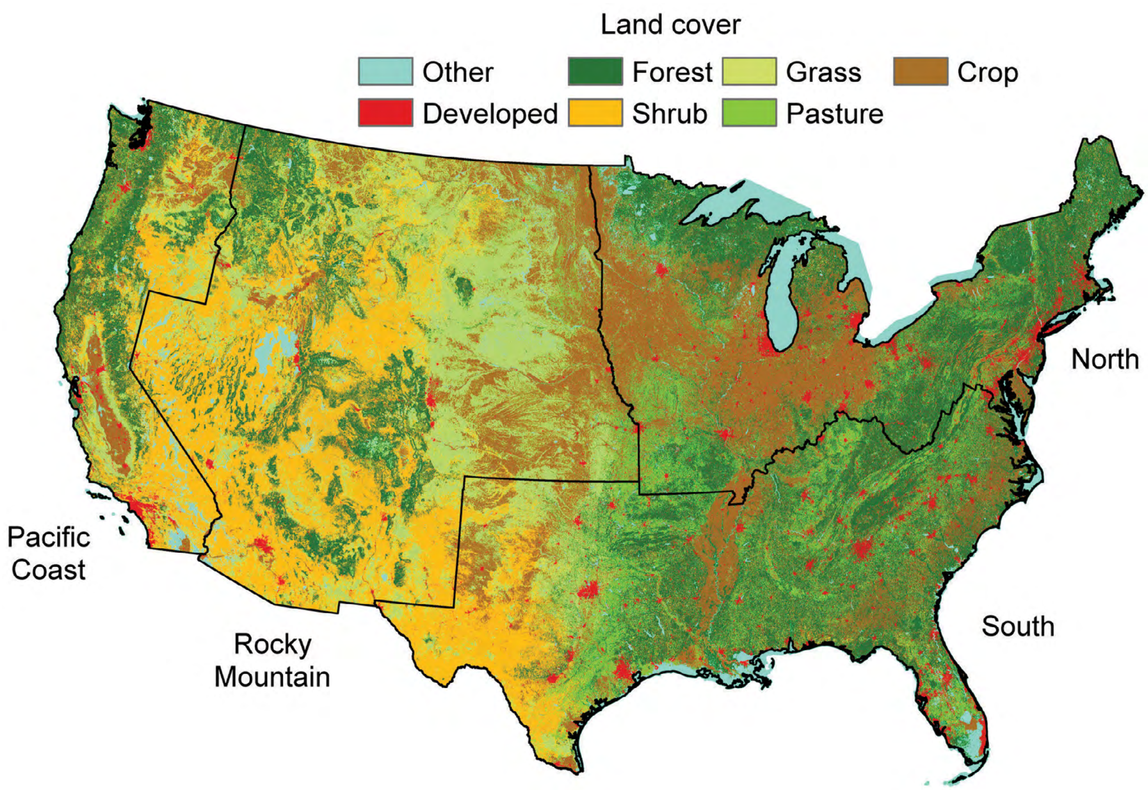

Figure 1—Land cover (including forest land) across the continental United States. The South has extensive forest land, with the exception of western Texas and parts of the Mississippi Delta. Map from National Land Cover Database (2016 edition), U.S. DOI Geological Survey, Sioux Falls, SD.

and weakening the remaining trees. In addition to their relatively frequent occurrence and contributions to widespread tree mortality (Everham and Brokaw 1996, Lemon 1961, Zeng and others 2009, and references therein), these perturbations can also increase the risk of subsequent losses by insects, diseases, and future disturbances (Beach and others 2010). Trees that survive natural disturbances may be of lower quality because of deformations to their boles or degradation to their wood from insect damage, fungal decay, or injury-triggered mineral stain (Bragg and others 2003, Panshin and de Zeeuw 1980, USDA Forest Service 1989). All of the newly created forest heterogeneity at spatial and temporal scales has major implications for other biotic elements (animal and plant species) as habitat templates and for future regeneration dynamics.

In this review, we consider catastrophic weather-related disturbances—events that significantly change forest composition and structure—and their impacts on associated pests and pathogens in the South. Surprisingly, such a synthesis does not currently exist, making this review particularly timely as weather-related disturbances become more prominent with climate change. Evidence shows, for example, that hurricanes are more rapidly intensifying and moving more slowly over land, resulting in far greater damage (Zhang and others 2020). Our review focuses primarily on wind, ice/snow, and hail storms and flooding, with some information presented on drought and fires (which will be the focus of subsequent reviews), and how these weather-related disturbances interact with forest pests and pathogens.

WEATHER EVENTS

Wind Storms

Given their nature, scale, and frequency, wind events are the most widely distributed broad-scale perturbations that occur across the South (Peterson and others 2016). Damaging wind events can range from massive tropical systems (hurricanes and tropical storms), to intense, fast-moving clusters of damaging thunderstorms (derechos), downbursts, and tornadoes, to widespread but low-severity impacts from frontal systems. At one level, wind events are broadly similar—the rapid and forceful movement of air that damages trees. However, their unique climatological signatures have impacts on forest communities that not only produce different damage outcomes, but potentially different responses from insects and disease. For this reason, we will review the primary wind-based perturbations that affect the South.

Because wind places stress along the entire tree, from its roots to the top of its crown, structural failure may occur at any place where the bending force exceeds the critical beam resistance (Peltola and others 1999). Bending force is the result of a number of factors, including the strength and duration of the wind gust, the drag of the crown (based on crown surface area), and the exposure of the tree to wind. Resistance is a function of wood strength and the size of the stem (or branches), as well as the strength and structural integrity of the root system (Quine and Gardiner 2007). Wind- and ice-resistant trees often have a number of attributes that serve to protect them: many have very strong wood or pliable boles and branches, and most also have strong root systems to anchor them against toppling or minimal decay that could lead to structural failure. Tree architecture can be very important, as some crowns are more streamlined to minimize wind exposure. Very tall trees—or at least those that are prominently exposed—can experience heightened wind damage, especially if suddenly exposed by cutting operations that removed nearby trees. Over time and under gradual exposure to more wind, roots, boles, and branches may develop considerable "windfirmness," making them less vulnerable to injury or death (Gardiner and others 2016). Large-diameter trees can often be more prone to windthrow and breakage than smaller diameter trees (Peterson 2007). Older trees vulnerable to windthrow may include those already infected by root rot, butt rots, and trunk rot pathogens, particularly in areas where hurricanes are a common occurrence (Nelson and Stanley 1959, Powers and Verrall 1962).

Hurricanes and tropical storms

Tropical cyclones (hurricanes and tropical storms) can form and strike the South any month of the year, but the Atlantic hurricane season extends from the beginning of June through the end of November. Between 1900 and 2005, 8 of the 10 most economically damaging tropical cyclones to impact the United States made landfall in the South (Pielke and others 2008), and since 2005 at least a half dozen systems have struck the South and inflicted at least $30 billion in losses per event (Smith and others 2019). Return periods for hurricanes of any strength across all coastal States in the South range from 5 to 20 years (U.S. DOC NOAA National Hurricane Center 2019). The return periods for the most damaging major hurricanes (Category 3, 4, or 5; sustained winds of $\geq$111 miles per hour [$\geq$96 kt]) range from about one to two storms per 20 years in southern Florida, the central Gulf Coast, and the coast of the Carolinas to perhaps one to two storms per century along the Virginia Coast (fig. 2).

In the South, damaging winds associated with tropical storms may leave extensive gaps in the forest canopy (Croker 1987, Xi 2015, Xi and others 2008), sometimes on a massive scale. For example, when Hurricane Michael struck the Florida Panhandle in October 2018 with Category 4-force winds, it catastrophically damaged (95 percent lost) timber on nearly 350,000 acres, left severe damage (75 percent lost) on an additional 1 million acres, and left moderate damage (15 percent lost) on just over 1.4 million acres (Florida Forest Service 2018). The extent and severity of damage left in a tropical cyclone's wake depends on a number of storm-related factors (for example, strength and speed of the storm, quantity and duration of the precipitation) and other site and vegetative conditions, such as the degree of exposure or soil saturation (Foster 1988, Foster and Boose 1992). For example, the most intensive and destructive winds of a hurricane typically occur at landfall along the "eyewall," but extensive windthrow can affect large areas of inland forest, especially if soils have been saturated by heavy rains (Kupfer and others 2008). Because of their more moderate windspeeds, tropical storms tend to produce far less wind damage to forests than hurricanes, although all tropical cyclones can spawn typically short-lived tornadoes with potentially major losses in limited areas. Hurricanes also cause localized hotspots of damage in complex terrain, perhaps due to embedded microbursts (Greenberg and McNab 1998, McNab and others 2004).

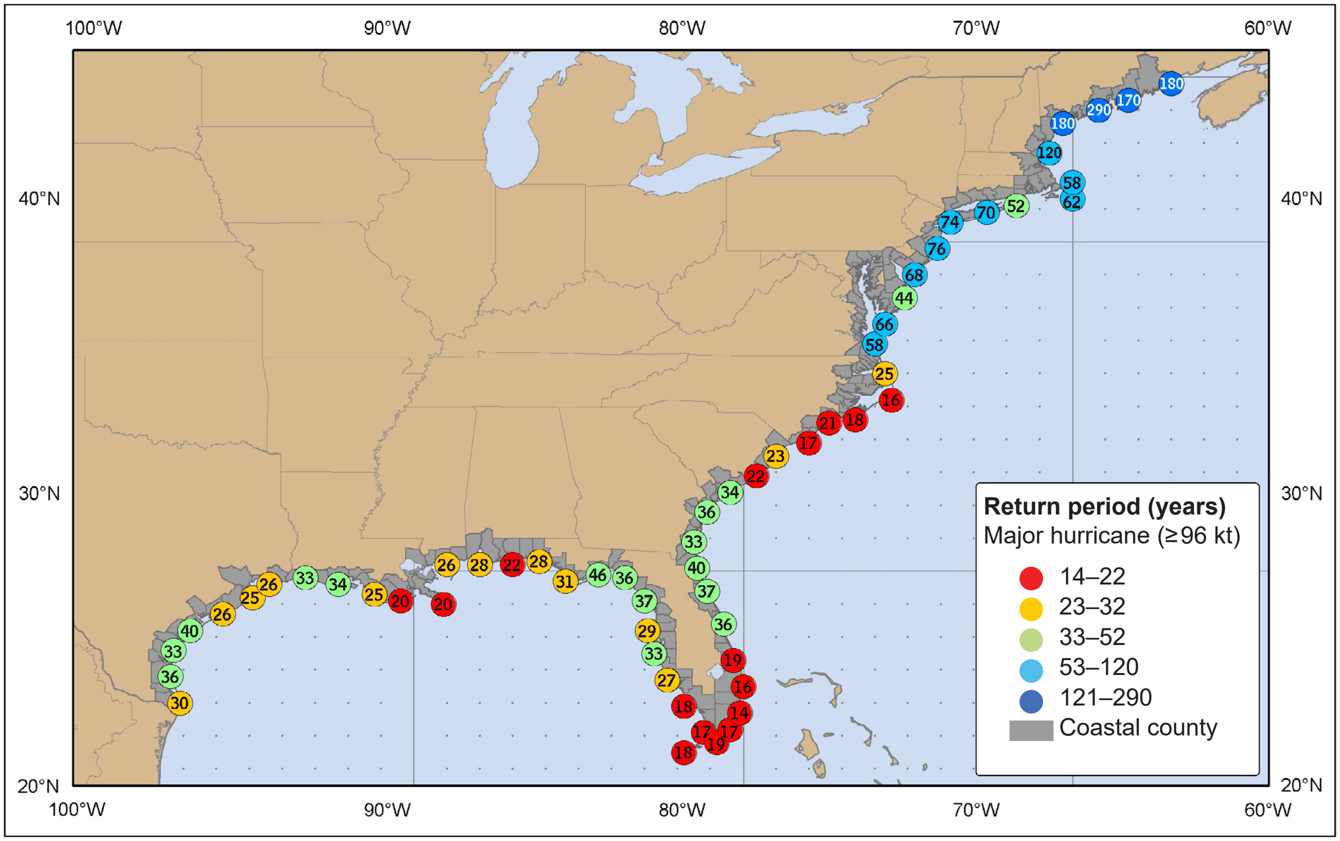

Figure 2—Return intervals for major hurricanes along the Gulf and Atlantic Coasts. Map from U.S. DOC NOAA National Weather Service.

Tornadoes

More tornadoes occur in the United States than anywhere else in the world, with the majority of them affecting the central region of the country (Boruff and others 2003, Dixon and others 2011, Goliger and Milford 1998). The South also experiences a relatively high frequency of tornadoes in spring and fall, in an area called “Dixie Alley” that spans from Arkansas and Louisiana in the west and as far east as Georgia and north into Tennessee (Dixon and others 2011). Dixie Alley is especially prone to strong, long-track tornadoes that move rapidly (≥ 50 miles per hour) (Coleman and Dixon 2014). Tornadoes often occur in outbreaks, such as the April 2011 event which was especially severe in Alabama and Mississippi and an April 2020 outbreak across the South that spawned 139 tornadoes over 2 days. Southwide, the average annual number of tornadoes ranges from a low of 18 in Virginia to a high of 155 in Texas (U.S. DOC NOAA NCEI 2019).

Tornado impacts can range from very limited damage from brief touchdowns or weak tornadoes to paths hundreds of yards wide carved for many miles. Generally, tornadoes create sharp edges between intact forest and windthrown areas (Goode and others 2020). The most intense tornadoes may topple all trees within their path (Peterson and Pickett 1995) unlike hurricanes, which typically have a gradient of damage and lower wind speeds in which tree age, size, and species affect likelihood of damage (Foster 1988). Tornado-based tree damage and mortality can be captured and mapped using the Normalized Difference Vegetation Index (NDVI) which shows vegetation properties and reveals the tracks of tornadoes through forested areas (fig. 3).

Macrobursts, microbursts, and derechos

Strong wind events resulting from downdrafts in convective thunderstorms are collectively termed “downbursts.” Our understanding of these weather phenomena is fairly recent. Fujita (1981, 1985) defined a downburst affecting an area at least 2.5 miles wide with peak winds lasting 5–20 minutes as a “macroburst,” and a downburst affecting a smaller area and lasting < 5 minutes a “microburst.” Derechos are currently defined as a family of long-lasting, damage-causing downburst clusters associated with a large-scale convective frontal

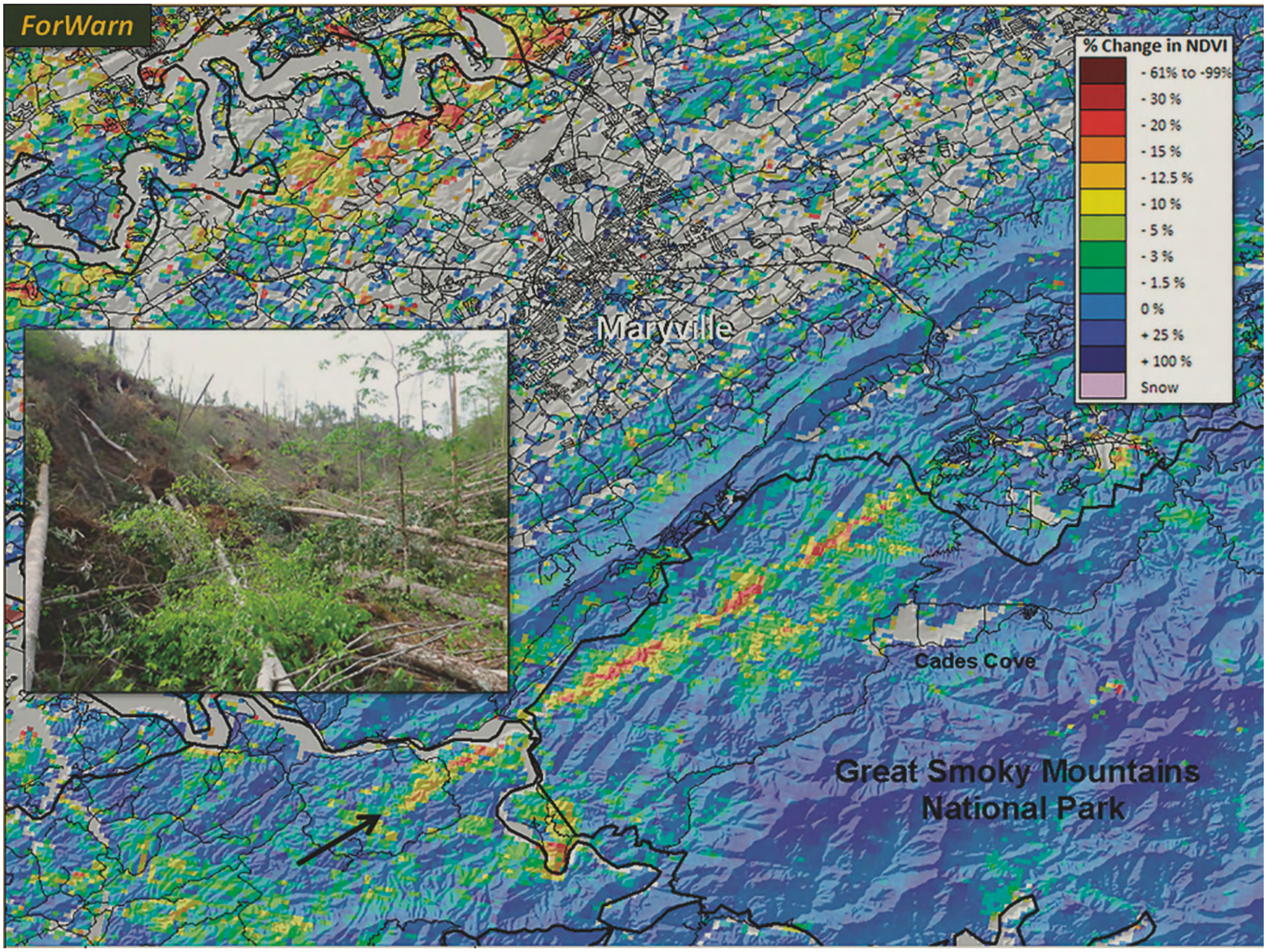

Figure 3—An example of a tornado path (Great Smoky Mountains tornado, April 2011) visible in a near-real-time change map based on Moderate Resolution Imaging Spectroradiometer (MODIS) Normalized Difference Vegetation Index imagery and captured from the U.S. Forest Change Assessment Viewer (https://forwarn.forestthreats.org).

system with one or more “bow echoes” that leave a swath of “straight-line” wind damage at least 60 miles wide and 400 miles long (Corfidi and others 2016). Derechos commonly occur in the South, sometimes as frequently as yearly (Ashley and Mote 2005) (fig. 4). They may originate in the Great Plains region and travel southeastward, or form in the Gulf Coast region and travel northeastward. Southern forests are at a higher level of risk from derechos in the spring, when they can develop anytime from late morning through the overnight hours. During the summer, derechos may impact western parts of the southern region (for example, Texas and Arkansas) as they form in the Great Plains and move southeast (Ashley and Mote 2005, Bentley and Mote 1998). Derechos may be far more complex than mere straight-line wind events, with embedded tornadoes, downbursts, and broader circulations, as indicated by damage patterns generated by the May 8, 2009 derecho that impacted an area stretching 1609 km from central Kansas to western Virginia and North Carolina (Vaughn 2013). Macrobursts and microbursts, with winds ranging up to 134 and 168 miles per hour, respectively, can cause major localized forest damage similar to that of tornadoes. Microbursts occur more frequently than tornadoes, and also generate characteristic patterns of forest damage that are easily discernible in aerial imagery (fig. 5). The damage to forests from downbursts tends to be much more widely distributed than that of tornadoes. While particularly strong macrobursts and derechos can flatten timber over large areas, tree damage from microbursts tends to be more locally concentrated.

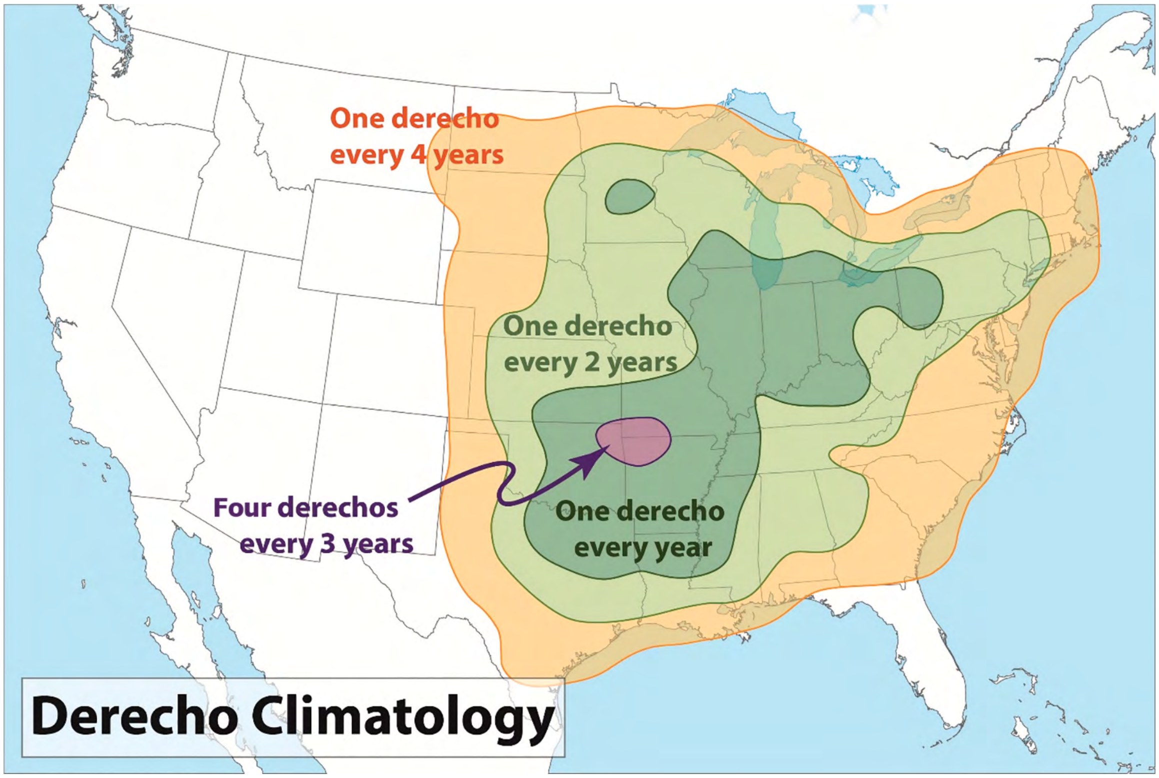

Figure 4—Average frequency of derechos in the United States. Map from Dennis Cain, U.S. DOC NOAA.

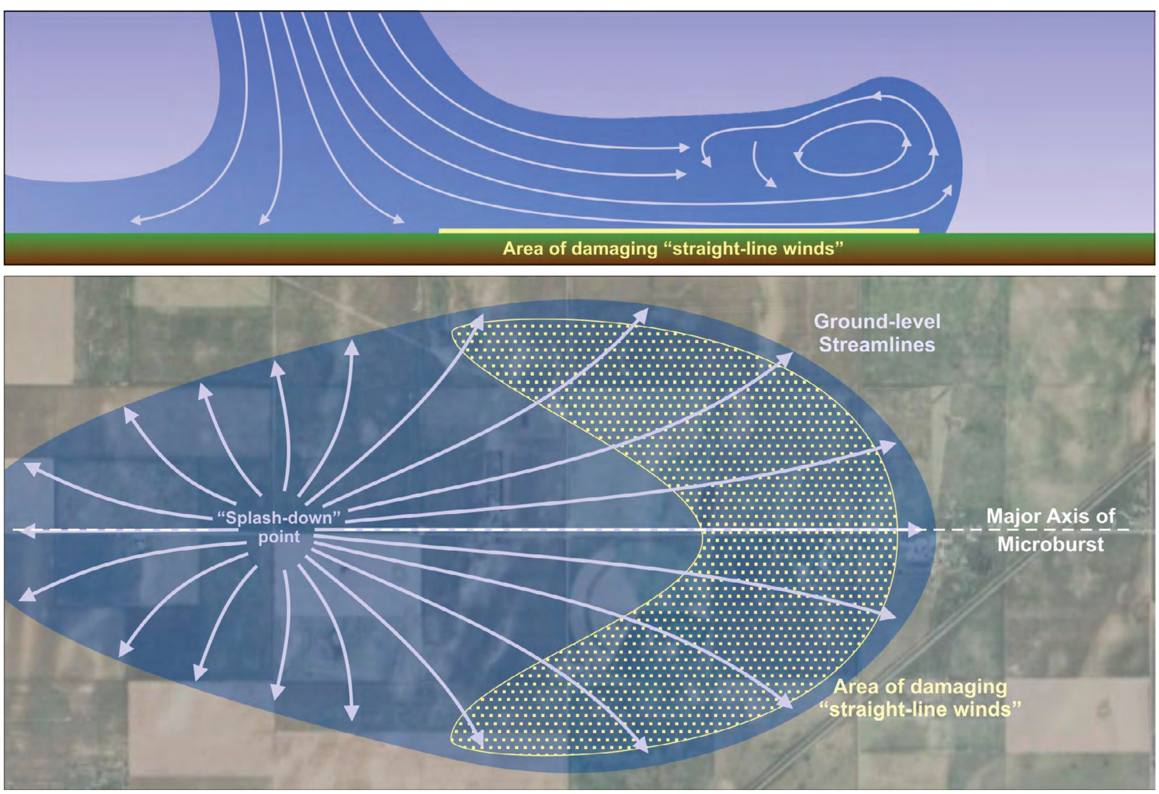

Figure 5—Graphic illustration of typical microburst wind patterns. Map from David Babb, Penn State University, Department of Meteorology and Atmospheric Science.

Severe Weather-Related Phenomena

Lightning and hail

Lightning strikes from thunderstorms usually result in localized injury to trees but are a widespread occurrence accompanying broad-scale severe weather events. Lightning can also start wildfires, leading to much wider forest impacts. Some have estimated that lightning may contribute 1 percent or even more of tree mortality in many places in the South (Komarek 1974); e.g., in a longleaf pine (*P. palustris*)-dominated ecosystem, lightning strike was the primary cause of tree mortality (Palik and Pederson 1996). Those areas more affected by thunderstorms[1] are more prone to lightning-based injuries. Lightning can be immediately lethal to struck trees, with some being literally blown apart when the massive surge of electricity explosively vaporizes moisture in the stem. More commonly, lightning travels from the top of the tree to the ground, blasting a strip of bark off along all or part of the branches, bole, and even roots (Taylor 1974).

Hail is a weather phenomenon that commonly accompanies severe thunderstorms in the South. Hailstones are solid ice accretions that grow radially as strong storm updrafts keep them suspended in the moist atmosphere. The stronger the updraft, the larger the hail can grow. Once hail grows to the point that the updrafts can no longer keep it suspended, the hailstones fall to the ground with considerable force. As a part of intense convective thunderstorms, hail is often also accompanied by strong winds (sometimes tornadoes) and lightning, both of which can magnify the damage. Hailstorms tend to be highly localized, and the most severe damage occurs even more locally where the quantity and duration of the falling hail accentuates the impact. However, some hail events cover large areas, such as a massive 1968 storm that struck near Camden, AR, and damaged about 180,000 acres, with spots of wind damage and post-storm insect attacks (Kucera and Hatch 1968).

Floods

Flood events are typically found only along stream channels and adjoining floodplains, range in duration from very short term (hours) to long term (months), and can be predictable seasonally or associated with specific precipitation events. Unless particularly intense (a forceful release or surge of water) or associated with a bank failure, short-term floods rarely kill or even injure trees in their path. There are times when rapidly rising water levels undercut banks, expose roots, or remove bark (fig. 6), or when debris can be forced upon standing trees causing them to break or topple, but these are usually spatially limited. In some large-scale, long-duration floods, water covers the root systems of trees for a long time period, which can eventually lead to tree decline or death. Soils saturated for extended periods by floodwaters lack the oxygen required for root respiration and can prove lethal to even the most flood-tolerant tree species under sufficient duration (Kozlowski 2002). Bottomland forests in the South are usually driven by the hydrological regime of the sites where they are found, and floods are often a controlling factor in species composition because of their effects on seedling success.

Figure 6—A large loblolly pine with a gradually exposed root system has survived multiple earlier floods but is vulnerable to eventual failure if this stream bank continues to experience erosion. Photo by Don C. Bragg, USDA Forest Service, Southern Research Station.

---

[1] There is variation in the frequency of lightning across the South (Orville and Huffines 2001).

Other Forest-Damaging Weather Phenomena

Ice and snow storms

Ice (sometimes called "glaze") storms and wet snowfalls are large-scale phenomena that occur when a coating of frozen precipitation accumulates to the point that the extra weight damages the tree. Although not as well-publicized as hurricanes, ice storms can be multiday events that damage or destroy timber across thousands to even millions of acres, producing economic losses on a massive scale (Bragg and others 2003, Irland 2000, Smith 2000). Ice storms and heavy wet snows are relatively common in Eastern North America, and much of the South experiences damaging events every few years to decades (Bennett 1959, Bragg and others 2003, Jones and others 2002, U.S. Army Corps of Engineers 2019). While most ice storms are not particularly severe or widespread, even a modest event can damage vulnerable trees and cause widespread power outages. In recent decades, major ice storms have struck Arkansas, Georgia, Mississippi, North Carolina, South Carolina, Tennessee, and Virginia (Bragg 2016, Bragg and others 2003, Halverson and Guldin 1995, U.S. Army Corps of Engineers 2019). For example, in December 2000 a pair of ice storms affected 40 percent of the forests in Arkansas, resulting in hundreds of millions of dollars of damage to timber, utility infrastructure, and buildings (Bragg and others 2003, 2004).

Ice storms occur when already cold rain falls onto a subfreezing surface or falls through subfreezing layers in the atmosphere causing the rain to become "supercooled"; the resulting accretion of ice adds weight to that surface (Degelia and others 2016). Wet snowfalls happen when it is relatively warm (near or just above freezing), leading to snow with a high moisture content that increases the likelihood of its adhering to surfaces. In either case, once the accumulation of frozen precipitation reaches the point where the added weight exceeds the load-bearing capacity of the tree's branches, bole, and/or root system, damage from stem bending, bole or branch breakage, or uprooting occurs (fig. 7). Glaze or snow load injuries can be accentuated by mitigating circumstances such as the size and load-bearing capacity of individual trees, bole or branch weakness due to decay or cankers, accompanying winds, saturated soils that weaken root support, recent density reductions via thinning, or

Figure 7—Example of severe ice damage in a recently thinned loblolly pine plantation in central Arkansas showing the most prominent and typical types of immediate damage: uprooting, stem breakage, stem bending, and branch (crown) loss. Additional injuries and tree death can also come later from insect attack or disease on affected trees. Photo by Don C. Bragg, USDA Forest Service, Southern Research Station.

locally higher elevations that increase precipitation accumulation. For instance, the same ice storm may inflict much more damage on a recently thinned 18- to 20-year-old loblolly pine plantation than an adjacent mature pine stand, given differences in individual tree resilience (Bragg and others 2003, 2004).

Frost damage

Damaging frosts are rarely considered to be a forest health threat in the South. However, a growing body of evidence shows that frost can be an aggravating factor (if not an outright contributor) to tree injury and mortality in this region. For example, Bendixsen and others (2015) reported that a late spring frost (a “false spring”) in an area of extreme drought may have triggered cavitation in the conducting vessels of drought-stressed oaks (*Quercus* spp.), making those trees more vulnerable to fungal infections that may have ultimately resulted in tree decline and death. Spring frost damage is thought to be increasing in a number of places, probably due to phenological responses to regional patterns associated with climate change (Augspurger 2013, Rigby and Porporato 2008), and may prove to be a growing concern across the South if it negatively impacts tree regeneration and forest health.

Drought and heat waves

Unlike most weather-related catastrophic forest disturbances, which tend to happen over a period of hours or a few days, droughts typically take weeks to months to build and can persist for many months or even years (megadroughts can last for 1 to 2 decades, if not longer). Drought is not an inherently catastrophic forest disturbance for much of the South; seasonal dryness is often experienced across much of the region in the late summer and early fall, as regional and even global weather patterns (such as El Niño and La Niña events) influence rainfall. Droughts can also be accentuated by local conditions, such as soil type, rooting zone depth and rock content, availability of supplemental water sources, forest composition, and stand age (Clark and others 2016a, 2016b). For a review of regional drought impacts on U.S. forests in the context of climate change and a discussion of research needs, see Hanson and Weltzin (2000).

Excessively high temperatures are generally not a major health threat to trees, which have considerable ability to tolerate extreme heat. However, heat waves that accompany droughts have been shown to exacerbate tree mortality and encourage insect outbreaks (Allen and others 2010). Combined, heat waves and drought also produce conditions favorable for the outbreak of wildfires in the South (McNulty and others 2019).

Wildfire

Although not a weather event itself, wildfires can be considered a weather-related phenomenon. The rate of fire growth, extent of damage, and severity of fire injury to forests are subject to weather-related influences, such as heat waves, strong winds, ignition sources (lightning), and the rapid accumulation of dead plant fuels. Wildfires occur when sufficient quantities of dry fuel are ignited and burn out of control, and can occur in hot or cool weather or dry to droughty conditions. Fire frequency in the South depends on the availability of and nature of fuels, sufficiently dry conditions, and presence of an ignition source. Bark beetle-induced mortality may alter fuel loads and fire behavior, but studies of these phenomena have largely been restricted to the Western United States and are controversial (Hart and others 2015, Hicke and others 2012). There is a need for research to better understand these relationships in the South.

Effects of Weather Events on Stand Characteristics and Tree Physiology

Direct storm impacts

Different kinds of weather events influence forests at different scales, from individual tree injuries (lightning strikes) to the stand scale (tornado) to a landscape scale (hurricanes, derechos). Landscape-scale disturbances often have smaller scale disturbances embedded within them, creating a mosaic of damage severity across the affected area. While characterizing and quantifying damage over large areas is challenging, we know much about how severe winds or glaze loads can affect individual trees, many of the variables that influence damage within stands, and some of the changes that occur within stands as a result of these agents (recently reviewed by Bragg and others [2003], Mitchell [2013], and Peterson [2007]). Broad generalizations (such as hardwoods versus softwoods) are not always useful, as storms impact many different aspects of trees and their stands. For example, in the South, softwood tree species that are common in the lower Coastal Plain region of South Carolina were damaged less by Hurricane Hugo than wider ranging hardwood species (Gresham and others 1991). Stand age is a factor as well; stands that withstood damage from Hurricane Michael in the Chipola Experimental Forest (near Clarksville, FL) were almost exclusively longleaf pine < 5 years old.[2]

At the stand level, severe wind events often result in characteristic damage. A hurricane generally leaves a gradient of damage corresponding to the gradient of wind speed across its track, whereas a strong tornado may destroy all the trees in its path. Tornado damage tracks are more often discontinuous and patchy, although they may nevertheless have sharp edges (Cannon and others 2016). A strong downburst may result in uprooting of all or nearly all trees in the affected area with little sign of disturbance in surrounding forest. Retrospective studies of stand and tree damage following hurricanes (for example, Kupfer and others 2008, Putz and Sharitz 1991, Walker 1991) have been most informative with regard to relative susceptibility of tree species and sizes as well as the effects of other abiotic factors such as topography and soils. The physical attributes of forests that experience severe weather also change—soil disturbance and coarse woody debris are both increased; environmental variables such as light, wind, temperature, and moisture change (Oliver and Larson 1996; Peterson and Leach 2008a, 2008b); and edges are formed (Webb 1999).

Not all tree species are equally susceptible to weather disturbance events. Ice storms present a good example of these differential responses. Over the years, a number of studies have considered differing amounts of damage in mixed-composition stands (both planted and natural) and have used these observations to discuss species-specific vulnerability to glazing. In general, it has been suggested that conifers with shorter needles, less dense foliage, and greater branch and bole flexibility are more likely to survive and have fewer and/or less severe injuries than species with long needles, dense crowns, or weak/inflexible wood. For instance, shortleaf pine is considered one of the most resilient southern pines to ice damage, followed by loblolly, and then slash and longleaf (Bragg and others 2003, Brender and Romancier 1960, McKellar 1942, Wahlenberg 1960). Some have even suggested that the varying resilience to glazing has helped control the distribution of some southern trees based on their ability to survive increasingly frequent ice storms with increasing latitude or elevation (for example, Lu and others 2020, Wahlenberg 1960). It is important to recognize the potential of other confounding factors (such as tree size, age, or landform position) on the apparent influence of species on damage response, so the most valid comparisons of ice damage resilience by taxa should control for mitigating factors. As an example, Bragg (2016) compared the response of loblolly and longleaf pine to a 2014 ice storm on the Savannah River Site in South Carolina using adjacent paired plantations to contrast these species and found loblolly had less damage and lower mortality rates than longleaf pines of the same diameter at breast height. This size-based comparison was necessary because even though they had been planted the same year on the same site and had received the same thinning treatments over time, the faster growing loblolly pines had grown larger (on average) than the longleaf, and larger trees are inherently more capable of supporting ice loads.

Regardless of the disturbance agent, tree damage is usually categorized as root injury, stem damage, branch damage, and/or canopy damage, whereas stand-level damage may be expressed as volume or mass loss, and/or mortality (Everham and Brokaw 1996). With the exception of certain extreme conditions, even a very damaging storm does not immediately kill most affected trees—many die in the following weeks, months, and even years, while others survive with major deformations (Cooper-Ellis and others 1999). In the same way, very few trees manage to escape the impacts of even a modest storm event, as small branches and foliage can be lost. Wind effects on individual trees vary according to tree species (Foster 1988, Francis and Gillespie 1993, Gresham and others 1991, Leininger and others 1997, Peterson 2007), age (Foster 1988), size (Foster 1988, Leininger and others 1997, Peterson 2007, Peterson and Pickett 1991), and rooting depth (Mueller and Cline 1959, Webb 1988). Easily discernable physical effects of severe wind events on trees include defoliation, limb breakage, bole breakage or snapping, abrasion, and toppling. In most southern pines, breakage of boles below the live crown results in a lethal injury. Younger hardwoods, in contrast, usually have the ability to resprout following topkill and may recover. Non-lethal injuries to surviving trees can range from the obvious, such as stem or branch breakage, leaning, or partial uprooting, to less apparent internalized damage to boles, branches, or roots. Permanent deformation (either severely bending or with non-lethal breakage of the bole) may appreciably diminish the economic value of the trees and make them more vulnerable to later injuries or damaging agents. As limbs, partial trees, or entire trees fall, they can damage neighboring trees: roots can be exposed, stumps or snags can be formed, and buds and

[2] Personal communication. 2020. J. Guldin, Senior Research Silviculturist, U.S. Department of Agriculture Forest Service, Southern Research Station, Hot Springs, AR 71902.

leaves can be stripped (though new buds and leaves may be available following defoliation). Root damage and damage to the vascular system of trees from bending are not as easily observed but can weaken trees. Indeed, trees of all sizes can topple in a sufficiently severe ice or wind storm if their root systems are too weak to support them or when soils are already saturated.

Ice damage manifests itself in many ways, from a barely noticeable loss of foliage to severe and sometimes lethal stem breakage, crown loss, bending, or uprooting (fig. 7). The actual injury experienced by any given tree depends on a number of circumstances, from the strength and resilience of its bole and branches to the rooting strength of the soil to the presence of aggravating weather factors (such as storm-related winds or persistence of icing conditions). Young trees are usually pliable enough to have their growing leaders bent all the way to the ground without bole breakage, allowing them to use various means to straighten their boles following release from ice or fallen storm debris (Bragg and others 2003). For larger trees with sufficiently strong boles (those capable of carrying the weight of the tree and accumulated ice), the damage is often limited to bent boles (which sometimes straighten but often permanently retain a degree of curvature) and the loss of smaller branches that break off when their individual ice coating exceeds their strength. Hail injuries to trees primarily result from stripped foliage and impact wounds on bark and other exposed tissues. Hail damage is often considered a passing concern in woody plants, most of which have the capacity to refoliate even if completely stripped of their leaves.

Floods, drought, temperature extremes, and fire

Because of their nature, floods, drought, heat waves, and fires present a different suite of forest health impacts than storm events. For example, flood damage to forests comes from physical injury to standing timber when banks get eroded from underneath a root system (causing toppling) or battered by water-borne debris, and from the impacts of long-term inundation resulting in the "drowning" of trees.

The process of toppling itself can happen very quickly when a current (often accelerated during a flood) rapidly undermines a tree alongside a stream channel; a stem can go from being firmly rooted to uprooted in minutes or hours under these circumstances. In other instances, the process of bank erosion is more gradual, and a tree can remain standing for many years with partially exposed root systems before it finally gets sufficiently undercut or otherwise structurally weakened. Any time tree root systems are exposed, they are subjected to increased levels of dieback and made vulnerable to infection, decay, and other forms of degradation from insects or disease. Floods, especially those along channels with substantial bank erosion and toppling of streamside trees, can move enormous quantities of dead wood. Much of this dead wood includes entire trees, from the root wad to the topmost branches, and these large objects can batter standing trees, causing injuries or even knocking over stems. In places, large "jams" or accumulations of dead wood will aggregate (fig. 8), and this cumulative load can likewise injure or kill trees along these parts of the channel. Coastal flooding of saltwater marshes may inundate trees without the ability to tolerate higher salinity and result in pronounced mortality, even if the species is generally flood tolerant (Kozlowski 1984). Widespread declines and mortality in coastal forests attributed to storm surges, elevated sea levels, and other geochemical processes have been reported in baldcypress (*Taxodium distichum*) and water tupelo (*Nyssa aquatica*), both of which are considered highly flood tolerant (for example, Allen and others 1996, Effler and Goyer 2006).

Floods can also result in tree injury and death via extended inundation. Physiologically, flooding (which includes waterlogged soils) negatively affects processes such as photosynthesis and respiration in trees by disrupting the flows of oxygen, water, and nutrients through biochemically triggered mechanisms and feedback loops (Kreuzwieser and Rennenberg 2014). Extended oxygen and moisture shortages arising from stomatal closures, higher root diffusion resistance, root death, and other cellular impacts can lead to many physiological stress responses including disruptions to metabolism, root senescence, leaf necrosis and shedding, bark loss, tree dieback, and death (Kozlowski 1984, Kreuzwieser and Rennenberg 2014). Although most species that live in bottomlands have adaptations to survive long periods of saturated soils and standing water, all trees have limits for how much excess water they can tolerate (fig. 9). Tolerance to flooding can vary by tree life-stage. For example, mature baldcypress and water tupelo are renowned for their long-term persistence in standing water, but their seeds must germinate and establish on relatively dry ground and seedling foliage must extend above floodwater depths, lest the germinants drown under extended inundation (Demaree 1932, Johnson 1990, Wilhite and Toliver 1990). Other studies have evaluated seedlings of many other taxa and noted significant differences in their ability to survive flooding of different durations. Hook (1984) rated a number of species in terms of "waterlogging [of the soil] tolerance" and placed them on a spectrum from most tolerant (for example, baldcypress and water tupelo) to highly

Figure 8—A debris jam that accumulated in the riparian forest along this river consists of trees that succumbed to bank undercutting or other toppling processes (e.g., windthrow) that placed the downed wood in the river. This flotsam can be hurled against bankside trees with considerable force during flood events, sometimes injuring or toppling other standing timber. Photo by Don C. Bragg, USDA Forest Service, Southern Research Station.

Figure 9—A seasonally flooded bottomland hardwood forest with a water control structure that allows this stand of timber to serve as a greentree reservoir. While the hardwoods and cypress found in this swamp are capable of tolerating long-term inundation (especially during the dormant season), even these species need some relief from waterlogged soils and standing water to grow and survive. Photo by Don C. Bragg, USDA Forest Service, Southern Research Station.

tolerant (for example, water hickory [*Carya aquatica*]) to moderately tolerant (for example, silver maple [*Acer saccharinum*] and loblolly pine) to weakly tolerant (for example, sugarberry [*Celtis laevigata*]) to least tolerant (for example, white oak [*Q. alba*] and shortleaf pine). This range of soil waterlogging tolerance helps to dictate species composition patterns along most areas affected by periodic flooding: it is, for example, a primary reason why loblolly and slash pines historically dominated wetter flatwood sites across the South and longleaf and shortleaf pines were rarely found in these seasonally flooded locations. Of course, season of flooding has a major role on the ability of a tree to survive inundation. Floods during the tree's dormant season are much less impactful than those that occur during the growing season (Broadfoot and Williston 1973).

Droughts (especially when they occur with high temperatures) can kill trees. This is especially true for young seed-origin trees and 1+0 planting stock (1-year-old bare-root seedlings) in the first year of outplanting, due to limited root development. Even if not lethal, prolonged drought or high temperatures can cause trees to greatly limit growth and reproductive effort, and lower their resistance to pests and pathogens. As with extreme high temperatures, frost events rarely prove lethal to trees, although it is common for foliage to be damaged sufficiently to require a new flush, thereby diminishing the carbon reserves of the affected individuals.

Fires can kill or wound healthy trees, depending on the severity of the burn, the susceptibility of the affected timber, and the presence of aggravating circumstances. Intense crown fires are the most lethal events and can result in near-complete death of large areas of forest of even the most fire-resistant species, if conditions are favorable. A full consideration of the complex interactions between wildfires, prescribed burns, pests, and pathogens is beyond the scope of this review; however, a few reports of insects and pathogens co-occurring with wildfire are included in table 1.

Table 1—Observations of insects and diseases during years 1955–2018 associated with various weather disturbances in the Southern United States

Weather/ abiotic event	Insect or pathogen	Observation	Host tree	Years reported
Drought	Actinopelte leaf spot (*Actinopelte dryina*)	Premature defoliation associated with drought	Oak (*Quercus* spp.)	1985, 1986
Drought	Heterobasidion (annosum) root disease (*Heterobasidion irregulare*)	Disease exacerbated by drought	Southern pines (*Pinus* spp.)	2004
Drought	Heterobasidion (annosum) root disease	Decline in disease due to relief from drought	Southern pines	2003
Drought	Balsam woolly adelgid (*Adelges piceae*)	Increased attacks and tree mortality	Fraser fir (*Abies fraseri*)	1986
Drought	Black turpentine beetle (*Dendroctonus terebrans*)	Increased insect activity	Southern pines	1963, 1968
Drought	Black turpentine beetle	Increased attacks and tree mortality	Southern pines	1969, 1971, 1981, 1982, 1983, 1985, 1986, 1987, 1988, 2000, 2001, 2002, 2003, 2005, 2006
Drought	Charcoal root rot (*Macrophomina phaseolina*)	Disease intensified as a result of extended drought	Loblolly pine (*Pinus taeda*)	1987
Drought	Cytospora canker (*Cytospora* spp.)	Aggravated by drought	Cottonwood (*Populus* spp.)	1987
Drought	Decay fungus (*Meruliopsis taxicola*)	Drought allowed fungus to cause significant decay	Cypress (*Taxodium* spp.)	2003
Drought	Dutch elm disease (*Ophiostoma novo-ulmi*)	Increased attacks and tree mortality	American elm (*Ulmus americana*)	1998
Drought	European elm bark beetle (*Scolytus multistriatus*)	Reduced tree vigor, beetle readily established broods in weakened trees	American elm	1955

(*continued*)

Table 1 (continued)—Observations of insects and diseases during years 1955–2018 associated with various weather disturbances in the Southern United States

Weather/ abiotic event	Insect or pathogen	Observation	Host tree	Years reported
Drought	Gypsy moth (*Lymantria dispar*)	*Entomophaga maimaiga* fungal outbreak subsided and gypsy moth rebounded	Hardwoods, especially oaks	2000, 2001
Drought	Gypsy moth	Populations of gypsy moth variable	—	2001, 2002
Drought	Hypoxylon canker (*Hypoxylon atropunctatum*)	Common and more widespread because of extended drought	Red oak group	1982, 1986, 1987, 1988, 1989, 1990, 1991, 1992, 2002, 2003, 2006
Drought	Linden looper (*Erannis tilaria*), eastern oak looper (*Phigalia titea*), fall cankerworm (*Alsophila pometaria*)	Increased attacks and tree mortality	Oaks	1983
Drought	Locust leaf miner (*Odontota dorsalis*)	Reduced tree vigor	Black locust (*Robinia pseudoacacia*)	2002
Drought	Eastern oak looper	Heavy defoliation	Oaks, hickories (*Carya* spp.)	1964
Drought	Nantucket pine tip moth (*Rhyacionia frustrana*)	Increased insect abundance	Loblolly, shortleaf (*Pinus echinata*) pines	1998, 1999, 2000
Drought	Pine bark adelgid (*Pineus strobe*)	Increased attacks and tree mortality	White pine (*Pinus strobus*)	2005, 2006
Drought	Pine colaspis beetle (*Colaspis pini*)	Some mortality in ornamental cypress	Southern pines, ornamental cypress	2003, 2004
Drought	Pine engraver beetles (*Ips avulsus*, *I. grandicollis*, *I. calligraphus*)	Increased attacks and tree mortality	Southern pines	1962, 1963, 1965, 1966, 1967, 1968, 1970, 1981, 1982, 1983, 1985, 1986, 1987, 1989, 1991, 1993, 1996, 1997, 1998, 1999, 2000, 2001, 2002, 2004, 2006, 2010, 2015
Drought	Pine sawflies (*Neodiprion* spp., *Diprion* spp.)	Drought exacerbated sawfly defoliation	Southern pines	2000
Drought	Red oak borer (*Enaphalodes rufulus*)	Increased attacks and tree mortality	Northern red oak (*Quercus rubra*), black oak (*Q. velutina*)	1999, 2000, 2001, 2002, 2003, 2006
Drought	Armillaria root rot (*Armillaria mellea*, *A. tabescens*), *Phaeolus schweinitzii*, *Phytophthora* spp.	More severe losses due to drought stress; more widespread due to drought	Southern trees	1980, 1981, 1986, 1987, 1989, 1992
Drought	Ganoderma root rot (*Ganoderma tsugae*, *G. lucidum*)	Active on droughty sites	Loblolly pine, oak	1982, 1983
Drought	Southern pine beetle (*Dendroctonus frontalis*)	Insect populations declined slightly during drought	Southern pines	1998
Drought	Southern pine beetle	Increased attacks and tree mortality	Southern pines	2000, 2001, 2015, 2017
Drought	Southern pine beetle	End of drought resulted in decrease of southern pine beetle population	Southern pines	2003

(*continued*)

Table 1 (continued)—Observations of insects and diseases during years 1955–2018 associated with various weather disturbances in the Southern United States

Weather/ abiotic event	Insect or pathogen	Observation	Host tree	Years reported
Drought	Sweet fern blister rust (*Cronartium comptoniae*)	Especially severe in droughty areas	Virginia (*Pinus virginiana*) and loblolly pine	1979
Drought	Texas leaf-cutting ant (*Atta texana*)	Insect abundant in areas of drought	—	1958
Flooding	Bald cypress leafroller (*Archips goyerana*)	Increased mortality	Baldcypress (*Taxodium distichum*)	1998, 1999, 2001, 2002
Flooding	Black turpentine beetle	Stands attacked	Southern pines	1957
Flooding	Black turpentine beetle	Increased attacks and tree mortality	Southern pines	1966, 1969, 1973, 2003, 2004
Flooding	Buck moth (*Hemileuca maia*)	Increased defoliation	Live oak (*Quercus virginiana*), other hardwoods	2005
Flooding	Gouty oak gall (*Callirhytis quercuspunctata*)	Increased mortality	Willow oak (*Quercus phellos*)	2003
Flooding	Longhorned beetle (*Lagocheirus aranaeformis strohеckeri*)	Increased attacks and tree mortality	Gumbo limbo (*Bursera simaruba*)	2006
Flooding	Pine engraver beetles	Increased attacks and tree mortality	Shortleaf pine	1973
Flooding	Red oak borer (*Enaphalodes rufulus*)	Increased attacks and tree mortality	Oak	2002
Frost	Elm spanworm (*Ennomos subsignaria*)	Insect decline	American elm	1963
Frost	Fall cankerworm (*Alsophila pometaria*)	Insect decline	—	1961
Frost	Gypsy moth	Population of gypsy moth declined	—	2002
Frost	Slime flux (*Erwinia* spp.)	Associated with frost cracks	Oak	1984, 1985
Frost	Stem cankers (*Cytospora* spp., *Sphaeropsis* spp., *Phoma* spp., *Fusarium solani*)	Disease exacerbated by late frost	Black cherry (*Prunus serotina*), oaks	1984
Frost	Virginia pine sawfly (*Neodiprion pratti pratti*)	Insect outbreak declined due to frost	Southern pines	1966
Frost	Yellow-poplar weevil (*Odontopus calceatus*)	Frost may affect weevil survival	Yellow-poplar (*Liriodendron tulipifera*)	1986
Hail	Pine engraver beetles	Increased activity and tree mortality	Loblolly pine	1968
Ice	Black turpentine beetle	Increased activity and tree mortality	Southern pines	1970
Ice	Pine engraver beetles	Increased attacks and tree mortality	Southern pines	1996
Lightning	Black turpentine beetle	Increased attacks and tree mortality	Southern pines	1969, 1972, 1974
Lightning	Pine engraver beetles	Insect populations confined to trees struck by lightning	Southern pines	1957, 1961

(*continued*)

Table 1 (continued)—Observations of insects and diseases during years 1955–2018 associated with various weather disturbances in the Southern United States

Weather/ abiotic event	Insect or pathogen	Observation	Host tree	Years reported
Lightning	Pine engraver beetles	Localized outbreaks occurred around strikes	Southern pines	1966
Lightning	Pine engraver beetles	Increased attacks and tree mortality	Southern pines	1968, 1972, 1974, 2010
Saltwater	Baldcypress leafroller	Insect defoliated stands that were flooded	Baldcypress	2005, 2006
Saltwater	Pine engraver beetles	Insects confined to trees damaged by saltwater	Southern pines	1961
Saltwater	Southern pine beetle	Many pines in outbreak stressed by saltwater	Southern pines	1997, 2015, 2016
Wildfire	Black turpentine beetle	Stands attacked	Southern pines	1957
Wildfire	Black turpentine beetle	Increased attacks and tree mortality	Southern pines	1985, 1986, 1987, 1988, 1992
Wildfire	Pine engraver beetles	Increased attacks and tree mortality	Southern pines	1968, 1971, 1985, 1986, 1987, 1998, 2005
Wildfire	Stem decay (Basidiomycetes)	Problematic in fire-damaged stands	Hardwoods	1984, 1985, 1986, 1988, 1989, 1990, 1991, 1992
Wind	Ambrosia beetle (*Xyleborus* spp.)	Increased attacks and mortality	Pines, hardwoods	1990, 1991, 1992
Wind	Black turpentine beetle	Increased attacks and mortality	Southern pines	1969, 2005, 2006
Wind	Coal fungus (*Ustulina vulgaris*)	Windthrow of diseased trees	Sugarberry (*Celtis laevigata*)	1973
Wind	Fusiform rust (*Cronartium quercuum* f. sp. *fusiforme*)	Tree mortality increased from wind and disease	Slash pine (*Pinus elliottii*)	2012
Wind	Maple petiole borer (*Caulocampus acericaulis*)	Resulted in premature defoliation	Sugar maple (*Acer saccharum*)	1985
Wind	Pine engraver beetles	Insect increased as a result from wind damage	Southern pines	1961
Wind	Pine engraver beetles	Increased attacks and tree mortality	Southern pines	1961, 1967, 1969, 1970, 1975, 1983, 1990, 1993, 1996, 2004, 2006
Wind	Pitch canker (*Fusarium moniliforme* var. *subglutinans*)	Greatest damage in orchards previously damaged by wind	Virginia, slash, shortleaf, longleaf (*Pinus palustris*), white, and Scots (*Pinus sylvestris*) pine	1980
Wind	Red oak borer (*Enaphalodes rufulus*)	Increased attacks and tree mortality	Black oak, red oaks	2006
Wind	Slime flux	Severe on previously storm-damaged trees	Hickory, oak	1987, 1988, 1989, 1991
Wind	Southern pine beetle	Increased attacks and tree mortality	Southern pines	1990, 1997
Wind	Stem decay (Basidiomycetes)	Problematic in wind-damaged stands	Hardwoods	1986, 1988, 1989, 1990, 1991, 1992

Data gathered from the annual "Major Forest Insect and Disease Conditions in the United States" reports (USDA Forest Service 1955–2020). Note that these data are non-quantitative and only indicate associations between biotic and abiotic agents. Cells containing '—' indicate information was not included in the published reports.

DISTURBANCE-ASSOCIATED INSECTS AND FUNGAL SPECIES

The immediate and cumulative physical effects of natural disturbance events such as wind, fire, ice, and flooding are only part of the longer term impacts of these events. As with all large-scale damaging phenomena in forests, these perturbations provide opportunities for a variety of other agents to arise and compound the forest impacts. Tree damage and weather-related environmental changes can have dramatic impacts on pests and pathogens in forests, as dead, injured, or emergent tissues all represent resources for herbivorous insects and/or pathogens. To better document these interactions, we compiled the non-quantitative observations of co-occurring weather disturbances and insects and diseases from the annual U.S. Department of Agriculture Forest Service "Major Forest Insect and Disease Conditions in the United States" reports (https://www.fs.fed.us/foresthealth/publications/fhp/index.shtml) spanning the years 1955 to 2018 in the South. Our search indicated that many different insects and diseases have been reported on trees stressed or disturbed by weather events, which affect their hosts in a variety of ways (table 1). While these sorts of observations were frequently noted, collecting data or conducting scientific analyses was not part of this effort. As such, the explanatory power of this extensive dataset is limited. While injured trees are more vulnerable to certain types of biotic agents, widespread outbreaks following a natural disturbance often do not occur due to many complicating factors (see reviews by Gandhi and others 2007, McNulty and others 1998, and Schowalter 2012). For example, while a few historical papers attest that ice or wind damage makes pines more susceptible to southern pine beetle (*Dendroctonus frontalis*; hereafter, SPB) damage, the evidence has been anecdotal (for example, Cain and Shelton 1996, Gooch 1943, Muntz 1947). Data on causal relationships between storm damage and SPB attacks is scarce to non-existent. Due to inherent differences among forest tree species, vulnerable trees typically respond differently to abiotic and biotic hazards. Hence, a better understanding of pest and pathogen influences is needed to understand the potential risks and impacts of complex perturbations.

Insect Pests

Because many bark and wood colonizing (or subcortical) insects exploit wounded, unhealthy, or otherwise stressed trees, severe weather events are often assumed to be causal, or at least inciting, agents in infestations by many subcortical insects including ants (Hymenoptera), beetles (Coleoptera), termites (Blattodea), and woodwasps (Hymenoptera) (Barry and others 1993; Gandhi and others 2007, 2009; Wilkinson and others 1978) (table 1). Species diversity of subcortical insects can increase substantially after a weather disturbance event (Gandhi and others 2009). However, direct evidence of causality by, or direct association of, severe weather events and secondary insect outbreaks and spread into surrounding relatively undisturbed stands is scarce in the South (for example, Overgaard 1970, Overgaard and Drake 1970, Wilkinson and others 1978). Bark and woodboring beetles (Buprestidae, Cerambycidae, Curculionidae [especially subfamily Scolytinae]), along with woodwasps (Siricidae) (fig. 10) are known to be associated with stressed and damaged trees in the South (Helbig and others 2016). The roles of these insects in successional colonization and decomposition of tree phloem and xylem is well-established. Such insect succession results in breakdown of woody debris and enhanced nutrient cycling within forests. Of course, many (likely all) of these insects also bring in multiple microbes, especially symbiotic fungi of ambrosia beetles, bark beetles, woodwasps (Hajek and others 2019), and other insects (Biedermann and Vega 2020) that may further enhance decomposition (Skelton and others 2019).

The South is subject to frequent hurricanes of varying intensity and severity. Secondary subcortical insects—colonizers of stressed or injured trees—tend to respond positively to hurricane damage. Ambrosia beetles (*Platypus* spp.), black turpentine beetle (*Dendroctonus terebrans*), pine engraver beetles (*Ips* spp.), deodar weevil (*Pissodes nemorensis*), root-feeding beetles (*Hylobius pales* and *Pachylobius picivorus*), and twig beetles (*Pityophthorus* spp.) have all been reported to colonize damaged trees and/or increase in numbers in affected stands (for example, Maguire 1995, Platt and others 2002, USDA Forest Service 1955–2020, Wilkinson and others 1978) (table 1). Most of these studies have focused on bark beetles that are among the first colonizers of damaged areas, with little focus on woodboring beetles and other insects such as tertiary colonizers that inhabit trees later. For example, *Ips* beetles were reported from damaged longleaf and loblolly pines after Hurricane Hugo (Hook and others 1991), on treetops of slash pines after Hurricane Donna (Wilkinson and others 1978), and from pines after Hurricane Ivan (Haley and others 2005). Black turpentine beetles were observed throughout wind-damaged areas in Louisiana after Hurricanes Katrina and Rita (Johnson 2007). After Hurricane Andrew in Florida,

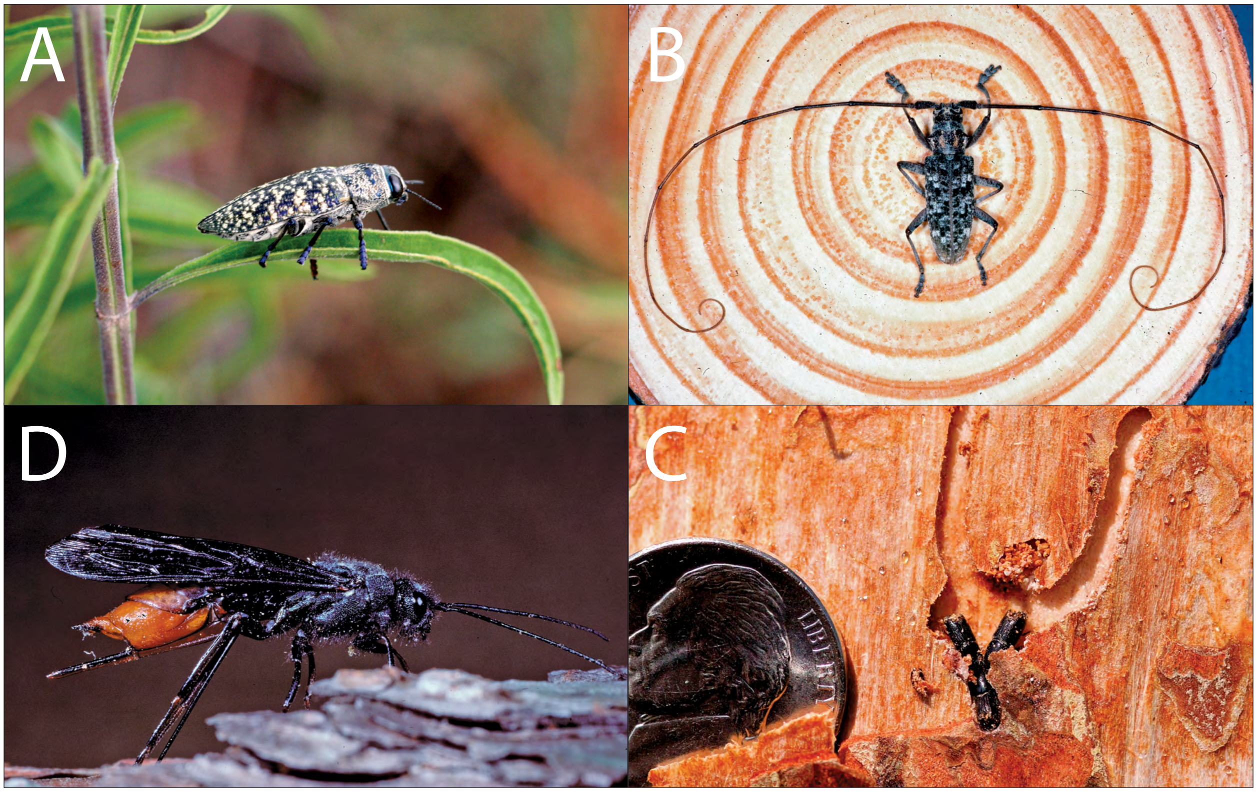

Figure 10—Bark and woodboring beetles, along with woodwasps, are known to be associated with stressed and damaged trees in the South. (A) Drummond's blue buprestid (*Lampetis drummondi*); (B) southern pine sawyer (*Monochamus titillator*); (C) sixspined ips (*Ips calligraphus*); and (D) a woodwasp (*Sirex nigricornis*). Photos by Whitney Cranshaw, Colorado State University; Lacy L. Hyche, Auburn University; Erich G. Vallery, USDA Forest Service, Southern Research Station; and Gerald L. Lenhard, Louisiana State University, respectively, courtesy of Bugwood.org.

sites with more tree damage had higher numbers of black turpentine beetles and *Hylobius salebrosus* (Maguire 1995). Similarly, *Ips* beetles and woodboring beetles colonized damaged shortleaf pines after two ice storm events in Ouachita National Forest (Hess and others 2001). Fredericksen and others (1995) simulated wind disturbance in loblolly pine stands and saw a resulting general increase in *Ips* beetles (especially small southern pine engravers [*I. avulsus*]).

In contrast to these secondary colonizers, SPB is a primary colonizer able to attack healthy pine trees and cause significant economic damage in pine stands throughout the South and isolated parts of the Northeastern United States. As mentioned above, there are few data indicating that SPB populations increase in wind- or ice-damaged trees. After Hurricane Hugo, SPB was trapped in wind-damaged areas but not recorded attacking trees (Hook and others 1991). Likewise, SPB was not recorded in stands after a tornado in 1983 and Hurricane Alicia the following year (Clarke and others 1999). In coastal areas, salinization due to Hurricane Hugo also resulted in stressed and dying trees (Gardner and others 1992). Both SPB and *Ips* beetle activity were seen in salt-killed and windthrown areas, and observed in and around the affected stands. Williams and Lipscomb (2002) likewise reported salt stress-associated SPB outbreaks. While Walker and Wiant (1966) mention that SPB is associated with ice-damaged trees, they do not present relevant data to that effect. If SPB is already present in a stand, a natural disturbance event may further contribute to the outbreak (such as SPB outbreaks exacerbated by ice storm damage [Cain and Shelton 1996]). The opposite, however, may also occur, as when stands classified as being at high hazard for SPB infestation become low hazard as trees are blown over (Clarke and others 1999) and the density of trees is decreased.

Lightning-struck trees can be important in the ecology of bark beetles (table 1). For example, Hetrick (1949) discussed lightning damage and its role in bark beetle attraction in the broader context of root injury. Hodges and Pickard (1971) reported that 31 percent of a total 2,100 spot infestations of SPB in Louisiana began in lightning-struck trees, and about 75 percent of beetle spots in August were associated with lightning strikes. They also linked lightning strikes to typical physiological changes in affected trees that encourage beetle attack—water relations, oleoresin flow, and oleoresin exudation pressure. Coulson and others (1983) presented a case for their hypothesis that lightning-caused disturbance in pines is largely responsible for the persistence of SPB and other bark beetles.

Patterns of this sort may vary outside the South. For example, Dodds and others (2019) found that a tornado and straight-line wind events caused extensive forest damage in northern Maine without any resulting outbreaks of the tree-killing spruce beetle (*Dendroctonus rufipennis*). Indeed, they captured spruce beetles more often in controls than in two disturbed treatments. However, bark beetle and woodborer species richness and abundance were higher in disturbed areas than in controls. So, in this case, the increase in downed, dead, and moribund wood provided suitable habitat for wood-inhabiting insects in treatments but without any alarming population increases of primary bark beetles. In another case, Gandhi (2005) reported that woodboring beetles, especially *Monochamus* spp., appeared to become the primary colonizer of residual and live jack pine (*P. banksiana*) trees after a severe wind disturbance event in northern Minnesota.

Little is known about responses of root-feeding beetles to weather-related disturbance. Yates and Miller (1996) reported a buildup of populations of root-feeding weevils 1 to 2 years after Hurricane Hugo; however, seedling mortality from these beetles was low. In addition, fungi, such as *Leptographium* spp., associated with root-feeding beetles have been recovered from windthrown pine roots and surrounding soil (Haley and others 2005). One can also draw some conclusions from work in closely related systems. In simulated disturbance (such as mechanical girdling) treatments of pines, root-feeding insects were more abundant and fed more near girdled loblolly pine trees (Helbig and others 2016). Though closely related, and with similar habits, to bark beetles, root weevils may have different responses to disturbance. Again, not directly related to weather, when wildfires burned > 500,000 acres of Florida forest in 1998, Hanula and others (2002) found that > 75 percent of the trees surviving severe fires had roots infected by root pathogens (*Leptographium* spp. and/or *Graphium* spp.). In fact, nearly 60 percent of these sampled roots were infected, whereas roots of unburned trees contained no such fungi. Larger numbers of the insect vectors (*H. pales* and *P. picivorus*) of these fungi were captured in moderate- and high-severity burned stands than in control stands. Conversely, secondary bark beetles (black turpentine beetle, *Hylastes salebrosus*, and *Ips grandicollis*) were less abundant in fire-damaged areas than in controls (Hanula and others 2002). Further to the north, red pine (*P. resinosa*) stands may suffer from red pine decline (Klepzig and others 1991). In this insect-disease complex, root-feeding beetles and weevils transmit pathogenic fungi and predispose trees to fatal attack by aboveground beetles (Aukema and others 2010).

Interactions may occur between multiple disturbances, leading to altered forest dynamics. Summer droughts following Hurricane Katrina presumably resulted in enhanced activity of both black turpentine beetles and *Ips* beetles (USDA Forest Service 2007) (table 1). Similarly, Hurricane Andrew damaged trees and their roots significantly which, coupled with drought, resulted in delayed mortality of surviving pine trees due to *Ips* beetles (Maguire 1995). Even when there isn't a direct interaction, trees that survive weather disturbance events can become susceptible to insects. For example, SPB killed 15 percent of Table Mountain pines (*P. pungens*) present on xeric sites that survived an ice storm in the Appalachian Mountains (Lafon and Kutac 2003). Both of these disturbances resulted in removal of 53 percent of pine basal area with loss in regeneration and greater dominance by hardwood species.

Defoliating species (Hymenoptera [sawflies] and Lepidoptera) have been reported to be associated with weather disturbance events, although these reports tend to be much rarer than those of subcortical insects (table 1). There could be direct and indirect effects of weather events on defoliating insects (Gandhi and others 2007). Direct effects due to frost would, for example, negatively affect defoliating insects at the individual level. Indirect effects would include changes in host quality due to drought, flooding, and saltwater which may increase association of defoliating insects with stressed trees (USDA Forest Service 1955–2020) (table 1).

It's noteworthy that there are almost no quantitative studies and few observational studies on other important guilds of forest insects such as gall-makers, sap-feeders, regeneration pests, and seed and cone insects (table 1). Weather disturbances may play a role in population dynamics and dispersal of nonnative species such as gypsy moth (*Lymantria dispar*) and balsam woolly adelgid (*Adelges piceae*), but such events are rarely documented (table 1). Similarly, ecologically important taxa such as wild pollinating, carrion-feeding, and soil- and litter-dwelling insects are virtually absent from the literature.

Diseases

Under favorable conditions, the risk of a disease outbreak may increase significantly, depending as well on the extent to which host trees are exposed to pathogens pre- or post-disturbance. To understand the effects of weather-related disturbances on pathogens and diseases of forest trees in the South, we examined the impacts of transient weather hazards and flooding on some important southern forest tree diseases, including Heterobasidion root disease (fig. 11), Armillaria root rot (fig. 12), fusiform rust (fig. 13), littleleaf disease of pine (fig. 14), and pitch canker (fig. 15).

Root rot pathogens can weaken the structural integrity of root systems (Dreaden and others 2016) and, through decay, decrease root anchorage and stem strength (Honkaniemi and others 2017). Although root rot pathogens are widespread in southern forests, they are often overlooked when assessing the health of forest stands (Coyle and others 2015). Disease impacts may include direct host mortality, losses due to decay and windthrow, reduction in the diameter growth of infected trees, and reduction in the resistance of stands to storm damage in certain locations (Garbelotto and Gonthier 2013). For instance, Heterobasidion root disease caused by *Heterobasidion irregulare* is an economically important disease of southern pine species that usually affects loblolly and slash pines. The disease can weaken root systems and increase the risk of windthrow in affected trees (Woodward and others1998). Basidiospores of the pathogen can be disseminated by wind over a long distance; however, production of spores is limited by dry, hot summer or freezing winter weather. The survival and severity of *H. irregulare* is reduced under cold and wet climatic conditions, and incidence is typically higher in the coastal States from Texas to Virginia than in the Northern States, where weather conditions limit the northward movement of the disease (Tainter and Baker 1996). Declining trees weakened by Heterobasidion root disease may become more susceptible to windthrow and mortality following hurricanes (Lugo 2008). Arefjev (2017) mentions increased susceptibility to bark beetles in trees with annosum root rot, but no data are presented.

Figure 11—Windthrow of a tree weakened by Heterobasidion root disease. Photo by USDA Forest Service, Region 8 (Southern Region), courtesy of Bugwood.org.

Armillaria root rot is a serious wood decay disease of pines and hardwoods around the world caused by *Armillaria* spp. including *A. mellea* (Kile and others 1991, USDA Forest Service 1989). The disease typically affects the overall growth of host trees, which may result in major losses due to mortality and heighten the risk of host susceptibility to infestation by bark beetles and other insect pests (Sturrock and others 2011). Affected trees are prone to windthrow damage and may create safety hazards in urban areas (USDA Forest Service 1989). The effect of the disease can be severe under drought conditions on forested sites and may lead to widespread mortality (Klopfenstein and others 2009, La Porta and others 2008, Shaw and Kile 1991). However, in eastern deciduous forests, *Armillaria* is considered a secondary pathogen that kills only stressed or weakened hosts (Wargo and Shaw 1985).

Another important disease of pines in the Southeastern United States is fusiform rust caused by the fungal pathogen *Cronartium quercuum* f. sp. *fusiforme*. This pathogen requires the presence of a primary host, a secondary or alternative host (primarily water oak [*Q. nigra*]), and extended periods of free moisture to complete its lifecycle. For example, the survival of infected slash pine from fusiform rust usually depends on the severity, year of first stem infection, site quality, and the initial number of trees per acre (Froelich and Schmidtling 1998). Not all impacts of fusiform rust are because of the lethality of the infection. In 1985,

Figure 12—Windthrow of a large bur oak weakened by Armillaria root rot on a golf course. Photo by Joseph O'Brien, USDA Forest Service, Southern Research Station, courtesy of Bugwood.org.

Figure 13—Fusiform rust deforms and weakens boles. Photo by Jaesoon Huang, USDA Service, Forest Health Protection.

Figure 14—Littleleaf disease dieback of pine trees caused by *Phytophthora cinnamomi*. Photo by USDA Forest Service, Region 8 (Southern Region), courtesy of Bugwood.org.

Figure 15—Deformity of pine main stem caused by pitch canker. This tree is prone to possible windstorm breakage. Photo by Robert L. Anderson, USDA Forest Service, courtesy of Bugwood.org.

Hurricane Elena made landfall near Biloxi, MS, and impacted some pine plantations in their 12th growing season, causing breakage at fusiform rust galls in all stands and death of infected trees, while rust-associated mortality from breakage was minimal during non-hurricane years (with the exception of trees that had fusiform rust from an early age) (Froelich and Schmidtling 1998). Similarly, in the wake of Hurricanes Frances and Jeanne in central Florida, fusiform rust galls on the stems of a significant number of leaning and toppled trees may have weakened affected trees (Roth and others 2007).

Forest stands in the South are at risk of several root diseases (some mentioned earlier) that may rely on specific soil site characteristics conducive for disease establishment. The alterations of soil carbon dioxide-oxygen ratio and nitrate availability by flooding can inhibit the growth of some microorganisms (Ahlgren and Hansen 1957, Blanche and others 1983). Eckhardt and Menard (2009) observed that deep sandy and well-drained soils are associated with Heterobasidion root disease, while poorly drained, heavy clay soils are associated with littleleaf disease. The causal agent of littleleaf disease, *Phytophthora cinnamomi* (Campbell and Copeland 1954, Lockman and Kearns 2016), is typically most abundant in waterlogged or poorly drained soil (Crandall 1948, Zentmyer 1980). An earlier study by Roth and others (1948) described littleleaf as a serious disease that primarily affects shortleaf and to a lesser degree loblolly pine, while barely affecting other pine species. It was observed that a significant level of nitrogen and calcium deficiency may occur in the foliage of the affected shortleaf pines stemming from reduction in absorptive capacity of rootlets due to poor soil aeration (Oak and Tainter 1988). Littleleaf disease may occur in pine stands established on eroded agricultural sites with clay soils in the southern Piedmont; however, pine hybrids have shown resistance to both littleleaf disease and fusiform rust (Oak and Tainter 1988, Schoenike and others 1977). The interaction of three important factors—stand age, soil drainage, and degree of erosion—facilitates littleleaf disease (Oak and Tainter 1988). While littleleaf disease is not necessarily associated with inundation events, pathogenicity has been linked to abundant soil moisture in a greenhouse study (Zak 1961), and by extension it is reasonable to suspect that rain and/or flooding events could increase disease incidence in the field.

Tree injuries and wounds can facilitate the incidence and severity of important diseases such as pitch canker (caused by the fungus *Fusarium circinatum*) at seed orchards. Pitch canker is a serious disease that affects several pine species including loblolly, shortleaf, and Virginia. Symptoms of the disease typically include crooks or deformity of the main stem, noticeable pitch flow in the affected areas of the stem, flagging at branch ends, slight swelling on the affected stems and twigs, and wilting of current candles (Mistretta and Bylin 1987). Severe outbreaks of pitch canker are frequently reported in years with high rainfall, high humidity, or following hurricane events (Dwinell and others 1985, Starkey and others 2007). Heavy losses from windthrow damage by hurricanes or tornadoes may occur with an average annual mortality of 0.4 trees per acre in mature longleaf pine stands (reported from long-term observations; Boyer 1979). Weather-related injuries and wounds caused by wind and hail in slash pine seed orchards may add to the risk of stem cankers that develop from infection entry points caused by mechanical injuries/wounds from cone harvesters (Dwinell and Barrows-Broaddus 1981, Dwinell and others 1985). In 1984, tree damage caused by Hurricane Diana, as it passed through the North Carolina coast, created infection points of access for *F. circinatum*. While hurricane winds may facilitate fungal spore dissemination, the associated rainfall may hinder disease management efforts by washing off fungicides and reducing their effectiveness in protecting host tissue from infections (Runion and Bruck 1988).

Certain types of disease (especially stem cankers) do increase the likelihood of damage from storms, and any factor that weakens the strength of the bole or roots puts a tree at greater risk for mechanical failure. Extensive heartrot in the bole, or decay in the roots, degrades trees' structural integrity. Previous or existing damage from diseases such as beech bark disease (a disease process, involving the scale insect *Cryptococcus fagisuga* and the fungi *Neonectria faginata* and *N. ditissima*) can make individual trees more susceptible to blowdown (Papaik and others 2005).

Disease-Environment Interactions

In the dogwood anthracnose pathogen-tree-environment interaction (causal agent *Discula destructiva*), disease severity increases with induced drought only on shaded trees (Erbaugh and others 1995). Likewise, the disease is less severe for trees growing in higher light conditions (Wyckoff and Clark 2002). As mentioned above, site quality is an important factor that clearly influences littleleaf disease (Eckhardt and Menard 2009), but not all pathogens respond similarly to site variables. Fusiform rust incidence is more frequent in loblolly and slash pine plantations in southeast Texas than in northeast Texas, where rust incidence was lower on poorly drained soils (Arabatzis and others 1991). Prolonged flooding and rapid fluctuation of soil water levels are among the environmental factors implicated in oak decline, a complex disease progression that cannot be attributed to a single cause (Manion 1981, Starkey and others 2004, Wargo and others 1983).

Fungal pathogens are highly adaptable and capable of coping with changing environmental conditions using their reproductive systems. For example, the causal pathogen of Heterobasidion root disease, an important disease of southern pines in the United States, is a nonnative pathogen in Italy, where it was reported to have caused high mortality of Corsican pine (*P. nigra*). Unlike the Southern United States, the climatic conditions in the central western coast of Italy are warm but drier, creating favorable conditions for the pathogen to spread into new forest areas, possibly hybridizing with the native species. Genetic analysis of the origin and spread of the fungus over geological time scales suggests the fungus has a high level of adaptability and mobility to cope with the changing environment. In the Southern United States, changing climate, particularly favorable drier conditions, may enable the fungus to inflict a high mortality on vulnerable hosts (Gonthier and others 2007, Olatinwo and others 2014).

MANAGEMENT IMPLICATIONS

Regardless of the cause of tree mortality, forest pests and pathogens can lead to the buildup of fuels, which can increase wildfire risk. Understanding the complex interactions among below- and aboveground diseases, insect impacts, fuels treatments, forest structure, species composition, stand history, and other environmental factors is important to reduce the overall risk of wildfire. Consequently, forest managers should consider possible impacts on pests and pathogens when developing fuel treatment plans (Rippy and others 2005).

Though the main reason for post-disturbance fuel reduction treatments in the Southern United States is to reduce the risk of impacts of wildfire, minimizing potential damage from insects and diseases is also considered (Gandhi and others 2007). Conventional wisdom, backed by anecdotal field observations, holds that bark beetles, ambrosia beetles, woodboring beetles, blue stain fungi, soft rot fungi, and wood decay fungi become problematic in unthinned, wind-damaged stands for 2 years after a storm event. Likewise, past history has led to concerns over bark beetle exploitation of wind-disturbed forests which were not salvaged quickly enough (Brazdil and others 2018). However, there are very few reports documenting that insects (mostly bark beetles) increase in sufficient numbers to add to the damage initially caused by the disturbance event.

While the main objective of post-storm salvage is reaping economic value from damaged timber, the process can be expensive and labor intensive, the mechanics of salvage logging are tricky and dangerous, and the value of salvaged timber can be tenfold lower than that from undamaged managed stands. While studies suggest that salvage operations are not always necessary to protect residual trees from attack by damaging primary bark beetles, there are other motivations for removing downed timber, such as ensuring the ability to conduct essential prescribed burns (Whelan and others 2018) and timely replanting of the stands for economic and ecological values. Increased weather disturbances and hence high volumes and types of coarse woody debris have resulted in an upswing in post-disturbance salvage logging and prescribed burning in many forest types (Karha and others 2018). These management responses will be largely driven by markets, which can be overwhelmed by large supplies of wood and fiber, and the ability of landowners and foresters to clean up post-disturbance.

In most weather-disturbed areas, trees may not die right away, causing a mortality lag-phase. Glaze-damaged trees may succumb more gradually over the course of months or even years by having their stem or root structural integrity weakened by the storm event, having their injuries attract insects (Cool and others 1971), or providing for avenues of fungal infection. Bragg and Shelton (2010) reported elevated mortality rates in surviving loblolly pine several years following a catastrophic ice storm, with most of the losses being found in the most damaged trees. While some of these trees died later due to physical bole failures months or even years after the ice storm, others probably died as a result of insect attack or disease. This suggests that heavily ice-damaged trees (whether the injury is crown loss, severe bole bending or breakage, or partial uprooting) should be salvaged if possible to reduce losses. In pine species, post-damage invasion by insects and diseases may occur within the first year, followed by decay fungi in the second year. In oak and hickory species, woodboring beetles, ambrosia beetles, and soft rot fungi can invade within the first year, followed by sapwood decay fungi after 2 years. Other hardwoods may experience heartwood decay fungi by the second year following the storm damage (Barry and others 1993, Stanturf and others 2007).

Droughts may also leave trees vulnerable to insects, disease, and fire. However, depending on the species, older, more established trees with extensive root systems may be less vulnerable to drought, as are certain tree species. Drought tolerance can be an ecosystem driver on many sites that regularly experience pronounced seasonal dryness (Clark and others 2016a, 2016b). This may also be the case when annual droughts are not the norm, but periodic severe droughts occur frequently enough to effectively eliminate drought-intolerant species.

Management may or may not cause further issues in forest stands. Several studies have assessed the responses of vegetation to post-disturbance salvage logging. In Tennessee, salvage logging after a wind disturbance event led to higher diversity and abundance of microsites and higher soil temperature (Peterson and Leach 2008b). However, 2 years following disturbance, there were few differences in herbaceous and tree seedling layers (Peterson and Leach 2008b). In Georgia, forest composition appears to be altered 6 years after post-wind disturbance salvaging activities with little change to tree species diversity (Oldfield and Peterson 2019). Post-hurricane salvage and other cleanup efforts, where management practices such as thinning or pruning are deployed, may leave behind fresh stumps and logging scars, providing several open routes for new infection by Heterobasidion root disease pathogens. New infections can spread to other vulnerable trees in the surrounding areas (Piri and Korhonen 2007, Rönnberg and others 2006). Freshly cut loblolly pine stumps may also attract colonization by *H. irregulare* for as long as 2 weeks after felling, while the pathogen can survive for several years in infected stumps (Tainter and Baker 1996). Prescribed fire after a wind disturbance event needs to be done carefully, as it may lead to immediate greater responses by bark and woodboring beetles. For example, 2 years after a catastrophic event in northern Minnesota, similar numbers of subcortical insects were found in the severe wind-disturbed and wind-disturbed/prescribed-burned areas (Gandhi and others 2009). However, catches in burned areas fell by 50 percent in subsequent years. Wind-disturbed salvaged and burned forests had a different species composition than undisturbed and untreated wind-disturbed forests. This indicates altered insect successional pathways, which may have implications for forest regeneration in the long term (Gandhi and others 2009).

Management practices and forest conditions prior to severe weather events can influence forest resilience (Beach and others 2010, Felt and Bromley 1939, Foster 1988, Platt and others 2002). In general, healthy forests are considered to be more resilient to many forest threats, from severe weather to insect or disease outbreaks. Typical silvicultural recommendations to improve forest health include managing for proper density management, matching appropriate species to suitable sites, avoiding treatments that injure residual trees, minimizing the accumulation of logging debris that can foster pests or pathogens, and treating emerging forest health issues immediately. Good management practices also include removal of hazard trees before they threaten human lives or property. For example, trees affected by root rot diseases are prone to windthrow and sometimes create a public safety hazard, particularly in urban parks or recreational sites.

Sometimes good silvicultural practices (such as thinning to reduce hazard from SPB) can lead to undesired outcomes. Historical logging regimes can increase the density of stumps acting as dispersion foci for *Heterobasidion* spp., eventually leading to dieback and higher levels of root rot infection (Sangüesa-Barreda and others 2015). Recently thinned plantations or overstocked natural stands of southern pines of 10 to 30 years of age also tend to be vulnerable to glaze damage, regardless of species. The residual pine timber following a thinning tends to be spindly, with a narrow bole supporting a concentration of needles at the crown. Close-grown trees in recently thinned stands are more susceptible to glaze damage than open-grown trees (Cool and others 1971). Thinning can also influence susceptibility to wind damage in stands, a phenomenon that has been particularly well-studied in North American balsam fir (*Abies balsamea*) forests (Ruel 1995). This is a good illustration of the need to balance risk among possible disturbances when making management decisions.

Disturbance agents can also shape planting decisions. In areas prone to hurricanes, slash pine is more resistant to wind damage than loblolly pine but not as resistant as longleaf pine (Johnsen and others 2009). Longleaf pine is recommended as a desirable species for mitigating the impacts of hurricanes in the South due to its resistance to breakage and uprooting, as well as its tolerance of fire and natural resistance to insect and disease outbreaks (McNulty 2002).

While there are few ways to mitigate natural flooding, there are a number of management options for conditions under human control. Greentree reservoirs (GTR) (fig. 9) involve impoundments constructed to regulate the length of time a bottomland forest holds water. These can significantly impact the composition of the affected forests (King and others 1998), increasing overstory mortality rates amongst most observed hard mast species. Regeneration of virtually all species in the affected GTR area is also greatly diminished such that avoiding artificial flooding to allow for recruitment of desired hard mast species such as willow oak (*Q. phellos*) and Nuttall oak (*Q. nuttallii*) is recommended. Maintaining proper drainage on associated roads is advised to avoid flooding-based tree declines and mortality.

CONCEPTUAL MODELS OF POST-DISTURBANCE FOREST DYNAMICS AND MANAGEMENT

We propose a conceptual model for ecological changes in forest composition and structure due to weather disturbance events and ensuing impacts on insects and diseases (fig. 16). Generally, there's not one but several weather disturbance events that happen on a landscape over time; these compounded disturbances can retrigger succession or result in further altered dynamics. As based on the intensity and frequency of weather disturbances and many stand characteristics (for example, tree species, soils, topography, etc.), variable levels of tree damage and mortality occur in forested areas. Damaged trees (broken boles, branches, tops, etc.) eventually die, though many times there are lag phases of mortality up to several years. Dead standing trees or snags and leaning trees can continue to fall down and may cause damage to residual live trees. Both damaged and dead trees contribute significantly to the types and amounts of coarse woody debris, and variable levels of canopy openings. These types of forest changes lead to altered habitat characteristics that either may enhance or disrupt resource availability to many plant and animal species. Changes in populations and communities of plants and animals eventually lead to successional trajectories that are different from undisturbed forest stands. Many feedback loops (in some cases negative) exist that trickle back into the system (red arrows, fig. 16). For example, increased insect and disease activity and invasion by exotic species in open gaps may further result in damage and mortality of residual trees; different tree species that become dominant in canopies after the disturbance may be more susceptible to weather events or exotic pests in the future. Southern forests are also subject to climatic changes, and further alterations in major disturbance regimes are expected which will result in compounded disturbance to the ecosystems.

A generalized second model is proposed for management considerations (fig. 17), although much research is still needed to understand management implications of

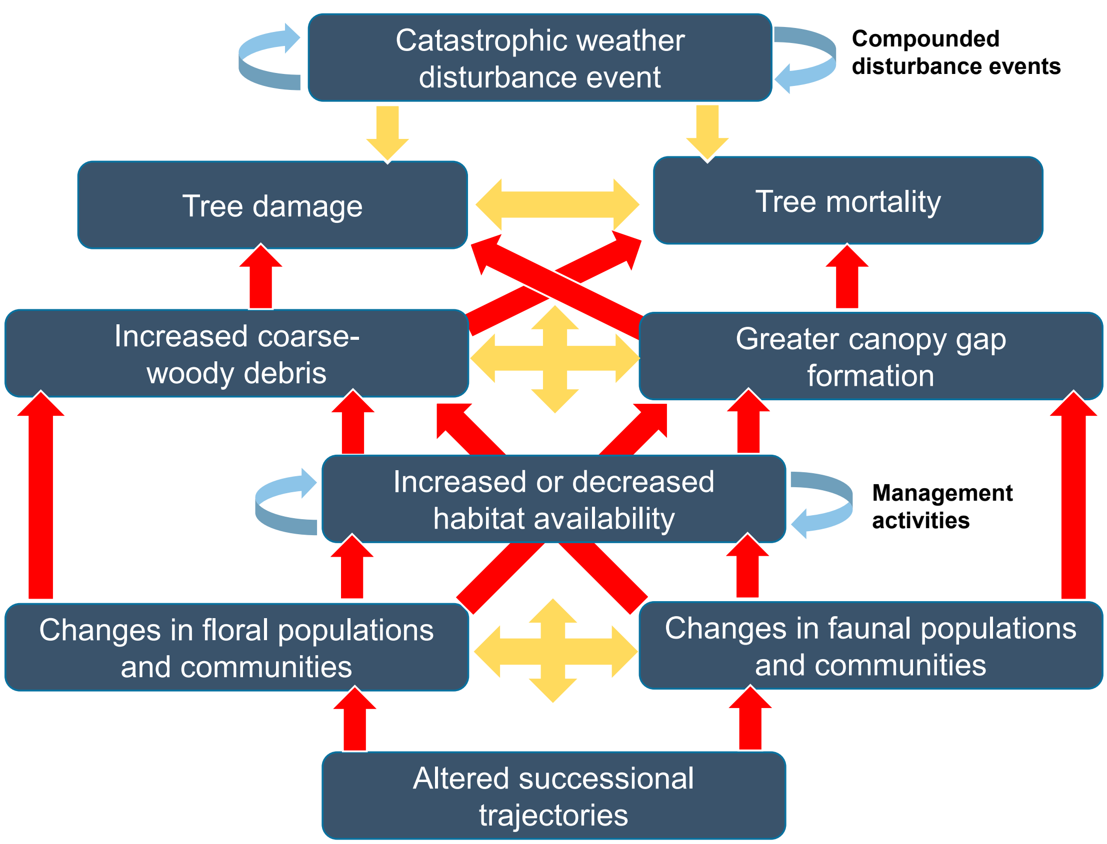

Figure 16—Conceptual model of changes in forest composition and structure due to weather disturbance events. Red arrows refer to potential negative feedback loops. Blue curved arrows for compounded disturbances and management activities refer to further changes in forest habitats and associated animals and plants.

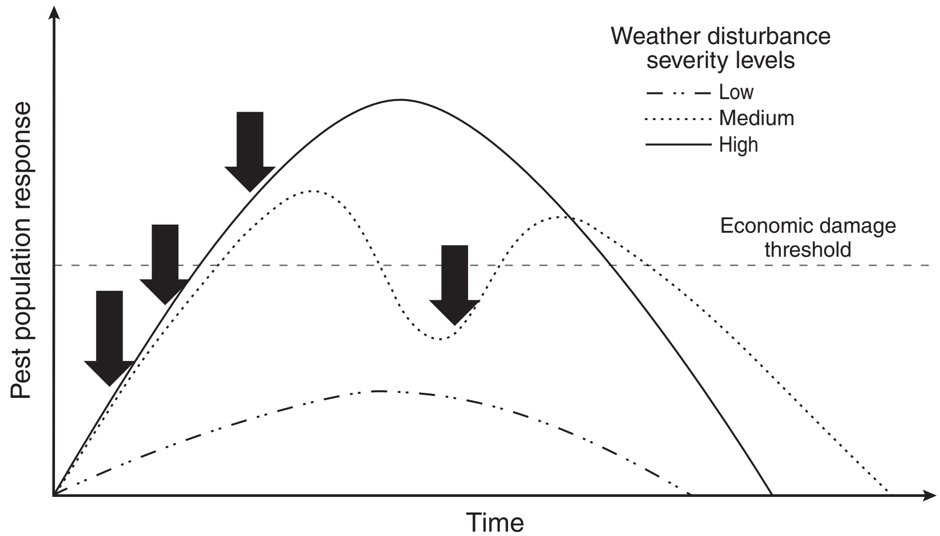

Figure 17—Hypothetical responses of herbivorous insect pest populations to different levels of severity of weather disturbances over time. Black arrows refer to post-disturbance pest management activities.

natural disturbances and subsequent insect and pathogen activity. For forests with low tree damage/mortality (disturbance severity levels), insect populations such as bark and woodboring beetles may respond positively but will remain at low levels. For forests with medium tree damage/mortality, beetles may show a bimodal response. They first colonize the trees that are dying and build up populations, may have some decline but still stay at relatively high levels, and then respond positively as the residual green trees start dying with time. It is also possible that medium-severity disturbance levels can result in higher beetle populations than high-severity levels. For forests with high tree damage/mortality, beetle populations continue to increase to high levels, and then decline gradually when all the suitable host material is used up. Post-disturbance management (dark arrows, fig. 17) to alleviate pest populations is conducted at the initial stages of pest population increases for both medium- and high-severity disturbances. Management may be needed at different times for forests with medium-severity disturbance levels due to several pulses of tree dieback. Management is generally not conducted for low-severity disturbances because pest populations stay below the economic damage threshold level. However, woody debris may still be cleared to facilitate replanting and forest regeneration. Long-term monitoring of pest populations is needed to better understand their responses under various disturbance severity levels and subsequent management activities. Acceptable economic damage threshold levels may vary based on land use objectives and price fluctuations following disturbance.

CONCLUSIONS AND FUTURE RESEARCH

Management is usually conducted to, among other things, reduce coarse-woody debris loads using several means, which can result in significantly different successional dynamics that may have variable effects on the populations and communities of target and non-target plant and animal species. Economic considerations, which are not addressed in this review, also come into play as larger catastrophic events may produce salvage gluts, impacting prices over larger areas. Timber managers must make decisions on both damaged and intact stands based on price and production risks (Prestemon and others 2001). Risks include the possibility of subsequent damage by insects or pathogens, highlighting the need for a better understanding of these factors following disturbance.

While weather disturbance agents operate frequently throughout the South, much remains unknown about their dynamics in forested areas. Hence, as based on these gaps in our knowledge, we propose the following avenues of research:

- What are the cascading effects of compounded disturbances (as based on their severity levels) on the abiotic and biotic components in the ecosystem?
- As most studies are conducted for only a few years (2 to 4 years) after a disturbance event, what are the long-term impacts of weather disturbances on biota?
- How do populations and communities of woodboring insects and other late insect colonizers of trees change over time?
- Does the level of disturbance result in different rates of residual tree mortality and associated different responses by insects and fungal pathogens?
- How do non-economically but ecologically important arthropods and fungal species (for example, litter- and soil-dwelling insects and wood-decaying fungi) respond to various weather disturbances?
- How do weather disturbances affect ecosystem services such as biodiversity, water, and nutrient cycling?
- Would we expect enhanced activity of invasive nonnative species in weather-disturbed areas?
- What are the management recommendations as related to levels of tree damage? For example, should the stands be salvaged at 10-, 20-, or 40-percent tree damage to prevent insect and disease outbreaks?
- As there is a great push for management to clear dead wood, if fuel reduction treatments such as burning or salvaging are not used, how would the forests regenerate by themselves?
- Do the timing and type of post-weather disturbance management activities affect biotic communities and regeneration dynamics?
- Are there ways to make southern forest stands more resilient to weather disturbances under current climatic changes?

At an operational level, there is a recognized need for greater communication and standardization in the Southern United States following broad-scale wind events such as hurricanes, especially events that cross State boundaries. Government agencies and land managers need rapid, reliable damage assessments, and duplication of efforts should be avoided. Addressing the research questions posed above, and improving coordination among State and Federal agencies as well as private and university partners, will improve our ability to inform land management decisions in the wake of catastrophic disturbances.

ACKNOWLEDGMENTS

We thank Brittany Barnes (University of Georgia, D.B. Warnell School of Forestry and Natural Resources) and Tom Sheehan (The Jones Center at Ichauway) for their technical support on the paper. James Meeker, Steve Clarke, and Wood Johnson (U.S. Department of Agriculture [USDA] Forest Service, Forest Health Protection) assisted with retrieval of publications. Chris Peterson (University of Georgia) and James Guldin (USDA Forest Service, Southern Research Station) provided many helpful comments that greatly improved the manuscript. Support was provided by The Jones Center at Ichauway; University of Georgia, D.B. Warnell School of Forestry and Natural Resources; and USDA Forest Service, Southern Research Station.

REFERENCES

Ahlgren, C.E.; Hansen, H.L. 1957. Some effects of temporary flooding on coniferous trees. Journal of Forestry. 55(9): 647–650.

Allen, C.D.; Macalady, A.K.; Chenchouni, H. [and others]. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. Forest Ecology and Management. 259(4): 660–684.

Allen, J.A.; Pezeshki, S.R.; Chambers, J.L. 1996. Interaction of flooding and salinity stress on baldcypress (*Taxodium distichum*). Tree Physiology. 16: 307–313. https://doi.org/10.1093/treephys/16.1-2.307.

Arabatzis, A.A.; Gregoire, T.G.; Lenhart, J.D. 1991. Fusiform rust incidence in loblolly and slash pine plantations in east Texas. Southern Journal of Applied Forestry. 15(2): 79–84. https://doi.org/10.1093/sjaf/15.2.79.

Arefjev, J.F. 2017. Free choice of the nature in the changing world. Universal Journal of Geoscience. 5: 117–137. https://doi.org/10.13189/ujg.2017.050501.

Ashley, W.S.; Mote, T.L. 2005. Derecho hazards in the United States. Bulletin of the American Meteorological Society. 86(11): 1577–1592. https://doi.org/10.1175/BAMS-86-11-1577.

Augspurger, C.K. 2013. Reconstructing patterns of temperature, phenology, and frost damage over 124 years: spring damage risk is increasing. Ecology. 94(1): 41–50. https://doi.org/10.1890/12-0200.1.

Aukema, B.H.; Zhu, J.; Moller, J. [and others]. 2010. Predisposition to bark beetle attack by root herbivores and associated pathogens: roles in forest decline, gap formation, and persistence of endemic bark beetle populations. Forest Ecology and Management. 259(3): 374–382. https://doi.org/10.1016/j.foreco.2009.10.032.

Barry, P.J.; Doggett, C.; Anderson, R.L.; Swain, K.M. 1993. How to evaluate and manage storm-damaged forest areas. Management Bulletin R8-MB63. Atlanta, GA: U.S. Department of Agriculture Forest Service, Southern Region. 11 p.

Beach, R.H.; Sills, E.O.; Liu, T.; Pattanayak, S. 2010. The influence of forest management on vulnerability of forests to severe weather. In: Pye, J.M.; Rauscher, H.M.; Sands, Y. [and others], eds. Advances in threat assessment and their application to forest and rangeland management. Gen. Tech. Rep. PNW-802. Portland, OR: U.S. Department of Agriculture Forest Service, Pacific Northwest and Southern Research Stations: 185–206.

Bendixsen, D.P.; Hallgren, S.W.; Frazier, A.E. 2015. Stress factors associated with forest decline in xeric oak forests of South-central United States. Forest Ecology and Management. 347: 40–48. https://doi.org/10.1016/j.foreco.2015.03.015.

Bennett, L. 1959. Glaze: its meteorology and climatology, geographical distribution, and economic effects. Technical Report EP-105. Natick, MA: U.S. Army Quartermaster Research and Engineering Command, Environmental Protection Research Division. 217 p.

Bentley, M.L.; Mote, T.L. 1998. A climatology of derecho-producing mesoscale convective systems in the Central and Eastern United States, 1986–95. Part 1: Temporal and spatial distribution. Bulletin of the American Meteorological Society. 79(11): 2527–2540. https://doi.org/10.1175/1520-0477(1998)079<2527:ACODPM>2.0.CO;2.

Biedermann, P.H.W.; Vega, F.E. 2020. Ecology and evolution of insect-fungus mutualisms. Annual Review of Entomology. 65: 431–455. https://doi.org/10.1146/annurev-ento-011019-024910.

Blanche, C.A.; Hodges, J.D.; Nebeker, T.E.; Moehring, D.M. 1983. Southern pine beetle: the host dimension. Bulletin 917. Mississippi State, MS: Mississippi Agricultural and Forestry Experiment Station. 29 p.

Boruff, B.J.; Easoz, J.A.; Jones, S.D. [and others]. 2003. Tornado hazards in the United States. Climate Research. 24: 103–117. https://doi.org/10.3354/cr024103.

Boyer, W.D. 1979. Mortality among seed trees in longleaf shelterwood stands. Southern Journal of Applied Forestry. 3: 165–167. https://doi.org/10.1093/sjaf/3.4.165.

Bragg, D.C. 2016. Initial mortality rates and extent of damage to loblolly and longleaf pine plantations affected by an ice storm in South Carolina. Forest Science. 62(5): 574–585. https://doi.org/10.5849/forsci.15-177.

Bragg, D.C.; Shelton, M.G. 2010. Recovery of planted loblolly pine 5 years after severe ice storms in Arkansas. Southern Journal of Applied Forestry. 34(1): 13–20. https://doi.org/10.1093/sjaf/34.1.13.

Bragg, D.C.; Shelton, M.G.; Heitzman, E. 2004. Relative impacts of ice storms on loblolly pine plantations in central Arkansas. In: Connor, K.F., ed. Proceedings of the 12th biennial southern silvicultural research conference. Gen. Tech. Rep. SRS–71. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station: 132–137.

Bragg, D.C.; Shelton, M.G.; Zeide, B. 2003. Impacts and management implications of ice storms on forests in the Southern United States. Forest Ecology and Management. 186: 99–123. https://doi.org/10.1016/S0378-1127(03)00230-5.

Brazdil, R.; Stucki, P.; Szabo, P. [and others]. 2018. The second most disastrous windstorm of the nineteenth century in the Czech Lands, 26–27 October 1870. Theoretical and Applied Climatology. 132(3–4): 1201–1216. https://doi.org/10.1007/s00704-017-2146-1.

Brender, E.V.; Romancier, R.M. 1960. Glaze damage in loblolly pine plantations. Southern Lumberman. 201: 168.

Broadfoot, W.M.; Williston, H.L. 1973. Flooding effects on southern forests. Journal of Forestry. 71(9): 584–587.

Cain, M.D.; Shelton, M.G. 1996. The R.R. Reynolds Research Natural Area in southeastern Arkansas: a 56-year study in pine-hardwood sustainability. Journal of Sustainable Forestry. 3(4): 59–74. https://doi.org/10.1300/J091v03n04_06.

Campbell, W.A.; Copeland, O.L. 1954. Littleleaf disease of shortleaf and loblolly pines. Circular 940. Washington, DC: U.S. Department of Agriculture. 41 p.

Cannon, J.B.; Hepinstall-Cymerman, J.; Godfrey, C.M.; Peterson, C.J. 2016. Landscape-scale characteristics of forest tornado damage in mountainous terrain. Landscape Ecology. 31: 2097–2114. https://doi.org/10.1007/s10980-016-0384-8.

Clark, J.S.; Iverson, L.; Woodall, C.W. [and others]. 2016a. The impacts of increasing drought on forest dynamics, structure, and biodiversity in the United States. Global Change Biology. 22: 2329–2352.

Clark, J.S.; Iverson, L.; Woodall, C.W. [and others]. 2016b. Impacts of increasing drought on forest dynamics, structure, diversity, and management. In: Vose, J.M.; Clark, J.S.; Luce, C.H.; Patel-Weynand, T., eds. Effects of drought on forests and rangelands in the United States: a comprehensive science synthesis. Gen. Tech. Rep. WO-93b. U.S. Department of Agriculture Forest Service, Washington Office: 59–96. Chapter 4.

Clarke, S.; Menard, R.; Bruce, W. 1999. Forest health evaluation of bark beetle activity in storm-damaged areas on the National Forests in Texas. Report No. 99-2-02. Pineville, LA: U.S. Department of Agriculture Forest Service, Forest Health Protection, Alexandria Field Office. 7 p.

Coleman, T.A.; Dixon, P.G. 2014. An objective analysis of tornado risk in the United States. Weather and Forecasting. 29: 366–376. https://doi.org/10.1175/WAF-D-13-00057.1.

Cool, B.M.; Goebel, N.B.; Wooten, T.E.; Loadholt, C.B. 1971. Glaze damage to pine trees in the Sandhills area of South Carolina. Forest Research Series Report 21. Clemson, SC: Clemson University Department of Forestry. 12 p.

Cooper-Ellis, S.; Foster, D.R.; Carlton, G.; Lezberg, A. 1999. Forest response to catastrophic wind: results from an experimental hurricane. Ecology. 80: 2683–2696. https://doi.org/10.1890/0012-9658(1999)080[2683:FRTCWR]2.0.CO;2.

Corfidi, S.F.; Coniglio, M.C.; Cohen, A.E.; Mead, C.M. 2016. A proposed revision to the definition of "derecho". Bulletin of the American Meteorological Society. 97(6): 935–949. https://doi.org/10.1175/BAMS-D-14-00254.1.

Coulson, R.N.; Hennier, P.B.; Flamm, R.O. [and others]. 1983. The role of lightning in the epidemiology of the southern pine beetle. Journal of Applied Entomology. 96(1–5): 182–193. https://doi.org/10.1111/j.1439-0418.1983.tb03659.x.

Coyle, D.R.; Klepzig, K.D.; Koch, F.H. [and others]. 2015. A review of southern pine decline in North America. Forest Ecology and Management. 349: 134–148. https://doi.org/10.1016/j.foreco.2015.04.007.

Crandall, B.S. 1948. *Phytophthora cinnamomi* root rot of avocados under tropical conditions. Phytopathology. 38: 123–130.

Croker, T.C. 1987. Longleaf pine: a history of man and a forest. Forestry Report RS-FR7. Atlanta, GA: U.S. Department of Agriculture Forest Service, Southern Region. 37 p. https://doi.org/10.5962/bhl.title.85034.

Curry, G.L.; Coulson, R.N.; Gan, J. [and others]. 2008. An optimization-based system model of disturbance-generated forest biomass utilization. Bulletin of Science, Technology, and Society. 28: 486–495.

Degelia, S.K.; Christian, J.I.; Barara, J.B. [and others]. 2016. An overview of ice storms and their impact in the United States. International Journal of Climatology. 36: 2811–2822. https://doi.org/10.1002/joc.4525.

Demaree, D. 1932. Submerging experiments with *Taxodium*. Ecology. 13(3): 258–262. https://doi.org/10.2307/1931552.

Dixon, P.G.; Mercer, A.E.; Choi, J.; Allen, J.S. 2011. Tornado risk analysis: Is Dixie Alley an extension of tornado alley? Bulletin of the American Meteorological Society. 92(4): 433–441. https://doi.org/10.1175/2010BAMS3102.1.

Dodds, K.J.; DiGirolomo, M.F.; Fraver, S. 2019. Response of bark beetles and woodborers to tornado damage and subsequent salvage logging in northern coniferous forests of Maine, USA. Forest Ecology and Management. 450: 117489. https://doi.org/10.1016/j.foreco.2019.117489.

Dreaden, T.J.; Smith, J.A.; Cram, M.M.; Coyle, D.R. 2016. Biology, diagnosis and management of Heterobasidion root disease of southern pines. SREF-FH-004. Athens, GA: Southern Regional Extension Forestry. 5 p.

Dwinell, L.D.; Barrows-Broaddus, J. 1981. Pitch canker in seed orchards. In: Proceedings of the 16th southern forest tree improvement conference; May 27–28, 1981; Virginia Polytechnic Institute and State University, Blacksburg, VA. Athens, GA: U.S. Department of Agriculture Forest Service, Forest Sciences Lab: 234–241.

Dwinell, L.D.; Barrows-Broaddus, J.; Kuhlman, E.G. 1985. Pitch canker: a disease complex of southern pines. Plant Disease. 69: 270–276. https://doi.org/10.1094/PD-69-270.

Eckhardt, L.G.; Menard, R.D. 2009. Declining loblolly pine stands: symptoms, causes, and management options. Alabama Treasured Forest Magazine. XXV111(2): 10–12.

Effler, R.S.; Goyer, R.A. 2006. Baldcypress and water tupelo sapling response to multiple stress agents and reforestation implications for Louisiana swamps. Forest Ecology and Management. 226: 330–340. https://doi.org/10.1016/j.foreco.2006.02.011.

Erbaugh, D.K.; Windham, M.T.; Stodola, A.J.; Augé, R.M. 1995. Light intensity and drought stress as predisposition factors for dogwood anthracnose. Journal of Environmental Horticulture. 13(4): 186–189.

Everham, E.M.; Brokaw, N.V.L. 1996. Forest damage and recovery from catastrophic wind. The Botanical Review. 62: 113–185. https://doi.org/10.1007/BF02857920.

Felt, E.P.; Bromley, S.W. 1939. The hurricane and the newer shade tree insect problems. Journal of Economic Entomology. 32: 203–205. https://doi.org/10.1093/jee/32.2.203.

Florida Forest Service. 2018. Hurricane Michael initial value estimate of altered, damaged or destroyed timber in Florida. [Unpublished report]. http://floridaforest.org/resources/hurricane-information/. [Date accessed: November 18, 2019].

Food and Agriculture Organization (FAO) of the United Nations. 2018. Forest products, 2016 yearbook. Rome, Italy: Food and Agriculture Organization. 243 p.

Foster, D.R. 1988. Species and stand response to catastrophic wind in central New England, USA. Journal of Ecology. 76: 135–151. https://doi.org/10.2307/2260458.

Foster, D.R.; Boose, E.R. 1992. Patterns of forest damage resulting from catastrophic wind in central New England, USA. Journal of Ecology. 80(1): 79–98. https://doi.org/10.2307/2261065.

Francis, J.K.; Gillespie, A.J.R. 1993. Relating gust speed to tree damage in Hurricane Hugo, 1989. Journal of Arboriculture. 19: 368–373.

Fredericksen, T.S.; Hedden, R.L.; Williams, S.A. 1995. Susceptibility of loblolly pine to bark beetle attack following simulated wind stress. Forest Ecology and Management. 76(1–3): 95–107. https://doi.org/10.1016/0378-1127(95)03552-L.

Froelich, R.C.; Schmidtling, R.C. 1998. Survival of slash pine having fusiform rust disease varies with year of first stem infection and severity. Southern Journal of Applied Forestry. 22(2): 96–100. https://doi.org/10.1093/sjaf/22.2.96.

Fujita, T.T. 1981. Tornadoes and downbursts in the context of generalized planetary scales. Journal of Atmospheric Science. 38: 1511–1534. https://doi.org/10.1175/1520-0469(1981)038<1511:TADITC>2.0.CO;2.

Fujita, T.T. 1985. The downburst: microburst and macroburst. SMRP Research Paper Number 210. Chicago: The University of Chicago. 124 p.

Gandhi, K.J.K. 2005. The responses of sub-boreal forest insects to a catastrophic wind-disturbance event and subsequent fuel-reduction practices in northeastern Minnesota, vols. I and II. St. Paul, MN: University of Minnesota. 466 p. Ph.D. dissertation.

Gandhi, K.J.K.; Gilmore, D.W.; Haack, R.A. [and others]. 2009. Application of semiochemicals to assess the biodiversity of subcortical insects following an ecosystem disturbance in a sub-boreal forest. Journal of Chemical Ecology. 35: 1384–1410. https://doi.org/10.1007/s10886-009-9724-3.

Gandhi, K.J.K.; Gilmore, D.W.; Katovich, S.A. [and others]. 2007. Physical effects of weather events on the abundance and diversity of insects in North American forests. Environmental Reviews. 15: 113–152. https://doi.org/10.1139/A07-003.

Garbelotto, M.; Gonthier, P. 2013. Biology, epidemiology, and control of *Heterobasidion* species worldwide. Annual Review of Phytopathology. 51: 39–59.

Gardiner, B.; Berry, P.; Moulia, B. 2016. Wind impacts on plant growth, mechanics and damage. Plant Science. 245: 94–118.

Gardner, L.R.; Michener, W.K.; Williams, T.M. [and others]. 1992. Disturbance effects of Hurricane Hugo on a pristine coastal landscape: North Inlet, South Carolina, USA. Netherlands Journal of Sea Research. 30: 249–263. https://doi.org/10.1016/0077-7579(92)90063-K.

Goliger, A.M.; Milford, R.V. 1998. A review of worldwide occurrence of tornadoes. Journal of Wind Engineering and Industrial Aerodynamics. 74: 111–121. https://doi.org/10.1016/S0167-6105(98)00009-9.

Gonthier, P.; Nicoletti, G.; Linzer, R. [and others]. 2007. Invasion of European pine stands by a North American forest pathogen and its hybridization with a native interfertile taxon. Molecular Ecology. 16: 1389–1400. https://doi.org/10.1111/j.1365-294X.2007.03250.x.

Gooch, W.L. 1943. Sleet storms—a forest scourge. American Forests. 49: 390–391.

Goode, J.D.; Kleinman, J.S.; Hart, J.L.; Bhuta, A.A. 2020. Edge influence on composition and structure of a *Pinus palustris* woodland following catastrophic wind disturbance. Canadian Journal of Forest Research. 50: 332–341. https://doi.org/10.1139/cjfr-2019-0292.

Greenberg, C.H.; McNab, W.H. 1998. Forest disturbance in hurricane-related downbursts in the Appalachian Mountains of North Carolina. Forest Ecology and Management. 104: 179–191. https://doi.org/10.1016/S0378-1127(97)00246-6.

Gresham, C.A.; Williams, T.M.; Lipscomb, D.J. 1991. Hurricane Hugo wind damage to Southeastern U.S. coastal forest tree species. Biotropica. 23: 420–426. https://doi.org/10.2307/2388261.

Hajek, A.E.; Morris, E.E.; Hendry, T.A. 2019. Context-dependent interactions of insects and defensive symbionts: insights from a novel system in siricid woodwasps. Current Opinion in Insect Science. 33: 77–83. https://doi.org/10.1016/j.cois.2019.03.006.

Haley, T.J.; Johnson, C.W.; Hess, N.J. 2005. Forest health evaluation of the Conecuh National Forest following Hurricane Ivan. Report No. 2005-02-01. Pineville, LA: U.S. Department of Agriculture Forest Service, Forest Health Protection, Alexandria Field Office. 20 p. https://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb5157193.pdf. [Date last accessed: July 2, 2020].

Halverson, H.G.; Guldin, J.M. 1995. Effects of a severe ice storm on mature loblolly pine stands in north Mississippi. In: Edwards, M.B., comp. Proceedings of the eighth biennial southern silvicultural research conference. Gen. Tech. Rep. SRS-1. U.S. Department of Agriculture Forest Service, Southern Research Station: 147–153.

Hanson, P.J.; Weltzin, J.F. 2000. Drought disturbance from climate change: response of United States forests. Science of the Total Environment. 262(3): 205–220.

Hanula, J.L.; Meeker, J.R.; Miller, D.R.; Barnard, E.L. 2002. Association of wildfire with tree health and numbers of pine bark beetles, reproduction weevils and their associates in Florida. Forest Ecology and Management. 170 (1–3): 233–247.

Hart, S.J.; Schoennagel, T.; Veblen, T.T.; Chapman, T.B. 2015. Area burned in the Western United States is unaffected by recent mountain pine beetle outbreaks. Proceedings of the National Academy of Sciences. 112: 4375–4380. https://doi.org/10.1073/pnas.1424037112.

Helbig, C.E.; Coyle, D.R.; Klepzig, K.D. [and others]. 2016. Colonization dynamics of subcortical insects on forest sites with relatively stressed and unstressed loblolly pine trees. Journal of Economic Entomology. 109(4): 1729–1740.

Hess, N.J.; Clarke, S.R.; Haley, T.J.; Kertz, R.C. 2001. Evaluation of ice storm damage on the Ouachita National Forest, Oden Ranger District. Report No. 2001-02-03. Pineville, LA: U.S. Department of Agriculture Forest Service, Forest Health Protection, Alexandria Field Office. 9 p.

Hetrick, L.A. 1949. Some overlooked relationships of southern pine beetle. Journal of Economic Entomology. 42: 466–469. https://doi.org/10.1093/jee/42.3.466.

Hicke, J.A.; Johnson, M.C.; Hayes, J.L.; Preisler, H.K. 2012. Effects of bark beetle-caused tree mortality on wildfire. Forest Ecology and Management. 271: 81–90. https://doi.org/10.1016/j.foreco.2012.02.005.

Hodges, J.D.; Pickard, L.S. 1971. Lightning in the ecology of the southern pine beetle, *Dendroctonus frontalis* (Coleoptera: Scolytidae). Canadian Entomologist. 103: 44–51.

Holzmueller, E.J.; Gibson, D.J.; Suchecki, P.F. 2012. Accelerated succession following an intense wind storm in an oak-dominated forest. Forest Ecology and Management. 279: 141–146. https://doi.org/10.1016/j.foreco.2012.05.036.

Honkaniemi, J.; Lehtonen, M.; Väisänen, H.; Peltola, H. 2017. Effects of wood decay by *Heterobasidion annosum* on the vulnerability of Norway spruce stands to wind damage: a mechanistic modelling approach. Canadian Journal of Forest Research. 47(6): 777–787. https://doi.org/10.1139/cjfr-2016-0505.

Hook, D.D. 1984. Waterlogging tolerance of lowland tree species of the South. Southern Journal of Applied Forestry. 8(3): 136–149. https://doi.org/10.1093/sjaf/8.3.136.

Hook, D.D.; Buford, M.A.; Williams, T.M. 1991. Impact of Hurricane Hugo on the South Carolina coastal plain forest. Journal of Coastal Research. Special Issue 8: 291–300.

Howard, J.L.; Liang, S. 2019. U.S. timber production, trade, consumption, and price statistics, 1965–2017. Res. Pap. FPL-701. Madison, WI: U.S. Department of Agriculture Forest Service, Forest Products Laboratory. 96 p.

Irland, L.C. 2000. Ice storms and forest impacts. Science of the Total Environment. 262: 231–242. https://doi.org/10.1016/S0048-9697(00)00525-8.

Johnsen, K.H.; Butnor, J.R.; Kush, J.S. [and others]. 2009. Hurricane Katrina winds damaged longleaf pine less than loblolly pine. Southern Journal of Applied Forestry. 33(4): 178–181. https://doi.org/10.1093/sjaf/33.4.178.

Johnson, R.D., II. 2007. Post hurricane black turpentine beetle damage. Lake Charles, LA: McNeese State University. M.S. thesis. 50 p. https://www.universal-publishers.com/book.php?method=ISBN&book=1581123914. [Date last accessed: July 7, 2020].

Johnson, R.L. 1990. Water tupelo, *Nyssa aquatica* L. In: Burns, R.M.; Honkala, B.H., tech. coords. Silvics of North America: volume 2. Hardwoods. Agric. Handb. 654. Washington, DC: U.S. Department of Agriculture Forest Service: 474–478.

Jones, K.; Thorkildson, R.; Lott, N. 2002. The development of a U.S. climatology of extreme ice loads. Technical Report 2002-01. Asheville, NC: U.S. Department of Commerce, National Climatic Data Center. 23 p.

Karha, K.; Anttonen, T.; Poikela, A. [and others]. 2018. Evaluation of salvage logging productivity and costs in windthrown Norway spruce-dominated forests. Forests. 9(5): 280. https://doi.org/10.3390/f9050280.

Kile, G.A.; McDonald, G.I.; Byler, J.W. 1991. Ecology and disease in natural forests. In: Shaw, C.G., III; Kile, G.A., eds. Armillaria root disease. Agric. Handb. 691. Washington, DC: U.S. Department of Agriculture Forest Service: 102–121.

King, S.L.; Allen, J.A.; McCoy, J.W. 1998. Long-term effects of a lock and dam and greentree reservoir management on a bottomland hardwood forest. Forest Ecology and Management. 112: 213–226. https://doi.org/10.1016/S0378-1127(98)00344-2.

Klepzig, K.D.; Raffa, K.F.; Smalley, E.B. 1991. Association of an insect-fungal complex with red pine decline in Wisconsin. Forest Science. 37: 1119–1139.

Klopfenstein, N.B.; Kim, M.S.; Hanna, J.W. [and others]. 2009. Approaches to predicting potential impacts of climate change on forest disease: an example with Armillaria root disease. Res. Pap. RMRS-76. Fort Collins, CO: U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station. 10 p. https://doi.org/10.2737/RMRS-RP-76.

Komarek, E.V. 1974. Introduction to lightning ecology. In: Komarek, E.V., ed. Proceedings of the Tall Timbers fire ecology conference, volume 13. Tallahassee, FL: Tall Timbers Research Station: 421–427.

Kozlowski, T.T. 1984. Plant responses to flooding of soil. BioScience. 34(3): 162–167. https://doi.org/10.2307/1309751.

Kozlowski, T.T. 2002. Physiological-ecological impacts of flooding on riparian forest ecosystems. Wetlands. 22(3): 550–561. https://doi.org/10.1672/0277-5212(2002)022[0550:PEIOFO]2.0.CO;2.

Kreuzwieser, J.; Rennenberg, H. 2014. Molecular and physiological responses of trees to waterlogging stress. Plant, Cell & Environment. 37(10): 2245–2259. https://doi.org/10.1111/pce.12310.

Kucera, D.R.; Hatch, C.L. 1968. Evaluation of insect conditions following severe hail damage to pine stands near Camden, Arkansas. Report #68-3-32. Pineville, LA: U.S. Department of Agriculture Forest Service, Southeastern Area State and Private Forestry. 4 p.

Kupfer, J.A.; Myers, A.T.; McLane, S.E.; Melton, G.N. 2008. Patterns of forest damage in a southern Mississippi landscape caused by Hurricane Katrina. Ecosystems. 11: 45–60. https://doi.org/10.1007/s10021-007-9106-z.

La Porta, N.; Capretti, P.; Thomsen, I.M. [and others]. 2008. Forest pathogens with higher damage potential due to climate change in Europe. Canadian Journal of Plant Pathology. 30(2): 177–195. https://doi.org/10.1080/07060661.2008.10540534.

Lafon, C.W.; Kutac, M.J. 2003. Effects of ice-storms, southern pine beetle infestation, and fire on Table Mountain pine forests of southwestern Virginia. Physical Geography. 24: 502–519.

Leininger, T.D.; Wilson, A.D.; Lester, D.G. 1997. Hurricane Andrew damage in relation to wood decay fungi and insects in bottomland hardwoods of the Atchafalaya Basin, Louisiana. Journal of Coastal Research. 13: 1290–1293.

Lemon, P.C. 1961. Forest ecology of ice storms. Bulletin of the Torrey Botanical Club. 88: 21–29. https://doi.org/10.2307/2482410.

Lockman, I.B.; Kearns, H.S. 2016. Forest root diseases across the United States. Gen. Tech. Rep. RMRS-342. Ogden, UT: U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station. 55 p.

Lu, D.; Pile, L.S.; Yu, D. [and others]. 2020. Differential response of tree species to a severe ice storm and their implications to forest composition in the Southeast United States. Forest Ecology and Management. 468: 118177. https://doi.org/10.1016/j.foreco.2020.118177.

Lugo, A.E. 2008. Visible and invisible effects of hurricanes on forest ecosystems: an international review. Austral Ecology. 33(4): 368–398. https://doi.org/10.1111/j.1442-9993.2008.01894.x.

Maguire, J. 1995. Restoration plan for Dade County's pine rockland forests following Hurricane Andrew. Miami, FL: Metro-Dade Department of Environmental Resources Management. 32 p. plus appendices. http://library.stu.edu/STUva/ERLIB/a044.pdf. [Date last accessed: July 7, 2020].

Manion, P.D. 1981. Tree disease concepts. Englewood Cliffs, NJ: Prentice Hall, Inc. 399 p.

McKellar, A.D. 1942. Ice damage to slash pine, longleaf pine, and loblolly pine plantations in the Piedmont section of Georgia. Journal of Forestry. 40: 794–797.

McNab, W.H.; Greenberg, C.H.; Berg, E.C. 2004. Landscape distribution and characteristics of large hurricane-related canopy gaps in a Southern Appalachian watershed. Forest Ecology and Management. 196: 435–447. https://doi.org/10.1016/j.foreco.2004.04.004.

McNulty, S.G. 2002. Hurricane impacts on U.S. forest carbon sequestration. Environmental Pollution. 116: S17–S24. https://doi.org/10.1016/S0269-7491(01)00242-1.

McNulty, S.G.; Baca, A.; Bowker, M. [and others]. 2019. Managing effects of drought in the Southeast United States. In: Vose, J.M.; Peterson, D.L.; Luce, C.H.; Patel-Weynand, T., eds. Effects of drought on forests and rangelands in the United States: translating science into management responses. Gen. Tech. Rep. WO-98. U.S. Department of Agriculture Forest Service, Washington Office: 191–220.

McNulty, S.G.; Lorio, P.L., Jr.; Ayres, M.P.; Reeve, J.D. 1998. Predictions of southern pine beetle populations using a forest ecosystem model. In: Mickler, R.A.; Fox, S., eds. The productivity and sustainability of southern forest ecosystems in a changing environment. New York: Springer: 617–634. https://doi.org/10.1007/978-1-4612-2178-4_33.

Mistretta, P.A.; Bylin, C.V. 1987. Incidence and impact of damage to Louisiana's timber, 1985. Resour. Bull. SO-117. New Orleans, LA: U.S. Department of Agriculture Forest Service, Southern Forest Experiment Station. 22 p. https://doi.org/10.2737/SO-RB-117.

Mitchell, S.J. 2013. Wind as a natural disturbance agent in forests: a synthesis. Forestry. 86: 147–157. https://doi.org/10.1093/forestry/cps058.

Mueller, O.P.; Cline, M.G. 1959. Effects of mechanical soil barriers and soil wetness on rooting of trees and soil mixing by blow-down in central New York. Soil Science. 88: 107–111. https://doi.org/10.1097/00010694-195988020-00009.

Muntz, H.H. 1947. Ice damage to pine plantations. Southern Lumberman. 175: 142–145.

Nelson, T.C.; Stanley, G.W. 1959. Hurricane damage related to thinning intensity in east Texas slash pine plantations. Journal of Forestry. 57: 39.

Oak, S.W.; Tainter, F.H. 1988. How to identify and control littleleaf disease. Protection Report R8-PR-12. Atlanta, GA: U.S. Department of Agriculture Forest Service, Southern Region. 14 p.

Olatinwo, R.; Guo, Q.; Fei, S. [and others]. 2014. Climate-induced changes in vulnerability to biological threats in the Southern United States. In: Vose, J.M.; Klepzig, K.D., eds. Climate change adaptation and mitigation management options: a guide for natural resource managers in southern forest ecosystems. Boca Raton, FL: CRC Press: 127–172.

Oldfield, C.A.; Peterson, C.J. 2019. Woody species composition, diversity, and recovery six years after wind disturbance and salvage logging of a southern Appalachian forest. Forests. 10: 129.

Oliver, C.D.; Larson, B.C. 1996. Forest stand dynamics. New York: John Wiley and Sons, Inc. 544 p.

Orville, R.E.; Huffines, G.R. 2001. Cloud-to-ground lightning in the United States: NLDN results in the first decade, 1989–98. Monthly Weather Review. 129: 1179–1193.

Oswalt, S.N.; Smith, B.W.; Miles, P.D.; Pugh, S.A. 2019. Forest resources of the United States, 2017: a technical document supporting the Forest Service 2020 RPA Assessment. Gen. Tech. Rep. WO-97. Washington, DC: U.S. Department of Agriculture Forest Service. 223 p. https://doi.org/10.2737/WO-GTR-97.

Overgaard, N.A. 1970. Evaluation of bark beetle infestations in storm-damaged timber on the DeSoto National Forest. Report No. 70-2-42. Pineville, LA: U.S. Department of Agriculture Forest Service, Southeastern Area State and Private Forestry. 3 p.

Overgaard, N.A,; Drake, L.E 1970. Evaluation of bark beetle infestations in storm-damaged timber on the DeSoto National Forest, Mississippi. Report No. 70-2-46. Pineville, LA: U.S. Department of Agriculture Forest Service, Southeastern Area State and Private Forestry. 4 p.

Palik, B.J.; Pederson, N. 1996. Overstory mortality and canopy disturbances in longleaf pine ecosystems. Canadian Journal of Forest Research. 26: 2035–2047. https://doi.org/10.1139/x26-229.

Panshin, A.J.; de Zeeuw, C. 1980. Textbook of wood technology. 3rd ed. New York: McGraw-Hill Book Company. 705 p.

Papaik, M.J.; Canham, C.D.; Latty, E.F.; Woods, K.D. 2005. Effects of an introduced pathogen on resistance to natural disturbance: beech bark disease and windthrow. Canadian Journal of Forest Research. 35: 1832–1843. https://doi.org/10.1139/x05-116.

Peltola, H.; Kellomä, S.; Väisänen, H.; Ikonen, V.-P. 1999. A mechanistic model for assessing the risk of wind and snow damage to single trees and stands of Scots pine, Norway spruce, and birch. Canadian Journal of Forest Research. 29: 647–661. https://doi.org/10.1139/x99-029.

Peterson, C.J. 2007. Consistent influence of tree diameter and species on damage in nine eastern North American tornado blowdowns. Forest Ecology and Management. 250: 96–108. https://doi.org/10.1016/j.foreco.2007.03.013.

Peterson, C.J.; Cannon, J.B.; Godfrey, C.M. 2016. First steps toward defining the wind disturbance regime in central hardwoods forests. In: Greenberg, C.H.; Collins, B.S., eds. Natural disturbances and historic range of variation: type, frequency, severity, and post-disturbance structure in central hardwood forests USA. Managing Forest Ecosystems 32. Cham, Switzerland: Springer International Publishing: 97–103.

Peterson, C.J.; Leach, A.D. 2008a. Limited salvage logging effects on forest regeneration after moderate-severity windthrow. Ecological Applications. 18: 407–420. https://doi.org/10.1890/07-0603.1.

Peterson, C.J.; Leach, A.D. 2008b. Salvage logging after windthrow alters microsite diversity, abundance and environment, but not vegetation. Forestry. 81: 361–376. https://doi.org/10.1093/forestry/cpn007.

Peterson, C.J.; Pickett, S.T.A. 1991. Treefall and resprouting following catastrophic windthrow in an old-growth hemlock-hardwoods forest. Forest Ecology and Management. 42: 205–217. https://doi.org/10.1016/0378-1127(91)90025-Q.

Peterson, C.J.; Pickett, S.T.A. 1995. Forest reorganization: a case study in an old-growth forest catastrophic blowdown. Ecology. 76: 763–774. https://doi.org/10.2307/1939342.

Pielke, R.A., Jr.; Gratz, J.; Landsea, C.W. [and others]. 2008. Normalized hurricane damage in the United States: 1900–2005. Natural Hazards Review. 9(1): 29–42. https://doi.org/10.1061/(ASCE)1527-6988(2008)9:1(29).

Piri, T.; Korhonen, K. 2007. Spatial distribution and persistence of *Heterobasidion parviporum* genets on a Norway spruce site. Forest Pathology. 37(1): 1–8. https://doi.org/10.1111/j.1439-0329.2007.00482.x.

Platt, W.J.; Beckage, B.; Doren, R.F.; Slater, H.H. 2002. Interactions of large-scale disturbances: prior fire regimes and hurricane mortality of southern pines. Ecology. 83: 1566–1572. https://doi.org/10.1890/0012-9658(2002)083[1566:IOLSDP]2.0.CO;2.

Powers, H.R., Jr.; Verrall, A.F. 1962. A closer look at *Fomes annosus*. Forest Farmer. 21(13): 8–9.

Prestemon, J.P.; Pye, J.M.; Holmes, T.P. 2001. Timber economics of natural catastrophes. In: Pelkki, M., ed. Proceedings of the 2000 southern forest economics workshop; March 23-35, 2000. Lexington, KY: University of Kentucky:132–141.

Putz, F.E.; Sharitz, R.R. 1991. Hurricane damage to old-growth forest in Congaree Swamp National Monument, South Carolina, U.S.A. Canadian Journal of Forest Research. 21: 1765–1770. https://doi.org/10.1139/x91-244.

Quine, C.P.; Gardiner, B.A. 2007. Understanding how the interaction of wind and trees results in windthrow, stem breakage, and canopy gap formation. In: Johnson, E.A.; Miyanishi, K., eds. Plant disturbance ecology: the process and the response. Amsterdam, The Netherlands: Elsevier: 103–155.

Rigby, J.R.; Porporato, A. 2008. Spring frost risk in a changing climate. Geophysical Research Letters. 35(12): L12703. https://doi.org/10.1029/2008GL033955.

Rippy, R.C.; Stewart, J.E.; Zambino, P.J. [and others]. 2005. Root diseases in coniferous forests of the Inland West: potential implications of fuels treatments. Gen. Tech. Rep. RMRS-141. Fort Collins, CO: U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station. 32 p. https://doi.org/10.2737/RMRS-GTR-141.

Rönnberg, J.; Sidorov, E.; Petrylaitė, E. 2006. Efficacy of different concentrations of Rotstop® and Rotstop® S and imperfect coverage of Rotstop® S against *Heterobasidion* spp. spore infections on Norway spruce stumps. Forest Pathology. 36(6): 422–433. https://doi.org/10.1111/j.1439-0329.2006.00476.x.

Roth, B.E.; Jokela, E.J.; Martin, T.A. [and others]. 2007. Genotype × environment interactions in selected loblolly and slash pine plantations in the Southeastern United States. Forest Ecology and Management. 238(1–3): 175–188. https://doi.org/10.1016/j.foreco.2006.10.010.

Roth, E.R.; Toole, E.R.; Hepting, G.H. 1948. Nutritional aspects of the littleleaf disease of pine. Journal of Forestry. 46(8): 578–587.

Ruel, J.C. 1995. Understanding windthrow: silvicultural implications. The Forestry Chronicle. 71: 434–445. https://doi.org/10.5558/tfc71434-4.

Runion, G.B.; Bruck, R.I. 1988. The effects of Thiabendazole on *Fusarium subglutinans*, the causal agent of pitch canker of loblolly pine. Plant Disease. 72(4): 297. https://doi.org/10.1094/PD-72-0297.

Sangüesa-Barreda, G.; Camarero, J.J.; Oliva, J. [and others]. 2015. Past logging, drought and pathogens interact and contribute to forest dieback. Agricultural and Forest Meteorology. 208: 85–94.

Schoenike, R.E.; Van Lear, D.H.; Benson, J.D. 1977. Comparison of shortleaf, loblolly, and putative hybrid pines in the Piedmont of South Carolina. Silvae Genetica. 26(5–6): 182–184.

Schowalter, T.D. 2012. Insect responses to major landscape-level disturbance. Annual Review of Entomology. 57: 1–20. https://doi.org/10.1146/annurev-ento-120710-100610.

Shaw, C.G., III; Kile, G.A. 1991. Armillaria root disease. Agric. Handb. 691. Washington, DC: U.S. Department of Agriculture Forest Service. 233 p.

Skelton, J.; Jusino, M.A.; Carlson, P.S. [and others]. 2019. Relationships among wood-boring beetles, fungi, and the decomposition of forest biomass. Molecular Ecology. 28(22): 4971–4986. https://doi.org/10.1111/mec.15263.

Smith, A.; Lott, N.; Houston, T. [and others]. 2019. U.S. billion-dollar weather & climate disasters 1980–2019. Asheville, NC: U.S. Department of Commerce National Oceanic and Atmospheric Administration, National Centers for Environmental Information. https://www.ncdc.noaa.gov/billions/. [Date accessed: November 17, 2019].

Smith, W.H. 2000. Ice and forest health. Northern Journal of Applied Forestry. 17: 16–19. https://doi.org/10.1093/njaf/17.1.16.

Stanturf, J.A.; Goodrick, S.L.; Outcalt, K.W. 2007. Disturbance and coastal forests: a strategic approach to forest management in hurricane impact zones. Forest Ecology and Management. 250(1–2): 119–135. https://doi.org/10.1016/j.foreco.2007.03.015.

Starkey, D.A.; Meeker, J.; Mangini, A. 2007. Pitch canker of southern pines and recent cases in Florida, Louisiana, Mississippi and Texas. In: Riley, L.E.; Dumroese, R.K.; Landis, T.D., eds. National proceedings: Forest and Conservation Nursery Associations - 2006. Proc. RMRS-P-50. Fort Collins, CO: U.S. Department of Agriculture Forest Service, Rocky Mountain Research Station: 97–103.

Starkey, D.A.; Oliveria, F.; Mangini, A.; Mielke, M. 2004. Oak decline and red oak borer in the interior Highlands of Arkansas and Missouri: natural phenomena, severe occurrences. Gen. Tech. Rep. SRS–73. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station: 217–222.

Sturrock, R.N.; Frankel, S.J.; Brown, A.V. [and others]. 2011. Climate change and forest diseases. Plant Pathology. 60(1): 133–149. https://doi.org/10.1111/j.1365-3059.2010.02406.x.

Tainter, F.H.; Baker, F.A. 1996. Principles of forest pathology. New York: Wiley. 805 p.

Taylor, A.R. 1974. Ecological aspects of lightning in forests. In: Komarek, E.V., ed. Proceedings of the Tall Timbers fire ecology conference, volume 13. Tallahassee, FL: Tall Timbers Research Station: 455–482.

U.S. Army Corps of Engineers. 2019. Damaging ice storm GIS. [Online database]. Vicksburg, MS: U.S. Army Corps of Engineers, Engineer Research and Development Center. http://rsgisias.crrel.usace.army.mil/ice/icegis.html. [Date accessed: September 19, 2019].

U.S. Department of Agriculture (USDA) Forest Service. 1955–2020. Forest insect and disease conditions in the United States. Washington, DC: U.S. Department of Agriculture Forest Service, Forest Health Protection. https://www.fs.fed.us/foresthealth/publications/fhp/index.shtml. [Date last accessed: July 7, 2020].

U.S. Department of Agriculture (USDA) Forest Service. 1989. Insects and diseases of trees in the South. 1997 reprint. Protection Rep. R8-PR16. Atlanta, GA: U.S. Department of Agriculture Forest Service, Southern Region. 98 p.

U.S. Department of Agriculture (USDA) Forest Service. 2007. Forest insect and disease conditions in the United States 2006. U.S. Department of Agriculture Forest Service, Forest Health Protection. https://www.fs.fed.us/foresthealth/publications/ConditionsReport_2006.pdf. [Date last accessed: July 7, 2020].

U.S. Department of Commerce (DOC) National Oceanic and Atmospheric Administration (NOAA), National Centers for Environmental Information (NCEI). 2019. U.S. tornado climatology. https://www.ncdc.noaa.gov/climate-information/extreme-events/us-tornado-climatology. [Date accessed: September 23, 2019].

U.S. Department of Commerce (DOC) National Oceanic and Atmospheric Administration (NOAA), National Hurricane Center. 2019. Tropical cyclone climatology. https://www.nhc.noaa.gov/climo. [Date accessed: October 16, 2019].

Vaughn, D.G. 2013. Derecho! The forgotten windstorm that changed the Ozarks. Forest History Today. Spring/Fall: 4–12.

Wahlenberg, W.G. 1960. Loblolly pine. Its use, ecology, regeneration, protection, growth and management. Durham, NC: Duke University School of Forestry. 603 p.

Walker, L.C.; Wiant, H.V., Jr. 1966. Silviculture of shortleaf pine. Forestry Bulletin No. 9. Nacogdoches, TX: Stephen F. Austin State College, School of Forestry. 60 p.

Walker, L.R. 1991. Tree damage and recovery from Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. Biotropica. 23(4a): 379–385.

Wargo, P.M.; Houston, D.M.; LaMadeleine, L.A. 1983. Oak decline. Forest Insect and Disease Leaflet 165. Washington, DC: U.S. Department of Agriculture Forest Service. 8 p.

Wargo, P.M.; Shaw, C.G., III. 1985. Armillaria root rot: the puzzle is being solved. Plant Disease. 69(10): 826–832. https://doi.org/10.1094/PD-69-826.

Webb, S.L. 1988. Windstorm damage and microsite colonization in two Minnesota forests. Canadian Journal of Forest Research. 18: 1186–1195. https://doi.org/10.1139/x88-182.

Webb, S.L.1999. Disturbance by wind in temperate-zone forests. In: Walker, L.R., ed. Ecosystems of disturbed ground. Ecosystems of the world 16. Amsterdam, The Netherlands: Elsevier Science: 187–222.

Whelan, A.W.; Bigelow, S.W.; Nieminen, M.F.; Jack, S.B. 2018. Fire season, overstory density and groundcover composition affect understory hardwood sprout demography in longleaf pine woodlands. Forests. 9(7): 423. https://doi.org/10.3390/f9070423.

Wilhite, L.P.; Toliver, J.R. 1990. Baldcypress, *Taxodium distichum* (L.) Rich. In: Burns, R.M.; Honkala, B.H., tech. coords. Silvics of North America: volume 1. Conifers. Agric. Handb. 654. Washington, DC: U.S. Department of Agriculture Forest Service: 563–572.

Wilkinson, R.C.; Britt, R.W.; Spence, E.A.; Seiber, S.M. 1978. Hurricane-tornado damage, mortality, and insect infestations of slash pine. Southern Journal of Applied Forestry. 2(4): 132–134. https://doi.org/10.1093/sjaf/2.4.132.

Williams, T.M.; Lipscomb, D.J. 2002. Natural recovery of red-cockaded woodpecker cavity trees after Hurricane Hugo. Southern Journal of Applied Forestry. 26: 197–206. https://doi.org/10.1093/sjaf/26.4.197.

Woodward, S.; Stenlid, J.; Karjalainen, R.; Hüttermann, R. 1998. *Heterobasidion annosum*: biology, ecology, impact and control. Wallingford, UK: CAB International. 589 p.

Wyckoff, P.H.; Clark, J.S. 2002. The relationship between growth and mortality for seven co-occurring tree species in the Southern Appalachian Mountains. Ecology. 90: 604–615. https://doi.org/10.1046/j.1365-2745.2002.00691.x.

Xi, W. 2015. Synergistic effects of tropical cyclones on forest ecosystems: a global synthesis. Journal of Forestry Research. 26: 1–21. https://doi.org/10.1007/s11676-015-0018-z.

Xi, W.; Peet, R.K.; Urban, D.L. 2008. Changes in forest structure, species diversity and spatial pattern following hurricane disturbance in a Piedmont North Carolina forest, USA. Journal of Plant Ecology. 1: 43–57. https://doi.org/10.1093/jpe/rtm003.

Yates, H.O., III; Miller, T. 1996. Post-Hurricane Hugo forest pest populations and damage. In: Haymond, J.L.; Hook, D.D.; Harms, W.R., eds. Hurricane Hugo: South Carolina forest land research and management related to the storm. Gen. Tech. Rep. SRS-5. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station: 380–386. https://doi.org/10.2737/SRS-GTR-5.

Zak, B. 1961. Aeration and other soil factors affecting southern pines as related to littleleaf disease. Tech. Bull. 1248. Asheville, NC: U.S. Department of Agriculture Forest Service, Southeastern Forest Experiment Station. 30 p.

Zeng, H.; Chambers, J.Q.; Negron-Juarez, R.I. [and others]. 2009. Impacts of tropical cyclones on U.S. forest tree mortality and carbon flux from 1851 to 2000. Proceedings of the National Academy of Sciences. 106(19): 7888–7892. https://doi.org/10.1073/pnas.0808914106.

Zentmyer, G.A. 1980. *Phytophthora cinnamomi* and the diseases it causes. Monograph No. 10. St. Paul, MN: American Phytopathological Society. 96 p.

Zhang, G.; Murakami, H.; Knutson, T.R. [and others]. 2020. Tropical cyclone motion in changing climate. Science Advances. 6: eaaz7610. https://doi.org/10.1126/sciadv.aaz7610.

Vogt, James T.; Gandhi, Kamal J.K.; Bragg, Don C.; Olatinwo, Rabiu; Klepzig, Kier D. 2020. Interactions between weather-related disturbance and forest insects and diseases in the Southern United States. Gen. Tech. Rep. SRS–255. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 37 p. https://doi.org/10.2737/SRS-GTR-255.

Forests in the Southern United States experience a wide variety of weather-related disturbances, from small-scale events which have management implications for one or a few landowners to major hurricanes impacting many ownerships across multiple States. The immediate impacts of catastrophic weather disturbance are obvious—trees are killed, stressed, or damaged due to wind, flooding, ice, hail, or some combination of events. How forests respond to disturbance depends on several factors such as forest types and attributes, ecoregion, local pressure from invasive plants, preexisting infestations of pests and pathogens, prior disturbance events, and other variables which interact in complex ways, influencing successional dynamics and management decisions. In this review, we synthesize the major weather perturbations affecting the forests of the Southern United States and current state of the knowledge surrounding interactions between these events, forest pests, and forest diseases. We present a compilation of non-quantitative observations between 1955 and 2018 from annual U.S. Department of Agriculture Forest Service “Major Forest Insect and Disease Conditions in the United States” reports describing where insects or diseases were found on trees that were stressed by weather disturbances. Two conceptual models are presented, one describing changes in forest structure and composition, and a generalized model of herbivorous pest population fluctuations following different severity levels of disturbance. Finally, we propose 11 questions that require additional research to better inform sustainable forest management decisions in preparation for and in response to catastrophic weather events.

Keywords: Flooding, forest pathogens, forest pests, ice storms, post-disturbance management, post-disturbance recovery, windstorms.

A copy of this general technical report is available for download at www.srs.fs.usda.gov/pubs/.