Forest Insect and Fungal Pathogen Responses to Drought

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Introduction

Recent changes in precipitation patterns and in the occurrence of extreme temperature and precipitation events have been documented in many forested regions of the United States (Ryan and Vose 2012). Changes in drought intensity and frequency have the potential to alter populations and impacts of tree-damaging forest insects and pathogens (Ayers and Lombardero 2000, Dale and others 2001, Weed and others 2013). Scientists, forest managers, and environmental policymakers need to better understand the role of drought in outbreaks of forest insects and diseases in order to anticipate the future condition of U.S. forests and to consider actions to mitigate undesirable changes.

Here we review evidence for a role of drought in outbreaks of, and tree damage by, herbivorous insects and fungal pathogens in forests of the United States. First, we describe our understanding of how drought affects host nutritional quality and susceptibility to attack, and how damage by insect herbivory and pathogens affect tree responses to drought. Second, we review the responses of herbivorous forest insects (bark beetles, defoliators, sapfeeders) and fungal pathogens to drought. Third, we highlight regional differences in the roles of drought on forest insects and diseases by contrasting the Western United States with the Eastern United States. Fourth, we discuss predictions of future drought-related insect and disease impacts to western and eastern forests. Finally, we summarize our findings and highlight important research needs.

Tree Responses to Drought

Host Tree Nutrition and Susceptibility to Attack

Drought affects many components of tree nutritional quality. Several reviews of hundreds of studies (Huberty and Denno 2004, Mattson and Haack 1987, Rouault and others 2006) have concluded that drought often increases plant tissue concentrations of nitrogen compounds such as amino acids and nitrate; osmolytes such as sugars and inorganic ions; and allelochemicals such as cyanogenic glycosides, terpenoids, and alkaloids. The responses of most of these compounds are hypothesized to be dome-shaped with increases in tissue concentration during mild or moderate drought, when water stress constrains growth more than photosynthesis and root uptake of nutrients, followed by decreases during long and severe drought when intense water stress constrains growth, photosynthesis, and root uptake (Mattson and Haack 1987).

Drought-induced changes in nitrogen content of tree tissues have been investigated in many studies because of the importance of nitrogen in insect metabolism and its influence on population growth (White 1984). Drought often increases nitrogen content of tree tissues. Positive effects of drought on tree damage by foliage-feeding insects are often attributed to increased nitrogen content of water-stressed leaves (Jactel and others 2012). For example, lepidopteran larval survival is positively associated with pine leaf nitrogen concentration (Hodar and others 2002).

Drought often causes early senescence of older leaves that remobilizes nitrogen into soluble forms through vascular tissues to younger tissues, where concentrations in water-stressed plants often exceed concentrations in non-stressed plants (White 1984). All forms of drought reduce tree tissue water content, which often interferes with insect utilization of nitrogen (Huberty and Denno 2004). Timing and duration of water stress are important controls over insect capacity to use concentrated zones of nitrogen in plants. For example, Huberty and Denno's (2004) pulsed stress hypothesis predicts that sapfeeding insects benefit by feeding on drought-stressed plants when drought is followed by wetter periods that increase plant turgor and hence allow insects to benefit from drought-induced increase in plant tissue nitrogen.

Drought often alters plant defenses. The growth-differentiation-balance hypothesis (GDBH) (Herms and Mattson 1992) predicts that drought has nonlinear impacts on carbon-based plant defenses, such as terpenes, and defenses that ultimately require carbohydrates to support metabolic costs of synthesis. Specifically, mild or moderate water stress that does not cause closure of plant stomata is predicted to increase carbon-based defense due to surplus carbohydrates that result from a negative effect of stress on the use of carbohydrates for growth that is greater than the production of carbohydrates by photosynthesis (Lorio 1986, Reeve and others 1995). In contrast, intense water stress causes plants to close stomata to avoid excessive water loss, which consequently reduces photosynthesis (McDowell and others 2008, Pallardy 2008). Prolonged periods of low photosynthesis during intense water stress are predicted by the GDBH to reduce carbohydrate supply and metabolism of all plant processes, including defense. Intense drought likely causes defense failure due to a combination of tree carbon starvation and hydraulic failure (McDowell and others 2011, Tague and others 2013). The current

understanding of drought impacts on chemical composition of tree defenses is poor and largely based on experiments with seedlings that may not scale directly to mature trees (Lusebrink and others 2011, Turtola and others 2003). The few experimental studies of mature trees (Gilmore 1977, Hodges and Lorio 1975) have shown that drought can alter chemical composition of resin monoterpenes in pines, but effects of such alterations on tree defense and insect populations are not known. Drought-induced changes in tree defense compounds are rooted in alterations in transcription of genes associated with stress resistance (Arango-Velez and others 2014).

Drought often alters insect feeding by increasing leaf toughness. Physical characteristics of plant tissues, such as leaf toughness, are strongly associated with plant resistance against insects. A recent review reported stronger roles of physical traits than chemical and secondary metabolic traits in plant resistance to insect herbivory (Carmona and others 2011). During drought, leaf water content decreases and leaf toughness and dry matter content increases (McMillin and Wagner 1996, Pasquier-Barre and others 2001). These changes are associated with reduction in folivore feeding and reproduction (Awmack and Leather 2002, Pasquier-Barre and others 2001, Wagner and Zhang 1993).

Drought can increase plant attractiveness to insects by altering clues used to identify hosts (Mattson and Haack 1987, Rouault and others 2006). Leaf yellowing that often accompanies drought may be a spectral clue detected by insects, and warmer temperature of drought-stressed plant tissues may be detected by insect thermal sensors. Xylem cavitation in plants caused by drought results in ultrasonic acoustic emissions that likely are detectable by some insects (Haack and others 1988). Insect chemoreceptors may detect drought-induced changes in suites of plant compounds. For example, drought may induce plant production of volatile compounds and ethanol that are olfactory attractants for some insects, such as bark beetles (Kelsey and Joseph 2001, Kelsey and others 2014, Manter and Kelsey 2008, Miller and Rabaglia 2009).

Influence of Pathogens and Herbivory in Tree Drought Response

Few studies have addressed the impact of previous insect herbivory on tree response to drought. Insect defoliation of conifers during experimentally induced drought has been reported to reduce water stress (e.g., less negative xylem water potential) of isolated potted trees (Kolb and others 1999), but to have little effect on water stress of trees sharing the same soil resources (Jacquet and others 2014). Feeding by the hemlock woolly adelgid (*Adelges tsugae*) on eastern and Carolina hemlocks (*Tsuga canadensis* and *Tsuga caroliniana*, respectively) increased tree water stress and predisposed trees to drought in a field observational study (Domec and others 2013, Gonda-King and others 2014). The few studies of the combined effects of previous herbivory and drought on tree growth and carbohydrate pools show largely additive effects. For example, an experimental study of 10-year-old maritime pine (*Pinus pinaster*) found additive effects with no interaction of artificial defoliation and water stress on tree growth and carbohydrate pools (Jacquet and others 2014). In this study, carbohydrate pools of whole trees, roots, and stems were lowest in water-stressed trees exposed to 100 percent defoliation. Defoliation also redistributed carbohydrates from roots to stems, a response which likely predisposes defoliated trees to future drought by reducing root growth. In another example, experimental defoliation of aspen (*Populus tremuloides*) reduced stem hydraulic conductance because of a decrease in xylem growth (Anderegg and Callaway 2012). This response likely predisposes aspen to water stress in future droughts. Moreover, defoliation of aspen reduced tree carbohydrate storage and increased occurrence of fungal cankers, stem borers, and bark beetle attacks (Anderegg and Callaway 2012). These findings show that previous herbivory that alters tree carbohydrate pools and defense metabolism can, in turn, influence tree response to future drought and insect and pathogen attacks. For example, whereas the associated mechanisms are not fully understood, previous tip moth (*Rhyacionia frustrana*) attacks predispose trees to higher levels of attack in subsequent generations (Coody and others 2000).

Fungal pathogens predispose trees to drought stress and drought-induced mortality. A recent framework (Oliva and others 2014) predicts that necrotrophs, which obtain nutrients from dead tree cells, accelerate drought-induced tree mortality by depleting tree resources as a result of repair and compartmentalization processes. Vascular wilts have been hypothesized to accelerate drought-induced tree mortality by reducing sapwood conductance of water and impairing phloem transport. Biotrophs, which obtain nutrients directly from living tree tissues, are expected to be negatively affected by drought because of the strong connection between their performance and tree nutritional status. However, if biotrophs are able to invade stressed

trees, they are expected to cause more severe drought impacts on trees because they deplete carbohydrate reserves important for tree drought tolerance (Oliva and others 2014).

Parasitic plants typically intensify negative impacts of drought on tree water stress and growth by obtaining water and nutrients from tree hosts (Sanguesa-Barreda and others 2012, Stanton 2007, Stewart and Press 1990). High transpiration rates by xylem-tapping parasites, such as the true mistletoes (*Phoradendron* spp.), often reduce xylem water potential, stomatal conductance, net photosynthetic rate, and water-use efficiency of host branches and leaves (Ehleringer and others 1986, Orozco and others 1990, Sanguesa-Barreda and others 2013, Zweifel and others 2012). Moreover, infection by xylem-tapping parasites can decrease xylem hydraulic conductivity of host branch portions distal to the infection (Tennakoon and Pate 1996). Xylem-tapping parasites often reduce ectomycorrhizae on tree roots (Gehring and Whitham 1992), which reduces host nutrient and water uptake. Phloem-tapping parasitic plants, such as the dwarf mistletoes (*Arceuthobium* spp.), predispose trees to drought by several processes including alteration of host hormones (Logan and others 2013) and hydraulic processes (Sala and others 2001), reduction of host net photosynthetic rate and water-use efficiency (Marias and others 2014, Meinzer and others 2004), and depletion of host carbohydrates transported in phloem (Knutson 1979, Stewart and Press 1990). These carbohydrate losses likely reduce tree capacity for metabolic processes of drought tolerance and reduce root uptake of water and nutrients because less carbohydrate is allocated to roots (Knutson and Toevs 1972, Stewart and Press 1990). Phloem-tapping parasitic plants, such as the dwarf mistletoes that occur on conifers, also predispose trees to lethal bark beetle attacks during drought (Kenaley and others 2008).

Insect and Pathogen Responses to Drought

Outbreaks of some herbivorous insects and fungal pathogens occur during or following drought (Koricheva and others 1998, Mattson and Hack 1987, Sturrock and others 2011). Performance and impacts of insects and pathogens during and following drought differ depending on the type of food substrate (i.e., woody or foliar), feeding guild, duration of stress, and the type and importance of host defenses. The intrinsic capacity for drought resistance, which can vary among individual trees, species, and regions, will also influence tree response to water stress, insect herbivory, and fungal pathogens. Below we review impacts of drought and tree water stress on performance and impacts of major tree-feeding insect guilds (i.e., bark beetles, defoliators, sapfeeders) and tree fungal pathogens.

Bark Beetles

Bark beetles are chewing insects that feed on phloem and woody tissue beneath the bark of trees. A few notable species feed on live tissues causing death of the host tree, resulting in extensive economic and ecological impacts when widespread population outbreaks occur (Wood 1982) (fig. 6.1). Host trees have evolved defensives, however, that include chemical, physical, and histological components. A variety of chemical groups are involved in tree defense against bark beetle attack including terpenes, which are both a constituent and an inducible component of tree resin. Terpene concentrations can increase to levels that are repellant and toxic in a matter of days following beetle attack (Franceschi and others 2005). Structural aspects of trees, such as the number and size of resin ducts in the xylem and phloem, are also important as they are responsible for the production and storage of resin (Kane and Kolb 2010). Both terpene production and resin duct formation are dependent on carbon allocation within a tree, and carbon allocation can be nonlinearly influenced

Figure 6.1—Mountain pine beetle (*Dendroctonus ponderosae*) is one of several bark beetle species that has caused extensive tree mortality in pine forests of western North America. Tree mortality increased in multiple areas during the mid-2000s following a severe drought in the early 2000s. On the Helena National Forest, Montana, tree mortality exceeded 70 percent in some lodgepole (*Pinus contorta*) and ponderosa (*P. ponderosa*) pine stands. (photo by Barbara Bentz, U.S. Department of Agriculture, Forest Service)

,by drought (Herms and Mattson 1992). Intense drought reduces carbon assimilation, water transport, and cell turgor, thereby decreasing the synthesis and mobilization of secondary metabolites, such as terpenes, that are used in defense against bark beetle attack (Sala and others 2012). The level of water stress, however, may influence the allocation of assimilated carbon to defense and growth, as described above using the GDBH. Although at severe levels of water stress both growth and defense are most likely reduced, moderate water stress could lead to increased resistance if only growth is constrained, providing a surplus of carbon for resin synthesis and duct formation (Herms and Mattson 1992, Lieutier 2004, Rouault and others 2006). Although water stress can reduce overall emissions of volatile compounds due to stomatal closure, the relative concentrations of some terpenes can change (e.g., ethanol, α-pinene and β-pinene), often making trees more attractive to bark beetles (Cates and Alexander 1982, Hodges and Lorio 1975, Kelsey and Joseph 2001, Kelsey and others 2014, Kimmerer and Kozlowski 1982).

Bark beetles that feed in phloem can be either positively or negatively affected by drought, depending on drought intensity, duration, and tree water stress (Jactel and others 2012). Positive feedbacks between drought and bark beetle outbreaks have occurred in semi-arid forests of the Western United States during intense drought (fig. 6.2), whereas negative feedbacks are more

Figure 6.2—The aftermath of a western pine beetle (*Dendroctonus brevicomis*) outbreak. In the early 2000s, the mountain ranges of southern California experienced elevated levels of tree mortality due to western pine beetle, which many experts associated with severe drought (i.e., precipitation was the lowest in recorded history during 2001–2002) although other predisposing, inciting, and contributing factors were likely important. Despite continuing drought and an availability of suitable hosts, western pine beetle populations rapidly declined in 2004. This outbreak is considered by many to be among the largest recorded for this species of bark beetle. (photo by Christopher Fettig, U.S. Department of Agriculture, Forest Service)

,likely in the more mesic forests of the Eastern United States that experience milder drought than in the West. Although severely water-stressed trees may be more attractive to bark beetles and easier to overcome due to low defense capability, low levels of carbohydrates and nitrogen and reduced moisture content of phloem in such trees may negatively affect development of bark beetles and their associated fungi. This suggests that continuously stressed trees could result in poor bark beetle population performance as observed for other feeding guilds (Huberty and Denno 2004).

Few studies have experimentally investigated the effect of drought on bark beetle performance (Gaylord and others 2013); instead most studies have retrospectively analyzed the effect of either moisture- or temperature-induced drought on tree mortality due to bark beetles. Empirical associations have been found between reduced precipitation in the current year and years leading up to outbreaks of mountain pine beetle (*Dendroctonus ponderosae*) (Chapman and others 2012, Creeden and others 2014, Evangelista and others 2011, Thomson and Shrimpton 1984), spruce beetle (*Dendroctonus rufipennis*) (DeRose and Long 2012, Hart and others 2014, Hebertson and Jenkins 2008), and pinyon ips (*Ips confusus*) (Raffa and others 2008). The role of drought in predisposing pinyon pine to pinyon ips attacks has been confirmed by a recent experimental manipulation of precipitation (Gaylord and others 2013). The effect of drought on tree mortality from bark beetles can also vary depending on the lag time (Preisler and others 2012), and the duration of the outbreak event will depend on the species. For example, mountain pine beetle and spruce beetle are capable of causing widespread tree mortality for several years after drought has ceased when positive feedbacks on their populations, due to extensive host abundance, concentrated beetle density, optimal symbiotic associations, and escape from natural enemies, amplify over spatial and temporal scales (Raffa and others 2008). Conversely, pinyon ips depends more directly on stressed trees for successful reproduction, as illustrated by a rapid reduction in the population outbreak and tree mortality in the Southwestern United States during the early 2000s when wetter conditions returned (Raffa and others 2008) (fig. 6.3). The drought in the early 2000s that influenced outbreaks of mountain pine beetle, spruce beetle, and pinyon ips created conditions of severe water stress (Breshears and others 2009, Gaylord and others 2007), as it was one of the most severe droughts in the past 500 years in many parts of the Interior Western United States (Pielke and

Figure 6.3—Mortality of pinyon pine (*Pinus edulis*) due to pinyon ips (*Ips confusus*) associated with intense drought in the Southwestern United States. In some areas, tree mortality exceeded 90 percent. Populations of pinyon ips rapidly declined when wetter conditions returned to the region. (photo by Thomas Kolb, Northern Arizona University)

others 2005). This drought was also associated with warm temperatures that can have a direct positive effect on bark beetle population survival and growth (Breshears and others 2005). Warm winters can reduce cold-induced mortality (Bentz and Mullins 1999, Trần and others 2007), and warm summers can reduce generation time (Bentz and others 2014, Thatcher and Pichard 1967). In general, warm summer temperatures positively influence bark beetle population success, and drought likely magnifies the effect. The effect of drought on bark beetle population growth is not straightforward, however, as increased precipitation can also have a positive effect on bark beetle population growth (Duehl and others 2011, Gumpertz and Pye 2000, Preisler and others 2012) by providing a more nutritious food resource for developing larvae, and by reducing tree defense because carbon is preferentially allocated to growth as predicted by the GDBH (Herms and Mattson 1992, McDowell and others 2011).

Defoliators
Forest defoliators consume, mine, and/or skeletonize the foliage of trees. A number of species may cause tree mortality depending on the timing, frequency, and severity of feeding, and a few are capable of causing extensive levels of tree mortality over large areas (e.g., eastern spruce budworm, *Choristoneura fumiferana*).

While outbreaks of forest defoliators have been linked to drought (Mattson and Haack 1987), much of the associated evidence supporting this relationship is largely circumstantial. There is considerable variation in the magnitude and direction of insect responses to drought, and this is perhaps best typified among defoliators. For example, several studies have shown drought increases the performance and impact of defoliators while others have shown the opposite (Jactel and others 2012). To that end, Jactel and others (2012) suggested that the type of trophic substrate impacted (e.g., foliage versus wood) may be a more appropriate criterion for evaluating the responses of forest insects to drought than feeding guild.

Research has focused on the indirect effects of drought on defoliators as mediated through changes in host tree physiology, primarily leaf chemistry and palatability. Due to the inherent difficulties of studying the responses of defoliators to drought-stressed mature trees in forest environments, much of what is known comes from laboratory studies on seedlings. These seedling data may or may not be indicative of responses to mature trees, and therefore a distinction should be made between them. Furthermore, it is important to emphasize that responses observed in laboratory studies are likely not indicative of responses that occur at the population level (Larsson 1989), and therefore such extrapolations should be viewed with some caution. Consequently, little is known about the direct effects of drought on populations and impacts of defoliators and their common associates, including predators, parasites, and competitors. Some insect fungal pathogens important in regulating defoliator populations are likely to be negatively impacted by drought. For example, *Entomophaga maimaiga*, which causes extensive epizootic outbreak in populations of the gypsy moth (*Lymantria dispar*) in the Eastern United States, requires high levels of moisture for conidial production and discharge (Hajek 1999). Interestingly, drought-stressed plants are consistently warmer than unstressed plants because reduced transpiration limits plant cooling, with differences as great as 15 °C being observed (Mattson and Haack 1987). This has obvious implications to populations and impacts of the insects colonizing them due to positive responses of many insects to increasing temperature.

Many defoliators preferentially feed on leaves with high protein and water content, low leaf toughness, and low concentrations of secondary metabolites (Dury and others 1998). As described earlier, drought often affects

the nutritional quality of foliage by causing changes in water, carbohydrate, and nitrogen concentrations. It has been well demonstrated that the magnitude and direction of responses to drought by defoliators are influenced by the severity and duration of drought stress (Jactel and others 2012). However, drought stress severity should be viewed in the context of the overall drought resistance of a given tree species. For example, trees that have narrow xylem conduits (gymnosperms) can generally maintain physiological function and recover from more severe drought than trees that have wide xylem conduits (most angiosperms) (Brodribb and Cochard 2009). Overall, compromised physiological function and reduced productivity often leads to a higher vulnerability to insect attack (Bolton 2009).

Nitrogen concentrations often increase in foliage during drought stress (White 1969, 1984), which may increase the performance of defoliators as nitrogen is often a limiting growth factor (Mattson and Haack 1987). Rouault and others (2006) commented that some defoliators benefited from increased nitrogen in plant tissues associated with moderate water stress during the drought and heat waves that occurred in Europe during 2003. For some insects, nutrients in unstressed foliage are below levels optimal for development and even moderate stress has been reported to cause significant changes in the quality of foliage that affect defoliator performance (Herms and Mattson 1992, Larsson 1989, Larsson and Björkman 1993, Mattson and Haack 1987, Rouault and others 2006). Alternatively, Craig and others (1991) found no consistent evidence that drought stress led to increased performance of sawflies (*Neodiprion* spp.) in ponderosa pine (*Pinus ponderosa*) trees. Furthermore, they reported that performance was better on nonstressed trees during some years. In another study, sawfly performance was greatest on needles from ponderosa pine seedlings exposed to intermittent rather than continuous water stress (McMillin and Wagner 1995). Severe drought stress is generally recognized as causing a deterioration of host tissue quality; however, some defoliators may be attracted to chlorotic foliage as many insects are attracted to yellow hues (Prokopy and Owens 1983).

Drought may negatively impact the performance of defoliators through reduced leaf water content, which usually increases leaf toughness resulting in reduced palatability and lower leaf consumption. For example, leaf water content is thought to be one of the most important factors influencing the growth of

autumnal moth (*Epirrita autumnata*) and winter moth (*Operophtera brumata*) in Europe (Henriksson and others 2003, Tikkanen and Lyytikäinen-Saarenmaa 2002). Similarly, Scriber (1977) showed that cecropia moth (*Hyalophora cecropia*) larvae reared on water-stressed leaves of black cherry (*Prunus serotina*) in the laboratory grew more slowly and were less efficient at utilizing plant biomass than larvae that fed on leaves fully supplemented with water.

Concentrations of secondary metabolites often increase in foliage as a result of drought stress, which has been shown to negatively impact defoliators. Hale and others (2005) demonstrated that concentrations of total phenolic glycosides, important secondary defensive compounds (Hemming and Lindroth 1995), were lower in well-watered black poplar (*Populus nigra*) seedlings, and higher in drought-stressed seedlings despite the latter being constrained by a smaller carbon budget. In their study, continuous drought stress decreased the growth of gypsy moth larvae likely as a result of decreased foliar nitrogen and increased total phenolic glycoside concentrations, but had no effect on white-marked tussock moth (*Orgyia leucostigma*) larvae, which is thought to be less sensitive to increases in phenolic glycosides than gypsy moth (Kopper and others 2002). In another study, Roth and others (1997) investigated the effects of carbon dioxide and water availability on quaking aspen and sugar maple (*Acer saccharum*) seedlings. Foliar nitrogen levels declined and secondary metabolite concentrations increased under enriched carbon dioxide, but starch and sugar levels were unaffected. All phytochemicals, with the exception of simple sugars, declined or did not change in response to drought. Carbon dioxide and drought-mediated changes reduced performance of forest tent caterpillar (*Malacosoma disstria*) (Roth and others 1997).

In a recent meta-analysis, Jactel and others (2012) concluded that primary agents that feed on tree foliage inflicted greater damage on drought-stressed trees than unstressed trees, but the effect was largely attributed to gall-making insects and fungal pathogens. Their meta-analysis included 100 comparisons of forest insects and fungi on drought-stressed and unstressed trees (based on 40 publications, 1975–2010). Among foliage feeders, such notable forest pests as gypsy moth and forest tent caterpillar, as well as several sawflies, aphids (Aphididae), and leaf pathogens, were included. Results for chewing insects on foliage were highly variable among 20 studies included in the meta-analysis, and the overall effect of drought on foliage damage by chewing

insects was positive, but not significantly different from zero based on a 95-percent confidence interval.

Sapfeeders

Water stress is hypothesized to positively influence phloem sapfeeders, such as aphids and adelgids (*Adelgidae*), through an increase in host tissue nitrogen content. Meta-analyses, however, suggest that the response is highly variable among studies and dependent on the level of stress and resultant turgor pressure of the tree (Huberty and Denno 2004, Jactel and others 2012, Koricheva and others 1998). Similar to other phloem feeders, spruce aphid (*Elatobium abietnum*) performance and population growth was greatest when water stress was intermittent and was lowest when the stress was continuous (Major 1990). Under continuous water stress, leaf and phloem nitrogen are diminished due to reduced turgor, but moderate or periodic stress provides available nitrogen during periods of periodic turgor recovery. These results suggest that the optimum host would be a plant that has experienced long-term intermediate stress, and then temporarily released from the stress by abundant precipitation during insect feeding (Mopper and Whitham 1992). The response of sapfeeders, such as the Eastern spruce gall adelgid (*Adelges abietis*), which has both a sucking and galling life stage, can also vary with life stage. The sucking stage is often positively influenced by drought, while the galling life stage, which requires expanding plant tissues for successful gall formation, is negatively influenced (Björkman 2000).

Fungal Pathogens

Relatively few studies have directly addressed the effects of drought on fungal tree pathogens. However, it has been predicted that drought could alter the prevalence, severity, and geographic patterns of many forest pathogens because forest diseases are strongly influenced by environmental conditions, such as humidity and temperature (Sturrock and others 2011). On one hand, drought that increases tree water stress and reduces resources available for defense could make trees more susceptible to pathogens. On the other hand, drought may retard the development, survival, reproduction, and dispersal of fungal pathogens because many rely on moisture availability to cause infection (Klopfenstein and others 2009). Changes in moisture availability could directly influence fungal pathogen sporulation and infection of host species (Sturrock and others 2011). However, it is not clear how drought affects pathogen survival, as fungal pathogens are highly adaptable and have diverse reproductive

systems that are designed for coping with changing environmental conditions (Olatinwo and others 2013).

Several recent reviews have addressed impacts of drought on tree fungal pathogens and have highlighted sources of variation in drought response. Desprez-Loustau and others (2006) suggested that duration of drought is an important predictor of forest disease impact on trees as more infections are likely to develop during or after prolonged drought. Jactel and others (2012) reported that the most important factors for determining disease severity under drought conditions were pathogen status (primary or secondary), affected tree part (foliar versus woody organs), and water stress severity. Further, they reported that primary pathogens that infect wood and foliage of healthy trees inflict less damage on trees during drought (Jactel and others 2012). Moreover, pathogens whose reproduction, spread, infection, and survival are directly tied to the availability of moisture have been predicted to be negatively impacted by drought (Sturrock and others 2011). In contrast, drought is expected to increase host damage by secondary pathogens that colonize stressed trees and woody organs, such as root rot pathogens, stem wound colonizers, and latent colonizers of sapwood (Desprez-Loustau and others 2006, Jactel and others 2012, Sturrock and others 2011).

Needle diseases, which are caused by rust pathogens, and diseases caused by *Phytophthora* species are sensitive to precipitation and humidity, as rates of reproduction, spread, and infection are greater when conditions are moist (Harvell and others 2002). Therefore, drought may decrease the incidence and severity of these diseases (Thompson and others 2014). Rates of infection for many needle pathogens, such as *Dothistroma septosporum* and *D. pini* that cause Dothistroma needle blight of pine, spruce, larch, and Douglas fir (*Pseudotusga menziesii*) (Barnes and others 2004), and *Phaeocryptopus gaeumannii* that causes Swiss needle cast of Douglas fir, are closely linked to temperature and moisture (Hansen and others 2000, Stone and others 2008). High levels of moisture were particularly critical for infection by *D. septrosporum.* This pathogen required 10 or more consecutive hours of needle wetness at temperatures ranging from 16 °C to 20 °C for infection to occur (Bulman 1993). High levels of moisture have also been shown to be required for infection by *P. gaeumannii.* High levels of *P. gaeumannii* incidence have been positively correlated with winter rainfall accumulation and leaf wetness hours (Manter and others 2005). Similar to needle and foliar diseases,

drought conditions could also decrease the severity of stem rust diseases.

It has been suggested that the incidence of rust diseases will be affected not only by drought conditions, but also by the presence or absence of alternate hosts. Many stem rust pathogens, such as fusiform rust and white pine blister rust, are unusual as pathogens because in addition to the requirement of extended periods of free moisture to complete their lifecycles, they also require the presence of primary and secondary hosts. Drought conditions could alter the geographic range of primary and secondary hosts (Olatinwo and others 2013). Fusiform rust is a significant pathogen on pine, especially in southeastern species. The alternative host in the Southeast is primarily water oak (*Quercus nigra*). Fusiform rust would not complete its lifecycle if the geographic range of water oak changes during future drought and climate change. White pine blister rust, caused by *Cronartium ribicola*, was introduced to North America from Asia in the early 1900s. Infection causes branch dieback, productive failure, and tree mortality (Bega 1978). Environmental requirements for disease progression of *C. ribicola* are well documented. Needle infection requires 48 hours of 100 percent relative humidity and temperatures less than 20 °C (Van Arsdel and others 1956). Drought will likely result in less white pine blister rust infection in regions where moisture is or becomes a limiting factor to the rust (Kinloch 2003).

Phytophthora ramorum, the causal agent of sudden oak death, is a serious and devastating pathogen. Recently introduced, this pathogen has had a significant impact on tanoak (*Notholithocarpus densiflorus*) and live oak (*Quercus agrifolia*) in California and Oregon forests. *P. ramorum* has been demonstrated to be a high risk pathogen to many forests in North America because of its ability to infect a wide range of hosts (Dodd and others 2008). However, like all *Phytophthora* species, extended periods of rainfall in fall or spring are essential to the persistence of *P. ramorum*. Therefore infections by *Phytophthora* spp. would likely decrease during extended drought unless drought is followed by periods with extended rainfall (Venette 2009, Weed and others 2013).

Root rot pathogens of trees, such as *Armillaria* spp. and *Heterobasidion* spp., are predicted to become more severe and move into new geographic regions during drought because these pathogens most successfully colonize stressed trees (Olatinwo and others 2013,

Sturrock and others 2011). Armillaria root rot is a global disease caused by both primary and secondary pathogens that infect primarily pines and hardwoods (Kile and others 1991). Infections cause wood decay, overall growth reduction and tree mortality, and increase tree susceptibility to colonization by bark beetles or other insect pests (Sturrock and others 2011). On forested sites under drought conditions causing tree stress, Armillaria root rot severity could increase significantly and cause widespread tree mortality (Klopfenstein and others 2009, La Porta and others 2008, Shaw and Kile 1991). Similarly, Heterobasidion root rot caused by *Heterobasidion irregulare* and *H. occidentale*, could increase in geographic range and incidence during drought (Kliejunas and others 2009, Otrosina and Garbelotto 2010). Currently in the Southeastern United States, Heterobasidion root rot causes significant losses on conifers, and it has been suggested that with increased drought, growing numbers of trees will be impacted by this disease (Duerr and Mistretta 2013). In the central western coast of Italy, where environmental conditions are becoming increasingly hotter and drier, widespread morality of Corsican pine (*Pinus nigra* var. maritime) was caused by Heterobasidion root rot (Gonthier and others 2007). In these drier conditions, the pathogen appears to be increasing its geographic range and incidence.

Several studies have reported increased severity of stem canker pathogens during drought because water-stressed trees are less effective at mechanisms of canker resistance, such as compartmentalization and callusing (Bevercombe and Rayner 1980, McIntyre and others 1996). Cankers caused by *Septoria musiva* on poplar (*Populus* spp.) stems were significantly larger on water-stressed trees compared to unstressed trees (Desprez-Loustau and others 2006, Maxwell and others 1997). Likewise, increased severity of Diplodia shoot blight caused by *Diplodia sapinea* has also been associated with water stress of trees in several studies (Blodgett and others 1997, Paoletti and others 2001).

Drought and forest pathogens often are implicated as causal factors in tree diseases of complex etiology or decline diseases (Manion 1981). Decline diseases are caused by a multitude of predisposing, inciting, and contributing factors including drought and fungal pathogens. In a review of aspen decline in North America, Worrall and others (2013) concluded that recent declines in many regions, including the Western United States, were primarily induced by drought, but biotic agents, including fungal pathogens, also played

a role. Primary pathogenic agents such as sooty-bark canker; multi-year defoliation by tent caterpillars (*Malacosoma* spp.); and secondary agents such as boring insects, fungal cankers, and Armillaria root disease have been associated with drought-induced aspen mortality in most studies (Worrall and others 2013). Previous defoliation likely increases aspen susceptibility to drought and secondary biotic agents via carbon limitation (Anderegg and Callaway 2012). Tree-ring studies in the Western United States show that chronically low growth rate predisposes aspens to die during severe drought (Hanna and Kulakowski 2012, Ireland and others 2014, Kane and Kolb 2014). Data from these studies strongly suggest that stresses leading to aspen death accrue over decades and that "sudden aspen death" is not due solely to recent severe drought. Overall, the role of drought and biotic agents in aspen mortality in the Western United States is consistent with Manion's decline disease framework (Manion 1981) with drought acting as an inciting factor and biotic agents as contributing factors.

Regional and Sub-Regional Differences and Interactions

In the West
Bark beetles are the main biotic agent of tree mortality in the Western United States. Multiple large outbreaks have killed hundreds of millions of trees in recent decades (Meddens and others 2012). Aggressive bark beetle species such as mountain pine beetle and spruce beetle are able to kill healthy trees when beetle populations are large, and climate plays an important role in driving epidemics of these beetles through effects on the insects and on host trees (Bentz and others 2010, Raffa and others 2008). Drought provides an increased source of susceptible host trees, which allows beetle populations to build. Temperature-induced drought in the 1990s in Alaska and moisture-induced drought in the early 2000s in the Western conterminous United States have been linked to bark beetle outbreaks (Berg and others 2006, Chapman and others 2012, Creeden and others 2014, Hart and others 2014, Shaw and others 2005). Others have also found a relationship between drought and historic spruce beetle outbreaks (DeRose and Long 2012, Hebertson and Jenkins 2008, Sherriff and others 2011). However, when drought is relieved, epidemics of some species, including mountain pine beetle and spruce beetle, can continue due to positive feedbacks that allow high numbers of beetles to overwhelm the defenses of trees, despite their recovery from drought stress (Creeden and others

2014, Raffa and others 2008). The northward range expansion of mountain pine beetle into the Canadian boreal forest and the extensive outbreaks in high-elevation five-needle pines of the Western United States have been attributed to warming (Carroll and others 2004, Logan and others 2010). Drought may have played a role in initiating these outbreaks and facilitating population increase to levels that killed healthy trees, but warming was the primary reason for these epidemics occurring in historically unknown or rare locations.

In contrast to aggressive beetle species, successful attacks of less aggressive bark beetles in the Western United States are limited to stressed hosts, and as such outbreaks are closely tied to drought and associated warm temperatures. The pinyon pine (*Pinus edulis* and *P. monophylla*) mortality caused by severe drought and pinyon ips is an excellent example. In the early 2000s, a "global-change-type drought" occurred in the Southwest in which extremely dry conditions occurred during a period of time when conditions were already warmer than in the past (Breshears and others 2005). *Ips* populations increased in conjunction with the drought and warm temperatures, and together with extreme tree physiological stress, caused mortality in millions of hectares of pinyon pine stands (Breshears and others 2005, Meddens and others 2012, Raffa and others 2008). When wetter conditions returned after several years, *Ips* populations declined (Raffa and others 2008). *Ips* lack the positive feedback mechanisms that allow for increased population growth with increased beetle numbers. Outbreaks of other bark beetle species, such as Douglas-fir beetle (*Dendroctonus pseudotsugae*), western balsam bark beetle (*Dryocoetes confusus*), fir engraver (*Scolytus ventralis*), and pine engraver (*Ips pini*), also caused extensive tree mortality in the early 2000s (Meddens and others 2012), although the role of drought is less clear.

The role of drought in the Western United States in influencing outbreaks of another class of insects—defoliators—is less understood. The primary defoliating insect of the West is western spruce budworm, which attacks multiple conifer species and periodically erupts, causing widespread tree damage and death. Budworm outbreaks have been linked to drought conditions that cause tree stress or are related to the important synchrony of caterpillar development and foliage phenology (Campbell and others 2006, Thomson and others 1984, Williams and Liebhold 1995a), although other studies have found that outbreaks

were associated with wetter conditions at the end of droughts that increase food resources (Flower and others 2014, Ryerson and others 2003, Swetnam and Lynch 1993). Multiple drought influences may be important, and they may vary regionally (Lynch 2012). For many defoliators, either drought is not important or its influence is unknown (Jactel and others 2012).

Pathogens are also important forest disturbance agents in the Western United States. As described earlier, some forest pathogens important in the West, such as those causing Phytophthora root rot, sudden oak death, Dothistroma needle blight, Swiss needle cast, and white pine blister rust, prefer moist conditions, thereby suggesting that drought plays a limiting role in these outbreaks (Jactel and others 2012, Sturrock and others 2011). Other fungal pathogens, such as those causing Armillaria root disease or various cankers, are indirectly affected by drought through increasing stress of host trees, implying that drought leads to more favorable conditions for outbreaks (Jactel and others 2012, Klopfenstein and others 2009, Sturrock and others 2011).

In the East
The role of drought in insect and fungal pathogen outbreaks is less clear in mesic forests of the Eastern United States than in the more arid regions of the Western United States, where drought has been linked to outbreaks of certain insects and diseases. The generally mild droughts of the Eastern United States (i.e., compared to portions of the Western United States) can increase the concentration of plant secondary metabolites that are important for resisting pathogens and insects (Hale and others 2005, Herms and Mattson 1992, Lombardero and others 2000).

Hardwood forests—Water stress of broad-leaved hardwood trees generally decreases water content and increases concentrations of soluble nitrogen and secondary metabolites in plant tissues, but these physiological changes may have positive, negative, or neutral effects on insect growth and fitness depending on the species (Hale and others 2005, Huberty and Denno 2004, Mattson and Haack 1987, Scriber 1977). For example, experimental water stress of black poplar led to reduced concentrations of total phenolic glycosides and reduced feeding performance of gypsy moth, but not white-marked tussock moth (Hale and others 2005). Chakraborty and others (2013) found no effects of drought in either of two ash species on constitutive or induced phenolics in the phloem. Roth and others (1997) reported a rare case of

drought-induced reductions in defensive compounds in quaking aspen.

In the East, aspen and poplar, maple, oak, hickory, beech, ash, and birch are all widely distributed, important components of mixed-hardwood forests. These forests are periodically subjected to outbreaks from forest tent caterpillar, gypsy moth, winter moth, and other defoliators, and significant effects on forest composition and structure are expected with the arrivals of the nonnative emerald ash borer (*Agrilus planipennis*), thousand cankers disease, and laurel wilt into the region. The impacts of these hardwood pests seem largely unrelated to drought (Olatinwo and others 2013, Weed and others 2013). One exception could be the recent epidemic of red oak mortality in the Ozark Mountains (Jones and others 2014) that has been associated with drought and the wood-boring beetle, *Enaphalodes rufulus* (Haavik and Stephen 2010). However, even this case is not simple to interpret due to potentially confounding influences of forest age, structure, and Armillaria root rot (Wang and others 2007).

Conifer forests—Insects and pathogens are also continuous threats to the health of conifer forests in the Eastern United States. The southern pine beetle (*Dendroctonus frontalis*) is the most important disturbance agent of southern pine ecosystems; white pine blister rust is a perennial stress on eastern white pine (*Pinus strobus*); invasive adelgids threaten the persistence of mature hemlock and Fraser fir (*Abies fraseri*) stands across the mid-Atlantic; and eastern spruce budworm outbreaks periodically disturb the eastern boreal forest. Early hypotheses suggested that water stress would improve host quality to herbivores by favoring the balance of nutrients that are important for insect growth (Mattson and Haack 1987. However, oleoresin is the primary mechanism in conifers conferring resistance to herbivores and especially bark beetles (Raffa and Berryman 1983), and oleoresin flow and its chemical composition are key determinants of bark beetle success (Lombardero and others 2000, Lorio 1986, Raffa and others 2005). There is a pervasive suggestion in the scientific literature and among forest health managers that drought stress compromises tree defenses to a point where outbreaks of aggressive species such as southern pine beetle are permitted, but the growing, albeit small body of scientific evidence indicates that constitutive resin defenses actually increase at the moderate levels of drought stress that occur in the Eastern United States (Dunn and Lorio

1993, Lombardero and others 2000, Lorio and others 1995, Reeve and others 1995).

Resin flow in loblolly pine (*Pinus taeda*), the most abundant pine of the Southeastern United States, increases significantly under conditions of moderate water deficit (Dunn and Lorio 1993, Lombardero and others 2000, Reeve and others 1995), and does not decrease until drought is extreme (Lorio and others 1995). This matches expectations derived from the GDBH, which we describe in earlier sections (Lorio 1986, Lorio and others 1982). Resin flow of loblolly pine tends to be highest during seasonal periods of suboptimal growth, such as under moderate water stress (Lombardero and others 2000). Studies of conifers from other regions also show that moderate drought can increase some tree defensives. For example, foliar tannins, another class of important phenolic anti-herbivore defenses, had a nonlinear response to soil water deficits with greatest concentrations in Douglas-fir needles occurring at moderate water stress (Horner 1990). In Europe, drought stress generally increased the concentrations of several individual monoterpenes and resin acids in the woody tissues and needles of Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) (Turtola and others 2003).

The hypothesis that drought triggers outbreaks of southern pine beetle has been under investigation for nearly a century (Dunn and Lorio 1993, Hodges and Lorio 1975, Lorio 1986, Lorio and others 1995, McNulty and others 1997, Reeve and others 1995, St. George 1930, Turchin and others 1991). However, drought tends to increase defenses of southern pines rather than decrease them (above). Furthermore, analyses of time series data have failed to reveal the expected relations between drought and southern pine beetle fluctuations (McNulty and others 1997, Turchin and others 1991); if anything, southern pine beetle outbreaks have been positively correlated with rainfall (Duehl and others 2011, Gumpertz and Pye 2000). This correlation is consistent with a broad pattern in which the secondary colonizers of dying trees benefit from drought, rather than the aggressive tree-killing species such as southern pine beetle (Jactel and others 2012). Diverse evidence argues against the hypothesis that southern pine beetle outbreaks are promoted by drought (fig. 6.4).

Figure 6.4—A local infestation ("spot") of southern pine beetle (*Dendroctonus frontalis*) in east Texas. In the Eastern United States, southern pine beetles are a dominant source of disturbance in pine forests from New Jersey to Texas. Epidemics are believed to be unrelated to drought, but instead are most prevalent in pine forests that are fast growing, unthinned, and overstocked. (photo by Ronald Billings, Texas A&M Forest Service)

Similar to hardwood species in the Eastern United States, we lack strong evidence that sustained population outbreaks of insects and pathogens on eastern conifers are triggered by water stress or drought. Whereas water stress and drought are often cited as a predisposing factor to pest and pathogen outbreaks (Edmonds and others 2000), evidence for a strong role of drought on insect and pathogen outbreaks in forests of the Eastern United States is not yet convincing. The few examples of positive correlations between spatial and temporal outbreak patterns of insects and pathogens in the Eastern United States (Haavik and Stephen 2010) may be spurious or associated with other mechanisms. One such mechanism could be the powerful effects of warming temperatures on developmental rates and fitness of insects and pathogens that together with reduced precipitation create drought-like conditions (Weed and others 2013).

Anticipating Impacts: Predictions of Future Drought-Related Insect and Disease Impacts

In the West

Future anthropogenic-induced changes to the Earth's climate are likely to include increases in temperature and significant changes in precipitation patterns. Across the Western United States, temperature increases are projected to exceed global mean increases and more frequent extreme weather events, such as droughts, are expected (Levinson and Fettig 2014). Winter precipitation is projected to increase in some areas, but to decrease by up to 20 percent in the Southwestern United States by the 2050s. Summer precipitation is projected to decrease by 10–30 percent throughout the West by the 2050s (Fettig and others 2013). Observed increases in temperature have been greater in winter and spring than in summer (IPCC 2007, Melillo and others 2014). Warming during winter will further exacerbate recent declines in snowpack. As such, many forests in the Western United States will experience further increases in drought stress whether associated with reductions in precipitation or increases in evaporative demand associated with elevated temperature. Williams and others (2013) reported that if the vapor-pressure deficit continues increasing in the Southwestern United States, as projected by climate models, by the 2050s mean forest drought stress will exceed that of the most severe droughts in the past 1,000 years.

As might be expected, an increase in the frequency and severity of some biotic disturbances is expected as a result of more intense drought stress and increasing temperature (Allen and others 2010, Bentz and others 2010, Fettig and others 2013, Sturrock and others 2011, Weed and others 2013). However, our understanding of these relationships in the Western United States is largely limited to select insects in conifer forests. Among insects, range expansions and increases in the frequency and severity of outbreaks by some bark beetle species have already been documented (Bentz and others 2009), and further changes are anticipated (Bentz and others 2010, Fettig and others 2013, Sambaraju and others 2012, Sturrock and others 2011, Williams and Liebhold 2002). It is thought that increasing temperatures and drought stress, exacerbated by high densities of suitable and susceptible hosts (Fettig and others 2007, Hicke and Jenkins 2008), have contributed to the positive feedbacks necessary for these range expansions and epidemic populations to occur (Raffa and others 2008). For example, Preisler and others (2012) reported that in addition to beetle pressure, climate variables with the largest effect on the odds of a mountain pine beetle outbreak exceeding a certain size in Oregon and Washington were minimum winter temperature and drought in the current and previous year. Precipitation levels the year prior to an outbreak had a positive effect on outbreak size, perhaps because of the positive influence of precipitation on the production of phloem, which is where larvae feed. While increases in the impact of several bark beetle species are expected with future climate change (Bentz and others 2010), it is important to note that significant areas of the Western United States have already suffered high levels of tree mortality due to bark beetles (Meddens and others 2012), and susceptible hosts may be currently depleted in these areas, which will dampen future outbreaks for decades.

Our understanding of the anticipated impacts of defoliators on drought-stressed forests in the Western United States is limited. This partially results from inconsistencies in the direction and magnitude of their responses to drought (see earlier), and because bark beetle outbreaks and wildfire have overshadowed the impacts of defoliators as primary disturbances associated with drought-stressed forests in the West, particularly in recent decades. Williams and Liebhold (1995a, 1995b) investigated potential changes in spatial distribution of outbreaks of western spruce budworm (fig. 6.5) in eastern Oregon under several climatic change scenarios. With an increase of 2 °C, the

Figure 6.5—Western spruce budworm (*Choristoneura occidentalis*) defoliation. Some experts suggest that defoliation due to western spruce budworm will decline in the future due to increasing drought. However, there is considerable uncertainty about the role of drought on the performance of defoliators and their influence on drought-stressed forests in the United States. (photo by Lia Spiegel, U.S. Department of Agriculture, Forest Service)

projected defoliated area decreased relative to ambient conditions, as was projected when temperature was increased and precipitation decreased. However, with an increase in temperature and precipitation, the defoliated area was projected to increase. Despite this, considerable uncertainty remains about the future impacts of defoliators to drought-stressed forests in the Western United States (Weed and others 2013).

Outbreaks of forest diseases caused by native and introduced pathogens are generally thought to become more frequent and severe as a result of climate change (Sturrock and others 2011). However, diseases caused by pathogens directly affected by climate (e.g., needle blights) are projected to have reduced impacts under warmer and drier conditions. These groups of pathogens may cause disease in healthy hosts if the pathogen's environmental requirements are met, many of which require moist conditions (Sturrock and others 2011).

In the East
In the Eastern United States, effects of drought on biotic disturbance in forests are anticipated to be modest relative to effects from warming and introductions of nonnative insects and pathogens (Duehl and others 2011, Olatinwo and others 2013, Weed and others 2013). In the Northeastern United States, droughts have been historically rare and are projected to remain

low in intensity through this century (Hayhoe and others 2007). Since projections of future changes in precipitation for the Eastern United States are generally flat (Ryan and Vose 2012), the eastern forests that are most likely to experience drought in the future are those already subject to occasional droughts (e.g., forests near the edge of the Great Plains). Forests with red oak may be at greater risk because drought can permit increased mortality from wood-boring beetles (Haavik and Stephen 2010) and *Armillaria* species (Clinton and others 1993). Impacts on ash from the emerald ash borer could be exacerbated by drought (Chakraborty and others 2013). There may be a tendency for drought to increase the susceptibility of hardwood trees to wood-boring beetles (Dunn and others 1990, Muilenburg and Herms 2012). Fortunately, the extensive and productive pine forests of the Southeastern United States do not seem dangerously vulnerable to drought-triggered outbreaks of tree-killing bark beetles (Duehl and others 2011, Duerr and Mistretta 2013, McNulty and others 1997, Weed and others 2013).

Summary and Research Needs for Insects and Pathogens

Bark Beetles
Our review of impacts of drought on bark beetle performance and tree mortality in U.S. forests is consistent with predictions of plant carbon allocation models (Herms and Mattson 1992, McDowell and others 2011) that suggest moderate drought/tree water stress can reduce bark beetle population performance and subsequent tree mortality, whereas intense drought increases bark beetle performance and tree mortality (fig. 6.6). Figure 6.6 provides a framework for understanding the apparent difference in the effect of drought on bark beetle performance and tree damage between eastern and western forests.

Most eastern forests have considerably higher precipitation and less severe drought than western forests, especially compared to forests east of the Sierra Nevada and Cascade Mountain crests and west of the Great Plains. Current evidence strongly suggests that the relatively moderate droughts that occur in eastern conifer forests do not increase performance and tree mortality from native bark beetles, but instead may reduce performance and impact. Because western arid forests are more water-limited than eastern mesic forests and at times experience more severe drought, insect-caused tree mortality has been more often

correlated with severe drought in the Western United States. The "global-change-type drought" that occurred in the Southwestern United States in the early 2000s (Breshears and others 2005) is an excellent example and provided an opportunity to examine the role of drought and temperature in bark beetle outbreak potential. We suggest that future research on the role of drought in bark beetle outbreaks should focus on:

● the relative role of temperature in drought-induced outbreaks of bark beetles;

● identification of species which are capable of self-perpetuating outbreaks after drought subsides;

● the level of drought-associated tree mortality that would occur without bark beetle attacks;

● the effectiveness of manipulating forest composition and structure to reduce drought stress and bark beetle attacks in semi-arid forests; and

● the level of drought intensity in pine forests of the Eastern United States that would shift the role of drought in beetle outbreaks from a negative to a positive driver (fig. 6.6).

Defoliators
In contrast to bark beetles, our review found inconsistent impacts of drought on defoliator performance and tree damage. Whereas individual studies have reported both positive and negative impacts of drought on defoliator performance and damage, cumulative results over many studies are too variable to allow generalization of drought impacts on this insect guild. While substantial inconsistency and uncertainty exist in the response of defoliators to drought, it is clear from climate-change projections (Melillo and others 2014, Ryan and Vose 2012) that forest defoliators will increasingly interact with drought-stressed hosts. As such, we underscore the need for a greater understanding of the impacts of drought on defoliators.

Sapfeeders
The collective response of tree sapfeeders to drought is nonlinear based on available evidence (fig. 6.7). Sapfeeders typically have the highest performance and cause the most tree damage at moderate drought intensity, and when periods of intense drought are interrupted by precipitation, resulting in plant tissues enriched with nitrogen and with high turgor.

Fungal Pathogens
Our review highlights a complex response of tree fungal pathogens to drought (fig. 6.8). The overall consensus of our review and others is that some forest pathogens will become less severe during drought whereas some diseases will become more severe (Desprez-Loustau and others 2006, Jactel and others 2012, Klopfenstein and others 2009, Sturrock and others 2011). Specifically, available evidence suggests that drought reduces performance and damage by primary pathogens that infect healthy trees and foliage,
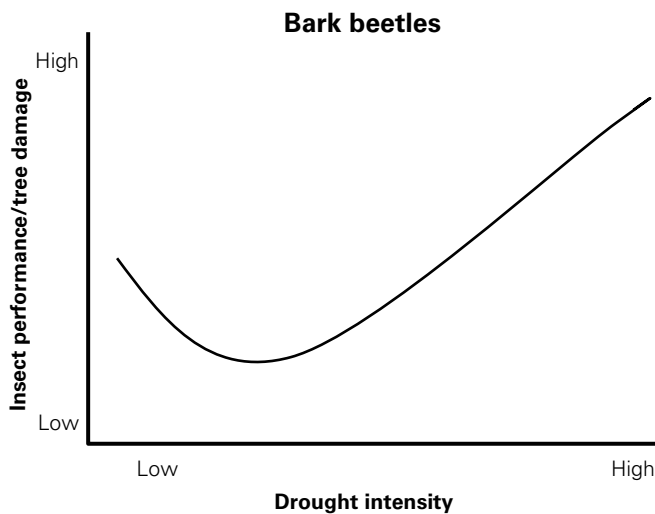

Figure 6.6—Nonlinear response trend of bark beetle performance and tree damage to drought intensity based on our literature review and tree carbon allocation frameworks.
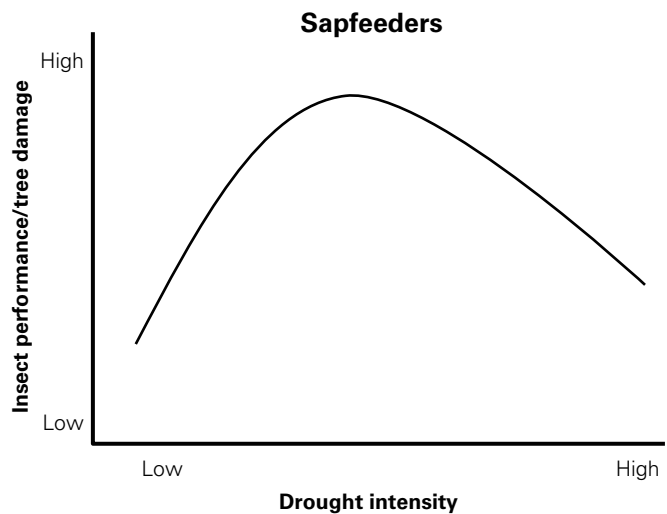

Figure 6.7—Nonlinear response trend of sapfeeder performance and tree damage to drought intensity for U.S. forests based on our literature review.

Fungal pathogens

Primary (e.g., rusts, *Phytophthora*, *Dothistroma*)

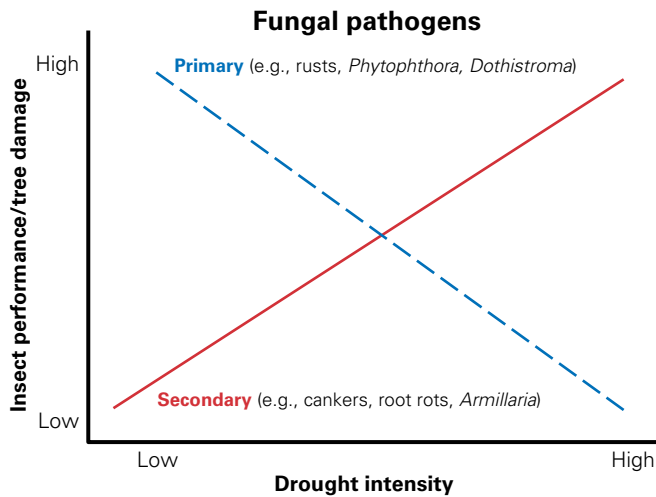**Secondary** (e.g., cankers, root rots, *Armillaria*)

Figure 6.8—Response trends of performance and tree damage by primary (dashed blue line) and secondary (solid red line) fungal pathogens to drought intensity for U.S. forests based on our literature review.

such as rusts (*Phytophtora* and *Dothistroma*) and pathogens whose performance is directly tied to high availability of moisture. In contrast, drought typically increases performance and damage by secondary pathogens that colonize stressed trees and woody organs, such as stem cankers, root rots, and *Armillaria*. The response trends in figure 6.8, however, are based on knowledge about the role of available water on fungal performance and spread, and a few empirical studies of impacts of drought or tree water stress on pathogen performance and damage. There is a strong need for empirical data and predictive tools on how changes in drought frequency and severity will alter forest fungal pathogens. Future research using these data to model and predict forest disease incidents for forest ecosystems under different drought conditions would be useful for management (Klopfenstein and others 2009), as it will give forest managers additional foresight into potential outbreak conditions of the future.

Conclusions

It is clear that drought and associated temperature changes can significantly influence outbreaks of forest insects and pathogens, both positively and negatively, and that both drought and temperature are projected to increase in many parts of the United States in future years. In this review, we highlight specific research on insect and pathogens that is needed to better predict future climate-related impacts to forest ecosystems across the United States. Because eastern forests are generally less limited by water availability than western forests, less is known about the potential for drought impacts on insects and their role in tree mortality in eastern forests. Climate-change projections, however, strongly suggest an increase in temperature in eastern forests, which will intensify drought even if precipitation does not change (Ryan and Vose 2012). Interactions between drought and biotic disturbances are crucial in determining continental-scale forest productivity, ecotones between forests and shrubland or grasslands, carbon balance, and many other forest ecosystem services. Emerging and new knowledge of the role of drought and associated temperature changes in forest insect and pathogen-caused tree mortality will be essential components of models and frameworks for future forest management planning.

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