



Review

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

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ARTICLE INFO

Article history:

Received 23 March 2015

Received in revised form 9 June 2015

Accepted 14 June 2015

Available online 2 July 2015

Keywords:

Emergent pest

Wood borer

Oak borer

Defoliator

*Enaphalodes rufulus**Agilus* spp*Lymantria dispar*

Forest decline

Forest succession

Climate change

Fire suppression

Callus

Hydraulic failure

Carbon starvation

Ozark Plateau

Carbon balance

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.

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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.

2. Common features of oak decline

Tree mortality and forest decline are important natural processes in successional development of forest stands. Forest declines are regional dieback and mortality events affecting one or a few closely related tree species, and result from several interacting causal factors (Sinclair, 1965; Mueller-Dombois, 1986; Manion, 1991). Because these factors interact at different stages of stand development, and persist for different periods of time, theories about which factors initiate and accelerate forest decline are difficult to test and can often only be based on correlational or observational evidence. However, because of the general intractability of the study of decline and the looming threat of global change's influence on forests, there has been much effort over the past few decades devoted to understanding the phenomena of forest declines. Many common elements seem to be increasingly apparent.

We define oak decline as a landscape-scale die-off event involving dominant and subdominant canopy oaks. Decline events can last for several years and are often preceded by a long period during which trees exhibit reduced radial growth. We consider canopy (crown) dieback as a symptom of decline, but also as a phenotypic indicator of adaptation to drought/poor environmental conditions (e.g. Thomas and Hartmann, 1996). Oak decline is common throughout the distribution of oaks, and is usually associated with some combination of over-mature, even-aged forests suffering from poor management practices (such as fire suppression, limited thinning, and/or high-grading), along with other stressful abiotic (climate extremes, poor soils or other predisposing site conditions) and biotic (insects and pathogens) factors (Sinclair, 1965; Houston, 1987; Millers et al., 1989; Manion, 1991; Tomiczek, 1993; Wargo, 1996; Gibbs and Greig, 1997; Führer, 1998; Thomas et al., 2002; Denman and Webber, 2009).

2.1. Forest history

Forest conditions and history, regional climate, along with edaphic or physiographic features, often termed predisposing factors, can dictate which sites are more severely affected by decline than others. For example, oaks growing in a Mediterranean climate are comparatively well-adapted to regularly occurring periods of drought, relative to oaks growing in a temperate climate. Poor quality sites of low nutrient content, high soil clay or sand content, and xeric exposures often experience large amounts of mortality during a decline (Sinclair, 1965; Starkey and Oak, 1989; Oak et al., 1996; Thomas and Hartmann, 1998; reviewed in Thomas et al., 2002). Stand dynamics, shaped by management practices, influence the degree of intra- and interspecific competition among oaks and between oaks and other species, and may affect resilience following stress events or resistance to biotic agents (Tainter et al., 1990; Oak et al., 1991; Rozas and García-González, 2012). Consequently, the degree to which a species is physiologically well-adapted to the site on which it grows becomes an important issue (Mueller-Dombois, 1986, 1987, 1992).

Loss of species from catastrophic events, changes in land use, and shifts in forest cover types may also be predisposing factors. In the eastern US, land-use changes associated with European settlement and high-grading harvest of virgin forest stands led to shifts in species composition from chestnut-, conifer- and white oak-dominated stands to stands dominated by red oak. Loss of American chestnut, *Castanea dentata* (Marsh.) Borkh., by chestnut blight (*Cryphonectria parasitica* (Murr.) Barr) also eliminated a dominant species highly adapted to poor sites, resulting in conversion to oak-dominated forests that may be less adapted to those sites (Elliott and Swank, 2008). With the absence of periodic wild-fire, conifer and white oak regeneration was limited; red oaks

re-sprouted from cut stumps, and became dominant pioneer species on sites to which they may not be as well-adapted as other species (Millers et al., 1989; Kessler, 1992; Abrams, 1996, 2003; Thompson et al., 2013).

2.2. Primary factors

Sometimes referred to as inciting factors, these are stressful events such as insect defoliation, drought, or damaging frost, which can occur repeatedly and/or act concurrently or sequentially (Sinclair, 1965; Manion, 1991). Primary factors initiate decline events by compromising the physiological capacity of oaks, rendering them increasingly susceptible to secondary agents such as diseases (caused by pathogens) and insects (Sinclair, 1965; Kozłowski, 1969; Waring, 1987; Manion, 1991; Wargo, 1996; Thomas et al., 2002). Extreme weather and defoliation by insect larvae and by fungi, often occurring simultaneously or sequentially, are the most common primary factors involved in oak decline (Houston, 1987; Millers et al., 1989; Tomiczek, 1993; Wargo, 1996; Gibbs and Greig, 1997; Donaubauer, 1998; Führer, 1998; Thomas et al., 2002; Marçais and Bréda, 2006).

Changes in normal rainfall patterns – which may include drought or excessive flooding – can adversely affect tree water relations, rendering trees susceptible to dieback and/or mortality agents (Mueller-Dombois, 1986; White, 1987; Rozas and García-González, 2012). For deciduous hardwoods, frost injury in winter can damage vascular tissues, and late spring frosts that follow bud burst can injure newly formed leaves or deplete carbon (C) reserves upon re-foliation (Horsley et al., 2002; Thomas et al., 2002; Frey et al., 2004).

Defoliating insects become primary mortality agents when they become capable of feeding, reproducing successfully, and increasing to epidemic population levels on healthy trees (e.g. Davidson et al., 1999). Outbreaks of defoliators are often widespread regionally and cyclic, lasting for several years, then repeating at intervals in the same locations (Myers, 1988; Berryman, 1996; Speer et al., 2001; Bouchard and Pothier, 2010). Factors that drive these cycles are not fully understood, but for some species, appear to be related to fluctuations in climate (Elkinton and Liebhold, 1990; Myers, 1998; Liebhold et al., 2000).

In North America, the introduced gypsy moth, *Lymantria dispar* L., is by far the most frequent defoliator of oaks. However, several native species including forest tent caterpillar, *Malacosoma disstria* Hübner; oak leaf tier, *Acleris semipurpurana* (Kearfott); walkingstick, *Diapheromera femorata* (Say); fall cankerworm, *Alsophila pometaria* (Harris); fruit-tree leafroller, *Archips argyrospila* (Walker); and elm spanworm, *Ennomos subsignarius* (Hübner) have also been reported to cause significant defoliation (Staley, 1965; Nichols, 1968; Dunbar and Stephens, 1975; Millers et al., 1989). Common native defoliators in Europe are winter moth, *Operophtera brumata* L.; European oak leafroller, *Tortrix viridana* L.; oak processionary moth, *Thaumetopoea processionea* L.; and gypsy moth, *L. dispar* (Gibbs and Greig, 1997; reviewed by Führer, 1998; Thomas et al., 2002; EFSA, 2009). In Europe, *L. dispar* and *T. processionea* cause more damage to oaks than the other caterpillars, because they feed longer during the growing season (Thomas et al., 2002; Nageleisen, 2008).

2.3. Secondary factors

Secondary biotic agents, often termed contributing factors, often arrive, attack, or spread after one or more consecutive seasons of defoliation. These include bark beetles and wood borers, mostly *Agrilus* spp. or other Buprestidae (although various species in the Cerambycidae and *Prionoxystus* spp. (Lepidoptera: Cossidae) have been reported); root pathogens (*Armillaria* spp., *Phytophthora*

spp., and/or *Collybia fusipes*); and less commonly, stem cankers (e.g. *Hypoxyylon* canker) (Balch, 1927; Mistretta et al., 1981; Bassett et al., 1982; Millers et al., 1989; Dunn et al., 1990; Gibbs and Greig, 1997; Führer, 1998; Thomas et al., 2002; Sallé et al., 2014). These agents are not commonly capable of killing healthy oaks, but they can kill oaks weakened by some other factor (Sinclair, 1965; Manion, 1991; Mueller-Dombois, 1992). *Agrilus biguttatus* (F.) (syn. *A. pannonicus* (Pill. et Mitt.)), in Europe, and *A. bilineatus* (Weber) in North America, are usually the first secondary insects to arrive and are the most important final contributors to oak mortality (Millers et al., 1989; Wargo, 1996; Moraal and Hilszczański, 2000; Thomas et al., 2002). Dying oaks can be colonized by more than one secondary biotic agent. For instance, *A. bilineatus* may colonize the main stem and upper branches of moribund oaks that are also infected with root rot, *Armillaria* spp. (Balch, 1927; Staley, 1965; Kegg, 1971, 1973; Dunbar and Stephens, 1975; Wargo, 1977).

2.4. Interactions among factors

Thomas et al. (2002) developed a model, based on experimental work in controlled conditions and on mature trees at several sites experiencing decline, that explains interactions among abiotic and biotic factors involved in oak decline in Central Europe. They theorized that the physiological effects of defoliation on oaks render them more susceptible to climate extremes, such as drought and frost (Thomas et al., 2002; Gieger and Thomas, 2002; Thomas et al., 2004; Marçais and Bréda, 2006). Specifically, they suggested that depletion of C reserves impairs fine-root production, through loss of photosynthetic surface area and reduced rates of photosynthesis (evidenced by reduced stomatal conductance) (e.g. Frost and Hunter, 2008). Reduced fine-root biomass limits water uptake during drought, and along with cavitation (breakage of the water column in xylem vessels) leading to embolism (formation of air bubbles in the xylem) caused by drought or damaging frost, severely compromises oak water relations (Gieger and Thomas, 2002; Thomas et al., 2004). Secondary agents, usually *A. biguttatus* and/or root pathogens, then attack/infect and kill the weakened oaks.

Wargo (1996) proposed a mechanism to explain the role of opportunistic pathogens in oak decline. Starch (primary form of C reserves/stores) levels in roots are reduced following defoliation (Staley, 1965; Parker and Patton, 1975; Parker, 1979). Of the simple sugars, sucrose levels decrease, but glucose and fructose increase: *Armillaria* spp. growth rates can be up to three times higher on glucose than on other C sources (Wargo et al., 1972; Wargo, 1980, 1996). This increase in glucose also allows *Armillaria* spp. to grow rapidly in the presence of inhibitory phenols (biotic resistance chemicals) such as gallic acid; and, *Armillaria* spp. can even use oxidized phenols as additional C sources to grow more vigorously than on glucose alone (Wargo et al., 1972; Wargo, 1980, 1996). *A. bilineatus* and *Prionoxystus* spp. more frequently attacked oaks with lower winter starch reserves (Dunn et al., 1987, 1990). However, oaks attacked by *A. bilineatus* did not have differing levels of resistance (phloem phenolics and callus formation) than those not attacked, indicating that patterns of C utilization or changes in source–sink relationships may be more important for borer colonization than total C stores (Dunn et al., 1990).

3. How drought leads to oak mortality

3.1. Oak adaptations to and recovery from drought

Oaks possess several adaptations to tolerate and/or avoid drought conditions, including osmotic and elastic adjustments;

deep rooting structure; and many have ring-porous anatomy to transport water with minimal hydraulic resistance (reviewed by Abrams, 1990; Dickson and Tomlinson, 1996). Cavitation is more likely in large-diameter earlywood vessels (Tyree and Dixon, 1986; Cochard and Tyree, 1990), but oaks also possess small-diameter latewood vessels, which are less vulnerable to cavitation and may be important during drought (Abrams, 1990; Granier et al., 1994). Well-established (extensive, deep, and dense) root systems may be the most important characteristic of drought-tolerant trees (Bréda et al., 2006). Briefly, physiological adjustments that occur at the onset of drought stress act to postpone dehydration through reduced stomatal conductance and increased water uptake via root growth, or to tolerate dehydration through osmotic adjustment (Geiger and Servaites, 1991; Pallardy, 2008). Osmotic adjustment has been documented in many oaks and is achieved by synthesis and mobilization of osmotic agents (organic anions, soluble carbohydrates: mostly sugars, and amino acids) to help tissues maintain turgor; cells essentially accumulate solutes to retain volume and relative water content at low water potentials (Abrams, 1988; Geiger and Servaites, 1991; Kozłowski and Pallardy, 2002; Pallardy, 2008). As drought conditions continue, leaf abscission (i.e. crown dieback) occurs, and root growth increases (Waring, 1987; Kozłowski, 1991; Dickson and Tomlinson, 1996; Bréda et al., 2006). Stored C may be mobilized and used for osmotic adjustment, repair of embolism, root growth, and regular cell and tissue maintenance, especially if production of new C has declined due to reduced rates of photosynthesis so that it can no longer support these functions (Geiger and Servaites, 1991; Dickson and Tomlinson, 1996; Bréda et al., 2006; Sala et al., 2012).

After drought, trees need time to recover and rebound from stress-imposed changes on physiology and growth. Available C is used for maintenance, repair of damaged tissues, and resistance to biotic agents (Bréda et al., 2006). If re-current droughts (or other stress events) take place too quickly in succession to permit sufficient repair of damaged tissues, then a progressive loss of resilience (i.e. inability to take advantage of favorable environmental conditions), or even mortality, can follow (Niinemets, 2010). Several studies have found that oak growth and other physiological functions are gradually weakened by successive droughts, whereby mortality may not occur until after a second or third debilitating drought is endured (Jenkins and Pallardy, 1995; Lloret et al., 2004; Voelker et al., 2008; Haavik et al., 2011). The severity and duration of a mortality-inducing drought may be less important than its timing in relation to the developmental stage of oaks or the forest as a whole, wherein older, over-mature oaks are most likely to die (Dwyer et al., 1995; Voelker et al., 2008).

3.2. Physiological effects of drought on oaks that indirectly affect insects

Current understanding of mechanisms involved in drought-induced tree mortality suggests that trees die either by C starvation or hydraulic failure (McDowell et al., 2008; McDowell and Sevanto, 2010; Sala et al., 2010, 2012), or simultaneously by both (Sevanto et al., 2014). Biotic agents can exacerbate or be exacerbated by C starvation or hydraulic failure (McDowell et al., 2008). Hydraulic failure occurs when water loss through transpiration exceeds uptake by roots, resulting from a loss of conductivity in the xylem (i.e. embolism) (McDowell et al., 2008). Carbon starvation essentially occurs through a complete (or functionally complete – see Sala et al., 2010) depletion of C reserves, such that maintenance processes and resistance to biotic agents can no longer be fueled (McDowell et al., 2008). Although not all C storage (non-structural carbohydrate) pools may have been diminished, trees could still die of C limitation or

reserve-depletion if processes used to transport stored C are somehow damaged or inhibited by drought stress (Sala et al., 2010, 2012). Additionally, some C pools may become compartmentalized or made inaccessible, and thus not available for use during drought (Sala et al., 2010, 2012). Such limitations on stored C and cellular metabolism would prevent production and mobilization of secondary metabolites for resistance to biotic agents (Sala et al., 2010, 2012). Carbon balance is especially important for deciduous hardwoods, because they rely heavily on C stores and mobilization to re-foliate in spring, when C supplies are low (Kozłowski, 1991). Because patterns of C supply and demand are seasonally asynchronous, and C reserves are clearly important to avoid and tolerate stress, Sala et al. (2012) propose that trees may actively maintain minimum thresholds in C storage pools that are much larger than previously thought, to sustain physiological functions and endure fluctuating environmental conditions.

There is evidence that insects and pathogens impair oak-water relations and that they benefit from, or cause, C balance dysfunction. Oaks self-impede water transport by plugging xylem vessels (formation of tyloses), especially in earlywood, as a resistance mechanism against pathogen attack (Kozłowski, 1969). Formation of tyloses has been observed in response to biotic agents associated with oak decline (Kaus et al., 1996; Vansteenkiste et al., 2004). Presence of fungal infections was associated with greater incidence of occluded xylem vessels (Kaus et al., 1996). Feeding by *A. biguttatus* (and probably other oak borers) can physically cut xylem vessels, also inhibiting water transport (Vansteenkiste et al., 2004). In contrast, *E. rufulus* infestation apparently had little influence on oak water-relations during drought (Haavik et al., 2008). Defoliators alter oak C balance by reducing C supply for a time, and exhausting C reserves upon re-foliation (Parker and Patton, 1975; Wargo, 1996; Thomas et al., 2002), which can impair production of fine roots necessary for enhanced water acquisition during drought (Gieger and Thomas, 2002; Thomas et al., 2002). Oaks with low C reserves were more attractive to and readily colonized by *A. bilineatus* (Dunn et al., 1987, 1990). Oaks with poor vigor (Haavik et al., 2010), and reduced capacity for compartmentalization and formation of callus tissue (wound periderm), were most likely to be colonized by *E. rufulus* (Fierke and Stephen, 2008; Haavik and Stephen, 2011). Vigorous growth to tolerate attack by biotic agents, formation of tyloses, and other mechanisms used by hardwoods to compartmentalize and heal wounded vascular tissue could require substantial C investment, certainly in excess of that needed for maintenance and repair processes following drought.

Carbon starvation, or some form of C balance dysfunction, is most likely a long-term affliction of oaks that eventually manifests itself in an episode of decline. In several instances, oak mortality is a long, slow process preceded by decades of reduced growth rates and compromised physiological functioning (Tainter et al., 1990; Jenkins and Pallardy, 1995; Pedersen, 1998; Haavik et al., 2008, 2011; Andersson et al., 2011; Fan et al., 2012). This process is likely driven by successive droughts, and facilitated by an increasing loss of resilience with age, perhaps via an inability to re-establish C balances. Hydraulic dysfunction is not likely to be the single cause of oak mortality during decline, because trees that die solely from hydraulic failure in response to drought often do so quickly (e.g. Sevanto et al., 2014). It is likely that both compromised water relations and C balance dysfunction are important during oak decline, although the relative contribution of each at different stages of the decline process, and in relation to biotic agents, is not yet clear.

3.3. Drought-stressed trees may be more suitable for insects

The idea that drought renders trees more suitable for insects (White, 1969, 1984; Rhoades, 1979, 1985; Mattson and Haack,

1987a,b) has received experimental support for bark beetles and wood borers, but results have been inconclusive for defoliators (Larsson, 1989; Larsson and Björkman, 1993; Koricheva et al., 1998; Huberty and Denno, 2004; Rouault et al., 2006; Jactel et al., 2012). Many of these meta-analyses found that experimentally-imposed drought influenced different insect feeding guilds differently. Type of mortality agent (primary vs. secondary) and plant organ affected (foliage vs. wood) also influenced whether the effects of drought on tree damage were positive or negative (Jactel et al., 2012). These differences may be important in regard to forest decline: defoliators are capable of feeding on healthy trees because they are adapted to process toxic plant secondary metabolites and other compounds that reduce biomass digestibility (e.g. tannins), whereas borers and other secondary agents are only successful in plants that are severely physiologically compromised.

In theory, insects could benefit if drought resulted in reduced tree resistance, improved tree nutrition, or both (White, 1969, 1984, 2015; Rhoades, 1979, 1985; Mattson and Haack, 1987a,b). Reduced resistance could occur by way of impaired water relations, C balance dysfunction, or both. Improved nutrition for insects would likely result from osmotic adjustment in tree tissues consumed by insects. Insect development and survival could be enhanced from solute mobilization and accumulation in trees afforded by the break-down of large compounds (proteins, starch) into more readily-useable, smaller molecules (amino acids, sugars) (White, 1969, 1984; Rhoades, 1979, 1985; Mattson and Haack, 1987a,b) that fuel osmotic adjustment, because plant tissues are very low in nutrition compared to insect physiological requirements (Mattson, 1980; Slansky, 1990). Although there is evidence that drought stress results in increased concentrations of sugars and/or amino acids in different tree tissues (e.g. Hodges and Lorio, 1969; Parker and Patton, 1975; Parker, 1979; reviewed by Mattson and Haack, 1987b; Thomas and Hodkinson, 1991; Caldeira et al., 2002; Tariq et al., 2012), with concomitant positive effects on insect development or survival (e.g. Thomas and Hodkinson, 1991; Caldeira et al., 2002; Tariq et al., 2012), it is difficult to extrapolate such effects to the scale of forest insect outbreaks (e.g. Larsson et al., 2000).

Evidence suggests that drought-induced changes in oak resistance may be favorable for stem-borers. Rates of processes involved in the wound response, compartmentalization, and production of callus tissue decrease in response to drought stress (Puritch and Mullick, 1975; Bevercombe and Rayner, 1980; McIntyre et al., 1996). The wound response is an especially important mechanism of resistance to stem-boring insects involved in oak decline (Dunn et al., 1990; Vansteenkiste et al., 2004; Fierke and Stephen, 2008; Haavik and Stephen, 2011). A recently developed theory, termed induced resource sequestration, suggests that plants actively and rapidly divert important resources away from tissues attacked by herbivores to tissues not accessible to herbivores (reviewed by Orians et al., 2011). There is evidence for this among some hardwoods in response to defoliation (reviewed by Orians et al., 2011). Leaf-feeding could trigger changes in C and nitrogen (N) allocation patterns (e.g. Frost and Hunter, 2008) that alter drought-induced changes in C availability and use, which may in turn slow or inhibit wounding in response to borer attack.

Concentrations of allelochemicals in plants typically increase in response to moderate drought stress, especially in leaves, because growth slows before photosynthetic rate, allowing excess C supplies to be used for synthesis of secondary metabolites (e.g. allelochemicals) (theory by Loomis, 1932; Lorio, 1988; reviewed by Mattson and Haack, 1987b; theory and review by Herms and Mattson, 1992). However, there is some evidence that allelochemicals in oaks may decrease in response to drought stress (Thomas and Schaffellner, 1999). Many other factors have been shown to

increase concentrations of C-based allelochemicals (phenols and tannins) in oak leaves, including defoliation itself (Schultz and Baldwin, 1982; Rossiter et al., 1988), silviculture treatments (Forkner and Marquis, 2004), and increased temperature and/or concentrations of atmospheric carbon dioxide (Dury et al., 1998). Alternatively, drought may improve the defoliator's ability to detoxify allelochemicals via faster enzymatic actions due to increases in temperature, and increased concentrations of allelochemicals in leaves on their own can stimulate insect detoxification enzymes (Mattson and Haack, 1987b; Slansky, 1990). This myriad of variables potentially influencing the quality of oak foliage could complicate the effects of drought alone.

4. Emergent insects and pathogens: novel decline scenarios

4.1. Emergent biotic agents involved in oak decline: insects

In North America, several oak pests have become more damaging in recent decades. From 2010 to 2012, an unprecedented outbreak of two native oak moths affected several counties in the southeastern US (Coyle et al., 2013). Following several years of drought and unusually warm winters, these spring-feeding moths, the black-dotted brown moth, *Cissusa spadix* (Cram.), and the common oak moth, *Phoberia atomaris* (Hübner), (both Lepidoptera: Noctuidae) defoliated several oak species for three consecutive years, possibly rendering them more susceptible to secondary agents (Coyle et al., 2013). These caterpillars were not previously recognized as species prone to large outbreaks, and whether the combination of drought and defoliation by them weakened oaks such that they might later experience an episode of decline remains to be seen.

In 2003, an unusual outbreak of the native Gambel oak borer, *Agilus quercicola* (Fisher), a species not previously reported to injure trees, occurred in Colorado, USA (Sever et al., 2012). This outbreak, which only lasted for one season, followed several seasons of environmental stress, including late spring frosts and drought (Sever et al., 2012). Although some of its congeners are common and aggressive secondary agents of oak mortality, this borer has yet to be linked to oak decline.

In Europe, the importance of *A. biguttatus* in oak decline was likely overlooked in the past, since as larvae, they feed cryptically, beneath the bark at the cambial interface between phloem and xylem; but, in association with drought, populations may also be on the rise (Table 1; Gibbs and Greig, 1997; Moraal and Hilszczanski, 2000; Thomas et al., 2002; Brown et al., 2015). *A. biguttatus* populations can persist on oaks several years following defoliation and an extreme climate event, and feeding injury can facilitate entry for fungi (*Fusarium* spp.) that infect oak vascular tissue and induce vessel blockage (tyloses) (Moraal and Hilszczanski, 2000; Thomas et al., 2002). In combination with a new genus and species of gram-negative bacteria (Brady et al., 2010), *A. biguttatus* appears to be a major player in a new type of oak decline in Great Britain, termed acute oak decline, that is characterized by a quick onset of mortality (3–5 years) followed by a 5–10 year period of additional mortality in those trees that survived the initial event (Denman and Webber, 2009; Denman et al., 2014). The combined action of both agents, infection by the bacterial pathogen and feeding by *A. biguttatus* larvae, is thought to girdle and kill oaks (Denman and Webber, 2009; Denman et al., 2014).

In the Mediterranean, a wood-borer in the family Cerambycidae, *Cerambyx welensii* Küster (syn. *C. velutinus* Brullé), has recently been documented as an important contributor to *Quercus suber* and *Quercus ilex* decline (Table 1; Torres-Vila et al., 2012, 2013). *C. welensii* was originally thought to only colonize

Table 1
Examples of recent oak declines in Europe and North America in which novel factors were involved and/or traditional factors were largely absent.

| Location | General timing | Oak spp. affected | Novel factors | Traditional factors present | Traditional factors largely absent | References |
|-----------------------|----------------|---|---|--|---|---|
| Ozark region, USA | 1999–2003 | <i>Q. rubra</i> , <i>Q. velutina</i> , <i>Q. coccinea</i> | <i>Enaphalodes rufulus</i> (b) | Drought (a), poor forest management (a) | <i>Agilus bilineatus</i> (b), defoliators (b) | Starkey et al. (2000, 2004), Stephen et al. (2001), Guldin et al. (2006) and Mullenburg et al. (2014) |
| Southern Ohio, USA | 2002–present | <i>Q. alba</i> | <i>Phytophthora cinnamomi</i> ^a (b) | Drought (a), defoliators (<i>Malacosoma disstria</i> ; <i>Phigalia itea</i> ; and <i>Phoberia atomaris</i>) (b), <i>A. bilineatus</i> (b), <i>Armillaria</i> spp. (b), hypoxylon canker (b), Drought (a) | Defoliators (b), <i>Armillaria</i> spp. (b), <i>Phytophthora</i> spp. (b) | Balci et al. (2007, 2010) and Nagle et al. (2010) |
| Great Britain | 1989–1994 | <i>Q. robur</i> | <i>A. biguttatus</i> (b) | Not yet known/reported | Not yet known/reported | Gibbs and Greig (1997) |
| Great Britain, France | 2006–present | <i>Q. robur</i> , <i>Q. petraea</i> | <i>Gibbella quercineans</i> (b) and other bacteria spp., <i>A. biguttatus</i> (b) | Not yet known/reported | Not yet known/reported | Denman and Webber (2009), Brady et al. (2010) and Denman et al. (2014); www.forestry.gov.uk |
| Spain | 1980–present | <i>Q. ilex</i> , <i>Q. suber</i> | <i>Cerambyx welensii</i> (b), | Poor forest management (a), <i>P. cinnamomi</i> (b) | | Torres-Vila et al. (2012, 2013) (and references therein) |

a = abiotic factor; b = biotic agent.

^a Non-native to the USA.

large, aging oaks; yet now it has been found in young, apparently healthy oaks (Torres-Vila et al., 2012).

In France, incidence of *Coraebus florentinus* Herbst damage has increased in recent years (2008–2013), with increased damage noted following drought (Sallé et al., 2014). *C. florentinus* develops in branches and shoots of oaks, and is considered a pest in its native Mediterranean habitat, where it is particularly successful in oaks suffering from drought stress (Buse et al., 2013). The range of this buprestid (subfamily Agrilinae) has expanded northward in Germany since 1950, likely in relation to increasing maximum temperatures, and models predict it will expand further into Central Europe as global temperatures continue to rise (Buse et al., 2013).

4.2. Emergent biotic agents involved in oak decline: pathogens

Increasing numbers of reports and detections of *Phytophthora* spp., root pathogens that primarily infect fine roots, have drawn attention to their importance in oak decline. *Phytophthora* spp. may be non-native to areas experiencing oak decline (Brasier, 1996). *Phytophthora cinnamomi*, *P. quercina* (an oak-specific species), and several other *Phytophthora* spp. have been detected in recent decades in Europe (Jung et al., 1999, 2002; Gallego et al., 1999; Vettraino et al., 2002; Balci and Halmschlager, 2003) and in North America (Table 1; Balci et al., 2007, 2010; Nagle et al., 2010). Although their role is not yet completely understood, it may be exacerbated by changing climate conditions (reviewed by Brasier, 1996; Jönsson, 2006). *P. cinnamomi* (widely distributed, with likely origin of Papua New Guinea) is a worldwide invasive pest, one of the most destructive root pathogens, and cold temperatures are thought to limit its distribution (Brasier, 1996). *Phytophthora* diseases are most prevalent in relatively alkaline, clay-rich soils (Thomas et al., 2002; Jönsson et al., 2005); recent evidence indicates that, contrary to earlier belief, they can also infect roots in acidic soils (Jönsson et al., 2003; Jönsson, 2004). *Phytophthora* diseases can infect fine roots during periods of excess or limited soil moisture, and may be particularly successful when conditions rapidly change from one moisture extreme to the other (Brasier, 1996; Jung et al., 2003; Jönsson, 2006). Warm, wet conditions allow for increased spread (via sporangia production) by *Phytophthora* spp., which may occur simultaneously with increased fine root production by oaks; when dry conditions quickly return, these new fine roots are then extremely susceptible to infection (Brasier, 1996; Jönsson, 2006).

Since Thomas et al.'s (2002) model was developed, some progress has been made to unravel the role of pathogens in oak decline in Europe. In addition to reports on *Phytophthora* spp., *Armillaria* spp. appear to be weak pathogens involved in oak decline; but those oaks infected may be less likely to survive defoliation (Marçais and Bréda, 2006). Other root pathogens have been shown to reduce rates of oak-seedling photosynthesis (Linaldeddu et al., 2009). Marçais et al. (2011) found that inoculating seedlings with a combination of pathogens known to be associated with oak decline (*C. fusipes*, *Armillaria mellea*, and two *Phytophthora* spp.) resulted in greater damage than inoculation of one species alone, implying that several species may act synergistically to weaken/kill oaks during episodes of decline.

4.3. Novel decline scenarios: oak, aspen, and birch

Similar to the *E. rufulus* epidemic, populations of other little-known native insects have reached pest status in other hardwood forests recently, likely as a result of changing climate. In these decline scenarios drought and/or rapidly changing climate conditions seem to be the central primary factors, there is an apparent absence of primary mortality agents (defoliators), and

secondary agents may have transitioned to a more aggressive tree-killing role than was observed in the past.

In the mid- to late-1990s, *A. biguttatus* was associated with oak mortality in several European countries, many in which it had not previously been reported as a pest (Moraal and Hilszczański, 2000). It is somewhat unclear whether *A. biguttatus* was not noticed before or whether it only recently became a more prevalent pest (Moraal and Hilszczański, 2000; Thomas et al., 2002; Brown et al., 2015). Regardless, its role in oak decline may be transitioning to a more aggressive one. Historically, *A. biguttatus* attack was associated with climatic stress, either drought or damaging frost, and defoliation (Hartmann and Blank, 1992; Gibbs and Greig, 1997; Thomas et al., 2002), but the 1990s outbreak in Great Britain occurred in the absence of defoliation and fungal pathogens (Table 1; Gibbs and Greig, 1997). Similar to the Ozark region decline, drought was apparently the only initiating factor that weakened oaks in Great Britain.

Following a severe, multi-year drought that peaked in 2002, a native aspen bark beetle, *Trypophloeus populi* Hopkins, experienced its first documented outbreak in association with sudden aspen decline in Colorado (Marchetti et al., 2011). During this mortality event, trembling aspen, *Populus tremuloides* Michx., were initially weakened by unusually hot drought (Worrall et al., 2008, 2010; Rehfeldt et al., 2009; Ziegler et al., 2012), which resulted in an abundance of susceptible host trees that were colonized by *T. populi*, whose populations reached unprecedented levels (Marchetti et al., 2011). A group of several seemingly interchangeable secondary agents were involved in this sudden aspen decline, including two species of bark beetles (*T. populi* and *Procyphalus mucronatus*; the latter colonized trees that were nearer to mortality than those colonized by the former); bronze poplar borer, *A. liragus* Barter & Brown; poplar borer, *Saperda calcarata* Say; Cytospora canker; white trunk rot; and sooty-bark canker – but little evidence for defoliation was found (Marchetti et al., 2011; Ziegler et al., 2012). The role of *Armillaria* spp. remains uncertain (Marchetti et al., 2011).

Historically, etiology of aspen decline requires an inciting event that weakens trees and includes insect defoliation, along with drought or freeze–thaw events in late winter (Frey et al., 2004). Root health, although it has not been studied extensively, is thought to be an important factor in aspen susceptibility to drought and capacity to regenerate clonally following dieback of main stems (Shepperd et al., 2001; Frey et al., 2004; Worrall et al., 2008, 2010). Climate change was an important driving factor in the recent sudden aspen decline, whereby the current range of this early successional species is becoming climatically unsuitable (i.e. too hot and dry) (Rehfeldt et al., 2009; Ziegler et al., 2012), and is expected to shrink substantially by the second half of the 21st century (Rehfeldt et al., 2009).

Bronze birch borer, *Agrilus anxius* Gory, (native to North America) has long been associated with birch, *Betula* spp., decline and mortality in North America (Balch and Prebble, 1940; Barter, 1957; Millers et al., 1989; Jones et al., 1993), and could potentially be a more aggressive pest in the future. Climate change-related stress (e.g. warmer temperatures, reduced rainfall) may increase the frequency and intensity of *A. anxius* outbreaks (Haack, 1996), as drought-sensitive, early successional birch species experience range contractions (Iverson and Prasad, 2001). Much like eastern oak forests, birch was extensively logged in the 1920s and 1930s, which resulted in even-aged, maturing stands, susceptible to decline by the late 20th century (Muilenburg and Herms, 2012). Stressors such as defoliation, high temperatures, and drought weaken birch and render them susceptible to *A. anxius* colonization (Balch and Prebble, 1940; Jones et al., 1993; reviewed in Muilenburg and Herms, 2012). A recent (1991) episode of decline in paper birch (*Betula papyrifera* Marshall), was linked to several

seasons of warmer and drier than normal weather (Jones et al., 1993). Some studies suggest that *A. anxius* is strictly a secondary mortality agent, whereas others suggest that it can act as a primary mortality agent if population densities are high enough (reviewed in Muilenburg and Herms, 2012). The latter situation could plausibly occur in association with changing climate conditions and would be consistent with the recent aggressive behavior observed in other secondary hardwood mortality agents such as *E. rufulus*, *A. biguttatus*, and *T. populi*.

5. Case study: oak mortality and an unexpected outbreak of a little-known beetle

Many of the ideas that have been discussed with respect to factors involved in oak decline and the implications for oaks and oak ecosystems can be illustrated by a recent oak decline event (1999–2003) in the Ozark and Ouachita Mountains of Arkansas, Missouri, and Oklahoma, US (hereafter referred to as the Ozark region) that was unprecedented for several reasons (Table 1; Starkey et al., 2000; Stephen et al., 2001; Riggins et al., 2009; Haavik and Stephen, 2010a). It was the largest-scale oak mortality event reported for the Ozark region since European colonization at the turn of the 19th century. Defoliation was largely absent. Moreover, the secondary biotic agent involved was unique. *E. rufulus* was not previously known as an insect to reach epidemic levels and had never been identified as a secondary agent in oak decline (Stephen et al., 2001). Also strange was the near absence of *A. bilineatus*, the secondary biotic agent that has been ubiquitously involved in several different oak decline events in eastern North America for the past century (Millers et al., 1989; Wargo, 1996; Muilenburg et al., 2014). The other common secondary agent in eastern North America, *Armillaria* spp. root rot, was present in many areas of the Ozarks that experienced decline (Bruhn et al., 2000; Kelley et al., 2009), but its relative contribution to oak mortality in the event remains unresolved. This situation provided a unique opportunity to study novel associations in a major episode of oak mortality, as well as an interesting setting in which to explore the potentially changing roles of forest history, drought, and insect outbreaks in oak decline.

5.1. Sequence of events that led to oak mortality

Recent drought (1998–2001) was initially implicated as the primary factor initiating the event, although previous droughts (especially in the early 1950s), forest history and the resulting competitive stand dynamics driven by these factors also played important roles (Starkey et al., 2000; Stephen et al., 2001; Voelker et al., 2008; Haavik et al., 2011). Oak decline initiated by drought is not unusual for the Ozark region; notable episodes were reported in 1959, 1974–1976, and 1980–1983 (Mistretta et al., 1981; Bassett et al., 1982; Law and Gott, 1987; reviewed by

Millers et al., 1989). Several investigations, most retrospective, facilitated temporal delineation of events leading up to and including the recent Ozark region decline. Through several spatial and temporal studies, we were able to piece together relationships among, and influences of factors acting at several different scales and times, from beetle populations within trees to regional climate patterns (Table 2). A point-by-point summary of the sequence of events depicted in Fig. 1 follows.

- After drought in the 1930s (Fig. 1b), evidence of *E. rufulus* appeared in the extant tree-ring record (Fig. 1a “borer density”) via uniquely-shaped scars created by larval feeding galleries (Muzika and Guyette, 2004).
- *E. rufulus* population growth rate (Fig. 1a “borer growth”, intrinsic rate of increase ‘r’, greater than zero indicates positive growth rate) increased during the severe 1950s drought (Fig. 1b). A wet period followed and population growth rate declined. The next dry period, in the mid-1960s, again brought a positive population growth rate.
- Meanwhile, tree-water relations revealed that *Quercus rubra* responded physiologically as expected to the sequence of dry-wet-dry-wet conditions, via relatively less photosynthetic discrimination of the heavier C isotope (^{13}C) during dry periods and more photosynthetic discrimination during wet periods (Fig. 1c “ ^{13}C discrimination, Δ ”; Haavik et al., 2008).
- During a drought in 1980 (Fig. 1b), *E. rufulus* densities increased slightly (Fig. 1a “borer density”).
- *Q. rubra* did not respond physiologically as expected to the 1980 drought, as determined by isotopic analysis of tree-rings studied using discrimination against ^{13}C during photosynthetic C fixation. After the 1980 drought, clear differences in growth patterns emerged among individual red oaks. Those trees that died later (when *E. rufulus* population densities reached extreme levels) began to show a declining growth trend; those that remained healthy and vigorous later maintained – or even increased – radial growth rates (Fig. 1c “ring width”).
- During a prolonged wet period in the 1990s, despite a past association with drought (Haavik and Stephen, 2010a), borer populations were building, and had been increasing, although virtually undetected, for at least 11 generations (>2 decades) prior to the outbreak itself (Fig. 1a).
- 1998 began a four-year period of dry conditions (Fig. 1b); an explosion of *E. rufulus* populations that lasted six years (three borer generations) (Fig. 1a); a marked decline in *Q. rubra* growth rates (Fig. 1c); and a surge in red oak mortality that by 2009 reached a cumulative loss of about 50% of red oak stem density (and basal area) in Ozark oak-hickory forests in Arkansas, over the course of the event (Haavik et al., 2012a).
- Not until the 1999–2003 decline event did differences in *Q. rubra* water-relations become evident among trees with distinct borer infestation levels (Fig. 1c “all trees” vs. “low, moderate,

Table 2

At multiple ecosystem scales, conditions in the Ozark and Ouachita Mountains that produced a forested landscape susceptible to a biotic disturbance (ca. 2000), and, associated with these conditions, specific variables that were investigated.

| Conditions engendering borer outbreak | Scale | Variables | Studies investigating specific variables |
|--|-------------------|---|---|
| Drought or alternating wet-dry periods | Region | PDSI; growth–climate patterns | Haavik et al. (2011) |
| Forest mature; over-crowded; even-aged | Landscape | Topography; red oak abundance; oak age and size | Aquino et al. (2008) and Jones et al. (2014) |
| Abundant susceptible hosts; competitive conditions for hosts | Stand | <i>Q. rubra</i> abundance; tree spp. diversity; topography | Fierke et al. (2007) and Haavik and Stephen (2010b) |
| Overall reduced vigor; reduced resistance; compromised water-relations | Tree | Vigor index; growth patterns; compartmentalization; wound healing; drought stress indicators; growth–climate response; $\delta^{18}\text{O}$ water-use patterns | Haavik et al. (2010, 2008, 2011), Haavik and Stephen (2011) and Boone et al. (in press) |
| Few/limited effectiveness of natural enemies | Beetle population | <i>Beauveria bassiana</i> ; cannibalism; intraguild predation; carpenter ants | Meyers et al. (2007, 2013), Ware and Stephen (2006), Muilenburg et al. (2008), Verble and Stephen (2009a,b) and Haavik et al. (2012b) |

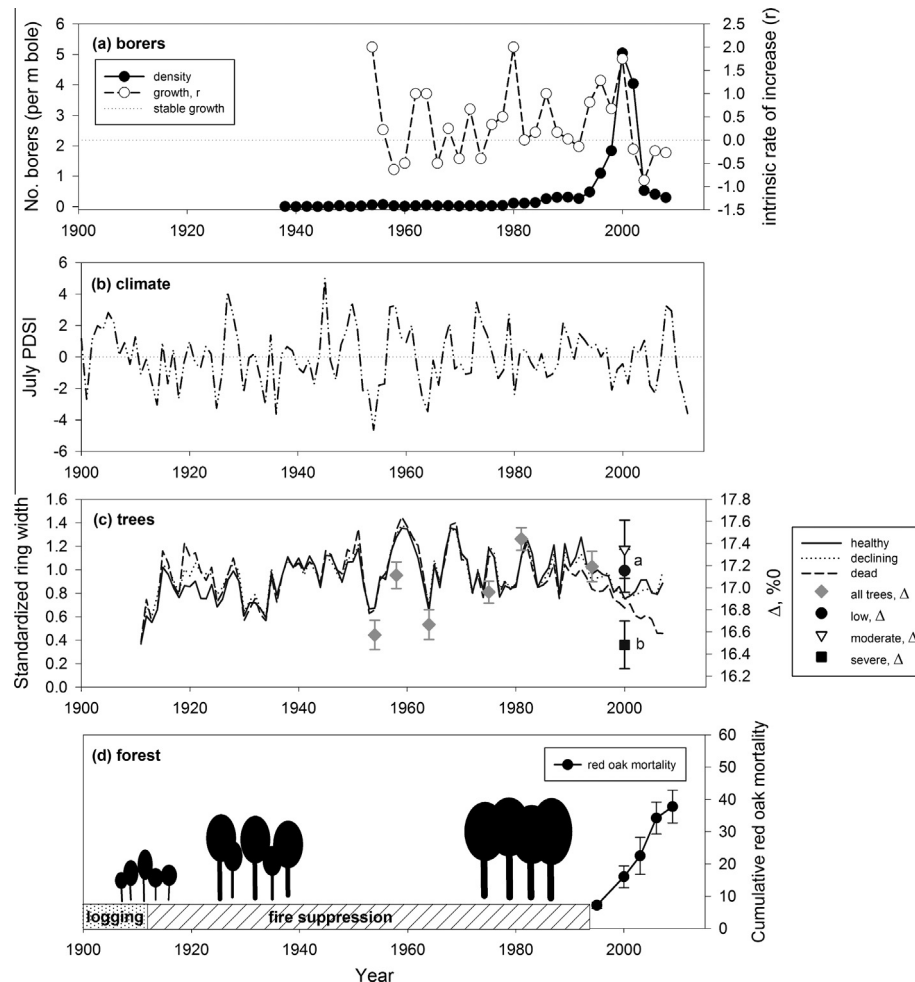


Fig. 1. Timeline of events leading up to and including the 1999–2003 Ozark and Ouachita oak decline in Arkansas. (a) Dendrochronological assessment of *E. rufulus* density and population growth from scars created by larval galleries (adapted from Haavik and Stephen, 2010a). (b) July palmer drought severity index (PDSI), found to be best explanatory climate variable for *Q. rubra* growth in Haavik et al. (2011). (c) *Q. rubra* radial growth indices (adapted from Haavik et al., 2011) and C discrimination (Δ) of *Q. rubra* (all trees = gray symbols; trees divided by different borer infestation levels, significant differences according to least squares means indicated by lowercase letters = white or black symbols) (adapted from Haavik et al., 2008). (d) Cumulative red oak mortality (% of stem density) in oak-hickory forests (adapted from Haavik et al., 2012a) and illustrations of management activities and different stages of oak forest development: stand initiation, stem exclusion, and understory re-initiation (left to right).

severe" infestation), likely as a consequence of extensive feeding by *E. rufulus* larvae in phloem and xylem tissues (Haavik et al., 2008).

5.2. Factors involved in oak mortality

By ca. 2000, oak forests in the Ozark region were vulnerable to decline. Stands, especially those on poorer sites, were dominated by drought-weakened oaks, rendering them susceptible to secondary mortality agents. Forest history in the Ozark region was similar to that in many other eastern North American oak forests. Clear-cutting and high-grading harvests of virgin stands in the early 20th century (1890–1910), followed by several smaller disturbances early in forest establishment (1920–1940s) favored oak dominance. Fire suppression (1910–1990) became especially effective with the rise in state forestry agencies after World War II, and that removal of fire from these ecosystems limited oak recruitment in the understory after 1950 (Strausberg and Hough, 1997; Soucy et al., 2005). Those acts eventually led to an aging, over-crowded oak forest with a simplified canopy structure – essentially a forested landscape susceptible to disturbance. Retrospective studies confirmed that live tree density (no. trees per ha) increased

during the 20th century (Foti, 2004; Chapman et al., 2006), and decreased following the decline episode (Fan et al., 2012; Haavik et al., 2012a). Between 1934 and 2002, in a portion of the Ozark Mountains, all canopy strata increased in density from 364 to 1029 trees/ha and in basal area from 10 to 23 m²/ha (Chapman et al., 2006). In that study, overstory oak density and basal area doubled during that time interval. Across the Ozark region in 2006, tree density was 583 trees/ha and basal area was 22 m²/ha, ~30% of which was red oak (Guldin et al., 2006). The red oak component declined by 50% in Ozark oak-hickory forests from the peak of the *E. rufulus* outbreak to after its collapse, from 20 to 11 red oaks/ha and from 12 to 6 m²/ha of red oak basal area (Haavik et al., 2012a).

Forests and stands with xeric topography, poor edaphic conditions, and an abundance of red oak were most severely affected (Fig. 2). Other oak declines in eastern North America have occurred persistently on poor quality sites (e.g. Tryon and True, 1958; Starkey and Oak, 1989; Stringer et al., 1989; Oak et al., 1991). Also characteristic of many oak declines in eastern North America, mortality and dieback in the red oak group (Section *Lobatae*) was much more substantial than in the white oak group (Section *Quercus*) (Heitzman, 2003; Guldin et al., 2006;

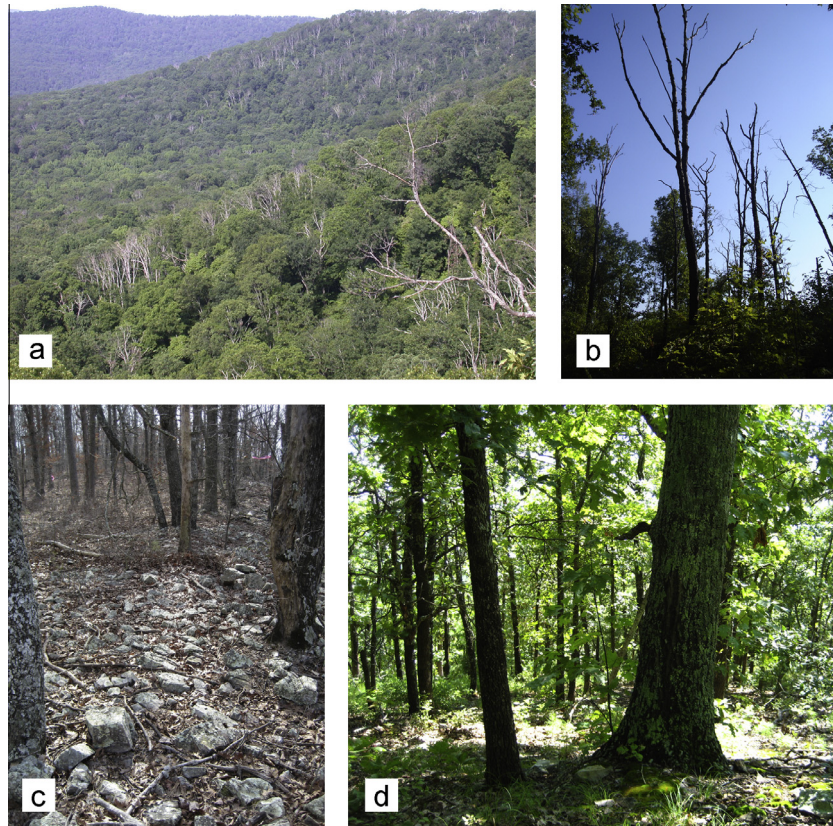


Fig. 2. Red oaks were abundant in areas that were most severely affected by the recent Ozark region oak decline, seen here as mortality to overstory, dominant oaks at the (a) landscape and (b) stand scales. Oak mortality was also high in areas with (c and d) xeric topography, on shallow, rocky soils.

Heitzman et al., 2007; Fan et al., 2008, 2011, 2012; Kabrick et al., 2008). Stands with high red oak basal area and density (no. trees per ha) experienced high levels of red oak dieback and mortality (Fierke et al., 2007; Aquino et al., 2008; Kabrick et al., 2008; Voelker et al., 2008; Wang et al., 2008): 40–70% of red oak basal area and 51–75% of red oak density (no. trees per ha) (Heitzman et al., 2007). Stands abundant in red oak existed on ridge-tops or upper slopes with south- or west-facing exposures on rocky, gravelly substrates with shallow, and sometimes clay-rich soils (Fierke et al., 2007; Heitzman et al., 2007; Aquino et al., 2008; Kabrick et al., 2008; Voelker et al., 2008; Wang et al., 2008). These are stressful growing conditions; water is limiting on ridge tops, and plant-available nitrogen appears to be in lower supply at such locations than on more mesic slope positions (S.A. Billings and F.M. Stephen, unpublished data). However, if red oak abundance was considered (i.e. amount of mortality assessed relative to the amount of red oak present), these poor quality sites did not necessarily experience proportionately more red oak mortality than higher quality sites; there were simply more red oaks growing on them (Kabrick et al., 2008; Voelker et al., 2008).

E. rufulus population densities were also higher in stands with more red oak, and lower in stands with higher tree species diversity (Fierke et al., 2007). Of *Q. rubra* growing on ridge-tops or other xeric aspects, a greater percentage of them experienced severe *E. rufulus* infestations compared with *Q. rubra* on mesic aspects (Fierke et al., 2007). Irrespective of topography, red oak mortality was greater in plots with higher *E. rufulus* population densities (Fierke et al., 2007), which suggests that at high population levels, *E. rufulus* became a more aggressive mortality agent. After the outbreak, a retrospective study confirmed that, compared to other xeric sites with lower borer densities, live *Q. rubra* basal area was

reduced in xeric areas that sustained higher borer densities (Haavik and Stephen, 2010b). In short, the total amount of oak mortality and dieback was greatest – and *E. rufulus* populations were highest – on sites with inherently stressful growing conditions.

Oaks in all canopy positions died or experienced dieback during the decline, but mortality levels were relatively higher in overtopped positions. Stand-level and landscape-scale studies that combined all red oak species for analyses, reported that all size classes experienced mortality (Heitzman, 2003; Guldin et al., 2006; Heitzman et al., 2007; Haavik et al., 2012a). Since oak forests in the Ozark region were primarily even-aged, size differences were less likely related to age than canopy position. These results may be, in part, because different oak species reach maturity at different ages and sizes (Guldin et al., 2006). In contrast, studies that examined species of red oak separately, found relatively more mortality in overtopped (suppressed and intermediate) crown positions than in dominant and co-dominant positions (Fan et al., 2008, 2011; Haavik and Stephen, 2010b). Suppressed oaks also supported higher *E. rufulus* larval survivorship, though not necessarily higher borer densities, than co-dominant oaks (Haavik and Stephen, 2010b). Although some studies of previous oak decline events found that declining oaks were older than healthy oaks (Tainter et al., 1990; Jenkins and Pallardy, 1995), we did not find any evidence for this (Haavik et al., 2011). Several studies agreed that by ca. 2000, oak forests in the Ozark region had likely reached an age susceptible to decline (Heitzman et al., 2007; Voelker et al., 2008; Haavik et al., 2011).

Drought alone, or the rapid change from a 6-year (1992–1997) wet period to abnormally dry conditions (1998–2001) (Fig. 1b), was almost certainly a factor that weakened oaks already suffering

from intense inter- and intra-specific competition, over-maturity, and stress from growing in extreme edaphic conditions. All of those factors likely rendered oaks more susceptible to *E. rufulus* infestation and subsequent mortality. Perhaps oaks that did not have the C reserves/supplies available for rapid callus formation and resistance to *E. rufulus* (Fierke and Stephen, 2008; Haavik and Stephen, 2011) were singularly weakened by drought, or by the sequence of sustained wet-then-dry conditions, which resulted in increased oak leaf area during wet conditions and consequently hydraulic demands that could not be met once drought and high borer populations arrived.

5.3. Differential effects of drought and forest history on co-occurring oaks

On the other hand, individuals that were good competitors and resilient following disturbance (i.e. drought and ensuing *E. rufulus* infestation) survived this event. Of oaks growing on the same aspect and slope position, healthy survivors were often larger in diameter and possessed higher radial growth rates over the past two decades than their declining or dying counterparts (Haavik and Stephen, 2010b). *Q. rubra* that sustained low borer infestations, compared with those that were dying and had severe borer infestations, exhibited higher indices of vigor (5-y basal area increment: sapwood area, Haavik et al., 2010), and greater capacity for

resistance to *E. rufulus* (Fierke and Stephen, 2008; Haavik and Stephen, 2011). Although these individuals possessed superior growth and vigor in years surrounding the oak decline, this was not always the case. Initially, during earlier stages of stand development (pre-1950), these *Q. rubra* were growing at a slower rate than *Q. rubra* that were declining or died ca. 2000 (Fig. 1c and d; Haavik et al., 2011). This grow-fast-die-early phenomenon appears to be a common pattern for oaks (Tainter et al., 1990; Biocca et al., 1993; Jenkins and Pallardy, 1995; Levanič et al., 2011) and possibly other temperate trees (e.g. Bugmann and Bigler, 2011).

Oak growth rates are influenced by multiple environmental factors, with soil moisture availability typically being the most important (Tainter et al., 1984, 1990; Helama et al., 2009; Speer et al., 2009; LeBlanc and Terrell, 2011). Leaf area indices of oaks fluctuate annually according to site moisture availability (Bréda and Granier, 1996; Hoff and Rambal, 2002), and crown dieback can be considered an adaptation to dry conditions (Thomas and Hartmann, 1996). Carbon allocation to below- vs. above-ground growth is also influenced by soil moisture availability, and rapid fluctuations between wet and dry periods can affect tree resilience to drought. Wet periods stimulate increases in leaf area, with concomitant reduced growth of roots and sapwood that result in high ratios of hydraulic demand to supply, which can increase susceptibility to subsequent drought (Waring, 1987; McDowell et al., 2008). Demands on C reserves for repair, maintenance, and defense of plant organs are also high during and following drought (Bréda et al., 2006).

Grow-slow-survive-longer oaks, those that were not initially competitively dominant (ca. 1960–1980 depending on tree age, see Haavik et al., 2011 for details), eventually may have become more resilient to drought than grow-fast-die-early oaks through differences in their root health and/or architecture. One possibility is that grow-fast-die-early oaks grew rapidly both above- and below-ground, and that during drought their extensive root systems became more severely affected by root pathogens (likely *Armillaria* spp.) which at some point affected resilience capacity following dry conditions enough so that they ultimately lost competitive dominance (Fig. 3a; Tainter et al., 1990; Biocca et al., 1993). Thus, having a root system that was comparably smaller than some neighboring oaks may have allowed grow-slow-survive-longer oaks to avoid extensive and debilitating root pathogen infection during and after drought, when demands for C reserves and water acquisition were high. A second possibility, perhaps related to the first, is that growing slowly initially enabled grow-slow-survive-longer oaks to maintain enough C reserves to later afford them better competitive and defensive capacity when their faster growing, dominant counterparts eventually succumbed to drought, root pathogen infection and/or borer infestation. A third possibility is that grow-slow-survive-longer oaks appeared to grow more slowly because radial growth did not increase as much as their faster growing counterparts, but their C reserves were instead allocated to more extensive root systems. If so, apparently slow-growing trees may have had access to deeper or different moisture sources than the (apparently) grow-fast-die-early oaks that invested more C into rapid above-ground growth (Fig. 3b).

In a recent synthesis, Sala et al. (2012) proposed that C storage pools may be actively regulated in woody plants, such that plants may somehow inhibit growth in the short term in favor of increasing C storage levels to enhance growth in the long term. Despite being consistent with that idea, there are inconsistencies with our second and third possibilities. Slow above-ground growth was probably dictated by some environmental variable, most likely light. Oaks are shade intolerant (Crow, 1988; Johnson et al., 2002). If light was limiting because of lack of competitive dominance in these individuals, then C may have also been in short

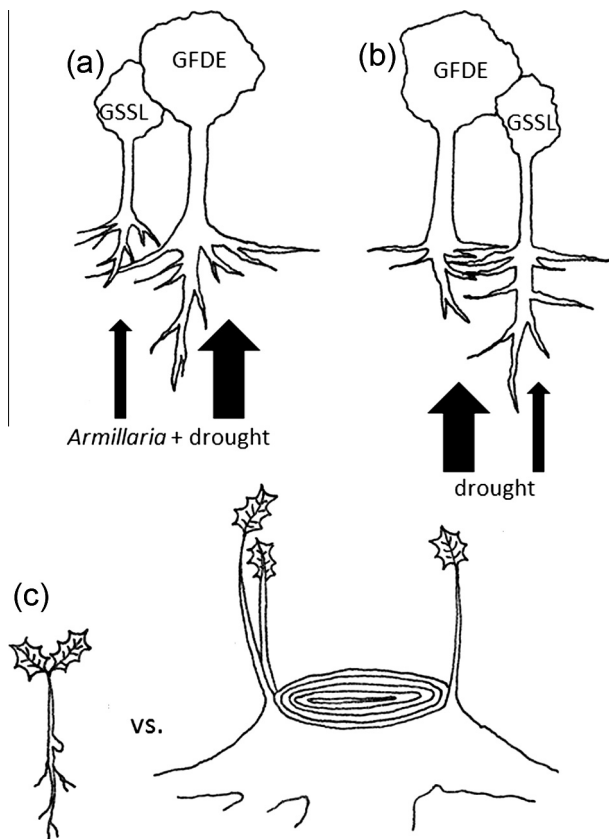


Fig. 3. Possible differences in root health, architecture, and/or origins that led to contrasting long-term growth patterns in grow-slow-survive-longer (GSSL) vs. grow-fast-die-early (GFDE) oaks. (a) GSSL oaks were conservative in above- and belowground growth relative to GFDE oaks, and during drought the extensive root systems of GFDE oaks were more susceptible to pathogens or other biotic agents, eventually resulting in a loss of GFDE competitive dominance. Alternatively, (b) GSSL oaks invested more in below- than aboveground growth, facilitating access to deeper or different water sources than those utilized by GFDE oaks during drought. Microsites and/or (c) root origins (seedling vs. sprout) may have influenced GSSL vs. GFDE growth patterns.



Fig. 4. *Quercus rubra* in the Ouachita Mountains, Arkansas, of sprout and seedling origins. (a) Mature *Q. rubra* of sprout origin that died in the recent decline event; (b) new sprouts from the root system of a mature *Q. rubra* that died; and (c) *Q. rubra* seedlings in a canopy gap created by mortality of over-story *Q. rubra*.

supply, either for reserves or investment in belowground growth. Thus, these possibilities seem unlikely unless some other variable influenced root architecture or health, such as variation in microsite conditions or root origin (Fig. 3c). Clues revealed by forecasting models suggesting that dying oaks had predictable, linear growth dynamics throughout their lives (Boone et al., in press) imply that nonlinear growth dynamics and, perhaps, an associated ability to respond nimbly to pulses of belowground resources may be consistent with these ideas.

Variation in microsite conditions has been suggested by several authors as a possible explanation for the grow-fast-die-early phenomenon (Biocca et al., 1993; Jenkins and Pallardy, 1995; Levanič et al., 2011), but without much detail as to what characteristics may have varied among microsites. Phillips and Marion (2004) proposed a model of self-reinforcing pedologic influences of trees to explain the extreme variability in soil properties observed within small areas in the Ouachita Mountains. The model predicted that trees non-randomly established on nutrient-rich, rock fragment-poor microsites. Rock displacement by tree growth, and accumulation of organic matter and nutrient turnover through decomposition maintained quality of microsites, which resulted in increased likelihood of future tree establishment in them. It is possible that favorable microsites could have facilitated better moisture and nutrient acquisition for some oaks, which would have been advantageous during drought.

Root origins may have also facilitated different resource allocation patterns. Grow-fast-die-early oaks may have been of sprout origin and grow-slow-survive-longer oaks may have been of seedling origin (Figs. 3c and 4). The taproot may be killed or damaged when mature trees are cut, which can seriously compromise water relations of sprout-origin oaks at early stages of stand development (Zadworny et al., 2014 and references therein). Sprouts that regenerate from cut stumps are initially more competitive, faster growers than seedlings (Zahner and Myers, 1984; Crow, 1988; Johnson et al., 2002) and would reach the canopy first, which could explain high radial growth rates at stand initiation (Fig. 1c and d). Furthermore, during episodes of decline, oaks of sprout origin are more likely to die than those of seedling origin (Führer, 1998), presumably because they are more susceptible to pathogen infection (Millers et al., 1989). Or, perhaps because sprout origin oaks can often have multiple stems (Fig. 4a), which might require too much C to support in a drought year.

6. Conclusions

- Many emergent insects and pathogens in oak and other hardwood declines are native species that have not caused noticeable levels of tree mortality in the past. Novel decline

situations often lack agents traditionally involved in decline and are associated with changes in climate. In particular, defoliation is sometimes absent, which implies that drought alone – and perhaps drought during periods of high temperature – is sufficiently debilitating to tree physiology that secondary agents are able to operate in a more aggressive manner than previously thought.

- Changing environmental conditions and anthropogenic influences have created hardwood forests currently vulnerable to disturbance. Changing climatic conditions complicate predictions of decline events of the future, but in general, will probably exacerbate tree mortality and encourage more rapid successional shifts in species dominance. Examples from North America and Europe suggest that parallels among different hardwood forest ecosystems exist.
- 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 source/sink relationships during drought and/or defoliation. This, in turn, might lead to limiting or depleting C reserves, and inhibiting translocation of stored C to repair damaged tissues and resist secondary biotic agents. Because C balance is tightly linked to rooting dynamics, the role of roots in drought tolerance (deep-rooting) and susceptibility (loss of fine roots) to drought is a critical avenue of research for understanding oak decline in the context of changing environmental conditions. Contrasting successive extremes of wet and dry periods appear to negatively affect oak C balance and water relations, which in turn may be advantageous for some secondary agents such as root pathogens (e.g. *Phytophthora* spp.). Furthermore, microsite characteristics and root origins (sprout vs. seedling) could influence different patterns of C balance and storage among oaks growing in similar environmental conditions, which may dictate which individuals survive or die during an episode of decline.
- We suggest that future studies focus on the relationship between tree physiology and insect and pathogen attack as well as the etiology of decline events. In particular, how do drought-induced physiological changes (e.g. osmotic adjustment, changes in C balance) in decline-affected trees influence insect and pathogen survival and population growth (i.e. via enhanced resistance or nutrition), and in turn, tree survival? Thorough description and understanding of the complete etiology of decline events and how different factors (forest history, primary and secondary factors) interact with one another is also critical. Drawing on what is known can help predict future scenarios and guide new avenues of study.

Acknowledgements

The research on red oak borer was supported in part by the University of Arkansas, Fayetteville and the UA Division of Agriculture, plus funding from the USDA Forest Service (Southern Forest Research Station, and Forest Health Monitoring Program). We greatly appreciate comments from Ken Raffa, Barbara Bentz, Jean-Claude Grégoire, Dan Herms, and three anonymous reviewers on an earlier version of the manuscript. We thank Dave Stahle and Rose Marie Muzika for insightful discussions and help with shaping our ideas. We also express our thanks to Vaughn Salisbury, Damon Crook, Rose Ann Barnhill, Larry Galligan and a myriad of students and technicians who collected the data summarized here.

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