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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.

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

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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).

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