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The importance of drought–pathogen interactions in driving oak mortality events in the Ozark Border Region

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Abstract

Forests are expected to become more vulnerable to drought-induced tree mortality owing to rising temperatures and changing precipitation patterns that amplify drought lethality. There is a crucial knowledge gap regarding drought–pathogen interactions and their effects on tree mortality. The objectives of this research were to examine whether stand dynamics and ‘background’ mortality rates were affected by a severe drought in 2012; and to evaluate the importance of drought–pathogen interactions within the context of a mortality event that killed 10.0% and 26.5% of white (*Quercus alba* L.) and black (*Q. velutina* Lam.) oak stems, respectively, in a single year. We synthesized (i) forest inventory data (24 years), (ii) 11 years of ecosystem flux data with supporting biological data including predawn leaf water potential and annual forest inventories, (iii) tree-ring analyses of individual white oaks that were alive and ones that died in 2013, and (iv) documentation of a pathogen infection. This forest displayed stand dynamics consistent with expected patterns of decreasing tree density and increasing basal area. Continued basal area growth outpaced mortality implying a net accumulation of live biomass, which was supported by eddy covariance ecosystem carbon flux observations. Individual white and black oaks that died in 2013 displayed historically lower growth with the majority of dead trees exhibiting *Biscogniauxia* cankers. Our observations point to the importance of event-based oak mortality and that drought–*Biscogniauxia* interactions are important in shaping oak stand dynamics in this region. Although forest function has not been significantly impaired, these drought–pathogen interactions could amplify mortality under future climate conditions and thus warrant further investigation.

1. Introduction

Forests account for ~45% of global terrestrial carbon stocks (Bonan 2008) and ~50% of gross primary production (GPP) (Beer *et al* 2010), and thus play a key role in the carbon–climate system. Severe regional-scale drought-induced tree mortality has drawn attention to the potential vulnerability of forests—and thus forest carbon stocks and sink strength—to future climate change (Allen *et al* 2010, 2015, Anderegg *et al* 2015). The loss of plant hydraulic function and carbon starvation during drought are important pathways leading to tree mortality (McDowell and Allen 2015, McDowell *et al* 2015, 2013, Anderegg *et al* 2016). It is thought that

rising atmospheric vapor pressure deficits (VPD)—a consequence of warming air temperatures—will play an increasingly important role in regulating stomatal conductance (g_s) and thus have important implications on the C and water economies of trees (Novick *et al* 2016). ‘Hotter’, more intense droughts are expected to amplify lethality, giving rise to increased tree mortality (Allen *et al* 2015, Williams *et al* 2012, McDowell and Allen 2015).

Much of the recent literature directed towards elucidating the coupled hydraulic impairment–carbon mechanisms of drought-induced tree mortality has examined highly xeric locations and responses to extreme long-term drought (Anderegg *et al* 2014,

2013, 2012, McDowell *et al* 2013) and do not directly address important interactions among drought and biotic agents of dieback (McDowell *et al* 2011, Oliva *et al* 2014), long-term declines in vigor (Berdanier and Clark 2016), or hydraulic deterioration (Pellizzari *et al* 2016). As an illustrative point, the importance of defoliation and root rot infection in modulating physiological decline during drought was recently demonstrated through careful observation (Aguadé *et al* 2015). Of particular interest here are the possible effects of increased frequency of short (sub-seasonal) ‘global-change’ type drought (i.e. high VPD and temperature) (Eamus *et al* 2013) on tree mortality.

Widespread oak decline has been documented in forests in Oklahoma (Bendixsen *et al* 2015), Arkansas (Haavik and Stephen 2010) and Missouri (Pallardy *et al* 1988, Jenkins and Pallardy 1995) in the 20th and early 21st centuries (Haavik *et al* 2015). While there may be spatial variation across the region regarding the precise sequence of events ultimately leading to mortality, some of the important factors include:

1. frequent droughts (Haavik *et al* 2015, Jenkins and Pallardy 1995, Voelker *et al* 2008),
2. high abundance of mature trees from the red oak group (Kabrick *et al* 2008),
3. infestation by the red oak borer (*Enaphalodes rufulus* (Haldeman) coleoptera: cerambycidae) (Haavik and Stephen 2010, Haavik *et al* 2015),
4. the presence of endemic pathogens such as *Armillaria* spp. (Bruhn *et al* 2000, Lee *et al* 2016) or *Biscogniauxia* spp. (Bassett and Fenn 1984, Bendixsen *et al* 2015), and
5. the presence of exotic pathogens such as *Phytophthora* spp. (Schwingle *et al* 2007).

Here, we re-examine a recent drought-induced mortality event, for which the precise mechanisms of death were not conclusively identified (Gu *et al* 2015) with emphasis on climate and drought–pathogen interactions.

We focus on upland oak–hickory forests of the Ozark Border Region of Missouri. Although the annual precipitation (climate normal) is 1083 mm, the distribution is such that late-season droughts are common, as is the over-winter recharge of soil water resources. Mortality significantly increased in response to an exceptional drought—of the ‘global-change’ type—during 2012 (Gu *et al* 2015) for black (*Quercus velutina* Lam.) and white (*Q. alba* L.) oaks that are typically tolerant of water stress. In the ensuing years, high incidence of cankers caused by *Biscogniauxia* spp. infection were visibly observed on many white oaks that died in 2013. It is possible that the proliferation of *Biscogniauxia* in predisposed, weaker individuals was promoted during frequent episodes of moderate water stress and that the exceptional drought of 2012 incited a shift to pathogenic behavior, accelerating mortality.

Here we address the following questions, with an emphasis on oak species:

1. Did a severe drought in 2012 alter trajectories of stand dynamics in oak–hickory forests in mid-Missouri?
2. Were there predisposing biogeographical factors driving spatial variation in mortality?
3. Is it plausible that drought–*Biscogniauxia* interactions caused the oak mortality event in 2013?
4. Were individuals that died in 2013 predisposed to mortality due to declining growth rates associated with ontogeny or *Biscogniauxia* infection?
5. Is tree mortality affecting ecosystem functioning and are there important legacy effects?

To answer these questions, we performed a novel synthesis of (i) forest inventory data spanning 24 years, (ii) 12 years (2005–2016) of ecosystem-scale carbon and water fluxes, and biological data including predawn leaf water potential (ψ_{pd}) and annual plot inventories, (iii) tree-ring analyses of individual white oaks that were alive and ones that died in 2013, (iv) documentation of pathogen infection.

2. Methods

2.1. Description of sites

2.1.1. Baskett Wildlife Research and Education Center (BWREC)

The University of Missouri’s BWREC (figure S1, available at stacks.iop.org/ERL/13/015004/mmedia) is a 900 ha reserve located in the Ozark Border Region of central Missouri (latitude 38.739, longitude −92.186). The dissected topography is characterized by numerous ridges separated by ravines that feed ephemeral and perennial streams. Ordovician and Mississippian limestones underlie BWREC soils that have a loess cap on ridge tops and slopes, with the latter being severely eroded. Dominant soils include Bardley gravelly silt loam (very-fine, mixed, active, mesic Typic Hapludalf) and Clinkenbeard very flaggy clay loam (clayey-skeletal, mixed, superactive, mesic Typic Argiudoll) along hillslopes, with Weller silt loam (fine, smectitic, mesic Aquertic Chromic Hapludalf) common on uplands and ridgecrests. The land cover is a mixture of abandoned agricultural fields, plantations, and second-growth hardwood forests (85–180 years old). Oak–hickory is the major forest type, with both northern and southern division species present, and species from the former being more abundant. Important oak species include *Q. alba*, *Q. velutina*, northern red (*Q. rubra* L.), bur (*Q. macrocarpa* Michx.), post (*Q. stellata* Wangenh.), blackjack (*Q. marilandica* Münchh.), shumard (*Q. shumardii* Buckley) and chinkapin (*Q. muehlenbergii* Engelm.). The most abundant hickory is shagbark

(*Carya ovata* (Mill.) Koch). Sugar maples (*Acer saccharum* Marsh.), ash (*Fraxinus* spp.) and eastern redcedar (*Juniperus virginiana* L.) are also found at BWREC.

2.1.2. Missouri Ozarks AmeriFlux site

The Missouri Ozarks AmeriFlux (MOFLUX) site (ID: US-MOz; latitude 38.7441, longitude -92.2000) that was established in 2004 is situated in second-growth upland oak-hickory forest (upper quartile of canopy heights ≈ 22 m; mean canopy height ≈ 18 m) (figure S1)—the dominant ecosystem type at BWREC (Pallardy *et al* 1988). Dominant soils at the site are Weller silt loam and Clinkenbeard very flaggy clay loam. Major tree species at MOFLUX include white oak, black oak, shagbark hickory, sugar maple, and eastern redcedar, with white ash (*Fraxinus americana* L.) scattered throughout the forest. For more complete details regarding the MOFLUX site and BWREC forests the reader is referred to the literature (Gu *et al* 2015, 2016a, 2016b, Pallardy *et al* 1988).

Net ecosystem exchanges of CO_2 (NEE), water vapor (i.e. latent heat flux, LE) and sensible heat (H) in the MOFLUX forest were measured using eddy covariance (Baldocchi 2003, Gu *et al* 2012, 2016b). Note that a negative NEE value represents net C uptake by the ecosystem, and we assume that net ecosystem production (NEP) is equal to minus NEE ($\text{NEP} \approx -\text{NEE}$). Supporting meteorological variables were also measured at the tower. Soil respiration (R_s) was measured using automated, flow-through non-steady state chamber systems. From 2004–2010, a custom built, eight-chamber system (Edwards and Riggs 2003, Gu *et al* 2008) was used, after which a commercially available sixteen-chamber system (Li-Cor Inc., Lincoln, NE) was used. All flux and meteorological observations were recorded at half-hourly resolution. The reader is referred to the literature for a more detailed description of the micrometeorological instrumentation and flux calculations (Yang *et al* 2010, 2007, Gu *et al* 2012, 2016b).

Predawn leaf water potential (ψ_{pd}) was measured each growing-season in the MOFLUX forest at weekly to bi-weekly intervals (Gu *et al* 2015). Samples (20–21 total) from canopy and sapling individuals comprising the major species were collected before dawn in rough proportion to their relative basal area contributions. Samples were excised from lower branches (<2 m), placed in humidified bags, and stored in a cooler on ice until analysis using the pressure chamber technique (Pallardy *et al* 1991). The predawn leaf water potential integral (PLWPI) was used as a metric to describe integrated water stress (Myers 1988, Gu *et al* 2015). For each year (and species), the ψ_{pd} time series was first interpolated linearly to fill gaps between observations. The PLWPI was then calculated from the interpolated time series ($\psi_{\text{pd},i}$) according to: $\text{PLWPI} = \sum \psi_{\text{pd},i}$ (Gu *et al* 2015), with units of MPa d.

2.1.3. Forest inventory and mortality

In 1968, a network of vegetation plots, hereafter referred to as the Rochow plots, was established across BWREC to characterize forest succession within representative forest types that capture environmental variability within the region (Rochow 1972). Initially, 75 permanent plots were established, with 53 plots re-measured in 1982, 1992, 2004, and 2016. Within each plot, forest vegetation was sampled using a nested sampling design. Diameter at breast height (DBH) and species were recorded for each tree ($\text{DBH} > 8.75$ cm) within 0.08 ha circular plots. In 1992, each living tree was mapped relative to the plot center, with distance and azimuth recorded. No spatial reference information was used in the 2004 sampling, but in 2016 the spatial data from 1992 were used to relocate and tag each tree. The dataset represents the longest continuous inventory in mid-Missouri and provides valuable and robust data on forest successional patterns across common forest types of the region (Rochow 1972, Jenkins and Pallardy 1995, Pallardy *et al* 1988, Belden and Pallardy 2009).

We used long-term data from the Rochow plots to describe stand dynamics across the landscape (figure S1). Previous analyses had classified the plots into four primary forest types (dry ridge and slope, mesic, glade-like, and bottomland) (Pallardy *et al* 1988, Belden and Pallardy 2009). We focused our analyses on the plots within the dry ridge and slope classification ($n = 26$) due to the similarity of the forest type with the MOFLUX site. For each plot, we recorded topographic characteristics, including soil series, aspect, slope, and elevation, and we tested for differences in mortality by soil series and for bivariate relationships with each continuous variable.

When the MOFLUX site was established, individual trees ($\text{DBH} > 9$ cm) were inventoried on circular plots ($n = 24$), each of area 0.08 ha (figure S1), and live trees were identified with numbered aluminum tags (Gu *et al* 2015). The plots were separated by 50 m along five linear transects that radiated out from the tower in SE, S, SW, W, and NW directions. In subsequent years, tree mortality was recorded during frequent (monthly) visits during the growing season. Ingrowth on the plots was added to the inventory each year in the autumn, and the DBH of all trees was measured at least once every three years. Subsequent to the documented 2013 mortality event (Gu *et al* 2015), evidence of widespread *Biscogniauxia* infection was noted. Closer monitoring of oaks (live and dead) in the inventory for the visible presence of *Biscogniauxia* was therefore initiated.

Assuming the probability of mortality was constant over time, annual mortality, m , over some time interval, t (years), was computed according to:

$$m = 1 - [1 - (N_0 - N_1)/N_0]^{1/t}, \quad (1)$$

where, N_0 and N_1 are stem counts or basal area at the start and end of the measurement interval (Sheil *et al* 1995). On MOFLUX plots, mortality was recorded at

sub-annual intervals, and all data were summarized to annual values prior to calculating m using equation (1)—note that we use the updated live numbers over time when calculating mortality in each subsequent year as opposed to referencing all values to the 2005 live inventory as in Gu *et al* (2015). On the Rochow plots, mortality was assessed over a much longer interval (1992–2016); therefore, these data do not capture the dynamics of mortality in response to stressors. However, the Rochow data provide a valuable window further back in time because the MOFLUX plots were established in 2005.

2.1.4. Tree-ring analysis

For the tree-ring analysis, in autumn 2013 we chose 25 pairs of white oaks within a limited area; each pair included a healthy looking tree and a tree that had died within the previous 2 years. Cores were collected from each tree. In the laboratory, cross-sections were surfaced with an electric hand planer and the cellular detail of annual rings and fire scar injuries were revealed by sanding with progressively finer sandpaper (80–1200 grit). A radius (pith-to-bark tree-ring series) of the cross-section with the least amount of ring-width variability due to fire injuries was chosen for measurement and cross-dating. The ring-width series from each tree was plotted and cross-dated to ensure years were correctly identified. The COFECHA computer program (Holmes 1983) was used as a check of tree-ring dating and measurement quality control.

3 Results

3.1. Baskett forest stand dynamics

From 1968 through 2016, the oak–hickory forests of BWREC demonstrated patterns consistent with expected stand development of second-growth forests (figure S2). Through time, the number of trees per hectare decreased ($p < 0.0001$) but the stand basal area increased ($p < 0.0001$), demonstrating tree mortality concomitant with growth of residual trees. The number of trees that died per plot was significantly related to tree density in 1992, but the mean annual mortality rate of 2.0% across plots was independent of tree density in 1992 (figure S3). We found no significant relationships between plot-level mortality rate and slope, aspect, elevation, or soil series, probably due to the similarity of conditions among plots.

We ranked the ten most abundant species by trees per hectare and basal area of live trees in 1992 across all plots (figure 1). White oak was the most abundant by both measures, yet the mortality rate of white oak was less than the community average based on trees per hectare ($1.8\% \text{ yr}^{-1}$ and $2.6\% \text{ yr}^{-1}$, respectively) and basal area ($1.1\% \text{ yr}^{-1}$ and $2.0\% \text{ yr}^{-1}$, respectively). Aside from red elm, which had low abundance but nearly complete mortality over the 24 year period, black oak had the highest mortality rate based on both tree

density ($3.2\% \text{ yr}^{-1}$) and basal area ($3.8\% \text{ yr}^{-1}$). White oak and sugar maple were abundant enough to test for relationships among plot level attributes and mortality rates, but no significant relationships were observed. For most species, there were no differences in the DBH in 1992 between trees that lived and trees that died by 2016 (figure 2). However, white oak mortality was concentrated on smaller trees ($p < 0.001$), and sugar maple mortality was concentrated on larger trees ($p = 0.005$). The difference in DBH between trees that lived and trees that died by 2016 was not affected by slope, elevation, aspect, or soil type for any species tested.

3.2. MOFLUX tree mortality and ecosystem function

The average annual mortality rates across all years except 2013 for white and black oaks were $1.7\% \pm 0.38\%$ and $2.1\% \pm 0.59\%$, respectively, and are in-line with estimates from the Rochow plots (white oak = 1.8% ; black oak = 3.2%). After the exceptional drought of 2012 (minimum community $\psi_{\text{pd}} \approx -4 \text{ MPa}$; figure S5(e)) there was a notable mortality event in 2013 (figures 3 and 4), for which annual white and black oak mortality was 10.0% and 26.5% , respectively. In general, the DBH distribution of dead individuals tended to span a wider range and include larger trees in the years after the more severe droughts (figure 3(b)). Interestingly, in 2013, substantial numbers of oak trees of all size classes died (figures 4(f) and (g)). There were, however, differences between species: (i) white oak mortality tended to affect trees of smaller DBH than the live population (and vice versa for black oak) (figures 4(f) and (g) and figure S4), (ii) the DBH distribution of dead black oaks was concentrated in the larger size classes compared to the more uniform distribution for white oak (figures 4(f) and (g)), and (iii) mortality tended to affect larger black oaks compared to white oaks (figures 4(f) and (g) and figure S4).

Water stress was related to mortality in the subsequent year (figure 5). Mortality of white oak and black oak was relatively stable down to PLWPIs of -150 MPa d , rising sharply between -150 and -250 MPa d (figure 5(a)). In contrast, the ensemble mortality–PLWPI relationship for the other major species was described by an exponential function (figure 5(b)). It is interesting that the oaks displayed a markedly larger mortality response to the 2012 drought given that they are more drought tolerant than the other major species. Indeed the range of PLWPI (oak vs other species; figures 5(a) vs (b), respectively) and the dynamics of ψ_{pd} (figure S5) show that the oak species tended to show lower susceptibility to water-stress than other species. It was particularly evident during years of moderate drought where there is separation according to relative capacities to tolerate and avoid drought (figures S5(a)–(c)). It is also noteworthy that irrespective of species, rapid recovery of ψ_{pd} after soaking rains was observed repeatedly within and across years, regardless of drought severity (figure S5).

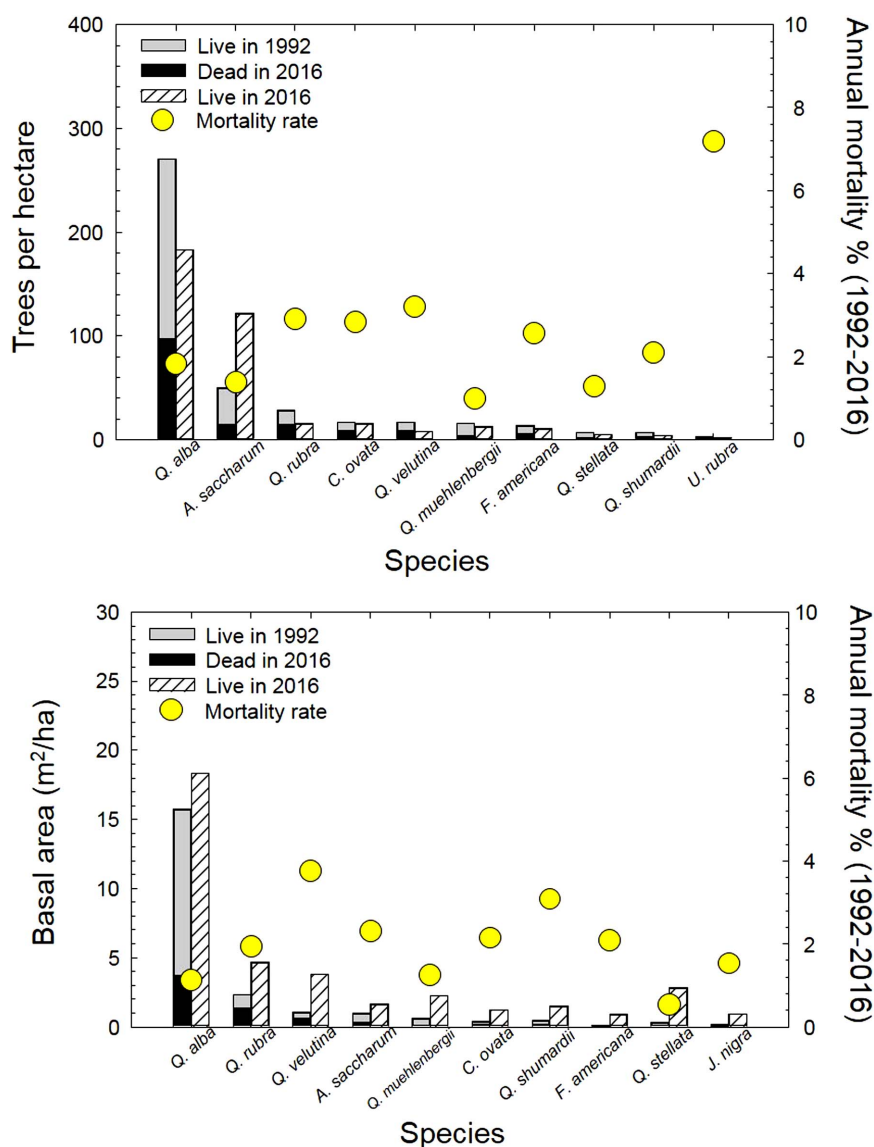


Figure 1. Mortality summary of the dry ridge and slope Rochow plots (1992–2016) presented in terms of tree density (top panel) and basal area (bottom panel). Species represented include white oak (*Quercus alba* L.), sugar maple (*Acer saccharum* Marsh.), northern red oak (*Q. rubra* L.), shagbark hickory (*Carya ovata* (Mill.) K. Koch), black oak (*Q. velutina* Lam.), chinkapin oak (*Q. muehlenbergii* Engelm.), white ash (*Fraxinus americana* L.), post oak (*Q. stellata* Wangenh.), shumard oak (*Q. shumardii* Buckley), red elm (*Ulmus rubra* Muhl.), and eastern black walnut (*Juglans nigra* L.).

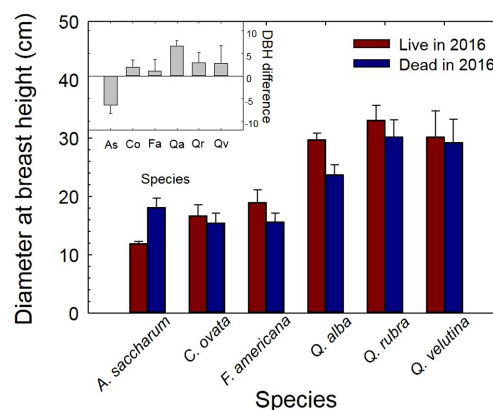


Figure 2. Average diameter at breast height (DBH) of trees that lived and died (1992–2016) on dry ridge and slope Rochow plots and the differences in mean DBH of live and dead trees (inset; negative and positive differences indicate larger and smaller trees were dying, respectively). Species included in the main panel are sugar maple (*Acer saccharum* Marsh.), shagbark hickory (*Carya ovata* (Mill.) K. Koch), white ash (*Fraxinus americana* L.), white oak (*Quercus alba* L.), northern red oak (*Q. rubra* L.) and black oak (*Q. velutina* Lam.), which are represented in abbreviated form in the inset panel as As, Co, Fa, Qa, Qr, and Qv, respectively.

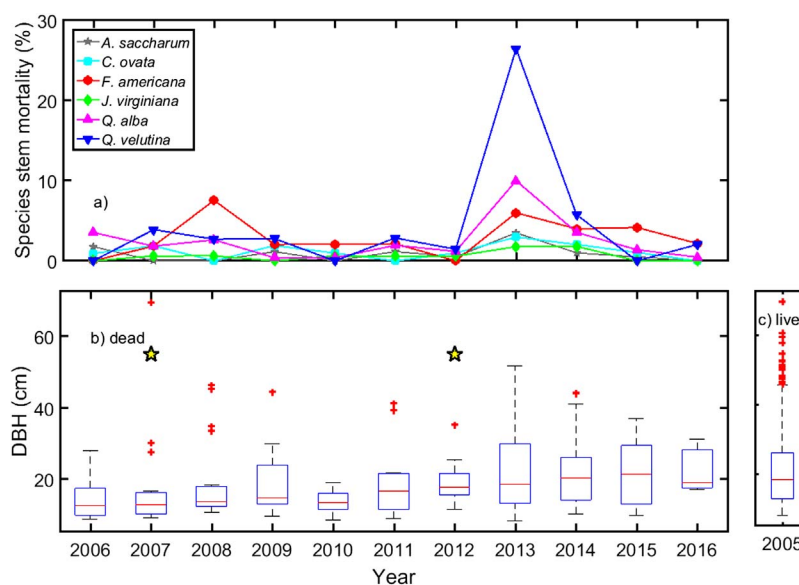


Figure 3. Time series of MOFLUX (a) species stem mortality, (b) the distribution of (community) diameter at breast height (DBH) of individuals that died, and (c) the DBH distribution of live individuals in 2005. In (b), the stars indicate the two years with the most severe drought. The major species included in the (a) panel are white oak (*Quercus alba* L.), black oak (*Q. velutina* Lam.), shagbark hickory (*Carya ovata* (Mill.) K. Koch), eastern redcedar (*Juniperus virginiana* L.), sugar maple (*Acer saccharum* Marsh.), and white ash (*Fraxinus americana* L.).

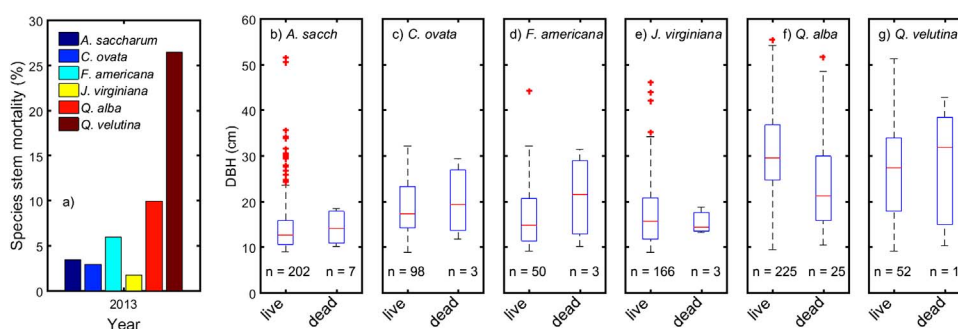


Figure 4. (a) Stem mortality of major tree species in the MOFLUX forest in 2013 relative to the live stems present during the 2012 drought. (b)–(g) Distribution of diameter at breast height (DBH, 1.3 m) of trees that were alive and those that died in 2013. The species are white oak (*Quercus alba* L.), black oak (*Q. velutina* Lam.), shagbark hickory (*Carya ovata* (Mill.) K. Koch), eastern redcedar (*Juniperus virginiana* L.), sugar maple (*Acer saccharum* Marsh.), and white ash (*Fraxinus americana* L.). Note that in (b), *A. saccharum* is abbreviated as *A. sacch* because of space constraints.

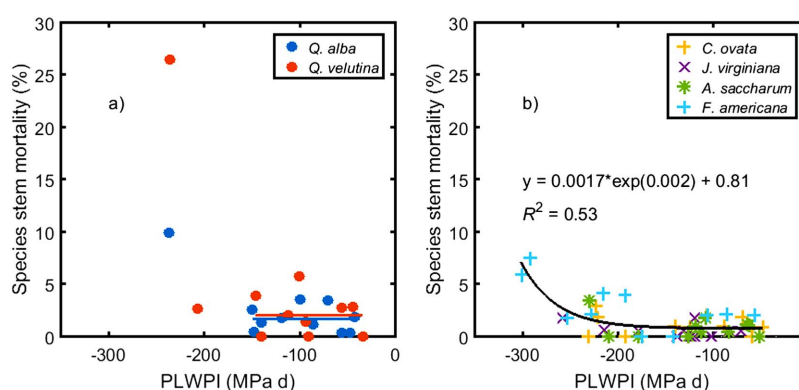


Figure 5. One-year lagged species stem mortality as a function of predawn leaf water potential integral (PLWPI) for (a) oak species and (b) other major species in the MOFLUX forest. In (a) the horizontal lines represent the ensemble mean species stem mortality across a range of PLWPI for which there was no relationship ($p > 0.7$) between the two variables. The species are white oak (*Quercus alba* L.), black oak (*Q. velutina* Lam.), shagbark hickory (*Carya ovata* (Mill.) K. Koch), eastern redcedar (*Juniperus virginiana* L.), sugar maple (*Acer saccharum* Marsh.), and white ash (*Fraxinus americana* L.).

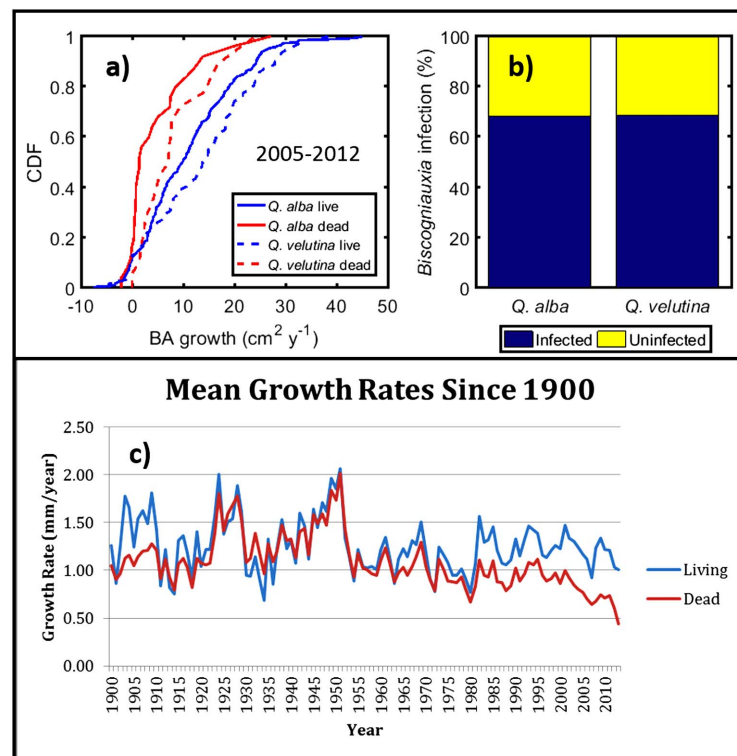


Figure 6. (a) Empirical cumulative distribution functions (CDF) of basal area growth rates from 2005 through 2013 of white oak (*Quercus alba* L.) and black oak (*Q. velutina* Lam.) individuals in the MOFLUX forest that were alive and those that died in 2013. (b) The incidence of *Biscogniauxia* infection on the trees that died as determined by visible presence of cankers and sloughing of bark, and (c) mean annual growth rates inferred from tree-ring chronologies obtained from cores collected from white oak that were alive ($n = 25$) and ones that died ($n = 25$) in 2013.

For both white and black oak, mortality preferentially affected individuals displaying lower growth rates (figure 6(a)) with visible cankers caused by *Biscogniauxia* on 68% of the individuals that died in 2013 (figure 6(b)) implying that weaker individuals may have been predisposed to pathogen infection. Tree-ring chronologies constructed for white oak individuals further substantiate the divergent growth rates (live versus dead trees in 2013) that can be traced to the early 1980s (figure 6(c)), coincident with another severe drought—in 1980 the mean PDSI in July and August was -3.31 (July/August PDSI in 2012 was -3.78). Approximately 3% of live oak trees in 2017 showed evidence of *Biscogniauxia* (usually in the crown) implying that the fungi are probably present in endophytic form in the forest. Interestingly, there was no observable evidence of fungal infection on non-*Quercus* individuals, underscoring the apparent importance of pathogens in regulating oak mortality in this system. Taken together, these observations support the hypothesis of slow *Biscogniauxia* infection during moderate water-stress with a significant increase in pathogenicity during and after the severe drought that ultimately caused death.

Meteorological variability (figure 7(a)) modulated the intensity of physiological drought during the growing seasons (PLWPIs in figure 7(b)). Water status was a key factor regulating the large growing season C ($\text{NEP} = 465 \pm 25 \text{ g C m}^{-2}$; $R_s = 645 \pm 35 \text{ g C m}^{-2}$) and water (evapotranspiration (ET) = $550 \pm 27 \text{ mm}$)

fluxes (figure 7(c) and figure S6). Despite respiratory losses of C during the non-growing season, the forest was a large annual C sink ($\text{NEP} = 330 \pm 25 \text{ g C m}^{-2}$)—even during the exceptional drought of 2012 ($\text{NEP} = 195 \text{ g C m}^{-2}$). High interannual PLWPI variability (figure 7(b)) yielded concomitant variability in the ecosystem C and water fluxes that was of sufficient magnitude to prevent the detection of significant linear trends over time (figure 7(d)). The suppression of NEP and ET during drought was confined to the years during which water stress occurred as evidenced by the strong linear relationships with PLWPI (figure 7(c)) and the absence of lags in recovery or trends in the time series (figure 7(d)). R_s dynamics were more decoupled from PLWPI (figure 7(c); lower R^2), with a lagged recovery to the 2012 drought that lasted for one year. Interestingly, there was a significant linear decline in peak canopy leaf area index (LAI) ($-0.06 \pm 0.014 \text{ yr}^{-1}$, $p < 0.01$).

4. Discussion and concluding remarks

This oak–hickory forest was displaying stand dynamics consistent with expected patterns of decreasing density being compensated by increasing basal area (figures 1 and S2) (Pallardy *et al* 1988). The increasing sugar maple tree density versus declines for major oak species (figure 1) is consistent with previous findings suggesting successional trends towards greater sugar maple

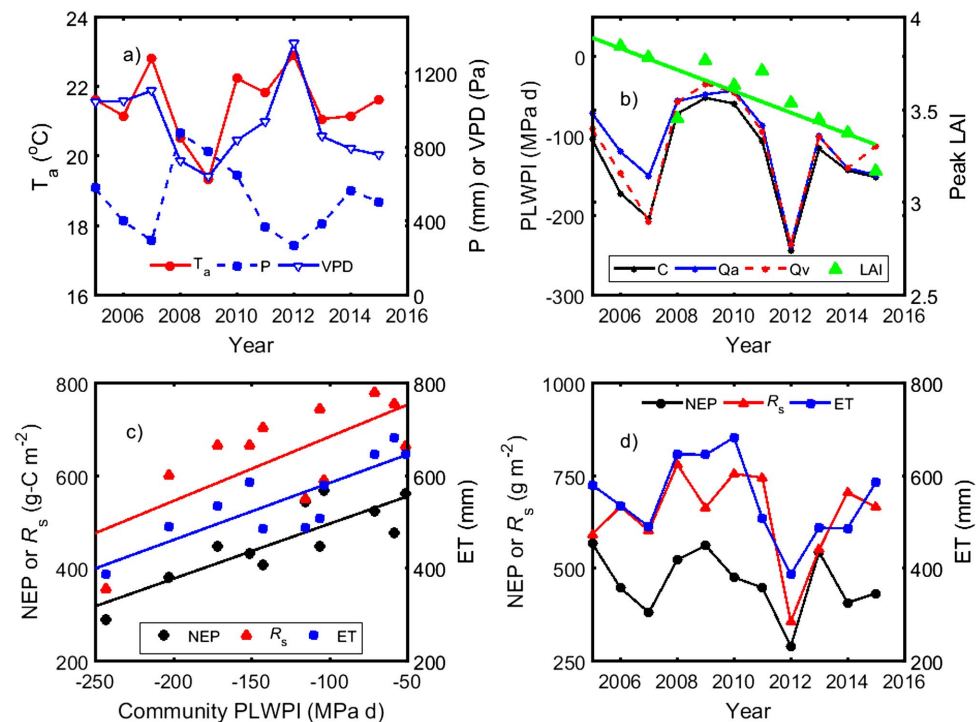


Figure 7. (a) Time series of growing season mean daily air temperatures (T_a), mean vapor pressure deficit (VPD), and total precipitation (P); (b) time series of growing season predawn leaf water potential integrals (PLWPI) for the community (C), white oak (Qa; *Quercus alba* L.) and black oak (Qv; *Quercus velutina* Lam.), and annual peak leaf area index (LAI); (c) growing season net ecosystem production (NEP; $R^2 = 0.68$), soil respiration (R_s ; $R^2 = 0.44$), and evapotranspiration (ET; $R^2 = 0.68$) as a function of community PLWPI; and (d) time series of growing season NEP, R_s and ET. Positive values of NEP and R_s represent gains and losses of carbon, respectively. There was a significant temporal trend for peak LAI decline (b); $-0.06 \pm 0.014 \text{ yr}^{-1}$, $p < 0.01$).

importance in these forests (Belden and Pallardy 2009). The continued basal area growth outpaced mortality (figures 1 and S2) implying a net accumulation of live biomass, which is supported by the large C sink measured at MOFLUX from 2005 through 2015 (figures 7 and S6). The community- and species-level mortality rates (1% – $3\% \text{ yr}^{-1}$ and 1% – $4\% \text{ yr}^{-1}$, respectively, on stem density or basal area basis) over the interval 1992–2016 (figure 1) were in line with reported estimates of typical background mortality (Gonzalez-Akre *et al* 2016). On average, mortality tended to affect larger and smaller sugar maples and white oaks, respectively (figures 2, 4 and S4(a)), which was expected for the canopy dominant white oaks based on typical stand dynamics. However, the preferential mortality of larger sugar maple individuals raises important questions regarding the expected successional trend towards increasing canopy importance of sugar maples (Belden and Pallardy 2009, Pallardy *et al* 1988).

The mortality rates observed on the Rochow plots were estimated over an interval of ~ 25 years and thus integrated over several known drought events, some of which were captured in the MOFLUX record (Gu *et al* 2015). At MOFLUX, we observed massive white (10.0%) and black oak (26.5%) mortality one year after the exceptional drought of 2012 (figures 3 and 4). The mean stem density mortality rates over all years excluding 2013 (white oak = $1.7\% \pm 0.38\% \text{ yr}^{-1}$, black oak = $2.1\% \pm 0.59\% \text{ yr}^{-1}$) were, however, in line with those

observed on the Rochow plots (white oak = $1.8\% \text{ yr}^{-1}$; black oak = $3.8\% \text{ yr}^{-1}$), implying that event-based mortality is an important mode of declining tree density for these species.

Observed ψ_{pd} repeatedly demonstrated rapid leaf rehydration after soaking rains within and across years (figure S5) (Gu *et al* 2015 2016a) implying that catastrophic hydraulic disconnection during the drought (Anderegg *et al* 2014, 2013, 2012, McDowell *et al* 2013) was unlikely to be the sole agent of tree death. Furthermore, oaks of all size classes died in 2013 (figures 4(f) and (g)), which is counter to the notion that larger trees are generally more susceptible to drought-induced mortality (Bennett *et al* 2015) due to greater hydraulic vulnerability (McDowell and Allen 2015) and crowns being exposed to direct sunlight (Nepstad *et al* 2007) versus smaller individuals. We found that white and black oak individuals that died in 2013 displayed lower growth rates according to inventory-based (figure 6(a)) and tree-ring evidence (figure 6(c)), which combined with the pervasiveness of *Biscogniauxia* (figure 6(b)) provides strong support that drought–pathogen interactions (Oliva *et al* 2014) and tree-level characteristics related to sustained growth modulate oak mortality in this forest. The proliferation of endophytic *Biscogniauxia* is favored in tissues subjected to water stress (Vannini *et al* 2009). When hosts are sufficiently stressed, *Biscogniauxia* can rapidly shift to pathogenic behavior and accelerate mortality

(Desprez-Loustau *et al* 2006, Capretti and Battisti 2007). It may be that oaks are susceptible to these mortality ‘pulses’ because of their ring-porous hydraulic architecture that limits water transport to the outer annual ring or two (Kozłowski and Winget 1963), giving less redundancy against an invasion of the sapwood by a pathogen compared to species where water transport occurs in multiple rings. Thus, when under severe drought stress and pathogen infection, the oaks may suffer greater acute effects because of the comparatively smaller area of the stem and branches actively conducting water. Taken together, these observations are supported by the fact that tree mortality was invariant until PLWPI decreased to -150 MPa d at which point there was a threshold response in mortality in the year after drought figure 5(a).

Oak forests in the wider region are known to harbor opportunistic root and stem canker pathogens such as *Armillaria* (Bruhn *et al* 2000, Lee *et al* 2016, Lee 2016) and *Biscogniauxia* (Bassett and Fenn 1984, Bendixsen *et al* 2015), respectively, that only become pathogenic when trees are stressed. These pathogens, in association with antecedent drought-stress, are important contributors to oak decline (Wargo 1996, Haavik *et al* 2015)—particularly for the decline of the red oak group (Bruhn *et al* 2000, Bendixsen *et al* 2015, Bassett and Fenn 1984, Voelker *et al* 2008, Haavik *et al* 2015). We have documented an extreme mortality event consistent with severe drought stress inducing *Biscogniauxia* pathogenicity. The predisposition of individuals that died in 2013 to lower antecedent growth rates (figures 6(a) and (c)) and the overall decline in peak LAI (figure 7(b)) is supportive of the notion that *Biscogniauxia* was slowly spreading and infecting sapwood and affecting crown structure and function during periods of moderate water-stress, and that the 2012 drought exceeded a threshold that permitted rapid development of infection and damage to the sapwood (Oliva *et al* 2014). Although *Armillaria* is also present in this forest, it has been found to be less abundant and important in more mature stands (Lee 2016) such as those studied here. We therefore suspect that *Armillaria* plays a comparatively minor role relative to *Biscogniauxia* in this forest, but further research is needed to conclusively ascertain this. Furthermore, the factors contributing to reduced growth in some trees are unclear at this juncture and warrant further investigation to better understand why some individuals are more susceptible to infection from deterministic and probabilistic perspectives.

Although the presence of *Biscogniauxia* in the wider region has been known for some time (Bassett and Fenn 1984), it has received comparatively less attention than root pathogens (Bruhn *et al* 2000, Lee *et al* 2016, Lee 2016). Numerous *Biscogniauxia* infections and associated oak mortality reported in Texas, Oklahoma, and Missouri after the global-change type droughts of 2011 and 2012 underscore the importance of this endophytic pathogen in the wider region.

While the drought–*Biscogniauxia* interaction has not yet manifested catastrophic mortality rates in the region, further attention is necessary because of expected climate warming and shifting precipitation patterns that are expected to increase drought frequency and severity, with alternating wet periods (Hubbart *et al* 2016). Amplified drought severity in response to rising temperatures has been documented elsewhere (Vicente-Serrano *et al* 2014), and hotter more intense droughts are expected to increase tree mortality (Allen *et al* 2015, Williams *et al* 2012, McDowell and Allen 2015). It is therefore plausible that white and black oaks in the region will become more susceptible to drought-induced mortality due to more frequent and intense water stress (and alternately wet periods) favoring the spread of pathogens (Hubbart *et al* 2016).

We propose that the drought–*Biscogniauxia* interaction will play an important role shaping stand dynamics in the Ozark Border Region and the wider Central Hardwoods Forest. Understanding the drought–*Biscogniauxia* interaction is therefore crucial towards our ability to forecast the trajectory of these forests and the resulting economic consequences (e.g. timber sales) and ecosystem services (e.g. large C sink, animal habitat). Important avenues of inquiry needed to fill knowledge gaps in this regard include:

1. Determining more precise water stress thresholds that govern the spread of *Biscogniauxia* and its shift to pathogenic behavior; and whether this sensitivity responds to factors such as tree age or accumulated stress.
2. Determining the factors that predispose trees to infection (e.g. genetics, competition, moisture gradients).
3. Assessing the importance of interactions with root pathogens such as *Armillaria*.
4. Modeling the drought–pathogen interaction(s) to permit implementation within land surface schemes and models of stand dynamics.

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