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Predictors and mechanisms of the drought-influenced mortality of tree species along the isohydric to anisohydic continuum in a decade-long study of a central US temperate forest

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Abstract

Using decade-long continuous observations of tree mortality and predawn leaf water potential (ψ_{pd}) at the Missouri Ozark AmeriFlux (MOFLUX) site, we studied how the mortality of important tree species varied along the isohydric to anisohydric continuum and how such variations may be predicted. Water stress determined inter-annual variations in tree mortality with a time delay of one year or more, which was predicted by predawn leaf water potential integral (PLWPI), mean effective precipitation interval (a time period with no daily precipitation rates exceeding a threshold) with a daily threshold precipitation at $5\,mm\,day^{-1}$ (MEPI5), and precipitation variability index (PVI). Positive temperature anomaly integral (PTAI) and vapor pressure deficit integral (VPDI) also worked reasonably well, particularly for moderate droughts. The extreme drought of the year 2012 drastically increased the mortality of all species in the subsequent year. Regardless of the degree of isohydry and drought intensity, the ψ_{pd} of all species recovered rapidly after sufficiently intense rain events. This, together with a lack of immediate leaf and branch desiccation, suggests that hydraulic disconnection in the xylem was absent even during extreme drought and tree death was caused by significant but indirect effects of drought. We also found that species occupying middle positions along the isohydric to anisohydric continuum suffered less mortality than those at either extremes (i.e. extremely isohydric or extremely anisohydric). Finally, our study suggested that species differences in mortality mechanisms can be overwhelmed and masked in extreme droughts and should be examined in a broad range of drought intensity.

1 Introduction

The world's forests are currently a large carbon sink (Pan et al., 2011), helping curtail the rising of atmospheric CO_2 concentrations due to anthropogenic emission. This present carbon sink, however, is vulnerable to factors that can alter forest structure and function. Among such factors, tree mortality influenced by drought has been increasingly of concern (McDowell et al., 2013a). In many regions of the world, drought-influenced tree mortality is believed to be accelerating (Philips et al., 2009; Allen et al., 2010; Peng et al., 2011; van Mantgem et al., 2011). Whether this acceleration is related to global and regional climate warming caused by fossil CO_2 emission is uncertain. However, climate warming is expected to lead to a drier land surface (Sherwood and Fu, 2014) and faster developing pace and elevated intensity of drought even if it may not directly result in a higher frequency of drought (Trenberth et al., 2014). Thus, understanding and being able to predict drought-influenced tree mortality are essential to assessing the sustainability of the world's forests as a carbon sink if the climate system warms as expected (Xu et al., 2013; McDowell et al., 2013b).

It is a challenge to predict tree mortality in general and drought-influenced tree mortality in particular. Drought may result in or contribute to tree death in multiple ways. Total hydraulic failure (catastrophic xylem cavitation causing loss of hydraulic conductivity and leading to shoot desiccation) is not uncommon in shallowly rooted seedlings (e.g., Williams et al., 1997), but has not been clearly established as a direct agent of mortality in mature plants (McDowell et al., 2008). Partial hydraulic failure and carbon starvation (stomatal closure to avoid hydraulic failure and protect the photosynthetic machinery resulting in reduced photosynthesis and negative plant carbon balance) have also been suggested as agents of tree death from drought (McDowell et al., 2008). These different mechanisms do not necessarily operate independently (McDowell, 2011; Sevanto et al., 2014). Further, they might not be the proximate cause of death; for example, they may simply weaken the trees by decreasing or preventing defensive chemical production and thus predispose the trees to attacks by insects and pathogens which eventually cause death (Waring, 1987; McDowell, 2011).

Different strategies of adaptation to drought are manifested by vascular homeohydric plants to balance the conflicting needs of adequate photosynthesis and plant hydration (Sperry et al., 2002). These suites of traits are often characterized into isohydric and anisohydric ideotypes. Isohydric, stress-avoiding plant species constrain the depression in leaf water potential and the level of tension in the xylem to narrow ranges through access to deep soil water via root system architecture and growth patterns (Hinckley et al., 1981), stomatal regulation (Tardieu, 1993) and osmotic (Blum, 2011) and hydraulic architectural adjustments and capacitance (Meinzer et al., 2009). In contrast, anisohydric species allow greater excursion of leaf water potential and xylem tension, a characteristic often associated with a more resilient photosynthetic apparatus and cavitation-resistant xylem (Tardieu and Simonneau, 1998). It is tempting to establish a correspondence between isohydric/anisohydric responses and drought-influenced mortality mechanisms. McDowell et al. (2008) suggested that isohydric plants risk carbon starvation due to stomatal closure while anisohydric plants are subject to hydraulic failure caused by uncontrolled xylem embolism.

Like the mortality concepts of hydraulic failure and carbon starvation, isohydric and anisohydric ideotypes are conceptualized descriptions of plant-water relationships. They are at the extremes of a continuum of plant adaptation responses to water stress. This isohydric to anisohydric continuum exists because plant species in natural conditions possess a wide range of capacities to regulate leaf water status and xylem tension in accordance with their life histories, niches in the ecosystem, and characteristics of precipitation regimes (Meinzer et al., 2009; Martínez-Vilalta, 2014). Drought intensity must also be a factor affecting the effectiveness of any water stress adaption response. On the one hand, if the drought is so severe, it can overwhelm any capacity of plants to control their internal water environment. On the other hand, increased availability of water may progressively mask effects of disparities in regulative capacities among different plant species. Thus the variations of drought-influenced tree mortality along the isohydric to anisohydric continuum must nonlinearly depend on drought intensities. An investigation of such nonlinear dependence will be important to the development of in-depth understanding of mortality mechanisms and models to predict impacts of drought on forest ecosystem structure and function in a warming world.

We have been monitoring the mortality of all tree species (the six most important ones are studied here) at the Missouri Ozark AmeriFlux (MOFLUX) site since 2005 and predawn leaf water potential (ψ_{pd}) since 2004 (Gu et al., 2006, 2007; Yang et al., 2009; Gu et al., 2015). The different tree species monitored at the MOFLUX site exhibited a range of hydration-regulating capacities (see the next sections). During our study period, a wide range of precipitation regimes from abundant rain to extreme drought occurred at the MOFLUX site, resulting in large inter-annual fluctuations in plant water stress levels (Gu et al., 2015) and associated tree mortality (see the next sections). The combination of species diversity, relatively long mortality time series, and broad range of precipitation regimes provided a rare opportunity to investigate how drought and precipitation variability affect tree mortality, how such impacts may be related to the position of a species along the isohydric to anisohydric continuum, and how drought-influenced tree mortality can be predicted effectively. We explore these issues in the present paper.

2 Materials and methods

2.1 Study site

The study was conducted at the Missouri Ozark AmeriFlux (MOFLUX) site. This site has been described several times before and the following site information is taken mostly from Gu et al. (2015) for the sake of convenience. The MOFLUX site, which has been operating since 2004 with a suite of meteorological and ecological instrumentation (Gu et al., 2006, 2007; Yang et al., 2010), is located in the University of Missouri's Baskett Wildlife Research and Education Area (BWREA, Lat. 38°44′39″ N, Long. 92°12′ W). BWREA is within the Ozark border region of central Missouri. Second-growth upland oak-hickory forests constitute the major vegetation type at the BWREA (Rochow, 1972; Pallardy et al., 1988). Major tree species include white oak (*Quercus alba* L.), black oak (*Q. velutina* Lam.), shagbark hickory (*Carya ovata* (Mill.) K. Koch), sugar maple (*Acer saccharum* Marsh.), and eastern redcedar (*Juniperus virginiana* L.). The climate of the area is warm, humid, and continental (Critchfield, 1966), with monthly mean temperature of −1.3 °C in January and 25.2 °C in July and an annual total precipitation average of 1083 mm (National Climatic Data Center 1981 to 2010 climate normals, Columbia Regional Airport, Missouri). Dominant soils at the site are Weller silt loam (Fine, smectitic, mesic Aquertic Chromic Hapludalf) and Clinkenbeard very flaggy clay loam (Clayey-skeletal, mixed, superactive, mesic Typic Argiudoll) (Young et al., 2001). The comparatively thin soils of these oak-hickory forests often exacerbate plant water stress when droughts occur (Bahari et al., 1985; Jenkins and Pallardy, 1995).

2.2 Measurements

2.2.1 Meteorological measurements

Measurements of precipitation, temperature and relative humidity made on the 30 m flux tower located at the site were used in the study to formulate potential meteorologically-based predictors for tree mortality. Precipitation was measured with a recording tipping bucket rain gauge (TR-525M, Texas Electronics, USA) mounted at the top of the tower. Data were totaled over 30 min periods. Data of temperature and relative humidity used in this study were also measured at the top of the tower. Atmospheric vapor pressure deficit (VPD) was computed from the measured temperature and relative humidity.

2.2.2 Tree mortality monitoring

Individual trees with diameter at breast height (DBH, 1.3 m height) larger than 9 cm were inventoried when the site was established in 2003–2004. The inventory used 24 circular plots, each with a size of 0.08 ha. These plots were placed at 50 m intervals away from the site flux tower along the southeast ($n = 5$ plots), south ($n = 5$), southwest ($n = 5$), west ($n = 5$) and northwest ($n = 4$) transects. The last transect had only 4 plots as it terminated in a pond. On each plot, living trees were identified with a numbered aluminum tag, identified to species and measured for DBH. In each subsequent year, death of tagged trees was noted and recorded during frequent visits to all plots.

2.2.3 Predawn leaf water potential (ψ_{pd})

Since early June of 2004, measurements of ψ_{pd} have been made periodically (weekly to bi-weekly) during the growing seasons. In each year except for 2004, the first measurements occurred in mid-May. In all years, the last measurements took place in late October. Leaf samples were collected before dawn for canopy and sapling individuals of common tree species at the site. A total of 20–21 samples were obtained each day with 6–7 taken from *Quercus alba*, and the rest distributed among *Q. velutina*, *Acer saccharum*,*Carya ovata*, *Fraxinus americana* L. (white ash), and *Juniperus virginiana*, roughly in proportion to their relative stem abundance in the stand. ψ_{pd} was measured with a pressure chamber (Turner, 1981; Pallardy et al., 1991).

2.3 Potential predictors for tree mortality

Successful approaches to predicting drought-influenced tree mortality remain elusive in the present and it is beneficial to explore a wide array of possibilities. To take advantage of our relatively long mortality dataset and a broad range of meteorological and physiological measurements, we examined a suite of potential predictors for tree mortality. These potential predictors included predawn leaf water potential integral (PLWPI), precipitation variability index (PVI), mean effective precipitation interval (MEPI), positive temperature anomaly integral (PTAI), and water vapor pressure deficit integral (VPDI). Gu et al. (2015) formulated these indices to study the variations of plant water stresses with precipitation regimes. Their definitions and the rationales for applying them to study tree mortality are described below. In addition, we also used the mean daily precipitation rate $\bar{p}$ as a potential predictor for tree mortality.

2.3.1 Predawn leaf water potential integral (PLWPI)

PLWPI is the area between the seasonal curve of the measured ψ_{pd} and the zero ψ_{pd} line (Myers, 1988; Gu et al., 2015). Myers (1988) showed that PLWPI provides a link between short-term water stress and long-term plant growth. Hanson et al. (2003) used soil water potential integral, which is correlated with PLWPI, to indicate forest water stress. Gu et al. (2015) showed that PLWPI is affected by interannual variability in precipitation regimes and varies widely among different species under the same precipitation regimes.

PLWPI is a direct, integrative measure of plant water stress over the growing season and can be used as a relative indicator of the position of co-occurring species along the isohydric to anisohydric continuum. PLWPI provides an estimate similar to the "static" component of water stress described by Tyree and Sperry (1988). Species with tight control of leaf water status (i.e. isohydric species) should have relatively high (less negative) PLWPI whereas anisohydric species should have lower (more negative) PLWPI. In the literature, isohydric and anisohydric behaviors have often been discussed in the context of stomatal regulation. However, a variety of factors besides stomatal regulation can affect species difference in ψ_{pd} and PLWPI for the same external water input. For example, species with deeper root distributions should have higher ψ_{pd} and PLWPI than those with shallower roots even if they have the same stomatal regulation capacity because surface soil layers dry first. Further, significant loss of stem hydraulic conductivity, if happens, should be captured in ψ_{pd} and PLWPI because appreciable loss of conductivity will delay and/or prevent overnight recovery in leaf water potential of the shoot. Although Tyree and Sperry (1988) included this source of stress in the "dynamic" component, in the case of PLWPI it is probably best considered as a component of the "static" contribution because it contributes to lower leaf water potentials whether or not there is any daytime flow in the soil-plant system. In this study, we consider water stress adaptation as a system-wide plant property that constrains the fluctuations in ψ_{pd} and PLWPI in response to water supply and demand. Consequently, differences in ψ_{pd} and

PLWPI among species in the same environment reflect their differences in the degree of water stress avoidance responses and therefore their relative degree of isohydry. An examination of the association of PLWPI with tree mortality of different species could lead to insights into mechanisms of drought-influenced tree mortality.

2.3.2 Precipitation variability index (PVI) and mean effective precipitation interval (MEPI)

To effectively evaluate impacts of drought on tree mortality, we needed to put particular droughts within the broader context of precipitation regimes. Following Gu et al. (2015), we used $\bar{p}$, PVI and MEPI to quantify precipitation regimes. PVI is defined as the following:

$$\mathrm{PVI} = \sqrt{\frac{\sum_{i=1}^{n} \left(R_i - \bar{R}\right)^2}{n}}, \tag{1}$$

where,

$$R_i = \frac{C_i}{E_i}. \tag{2}$$

$$\bar{R} = \frac{\sum_{i=1}^{n} R_i}{n}. \tag{3}$$

$$C_i = \sum_{j=1}^{i} p_j, \tag{4}$$

$$E_i = i\bar{p}. \tag{5}$$

Here, $\{p_1, p_2, ..., p_n\}$ is a time series of precipitation measurements and $i = 1, ..., n$. It is assumed that the values of p_i, $i = 1, ..., n$, are measured at regular intervals. The intervals can be hourly, daily, or weekly, or longer, depending on the intended use of the resultant PVI. For the purpose of this study, we assume that the values of p_i are measured daily in a unit of mm day^{-1}. PVI is dimensionless. It has a value of zero for perfectly uniform precipitation and increases as precipitation events become more sporadic.

Because PVI is strictly an index of variability and does not contain information about precipitation quantity, Gu et al. (2015) proposed MEPI to incorporate both precipitation variability and quantity into a single measure. MEPI is defined as the average of all time intervals during which no precipitation exceeding a threshold daily precipitation rate (p_t) occurs (Gu et al., 2015). It is based on the concept of effective precipitation (Noy-Meir, 1973; Porporato et al., 2002). For a precipitation event to contribute effectively to relieving plant water stress, it has to be sufficiently intense so that it can penetrate the canopy and litter layer to wet the mineral soil. Gu et al. (2015) found that at the MOFLUX site, MEPI with a p_t of 5 mm day^{-1} explained interannual variations in plant water stress levels most effectively. Following the notation of Gu et al. (2015), we use MEPI5 to denote MEPI with $p_t = 5$ mm day^{-1}. MEPI5 was evaluated as one of the potential predictors of tree mortality.

2.3.3 Positive temperature anomaly integral (PTAI) and water vapor pressure deficit integral (VPDI)

It has been suggested that temperature and atmospheric VPD may play elevated roles in tree mortality influenced by global change-type droughts (Breshears et al., 2009; Adams et al., 2009; Weiss et al., 2009; Eamus et al., 2013). To complement the water availability-based potential predictors ($\bar{p}$, PLWPI, PVI and MEPI5) for tree mortality, we applied PTAI and VPDI in an attempt to capture effects of high temperature and VPD, respectively:

$$\mathrm{PTAI} = \sum_{i=1}^{n} \max\left(T_i - T_{ci}, 0\right)/48, \tag{6}$$

$$\mathrm{VPDI} = \sum_{i=1}^{n} \mathrm{VPD}_i/48. \tag{7}$$

In Eq. (6), T_i is the observed half-hourly temperature at the time step i and T_{ci} is the daily mean temperature climate normal of the day during which the time step i occurs. "max" in the right hand side of Eq. (6) means that in any day, only those half-hourly temperatures above the normal of that day (i.e. positive temperature anomaly) is included in the calculation of PTAI and any negative temperature anomaly is replaced by the value of zero in the calculation. The daily mean temperature climate normals were computed by the US National Climatic Data Center (NCDC) with observations of the period 1981 to 2010 at the Columbia Regional Airport (less than 10 km to the northwest of the MOFLUX site). The half-hourly temperature data were from measurements made at the top of the MOFLUX tower. In Eq. (7), VPD_i is the vapor pressure deficit in the unit of kPa at i. The VPD values were half-hourly and computed from half-hourly temperature and relative humidity observed at the top of the tower. The division by 48 in Eqs. (6) and (7) allows PTAI and VPDI to be expressed in a unit of °C day and kPa day, respectively.

3 Data processing and analysis

Mortality data from 2005 to 2014 and measurements of precipitation, ψ_{pd}, temperature and VPD from 2004 to 2013 were used in this study. For precipitation, ψ_{pd}, temperature and VPD, only growing-season measurements were used. We used days 120 and

300 as the start and end of the growing season, respectively, based on the seasonal patterns of leaf area index (LAI) measured at the site (data not shown). While the onset and senescence of vegetation activities varied somewhat from year to year (which was not found to have any direct effect on tree mortality), using the same dates to mark the growing season for all years eliminated uncertainties in the calculated predictors that may be caused by inter-annual variations in the length and timing of the growing season. We linearly interpolated measurements of ψ_{pd} for days that predawn measurements were not made. It was assumed that the ψ_{pd} on days 120 and 300 was zero so that any day before the first (mid-May in every year except for 2004 and early-June for 2004) or after the last measurement (late October for all years) could be properly interpolated. This assumption was a reasonable approximation because the first and last measurements of ψ_{pd} were always close to zero even during years when severe drought occurred (see Sect. 4).

Because meteorological and physiological measurements started in early June 2004 at the MOFLUX site, there was a measurement gap of about 40 days (day 120 to 160) in the growing season of 2004. We tested three strategies for dealing with this measurement gap. In the first strategy, we filled the measurement gap with the data from the same period of 2008 to compute the growing-season $\bar{p}$, PVI, MEPI5, PLWPI, PTAI and VPDI in 2004. This strategy was based on the fact that both the years 2004 and 2008 were relatively wet and the measured seasonal variations inψ_{pd} of these two years were broadly similar to each other (see Sect. 4). The second strategy was simply to compute the potential predictors with available data in 2004 while the third was to exclude 2004 from the analysis. All three strategies led to similar findings in terms of how the predictors were related to tree mortality. We reported the results based on the first strategy.

We expressed the mortality of trees (DBH > 9 cm) in different ways based on the specific requirements of analysis. First, we analyzed the total mortality from 2005 to 2014 for each species within each DBH class. Each DBH class had a width of 6.3 cm and 10 DBH classes covered all trees sampled. For the DBH-based mortality analysis, the total mortality of each species was expressed as a percentage relative to the total number of dead trees of all species with each DBH class. This total mortality percentage of a species within each DBH class was then compared to this species' relative stand abundance in this DBH class (also a percentage number) in the 2005 forest inventory data. This comparison indicated whether trees of a species died proportionally or disproportionally to its stand abundance.

Second, we analyzed interannual variations of species mortality and their relationships with those of $\bar{p}$, PVI, MEPI5, PLWPI, PTAI and VPDI. In this second analysis, DBH classes were not differentiated. The mortality of each species in each year was expressed relative to either the total stem number or the total basal area of this species in the 2005 forest inventory data. The former was termed stem mortality and the latter basal area mortality, all expressed in %.

In addition to the mortality analysis at the species level, we also analyzed mortality at the community level. In this case, the community mortality in each year was expressed relative to either the total stem number or the total basal area of the whole stand in the 2005 forest inventory data. A community PLWPI was also calculated, which was the mean of species PLWPI weighted by species relative abundance in the stand.

4 Results

4.1 Inter-annual variations in precipitation regimes and potential predictors of tree mortality

Figure 1 documents that from 2004 to 2013, potential abiotic predictors of tree mortality varied widely in association with changing precipitation regimes at the MOFLUX site. Ranked with the mean daily precipitation rate $\bar{p}$ of the growing season, the driest (wettest) and second driest (wettest) growing seasons occurred in 2012 (2008) and 2007 (2009), respectively (Fig. 1a). Although 2012 and 2007 did not differ much in terms of $\bar{p}$, (1.4 vs. 1.6 $\mathrm{mm\,day^{-1}}$), both PVI (Fig. 1b) and MEPI5 (Fig. 1c) were considerably higher in 2012 than in 2007. In addition, the PTAI (Fig. 1d) and VPDI (Fig. 1e) were also higher in 2012 than in 2007. Thus the growing season of 2012 had not only more variable precipitation but also higher heat stress and atmospheric evaporative demand than that of 2007. This difference had consequences on the tree mortality caused by the droughts of these two years. Figure 1 also shows that the interannual variations in $\bar{p}$, PVI, MEPI5, PTAI and VPDI are not independent but are also not perfectly correlated either, suggesting that these potential predictors contain independent information at least to some degree that may be useful for relating to inter-annual variations in tree mortality.

4.2 Seasonal, inter-annual and species variations in ψ_{pd}

Large inter-annual variations in precipitation regimes led to contrasting seasonal patterns in ψ_{pd} for different years and for different species (Figs. 2 and 3). For much of the growing seasons of the two driest years 2012 (Fig. 3c) and 2007 (Fig. 2d), ψ_{pd} of all species measured was consistently below the severe water stress threshold (−1.5 MPa) suggested by Hsiao (1973). Because ψ_{pd} generally marks the highest leaf water potential in the diurnal cycle, the maximal water stress that the plants at the MOFLUX site experienced during the day (i.e. noon to early afternoon) were likely even more severe than indicated by ψ_{pd}. During the peak of the drought in 2012, ψ_{pd} of all species approached or declined below −4 MPa while in 2007 the lowest value varied considerably across species, ranging from around −2 MPa (white oak) to below −4 MPa (white ash). In 2005 (Fig. 2b), ψ_{pd} steadily decreased initially as the growing season progressed but the decreasing trend was interrupted by heavy mid-season rain which rehydrated the trees. In 2006, 2011 and 2013 (Figs. 2c, 3b, and 3c, respectively), repeated drying and rehydrating cycles caused fluctuations in ψ_{pd}. The years 2004, 2008, 2009 and 2010 were relatively wet and for the entire growing seasons of these years, no species had ψ_{pd} below −1 MPa except for white ash. It is significant to note that the recovery of ψ_{pd} after soaking rains was prompt and complete, even during severe drought years (e.g., 2007, Fig. 2d and 2012, Fig. 3c).

Large differences in seasonal patterns of ψ_{pd} existed among different species under the same precipitation regimes. White ash consistently had the lowest ψ_{pd} among all species when the community in general had ψ_{pd} below −1 MPa. Above −1 MPa, eastern redcedar tended to have the lowest ψ_{pd}. Therefore the relative positions of different species in the cross-species variations in ψ_{pd} were not fixed in time, depending on the level of water availability at a particular moment. When well hydrated, all species had similar ψ_{pd} except for eastern redcedar whose ψ_{pd} slightly departed from those of other species (for example, Fig. 2e for the early growing season of 2008). Because white ash tended to have the lowest ψ_{pd} under dry conditions but similar ψ_{pd} as other species under wet conditions, the ψ_{pd} of white ash fluctuated more widely than other species both within and across the years, suggesting that it was the most anisohydric species among the species investigated in this study. At the opposite side, white oak tended to have the highest (least negative) and least variable ψ_{pd} among all species, suggesting that it the most isohydric species in our study. However, this classification is relative and a species' capacity in preserving ψ_{pd} depends on the intensity of drought. This relativity can be most clearly seen by comparing the seasonal variations in white oak ψ_{pd} between 2007 and 2012. During the second driest year of 2007, white oak had ψ_{pd} considerably higher than other species. However, during the driest year of 2012, its ψ_{pd} was within the variations of that of other species. In fact differences among all species were much diminished in 2012 compared with 2007.

Species differences in ψ_{pd} were reflected and more clearly seen in the inter-annual variations of PLWPI (Fig. 4). White ash had the lowest PLWPI among all species for all years except for the relatively wet year of 2009 when eastern redcedar had lower PLWPI than white ash did. White oak tended to have the highest PLWPI for most years. The exceptions were wet years (e.g., 2008 and 2009) for which black oak had slightly higher PLWPI and the driest year of 2012 for which shagbark hickory and sugar maple had slightly higher values. As expected from the seasonal patterns in ψ_{pd} among species across years, the maximal difference in PLWPI among species (max – min species PLWPI in each year) reached a maximum at an intermediate value of community PLWPI (Fig. 5), suggesting that the differences in ψ_{pd} and PLWPI among species reached maximum when the site was under some intermediate levels of water stress and diminished towards either extreme wet or extreme dry conditions.

4.3 Variations of tree mortality with species, DBH classes and year

At the MOFLUX site, white oak and black oak dominated the largest DBH classes of the stand while the abundance of other species increased in smaller DBH classes (Fig. 6a). Over the whole mortality monitoring period (2005 to 2014), the total mortality rate of a species as a percentage relative to the stand mortality in each DBH class (Fig. 6b) differed from this species' abundance in this given DHB class for most DBH classes and for most species (i.e. compare the bar lengths indicating relative abundance in Fig. 6a with the bar lengths indicating relative mortality in Fig. 6b for the corresponding DBH classes). For example, in DBH classes 1 to 6 (DBH from 9 to 47 cm), black oak had a mortality rate relative to the stand consistently higher than its relative abundance in the corresponding stand DBH classes as shown in the forest inventory data, indicating that black oaks died at a disproportionately higher rate within these DBH classes. In contrast, eastern redcedar and shagbark hickory had relative mortality rates lower than their relative abundances in each DBH class, suggesting that these two species had better survivability compared with other species.

The total mortality of the 2005–2014 period shown in Fig. 6b was dominated by exceptionally high mortality in 2013 for most species, one year after the driest year of 2012. Figure 7 showed the inter-annual variations of the yearly mortality rate expressed relative to species abundance in 2005, based on either stem number density (Fig. 7a) or basal area (Fig. 7b). For all species, the highest stem mortality occurred in 2013. This is also true for the basal area mortality; the only exception was white ash which had slightly higher basal area mortality in 2014 than in 2013, largely due to one very large tree that died in 2014. Considering that 2013 was a year with only modest water stress (Fig. 4), the mortality in 2014, two years after the driest year of 2012, appeared to be unusually high for most species and also for the community as a whole.

4.4 Variations of tree mortality with potential predictors with time lag

We analyzed how mortality changed with $\bar{p}$, PVI, MEPI5, PLWPI, PTAI, and VPDI for each species as well as for the community at different lag years (0, 1, 2 and 3 years – there were not enough data to test for more lag years). We found that the relationships were strongest at one year lag in all cases; i.e. the mortality in one year was best explained in terms of variance (R^2) by the $\bar{p}$, PVI, MEPI5, PLWPI, PTAI and VPDI in the previous year. This one-year lag can be already expected from the fact that the highest mortality occurred in 2013, one year after the driest year of 2012. Both at the species and community levels, stem mortality rates decreased with an increase in the previous year's $\bar{p}$ (Figs. 8a and S1 in the Supplement) and PLWPI (Figs. 8b and 9) and increased with an increase in the previous year's PVI (Figs. 8c and S2), MEPI5 (Figs. 8d and 10), PTAI (Figs. 8e and S3) and VPDI (Figs. 8f and S4). Based on the explained variance, the best predictors of tree mortality are PLWPI and MEPI5 and the worst is $\bar{p}$ with the performance of PVI, PTAI and VPDI intermediate among the six predictors. The results from the analyses with the basal area mortality rates showed similar patterns and therefore are not presented here.

Although we found that the relationships between mortality and predictors appear to be strongest with 1 year lag, this does not imply droughts don't have longer-term impacts. Figure 7 suggests that the unusually high mortality of tree species in 2014 may be a result of lingering impact of the extreme drought of 2012. When the previous two year's MEPI5s were used to form a composite MEPI5 in year t[= MEPI5($t-1$)+0.5× MEPI5($t-2$)], the composite MEPI5 explained more variance in tree mortality than the previous year's MEPI5 alone (Fig. 11). The better performance of the composite MEPI5 suggests a drought can affect tree mortality two years later.

The variations of mortality rates with the previous year's $\bar{p}$, PVI, MEPI5, PLWPI, PTAI and VPDI were clearly dominated by the impact of the extreme drought of 2012. However, the impact of 2012 was not the sole determinant of the relationships. When the mortality data for 2013 and 2014 were excluded from the analysis, a linear regression still explained much of the variance in the inter-annual variations of mortality (Fig. S5). In fact, PTAI (Fig. S5e) and VPDI (Fig. S5f) even explained higher variances when the ‘outliers’ were removed, suggesting that these two predictors may work well for moderate drought.

4.5 Mortality of tree species along the isohydric to anisohydric continuum

Within the same species, mortality decreased with an increase (i.e. becoming less negative) in the previous year’s PLWPI. However, the mortality-PLWPI relation across species is more complicated and is not monotonic. For example, white and black oaks generally had higher (less negative) PLWPI than sugar maple, shagbark hickory, and eastern redcedar (Fig. 4), but their mortality was also higher than the latter three species, especially after the most severe drought year of 2012 (Fig. 7). In contrast, white ash exhibited lower PLWPI (Fig. 4) but higher mortality than sugar maple, shagbark hickory, and eastern redcedar (Fig. 7). These differences across species can also be inferred from plots of annual mortality as a function of the previous year’s PLWPI (Fig. 9).

A more clear demonstration of how the mortality of a species is related to its capacity in regulating ψ_{pd} and PLWPI is given by Fig. 12. Because the mortality sampling population for any particular year was relatively small for species with less abundance in the community (e.g. white ash and shagback hickory, Fig. 6a), in Fig. 12 we pooled the decade-long data to focus on the mortality difference of species along the isohydric-anisohydric continuum. The PLWPI of a species in a year was normalized by the absolute value of the community PLWPI of this year and then averaged across the 10-year period. Because the PLWPI of all species was divided by the same value in a given year, this standardization procedure preserved their relative positions along the isohydric-anisohydric continuum as indicated by their PLWPI values and yet allowed different years of widely varying water stress levels to be averaged. Similarly, the annual mortality of a species in a year was normalized by the community mortality of this year and then averaged across the 10-year period. Figure 12 showed that species occupying the middle of the isohydric-anisohydric continuum (eastern redcedar, shagbark hickory and sugar maple) suffered less mortality than those in the isohydric end (white and black oaks) or in the anisohydric end of the continuum (white ash).

5 Discussion

A wide range of precipitation regimes from ample seasonal moisture to extreme drought was observed over the ten-year tree mortality study period at the MOFLUX site, as reflected in both precipitation variables and PLWPI, which themselves were closely inter-correlated (Gu et al., 2015). The generally tight correlation between precipitation regimes and time-delayed (one year or more) interannual variations in the mortality of tree species strongly supports the assertion that drought was an important factor in death of trees during the study. Although different species had variable degrees of water stress and drought tolerance, the mortality of all species increased after the extreme drought of 2012. These results are consistent with world-wide syntheses of drought-related mortality reports (e.g., Breshears et al., 2009; Allen et al., 2010). Further, the close relationships of mortality with various predictors, specifically PLWPI, MEPI5, PTAI and VPDI, even without considering the severe drought year of 2012, indicate the apparent importance of non-extreme plant water stress in promoting mortality (cf. Breshears et al., 2009).

Non-extreme water stress is also important for understanding species difference in regulating their internal water environment. Under very wet conditions, all species are hydrated equally well while under extreme drought conditions, any capacity of species in maintaining ψ_{pd} and PLWPI is overwhelmed by a lack of water even in deep soil. Only under intermediate drought levels can any regulatory mechanism that a species might have functions effectively (Fig. 5). Thus non-extreme water stress may be the optimal conditions for revealing differences in plant water relations across different species.

Significantly, our results provide evidence relating to the postulated relationships between mortality and the putatively vulnerable anisohydric ideotype and the role of hydraulic disconnection as a direct agent of mortality in established trees in natural stands (e.g., McDowell et al., 2008; Allen et al., 2010; Anderegg et al., 2013, 2014). Whereas one species that exhibited the most anisohydric behavior (white ash) exhibited relatively high mortality after the severe drought of 2012, the other two species exhibiting as high (white oak) or higher (black oak) mortality had the highest values of PLWPI (indicating a relative isohydric pattern of water relations). Further, two lines of evidence indicated there was no catastrophic loss of xylem hydraulic conductivity in any species. First, mortality lagged PLWPI by a year without the evidence of nearly immediate shoot desiccation that would follow hydraulic disconnection. There was some leaf scorching at the top of the canopy during 2012 associated with the drought and high temperatures (e.g., during July ψ_{pd} fell below −3 MPa and average temperature was 5 °C above the 1980–2010 average), but no signs of leaf desiccation (leaf curling, cracking or green hue change in laminae). Second, even during severe drought, ψ_{pd} recovered rapidly after wetting rains and such rapid recovery was often seen throughout the ten-year study period. This type of response would not be expected if significant hydraulic disconnection had occurred (via immediate hydraulic failure or after "cavitation fatigue", Hacke et al., 2001); rather, one would have expected little or no recovery in ψ_{pd}. One might argue that xylem refilling might occur with rainfall, but no accepted mechanism exists for this phenomenon and the source of the refilling water in a hydraulically disconnected and severely dehydrated xylem appears absent. Hence, drought-related mortality, at least in this forest, likely cannot be directly linked to hydraulic failure (McDowell et al., 2008; Anderegg et al., 2014). Rather, a significant but indirect role for drought as one determinant of mortality seems far more likely (McDowell et al., 2013b).

Species exhibited differences in the static component of water stress represented by ψ_{pd}, notably with white ash having generally greater anisohydric behavior than other species. With ample rain and thus adequate soil moisture, eastern redcedar had lower ψ_{pd}. This last response has been observed before (Ginter-Whitehouse et al., 1982; Bahari et al., 1985) and likely relates to the higher-resistance tracheid anatomy of redcedar which prevents full overnight equilibration in moist soil. Relative placement on the isohydric-anisohydric continuum based on comparisons of water relations, while not arbitrary, must necessarily be limited to the species studied. In a broader context of previous studies in this forest, it is worth noting that another fairly common tree species at the site (viz., black walnut (*Juglans nigra* L.)) exhibited more extreme isohydric behavior than the oak species studied here, and that white ash (heretofore not studied extensively in this forest) exhibited responses similar to flowering dogwood (*Cornus florida* L.) (Bahari et al., 1985; Ni and Pallardy, 1991; Loewenstein and Pallardy, 1998). It must be emphasized that none of these species showed any indication of hydraulic disconnection, as determined by failure in recovery of ψ_{pd} after significant rainfall (e.g., Bahari et al., 1985; Lowenstein and Pallardy, 1998). Thus, these results also suggest the established link between PLWPI and mortality must be mediated indirectly.

PLWPI was a monotonic predictor of drought-influenced tree mortality within a species and for the plant community as a whole; i.e. the lower it was, the higher was the subsequent year's mortality. However, the PLWPI – mortality relationship varied substantially across species. Our data indicated that species with extreme (lowest or highest) positions in the continuum of PLWPI suffered higher mortality than species with intermediate values of PLWPI. This finding provides a potential explanation to an apparent contradiction in previous tree mortality studies. Rice et al. (2004) compared the drought-influenced stem mortality of the ironbark species complex of eucalypts (*Eucalyptus crebra – E. xanthoclada*) with that of the bloodwood species *Corymbia erythrophloia*. Ironbark species suffered higher mortality than bloodwood species did. Rice et al. (2004) attributed the higher mortality of ironbarks to this species complex's greater water stress as indicated by more negative predawn and midday xylem water potentials compared to predawn values of bloodwoods. In agreement with the results of Rice et al. (2004), Hoffmann et al. (2011) found that species with lower leaf water potential were associated with higher drought-influenced mortality. In contrast, McDowell (2011) reported that in the southwestern US, *Pinus edulis* had much higher drought-influenced mortality than *Juniperus monosperma* did even though the former was an isohydric species and maintained higher ψ_{pd} than the anisohydric *Juniperus* *monosperma*. The non-monotonic relationship between PLWPI and mortality across species first reported in our study thus reconciles contradictory findings in previous studies (Fig. 12).

Forest composition at the MOFLUX site is undergoing change today. In a long-term permanent plot study in the forests at the Baskett Area, Pallardy et al. (1988) and Belden and Pallardy (2009) found that saplings of oak species were being replaced by those of sugar maple. The disproportionally high mortality of black and white oaks and white ash in the present study suggest that the forest may be transitioning to a plant community that is composed of species occupying intermediate positions in the isohydric-anisohydric continuum.

Unless being killed outright, a tree's life terminates when sufficient resources are either not available (Waring, 1987) or come too late to revive vital coordinated organ activities. This death process is an end-point response that integrates past internal and external dynamics (Hanson et al., 2003) and is thus hard to predict mechanistically. However, tree mortality is unique as a life-ending process due to two fundamental characteristics of tree's life. First, trees are sessile and thus have very limited capacity to evade environmental stresses. Second, trees can be potentially immortal due to their integrated biology of modular structure and meristem dormancy and thus some external agent must occur to induce their death. The combination of these two characteristics means that while it is difficult to mechanistically predict tree mortality, possibility exists to make robust empirical predictions if sufficiently long concerted observations are made on both tree mortality and responsible external agents.

Our study demonstrates that this strategy can be particularly fruitful for predicting drought-influenced tree mortality. PLWPI and MEPI in the growing season of the prior year are good predictors of tree mortality in the current year. The mean precipitation rate does not contain information about precipitation variability while PVI lacks information about precipitation amount. Thus individually they are not as good as PLWPI or MEPI in predicting tree mortality except for mortality caused by severe droughts; they must be used jointly to serve as predictors of tree mortality. PTAI and VPDI apparently work better for non-extreme drought-influenced tree mortality but may have limited capacity for a broad range of water stress including extreme drought. Obviously these predictors will need to be tested at other sites with longer datasets before any conclusion can be drawn with respect to which predictor(s) are the best for predicting drought-influenced tree mortality.

6 Conclusions

Our study has revealed that the drought-influenced mortality of tree species varies nonlinearly along the isohydric to anisohydric continuum and such variations can be predicted by multiple, simply constructed indices with a one-year time lag. These indices include predawn leaf water potential integral (PLWPI), mean effective precipitation interval (MEPI), precipitation variability index (PVI), positive temperature anomaly integral (PTAI), and vapor pressure deficit integral (VPDI). While hydraulic disconnection in the xylem has been postulated as a mechanism for drought-influenced tree mortality, significant but indirect effects of drought are more likely the main cause of tree depth in our study. Extreme isohydric or extreme anisohydric responses apparently all lead to an increased risk of drought-influenced mortality and species with intermediate responses survive better. While severe droughts tend to attract more attention, it is important to study the impacts of a broad range of drought intensities. Less severe droughts can not only be significant promotors of tree death but also reveal species differences in mortality mechanisms more effectively because any such differences may be overwhelmed and masked by severe droughts. Thus response differences among species are related to drought intensities.

Although reports of tree mortality caused by episodic drought events have been extensive in the literature, studies based on long-term, continuous observations such as represented by this present study have been rare (e.g., Breshears et al., 2009). Yet, understanding tree mortality mechanisms and developing predictive models of tree mortality require long-term continuous monitoring of tree mortality and environmental factors. Tree mortality caused by episodic drought events must be investigated in the long-term background of mortality and environmental dynamics. There is a need for increased investment on coordinated long-term observations of tree mortality and responsible external forcing agents in global forests.

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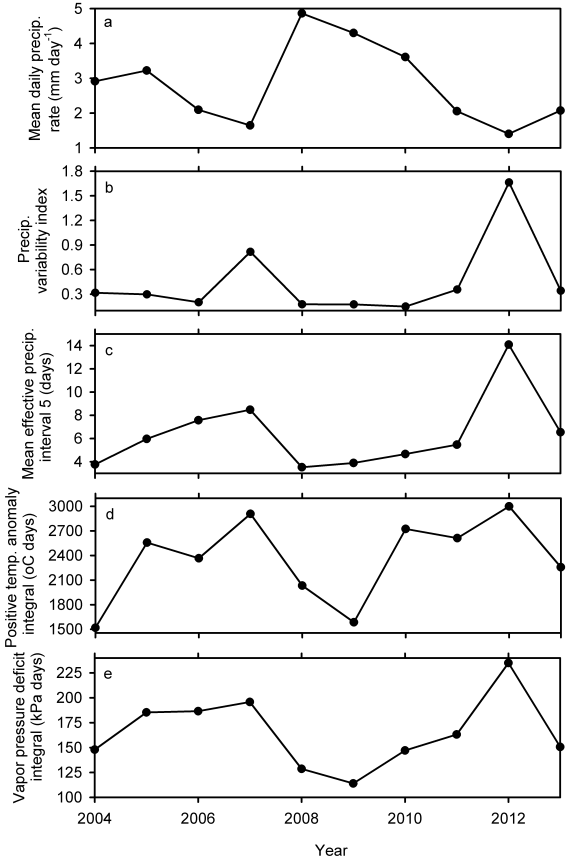

Figure 1. Inter-annual variations in the mean daily precipitation rate **(a)**, precipitation variability index **(b)**, mean effective precipitation interval with a threshold daily precipitation rate of 5 mm day^{-1} **(c)**, positive temperature anomaly integral **(d)** and vapor pressure deficit integral **(e)**. Only growing-season data (day 120 to 300) are used in the calculation.

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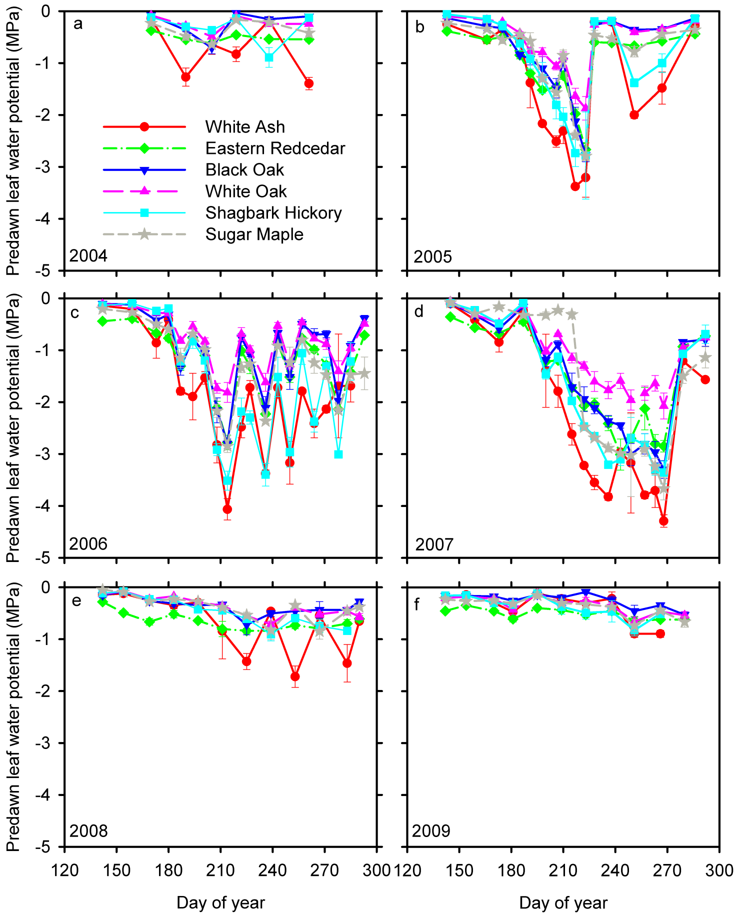

Figure 2. Seasonal variations in predawn leaf water potential of different species from 2004 to 2009. Data for 2006 and 2009 are from Gu et al. (2015) and are included here for the purpose of completeness; the rest are first reported in the present study.

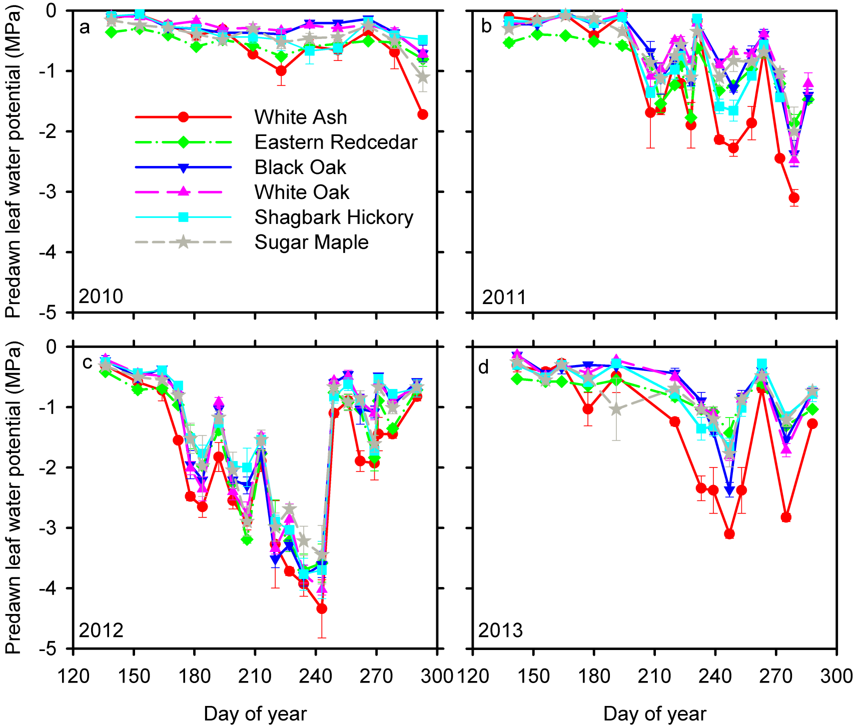

Figure 3. Seasonal variations in predawn leaf water potential of different species from 2010 to 2013. Data for 2012 are from Gu et al. (2015) and are included here for the purpose of completeness; the rest are first reported in the present study.

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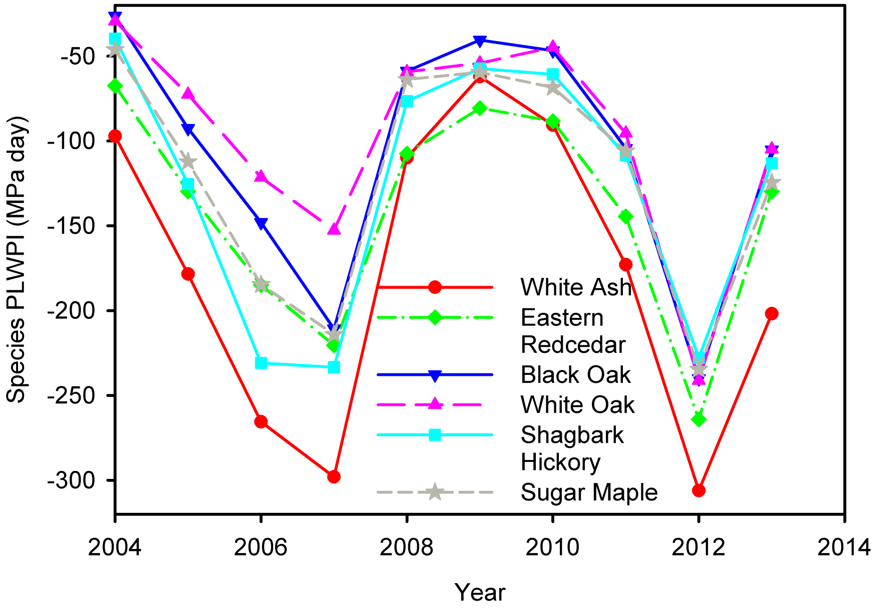

Figure 4. Inter-annual variations in predawn leaf water potential integral (PLWPI) of different species from 2004 to 2013.

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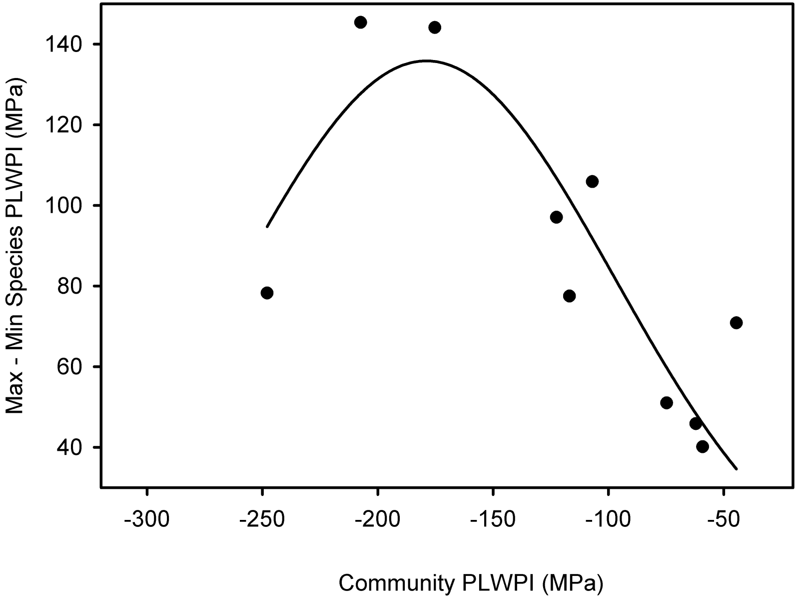

Figure 5. The difference between the maximum and minimum predawn leaf water potential integral (PLWPI) among the six species studied as a function of the community PLWPI. The community PLWPI serves as a measure of overall water stress of a year. This figure shows that species differences in PLWPI reach the maximum at an intermediate level of water stress.

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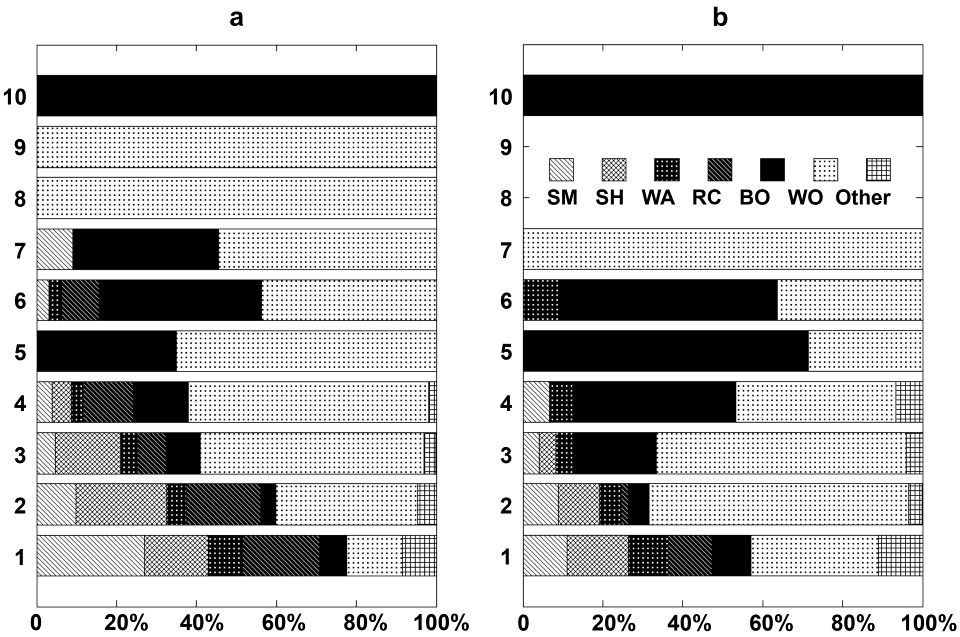

Figure 6. The relative abundance according to the 2005 forest inventory **(a)** and the total relative mortality of each species from 2005 to 2014 **(b)** in each diameter at breast height (DBH at 1.3 m) class. The relative abundance is expressed as a percentage of stem number of each species relative to the total stand stem number in each DBH class. Similarly, the relative mortality is expressed as a percentage of total mortality of each species relative to the total stand mortality in each DBH class. This figure shows whether members of a species die proportionally or disproportionally to its abundance in the stand. SM, sugar maple; SH, shagbark hickory; WA, white ash; RC, eastern redcedar; BO, black oak; WO, white oak; Other, the rest species together.

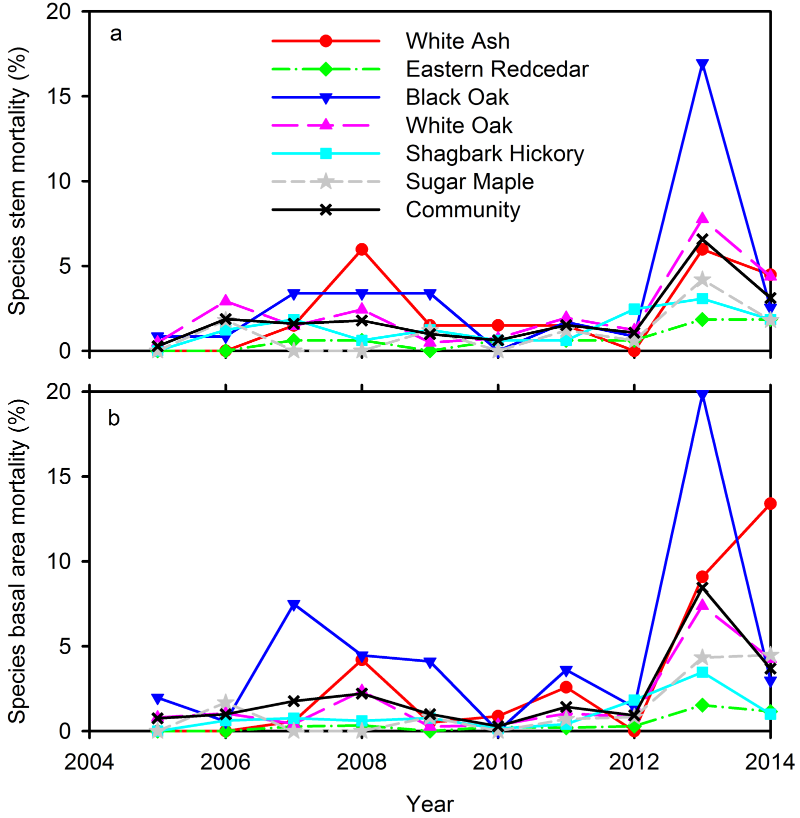

Figure 7. Inter-annual variations in the species mortality expressed relative to either the stem number density **(a)** or the basal area **(b)** of a species in 2005.

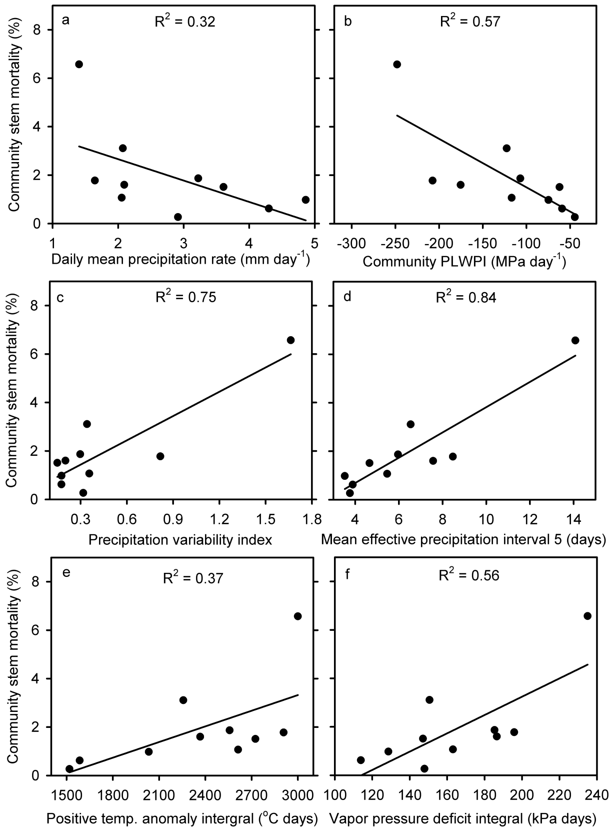

Figure 8. The mortality of the plant community as a whole expressed relative to the stem number density of 2005 as a function of the previous year's daily mean precipitation rate **(a)**, predawn leaf water potential integral (PLWPI) at the community level **(b)**, precipitation variability index **(c)**, mean effective precipitation interval with a threshold daily precipitation rate of 5 mm day^{-1} **(d)**, positive temperature anomaly integral **(e)**, and vapor pressure deficit integral **(f)**.

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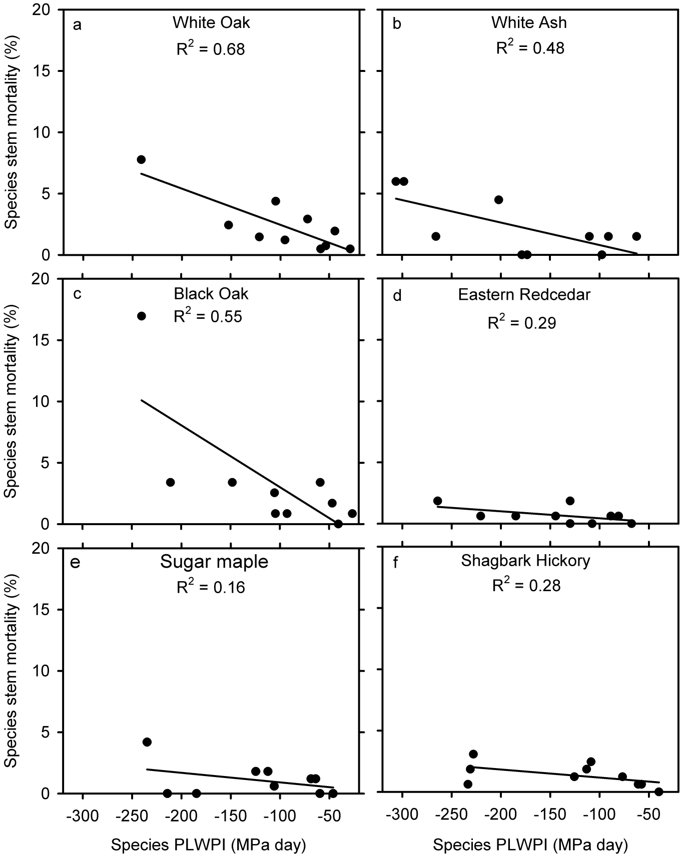

Figure 9. The species mortality expressed relative to the stem number density of 2005 as a function of this species' predawn leaf water potential integral (PLWPI) in the previous year.

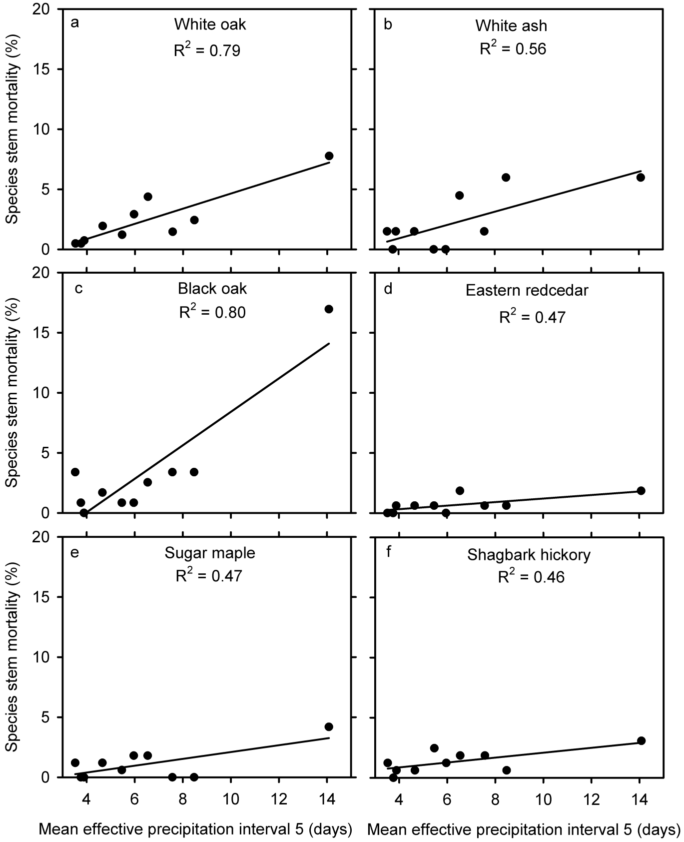

Figure 10. The species mortality expressed relative to the stem number density of 2005 as a function of the mean effective precipitation integral with a threshold daily precipitation rate of 5 mm day^{-1} (MEPI5) in the previous year.

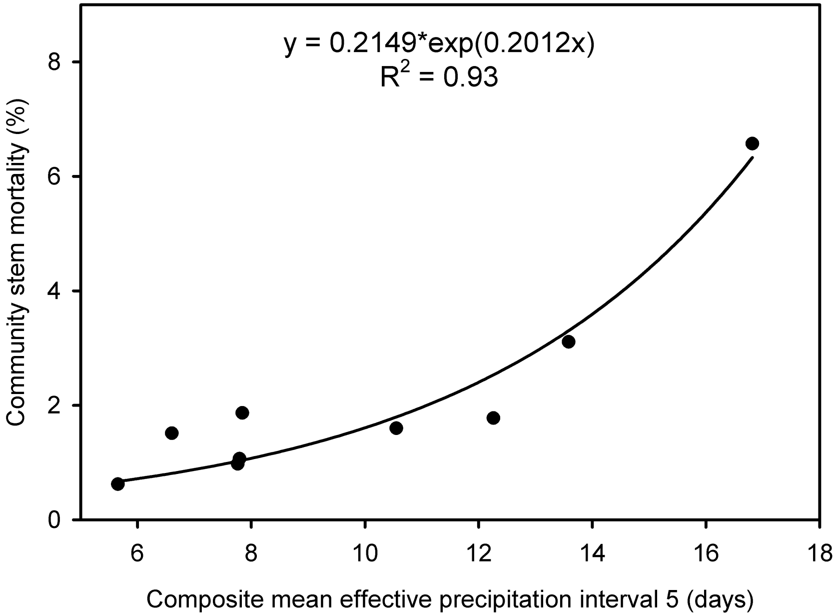

Figure 11. The mortality of the plant community as a whole expressed relative to the stem number density of 2005 as a function of the composite mean effective precipitation interval with a threshold daily precipitation rate of 5 mm day^{-1} (MEPI5). The composite MEPI5 is the previous year's MEPI5 plus the halved MEPI5 two years earlier.

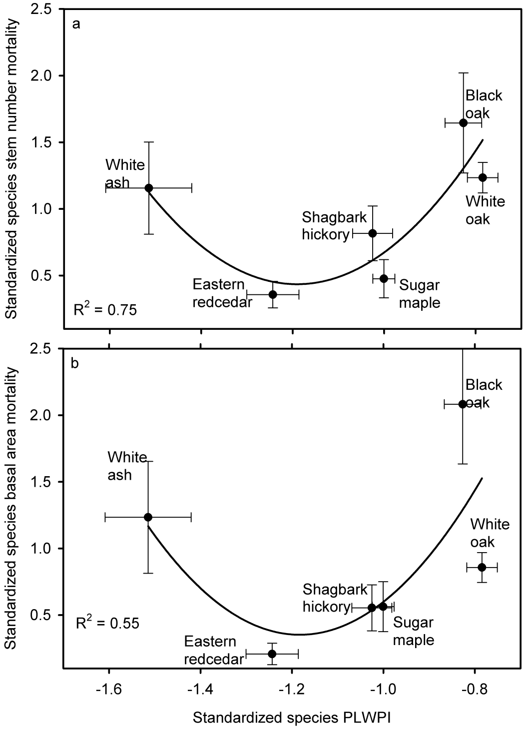

Figure 12. The mean standardized species mortality as a function of the mean standardized predawn leaf water potential integral (PLWPI). In each year and for each species, the standardization is done by diving a species mortality by the community mortality or by dividing a species PLWPI by the absolute value of the community PLWPI. The standardized yearly values are then averaged across the years. The standardization preserves the relative positions of species in the isohydric to anisohydric continuum. Mortality is either expressed based on stem number density **(a)** or basal area **(b)**. This figure shows that species occupying middle positions along the isohydric to anisohydric continuum suffered less mortality than those at either extremes (i.e. extremely isohydric or extremely anisohydric).