

Earth, wind, and fire: abiotic factors and the impacts of global environmental change on forest health

J.E. LUNDQUIST, A.E. CAMP, M.L. TYRRELL, S.J. SEYBOLD,
P. CANNON, AND D.J. LODGE

7.1 Introduction

Trees do not just die; there is always a primary cause, and often contributing factors. Trees need adequate quantities of water, heat, light, nutrients, carbon dioxide, oxygen, and other abiotic resources to sustain life, growth, and reproduction. When these factors are deficient or excessive, they cause mortality. According to the concept of baseline mortality (Chapters 1, 2, and 3), a certain number of trees must die as a forest ages to maintain a healthy condition. Abiotic factors kill trees in different ways, e.g., starvation, desiccation, uprooting, or stem breakage. The patterns of mortality and how the forest responds determine how changing stand structures impact sustainability and productivity. Here, we discuss abiotic factors, and how they influence diameter and age class distributions. We conclude this chapter by suggesting general principles about the impacts of abiotic disturbances on stand structures within forest ecosystems.

7.2 Weather events

Weather is the set of all phenomena occurring in a given atmosphere at a given time. Weather phenomena include wind, clouds, rain, snow, fog, dust storms, ice storms, hurricanes, tornadoes, and others. Some weather events can reset forest succession directly by killing trees. Weather events also can influence the rate and direction of forest succession indirectly by increasing fuels to enhance fire risk or by predisposing trees to other stresses. Previous assessments of annual forest impacts (Dale *et al.* 2001) show that ice storms are the least

extensive (> 180 000 ha) and costly (> US\$10 million), whereas wind events (hurricanes and tornadoes) are the most extensive (> 1 600 000 ha) and costly (> US\$800 million) weather phenomena.

7.2.1 Drought

Drought is an extended period (months or years) of water supply deficiency. Generally, this occurs when a region receives consistently below average precipitation, although land use practices (overfarming, excessive irrigation, massive water diversion, deforestation, or erosion) can trigger a drought. Cessation of rainfall may be related to reductions in the amount of water vapor in the atmosphere, or reduction in upward forcing of the air mass containing that water vapor. Both can be caused by more frequent high pressure systems, winds carrying continental, rather than oceanic air masses (i.e., reduced water content), and ridges of atmospheric high pressure that restrict local thunderstorm activity or rainfall. Although humans tend to be most cognizant of the impact of drought in the context of food production and desertification of agricultural lands, drought stress can also have significant impacts on forested landscapes, especially in concert with tree-killing bark beetles (see case study below). Drought reduces net primary production and water use in forests; plants can die during moderate (seedlings, saplings) or severe droughts (large trees) (Dale *et al.* 2001). Drought can also reduce nutrient cycling and decomposition, which result in a buildup of flammable organic matter that can increase the frequency and/or intensity of fires (Dale *et al.* 2001).

For many trees, water is the most limiting resource. Different tree species respond differentially to water stress. Coder (1999) categorized the various responses of plants, short of death, to drought of increasing severity: “1) recognizing (“sensing”) soil/root water availability problems; 2) chemically altering (osmotic) cell contents; 3) closing stomates for longer periods; 4) using food storage reserves; 5) closing-off or closing-down root activities (suberizing roots); 6) initiation of foliage, branch and /or root senescence; 7) setting-up abscission and compartment lines; and 8) sealing-off (allowing to die) and shedding tissues/organs that are unable to maintain health.” Under extreme conditions of intensity or duration or both, drought stress can kill trees, but exactly how is not well defined. Two hypotheses of how tree death occurs in response to drought have been frequently recognized (McDowell *et al.* 2008): (1) the *carbon-starvation hypothesis* states that when stomata close, photosynthesis stops, resulting in a carbohydrate deficit in metabolizing living tissues and eventual starvation and death of a tree, and (2) the *hydraulic-failure hypothesis* states that cavitation of the water column in the xylem leads to desiccation of tree tissues and eventual tree death.

Trees display many mechanisms to avoid drought impacts. Drought avoiders close their stomata under low moisture, whereas drought endurers continue to

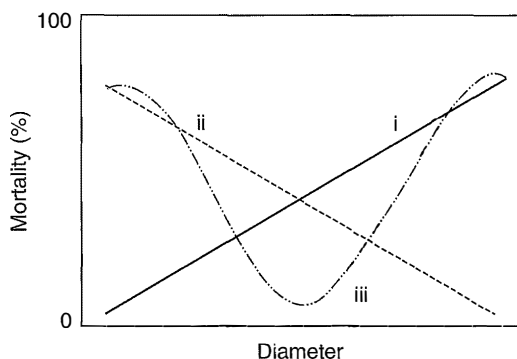


Figure 7.1 Stylized curves corresponding to various patterns of mortality reported in studies of drought in forest stands. The curve marked i, for example, shows heaviest mortality in larger diameter classes. The curve marked ii shows just the opposite with heaviest mortality occurring in the smallest diameter classes. Curve iii shows peaks of mortality in both the small and large diameter classes.

transpire. Certain species are more vulnerable than others, and in mixed stands, these species tend to be replaced by more drought-hardy trees.

The relationship between tree age and drought-associated mortality depends on many interacting variables, including among others: intensity and duration of the drought event/s, previous drought history, topography, species, stand structure, and previous harvest history. Studies examining the impacts of drought on age distribution have shown that drought can have a major impact on mortality and that usually trees of either young or old ages or both die during extreme drought episodes (Mueller *et al.* 2005). The small root volume of seedlings and young trees limits their ability to acquire soil water, making them relatively vulnerable to drought damage or death. Large trees require more water to maintain their relatively large crowns, making these age classes also relatively vulnerable to drought damage or death.

The interaction of drought, diameter class, and tree mortality has been recently studied in many different forest types worldwide. Mueller *et al.* (2005) examined the effects of age on mortality during a severe summer drought in 2003 in pinyon-juniper woodlands in the southwestern USA. They found that mortality impacts differed between the two co-dominant tree species (*Pinus edulis* and *Juniperus monosperma*), and that mortality was positively correlated with diameter (Figure 7.1i). The authors speculate that because *P. edulis* was more severely impacted than *J. monosperma*, the latter would eventually gain dominance in affected stands, resulting in a species shift at the stand level. Nepstad *et al.* (2007) came to the same conclusions when they examined drought effects on mortality of tropical forest stands in experimental dry and wet plots in the

Amazon basin in Brazil (Figure 7.1i). In contrast, following droughts in 1985 and 1994, Lloret *et al.* (2004) reported more mortality among smaller trees than larger (i.e., older) trees in holm oak (*Quercus ilex*) forests in Spain (Figure 7.1ii). Vygodskaya *et al.* (2002) describe mortality of both small and large trees in *Picea abies* forests of the southern taiga in Russia over a 30-year observation period (Figure 7.1iii). Slik (2004) found a disproportionate number of dead trees in large diameter classes and an increase in abundance of newly established small diameter classes in drought-stricken dipterocarp forests in Borneo (Figure 7.1ii to 1iii). These studies illustrate how drought can have a significant effect on age class distribution, and that the effects vary among different forest ecosystems.

A third hypothetical mechanism for drought-caused tree mortality is the *biotic agent demographic hypothesis*, which states “drought drives changes in demographics of mortality agents that subsequently drive forest mortality” (McDowell *et al.* 2008). The direct effects of drought leading to mortality are usually minor compared to the indirect effects that result from enhanced vulnerability to other abiotic stresses, insect pests, and pathogens, or other secondary disturbances (Rouault *et al.* 2006). The effects on age class distribution depend on the nature, extent, and magnitude of these interactions within a complex environment.

Textbox 7.1 Drought, forest dieback, and bark beetles in Western North America

Conifers such as piñon pine, ponderosa pine, lodgepole pine, and Engelmann spruce died in large numbers throughout western North America as a consequence of an historically severe drought in 2000–2004. On the Colorado Plateau alone, 1.5 million ha of piñon pine and 1.0 million ha of ponderosa pine were affected by drought-catalyzed population increases of piñon ips (*Ips confusus* [LeConte]) and a complex of *Dendroctonus* spp. and *Ips* spp., respectively (CIRMOUNT Committee 2006). Over a longer time period centered on this turn-of-the-century drought, nearly 15 million ha of lodgepole pine were killed in Alberta and British Columbia by the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (Nealis and Peter 2008). In the San Bernardino Mountains of southern California, Grulke, *et al.* (2009) report a long-term correlation between below-average annual precipitation and regional pest report records of bark beetle outbreaks in the mixed conifer forest, dominated by Coulter, Jeffrey, and ponderosa pines (Figure 7.2). The mechanism that explains the role of drought stress and successful colonization, reproduction, and population increase by bark beetles on conifers is an area of intensive study.

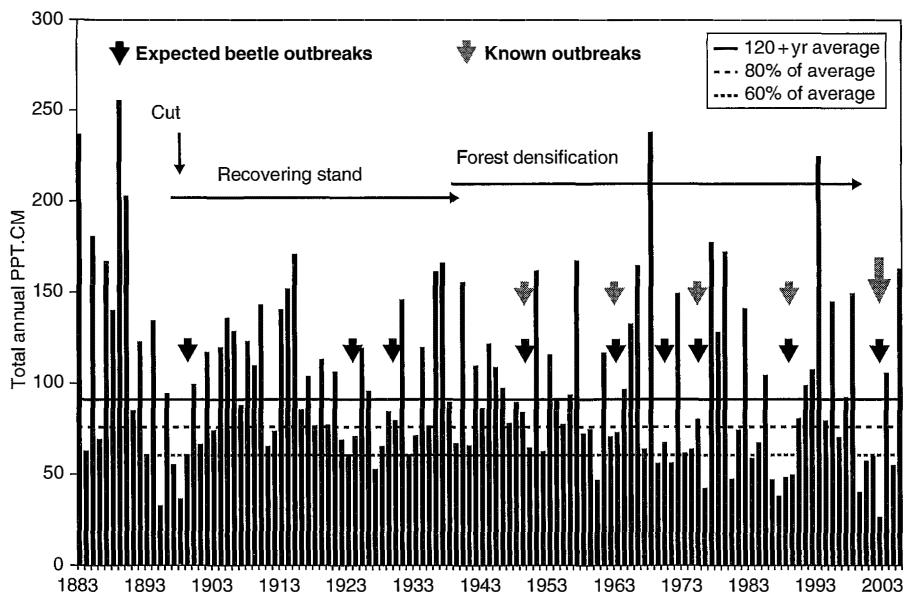


Figure 7.2 Long-term (123 yr) precipitation record from the Big Bear Dam in the eastern San Bernardino Mountains, CA, USA. Total annual precipitation (hydrological year, Oct. 1 to Sept. 30) in cm is shown along the y-axis. The long-term average (96 cm) is indicated with a solid line. Periods of three- to four-years of moderate drought stress (<80% of the average, dashed line) are common; periods of extreme drought stress (<60% of the average, dotted line) often were coincident with bark beetle outbreaks. Known occurrences of bark beetle outbreaks (grey triangles) were documented in annual California Pest Reports (1949 to present). (From Grulke *et al.* 2009, with permission.)

7.2.2 Wind storms

Windthrow is the uprooting of trees by the wind, and **windfall** occurs when a tree is thrown down or stems are broken off by the wind (Natural Resources Canada 1995). Windfall also describes the area on which trees have been thrown down or broken by the wind. In some areas of the world, wind is the dominant natural disturbance shaping forest stand structure (see front and back covers). In the coastal temperate rain forests of southeastern Alaska, for example, frequent small-scale wind events cause treefall gaps and patches (Figure 7.3), which are a major determinant of the structure of these forests (Deal *et al.* 1991, 2002; Nowacki and Kramer 1998). These highly frequent events result in small to moderate-sized gaps (less than 20 ha) in this forest type, but large blowdowns do sometimes occur. For example, on Prince of Wales Island in 1968, partial and complete blowdown of over 1000 patches (each 0.8 to 56 ha) merged in a single major wind event (Harris 1989). In contrast, large-scale



Figure 7.3 Uprooted white spruce following wind storm in Alaska. Photo by J. E. Lundquist.

windthrow events that create large clearings are more frequent than treefall gaps in tropical forests subjected to hurricane-force winds (Lugo and Scatena 1996). In Nicaraguan forests, for instance, windfall from Hurricane Joan affected 80% of the canopy trees in an area of 500 000 ha (Boucher 1990; Tanner and Kapos 1991), and on the island of Dominica in the Caribbean, windfall from Hurricane David killed about 5 million trees (Lugo and Scatena 1996). In the northern hemisphere, straightline winds, or derechos, that are associated with severe thunderstorms cause significant losses of trees in areas not affected by hurricanes. Here, we focus the discussion on small- to moderate-scale wind events.

Not all forest stands are equally susceptible to wind damage. The impacts of wind events on diameter distribution depend upon endogenous factors like species composition and stand structure, and on exogenous factors like scale (extent or magnitude), frequency (return time), intensity, and severity of each disturbance (Lorimer 1977; Canham and Loucks 1984; Whitney 1986; Frelich and Lorimer 1991; Peterson and Pickett 1991; Frelich and Reich 1995; Palik and Robl 1999). Furthermore, risk to wind damage is a scale-dependent property = tree size and tree species are important at the stand scale, topography site and stand factors at the landscape scale, and rainfall and wind speed at the regional scale (Xi *et al.* 2008). Shorohova and his coworkers (2008) showed that damage by severe winds often increases with increasing evenness of unharvested white spruce stands in northern Europe and with increasing average stem diameter.

Evans *et al.* (2007) showed that stand structure, average tree age, mean elevation, range of elevations across stands, topographic position, and placement with respect to neighboring stands were significant factors predicting wind impacts in over 1000 disturbance gaps and patches following the 2003 ice storm in eastern North America (see next section). Several models have been developed to predict wind damage in forest stands (Kenderes *et al.* 2007; Kamimura and Shiraishi 2007; Zeng *et al.*, 2007; Gardiner *et al.* 2008; Xi *et al.*, 2008; Kamimura *et al.* 2009; and many others). One model developed by Ancelin *et al.* (2004) predicts that mortality is differentially distributed among sizes and species in irregular stands, but uniformly distributed in uniform stands, and that the most susceptible trees were small diameter, tall, and with small crowns. A common prediction among these models is that risk to wind damage varies in space and time across forest landscapes, and this is reflected in the spatial heterogeneity of stand structure.

Textbox 7.2 Impact and interaction of windthrow and other factors on stand structure in unharvested boreal forests

McCarthy and Weetman (2007) examined the diversity of stand structures in previously unharvested balsam fir stands in Newfoundland at various times following succession resetting infestations of spruce budworm (*Choristoneura fumiferana*) and the hemlock looper (*Lambdina fuscicollis*). They identified four different stand structures based on diameter distributions (Figure 7.4): (1) Modal distributions were composed of a uniform cohort of trees established soon after a stand-replacing event; (2) Bimodal distributions were composed of gaps in the canopy of a uniform overtopping layer of trees with established regeneration; (3) Reverse-j distributions representing trees with a range of diameters and is commonly associated with old-growth; and (4) Bi-staged distributions where widely scattered dominant individuals overtopped a dense layer of regeneration. Windthrow along with minor insect herbivory, and root and stem pathogens played a major role. According to McCarthy and Weetman (2007), stands with a bimodal distribution “are beginning to break-up from partial insect herbivory, windthrow, and butt and root rots, and show irregular tree distributions. Given time, and the absence of stand-replacing insect disturbance, these stands may develop into ‘true old-growth’. Some of the old reverse-j stands and all of the irregularly structured bimodal stands are probably the product of this process transition from modal to bimodal to reverse-j distributions.”

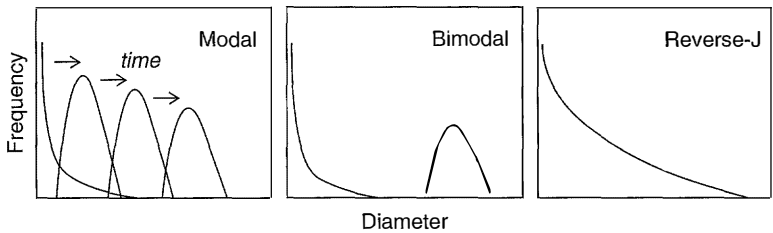


Figure 7.4 Stylized curves based on the study by McCarthy and Weetman (2007) showing chronosequence of stand structure changes following a major stand replacing event.

Light to moderate wind events commonly cause little impact on age distribution. In fact, these events may serve to speed up stand succession. Rich *et al.* (2007), for example, examined the influence of tree species, age, diameter, and intensity of wind events on wind-driven patterns of mortality in unharvested stands in the southern boreal forest in Minnesota. Rates of mortality were higher in mature stands less than 125 years old. Of the nine species examined, early successional and shade-intolerant species were most susceptible to being killed, and shade-tolerant least. The authors concluded that these patterns support the role of wind in accelerating succession, and use the term “wind-induced weeding” to describe this phenomenon.

Wind events commonly interact with other disturbance agents (Gandhi *et al.* 2007; 2009). When this happens, the impacts on age class distribution can result from the interaction in unanticipated ways. Uprooted trees cause soil disturbance, exposure of rocks, and root damage to neighboring trees. Broken trees contribute dead branches, stems, and stressed or moribund broken standing trees to the **coarse woody debris** (CWD) pool, which may increase the risk and potential impacts of wildfires. Heavy rains may amplify a wind-caused disturbance by loosening soil allowing extensive uprooting of trees (Foster 1988). Uprooting of trees during a wind event significantly alters the physical and chemical properties of the soil through mixing of soil layers (Mueller and Cline 1959; Bormann *et al.* 1995), and creation of pit-and-mound topography (Lyford and MacLean 1966). Because pits and mounds are generally preserved for a long time, they may affect tree regeneration for a correspondingly long time (Schaetzl *et al.* 1989; Oliver and Larson 1996), and thus enhance and enlarge frequency among smaller diameter classes. Many kinds of insects and pathogens sustain their populations in wood fallen during wind events, and some of these are induced to outbreak levels when windthrow levels are severe (Gandhi *et al.* 2007, 2009). Interactions of wind with other disturbance agents can be complex, leading to what has been termed “ecological surprises” (Peterson and Leach 2008), with resulting impacts on diameter distribution that are difficult to generalize.

7.2.3 Ice damage

Ice storm damage occurs when supercooled precipitation creates layers of ice (glaze) on leaves, twigs, branches, and boles (Lemon 1961; Irland 1998; 2000). Impact on individual trees depends on the thickness of the ice layers. The weight of ice borne by tree crowns during an ice event may increase the weight of twigs 30-fold (Hauer *et al.* 1993; Irland 1998). Oliver and Larson (1996) estimate that a 15 m-tall conifer with a mean crown width of 6 m can accumulate 5 tons of ice during a severe storm. Ice storms occur primarily in eastern North America (Lemon 1961). From 1900 to 1960, two to eight minor ice storms were recorded each decade in the eastern USA (Irland 1998). The recurrence time of 20 to 100 years for major ice storms in eastern North America makes them more frequent than all other weather-related disturbances (Irland 1998, 2000). Proulx and Greene (2001), for instance, state that ice storms caused around 50% of all mortality of canopy trees in northern forests in Quebec, and that this type of disturbance is the most frequent among all disturbances, including insect pests and tree pathogens, wildfires, and wind damage.

Tree damage is related to tree species, size and crown position, crown architecture, tree age and conditions, and site characteristics, especially slope, aspect, soil texture and depth (Rhoads *et al.* 2002). Mortality results from stem snap and root upwelling. Stem breakage depends on the weight of the ice, the arrangement of the branches, and wood strength (Lemon 1961). Broad-crowned trees with large stem diameters are more susceptible to ice storm damage than those with smaller diameters (Hauer *et al.* 1993). Most damage results from mechanical damage like twig, branch, and bole breakage, and uprooting. Ice thicknesses of 5–10 mm cause breakage of smaller branches; thicknesses of 10–25 mm cause breakage of healthy young branches and even the stems of young trees (Lemon 1961).

Textbox 7.3 Effects of the 1998 ice storm in eastern North America

A severe and widespread ice storm in January 1998 affected an area of 2000 × 400 km in South-central Canada and the northeastern USA. This major weather event and the ensuing research response marked a major increase in our knowledge of this type of disturbance on the dynamics of stand structure (Duguay, *et al.* 2001; Hooper, *et al.* 2001; Rhoads, *et al.* 2002; Hopkin, *et al.* 2003; Lafon and Kutac 2003; Shortle, *et al.* 2003; Lafon 2004; Millwood and Kraft 2004; Aril, *et al.* 2007; Takahashi, *et al.* 2007). Severity and patterns of impact varied among forest type and location. Conifers were less damaged than hardwoods (Hopkin, *et al.* 2003). Rhoads,

Textbox 7.3 (cont.)

et al. (2002) noted the inconsistency in key factors causing damage among storms and locations. Lafon (2004), however, suggested that some common damage patterns occurred, specifically, (1) loss of smaller diameter trees (Figure 7.1ii), which could create a pulse of an overdense age class, (examples presented in Chapter 1); and (2) loss of canopy in larger overstory trees (Figure 7.1i), which could facilitate late succession understory tree species or allow an increased establishment of early successional tree species (Figure 7.1iii). In a study of even-aged northern forest mixed hardwoods, Rhoads, *et al.* (2002) concluded that stands younger than 15–20 years were much less vulnerable to ice damage than older stands, and that ice damage was age-related. Takahashi, *et al.* (2007) examined an old growth beech-maple forest in eastern Canada nearly a decade after the 1998 ice storm and found that although basal area in the recovering forest was reduced by 37% and tree density decreased 61%, the species composition or diameter class distribution changed little or not at all. Aril, *et al.* (2007) found that canopy cover thinned from 93% to 83% immediately following an ice storm in beech-maple forests in eastern USA, but canopies recovered after three years, which was too soon for overstory-intolerant species to become established in *Acer-Fagus* forests.

7.3 Fire

Fire is a ubiquitous disturbance agent that operates at many spatial and temporal scales. Fire-associated mortality is a function of forest type, development stage, and fire intensity; other disturbance agents can exacerbate the effects of fire. Even large, intense fires have a role in maintaining healthy forests, despite their role in causing extensive tree mortality.

7.3.1 Fire regimes and ecosystems

Fire effects are best assessed in terms of the parameters of the **fire regime**; including fire frequency, predictability, extent, magnitude (intensity and/or severity), timing, and potential synergistic effects on future disturbances (Heinselman 1981; White and Pickett 1985; Agee 1993). A fire regime typifies the historical role of fire for a particular ecosystem, and emphasizes the complexity with which fire interacts with ecosystem patterns and processes. Heinselman developed a system of classifying fires that attempts to characterize this complexity using fire frequency and magnitude:

0. Very little natural fire
1. Infrequent (> 25 years between successive fires) light surface fires
2. Frequent (< 25 years between successive fires) light surface fires
3. Infrequent severe surface fires
4. Combined frequent severe surface fires and crown fires (25 to 100 years between fires)
5. Combined infrequent crown fires and severe surface fires (100 to 300 years between fires)
6. Infrequent (> 300 years) crown fires and severe surface fires

Subsequent researchers (Davis *et al.* 1980; Johnson and Van Wagner 1985; Davis and Mutch 1994) have refined Heinselman's classification to better describe particular ecosystems or regions; however, Heinselman's classification has the flexibility to address fire regimes globally.

Many forest ecosystems are characterized as being adapted to fire (Pyne 1995; Jurskis 2005). Various plant species have developed the ability to survive fires by means of traits, such as thick bark or regeneration following fires by sprouting or cone serotiny (Rowe 1981). Such traits are not adaptations to fire, *per se*, but to a particular fire regime. The regime serves as a coarse filter that selects for certain species while eliminating others. To persist under a particular fire regime, plants require traits that enable them to complete their life cycle (Gill 1981). To persist under a fire regime characterized by lethal high-intensity fires, plants must achieve sexual maturity within the interval between successive fires or be able to regenerate vegetatively by sprouting. For example, lodgepole pines (*Pinus contorta*) produce viable seed within a decade of germination, and their cones often require the heat of a fire to release seed; oaks re-sprout after being killed back to the root collar; and many shrubs in fire-prone environments develop lignotubers or have seeds that require scarification by fire prior to germination.

Distinguishing between intensity and severity is important to characterize the effects of fire on forest ecosystems. **Intensity** is the energy output of a fire, and is a function of the energy content of the fuel, the amount of fuel consumed, and the rate of fire spread. Fire intensity is measured as the amount of energy released per unit length of the fireline. **Fire severity** is its ecological impact, and is most often measured as a percentage of overstory mortality.

7.3.2 Large-scale fire

Agee (1990, 1993) described three levels of fire severity that are useful in characterizing the extent to which a particular fire matches or deviates from the average for a particular fire regime. Low-severity fires remove less than 20% of

the basal area, whereas high-severity fires kill 70% or more of the basal area. Fires of moderate severity fall between these endpoints. Differences in forest composition and structure result in fires of similar intensities having dissimilar severities (mortality).

Different fire regimes result in different spatial and temporal patterns of tree mortality at a variety of spatial scales. High-severity fires remove most of the basal area and leave few to no survivors. Very large high-intensity fires, such as those typical of boreal regions, are also high-severity fires in that mortality levels are high because trees do not have traits that allow them to survive high-intensity burns. Unburned areas within landscape-scale fires may actually increase with increasing fire size (Eberhart and Woodward 1987). Light wind-blown seeds that can travel great distances over crusted snow quickly regenerate burned-over areas to a single age cohort. Thus, fire in the boreal forests of North America and Eurasia is a landscape-scale phenomenon with periodic high mortality levels and resultant single age classes at large spatial scales.

Topography combines with fire regime to mitigate or exacerbate fire effects at smaller spatial scales (Camp *et al.* 1997). High-severity fires in topographically complex landscapes are constrained by areas that contain less abundant fuels or fuels too wet to ignite. Poulos *et al.* (2007) mapped fuels across large landscapes in western Texas and Mexico, and found topographic differences in fuel amounts that could alter patterns of fire intensity and thus tree mortality. Steep slopes accelerate fire spread and decrease the aspect duration of fire, often allowing some trees to survive. Age classes in topographically complex landscapes will mirror the complexity of burn patterns, resulting in a mosaic of age classes (Flanagan *et al.* 1998).

Use of age or size-class distributions to evaluate the health of forests in fire-prone regions must consider inherent fire regimes and their corresponding effect on forest age and structure (Ryan 2002; Wallenius 2002). Moderate-severity fire regimes have been less studied than high and low-severity regimes. Vegetation patterns in moderate-severity fire regimes are complex given the wide range of fire intensities and return intervals (but see Schellhaas *et al.* 2000; Pennanen 2002). The persistence of more species with different traits and life cycle requirements is potentially high; thus, a larger distribution of age classes would be expected, especially over longer temporal scales. Multiaged forests with age/size distributions approaching a reverse-J shape are more typical of low-severity fire regimes (Peterson and Ryan 1986; Johnson 1992). Low-severity fires proportionally damage more young and late-successional species.

When a wildfire moves through a forest stand, it can kill all of the trees if it is especially intense. But more commonly it will kill only a proportion of the trees, and leave the rest singed and scarred but able to recover, at least partially. Some

survivors may be able to supply critical seed crops. Several species-specific equations have been developed to predict the probability of mortality of individual survivors (Hood *et al.* 2007). For example:

$$P_m = \frac{1}{-(-6.8243 + 0.000568PCLC^2 + 0.6688CKR - 0.0285DBH)1 + 1 + e}$$

where:

P_m = probability of survival;

$PCLC$ = percentage of crown length scorched;

CKR = cambium kill rating (percentage of the cambium killed around the circumference at the base of the tree);

DBH = diameter at breast height.

7.3.3 Changing fire regimes

Understanding inherent fire regimes is essential to properly assessing the impact of fire on forest health. Changes to historical fire regimes alter forest development patterns, including the establishment, growth, and mortality of trees. Removal of fire as a forest process may increase forest complexity, and give rise to reverse-J age/size distributions. However, forests that historically were maintained under a particular fire regime often become less healthy with removal of fire (Hessburg *et al.* 1994; Covington *et al.* 1997; Allen *et al.* 2002). In the absence of fire, forests shift in composition, leading to changes in future fire regimes and in the patterns of mortality from other disturbances, particularly disease and insect outbreaks. Fires, especially low-intensity frequent fires, maintain low forest density by killing seedlings and small trees. With fewer individuals competing for moisture and other resources, these forests are more resilient to other disturbances. Changes in fire intensity or recurrence are more likely to result in decreased forest resilience and persistence. In the western coterminous USA a complete set of statistics has been collected for every wildfire from 1970–2003. Westerling *et al.* (2006) concluded following a thorough analysis of data from all 1116 large (greater than 400 ha) wildfires that there had been a sudden and dramatic increase in the frequency and duration of large wildfires, and that the wildfire season had become extended. Wildfires were four times more frequent and extended over six times the land area for 1987–2003 compared to 1970–1986.

7.3.4 Fire suppression

Fire suppression has created forest health problems. Studies of eucalyptus decline in Australia (Jurskis 2005) and oak decline in Arkansas (Guyette *et al.* 2006) implicate fire exclusion as a contributing factor in decline. See also

the textbox on fusiform rust in Chapter 4. In interior western North America, increased forest density resulting from fire exclusion has exacerbated forest health problems associated with drought (Guarin and Taylor 2005; Fule 2008), bark beetles (Klenner *et al.* 2008; Fonseca-Gonzales *et al.* 2008), herbivores (Swetnam and Lynch 1993; Veblen *et al.* 2000; Ryerson *et al.* 2003), and root disease pathogens (Thies 2001 Parker *et al.* 2006). Mortality resulting from these disturbance agents along with increased complexity in forest structure resulting from fire exclusion that increased the vertical and horizontal contiguity of fuels, predisposed stands to large, intense (and severe) fires.

Aboriginal peoples used fire to manage their environment. It is often difficult to differentiate between the effects of natural and anthropogenic fire on ecosystems. In some instances, fire-adapted ecosystems developed because anthropogenic activities favored plants with traits that conferred a competitive advantage under frequent burning. The original human inhabitants of Australia and western North America used fire extensively over millennia, giving rise to ecosystems adapted to the frequency and magnitude of their burning (Pyne 1995). More recently, fires were excluded from ecosystems previously adapted to periodic fires. Livestock grazing eliminated the grasses that carried fires across the landscape. Roads also broke up fine fuel continuity, decreasing fire size and spread. Direct fire suppression was effective when fuel levels were low, but now suppressing fires under extreme weather conditions in forests choked by decades of fuel buildups is impossible. Humans still affect fire regimes through fire use and fire suppression. In tropical forests that may have historically burned only once or twice a millennium and then only during severe ENSO (El Niño–Southern Oscillation) periods, agricultural conversion and population pressure have greatly increased fire frequency. In the Brazilian Amazon, anthropogenic burning of previously forested land to increase pasture productivity has led to fire incursion into adjacent rain forest. Together with logging, fire increases the vulnerability of tropical forests to future burning (Goldammer 1999); however, multiple fires so reduce fuel loads that in some cases this vulnerability dampens over time.

7.3.5 Intensifying fire regimes

Various factors influence fire frequency and severity including geographic location, forest type, elevation band, previous land-use history, and temperature and precipitation patterns. In the western USA, the factor with the greatest influence on fire frequency and severity was spring temperatures. Specifically, unusually warm spring temperatures coupled with reduced precipitation and earlier snowmelt dates caused drought conditions and more rapid and thorough drying of coarse woody debris and other forest fuels. The moisture

equilibrium relationship between dead woody tissue and the ambient air is fairly clear, but the relationship between low soil moisture and tree mortality is not. It often takes three to four consecutive drought years before conifer mortality rates increase in most western forests (N. Grulke, Research Plant Pathologist, USDA Forest Service, Pacific Southwest Research Station, Riverside, California, pers. comm.). Background mortality rates have increased in recent decades in 76 unmanaged forests older than 200 years in the western USA (van Mantgem *et al.* 2009). Increases in mortality also are appearing widely across elevations, tree sizes, dominant genera, and past fire histories. Forest density and basal area declined slightly suggesting that increasing mortality was not caused by endogenous increases in competition. Because mortality increased in small trees, the overall increase in mortality rates cannot be attributed solely to aging of large trees. From the 1970s to 2006 in these 76 plots, the mean annual temperature of the Western United States increased at a rate of 0.3 to 0.4°C per decade. May this be the dominant contributor to the increases in tree mortality rates across the region?

7.3.6 Impacts of wildfires

From a utilitarian forest health perspective, a fire event well within inherent fire regime parameters, may still result in an “unhealthy” condition, if postfire forest structure no longer meets societal expectations (management objectives). For example, the much publicized 1988 Yellowstone fires in the western USA were well within historical parameters but the public outcry curtailed all efforts to restore the role of fire in ecosystem sustainability. Infrequent, high-intensity fires are generally considered catastrophic because the forests are unable to recover. Although many recent fires across the globe have resulted in extreme loss of property, damage to infrastructure, and even loss of human life, they are not necessarily without historical precedent (Strauss *et al.* 1989; Gill and Grant 2008; Keane *et al.* 2008).

In the Mediterranean Basin, large fires were common during the late Quaternary (Carrion *et al.* 2003). But in the current human-dominated and more frequently ignited landscape, fire may pose an ecological threat (Pausas 2008). Although coastal shrub ecosystems and oak forests are resilient to a higher incidence of fire, pine woodland ecosystems are less able to recover from frequent fire; especially problematic are the effects of fire on highly erodible soils. In some cases, vulnerability to fire in the Mediterranean Basin is a by-product of millennia of questionable land use policies (see Chapter 8).

Extreme fires in *Nothofagus* forests within historical ranges of variability for the region occurred in southern Argentina and Chile during the last two decades (Kitzberger and Veblen 1997; Veblen *et al.* 1999), underscoring the need

to understand their historical antecedents and the role of fire. These fires were associated with droughts, and not just with more recent colonial land management practices. Nonetheless, the forest health consequences from current large, intense fires are exacerbated by increased fuel flammability resulting from natural forest conversion to exotic conifer plantations (Veblen *et al.* 2008). More frequent ignitions resulting from human incursion into wildlands is also increasing forest vulnerability to fire. The rain forests of Southeast Asia were thought to be immune to the effects of natural fires. The fires that did occur were a direct result of recent logging and land conversion. But more recent evidence has shown that these forests burn only during extreme ENSO events (Goldammer 1993; Hope *et al.* 2005). During the ENSO events of 1982–83 and 1997–98, continental and insular Southeast Asia experienced extreme droughts accompanied by extensive fires. In Kalimantan, the fires burned as much as 5 million ha during each event (Malingreau *et al.* 1985; Siebert *et al.* 2001). For fire to occur, even with extreme drought, there must be a source of ignition. Burning for land clearing adjacent to intact rain forest may play an important role. Small fires at the periphery of the HKK Wildlife Sanctuary in Thailand became the burning front that ignited hundreds of square kilometers of forest in January 1998 (Baker *et al.* 2008). Even where fire intensity was low, fire severity was extremely high, likely the result of rain forest trees lacking fire-adapted traits (Baker *et al.* 2008). Increased fire frequency in these non-adapted forests could lead to loss of both plant and animal biodiversity. A recent prolonged drought in Australia has led to large, high-intensity fires with loss of property and life (McLeod 2003), leading to the conclusion that burn severity was uniformly high (Bowman 2003), and that such fires were negatively impacting forest health and biodiversity (Hardy 2005). Although some areas within the fires' perimeters did experience high-severity burning, other areas were less impacted (Bradstock 2008).

7.3.7 Increased frequency of less-intense fires also impacts forest communities

A decrease in *Pinus cembra* populations in the European Alps is consistent with 20th-century increases in fire frequency. In other forest types, fire frequency is decreasing (Heyerdahl *et al.* 2007), allowing the incursion of species less adapted to frequent fires. As described above, the resulting increase in forest density greatly affects forest health, especially during dry periods.

7.4 Air pollution

The air pollutants of primary concern to forest health are acid deposition and ozone. Acid deposition increases soil acidity, affects nutrient availability, and weakens the ability of plants to withstand disturbances such as drought,

winter freezing, and pest outbreaks (Shortle and Smith 1988; de Hayes *et al.* 1999; Driscoll *et al.* 2001; Schaberg *et al.* 2001). In sensitive populations and at high concentrations, acid deposition also causes direct foliar injury (Siccama *et al.* 1982; Craig and Friedland 1991; Zeng *et al.* 2005; Fischer *et al.* 2007). High levels of ozone (O_3) can be toxic to plants, causing cellular damage resulting in foliar injury and consequent growth reduction (Augustaitis and Bytnerowicz 2008).

7.4.1 Acid deposition

The primary ingredients of **acid deposition** are sulfur dioxide (SO_2), a by-product of burning coal, and nitrogen oxides (NO_x) emitted from burning fossil fuels. Both react with oxygen and water in the atmosphere to form strong, highly water-soluble acids. These acids are readily removed from the atmosphere with precipitation, and disassociate in the soil solution as hydrogen (H^+), sulfate (SO_4^{2-}) and nitrate (NO_3^-) ions. The resulting decrease in pH causes plant nutrients, such as the bivalent cations (calcium [Ca^{2+}]) and (magnesium [Mg^{2+}]) to leach from the soil, and mobilizes toxic cations, such as aluminum (Al^{3+}) (Likens and Borman 1995; Driscoll *et al.* 2001; Puhe and Ulrich 2001).

Global critical loads of nitrogen and sulfur deposition have been modeled to identify forest areas sensitive to acid deposition (Bouwman *et al.* 2002). According to this model, areas with low temperatures, dry soil conditions, long frost periods, and low base saturation have high-sensitivity (Bouwman *et al.* 2002). Critical loads of acidity are exceeded in most of Europe, eastern North America, southeastern Brazil and the La Plata region, parts of Siberia, the southern part of West Africa, Central Africa, and South China (Tao and Feng 2000).

Acid deposition affects forests at three levels: (1) individual plant, (2) sensitive species and populations, and (3) ecosystem. Specific effects on forest health include direct foliar injury, growth reduction, nitrogen fertilization, increased susceptibility to other stressors, heavy metal toxicity, and nutrient impoverishment (deHayes *et al.* 1999; Schaberg *et al.* 2001; Bytnerowicz *et al.* 2007, among others). Nonetheless, there is little evidence of direct cause and effect between acid deposition alone and any of these factors (Driscoll *et al.* 2001). In all cases, acid deposition acts within a complex of stressors including climate change, drought, insects, diseases, and other air pollutants.

Plant-level effects. Acid deposition can cause acute, direct foliar injury and crown damage especially harmful to conifers, which cannot withstand extensive defoliation (Craig and Friedland 1991; deHayes *et al.* 1999; Schaberg *et al.* 2001; Fischer *et al.* 2007). In nitrogen-limited systems, such as most temperate forests, nitrogen deposition may act as a fertilizer; however, excess nitrogen can lead to

deficiencies in other nutrients, particularly calcium (Driscoll *et al.* 2001). Acid deposition may interfere with calcium and magnesium nutrition and calcium-dependent processes, although the mechanisms are poorly understood (Schauberg *et al.* 2001; Puhe and Ulrich 2001). Nutrient deficiencies can lead to increased susceptibility to other stressors and disturbances, fine root decline (Puhe and Ulrich 2001; Park *et al.* 2008), aluminum toxicity (Puhe and Ulrich 2001), and growth reduction.

Sensitive species. Most published research about acid deposition and forest effects has been conducted in the northeastern United States and Europe, although there have been studies in Asia as well. Extensive work has been done in the United States on high-elevation red spruce (*Picea rubens*) in northern New England, which experienced high mortality in the 1980s (Siccama *et al.* 1982). Exposure to acidic mist and cloud water may have reduced the cold tolerance of red spruce by leaching membrane-associated calcium from the needles causing increased susceptibility to winter freezing (de Hayes *et al.* 1999; Driscoll *et al.* 2001).

Episodic sugar maple (*Acer saccharum*) dieback over large areas of northwestern Pennsylvania and southwestern New York has been attributed to acid deposition in combination with other stressors (Drohan *et al.* 1999; Horsley *et al.* 1999; Driscoll *et al.* 2001). It is hypothesized that dieback was caused in part by depletion of nutrient cations from marginal soils (Horsley *et al.* 1999; and Chapter 6).

Scots pine (*Pinus sylvestris*) defoliation has been attributed to acid deposition in Lithuania (Augustaitis and Bytnerowicz 2008), and high sulfate deposition is significantly related to higher defoliation in Norway spruce (*Picea abies*) and Scots pine in Europe (Puhe and Ulrich 2001).

Ecosystems. The most significant effect of acid deposition on forests is a change in soil chemistry. Increased input of H^+ from dissolved acids increases soil acidity, decreases availability of nutrient cations, and mobilizes toxic metals (Driscoll *et al.* 2001; Bailey *et al.* 2005). Addition of nitrogen in previously nitrogen-limited forest ecosystems can cause a decline in mycorrhizae populations and inhibition of nitrogen fixation (Parrent *et al.* 2006, also see Chapter 6). Cation depletion may result in a decreased productivity. However, the added nitrogen may act as a fertilizer in the short term. Increased nitrogen may improve foliage nutrition thus increasing insect herbivory (Throop and Lerdau 2004). Complex interactions between resource availability, climate change, acid deposition, ozone pollution, and other forms of disturbance will determine productivity; changes in nutrient status are just part of the equation. Some mosses, lichens, and phytopathogenic fungi are highly sensitive to SO_2 . Decline in populations of these species could significantly affect productivity in boreal and alpine forest ecosystems (Harden *et al.* 1997).

Species composition may change in ecosystems where sensitive species have a higher than baseline mortality rate. There is generally a long ecosystem response time to environmental stresses such as air pollution. Studies have not yet shown widespread ecosystem changes that can be attributed to air pollution, except in areas of high deposition from point sources, such as smelters and dirty-coal-burning power plants (Munton 2002; Bernal-Salazar *et al.* 2004). Where species experience decline and higher than baseline mortality, age class distribution will shift to a younger cohort, providing that adequate advance regeneration is present. At the ecosystem level, age class distribution may or may not change depending on the extent of species decline, the change in baseline mortality of sensitive species, the mix between sensitive and non-sensitive species at the stand and landscape scales, and the mosaic of species composition and structure across the landscape.

7.4.2 Ozone

Ozone is formed in the atmosphere through the interaction of nitric oxide (NO), sunlight, and hydrocarbons, and is highest in areas with high levels of both sunlight and fossil fuel emissions. Such areas include the southwestern and eastern USA, eastern Europe, the Mediterranean, western Asia, and north-eastern China (Felzer *et al.* 2007). It is projected that 50% of the northern hemisphere forests will be affected by toxic levels of ozone by 2100 (Fowler *et al.* 1999).

Plant-level effects. Damage from current ambient ozone levels on northern hemisphere trees causes crown defoliation, and reduced leaf area, tree height, diameter growth, and root-shoot ratios, with consequent loss of photosynthetic capacity and lower biomass production (Skärby *et al.* 1998; Felzer *et al.* 2007; Augustaitis and Bytnerowicz 2008; Wittig *et al.* 2009). Ozone enters with water through stomata, causing direct cellular damage. Drought may reduce risk of O₃ injury because plants close stomata under moisture stress (Wittig *et al.* 2007). Populations are most sensitive when peak ozone concentrations coincide with the growing season and no moisture stress.

Sensitive species. Sensitive species in the United States include certain genotypes of eastern white pine (*Pinus strobus*), trembling aspen (*Populus tremuloides*), southern pines, black cherry (*Prunus serotina*) (Karnosky *et al.* 2007) and western pines (Richardson *et al.* 2007; Bytnerowicz *et al.* 2008). Ambient ozone levels have been associated with growth reduction in mature southern pines, particularly loblolly pine (*Pinus taeda*) (Felzer *et al.* 2007). In Europe, Aleppo pine (*Pinus halepensis*) in the Mediterranean Basin as well as Swiss stone pine (*Pinus cembra*) in the timberline ecotone of the European mountains have shown signs of ozone damage (Richardson *et al.* 2007). Ozone has been implicated in reduced stem growth of Scots pine in Central Europe (Augustaitis and Bytnerowicz 2008).

Several pine species in Mexico show ozone-induced damage similar to pines in the western United States (Richardson *et al.* 2007).

Ecosystems. Where species experience decline and higher mortality than baseline mortality, age-class distribution will shift to a younger cohort, so long as there is adequate advanced regeneration. If the disturbance is chronic, mortality will remain higher than baseline.

7.5 Large-scale infrequent disturbances

Disturbances are a natural part of every forest ecosystem. Some occur at more or less predictable intervals, and occur over limited areas; others (e.g., hurricanes, volcanic eruptions, floods) occur rarely, or at irregular intervals, or both, and over large areas. The latter have been termed “**large infrequent disturbances (LIDs)**”. Whether LIDs qualitatively differ from small-scale disturbances, or are only quantitative extensions of the latter is a debated topic (Romme *et al.* 1998). Some well-known and well-studied LID examples are the Mount St Helens eruption in 1980, the Yellowstone wildfires in 1988, floods along the Mississippi in 1993, and the spruce beetle outbreaks on the Kenai Peninsula in the mid-1990s.

7.5.1 Tropical storms

Tropical storms are large-scale extreme wind events. Meteorologists classify them based on their scale, wind intensity, and location. Some of the more common definitions based on windspeeds are: tropical depression (winds less than 61 kph), and tropical storm (winds between 61 and 119 kph). There are several equivalent terms for storms with the higher wind velocities: hurricanes (North Atlantic Ocean, the northeast Pacific Ocean east of the dateline, or the South Pacific Ocean east of 160°E); typhoons (northwest Pacific Ocean west of the dateline); severe tropical cyclones (southwest Pacific Ocean west of 160°E or southeast Indian Ocean east of 90°E); severe cyclonic storms (Indian Ocean and tropical cyclones in the southwest Indian Ocean).

These latter storms can cause catastrophic tree mortality in both tropical and temperate forests, where the width of catastrophic damage is usually limited to the width of the eyewall (where the most damaging winds and most intense rain occur), which rarely exceeds 50 km (Foster and Boose 1994). The amount of forest area affected by catastrophic wind events at locations such as the Luquillo Mountains of Puerto Rico, for example, is actually less than background mortality of wind events when return times and frequency of events are factored in (Lugo and Scatena 1996). Other catastrophic wind events have eyewalls that approach the entire width of the Caribbean islands they impact, such as the track of Hurricane Gilbert over Jamaica in 1988 (Wunderle *et al.* 1992). In addition, the

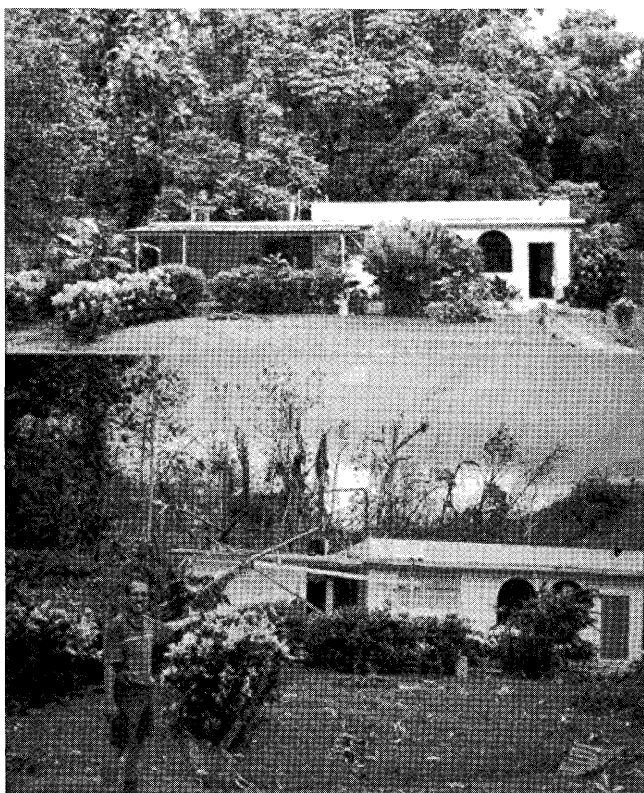


Figure 7.5 Effect of Hurricane Georges in 1988 on forest canopy in Sabana, a valley closest to the point of landfall in El Yunque National Forest of Puerto Rico. Note the heterogeneity of damage due to embedded meteorological events and topographic exposure in the lower, post-hurricane photo. Mortality from treefalls occurred on steep unstable slopes just behind the building, whereas the larger trees behind them on the ridge that were either delimbed or topped mostly survived and recovered. Photo by D. J. Lodge.

long tracks of some hurricanes can induce catastrophic wind damage in forests in widely separated areas. Hurricane Gilbert struck both Jamaica and the Yucatan Peninsula (Whigham *et al.* 1991; Wunderle *et al.* 1992); Hurricane Hugo damaged forests in Guadeloupe (Benito-Espinal and Benito-Espinal 1991), Puerto Rico (Walker 1991; Zimmerman *et al.* 1994; Lugo and Scatena 1996) and South Carolina (Gresham *et al.* 1991); and Hurricane David devastated both Dominica and the Dominican Republic, and then spawned tornado damage in the USA from the middle-Atlantic States to New England in 1979.

Patterns of wind damage, although appearing chaotic when viewed at local scales (Figure 7.5), are controlled by a set of predictive factors (Foster and Boose 1992; Boose *et al.* 1994; Foster *et al.* 1998, 1999). At larger, regional scales (100 to

500 km), patterns of forest damage are determined by hurricane size, intensity, and storm track; weakening of storms through interactions with coastlines and mountains; and regional variation in vegetation. At smaller landscape scales of about 10 km, storm damage is controlled by interactions of gradients in wind speed and direction, embedded meteorological phenomena such as downbursts and tornadoes, topographic exposure, and differential stand susceptibility to wind (Figure 7.5). Stand susceptibility to wind is determined by factors such as site conditions (steep, unstable slopes or shallow rooting owing to waterlogged soils; Figure 7.5) (Basnet *et al.* 1992; 1993; Scatena and Lugo 1995; Everham and Brokaw 1996), and stand structure and composition, both of which are strongly influenced by previous natural and human disturbances (Zimmerman *et al.* 1994, 1995; Foster *et al.* 1998, 1999).

The effects of hurricanes on the diameter distribution of residual forest stands following a storm depend on topographic position, exposure to wind, and previous disturbances. Background tree mortality in tropical forests ranges from ca. 0.5% to 3.5%, with a mean of 1.6% per year (Lugo and Scatena 1996).

Direct mortality from hurricane winds in the Caribbean can be as high as 46%, such as the impact of Hurricane David on Dominica, which killed about 5 million trees in 10 hours (Lugo and Scatena 1996). Bole breaks plus uprooting can be as high as 80% (Tanner and Kapos 1991). Hurricane Joan broke or uprooted 80% of the trees in Nicaragua (Boucher 1990; Yih *et al.* 1991), and Hurricane Hugo caused similar damage to 25% to 55% of the trees in wet forest of Guadeloupe, depending on size class (Benito-Espinal and Benito-Espinal 1991). Generalizations regarding differential damage according to size classes are unreliable and site-specific (Tanner and Kapos 1991) because the effect of hurricane winds on diameter distributions of the residual forest varies greatly depending on wind-speed, the initial forest structure and species composition, previous disturbances, and various state factors previously noted. In tabonuco forests in the Luquillo Mountains of Puerto Rico, catastrophic tree mortality was higher on slopes than on ridges owing to the ability of the dominant trees on ridges to withstand winds (Basnet *et al.* 1993; Scatena and Lugo 1995) and the ability of most trees to resprout (Walker 1991). Stands of uniform, young, flexible trees had little mortality from Hurricane Gilbert in Jamaica (Wunderle *et al.* 1992), Hurricane Hugo in South Carolina (Gresham *et al.* 1991), or Hurricane Georges in limestone forest of the Dominican Republic (Uriarte *et al.* 2004). In contrast, young stands with large remnant trees in human-impacted coastal forests and wet limestone forests with mixtures of large and small trees in Jamaica had disproportionately higher mortality in the intermediate size classes (> 8 to 23 cm diameter) caused by branches falling from the larger trees. Greatest reduction in

intermediate size classes was also observed in the Bisley Watersheds in Puerto Rico, an area with the highest impact by Hurricane Hugo in the Luquillo Mountains because they were closest to the point of landfall and faced directly into the storm winds (50% overall mortality, data of Scatena and Lugo cited in Walker 1991; Basnet *et al.* 1992; Heartsill-Scalley *et al.* 2007). Although the largest trees had the lowest proportion of stems lost of any size class from Hurricane Gilbert on Jamaica (Wunderle *et al.* 1992), Hurricane Hugo in wet forest on Guadeloupe (25% vs. 55%, Benito-Espinal and Benito-Espinal 1991), and Hurricane Hugo on the windward side of Puerto Rico. Walker (1991) found at El Verde on the leeward side of the Luquillo Mountains in Puerto Rico that large trees had proportionately more damage, and Dittus (1985) found that a cyclone that struck Sri Lanka killed disproportionately more canopy than smaller diameter subcanopy trees (46% vs. 29%).

Disturbance history greatly influences damage from hurricanes. For example, clearcutting subtropical wet forest in Puerto Rico about 60 years prior to Hurricane Hugo resulted in stands dominated by fast-growing secondary tree species (especially *Casearia arborea*) that were differentially more susceptible to direct hurricane mortality (Zimmerman *et al.* 1994; Thompson *et al.* 2002). Selective cutting can lead to stands with mixed canopy heights that result in greater mortality of the intermediate diameter classes when exposed to extreme hurricane winds. In addition, fire history can influence damage from subsequent hurricanes. Platt *et al.* (2002) compared mortality from stem breakage and delayed mortality (primarily bark beetle attack) in Everglades slash pine (*Pinus elliotii*) savannas with different fire histories during the decade preceding Hurricane Andrew (1992) in south Florida. Direct mortality from wind and delayed mortality were lowest in stands burned during the wet (lightning fire) season, intermediate in unburned stands, and highest in stands burned during the dry (anthropogenic fire) season.

Hurricane damage to forests is not restricted to wind damage. Wet hurricanes in mountainous terrain are frequently associated with landslides. There were 285 landslides associated with Hurricane Hugo in Puerto Rico, primarily in areas receiving over 200 mm of rain (Scatena and Larsen 1991). In coastal areas, salt intrusion from overwash caused by storm surge often causes longer-lasting effects on forest ecosystems than direct wind damage (Blood *et al.* 1991; Gardner *et al.* 1991; Liu *et al.* 2008). Storm surge in South Carolina from Hurricane Hugo extended several hundred kilometers inland and more than 150 m into the forest from the marsh edge, leading to persistent changes in soil chemistry and structure in addition to direct tree mortality (Blood *et al.* 1991; Gardner *et al.* 1991). Furthermore, hurricane damage to forests in the Caribbean Basin and Gulf Coast frequently predispose these areas to catastrophic fires, which have a

much greater impact on subsequent forest recovery than direct damage from wind (Furley and Newey 1979; Whigham *et al.* 1991; Myers and van Lear 1998; Liu *et al.* 2008).

7.6 Geological events

Landslides, volcanic eruptions, tsunamis, and other geological events can be extraordinarily destructive because they often occur in highly populated locations. **Landslides** are gravity-driven, massive down-slope movements of the landscape. Mudflows, creep, block slide, avalanches, slumps, and other similar events are called landslides. Damage depends on the rate of movement of soil, rock, and other debris, which, in turn, depends on such factors as steepness of the slope, freeze and thaw temperature patterns, amount of water saturation, earth movements, and instabilities caused by recent construction or streambank erosion. Landslides are usually associated with very wet periods with heavy precipitation or rapidly warming times with rapid snowmelt. Impacts differ because the rate and magnitude of movement differ. Debris flow is a type of landslide commonly referred to as mudflows/slides or lahars. Areas where forest vegetation has been destroyed by wildfires are particularly susceptible to landslides following rainstorms. Debris flows can be extremely destructive when caused by volcanic activity. Landslides can cause severe, sometimes complete, loss of vegetation and concurrent extreme impacts of diameter class distribution and thus sustainability, but the spatial scales are usually limited, and have little impact on the overall diameter distribution forest-wide.

Volcanic eruptions range from explosive blasts with volcanic dust and rock (tephra) to gurgling lava spreading locally. The former, referred to as felsic volcanoes, can influence forest ecosystems for great distances by spreading tephra, which settles on the landscape surface, eventually working its way into the soil. The latter, referred to as mafic volcanoes, are associated with flowing basaltic lava that smothers and burns any and all vegetation in its path, covering existing soils to varying depth, but impacting only nearby forest ecosystems. Some volcanoes have characteristics of both the mafic and felsic types. Perhaps the most well-known and well-studied recent example is Mount St. Helens in Washington State in the western USA. Forested areas near the volcano were leveled by the blast. The diameter class distribution within these areas were changed dramatically, if only locally (Weber *et al.* 2006) – health, as defined in Chapter 1, is obviously a scale-dependent phenomenon. The vast amounts of tephra belched by this volcano stimulated a great deal of research on the impacts of this substance on forest ecosystems. Impacts ranged from restricting photosynthesis by coating leaf surfaces and reducing light to causing tree mortality.

The impacts of tephra are broadly distributed across tree diameter classes and probably have little impact on diameter distribution or basal mortality.

Coastal mangrove forests and tsunamis have a unique relationship to forest health. Tsunamis highlight the important role played by coastal forests, and the value to human health and property serviced by sustained health of these ecosystems. **Tsunamis**, or tidal waves, are created by geological events above or beneath the sea that cause a rapid displacement of water. Powerful earthquakes, underwater landslides, or other causes of mass movements of earth and water can cause exceptionally big tsunamis that can cross oceans creating waves thousands of miles away from the source. The distance between waves of a tsunami can be many miles and much longer than wavelengths of common wind-generated waves, which are usually measured by hundreds of feet. When a tsunami meets the shoreline, its height is modest but its persistence is long. The power embedded in a tsunami and the huge amount of water that it carries provide the potential for great damage. Coastal forests can mediate the effects of tsunami. The ability to reduce impacts of the tsunami is a function of stem density, stem diameter, wave period, path width, and inundation depth.

Textbox 7.4 Tsunami protection by coastal forests in Sumatra

On December 26, 2001, a tsunami washed ashore on Sumatra. By the time the ocean settled, over 300 000 people had perished. Coastal mangrove forests were less impacted than other areas along the coast (Tanaka 2009). Gaps in this forest amplified flow rates of water and debris, which damaged buildings and other physical assets and harmed and killed people. A 30% attenuation occurred in forest groves where tree density was 0.2 trees/m² and average diameter at breast height was 15 cm under a 30-minute wave period. The mediating effect of the forest was reduced when inundation depth was greater than 3 m, and nearly lost when it exceeded 10 m. The impact of the Sumatra tsunami on coastal forest health varied and depended on the interacting characteristics of the inundation and the forest. Stem diameters in mangrove forests were related to survival of trees (Yanagisawa, *et al.* 2009). Diameter distributions in these forests were affected because smaller diameter trees were less likely to survive than larger trees. Specifically, trees with diameters between 25 and 30 cm had a 72% chance of survival, whereas those with diameters between 15 and 20 cm had only a 19% chance of survival. With a decreased frequency of small diameter classes, mid-sized classes will be reduced in the future. The tsunami created an unhealthy condition where forests were affected.

7.7 Emergent stressors in a changing climate

Climate is the average of weather phenomena over a period of time, usually 30 years (IPCC 2007). Many believe that the climate is changing. In many regions of the world, the last several decades have shown weather patterns not inconsistent with climate change. During this time, a significant increase in mean global temperature has been reported (CIRMOUNT 2006). Many believe that this trend will continue for the foreseeable future. Although tropical forests are not immune from effects of climate change, northern boreal and sub-boreal forests are expected to be most affected (IPCC 2001; Wunderle *et al.* 2009). A changing climate would lead to novel ecosystems (Hobbs *et al.* 2006), increased frequency and intensity of disturbances (Dale *et al.* 2001; Emanuel 2005; Hoyos *et al.* 2006; Klotzbach 2006), and unanticipated impacts on stand structure (IPCC 2001). Insect pests, diseases, and other stress agents, for example, would become increasingly prevalent as vegetation readjusts itself to new climatic norms, and would facilitate and catalyze these adjustments largely by killing stressed trees and other vegetation. Descriptions of the potential effects of climate change on forest insect pests and diseases have appeared (e.g., Williams and Liebhold 1995; Ayres and Lombardero 2000; Kliejunas *et al.* 2008). Many more have been published for specific forest host-pest-disease systems.

Although climate change usually is portrayed as increasing temperature, or global warming, the phenomenon actually expresses itself in many other ways as well. Along with a changing temperature, acid rain, precipitation, UV-B radiation, metal deposition, tropospheric ozone, atmospheric carbon dioxide, and other climatic attributes are changing also (Valladares 2008). The phenomenon called climate change is a truly multivariate phenomenon.

Climatic factors are pervasive in time and space, occur on spatial scales not normally perceived by humans, and are thus outside of our day to day experience. Therefore, evidence of a changing climate effects on forest health is difficult to document. In some forests, wildfires occur earlier and more frequently, severe droughts persist longer (IPCC 2001), thaw-freeze events are more frequent and widespread, bark beetle and defoliator outbreaks are more frequent and severe, and decline diseases and other complex multiple-agent diseases are more common and widespread, and more difficult to diagnose (Jurskis 2005). Many believe that these occurrences are connected to a changing climate (Dale *et al.* 2001).

Deforestation and other changes in land use can affect local or regional climate, which in turn can affect forest health, especially at higher elevations. Conversion of forest to pasture in lowland Costa Rica was associated with changes in cloud forests. Such local or regional climate changes can interact

with global climate change with loss of cumulus cloud formation during the dry season and lifting of the cloud base in adjacent mountain ranges (Lawton *et al.* 2001). Conversion of coastal forest to pasture on the island of Puerto Rico disrupted the advective flow of moisture from the Atlantic Ocean thereby reducing cloud formation at higher elevation (Scatena 1998; Schellekens *et al.* 2000; Van der Molen 2002). Such local or regional changes will likely exacerbate the effects of increased summer drying in the Caribbean and Central American region brought about by global climate change (Neelin *et al.* 2006), and result in a contraction or extirpation of cloud forests on tropical mountains. Loss of cloud forests may already be occurring in Central America (Foster 2001; Benning *et al.* 2002), and global climate change is expected to reduce the extent of cloud forests in biodiversity hotspots of the Andes (Bush *et al.* 2004) and Hawaii (Benning *et al.* 2002).

Emerging stressors in a changing climate are illustrated below by drought in the boreal forest, yellow cedar decline in coastal temperate forests of south-eastern Alaska, and intensifying fire regimes in tropical forests.

7.7.1 Boreal drought

The boreal forest occupies an area of not less than 1.2 billion ha equivalent to approximately 17% of the Earth's land surface, and occurs between 45° and 70° N latitude (Larsen 1980). One-third of this forest is in Central and western Alaska and in Canada from the Yukon Territory to Labrador. The rest is in Eurasia from northern Europe across Siberia to the Pacific Ocean. The major trees include various species of larch (*Larix*), spruce (*Picea*), fir (*Abies*), birch (*Betula*), poplar (*Populus*), willow (*Salix*), and alder (*Alnus*). This forest biome is expected to experience the greatest impacts of climate change sooner than forest biomes southward (ICPP 2001). Temperature is a limiting factor of tree distribution in the boreal forest. Atmospheric temperatures are expected to increase significantly in the northern portion of the boreal forest (IPCC 2001). Growth rates of trees are expected to increase because photosynthesis is correlated with increasing temperature. Indeed, many studies indicate that growth and tree species distribution is increasing and expanding in the boreal zones (Myneni *et al.* 1997; Sturm *et al.* 2001). Other studies, however, indicate otherwise (Chapin *et al.* 2006a).

The relationship between tree growth and survival and global warming in the boreal region is more complicated than it appears. According to Soja *et al.* (2006), "Despite its relative simplicity, boreal forest composition results from a complex interaction between climate, solar radiation, topography, geology, nutrient availability, soil moisture, soil temperature, permafrost, depth of forest floor organic layer, ecology of species, forest fires, and infestations." Trees growing in

certain locations in boreal Alaska, particularly those on north-facing slopes, actually showed a decreased growth rate with increasing summer temperatures (Barber *et al.*, 2000; Lloyd and Fastie 2002; Wilmking *et al.* 2004). The cause of this growth decline is not perfectly known, but it is assumed that evapotranspiration during the summer warm season is greater than the precipitation replenishing the water used, creating moisture stress, a condition that some have referred to as “boreal drought” (Chapin *et al.* 2006b).

Textbox 7.5 Impacts of drought on aspen stands in the prairie provinces of Canada

The northern forest is expected to migrate northward as the climate changes. It is less appreciated that the southern fringes of this forest will become a zone of increasing stress to resident trees. Some of these populations are expected to recede northward and to be eliminated from the ecotone by invading southern species and by stress-related insect pests and pathogens. Trembling Aspen has a widespread distribution across North America and is a dominant tree species in prairie woodlots in the western Canadian interior at the northern fringe of the Great Plains. A 300% increase in aspen mortality rate and 30% reduction in growth rate followed a severe drought here in 2001–02. Variation in productivity was positively correlated to site conditions, as measured by climate moisture index and mineral soil silt content, and negatively correlated to insect feeding, which included defoliation by the large aspen tortrix (*Choristoneura conflictana*) and wood boring by the poplar borer (*Saperda calcarata*), the flatheaded borers (*Agrilus liragus* and *Dicercas* spp.), and the ambrosia beetle (*Trypodendron retusum*). Mortality, in turn, was strongly correlated to drought severity (measured by minimum annual climate moisture index). Regeneration apparently does not replace the more mature aspen trees lost. In this case, aspen will eventually no longer be sustainable in this ecosystem.

7.7.2 Shifting vegetation zones

Many climate change impact forecasts are based on complex computer models, which predict existing forest vegetation will expand into new environments displacing current residents. Predicting patterns, extent, and rates of these shifting tree distributions is vital to forest managers who need to make decisions about adapting to and mitigating these impacts. Climatic envelope modeling is one method of predicting the future distributions of organisms under a changing climate (Berry *et al.* 2002). With this method, climatic factors associated with

current distributions are used to project distributions under different climate change scenarios. As community members differ in their threshold response levels, phenotypic plasticity characteristics, genetic diversity, resilience to change, adaptability to new habitats, competitive abilities, and other invasive abilities, intact communities are not likely to move in concert (Bazzaz *et al.* 1995). Instead, different organisms will survive, migrate, or recover at different rates or not at all. New stresses likely will confront these organisms, especially at the moving fronts. In these ecotones, novel pathosystems will determine patterns of death for different species in different stand types.

Textbox 7.6 Yellow cedar decline in Alaska

Yellow cedar is a valuable tree species in southeast coastal Alaska that has been dying since the late 1800s. Mortality of this long-lived tree species has occurred over an area of approximately 200 000 ha. Alaska is the northern edge of its range. Southward, this species is limited to higher elevations. In affected stands, 70% or more of the trees are affected. The condition was first noticed in 1909, subsequently continuing with a noticeable increase after 1970. Dead trees remain standing for up to 100 years, creating what can be called a ghost forest. Affected trees grow at low elevations in soils that stay wet for extended periods mostly on south and west slopes. Mortality is distributed where snow accumulations are limited and winter temperatures are relatively warm. Determining the etiology of this decline required efforts over nearly 30 years by a diverse range of experts. At first, various biotic agents including pathogens and insect pests were examined. Later, the cause was found to involve a complex interaction of abiotic factors and timing and has been explained as follows. “Yellow cedar trees growing on poorly drained soils have shallow roots. Exposure on these wet sites is created from open canopy conditions that allow for solar radiation to warm soil and shallow roots. Canopy exposure also promotes rapid temperature fluctuation and more extreme cold temperatures. Premature dehardening of roots due to warmer springs and earlier melting and less abundant snow pack coincide resulting in root freezing as the primary injury mechanism (Hennon, *et al.* 2008).

7.7.3 Intensifying fire regimes in tropical forests

Periodic climate oscillations influence fire intensity and duration, especially in the tropics. The most powerful of these is the Pacific Decadal Oscillation, also known as the El Niño Southern Oscillation (ENSO). During an El Niño event,

a significant rise in temperature occurs over a large (approximately 15 000 000 km²) portion of the western tropical Pacific Ocean, and this condition lasts 6 to 18 months. El Niño phenomena occur approximately three to seven years apart (Drollette 2005), alternating with a condition of extreme cooling in the central and east-central Pacific, a condition known as La Niña. During an El Niño year, severe drought occurs in Australia, Indonesia, and the Philippines as high-pressure cells develop over the northern part of these land masses creating persistent hot and dry conditions. El Niño events also affect weather in western North America by raising temperatures, but its effects on wildfire in that region are unclear because rising temperatures also are accompanied by increased rainfall (Miller *et al.* 2009; Westerling *et al.* 2006). The intensity of El Niño events has been increasing in the last half century, and the severity of the droughts associated with them intensifying (Slik 2004).

Wildfires in Australia during El Niño events have become legendary for their intensity and size. The most recent of these occurred in 2009. Fortunately, a majority of the fire-adapted Australian tree species have special mechanisms that allow them to survive or reforest quickly during or following fire. For example, some of the eucalyptus species possess thick bark, white bark (which allows the reflection of heat), an ability to sprout from epicormic branches under the bark of trunks and limbs, the regrowth from lignotubers, and an ability to produce copious amounts of seed with a genetic constitution geared for rapid growth soon after germinating in the nutrient-rich natural seed-bed left in the wake of these fires (Costermans 1983). The impacts of climate change combined with El Niño years remains to be seen. Responses to massive ENSO-related forest fires in dipterocarp forests of Indonesia have been quite different, resulting in massive deforestation and lack of regeneration. A graphic example from the Island of Kalimantan is described in the case study below.

Textbox 7.7 El Niño-related fire causing deforestation on the Kalimantan Island, Indonesia

Drought associated with the ENSO is the “most significant” type of natural catastrophic disturbance” in Borneo (Harrison 2001). Wildfires precipitated by drought can significantly impact stand structure and sustainability. In late 1982 and early 1983, a major El Niño event caused extensive fires in Southeast Asia. The fires on East Kalimantan Island in Borneo were permitted to burn until rains returned the following year. Many of the fires were in old-growth dipterocarp forests that require shade for regeneration; conditions destroyed by the fires. The high intensity and

Textbox 7.7 (cont.)

large extent of these fires (up to 12 500 km²) eliminated viable seed sources for regeneration. The grasses and mosses that colonized the burns provided neither food nor perches to potential seed dispersers such as birds and bats, limiting forest regeneration even near the forest edge. Small diameter classes were restricted, and the change in diameter distribution significantly varied from baseline mortality pattern that challenged the sustainability of the current structure in affected stands. After 10 years without forest regeneration, the Indonesian government granted forest concessions to companies that established nurseries and regenerated forest in exchange for a tax-free portion of the profits on subsequent harvest of the new timber. Although four tree nurseries were established beginning in 1991, no suitable native species were available for this task. *Pinus caribaea* was planted on one small area (50 000 ha) of acid sands. All other soils and climates required hardwoods. Among the successful species were a few eucalypts, *Gmelina arborea*, *Acacia mangium*, and *Paraserianthes (Albizia) falcataria*. The hope was that after just a few rotations of these pioneer species the original “climax,” shade-requiring species could be successfully reintroduced. The strategy has worked well in some parts of the tropics (Parrotta 1993; Parrotta, *et al.* 1997).

7.8 Conclusion

The abiotic disturbance factors examined above represent only a small sampling of the many different abiotic stresses that exist in forests. Numerous studies have addressed the impacts of abiotic disturbances on some aspect of stand structure, but few examine the impact on diameter distributions across the entire range of size classes. Nonetheless, available studies clearly show that these factors can significantly influence diameter and age class distributions during the life of a forest. They also emphasize that trees growing in the forest interact simultaneously with a multitude of disturbances and other types of ecological processes, and that distribution, scale, patterns, and magnitude in time and space vary among these different processes, which often, but not always interact in complex ways. Comparing observed mortality to baseline mortality is a potentially useful way of sorting out the relative impacts of different abiotic factors on sustainability of forest ecosystems, and an operationally useful way of defining, assessing, and monitoring forest health.

Although each specific case will have its own specific cause and affect characteristics, some general principles about the impacts of abiotic disturbances on stand structure and diameter/age distribution can be proposed:

- (1) Larger diameter trees are more exposed to exogenous mortality agents, like strong wind and temperature shift events.
- (2) Stands with an uneven-age/diameter composition have a lower risk of catastrophic damage due to abiotic disturbances.
- (3) Impact and health are scale-dependent properties. Small-scale disturbances can be catastrophic if they impact valuable management objectives. Relevant scale depends on management objectives.
- (4) Severe large-scale disturbances usually leave patches of pre-existing vegetation, which act as biotic legacies for future stand development.
- (5) Mild or moderate and uniformly distributed disturbances can impact diameter distribution by enhancing conditions for regeneration, usually by thinning overstory crown density.
- (6) Abiotic factors interact with other stresses that also can cause trees to die. Because there can be so many interconnected relationships among these factors, determining cause and effect can be complicated.
- (7) Severe storms tend to reset succession; moderate storms tend to speed it up.

References

- Agee, J. K. 1990. The historical role of fire in Pacific Northwest forests. In: *Natural and Prescribed Fire in Pacific Northwest Forests*. Walstad, J. et al. (eds). Oregon State University Press, Corvallis.
- Agee, J. K. 1993. *Fire Ecology of Pacific Northwest Forests*. Island Press, Washington DC, USA.
- Agrios, G. N. 2005. *Plant Pathology*. 5th edition. Elsevier Academic Press, Burlington, MA.
- Allen, C. D., Savage, M., and Falk, D. A. 2002. Ecological restoration of southwestern ponderosa pine ecosystems: a broad perspective. *Ecological Applications* 12: 1418–1433.
- Amatulli, G., Pérez-Cabello, F., and de la Riva, J. 2007. Mapping lightning/human-caused wildfires occurrence under ignition point location uncertainty. *Ecological Modelling* 200: 321–333.
- Ancelin, P., Courbaud, B., and Fourcaud, T. Y. 2004. Development of an individual tree-based mechanical model to predict wind damage within forest stands. *Forest Ecology & Management* 203: 101–121.
- Aril, K. and Lechowicz, M. J. 2007. Changes in understory light regime in a beech-maple forest after a severe ice storm. *Canadian Journal Forest Research* 37: 1770–1776.
- Augustaitis, A. and Bytnerowicz, A. 2008. Contribution of ambient ozone to Scots pine defoliation and reduced growth in the Central European forests: A Lithuanian case study. *Environmental Pollution* 155: 436–445.

- Ayres, M. P. and Lombardero, M. J. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *The Science of the Total Environment* 262: 263–286.
- Bailey, S. W., Horsley, S. B., and Long, R. P. 2005. Thirty years of change in forest soils of the Allegheny Plateau, Pennsylvania. *Soil Science Society of America Journal* 69: 681–690.
- Baker, P. J., Bunyavejchewin, S., and Robinson A. P. 2008. The impacts of large-scale low- intensity fires on the forests of continental South-east Asia. *International Journal of Wildland Fire* 17: 782–792.
- Baker, W. L. 1992. The landscape ecology of large disturbances in the design and management of nature reserves. *Landscape Ecology* 7: 181–194.
- Bale, J. S., Masters, G. J., Hodkinson, I. D., et al. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology* 8: 1–16.
- Barber, V. A., Juday, G. P., and Finney, B. P. 2000. Reduced growth of Alaska white spruce in the twentieth century from temperature-induced drought stress. *Nature* 405: 668–673.
- Brasier, C. M. 1996. *Phytophthora cinnamomi* and oak decline in southern Europe. Environmental constraints including climate change. *Annales Des Sciences Forestieres* 53: 347–358.
- Basnet, K., Likens, G. E., Scatena, F. N., and Lugo, A. E. 1992. Hurricane Hugo: damage to a tropical rain forest in Puerto Rico. *Journal Tropical Ecology* 8: 47–55.
- Basnet, K., Likens, G. E., Scatena, F. N., and Lugo, A. E. 1993. Ecological consequences of root grafting in tabonuco (*Dacryodes excelsa*) trees in the Luquillo Experimental Forest, Puerto Rico. *Biotropica* 25: 28–35.
- Battles, J., Robards, T., Das, A., et al. 2008. Climate change growth on forest growth and tree mortality: a data-driven modeling study in mixed conifer forest of the Sierra Nevada, California. *Climatic Change* 87(Suppl 1): S193–S213.
- Bazzaz, F. A., Jasienski, M., Thomas, S. C., and Wayne, P. 1995. Microevolutionary responses in experimental populations of plants to CO₂-enriched environments: parallel results from two model systems. *Proceedings National Academy Science USA* 92: 8161–8165.
- Beatty, S. W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plants. *Ecology*: 65: 1406–1419.
- Benito-Espinal, F. P and Benito-Espinal, E. 1991. *L'Ouragan Hugo. Genèse, Incidences, Géographiques et Ecologiques su la Guadeloupe*. Les Presses de l'Imprimerie Désormeaux à Fort-de-France, Guadeloupe.
- Benning, T. L., LaPointe, D., Atkinson, C. T., and Vitousek, P. M. 2002. Interactions of climate change with biological invasions and land use in the Hawaiian Islands: modeling the fate of endemic birds using a geographic information system. *Proceedings National Academy Science USA* 99: 14246–14249.
- Bernal-Salazar, S., Terrazas, T., and Alvarado, D. 2004. Impact of air pollution on ring width and tracheid dimensions in *Abies religiosa* in the Mexico City basin. *Iawa Journal* 25: 205–215.
- Berry, P. M., Dawson, T. P., Harrison, P. A., and Pearson, R. G. 2002: Modelling potential impacts of climate change on the bioclimatic envelope of species in Britain and Ireland. *Global Ecology and Biogeography* 11: 453–62.

- Black, M. P., Mooney, S. D., and Haberle, S. G. 2007. The fire, human, and climate nexus in the Sydney Basin, eastern Australia. *The Holocene* 17: 469–480.
- Blood, E. R., Anderson, P., Smith, P. A., *et al.* 1991. Effects of Hurricane Hugo on coastal soil solution chemistry in South Carolina. *Biotropica* 23(suppl.): 348–355.
- Boose, E. R., Foster, D. R., and Fluet, M. 1994. Hurricane impacts to tropical and temperate forest landscapes. *Ecological Monographs* 64: 369–400.
- Bormann, F. H. and Likens, G. E. 1979. Catastrophic disturbance and the steady-state in northern hardwood forests. *American Scientist* 67: 660–669.
- Bormann, F. H., Spaltenstein, H., McClellan, M. H., *et al.* 1995. Rapid soil development after windthrow disturbance in pristine forests. *Journal Ecology* 83: 747–757.
- Boucher, D. H. 1990. Growing back after hurricanes; catastrophes may be critical to rain forest dynamics. *BioScience* 40: 163–166.
- Bouget, C. and Duelli, P. 2004. The effects of windthrow on insect communities: a literature review. *Biological Conservation* 118: 281–299.
- Bouwman, A. F., Van Vuuren, D. P., Derwent, R. G., and Posch, M. 2002. A global analysis of acidification and eutrophication of terrestrial ecosystems. *Water Air Soil Pollution* 141: 349–382.
- Bowman, D. M. J. S. 2003. Australian landscape burning: a continental and evolutionary perspective. In: *Fire in Ecosystems of South-West Western Australia: Impacts and Management*. Abbott, I. and Burrows N. (eds). Backhuys.
- Boykoff, M. 2007. Changing patterns in climate change reporting in United States and United Kingdom media. *Presentation at Carbonundrums: Making Sense of Climate Change Reporting around the World, Reuters Institute for the Study of Journalism and Environmental Change* June 27, 2007.
- Bradstock, R. A. 2008. Effects of large fires on biodiversity in south-eastern Australia: disaster or template for diversity? *International Journal of Wildland Fire* 17: 809–822.
- Bréda, N., Roland, H., Granier, A., and Dreyer, E. 2006. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Annals Forest Science* 63: 625–644.
- Bush, M. B., Silman, M. R., and Urrego, D. H. 2004. 48 000 years of climate change in a biodiversity hotspot. *Science* 303: 827–829.
- Bytnerowicz, A., Arbaugh, M., Schilling, S., *et al.* 2008. Ozone distribution and phytotoxic potential in mixed conifer forests of the San Bernardino Mountains, Southern California. *Environmental Pollution* 155: 398–408.
- Bytnerowicz, A., Omasa, K., and Paoletti, E. 2007. Integrated effects of air pollution and climate change on forests: A northern hemisphere perspective. *Environmental Pollution* 147: 438–445.
- Camp, A., Oliver, C., Hessburg, P., and Everett, R. 1997. Predicting late-successional fire refugia pre-dating European settlement in the Wenatchee Mountains. *Forest Ecology & Management* 95: 63–77.
- Canham, C. D. and Loucks, O. L. 1984. Catastrophic windthrow in the presettlement forests of Wisconsin. *Ecology* 65: 803–809.
- Carrion, J. S., Sanchez-Gomez, P., Mata, J. F., *et al.* 2003. Holocene vegetation dynamics, fire, and grazing in the Sierra de Gader, southern Spain. *The Holocene* 13: 839–849.

- Chakraborty, S. 2005 Potential impact of climate change on plant-pathogen interactions. *Aust. Plant Pathol* 34: 443-448.
- Chakraborty, S., Tiedemann, A. V., and Teng, P. S. 2000. Climate change: potential impact on plant diseases. *Environmental Pollution* 108: 317-326.
- Chapin, F. S. III, Yarie, J., Van Cleve, K., and Viereck, L. A. 2006a. The conceptual basis of LTER studies in the Alaskan boreal forest. In: *Alaska's Changing Boreal Forest*. Chapin, F. S. III, Oswood, M. W., and Van Cleve, K., et al. (eds). Oxford University Press, New York.
- Chapin, F. S. III, Oswood, M. W., Van Cleve, K., et al. (eds). 2006b. *Alaska's Changing Boreal Forest*. Oxford University Press, New York.
- CIRMOUNT Committee. 2006. Mapping new terrain: climate change and America's West. *Report of the Consortium for Integrated Climate Research in Western Mountains (CIRMOUNT)*. Misc. Pub., PSW-MISC-77, Albany, CA. Pacific Southwest Research Station, USDA Forest Service.
- Coakley, S. M., Scherm, H., and Chakraborty, S. 1999. Climate change and plant disease management. *Annual Review Phytopathology* 37: 399-426.
- Coder K. D. 1999. Drought damage to trees. *University of Georgia School of Forest Resources Extension Publication FOR99-010*
- Cohen, D., Dellinger, B., Klein, R., and Buchanan, B. 2007. Patterns in lightning-caused fires at Great Smoky Mountains National Park. *Fire Ecology* 3: 68-82.
- Condit, R., Hubbell, S. P., and Foster, R. B. 1995. Mortality rates of 205 neotropical tree and shrub species and the impact of a severe drought. *Ecological Monographs* 65: 419-439.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302-1310.
- Costermans, L. 1983. *Native Trees and Shrubs of South-eastern Australia*. Weldon, Sydney, Australia.
- Coulson, R. N., Hennier, P. B., Flamm, R. O., et al. 1983. The role of lightning in the epidemiology of the southern pine beetle. *Z. Ang. Entomol* 96: 182-193.
- Covington, W. W., Fule, P. Z., Moore, M. M., et al. 1997. Restoring ecosystem health in ponderosa pine forests of the southwest. *Journal Forestry* 95: 21-29.
- Craig, B. W. and Friedland, A. J. 1991. Spatial patterns in forest composition and standing dead red spruce in montane forests of the Adirondacks and Northern Appalachians. *Environmental Monitoring and Assessment* 18: 129-143.
- Dale, V. H., Joyce, L. A., McNulty, S., et al. 2001. Climate change and forest disturbances. *BioScience* 51: 723-734.
- Davis, K. M. and Mutch, R. W. 1994. Applying ecological principles to manage wildland fire. In: *Fire in Ecosystem Management*. National Advanced Resources Technology Center.
- Davis, K. M., Clayton, B. D., and Fischer, W. C. 1980. Fire ecology of Lolo National Forest habitat types. *USDA Forest Service Gen. Tech. Rep. INT-79*.
- de Hayes, D. H., Schaberg, P. G., Hawley, G. J., and Strimbeck, G. R. 1999. Acid rain impacts on calcium nutrition and forest health-alteration of membrane-associated calcium leads to membrane destabilization and foliar injury in red spruce. *BioScience* 49: 789-800.

- Deal, R. L., Oliver, C. D., and Bormann, B. T. 1991. Reconstruction of mixed hemlock-spruce stands in coastal southeast Alaska. *Canadian Journal Forest Research* 21: 643–654.
- Deal, R. L., Tappeiner, J. C., and Hennon, P. E. 2002. Developing silvicultural systems based on partial cutting in western hemlock-Sitka spruce stands of southeast Alaska. *Forestry* 75: 425–431.
- Deuber, C. G. 1940. The glaze storm of 1940. *American Forests* 46: 210–211, 235.
- Dickson, R. E. and Isebrands, J. G. 1991. Leaves as regulators of stress response. In: *Response of Plants to Multiple Stresses*. Mooney H. A., Winner, W. E., and Pell, E. J. (eds). Academic Press, New York.
- Dittus, W. P. J. 1985. The influence of cyclones on the dry evergreen forest of Sri Lanka. *Biotropica* 17: 1–14.
- Doyle, T. W. 1981. The role of disturbance in the gap dynamics of a montane rain forest: an application of a tropical succession model. In: *Forest Succession Concepts and Application*. West, D. C., Shugart, H. H., and Botkin, D. B. (eds). Springer-Verlag, New York.
- Driscoll, C. T., Lawrence, G. B., Bulger, A. J., et al. 2001. Acidic deposition in the northeastern United States: Sources and inputs, ecosystem effects, and management strategies. *BioScience* 51: 180–198.
- Drohan, P., Stout, S., and Petersen, G. 1999. Spatial relationships between sugar maple (*Acer saccharum* Marsh), sugar maple decline, slope, aspect, and atmospheric deposition in northern Pennsylvania. In: *Sugar Maple Ecology and Health: Proceedings of an International Symposium*. USDA Forest Service, Northeastern Research Station, Radnor, PA, Warren, PA, U.S.A. Horsley, S. B. and Long, R. P. (eds).
- Drollette, D. 2005. Fire down under. *Natural History* 114: 44–50.
- Duguay, S. M., Arie, K., Hooper, M., and Lechowicz, M. J. 2001. Ice storm damage and early recovery in an old-growth forest. *Environmental Monitoring and Assessment* 67: 97–108.
- Eberhart, K. E. and Woodward, P. M. 1987. Distribution of residual vegetation associated with large fires in Alberta. *Canadian Journal Forest Research* 17: 1207–1212.
- Eckberg, T. B., Schmid, J. M., Mata, S. A., and Lundquist, J. E. 1994. Primary focus trees for the mountain pine beetle in the Black Hills. *USDA For. Serv. Res. Note* RM-531.
- Emanuel, K. 2005. Increasing destructiveness of tropical cyclones over the past 30 years. *Nature* 436: 686–688.
- Evans, A. M., Camp, A. E., Tyrrell, M. L., and Riely, E. E. 2007. Biotic and abiotic influences on wind disturbance in forests of NW Pennsylvania, USA. *Forest Ecology & Management* 245: 44–53.
- Everham, E. M. and Brokaw, N. V. L. 1996. Forest damage and recovery from catastrophic wind. *Botanical Reviews* 62: 113–185.
- Felzer, B. S., Cronin, T., Reilly, J. M., et al. 2007. Impacts of ozone on trees and crops. *C. R. Geoscience* 339: 784–798.
- Fischer, R., Mues, V., Ulrich, E., et al. 2007. Monitoring of atmospheric deposition in European forests and an overview on its implication on forest condition. *Applied Geochemistry* 22: 1129–1139.

- Flanagan, P. T., Morgan, P., and Everett, R. L. 1998. Snag recruitment in subalpine forests. *Northwest Science* **72**: 303–309.
- Fonseca Gonzalez, J., Santos Posadas, H. M. D., Llanderal Cazares, C., et al. 2008. Ips and woodborer insects in *Pinus montezumae* trees damaged by fire. *Madera y Bosques* **14**: 69–80. [In Spanish].
- Foster, D. R. 1988. Species and stand response to catastrophic wind in central New England, USA. *Journal Ecology* **76**: 135–151.
- Foster, D. R. and Boose, E. R. 1992. Patterns of forest damage resulting from catastrophic wind in central New England, USA. *Journal Ecology* **80**: 79–98.
- Foster, D. R. and Boose, E. R. 1994. Hurricane disturbance regimes in temperate and tropical forest ecosystems. In: *Wind Effects on Trees, Forests and Landscapes*. Coutts, M. (ed.). Cambridge University Press, New York.
- Foster, D. R., Knight, D. H., and Franklin, J. F. 1998. Landscape patterns and legacies resulting from large, infrequent forest disturbances. *Ecosystems* **1**: 497–510.
- Foster, D. R., Fluet, M., and Boose, E. R. 1999. Human or natural disturbance: Landscape-scale dynamics of the tropical forests of Puerto Rico. *Ecological Applications* **9**: 555–572.
- Foster, P. 2001. The potential negative impacts of global climate change on tropical montane cloud forests. *Earth-Science Reviews* **55**: 73–106.
- Fowler, D., Cape, J. N., Coyle, M., et al. 1999. The global exposure of forests to air pollutants. *Water Air Soil Pollution* **116**: 5–32.
- Frelich, L. E. and Lorimer, C. G. 1991. Natural disturbance regimes in hemlock-hardwood forests of the upper Great Lakes Region. *Ecological Monographs* **61**: 145–164.
- Frelich, L. E. and Reich, P. B. 1995. Spatial patterns and succession in a Minnesota southern-boreal forest. *Ecological Monographs* **65**: 325–346.
- Fule, P. Z. 2008. Does it make sense to restore wildland fire in a changing climate? *Restoration Ecology* **16**: 526–531.
- Furley, P. A. and Newey, W. W. 1979. Variations in plant communities with topography over tropical limestone soils. *Journal Biogeography* **6**: 1–15.
- Gandhi, K. J. K., Gilmore, D. W., Katovich, S. A., et al. 2007. Physical effects of weather events on the abundance and diversity of insects in North American forests. *Environmental Reviews* **15**: 113–152.
- Gandhi, K. J. K., Gilmore, D. W., Haack, R. A., et al. 2009. Application of semiochemicals to assess the biodiversity of subcortical insects following an ecosystem disturbance in a sub-boreal forest. *Journal Chemical Ecology* **35**: 1384–1410.
- Gardiner, B., Byrne, K., Hale, S., et al. 2008. A review of mechanistic modeling of wind damage risk to forests. *Forestry* **81**: 447–463.
- Gardner, L. R., Michner, W. K., Blood, E. R., et al. 1991. Ecological impacts of Hurricane Hugo-salinization of a coastal forest. *Journal Coastal Research* **8**: 301–317.
- Garrett, K. A., Dendy, S. P., Frank, E. E., et al. 2006. Climate change effects on plant disease: genomes to ecosystems. *Annual Review Phytopathology* **44**: 489–509.
- Gill, A. M. 1981. Fire adaptive traits of vascular plants. In: *Fire Regimes and Ecosystem Properties*. USDA Forest Service Gen. Tech. Rep. WO26. Mooney H. A. et al. (eds).

- Gill, A. M. and Grant, A. 2008. Large fires, fire effects and the fire-regime concept. *International Journal Wildland Fire* **17**: 688–695.
- Goldammer, J. G. 1993. Historical biogeography of fire: tropical and subtropical In: *Fire in the Environment: The Ecological, Atmospheric, and Climatic Importance of Vegetation Fires*. Crutzen, P. J. and Goldammer, J. G. (eds). Wiley and Sons, New York.
- Goldammer, J. G. 1999. Forests on fire. *Science* **284**: 1782–1783.
- Gregory, F. A. and Sabat, A. M. 1996. The effect of hurricane disturbance on the fecundity of sierra palms (*Prestoea montana*). *Bios* **67**: 135–139.
- Gresham, C. A., Williams, T. M., and Lipscomb, D. J. 1991. Hurricane Hugo wind damage to southeastern U.S. coastal forest tree species. *Biotropica* **23**: 420–426.
- Grulke, N. E., Minnich, R. A., Paine, T. D., et al. 2009. Air pollution increases forest susceptibility to wildfires: A case study in the San Bernardino Mountains in southern California. In: *Air Pollution and Fire, Developments in Environmental Science*, Vol. 8. Bytnerowicz, A., Arbaugh, M., Riebau, A., and Anderson, C. (eds). Elsevier, Amsterdam.
- Guarin, A. and Taylor A. H. 2005. Drought-triggered tree mortality in mixed conifer forests in Yosemite National Park, California, USA. *Forest Ecology & Management* **218**: 229–244.
- Guyette, R. P., Spetich, M. A., and Stambaugh, M. C. 2006. Historic fire regime dynamics and forcing factors in the Boston Mountains, Arkansas, USA. *Forest Ecology & Management* **234**: 293–304.
- Harden, J. W., Trumbore, S. E., Veldhuis, H., and Stocks, B. J. 1997. Moss and soil contributions to the annual net carbon flux of a maturing boreal forest. *Journal of Geophysical Research-Atmospheres* **102**: 28805–28816.
- Hardy, C. C. 2005. Wildland fire hazard and risk: problems, definitions, and context. *Forest Ecology & Management* **211**: 73–82.
- Harrington R., Fleming, R. A., and Woiwod, I. P. 2001. Climate change impacts on insect management and conservation in temperate regions: can they be predicted? *Agricultural and Forest Entomology* **3**: 233–240.
- Harris, A. S. 1989. Wind in the forests of southeast Alaska and guides for reducing damage. *USDA Forest Service, Pacific Northwest Research Station, Gen. Tech. Rep.* PNW-GTR-244.
- Harrison, R. D. 2001. Drought and the consequences of El Nino in Borneo: a case study of figs. *Population Ecology* **43**: 63–75.
- Hauer, R. J., Wang, W., and Dawson, J. O. 1993. Ice storm damage to urban trees. *Journal Arboriculture* **19**: 187–194.
- Heartsill-Scalley, T., Scatena, F., Estrada, N. C., et al. 2007. Disturbance and long-term patterns of rainfall and throughfall nutrient fluxes in a subtropical wet forest in Puerto Rico. *Journal Hydrology* **333**: 472–485.
- Heinselman, M. L. 1973. Fire in the virgin forest of the Boundary Waters Canoe Area, Minnesota. *Quaternary Research* **3**: 329–382.
- Heinselman, M. L. 1981. Fire intensity and frequency as factors in the distribution and structure of northern ecosystems. In: *Fire Regimes and Ecosystem Properties: USDA Forest Service Gen. Tech. Rep. WO 26*. Mooney, H. A. et al. (eds).

- Hennon, P. E., D'Amore, D. V., Wittwer, D. T., and Caouette, J. P. 2008. In: *Integrated Restoration of Forested Ecosystems to Achieve Multiresource Benefits: Proc. 2007 National Silviculture Workshop*. Gen. Tech. Rep. PNW-GTP73. Deal, R. L. (tech. ed.). Portland OR: USDA Forest Service Pacific Northwest Research Station.
- Hessburg, P. F., Mitchell, R. G., and Filip, G. M. 1994. Historical and current roles of insects and pathogens in eastern Oregon and Washington forested landscapes. *USDA For. Serv. Gen. Tech. Rep. PNW-GTR-327*.
- Heyerdahl, E. K., Lertzman, K., and Karpuk, S. 2007. Local-scale controls of a low-severity fire regime (1750–1950), southern British Columbia, Canada. *Ecoscience* **14**: 40–47.
- Hildebrand, D. 2003. Lightning tracking an important tool in land management and wildland fire suppression. *Vaisala News* **162**: 32–33.
- Hobbs, R. J., Arico, S., Aronson, J., et al. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography* **15**: 1–7.
- Hood, S. M. 2007. Evaluation of a post-fire tree mortality model for western USA conifers. *International Journal of Wildland Fire* **16**: 679–689.
- Hood, S. M., Smith, S. L., and Cluck, D. R. 2007. Delayed conifer tree mortality following fire in California. In: *Restoring Fire-adapted Ecosystems: Proceedings 2005 National Silviculture Workshop*. Gen. Tech. Rep. PSW-GTR-203. Powers, R. F. (tech. ed.). USDA Forest Service, Albany, CA: Pacific Southwest Research Station.
- Hooper, M. C., Arai, K., and Lechowicz, M. J. 2001. Impact of a major ice storm on an old-growth hardwood forest. *Canadian Journal Botany* **79**: 70–75.
- Hope, G., Chokkalingam, U., and Anwar, S. 2005. The stratigraphy and fire history of the Kutai Peatlands, Kalimantan, Indonesia. *Quaternary Research* **64**: 407–417.
- Hopkin, A., Williams, T., Sajan, R., et al. 2003. Ice storm damage to eastern Ontario forests: 1998–2001. *Forestry Chronicle* **79**: 47–53.
- Horsley, S. B., Long, R. P., Bailey, S. W., et al. 1999. Factors contributing to sugar maple decline along topographical gradients on the glaciated and unglaciated Allegheny Plateau. In: *Sugar Maple Ecology and Health: Proceedings International Symposium*. Horsley, S. B. and Long, R. P. (eds). USDA Forest Service, Northeastern Research Station, Radnor, PA.
- Hoyos, C. D., Agudelo, P. A., Webster, P. J., and Curry, J. A. 2006. Deconvolution of the factors contributing to the increase in global hurricane intensity. *Science* **312**: 94–97.
- IPCC (Intergovernmental Panel on Climate Change). 2001. *Climate Change 2001: the Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, New York.
- IPCC (Intergovernmental Panel on Climate Change). 2007. *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, New York.
- IPCC (Intergovernmental Panel on Climate Change). 2007. Summary for policymakers. In: *Climate Change 2007: the Physical Science Basis. Contribution of Working Group 1 to the*

- Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Solomon, S., Qin, D., Manning, M., *et al.* (eds). Cambridge University Press, New York.
- Irland, L. C. 1998. Ice storm 1998 and the forests of the northeast. *Journal Forestry* **96**: 32–40.
- Irland, L. C. 2000. Ice storms and forest impacts. *Science of the Total Environment* **262**: 231–242.
- James, A. and Dupuis, J. 2005. The impacts of brush fires on the vegetation of Dominica. In: *12th Meeting of the Caribbean Foresters*. Weaver, P. L. and González, K. A. (eds). USDA Forest Service, International Institute of Tropical Forestry, Río Piedras.
- Johnson, E. A. 1992. *Fire and Vegetation Dynamics: Studies from the North American Boreal Forest*. Cambridge University Press, Cambridge.
- Johnson, D. W. and Curtis, P. S. 2001. Effects of forest management on soil C and N storage: meta analysis. *Forest Ecology & Management* **140**: 227–238.
- Johnson, E. A. and Van Wagner, C. E. 1985. The theory and use of two fire history models. *Canadian Journal Forest Research* **15**: 214–220.
- Jones, N. 2005. Wildland fires, management, and restoration in Barbados. In: *12th Meeting of the Caribbean Foresters*. Weaver, P. L. and González, K. A. (eds). USDA Forest Service, International Institute of Tropical Forestry, Río Piedras.
- Jurskis, V. 2000. Vegetation changes since European settlement of Australia: an attempt to clear up some burning issues. *Australian Forestry* **63**: 166–173.
- Jurskis, V. 2005. Eucalypt decline in Australia, and a general concept of tree decline and dieback. *Forest Ecology & Management* **215**: 1–20.
- Kamimura, K. and Shiraishi, N. A review of strategies for wind damage assessment in Japanese forests. *Journal Forest Research* **12**: 162–176.
- Kamimura, K., Gardiner, B., Kato, A., *et al.* 2008. Developing a decision support approach to reduce wind damage risk – a case study on sugi (*Cryptomeria japonica* (L.f.) D. Don) forests in Japan. *Forestry* **81**: 429–445.
- Karnosky, D. F., Skelly, J. M., Percy, K. E., and Chappelka, A. H. 2007. Perspectives regarding 50 years of research on effects of tropospheric ozone air pollution on US forests. *Environmental Pollution* **147**: 489–506.
- Katovich, S. A., McDougall, D., and Chavez, Q. 1998. Impact of forest stressors on the tree species of the Nicolet National Forest- past, present and future. *USDA Forest Service, Northeastern Area State and Private Forestry, Forest Health Protection, NA-TP-02-98*.
- Kayll, A. J. 1968. Heat tolerance of tree seedlings. *Proceedings Tall Timbers Fire Ecology Conference* **8**: 89–105.
- Keane, R. E., Agee, J. K., Fule, P., *et al.* 2008. Ecological effects of large fires on US landscapes: benefit or catastrophe. *International Journal of Wildland Fire* **17**: 696–712.
- Keane, R. E., Austin, M., Field, C., *et al.* 2001. Tree mortality in gap models: application to climate change. *Climate Change* **51**: 509–540.
- Kenderes, K., Aszalos, R., Ruff, J., *et al.* 2007. Effects of topography and tree stand characteristics on susceptibility of forests to natural disturbances (ice and wind) in Borzsony Mountains (Hungary). *Community Ecology* **8**: 209–220.
- Kershaw, A. P., Clark, J. S., Gill, A. M., and D'Costa, D. M. 2002. A history of fire in Australia. In: *Flammable Australia: the Fire Regimes and Biodiversity of a Continent*. Bradstock, R. A. *et al.* (eds). Cambridge University Press, Cambridge.

- Kimmins, J. P. 2003. *Forest Ecology*. 3rd edition. Benjamin Cummings Publishing Co., San Francisco, CA.
- Kitzberger, T. and Veblen, T. T. 1997. The influence of humans and ENSO on fire history of *Austrocedrus chilensis* woodlands in northern Patagonia, Argentina. *Ecoscience* 4: 508–520.
- Klenner, W., Walton, R., Arsenault, A., and Kremsater, L. 2008. Dry forests in the southern interior of British Columbia: historic disturbances and implications for restoration and management. *Forest Ecology & Management* 256: 1711–1722.
- Kliejunas, J. T., Geils, B., Micales Glaeser, J., et al. 2008. Climate and forest diseases of western North America: A literature review. White Paper prepared for The Western Wildlands Environmental Threat Assessment Center, Prineville, OR.
- Klotzbach, P. J. 2006. Trends in global tropical cyclone activity over the past twenty years (1986–2005). *Geophysical Research Letters* 33: L10805.
- Krieger, D. J. 2001. *Economic Value of Forest Ecosystem Services: A Review*. The Wilderness Society, Washington DC.
- Kulakowski, D. and Veblen, T. T. 2002. Influences of fires history and topography on the pattern of a severe wind blowdown in a Colorado subalpine forest. *Journal Ecology* 90: 806–819.
- Lafon, C. W. 2004. Ice-storm disturbance and long-term forest dynamics in the Adirondack Mountains. *Journal Vegetation Science* 15: 267–276.
- Lafon, C. W. and 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.
- Larsen, J. A. 1980. The boreal ecosystem. *Physiological Ecology*. Academic Press, New York.
- Larjavaara, M., Kuuluvainen, T., and Rita, H. 2005. Spatial distribution of lightning-ignited forest fires in Finland. *Forest Ecology & Management* 208: 177–188.
- Lawton, R. O., Nair, U. S., Pielke Sr., R. A., and Welch, R. M. 2001. Climate impact of tropical lowland deforestation on nearby montane cloud forests. *Science* 294: 584–587.
- Lemon, P. C. 1961. Forest ecology of ice storms. *Bulletin Torrey Botanical club* 88: 21–29.
- Likens, G. E. and Bormann, F. H. 1995. *Biogeochemistry of a Forested Ecosystem*. 2nd edition. Springer-Verlag New York Inc.
- Liu, K. B., Lu, H., and Shen, C. 2008. A 1200-year proxy record of hurricanes and fires from the Gulf of Mexico coast: testing the hypothesis of hurricane-fire interactions. *Quaternary Research* 69: 29–41.
- Lloret, F., Siscart, D., and Dalmases, C. 2004. Canopy recovery after drought dieback in holm-oak Mediterranean forests of Catalonia (NE Spain). *Global Change Biology* 10: 2092–2099.
- Lorimer, C. G. 1977. The presettlement forest and natural disturbance cycle of Northeastern Maine. *Ecology* 58: 139–48.
- Lugo, A. E. and Scatena, F. N. 1995. Ecosystem-level properties of the Luquillo Experimental Forest with emphasis on the tabonuco forest. In: *Tropical Forests:*

- Management and Ecology*. Lugo, A. E. and Lowe, C. (eds). Springer-Verlag, New York.
- Lugo, A. E. and Scatena, F. N. 1996. Background and catastrophic tree mortality in tropical moist, wet and rain forests. *Biotropica* **28** (suppl.): 585–599.
- Lundquist, J. E. and Hamelin, R. C. (eds.). *Forest Pathology – From Genes to Landscapes*. APS Press, St. Paul, MN, USA.
- Lundquist, J. E. and Negron, J. F. 2000. Endemic forest disturbances and stand structure of ponderosa pine (*Pinus ponderosa*) in the Upper Pine Creek Research Natural Area, South Dakota, USA. *Natural Areas Journal* **20**: 126–132.
- Lyford, W. H. and MacLean, D. W. 1966. Mound and pit relief in relation to soil disturbance and tree distribution in New Brunswick, Canada. *Harvard Forest Paper* 15.
- Major, J. 1951. A functional factorial approach to plant ecology. *Ecology* **32**: 392–412.
- Malingreau, J. P., Stephens, G., and Fellows, L. 1985. Remote sensing of forest fires: Kalimantan and North Borneo in 1982–83 El Niño-Southern Oscillation event. In: *Tropical Forests and the World Atmosphere*. AAAS Selected Symposium 101. Prance, G. T. (ed.). American Association for the Advancement of Science, Washington, DC.
- Manion, P. D. 1991. *Tree Disease Concepts*. 2nd edition. Prentice-Hall, Englewood Cliffs, NJ.
- Manion, P. D., Griffin, D. H., and Rubin, B. D. 2001. Ice damage impacts on the health of northern New York State Forest. *Forestry Chronicle* **77**: 619–625.
- Mann, M. E. and Emanuel, K. A. 2006. Atlantic hurricane trends linked to climate change. *EOS* **87**: 233–244.
- Martin, H. C. and Weech, P. S. 2001. Climate change in the Bahamas? Evidence in the meteorological records. *Bahamas Journal of Science* **5**: 22–32.
- McCarthy, J. W. and Weetman, G. 2007. Stand structure and development of an insect-mediated boreal forest landscape. *Forest Ecology & Management* **241**: 101–114.
- McDowell, N., Pockman, W. T., Allen, C. D., et al. 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? *New Phytologist* **178**: 719–739.
- McLeod, R. 2003. *The inquiry into the operational response to the January 2003 bushfires*. Australia Capital Territory Government report prepared for Chief Minister. Canberra.
- Millenium Ecosystem Assessment. 2005. *Ecosystems and Human Well-Being: Synthesis*. Island Press, Washington DC, USA.
- Miller, J. D., Saafford, H. D., Crimmins, M., and Thodes, A. E. 2009. Quantitative evidence for increasing forest fire severity in the Sierra Nevada and Southern Cascade Mountains, California and Nevada, USA. *Ecosystems* **12**: 16–32.
- Miller, M. J. and Smolarkiewicz, P. K. 2008. Predicting weather, climate, and extreme events. *Journal of Computational Physics* **227**: 3429–3430.
- Miller, R. M. and Lodge, D. J. 2007. Fungal responses to disturbance—Agriculture and Forestry In: *The Mycota, IV, Environmental and Microbial Relationships*. 2nd edition. Esser, K., Kubicek, P., and Druzhinina, I. S. (eds). Springer-Verlag, Berlin.

- Millward, A. A. and Kraft, C. E. 2004. Physical influences of landscape on a large-extent ecological disturbance: The northeastern North American ice storm of 1998. *Landscape Ecology* 19: 99–111.
- Mueller, O. P. and 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.
- Mueller, R. C., Scudder, C. M., Porter, M. E., et al. 2005. Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. *Journal Ecology* 93: 1085–1093.
- Munton, D. 2002. Fumes, forests and further studies: environmental science and policy inaction in Ontario. *Journal of Canadian Studies* 37: 130–163.
- Myers, R. K. and van Lear, D. H. 1998. Hurricane-fire interactions in coastal forests of the south: a review and hypothesis. *Forest Ecology & Management* 103: 265–276.
- Myneni, R. B., Keeling, C. D., Tucker, C. J., et al. 1997. Increased plant growth in the northern high latitudes due to enhanced spring time warming. *Nature* 386: 698–702.
- Natural Resources Canada. 1995. Silvicultural terms in Canada. *Natural Resources Canada, Canadian Forest Service*. 2nd edition. Ottawa.
- Nealis, V. and Peter, B. 2008. Risk assessment of the threat of mountain pine beetle to Canada's boreal and eastern pine forests. *Natural Resources Canada, Canadian Forest Service, Information Report BC-X-417*, Victoria, British Columbia.
- Neelin, J. D., Münnich, M., Su, H., et al. 2006. Tropical drying trends in global warming models and observations. *Proceedings National Academy Science USA* 103: 6110–6115.
- Negri, A. J., Burkardt, N., Golden, J. H., et al. 2005. The hurricane-flood-landslide continuum. *Bulletin American Meteorological Society* 86: 1241–1247.
- Nepstad, D. C., Tohver, I. M., Ray, D., et al. 2007. Mortality of large trees and lianas following experimental drought in an Amazon forest. *Ecology* 88: 2259–2269.
- Nowacki, G. J. and Kramer, M. G. 1998. The effects of wind disturbance on temperate rain forest structure and dynamics of southeast Alaska. *USDA Forest Service, Pacific Northwest Research Station, Gen. Tech. Rep. PNW-GTR-421*.
- Oliver, C. D. and Larson, B. C. 1996. *Forest Stand Dynamics*. John Wiley and Sons, Inc., New York.
- Palik, B. J. and Robl, J. 1999. Structural legacies of catastrophic windstorm in a mature Great Lakes aspen forest. *North Central Research Station Res. Pap. NC-337*, St. Paul, MN.
- Park, B. B., Yanai, R. D., Fahey, T. J., et al. 2008. Fine root dynamics and forest production across a calcium gradient in northern hardwood and conifer ecosystems. *Ecosystems* 11: 325–341.
- Parker, T. J., Clancy, K. M., and Mathiasen, R. L. 2006. Interactions among fire, insects, and pathogens in coniferous forests of the interior western United States and Canada. *Agricultural and Forest Entomology* 8: 167–189.
- Parrent, J. L., Morris, W. F., and Vilgalys, R. 2006. CO₂-enrichment and nutrient availability alter ectomycorrhizal fungal communities. *Ecology* 87: 2278–2287.

- Parrotta, J. A. 1993. Secondary forest regeneration on degraded tropical lands. In: *Restoration of Tropical Forest Ecosystems*. Lieth, H. and Lohmann, M. (eds). Kluwer Academic Publishers, The Hague.
- Parrotta, J. A. and Lodge, D. J. 1991. Fine root dynamics in a subtropical wet forest following hurricane disturbance. *Biotropica* **23**: 343–347.
- Parrotta, J. A., Turnbull, J. W., and Jones, N. 1997. Catalyzing native forest regeneration on degraded tropical lands. *Forest Ecology & Management* **99**: 1–7.
- Parsons, M., McLoughlin, C. A., Kotschy, K. A., et al. 2005. The effects of extreme floods on the biophysical heterogeneity of river landscapes. *Frontiers in Ecology and the Environment* **3**: 487–494.
- Pausas, J. G., Llovet, J., Rodrigo, A., and Vallejo, R. 2008. Are wildfires a disaster in the Mediterranean Basin? A review. *International Journal of Wildland Fire* **17**: 713–723.
- Pennanen, J. 2002. Forest age distribution under mixed-severity fire regimes: a simulation-based analysis for middle boreal Fennoscandia. *Silva Fennica* **36**: 213–231.
- Peterson, C. J. 2000. Catastrophic wind damage to North American forests and the potential impact of climate change. *The Science of the Total Environment* **262**: 287–311.
- Peterson, C. J. and Leach, A. D. 2008. Limited salvage logging effects on forest regeneration after moderate-severity windthrow. *Ecological Applications* **18**: 407–420.
- Peterson, C. J. and Pickett, S. T. A. 1991. Treefall and resprouting following catastrophic windthrow in old-growth hemlock-hardwoods forest. *Forest Ecology & Management* **42**: 205–217.
- Peterson, C. J. and Rebertus, A. J. 1997. Tornado damage and initial recovery in three adjacent, lowland temperate forests in Missouri. *Journal Vegetation Science* **8**: 559–564.
- Peterson, D. L. and Ryan, K. C. 1986. Modeling post-fire conifer mortality for long-range planning. *Environmental Management* **10**: 797–808.
- Phillips, J. D. 2002. Global and local factors in earth surface systems. *Ecological Modelling* **149**: 257–272.
- Platt, W. J. B., Beckage, R., Doren, F., and Slater, H. H. 2002. Interactions of large-scale disturbances: prior fire regimes and hurricane mortality of Savanna pines. *Ecology* **83**: 1566–1577.
- Platt, W. J. and Connell, J. H. 2003. Natural disturbances and directional replacement of species. *Ecological Monographs* **73**: 507–522.
- Podur, J. J., Martell, D. L., and Csillag, F. (2003) Spatial patterns of lightning caused forest fires in Ontario, 1976–1998. *Ecological Modeling* **164**: 1–20.
- Poulos, H. M., Camp, A. E., Gatewood, R. G., and Loomis, L. 2007. A hierarchical approach for scaling forest inventory and fuels data from local to landscape scales in the Davis Mountains, Texas, USA. *Forest Ecology & Management* **244**: 1–15.
- Proulx, O. J. and Greene, D. F. 2001. The relationship between ice thickness and northern hardwood tree damage during ice storms. *Canadian Journal Forest Research* **31**: 1758–1767.
- Puhe, J. and Ulrich, B. 2001. Implications of the deposition of acid and nitrogen. In: *Global Climate Change and Human Impacts on Forest Ecosystems*. Puhe, J. and Ulrich, B. (eds). Springer, Berlin.

- Pyne S. J. 1995. *World Fire: The Culture of Fire on Earth*. Henry Holt, New York, USA.
- Resh, V. H., Brown, A. V., Covich, A. P., *et al.* 1988. The role of disturbance in stream ecology. *Journal North American Benthological Society* 7: 433–455.
- Rhoads, A. G., Hamburg, S. P., Fahey, T. J., *et al.* 2002. Effects of an intense ice storm on the structure of a northern hardwood forest. *Canadian Journal Forest Research* 32: 1763–1775.
- Rich, R. L., Frelich, L. E., and Reich, P. B. 2007. Wind-throw mortality in the southern boreal forest: effects of species, diameter and stand age. *Journal Ecology* 95: 1261–1273.
- Richardson, D. M., Rundel, P. W., Jackson, S. T., *et al.* 2007. Human impacts in pine forests: past, present, and future. *Annual Review of Ecology, Evolution and Systematics* 38: 275–297.
- Romme, W. H. and Knight, D. H. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. *Ecology* 62: 319–326.
- Romme, W. H., Everham, E. H., Frelich, L. E., *et al.* 1998. Are large, infrequent disturbances qualitatively different from small, frequent disturbances? *Ecosystems* 1: 524–534.
- Rouault, G., Candau, J. N., Lieutier, F., *et al.* 2006. Effects of drought and heat on forest insect populations in relation to the 2003 drought in Western Europe. *Annals of Forest Science* 63: 613–624.
- Rowe, J. S. 1981. Concepts of fire effects on plant individuals and species. In: *The Role of Fire in Northern Circumpolar Ecosystems*. Wein, R. W. and Maclean D. A. (eds). John Wiley and Sons, New York.
- Ryan, K. C. 2002. Dynamic interactions between forest structure and fire behavior in boreal ecosystems. *Silva Fennica* 36: 13–39.
- Ryerson, D. E., Swetnam, T. W., and Lynch A. M. 2003. A tree-ring reconstruction of western spruce budworm outbreaks in the San Juan Mountains, Colorado, USA. *Canadian Journal Forest Research* 33: 1010–1028.
- Sanford, R. L., Jr., Parton, W. J., Ojima, D. S., and Lodge, D. J. 1991. Hurricane effects on soil organic matter dynamics and forest production in the Luquillo Experimental Forest, Puerto Rico: Results of simulation modelling. *Biotropica* 23: 364–372.
- Sartwell, C. 1971. Thinning ponderosa pine to prevent outbreaks of Mountain Pine Beetle. In: *Proceeding Short Course on Precommercial Thinning of Coast and Intermountain Forests in the Pacific Northwest, February 3–4, 1971*, Pullman, Washington, DC.
- Scatena, F. N. 1998. Climate change and the Luquillo Experimental Forest of Puerto Rico: Assessing the impacts of various climate change scenarios. *American Water Resources Association TPS-98-2*: 193–198.
- Scatena, F. N. and Larsen, M. C. 1991. Physical aspects of Hurricane Hugo in Puerto Rico. *Biotropica* 23(suppl.): 317–323.
- Scatena, F. N. and Lugo, A. E. 1995. Geomorphology, disturbance, and -the soil and vegetation of two subtropical wet steep-land watersheds of Puerto Rico. *Geomorphology* 13: 199–213.
- Schaberg, P. G., DeHayes, D. H., and Hawley, G. J. 2001. Anthropogenic calcium depletion: A unique threat to forest ecosystem health? *Ecosystem Health* 7: 214–228.
- Schaetzl, R. J., Johnson, D. L., Burns, S. F., and Small, T. W. 1989. Tree uprooting: a review of terminology, process, and environmental implications. *Canadian Journal Forest Research* 19: 1–11.

- Schellekens, J., Bruijnzeel L. A., Scatena F. N., *et al.* 2000. Evaporation from a tropical rain forest, Luquillo Experimental Forest, eastern Puerto Rico. *Water Resources Research* **36**: 2183–2196.
- Schellhaas, R., Camp, A. E., Spurbeck, D., and Keenum, D. 2000. Report to the Colville National Forest on the results of the South Deep watershed fire history research. USDA Forest Service PNW Research Station, Wenatchee Forestry Sciences Laboratory.
- Shepon, A. and Gildor, H. 2007. The lightning-biotic climatic feedback. *Global Change Biology* **14**: 440–450.
- Shinneman, D. J. and Baker, W. I. 1997. Nonequilibrium dynamics between catastrophic disturbances and old-growth forests in ponderosa pine landscapes of the Black Hills. *Conservation Biology* **11**: 1276–1288.
- Shorohova, E., Fedorchuk, V., Kuznetsova, M., and Shvedova, O. 2008. Wind-induced successional changes in pristine boreal *Picea abies* forest stands: evidence from long-term permanent plot records. *Forestry* **81**: 335–359.
- Shortle, W. C. and Smith, K. T. 1988. Aluminum-induced calcium deficiency syndrome in declining red spruce. *Science* **240**: 1017–1018.
- Shortle, W. C., Smith, K. T., and Dudzik, K. R. 2003. Tree survival and growth following ice storm injury. *USDA Forest Service Northeastern Research Station, Research Paper NE-723*
- Siccama, T. G., Bliss, M., and Vogelmann, H. W. 1982. Decline of red spruce in the Green Mountains of Vermont. *Bulletin Torrey Botanical Club* **109**: 162–168.
- Siegert, F., Ruecker, G., Hinrichs, A., and Hoffman, A. A. 2001. Increased damage from fires in logged forests during droughts caused by El Nino. *Nature* **414**: 437–440.
- Skärby, L., Ro-Poulsen, H., Wellburn, F. A. M., and Sheppard, L. J. 1998. Impacts of ozone on forests: a European perspective. *New Phytologist* **139**: 109–122.
- Slik, J. W. F. 2004. El Niño droughts and their effects on tree species composition and diversity in tropical rain forests. *Oecologia* **141**: 114–120.
- Soja A. J., Tchebakova, N. M., French, N. H. F., *et al.* 2006. Climate-induced boreal forest change: Predictions versus current observations. *Global and Planetary Change* **56**: 274–296.
- Stark, R. W. 1987. Impacts of forest insects and diseases: significance and measurement. *CRC Critical Reviews in Plant Sciences* **5**: 161–201.
- Stone, R. 2008. Natural disasters: Ecologists report huge storm losses in China's forests. *Science* **319**: 1318–1319.
- Strauss, S., Bednar, L., and Mees, R. 1989. Do one percent of the forest fires cause ninety-nine percent of the damage? *Forest Science* **35**: 319–328.
- Sturm, M., Racine, E., and Tape, K. 2001. Climate change: increasing shrub abundance in the Arctic. *Nature* **411**: 546–547.
- Swetnam, T. W. and Lynch, A. M. 1993. Multi century, regional-scale patterns of western spruce budworm outbreaks. *Ecological Monographs* **63**: 241–246.
- Takahashi, K., Aril, K. and Lechowicz, M. J. 2007. Quantitative and qualitative effects of a severe ice storm on an old-growth beech-maple forest. *Canadian Journal Forest Research* **37**: 598–606.
- Tainter, F. H. and Baker, F. A. 1996. *Principles of Forest Pathology*. John Wiley & Sons, Inc., New York.

- Taiz, L. and Zeiger, E. 2006. *Plant Physiology*. 4th edition. Sinauer Associates, Inc., Sunderland, MA.
- Tanaka, N. 2009. Vegetation bioshields for tsunami mitigation: review of effectiveness, limitations, construction, and sustainable management. *Landscape Ecological Engineering* 5: 71–79.
- Tanner, E. J. V. and Kapos, V. 1991. Hurricane effects on forest ecosystems in the Caribbean. *Biotropica* 23: 513–521.
- Tao, F. and Feng, Z. 2000. Terrestrial ecosystem sensitivity to acid deposition in South China. *Water, Air and Soil Pollution* 118: 231–243.
- Thies, W. G. 2001. Root diseases in eastern Oregon and Washington. *Northwest Science* 75: (Special Issue) 38–45.
- Thompson, J., Brokaw, N. V. L., Zimmerman, J., et al. 2002. Land use history, environment, and tree composition in a tropical forest. *Ecological Applications* 12: 1344–2002.
- Throop, H. L. and Lerdau, M. T. 2004. Effects of nitrogen deposition on insect herbivory: Implications for community and ecosystem processes. *Ecosystems* 7: 109–133.
- Turner, M. G., Baker, W. L., Peterson, C. J., and Peet, R. K. 1998. Factors influencing succession: lesson from large, infrequent, natural disturbances. *Ecosystems* 1: 511–523.
- Turner, M. G. and Dale, V. H. 1998. Comparing large, infrequent disturbances: what have we learned? *Ecosystems* 1: 493–496.
- Uriarte, M., Rivera, L. W., Zimmerman, J. K., et al. 2004. Effects of land use history on hurricane damage and recovery in a neotropical forest. *Plant Ecology* 174: 49–58.
- Valladares, F. 2008. A mechanistic view of the capacity of forests to cope with climate change. In: *Managing Forest Ecosystems: The Challenge of Climate Change*. Bravo, F. et al. (eds). Kluwer Academic Press.
- Van der Molen, 2002. Meteorological impacts of land use change in the maritime tropics. PhD dissertation, Vrije Universiteit, Amsterdam.
- Van Dyke, O. 1999. A literature review of ice storm impact on forests in Eastern North America. *SCSS Technical Report #112*. Pembroke, Ontario: Landmark Consulting.
- Van Mantgem, P. J., Stephenson, N., Byrne, J. C., et al. 2009. Widespread increase in tree mortality rates in the Western United States. *Science* 323: 521–524.
- Van Wagner, C. E. 1973. Height of crown scorch in forest fires. *Canadian Journal Forest Research* 3: 373–378.
- Veblen, T. T., Kitzberger, T., and Donnegan, J. 2000. Climatic and human influences on fire regimes in ponderosa pine forests in the Colorado Front Range. *Ecological Applications* 10: 1178–1195.
- Veblen, T. T., Kitzberger, T., Raffaele, E., et al. 2008. The historical range of variability of fires in the Andean – Patagonian *Nothofagus* forest region. *International Journal of Wildland Fire* 17: 724–741.
- Veblen, T. T., Kitzberger, T., Villalba, R., and Donnegan J. 1999. Fire history in northern Patagonia: the roles of humans and climatic variation. *Ecological Monographs* 69: 47–67.
- Vygodskaya, N. N., Schulze, E. D., Tchebakova, N. M., et al. 2002. Climatic control of stand thinning in unmanaged spruce forests in the southern taiga in European Russia. *Tellus Series B – Chemical and physical meteorology* 54: 443–461.

- Walker, L. R. 1991. Tree damage and recovery from Hurricane Hugo in the Luquillo Experimental Forest, Puerto Rico. *Biotropica* 23(suppl.): 379–385.
- Walker, L. R., Zimmerman, J. K., Lodge, D. J., and GuzmánGrajales, S. 1996. An elevational comparison of growth and species composition in hurricane-damaged forests in Puerto Rico. *Journal Ecology* 84: 877–889.
- Wallenius, T. 2002. Forest age distribution and traces of past fires in a natural boreal landscape dominated by *Picea abies*. *Silva Fennica* 36: 201–211.
- Wallenius, T., Kuuluvainen, T., Heikkilä, R., and Lindholm, T. 2002. Spatial tree age structure and fire history in two old-growth forests in eastern Fennoscandia. *Silva Fennica* 36: 185–199.
- Weaver, P. L. 1989. Forest changes after hurricanes in Puerto Rico's Luquillo Mountains. *Interciencia* 14: 181–192.
- Weaver, P. L. and González, K. A. 2005. Wildland fire management and restoration. In: *12th Meeting of the Caribbean Foresters*. Weaver, P. L. and González, K. A. (eds). USDA Forest Service, International Institute of Tropical Forestry, Río Piedras.
- Weber, M. H., Hadley, K. S., Frenzen, P. M., and Franklin, J. F. 2006. Forest development following mudflow deposition, Mount St. Helens, Washington. *Canadian Journal Forest Research* 36: 437–449.
- Westerling, A. L., Hidalgo, H. G., Cayan, D. R., and Swetnam, T. W. 2006. Warming and earlier spring increases western U.S. forest wildlife activity. *Science* 313: 940–943.
- Whigham, D. F., Olmsted, I., Cabrera Cano, E., and Harmon, M. E. 1991. The impact of Hurricane Gilbert on trees, litterfall, and woody debris in a dry tropical forest in the northeastern Yucatan Peninsula. *Biotropica* 23(suppl.): 434–441.
- White, P. S. and Jentsch, A. 2001. The search for generality in studies of disturbance and ecosystem dynamics. *Prog. Bot* 62: 399–450.
- White, P. S. and Pickett, S. T. A. 1985. Natural disturbance and patch dynamics: An introduction. In: *The Ecology of Natural Disturbance and Patch Dynamics*. Pickett, S. T. A. and White, P. S. (eds). Academic Press, New York.
- Whitney, G. G. 1986. Relation of Michigan's presettlement pine forests to substrate and disturbance history. *Ecology* 67: 1548–1559.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* 3: 385–397.
- Williams, D. W. and Liebhold, A. M. 1995. Herbivorous insects and global change – potential changes in the spatial-distribution of forest defoliator outbreaks. *Journal Biogeography* 22: 665–671.
- Williams, R. J. and Bradstock, R. A. 2008. Large fires and their ecological consequences: an introduction to the special issue. *International Journal Wildland Fire* 17: 685–687.
- Wilmking, M., Juday, G. P., Barber, V. A., and Zald, H. S. 2004. Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds. *Global Change Biology* 10: 1724– 1736.
- Wittig, V. E., Ainsworth, E. A., and Long, S. P. 2007. To what extent do current and projected increases in surface ozone affect photosynthesis and stomatal conductance of trees? A meta-analytic review of the last 3 decades of experiments. *Plant Cell and Environment* 30: 1150–1162.

- Wittig, V. E., Ainsworth, E. A., Naidu, S. L., *et al.* 2009. Quantifying the impact of current and future tropospheric ozone on tree biomass, growth, physiology and biochemistry: a quantitative meta-analysis. *Global Change Biology* **15**: 396–424.
- Wolf, A., Kozlov, M. V., and Callaghan, T. V. 2008. Impact of non-outbreak insect damage on vegetation in northern Europe will be greater than expected during a changing climate. *Climate Change* **87**: 91–106.
- Wunderle Jr., J. 2009. From the past to the globalized future of Caribbean birds. *Journal Caribbean Ornithology* **21**: 69–79.
- Wunderle Jr., J. M., Lodge, D. J., and Waide, R. B. 1992. Short-term effects of Hurricane Gilbert on terrestrial bird populations on Jamaica. *Auk* **109**: 148–166.
- Xi, W. N., Reet, R. K., Decoster, J. K., and Urban, D. L. 2008. Tree damage risk factors associated with large, infrequent wind disturbances of Carolina forests. *Forestry* **81**: 317–334.
- Yanagisawa, H., Koshimura, S., Goto, K., *et al.* 2009. The reduction effects of mangrove forest on a tsunami based on field surveys at Pakarang Cape, Thailand and numerical analysis. *Estuarine Coastal and Shelf Science* **81**: 27–37.
- Yih, K., Boucher, D. H., Vandermeer, J. H., and Zamorra, Z. 1991. Recovery of the rain forest of southwestern Nicaragua after destruction by Hurricane Joan. *Biotropica* **23**: 106–113.
- Zausen G. L., Kolb, T. E., Bailey, J. D., and Wagner, M. R. 2005 Long-term impacts of stand management on ponderosa pine physiology and bark beetle abundance in northern Arizona: A replicated landscape study. *Forest Ecology & Management* **218**: 291–305.
- Zeng, G. M., Zhang, G., Huang, G. H., *et al.* 2005. Exchange of Ca^{2+} , Mg^{2+} and K^{+} and uptake of H^{+} , NH_4^{+} for the subtropical forest canopies influenced by acid rain in Shaoshan forest located in Central South China. *Plant Science* **168**: 259–266.
- Zeng, H. C., Talkkari, A., Peltola, H., and Kellomaki, S. 2007. A GIS-based decision support system for risk assessment of wind damage in forest management *Environmental Modelling & Software* **22**: 1240–1249.
- Zimmerman, J. K., Everham, III, E. M., Waide, R. B., *et al.* 1994. Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life histories. *Journal Tropical Ecology* **82**: 911–922.
- Zimmerman, J. K., Aide, T. M., Rosario, M., *et al.* 1995. Effects of land management and a recent hurricane on forest structure and composition in the Luquillo Experimental Forest in Puerto Rico. *Forest Ecology & Management* **77**: 65–76.