



Observed and anticipated impacts of drought on forest insects and diseases in the United States [☆]



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ABSTRACT

Future anthropogenic-induced changes to the earth's climate will likely include increases in temperature and changes in precipitation that will increase the frequency and severity of droughts. Insects and fungal diseases are important disturbances in forests, yet understanding of the role of drought in outbreaks of these agents is limited. Current knowledge concerning the effects of drought on herbivorous insect and pathogen outbreaks in U.S. forests is reviewed, and compared between the relatively mesic and structurally diverse forests of the eastern U.S. and the more xeric forests of the western U.S. Theory and limited evidence suggests a non-linear relationship between drought intensity and outbreaks of aggressive bark beetle species (i.e., those capable of causing extensive levels of tree mortality), where moderate droughts reduce bark beetle population performance and subsequent tree mortality, whereas intense droughts, which frequently occur in the western U.S., increase bark beetle performance and tree mortality. There is little evidence for a role of drought in outbreaks of the southern pine beetle (*Dendroctonus frontalis*), the only bark beetle species that causes large amounts of tree mortality in the eastern U.S. Defoliators do not show consistent responses to drought. The response of sapfeeders to drought appears non-linear, with the greatest performance and impacts at intermediate drought intensity or when drought is alleviated by wetter periods. Interactions between tree pathogens and drought are poorly understood, but available evidence suggests reduced pathogen performance and host impacts in response to drought for primary pathogens and pathogens whose lifecycle depends directly on moisture (humidity). In these cases, rates of reproduction, spread, and infection tend to be greater when conditions are moist. In contrast, secondary fungal pathogens (i.e., those that depend on stressed hosts for colonization) are anticipated to respond to drought with greater performance and host impacts. In the western U.S., drought increases stress on trees severely infected by mistletoes thereby predisposing mistletoe-infected trees to attack by insects, particularly bark beetles and wood borers. Research needed to advance understanding of drought impacts on forest insects and diseases, and the role of forest management in mitigation of infestations during drought are discussed.

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1. Introduction

Recent increases in drought intensity (i.e., magnitude of reduction in precipitation or soil moisture) resulting from increases in atmospheric temperature and changes in precipitation have been documented in many regions, including forests of the U.S. (Allen et al., 2010; Ryan and Vose, 2012). Mean annual temperature

projected by multiple climate models for the next century indicate 3–9 °C of warming in the U.S. combined with reductions in summer precipitation in some places (Walsh et al., 2014), strongly suggesting future increases in drought frequency, extent, and intensity in many U.S. forests. Changes in drought intensity and frequency have the potential to alter populations and impacts of forest insects, forest tree pathogens, and parasitic plants (Ayres and Lombardero, 2000; Dale et al., 2001; Sturrock et al., 2011; Weed et al., 2013). Scientists, forest managers, and environmental policy makers request a better understanding of the role of drought in outbreaks of forest insects and diseases in order to better anticipate future conditions, and to inform actions aimed at mitigating undesirable changes.

Here we review current understanding about the role of drought in outbreaks of herbivorous insects and tree diseases caused by fungal and oomycete pathogens and parasitic plants (e.g., mistletoes) in U.S. forests. We address this topic using our collective research on insects and diseases of North American forests (Bentz et al., 2010; Gaylord et al., 2013; Weed et al., 2013; Creeden et al., 2014) as well as that of others concerning interactions among climate change, drought, herbivorous insects, and disease pathogens in forests (Mattson and Haack, 1987; Koricheva et al., 1998; Ayres and Lombardero, 2000; Desprez-Loustau et al., 2006; Sturrock et al., 2011; Jactel et al., 2012; Olatinwo et al., 2013). First, we describe how drought affects host nutritional quality and tree susceptibility to colonization by forest insects and diseases. Second, we review responses to drought of the most important biotic agents of tree health in U.S. forests, including herbivorous forest insects (bark beetles, defoliators, and sapfeeders), fungal and oomycete pathogens, and mistletoes. Third, we highlight regional differences in past and projected future impacts of drought on forest insects and diseases by contrasting the western U.S. with the eastern U.S. Finally, we summarize our findings, highlight research needed to advance understanding of future drought impacts, and discuss the role of forest management in mitigation of impacts. Little is known about the effects of drought on bacterial and viral forest tree diseases, and therefore these are not discussed.

2. Tree responses to drought

2.1. Host tree nutrition and susceptibility to attack

Drought affects many components of tree nutritional quality. Several reviews of hundreds of studies (Mattson and Haack, 1987; Huberty and Denno, 2004; Rouault et al., 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 insect population growth (White, 1984). Positive effects of drought on tree damage by foliage-feeding insects are often attributed to increased nitrogen content of water-stressed leaves (Jactel et al., 2012). For example, caterpillar survival is often positively associated with conifer leaf nitrogen concentration (Shaw et al., 1978; Mattson,

1980; Hodar et al., 2002) until very high concentrations are reached (Brewer et al., 1987). Drought often causes early senescence of older leaves that remobilize 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). Reduction of tree tissue water content often interferes with insect utilization of nitrogen (Huberty and Denno, 2004). Timing and duration of water stress are important controls over insect ability 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.

Drought often alters plant defenses. The growth-differentiation-balance hypothesis (GDBH; Herms and Mattson, 1992) predicts that drought has non-linear impacts on carbon-based plant defenses that 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 greater negative effect of stress on the use of carbohydrates for growth than the production of carbohydrates by photosynthesis (Lorio, 1986; Reeve et al., 1995). In contrast, intense water stress causes plants to close stomata to avoid excessive water loss, which consequently reduces photosynthesis (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 et al., 2011; Tague et al., 2013). 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 (Turtola et al., 2003; Lusebrink et al., 2011). The few experimental studies of mature trees (Hodges and Lorio, 1975; Gilmore, 1977; Reeve et al., 1995; Gaylord et al., 2013) have shown that water stress can alter the amount and chemical composition of resin defenses in pines, sometimes with demonstrable consequences for reproductive success of bark beetles (Reeve et al., 1995). Drought-induced changes in tree defense compounds are rooted in alterations in transcription of genes associated with stress resistance (Arango-Velez et al., 2014).

Plant resistance to insect herbivory can include physical traits, such as leaf toughness, in addition to chemical and secondary metabolic traits (Carmona et al., 2011). Drought often alters insect feeding by increasing leaf toughness, which is positively associated with plant resistance against foliage-feeding insects. During drought, leaf water content decreases and leaf toughness and dry matter content increases (McMillin and Wagner, 1996; Pasquier-Barre et al., 2001). These changes are associated with reduction in folivore feeding and reproduction (Wagner and Zhang, 1993; Awmack and Leather, 2002).

Drought can increase plant attractiveness to insects by altering clues used to identify hosts (Mattson and Haack, 1987; Rouault et al., 2006; Kelsey et al., 2014). 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 (Mattson and Haack, 1987). Xylem cavitation in plants caused by drought results in ultrasonic acoustic emissions that likely are detectable by some insects (Haack et al., 1988). Insect chemoreceptors may detect drought-induced changes in suites of plant compounds. For example, drought can induce plant production of volatile compounds and ethanol that are olfactory attractants for some insects (Miller and Rabaglia, 2009; Miller et al., 2013; Kelsey et al., 2014).

3. Insect and pathogen responses to drought

Outbreaks of some herbivorous insects and fungal pathogens occur during or following drought (Koricheva et al., 1998; Sturrock et al., 2011). Performance and impacts of insects and pathogens during and following drought differ depending on the type of food substrate, feeding guild, duration of stress, and host defenses, among other factors. Intrinsic capacity for drought resistance, which can vary among individual trees, species and regions, also will 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, fungal and oomycete pathogens, and parasitic plants.

3.1. Bark beetles

Bark beetles feed on tree phloem and woody tissue and fungal associates. A few notable species cause death of the host tree, resulting in extensive economic and ecological impact when widespread outbreaks occur (Wood, 1982; Raffa et al., 2008; Bentz et al., 2010) (Fig. 1). 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 and phenolic concentrations increase following beetle attack and become more toxic and repellent shortly after attack (Franceschi et al., 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, storage, and transport of resin (Kane and Kolb, 2010; Hood and Sala, 2015). Intense drought reduces carbon assimilation, water transport, and cell turgor, thereby decreasing synthesis and mobilization of secondary metabolites, such as terpenes (McDowell et al., 2011; Sala et al., 2012). Water stress intensity may influence allocation of assimilated carbon to defense and growth, as described above using the GDBH. Although with chronic severe water stress both growth and defense are most likely reduced, moderate water stress could increase resistance if growth is constrained more than photosynthesis, thereby providing surplus carbon for resin synthesis and duct formation (Herms and Mattson, 1992; Lieutier, 2004). Although water stress can reduce overall emissions of volatile compounds due to stomatal closure (Lusebrink et al., 2011), the relative concentrations of some terpenes can change, perhaps making drought-stressed trees more attractive to bark beetles (Hodges

and Lorio, 1975; Kimmerer and Kozlowski, 1982; Kelsey et al., 2014).

Bark beetles can be positively or negatively affected by drought, depending on drought intensity, duration, and tree water stress (Raffa et al., 2008). Positive feedbacks between drought and bark beetle outbreaks have occurred in semi-arid forests of the western U.S. during intense drought (Fig. 1b and c) (Greenwood and Weisberg, 2008; Negrón et al., 2009; Bentz et al., 2010; Gaylord et al., 2013, 2015; Fettig, 2016), whereas negative feedbacks on southern pine beetle (*Dendroctonus frontalis*) are more likely in the more mesic forests of the eastern U.S. (Lombardero et al., 2000). Although severely water-stressed trees may be more attractive to bark beetles, low resource levels in chronically stressed trees may negatively affect development of some bark beetles, their associated fungi, and perhaps other phoretic organisms (Raffa and Berryman, 1983; Waring and Pitman, 1983; Croisé and Lieutier, 1993; Storer and Speight, 1996; Huberty and Denno, 2004; Mercado et al., 2014). This suggests that continuously-stressed trees could result in poor bark beetle population development as observed for other feeding guilds (Huberty and Denno, 2004).

Few studies have experimentally investigated effects of drought on bark beetle populations. Instead, most studies have retrospectively investigated associations between drought and tree mortality due to bark beetles to infer drought impacts on bark beetle populations. Associations have been reported between reduced precipitation and outbreaks of fir engraver (*Scolytus ventralis*) (Ferrell et al., 1994), Douglas-fir beetle (*Dendroctonus pseudotsugae*) (Kane et al., 2014), Jeffrey pine beetle (*Dendroctonus jeffreyi*) (Fettig, 2016), mountain pine beetle (*Dendroctonus ponderosae*) (Thomson and Shrimpton, 1984; Evangelista et al., 2011; Chapman et al., 2012; Creeden et al., 2014), roundheaded pine beetle (*Dendroctonus adjunctus*) (Negrón et al., 2009), spruce beetle (*Dendroctonus rufipennis*) (Hebertson and Jenkins, 2008; DeRose and Long, 2012; Hart et al., 2014), western pine beetle (*Dendroctonus brevicomis*) (Jones et al., 2004; Negrón et al., 2009), and several engraver beetles, most notably Arizona fivespined ips (*Ips lecontei*) (Negrón et al., 2009; Ganey and Vojta, 2011), California fivespined ips (*Ips paraconfusus*) (Fettig, 2016), eastern fivespined ips (*Ips grandicollis*) (Conner and Wilkinson, 1983), pine engraver (*Ips pini*) (Negrón et al., 2009; Ganey and Vojta, 2011), sixspined ips (*Ips calligraphus*) (Negrón et al., 2009), and pinyon ips (*Ips confusus*) (Shaw et al., 2005). The role of drought in predisposing pinyon pine (*Pinus edulis*) to pinyon ips attacks has been confirmed



Fig. 1. Examples of extensive tree mortality in the western U.S. caused by bark beetles during severe drought in the early 2000s. (a) Pine forests of the Intermountain West due to mountain pine beetle (*Dendroctonus ponderosae*) (photo B. Bentz, USDA Forest Service). (b) Pine forests of southern California due to western pine beetle (*Dendroctonus brevicomis*) (photo: C. Fettig, USDA Forest Service). (c) Pinyon pine forests (e.g., *Pinus monophylla*) of the southwestern U.S. due to pinyon ips (*Ips confusus*) (photo: C. Fettig, USDA Forest Service).

by a recent experimental manipulation of precipitation (Gaylord et al., 2013). The effect of drought on tree mortality from bark beetles can vary depending on lag time and outbreak duration (Preisler et al., 2012). 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 favorable temperatures, extensive host abundance, concentrated beetle density, optimal symbiotic associations, and escape from natural enemies, amplify over spatial and temporal scales (Raffa et al., 2008, 2015). Conversely, pinyon ips (Fig. 1c) depends more directly on water-stressed trees for successful reproduction as illustrated by a rapid reduction in the population outbreak and tree mortality in the southwestern U.S. during the early 2000s when wetter conditions returned (Raffa et al., 2008). The drought in the early 2000s that coincided with outbreaks of several bark beetle species created conditions of severe water stress (Gaylord et al., 2007; Breshears et al., 2009; Negrón et al., 2009), as it was one of the most severe droughts in the past 500 years in many parts of the interior western U.S. (Pielke et al., 2005). This drought had warmer than average temperatures that likely positively influenced bark beetle survival and population growth (Breshears et al., 2005). Warm winters can reduce cold-induced mortality of beetles (Bentz and Mullins, 1999; Tran et al., 2007) and warm summers can reduce generation time (Thatcher and Pichard, 1967; Bentz et al., 2014). The effect of drought on bark beetle population growth is not straightforward, however, as increased precipitation may positively influence bark beetle population growth by providing a more nutritious food resource for developing larvae, and by reducing tree defense when carbon is preferentially allocated to growth as predicted by the GBDH (Herms and Mattson, 1992; Lombardero et al., 2000; McDowell et al., 2011).

3.2. Defoliators

Forest defoliators consume, mine, or skeletonize foliage. 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 (e.g., eastern spruce budworm, *Choristoneura fumiferana*). While outbreaks of forest defoliators have been linked to drought (Mattson and Haack, 1987), much of the evidence supporting this relationship is circumstantial. Magnitude and direction of defoliator responses to drought are variable. For example, several studies have shown drought increases performance and impact of defoliators while others have shown the opposite (Jactel et al., 2012). The meta-analysis by Jactel et al. (2012) concluded that the overall effect of drought on the amount of foliage damaged by chewing insects was positive, but not significantly different from zero based on a 95% confidence interval. Moreover, defoliators inflicted greater damage on drought-stressed than unstressed trees, but the effect was largely attributed to galling insects (Jactel et al., 2012).

Most research has focused on indirect effects of drought on defoliators as mediated through changes in host tree physiology, primarily leaf chemistry and palatability. Most current knowledge comes from laboratory studies on seedlings due to the inherent difficulties of studying responses of defoliators to drought-stressed mature trees in forest environments. Seedling studies may or may not reflect responses of mature trees. Little is known about 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 epizootics in outbreak populations of the gypsy moth (*Lymantria dispar*) in the eastern U.S., requires high levels of moisture for

conidial production and discharge (Hajek, 1999). As indicated earlier, drought-stressed plants are consistently warmer than unstressed plants because reduced transpiration limits plant cooling (Mattson and Haack, 1987). This has important implications to the insects colonizing them and their impacts to the host, given inherent increases in insect performance (e.g., regarding growth rate, consumption rate, and reduced developmental time) associated with elevated temperature (Levesque et al., 2002).

Many defoliators preferentially feed on leaves with high protein and water content, low leaf toughness, and low concentrations of secondary metabolites (Dury et al., 1998). Drought often affects nutritional quality of foliage by causing changes in water, carbohydrate, and nitrogen concentrations. The magnitude and direction of responses to drought by defoliators are influenced by intensity and duration of drought stress (Jactel et al., 2012). However, drought stress intensity 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 during severe drought better than trees that have wide xylem conduits (most angiosperms) (Brodrigg and Cochard, 2009). Overall, compromised physiological function and reduced productivity often leads to a higher vulnerability to insect attack (Bolton, 2009).

Nitrogen concentration often increases in foliage during drought (White, 1969, 1984), which may increase performance of defoliators because nitrogen is often a limiting growth factor (Mattson and Haack, 1987; Rouault et al., 2006). For some insects, nutrients in unstressed foliage are below levels optimal for development and even moderate stress can cause significant changes in the foliage quality that increase defoliator performance (Mattson and Haack, 1987; Larsson and Björkman, 1993; Rouault et al., 2006). Alternatively, Craig et al. (1991) found no consistent evidence that drought stress led to increased performance of sawflies (*Neodiprion* spp.) in ponderosa pine (*Pinus ponderosa*) trees. 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). Interestingly, Athey and Connor (1989) showed black locust (*Robinia pseudoacacia*) with high concentrations of foliar nitrogen received more herbivory by adult, but not larval, locust needleminer (*Odontota dorsalis*). Adult beetles skeletonize and chew holes in the leaves, whereas larvae mine the tissue between the upper and lower leaf surfaces, which tends to be more damaging.

Drought may negatively impact defoliator performance through reduced leaf water content, which usually increases leaf toughness and reduces palatability and consumption. 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 (Tikkanen and Lyttikäinen-Saarenmaa, 2002; Henriksson et al., 2003). 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 than larvae fed leaves fully supplemented with water.

Concentrations of secondary metabolites often increase in foliage as a result of drought stress, which negatively impacts most defoliators. Hale et al. (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 compared with drought-stressed seedlings despite the latter having smaller carbohydrate stores. In their study, continuous drought stress decreased growth of gypsy moth (*L. dispar*) larvae likely as a result of decreased foliar nitrogen and increased total phenolic glycoside concentrations, but had no effect on white-marked tussock moth (*Orygia leucostigma*) larvae, which is thought to be less sensitive

to increases in phenolic glycosides than gypsy moth (Kopper et al., 2002). Roth et al. (1997) investigated effects of carbon dioxide and water availability on quaking aspen (*Populus tremuloides*) 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. These carbon dioxide and drought-mediated changes reduced performance of forest tent caterpillar (*Malacosoma disstria*) (Roth et al., 1997).

Insect defoliation may alter tree response to drought. Insect defoliation of conifers during experimental drought has been reported to have little effect (Jacquet et al., 2014), reduce (Kolb et al., 1999), or increase tree water stress (Domec et al., 2013; Gonda-King et al., 2014). The few studies of the combined effects of previous herbivory and drought show largely additive effects with the lowest carbohydrate pools in water-stressed trees exposed to 100% defoliation (Jacquet et al., 2014). Defoliation can reduce tree carbohydrate storage, redistribute carbohydrates from roots to stems, and reduce stem hydraulic conductance due to decreased xylem growth (Anderegg and Callaway, 2012; Jacquet et al., 2014). These responses should increase vulnerability of defoliated trees to drought. Moreover, defoliation can increase occurrence of fungal cankers, stem borers, and bark beetle attacks (Anderegg and Callaway, 2012). Further, insect herbivory on roots increases tree susceptibility to drought by reducing root growth (Zvereva and Kozlov, 2012). These findings show that previous defoliation and other types of herbivory can influence tree response to future drought.

3.3. Sapfeeders

Water stress is hypothesized to positively influence phloem sapfeeders, such as aphids (Aphididae) and adelgids (Adelgidae), through an increase in phloem nitrogen content. Meta-analyses, however, suggest the response is variable, and dependent on the level of stress and resultant turgor pressure of the tree (Koricheva et al., 1998; Huberty and Denno, 2004). Spruce aphid (*Elatobium abietum*) performance and population growth, for example, were greatest when water stress was intermittent and lowest when stress was continuous (Major, 1990). Lynch (2003) reported that spruce aphid outbreaks tend to occur after dry winter and spring conditions in high-elevation forests in Arizona, but do not seem to be influenced by the amount of moisture received during the summer monsoon. Under continuous water stress, availability of leaf and phloem nitrogen to sap-feeders is diminished due to reduced turgor, but moderate or periodic stress increases nitrogen availability during periods of turgor recovery. These results suggest that the optimum host is a plant that has experienced long-term intermediate stress, and then temporarily released from stress by abundant precipitation during insect feeding (Mopper and Whitham, 1992). The response of sap-feeders to water stress also can vary with life stage. The sucking stage of the eastern spruce gall adelgid (*Adelges abietis*) is positively influenced by drought, whereas the galling life stage, which requires expanding plant tissues for successful gall formation, is negatively influenced (Björkman, 2000). The effect of host water stress on sap-feeder performance is also likely to be affected by the history and severity of the infestation and local site conditions. For instance, adelgid feeding decreases whole tree water potential (Arthur and Hain, 1986; Domec et al., 2013) which, may have a negative feedback on adelgid performance if infestation density and site conditions resulted in continuous water stress. Both the balsam woolly adelgid (*Adelges piceae*) and hemlock woolly adelgid (*Adelges tsugae*), two notable exotic, sapfeeding species, cause significant tree mortality in eastern North America, and their impacts are expected

to intensify as a result of climate change (Dale et al., 2001; Paradis et al., 2008), particularly warm winters and summer drought (Eschtruth et al., 2013).

3.4. Fungal and oomycete pathogens

Few studies have directly addressed the effects of drought on fungal and oomycete tree pathogens. However, it has been predicted that drought could alter the prevalence, severity, and geographic patterns of many tree pathogens because fungi are strongly influenced by humidity and temperature (Sturrock et al., 2011). On one hand, drought that increases tree water stress and reduces resources available for defense could make trees more susceptible to pathogen colonization and impacts. On the other hand, drought may retard the development, survival, reproduction, and dispersal of fungal pathogens because many rely on moisture to cause infection (Klopfenstein et al., 2009). Changes in moisture availability could directly influence fungal pathogen sporulation and infection of host species (Sturrock et al., 2011). However, it is not clear how drought affects pathogen survival, as fungal pathogens are highly adaptable and have diverse reproductive systems adapted to changing environmental conditions (Olatinwo et al., 2013).

Desprez-Loustau et al. (2006) suggested that drought duration is an important predictor of forest disease impacts on trees because more infections are likely to develop during or after prolonged drought. Jactel et al. (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 intensity. They reported that primary pathogens that infect wood and foliage of healthy trees inflict less damage on trees during drought (Jactel et al., 2012). 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 et al., 2011). In contrast, drought is expected to increase host damage by secondary pathogens that colonize woody organs of stressed trees, such as root rot pathogens, stem wound colonizers, and latent colonizers of sapwood (Desprez-Loustau et al., 2006; Sturrock et al., 2011; Jactel et al., 2012).

Needle diseases 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 et al., 2002). Therefore, drought will likely decrease the incidence and severity of these diseases (Thompson et al., 2014). Rates of infection by other needle pathogens, such as *Dothistroma septosporum* and *Dothistroma pini* that cause *Dothistroma* needle blight of pine (*Pinus*), spruce (*Picea*), larch (*Larix*), and Douglas-fir (*Pseudotsuga menziesii*) (Barnes et al., 2004), and *Phaeocryptopus gaumannii* that causes Swiss needle cast of Douglas-fir, are also closely linked to temperature and moisture (Hansen et al., 2000; Stone et al., 2008). High levels of moisture were critical for infection by *D. septosporum* where ten or more consecutive hours of needle wetness at temperatures between 16 and 20 °C were needed for infection (Bulman, 1993). High levels of *P. gaumannii* incidence have been positively correlated with winter rainfall accumulation and leaf wetness hours (Manter et al., 2005).

The incidence of rust diseases may be affected not only by drought, but also by the presence or absence of alternate hosts. Many stem rust pathogens, such as fusiform rust (*Cronartium quercuum*, or *Cronartium fusiforme*) and white pine blister rust (*Cronartium ribicola*), require primary and secondary hosts in addition to extended periods of ample moisture to complete their lifecycles. Drought could alter the geographic range of these hosts (Olatinwo et al., 2013). Fusiform rust is a significant pathogen on

pinus in the southeastern U.S. The alternative host in the Southeast is primarily water oak (*Quercus nigra*). In some areas, fusiform rust may not complete its lifecycle if the geographic range of water oak changes during future drought. The fungus that causes white pine blister rust was introduced to North America from Europe in the early 1900s, and environmental requirements for disease progression are well documented. Needle infection requires 48 h of 100% relative humidity and temperatures less than 20 °C (Van Arsdell et al., 1956). Multiple *Ribes* species, the alternate host for WPBR, are distributed throughout the western U.S. (Hummer and Dale, 2010), and large changes in their distributions are unlikely. However, drought will likely result in less infection by white pine blister rust in regions where moisture is or becomes a limiting factor to *C. ribicola* because of dependence of water for sporulation (Kinloch, 2003; Kliejunas, 2011).

Phytophthora ramorum, the causal agent of sudden oak death, has had a significant impact on tanoak (*Notholithocarpus densiflorus*) and live oak (*Quercus agrifolia*) in California and Oregon. *P. ramorum* has been demonstrated to be a high-risk pathogen to wetter forests in North America because of its ability to infect a wide range of hosts (Dodd et al., 2008). However, like all *Phytophthora* species, extended periods of rainfall in fall or spring are essential to its persistence. Therefore infections by *Phytophthora* spp. would likely decrease during extended drought, unless drought is followed by periods with extended rainfall (Venette, 2009; Weed et al., 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 (Sturrock et al., 2011; Olatinwo et al., 2013). *Armillaria* root rot is caused by primary and secondary pathogens that infect conifers and hardwoods (Kile et al., 1991). Infections cause wood decay, growth reduction, and tree mortality, and increase tree susceptibility to colonization by insects (Sturrock et al., 2011). Drought may increase incidence of *Armillaria* root rot (La Porta et al., 2008; Klopfenstein et al., 2009). Similarly, *Heterobasidion* root rot, caused by *Heterobasidion irregulare* and *Heterobasidion occidentale*, could increase in geographic range and incidence during drought (Kliejunas et al., 2009; Otrosina and Garbelotto, 2010). Currently the disease in the southeastern U.S. causes significant mortality to conifers, and drought may increase impacts there (Duerr and Mistretta, 2011). In the western coast of Italy, where environmental conditions are becoming increasingly hotter and drier, widespread mortality of Corsican pine (*Pinus nigra* var. *maritime*) was caused by *Heterobasidion* root rot (Gonthier et al., 2007). In these drier conditions, incidence and distribution of the pathogen appears to be increasing.

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 et al., 1996; Kliejunas, 2011). Cankers caused by *Cytospora umbrina* on thinleaf alder (*Alnus incana*) have been found in epidemic levels in the Rocky Mountains in Colorado and riparian areas of Alaska. Drier and hotter conditions will further stress trees, exacerbating disease pressure by *Cytospora* (Kliejunas, 2011). Cankers caused by *Septoria musiva* on poplar (*Populus* spp.) stems were significantly larger on water-stressed trees compared to unstressed trees (Maxwell et al., 1997; Desprez-Loustau et al., 2006). Likewise, increased severity of Diplodia shoot blight caused by *Diplodia sapinea* has been associated with water stress of trees in several studies (Blodgett et al., 1997; Paoletti et al., 2001).

Fungal pathogens often predispose trees to drought stress. A recent framework (Oliva et al., 2014) predicts that necrotrophs, which obtain nutrients from dead cells, accelerate drought-

induced tree mortality by depleting tree resources used for compartmentalization. Vascular wilts are predicted to accelerate drought-induced tree mortality by reducing sapwood hydraulic conductance and phloem transport. Biotrophs, which obtain nutrients directly from living tree tissues, are predicted to be negatively affected by drought because their performance is linked to tree nutritional status. Biotrophs that successfully invade stressed trees, however, are predicted to exacerbate drought impacts because they deplete carbohydrate reserves important for tree drought tolerance (Oliva et al., 2014).

Drought and forest fungal and oomycete pathogens often are implicated as causal factors in tree diseases of complex etiology, or decline diseases (Manion, 1991). Decline diseases are caused by a multitude of pre-disposing, inciting, and contributing factors including drought and fungal pathogens. In a review of aspen decline in North America, Worrall et al. (2013) concluded that recent declines in many regions, including the western U.S., were primarily induced by drought, but that other abiotic and biotic agents, including fungal pathogens, also played a role. Primary pathogenic agents such as sooty-bark canker (*Encoelia pruinosa*), multi-year defoliation by tent caterpillars (*Malacosoma* spp.), and secondary agents such as boring insects, fungal cankers, and *Armillaria* root disease were associated with drought-induced aspen mortality in most studies (Worrall et al., 2013). Tree-ring studies in the western U.S. show that chronically low growth rates predispose aspens to mortality during severe drought (Hanna and Kulakowski, 2012; Ireland et al., 2014; Kane and Kolb, 2014). These studies 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 U.S. is consistent with Manion’s decline disease framework (Manion, 1991) with drought acting as an inciting factor and biotic agents as contributing factors.

3.5. Parasitic plants

Parasitic plants typically intensify negative impacts of drought on tree water stress and growth by obtaining water and nutrients from tree hosts (Stewart and Press, 1990; Sanguesa-Barreda et al., 2012). High transpiration rates of xylem-tapping parasites, such as mistletoes (e.g., *Phoradendron* spp.), often reduce xylem water potential, stomatal conductance, net photosynthetic rate, and water-use efficiency of host branches and leaves (Ehleringer et al., 1986; Zweifel et al., 2012; Sanguesa-Barreda et al., 2013). 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 (e.g., *Arceuthobium* spp.), predispose trees to drought by altering host hormones (Logan et al., 2013) and hydraulic processes (Sala et al., 2001), reducing net photosynthetic rate and water use efficiency (Meinzer et al., 2004; Marias et al., 2014), and depleting carbohydrates (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 (Knutson and Toevs, 1972; Stewart and Press, 1990). Dwarf mistletoes may also predispose conifers to lethal bark beetle attacks during drought (Hawksworth and Wiens, 1996; Kenaley et al., 2008; Kliejunas, 2011).

Trees severely infected by dwarf mistletoes are frequently the first to die during drought (Byler, 1978; Hawksworth and Wiens, 1996; Millar et al., 2005; Kliejunas, 2011). This is particularly evident in pine forests in southern California with severe infestations of western dwarf mistletoe (*Arceuthobium campylopodum*), and in true fir forests in the Sierra Nevada of California infested with fir dwarf mistletoe (*Arceuthobium abietinum*) (Kliejunas, 2011). In addition, mortality of dwarf mistletoe-infected trees during

droughts is exacerbated by the high stand densities in many western forests due to the additional competition for water placed on infected trees (Byler, 1978; Negrón and Wilson, 2003). Immediately after the 1975–1977 drought in California, mortality of ponderosa pine infected with western dwarf mistletoe was reported to be more than four times greater than that of noninfected pines (Page, 1981; Smith, 1983). During droughts in northern Arizona in 1989–1990 and 2000–2002 mortality of pinyon pine was associated with pinyon dwarf mistletoe (*Arceuthobium divaricatum*) infection as well as high stand densities and attacks by pinyon ips (Wilson and Tkacz, 1992; Negrón and Wilson, 2003). Because the effects of climate change are predicted to cause warmer and drier conditions during the winter in the western U.S., it is probable that droughts will be more common, thereby increasing the negative impacts of dwarf mistletoes on coniferous forests (Kliejunas, 2011).

Mistletoes in the genus *Phoradendron* have also been shown to increase stress on their hosts during intense drought because these parasites are efficient at extracting large amounts of water from severely infected trees (Fisher, 1983; Kolb, 2002). Although severely mistletoe-infected trees suffer mortality during intense drought, only a few studies in the U.S. have investigated this relationship (Mathiasen et al., 2008). Lei (2001) found that severe infection by desert mistletoe (*Phoradendron californicum*) increased mortality of catclaw acacia (*Acacia greggii*) during an intense drought in southern Nevada from 1995 to 1997. Another facet of the severe drought was that the more severely infected acacia had greater reductions in canopy volume and flower/fruit/seed production than acacia with low or no mistletoe infection. The drought also increased the mortality of mistletoe plants and reduced mistletoe canopy volume and fruit production. Lei (2001) concluded that the severe drought actually had a greater impact on the survival of the mistletoe than its host. Jordan et al. (1997) reported similar findings for the same host-mistletoe relationship in southeastern California during a severe drought, and further concluded that the drought caused substantial levels of mistletoe mortality and may have limited the long-term success of the mistletoe; the drought also caused greater mortality of severely infected host trees. Another study of the effects of desert mistletoe in the Mojave Desert reported that nearly 60% of the mistletoe-infected blue palo verde (*Cercidium floridum*) died during a severe drought from 2001 to 2002 (Spurrier and Smith, 2007). In contrast, only about 3% of the uninfected palo verde died during the same period. These studies all support the hypothesis that mistletoe infection increases tree mortality during intense drought, presumably because of greater water stress on mistletoe-infected trees. Drought-induced die-back of mistletoe-infected branches has been commonly reported for other mistletoe-host associations, but the degree of damage to the hosts and mistletoes has not been thoroughly quantified (Childs, 1960; Mathiasen et al., 2008).

4. Regional differences in observed and future impacts

4.1. Western U.S.

Bark beetles are currently the most important biotic agent of tree mortality in the western U.S. and recent outbreaks have impacted a larger area than wildfires (Hicke et al., 2016). Multiple large outbreaks have killed hundreds of millions of trees in recent decades (Meddens et al., 2012). Aggressive 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 epidemics through effects on both insects and host trees (Raffa et al., 2008; Bentz et al., 2010). Drought produces an

increased source of susceptible host trees, which allows beetle populations to build. For example, spruce beetle outbreaks in Alaska in the 1990s were linked to temperature-induced drought (Berg et al., 2006; Sherriff et al., 2011), and in multiple outbreaks in Utah and Colorado, drought was identified as an important influence (Hebertson and Jenkins, 2008; DeRose and Long, 2012; Hart et al., 2014). Moisture-induced drought has been linked to recent outbreaks of mountain pine beetle in the western North America (Raffa et al., 2008; Preisler et al., 2012; Chapman et al., 2012; Creeden et al., 2014). Similarly, there is evidence that some bark beetle species initiate infestations in hosts growing in drier landscape positions, such as south-facing slopes (Kaiser et al., 2013). 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 U.S. have been attributed to warming (Carroll et al., 2004; Logan et al., 2010; Weed et al., 2015). Drought played a role in initiating these outbreaks and facilitating population increases to levels that killed healthy trees, but warming was the primary reason for these epidemics occurring in historically unknown or rare locations (Bentz et al., 2010).

In contrast to aggressive bark beetle species, successful attacks of less aggressive bark beetles in the western U.S. are usually limited to stressed hosts, and as such outbreaks are closely tied to drought and associated warm temperatures. In the early 2000s, a “global-change-type drought” occurred in the southwestern U.S. in which extremely low precipitation occurred during unusually warm weather (Breshears et al., 2005). *Ips* populations increased and together with extreme tree physiological stress, caused mortality over large areas of pinyon pine (Shaw et al., 2005; Meddens et al., 2012) and ponderosa pine (Negrón et al., 2009) forests. When wetter conditions returned, *Ips* populations declined. Outbreaks of other bark beetle species, such as Douglas-fir beetle, western balsam bark beetle (*Dryocoetes confusus*), and fir engraver, also caused extensive tree mortality in the early 2000s (Meddens et al., 2012), although the role of drought has not been quantitatively established. In southern California, severe drought stress (i.e., precipitation was the lowest in recorded history during 2001–2002) was important in facilitating a western pine beetle outbreak (Fig. 1b). In addition, elevated ozone and nitrogen deposition were likely predisposing factors (Jones et al., 2004; Fettig, 2016).

The role of drought in the western U.S. in defoliator outbreaks is less well understood than for bark beetles. One of the most important defoliating insects in the West is western spruce budworm (*Choristoneura occidentalis*), which attacks multiple conifer species and causes widespread tree mortality. Budworm outbreaks are related to environmental factors that promote synchrony between caterpillar development and foliage phenology, and to drought (Thomson et al., 1984; Williams and Liebhold, 1995a; Campbell et al., 2006). Budworm outbreaks are associated with wetter conditions at the end of droughts that increase food resources (Swetnam and Lynch, 1993; Ryerson et al., 2003; Flower et al., 2014). Multiple influences of drought may be important to budworm outbreaks, and likely vary regionally (Lynch, 2012). Outbreaks of other defoliators in the western U.S. may be influenced by drought as well, although studies are lacking for many insects (e.g., Douglas-fir tussock moth, *Orgyia pseudotsugata*) or may be conflicting for others. For example, a study reported that outbreaks of Pandora moth (*Coloradia pandora*) occurred during dry conditions (Pohl et al., 2006), whereas an earlier study reported drought had no impact on outbreaks of *C. pandora* (Speer et al., 2001).

Future impacts of defoliators on drought-stressed forests in the western U.S. are unclear. This partially results from inconsistencies in the direction and magnitude of defoliator responses to drought, and because recent bark beetle outbreaks and wildfire have

overshadowed impacts of defoliators. Williams and Liebhold (1995a, 1995b) investigated potential changes in spatial distribution of outbreaks of western spruce budworm in eastern Oregon under several climatic change scenarios. With a temperature increase of 2 °C and a decrease in precipitation, the projected defoliated area decreased relative to ambient conditions. However, with an increase in temperature and precipitation, the defoliated area was projected to increase. Considerable uncertainty remains about future impacts of defoliators on drought-stressed forests in the western U.S.

Pathogens are important forest disturbance agents in the western U.S. As described above, some fungal and oomycete 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 little role of drought in outbreaks of these pathogens (Sturrock et al., 2011; Jactel et al., 2012). Other fungal pathogens, such as those causing *Armillaria* root disease or various cankers such as *Cytospora*, are indirectly affected by drought through increasing stress of host trees, implying that drought leads to more favorable conditions for outbreaks (Klopfenstein et al., 2009; Kliejunas, 2011; Sturrock et al., 2011; Jactel et al., 2012). Overall, outbreaks of forest diseases caused by native and introduced fungal and oomycete pathogens are generally thought to become more frequent and severe as a result of drought (Sturrock et al., 2011). Mistletoe infestations can predispose conifers in the western U.S. to drought stress and subsequent lethal bark beetle attacks.

Across the western U.S., temperature increases are projected to exceed global mean increases and more frequent extreme weather events, such as drought, are expected (Levinson and Fettig, 2014). Winter precipitation is projected to increase in some areas, but to decrease by up to 20% in the southwestern U.S. by the 2050s. Summer precipitation is projected to decrease by 10–30% throughout the West by the 2050s (Fettig et al., 2013). Observed increases in temperature have been greater in winter and spring than summer (National Climate Assessment, 2014). Warming during winter will further accelerate recent declines in snow pack. As such, many forests in the western U.S. will experience further increases in drought stress whether associated with reductions in precipitation and/or increases in evaporative demand associated with elevated temperature. Williams et al. (2013) reported that if the vapor-pressure deficit continues increasing in the southwestern U.S., as projected by climate models, by the 2050s mean forest drought stress will exceed that of the most severe droughts in the past 1000 years.

An increase in the frequency and severity of some biotic disturbances is expected in the western U.S. as a result of more intense drought stress and increasing temperature (Bentz et al., 2010; Fettig et al., 2013; Weed et al., 2013). However, our understanding of these relationships is mostly limited to a small number of insect species in conifer forests. For insects, range expansions and increases in the frequency and severity of outbreaks by some bark beetle species have already been documented (Bentz et al., 2009) and further increases are anticipated (Williams and Liebhold, 2002; Bentz et al., 2010; Sambaraju et al., 2012). Moreover, population response will not always be positive as adaptive seasonality (i.e., life stage-specific developmental thresholds that aid in synchronizing adult emergence to appropriate times of the year) can be disrupted in some new thermal habits (Bentz et al., 2016). Increasing temperatures and drought stress, exacerbated by high densities of suitable and susceptible hosts (Fettig et al., 2007; Hicke and Jenkins, 2008), have contributed to the positive feedbacks necessary for range expansions and epidemic populations of insects to occur (Raffa et al., 2008). Although geographically variable, increases in the impact of several bark beetle species are expected with future climate change (Bentz et al., 2010). It is

important to note, however, that significant areas of the western U.S. have already experienced high levels of tree mortality due to bark beetles (Meddens et al., 2012), and susceptible hosts may be depleted in some areas, which would dampen future outbreaks for decades.

4.2. Eastern U.S.

4.2.1. Hardwood forests

In the East, aspen, poplar (*Populus*), maple (*Acer*), oak (*Quercus*), hickory (*Carya*), beech (*Fagus*), ash (*Fraxinus*), and birch (*Betula*) are 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 expansions of the nonnative emerald ash borer (*Agrilus planipennis*), thousands cankers disease, and laurel wilt in the region. The impacts of these biotic agents seem largely unrelated to drought (Olatinwo et al., 2013; Weed et al., 2013). One exception is the recent epidemic of red oak mortality in the Ouachita and Ozark Mountains (Jones et al., 2014; Haavik et al., 2015) 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 et al., 2007), along with effects of warming temperatures on insect developmental rates and fitness (Weed et al., 2013).

4.2.2. Conifer forests

Insects and pathogens are continuous threats to the health of conifer forests in the eastern U.S. The southern pine beetle 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 (*Tsuga canadensis* and *Tsuga caroliniana*) and Fraser fir (*Abies fraseri*) stands; and eastern spruce budworm outbreaks periodically disturb the eastern boreal forest.

The hypothesis that drought triggers outbreaks of southern pine beetle has been under investigation for nearly a century (Hodges and Lorio, 1975; Lorio, 1986; Reeve et al., 1995). As with conifers in the western U.S., oleoresin is the primary mechanism in conifers conferring resistance to southern pine beetle (Lorio, 1986; Lombardero et al., 2000; Raffa et al., 2005). Resin flow in loblolly pine (*Pinus taeda*), the most abundant pine of the southeastern U.S., increases under conditions of moderate water deficit (Dunn and Lorio, 1993; Reeve et al., 1995; Lombardero et al., 2000), and does not decrease until drought is extreme (Lorio et al., 1995). This matches expectations derived from the GDBH described in earlier sections. Resin flow of loblolly pine tends to be highest during seasonal periods of suboptimal growth, such as under moderate water stress (Lombardero et al., 2000). Furthermore, analyses of time series data have failed to reveal the expected relations between drought and southern pine beetle fluctuations (Turchin et al., 1991; McNulty et al., 1997). Diverse evidence argues against the hypothesis that southern pine beetle outbreaks are promoted by drought, but rather are linked to warming winter temperatures (Ungerer et al., 1999; Tran et al., 2007) and an abundance of susceptible hosts (Nowak et al., 2015).

In addition to southern pine beetle, there are three species of engraver beetles in the southern U.S., the sixspined engraver, five-spined engraver, and the small southern pine engraver (*Ips avulsus*), that attack pines, and for which drought has been implicated as an inciting factor (Conner and Wilkinson, 1983). These species usually colonize weakened, dead and dying trees and logging debris. If favorable climatic conditions coincide with large quantities of suitable host material, populations of these

species may erupt and result in mortality of apparently-healthy trees. While no studies have investigated the effects of drought on these species in mature pines in the southern U.S., studies of lightning-struck trees (Anderson and Anderson, 1968) indicate a negative relationship between oleoresin exudation rate and *Ips* attacks and brood development. Low phloem moisture limited brood development only when desiccation was severe (Anderson and Anderson, 1968).

In summary for the eastern U.S., we lack strong evidence that outbreaks of forest insects, fungal pathogens, and mistletoes are triggered by water stress or drought. The future effects of drought on forest insects and diseases in eastern U.S. forests are anticipated to be modest relative to effects from warming and introductions of non-native insects and pathogens (Duehl et al., 2011; Olatinwo et al., 2013; Weed et al., 2013). Precipitation has increased over the last century in much of the eastern U.S. and changes in temperature over this period have been smaller than in much of the western U.S. and Alaska (Ryan and Vose, 2012). For example, droughts in the northeastern U.S. have been historically rare and are projected to remain low in intensity through this century (Hayhoe et al., 2007; Peters et al., 2015). Whereas temperature is projected to increase in the eastern U.S., with the magnitude of this increase dependent on the amount of carbon emissions, precipitation projections range from no change to increases of up to 10% depending on the climate model and location within the eastern U.S. (Ryan and Vose, 2012). Outbreaks of several forest insects of eastern forests are linked to warm winter temperatures (e.g., southern pine beetle, Ungerer et al., 1999; Tran et al., 2007; hemlock woolly adelgid, Paradis et al., 2008) and it is expected that the outbreak ranges of these species will expand northward given the projected trend in winter temperatures. Warmer temperatures with no change in precipitation will increase vapor pressure deficit, which will tend to reduce water availability in surface soil due to higher evaporation, and reduce forest photosynthesis due to more frequent stomatal closure (Eamus et al., 2013). The ultimate effect of interactions between future projected changes in temperature and precipitation on drought intensity and forest response to drought in the eastern U.S. is unknown, but impacts are expected to be smaller than in semi-arid forests of the western U.S. The eastern forests most likely to experience increases in extreme drought in the future are those already subject to occasional droughts, such as forests near the edge of the Great Plains. In these forests there may be a tendency for drought to increase susceptibility of hardwood trees to wood boring beetles (Dunn et al., 1990; Muilenburg and Herms, 2012), for example, as observed in the Ouachita and Ozark Mountains (Haavik and Stephen, 2010). Impacts on ash from the emerald ash borer could also be exacerbated by drought (Chakraborty et al., 2013).

5. Summary, research needs, and management

5.1. Bark beetles

Our review about impacts of drought on bark beetle performance and associated levels of tree mortality in U.S. forests is consistent with predictions of plant carbon allocation models (Herms and Mattson, 1992; McDowell et al., 2011) that moderate drought or tree water stress reduces bark beetle population performance and subsequent tree mortality, whereas intense drought increases bark beetle performance and tree mortality. Fig. 2a provides a framework for understanding the apparent difference in the effect of drought alone on bark beetle performance and associated levels of tree mortality between eastern and western U.S. forests. Most eastern forests have considerably higher precipitation and less intense drought, especially compared to forests east of the Sierra

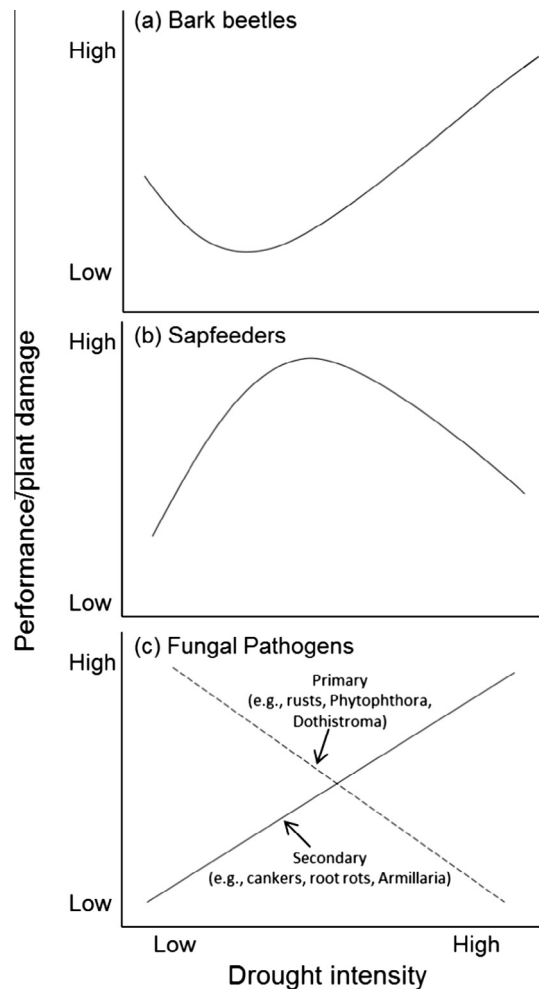


Fig. 2. Response trends of forest insect or pathogen performance and tree damage/plant mortality caused by bark beetles (a), sapfeeders (b), and primary and secondary fungal and oomycete pathogens (c) to drought intensity based on our literature review and synthesis.

Nevada and Cascade Mountain crests and west of the Great Plains (Peters et al., 2015). Eastern conifer forests also differ from most western conifer forests in other ways that make them less susceptible to drought-induced bark beetle outbreaks, such as greater structural diversity, greater species diversity, and younger stands that are more intensively managed. Current evidence strongly suggests that the relatively moderate droughts that occur in eastern conifer forests do not increase tree mortality from native bark beetles.

Because western arid forests are more water-limited than eastern mesic forests and at times experience more intense drought, insect-caused tree mortality has been more often correlated with severe drought in western U.S. forests. The “global-change-type drought” that occurred in the western U.S. in the early 2000s (Breshears et al., 2005) is an informative example, and provided an opportunity to examine the combined role of drought and temperature in bark beetle outbreak potential. In addition to drought effects on tree susceptibility to bark beetle attack, warm temperatures can be beneficial to populations as generation time is reduced and survival increased. We recommend that future research on the role of drought in bark beetle outbreaks should focus on: (1) the role of temperature in drought-induced outbreaks of bark beetles; (2) identification of bark beetle species that are capable of self-perpetuating outbreaks after drought subsides; (3) the level of drought-associated tree mortality that would occur without bark

beetle infestation; (4) the effectiveness of manipulating forest composition and structure to reduce drought stress and bark beetle infestations; (5) the level of drought intensity in pine forests of the eastern U.S. that would shift the role of drought in southern pine beetle outbreaks from a negative to a positive driver (Fig. 2a); (6) integration of mechanistically-based models of bark beetle response to drought and temperature into models that predict climate impacts on forest vegetation (e.g., Anderegg et al., 2015).

5.2. Defoliators

In contrast to bark beetles, our review found inconsistent impacts of drought on defoliator performance and associated levels of tree damage and tree mortality. 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 exists in the response of defoliators to drought, it is clear from climate-change projections (Ryan and Vose, 2012; IPCC, 2007; National Climate Assessment, 2014) that forest defoliators will increasingly interact with drought-stressed hosts. Moreover, the range of Douglas-fir tussock moth is expanding in the southwestern U.S. and into northern Mexico (Coleman et al., 2014), which has been attributed to changes in tree species composition and forest densification that benefit this species. As such, we underscore the need for a greater understanding of the response of Douglas-fir tussock moth and other forest defoliators to drought and the implications on local to regional patterns of host tree mortality.

5.3. Sapfeeders

The collective response of tree sapfeeders to drought is non-linear (Fig. 2b). Sapfeeders typically have the highest performance and cause the most tree damage at moderate drought intensity, and when drought is abated by precipitation, resulting in plant tissues enriched with nitrogen and with high turgor. Given large projected increases in the range of hemlock woolly adelgid in eastern North America, additional research should focus on the direct effects of drought on hemlock survival during active adelgid infestation. Although adelgid populations in western forests have historically remained at low levels, an understanding of the role of drought and warming temperature on future population increases in western US hemlock forests is needed.

5.4. Fungal and oomycete pathogens and parasitic plants

Our review highlights a complex response of tree fungal pathogens to drought (Fig. 2c). The overall consensus of our review and others (Desprez-Loustau et al., 2006; Klopfenstein et al., 2009; Sturrock et al., 2011; Jactel et al., 2012) is that some fungal and oomycete pathogens will become less severe whereas others will become more severe during drought. Specifically, evidence suggests that drought reduces performance and damage by primary pathogens that infect healthy trees and foliage, and pathogens whose performance is directly tied to high availability of moisture (e.g., rusts, *Phytophthora*, and leaf and needle pathogens). In contrast, drought typically increases performance and damage by secondary pathogens that colonize stressed trees and woody organs (e.g., stem cankers and root rots). The response trends in Fig. 2c, however, are based on knowledge about the role of available water on fungal performance and spread, and a few empirical studies on impacts of drought or tree water stress on fungal pathogen performance and tree damage. There is a large need for empirical data and predictive tools on how changes in drought frequency and intensity will alter 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 et al., 2009), as it will give forest managers additional foresight into conditions that foster outbreaks. Impacts of drought on populations of forest parasitic plants, such as mistletoes, are poorly understood due to a small number of investigations. More research that compares impacts of intense drought between mistletoes and their host trees is needed.

5.5. Role of forest management in mitigating drought-related impacts

Multi-way interactions between drought and disturbances caused by biotic and abiotic agents (e.g., Parker et al., 2006) and anthropogenic stressors (Millar and Stephenson, 2015) are important in determining continental-scale forest productivity, carbon balance, ecotones between forests, shrublands and grasslands, and many other forest ecosystem services. Emerging 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.

Given future projections of more frequent and intense drought in some U.S. forests and anticipated responses of forest insects and diseases to drought (Fig. 2), what can forest managers do to mitigate future outbreaks? First are management actions that help reduce atmospheric warming, which intensifies drought, such as increasing forest carbon storage (McKinley et al., 2011) and manipulating forest cover to alter site radiation balance (Luysaert et al., 2014; Alkama and Crescatti, 2016). Second are actions that actively facilitate a transition to new and better-adapted tree species in forests that are highly vulnerable to drought (Millar and Stephenson, 2015). Third are actions that use silvicultural tools, such as thinning to control tree density, to reduce future levels of tree mortality attributed to interactions between drought and forest insects and diseases. The premise of the latter approach is that thinning reduces competition among residual trees (e.g., for water) and alters stand microclimate (Kolb et al., 1998, 2007; Fettig et al., 2014a). Our findings support management actions that reduce tree density to reduce impacts of drought for certain forest insects and diseases. Proactive thinning of dense conifer stands by mechanical treatments or low-intensity burning has been shown to reduce subsequent tree mortality during drought by bark beetles in forests of the western U.S. (Fettig et al., 2007, 2010, 2014b; Gillette et al., 2014). There is also strong evidence that thinning reduces outbreaks of southern pine beetle in pine forests of the southeastern U.S. (Thistle et al., 2011; Nowak et al., 2015) by disrupting beetle pheromone plumes, among other factors. Model simulations suggest the same phenomena for mountain pine beetle in the Rocky Mountains (Powell et al., 2000). As such, there is growing scientific support that proactive thinning in dense conifer forests of the western and southeastern U.S. reduces the severity of future bark beetle infestations (Fettig et al., 2007, 2014b; Nowak et al., 2015) and wildfires (Stephens et al., 2012; McIver et al., 2013) (but see Six et al., 2014). In contrast to the case of bark beetles, there is no clear argument that thinning mitigates risks from defoliators and sapfeeders (Fig. 2b). For defoliators, thinning to favor non-host tree species has been recommended to reduce damage by western spruce budworm (Carlson and Wulf, 1989), but the use of thinning to reduce tree damage from defoliators has been questioned due to little empirical data, inconsistent effects, and poor understanding of related mechanisms (Muzika and Liebhold, 2000). Empirical data regarding effects of drought on forest pathogens are limited, but a preliminary theoretical model (Fig. 2c) suggests that thinning may reduce tree damage by secondary pathogens, but would have little effect or increase damage by primary pathogens.

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