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Review

Emergent insects, pathogens and drought shape changing patterns in oak decline in North America and Europe

Laurel J. Haavik [a,*], Sharon A. Billings [b], James M. Guldin [c], Fred M. Stephen [d]

[a] Department of Entomology, The Ohio State University, Ohio Agricultural Research and Development Center, 1680 Madison Avenue, Wooster, OH 44691, USA
[b] Department of Ecology and Evolutionary Biology and Kansas Biological Survey, University of Kansas, 2101 Constant Ave, Lawrence, KS 66044, USA
[c] USDA Forest Service, Southern Research Station, 607 Reserve Street, Hot Springs, AR, 71902, USA
[d] Department of Entomology, University of Arkansas, 319 Agriculture, Fayetteville, AR, 72701, USA

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ABSTRACT

Forest declines are well-studied phenomena. However, recent patterns suggest that the traditional sequence of events and factors involved in forest decline are changing. Several reports in recent decades involve emergent mortality agents, many of which are native insects and diseases. In addition, changing climate and weather patterns place increasing emphasis on root dynamics in forest decline, given the critical role of roots in susceptibility (loss of fine roots) and tolerance (deep-rooting) to drought. Contrasting successive extremes of wet and dry periods could negatively affect tree carbon (C) balance and water relations, which may provide an advantage to secondary agents such as root pathogens (e.g. *Armillaria* and *Phytophthora* spp.). We searched for patterns potentially implying mechanisms of mortality among several recent hardwood decline events (mostly in oak forests, *Quercus* spp.) linked to novel associations often involving drought – or hot drought, an apparent absence of defoliation, and a secondary bark- or wood-boring insect in a more aggressive tree-killing role than has been typically observed. To further explore one likely mechanism, we utilized a case study featuring an emergent mortality agent, the red oak borer, *Enaphalodes rufulus* (Haldeman) (Coleoptera: Cerambycidae), which, interacting with drought and forest history, resulted in an unprecedented oak mortality event (1999–2003, Ozark region, USA). Examination of long-term patterns of radial growth revealed that oaks surviving decline episodes often exhibited slow growth early during forest development, yet became superior competitors later on, and exhibited non-linear growth dynamics throughout their lives; trees that died often exhibited the opposite pattern, with rapid growth early in life and linear growth dynamics. We speculate that these different growth strategies could be related to patterns of resource allocation facilitated by root origins (sprout vs. seedling) and/or microsite conditions, and driven or influenced by repeated drought. Carbon balance dysfunction, a long-term affliction of oaks that eventually manifests itself in an episode of decline, may be the underlying mechanism of oak mortality during decline. It is likely caused by changes in C supply and demand during drought and/or defoliation that compromise oaks by depleting C reserves, or somehow inhibiting translocation of stored C to repair damaged tissues and resist secondary biotic agents. Ultimately, successive drought and persistent activity by these insects and pathogens kill affected oaks. Parallels among different hardwood ecosystems exist, and can be used to help predict future scenarios and guide new avenues of study.

Contents

* Corresponding author.
E-mail addresses: ljhaavik@gmail.com (L.J. Haavik), sharonb@ku.edu (S.A. Billings), jguldin@fs.fed.us (J.M. Guldin), fstephen@uark.edu (F.M. Stephen).

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1. Introduction

Forest declines (major die-offs of trees at the genus or species level) are not new phenomena, and have been reported worldwide throughout the 19th and 20th centuries (Millers et al., 1989; Manion and Lachance, 1992; Tomiczek, 1993). Whether these events are becoming more common as a result of increasingly severe weather events and/or anthropogenic shaping of 20th and 21st century forests is difficult to determine, and may be confounded with increased reporting in recent decades. Many theories have been proposed to explain episodes of decline (e.g. Sinclair, 1965; Mueller-Dombois, 1987; White, 1987; Manion, 1991; Auclair et al., 1992; Houston, 1992). Declines involve a complicated and poorly understood group of abiotic and biotic initiators and contributors to reductions in tree growth and vigor, degradation of foliage and root systems, and ultimately to tree mortality. Insects and/or pathogens are invariably associated with declines at some point, often as mortality agents. These mortality agents may themselves be affected directly by changes in climate and weather, and indirectly through responses of their host trees. Several recent accounts of decline in oak forests involve emergent insects and pathogens, many of which are native species. It is unclear why these biotic agents have suddenly become notable pests associated with landscape-scale tree mortality events. The seemingly sudden appearance of emergent insects and pathogens further complicates the nature of changing patterns in forest decline in response to changing environmental conditions.

Multiple ecosystem drivers, including frequent drought, land-use change, loss of foundation species, and herbivore population dynamics, have shaped eastern North American hardwood forests of today (Abrams, 1996; McEwan et al., 2011). This has created an interesting and complex setting in which to study how land management, climate, disturbances, and regeneration interact to shape forest dynamics. Recent literature has examined how rapidly changing environmental conditions have already affected interactions between forest insect populations and the forests that they inhabit, and has speculated what future effects might be (e.g., Ayres and Lombardero, 2000; Logan et al., 2003; Rouault et al., 2006; Dobbertin et al., 2007; Fettig et al., 2013; Weed et al., 2013). However, these studies have mainly focused on non-native invasive species, or native or introduced species (non-native) residing in conifer forests. Considerably less is known about native bark beetles and wood-borers in hardwood ecosystems, and how changing conditions – such as more frequent and severe drought – are likely to affect their interactions with host trees, and more broadly, their population dynamics.

Droughts of unprecedented severity and/or duration, often termed 'global-change-type' droughts, followed by major tree die-offs have sparked investigations into the factors and mechanisms involved in tree mortality, and whether their occurrence and activity are being altered as climatic changes occur (e.g. Hanson and Weltzin, 2000; Breshears et al., 2005; Mueller et al., 2005; Bréda et al., 2006; McDowell et al., 2008; Allen et al., 2010). Changes in intensity, duration, and frequency of dry periods will likely affect forest vulnerability to and resilience from attack by biotic agents (Desprez-Loustau et al., 2006; Rouault et al., 2006; Jactel et al., 2012). The frequency of pan-continental droughts – such as that experienced by the United States (US) in 2012 – could increase in the future, along with warmer, and more extreme regional droughts (Cook et al., 2014; Overpeck, 2013; IPCC, 2014).

These questions are particularly interesting in oak-dominated forests, which have been the subject of oak decline studies for multiple decades (Millers et al., 1989; Wargo, 1996; Thomas et al., 2002; Kabrick et al., 2008; Fan et al., 2012; Haavik et al., 2012a). Oaks are widely distributed throughout North America, Asia, and Europe (Logan, 2005), represent ~50% of all forest cover (Oswalt et al., 2014), and provide many ecosystem services (Pavlik et al., 1993; Logan, 2005; Marañón et al., 2013). Aside from beech, oaks are the most important broadleaved trees in Europe, occupying both temperate and Mediterranean climates (Thomas et al., 2002). Although oaks possess multiple physiological adaptations to tolerate drought (Abrams, 1990), recent work suggests that phenotypic and genotypic changes in individual oak populations may occur in response to selection pressures exerted by long-term droughts of increasing severity (e.g. Cavin et al., 2013), potentially making oaks yet more resilient to drought over time.

In this paper, we draw on the literature of insects and pathogens involved in hardwood (mainly oak) decline events, with emphasis on emergent pests and mechanisms of mortality during decline. We define emergent pests as insects or pathogens that have been implicated in forest decline or tree mortality in the past few decades, but were not historically reported or detected in this role – at all or as major contributors. We present a case study using an emergent oak pest, red oak borer, *Enaphalodes rufulus* (Haldeman) (Coleoptera: Cerambycidae), in the Ozark Highlands of Arkansas, US, and the roles played by *E. rufulus*, drought, and forest history in this unprecedented oak mortality event. Finally, we synthesize current understanding of mechanisms involved in drought-related tree mortality to provide insight into mechanistic explanations of oak decline, with the aim of identifying future avenues of study.