Response to Anonymous Referee #1

General comments: In this study, the authors use an extensive dataset of predawn water potentials of 6 species over 10 years, which included a severe drought and several moderate ones, to examine potential predictors in cross-species patterns of mortality. I found this study to be very interesting and insightful. Such datasets of plant water potential, especially those that span many years, many species, and mortality-causing droughts, are exceptionally rare. Thus, this is a very important study. ***Response:*** *Many thanks for the support of our research.*

Comment: I do, however, think that several major issues need to be addressed before the study is suitable for publication. ***Response:*** *We have carefully considered all issues raised by this reviewer and revised the manuscript accordingly.*

Comment: The statistics need to be better explained and in some cases redone. The authors never explain the statistical analyses they did, but based on the figures, it seems to be a large number of OLS linear regressions with no checking of the assumptions. The authors need to explain what was done, check the assumptions of linear regression (as mortality data often violates theses assumptions), and also need to re-do their model comparison with a formal model selection criteria, such as AIC. Using R-squared to compare between models is not a robust/valid approach. ***Response:*** *We have now explained the model selection process (with AICc). Most our regressions are simple one-independent variable fitting. All are linear with only a minimal two free parameters (intercept and slope) except for one nonlinear two-parameter and one nonlinear three-parameter fitting. The normality and homogeneity tests are difficult to conduct for a dataset of mortality with only 10 points. But this is not a critical issue for this study because we don't depend on statistical inference for main conclusions. Note that AIC or AICc is only valid when the dependent variable is identical. Also it is only useful in a relative sense, i.e., a single AIC or AICc value has no meaning. If ALL models tested are bad, AIC or AICc would not be able to tell that, but R2 can. So R2 is still useful in this sense. Also, for linear regresions, R2 is comparable across different predictors because they have the same number of parameters (2), i.e., they are equally parsimonious.*

Comment: The discussion of mortality mechanisms in the manuscript is weakly supported by the authors data and should be scaled back or removed from the paper. The authors do not measure any of the appropriate variables (e.g. hydraulic conductivity, percent loss conductivity, hydraulic vulnerability curves, midday water potentials, stomatal conductance, nonstructural carbohydrates, pest attack, etc.) to examine mortality mechanisms and thus the inferences based on whether trees "looked" like they wilted and lags between drought and mortality are very weak and extending far beyond the data collected. The paper is a very interesting contribution to examine the water potential patterns and how mortality occurred along the isohydric-anisohydric spectrum. It does not need to stray beyond the data collected into mortality mechanisms to be an interesting, strong contribution. Thus, I strongly recommend cutting those sections, as they are also not supported by the authors data or the literature which has documented hydraulically-driven mortality in both of the situations observed by the authors in their system (lack of immediate wilting and lags between drought and death). ***Response:*** *We appreciate this suggestion. We have scaled back discussion on mechanisms and focused on what can be directly supported by our data. The word' mechanisms' was also removed from the title.*

This and other referees make several comments about our assertions concerning hydraulic properties and our results. We would like to address them below in three labeled points and then make reference to these three points as we address individual comments.

Author Point 1

There seems to be some confusion about what we are trying to assert about our results, a situation that is probably attributable to imprecise terminology. We assert that our predawn water potential patterns, specifically the rapid, repeated recovery seen after soaking rains follow drought, are evidence that even during severe droughts there is no catastrophic hydraulic disconnection [p. 12] between roots and shoots that would result from "runaway cavitation." [We address the refilling possibility below in #2]. Referees criticized in several places that "Hydraulic Failure" had been shown to be involved in some episodes of mortality, showing lagged effects that resulted in delayed mortality, thus associating our strict definition with another term. It is true that measurements of elevated loss of hydraulic conductivity are observed in some stems that eventually die (Anderegg et al., 2013, but see comments on methods issues in #2 below), but others maintain viability at the same level of conductance loss (e.g., See Fig. 1 of Anderegg et al.). Further, the word "failure" is probably a poor choice for the concept as it has developed in the literature, as it suggests direct, immediate impacts at the whole-plant level, when it really means some level of loss of hydraulic function that has a downstream impact on plant function mediated by increased leaf water stress (e.g., gas exchange, Brodersen and McElrone, 2013). Such follow-on impacts on shoot water potentials are sometimes seen (e.g., Nardini et al., 2013), but in other cases there are no impacts on water potentials (e.g., Anderegg et al., 2013, Fig. 2). So together with the methodology issues discussed below, the science supporting the role of partial loss of conductivity as a direct agent of mortality is not so settled as the referees seem to think. Follow-on effects of partial loss, if it occurs, might be better considered as an additional sub-lethal burden just as other agents of stress like extreme or unseasonal temperature events, pathogens and insect defoliation. If climate predictions of a drought on the scale of the one suggested by Cook et al. (2015) emerge, we may indeed see direct effects on forests through total hydraulic disconnection. However, our results indicate that even during *severe contemporary droughts, we're not there yet. In revision, we have tried to be clear we're talking about this latter instance.*

Author Point 2

There is an emerging issue in xylem conductivity measurement and the large literature which has employed it (including nearly all the studies the referees cite in support of hydraulically-associated mortality). There is an expanding, substantive body of research that has called into question the widely used Sperry et al. 1988 technique (and its variations) (e.g., Choat et al. (2011) Plant, Cell Environ. 33: 1502-1512; Suuronen et al. (2013). Plant Methods 9: 11; Cochard and Delzon, 2013. Ann. For. Sci. 70: 659-6; Wheeler et al. (2014) Plant, Cell Environ. 36: 1938-1949; Rockwell et al. (2014) Plant Physiol. 164: 1649-1660; Wang et al. (2014). Plant, Cell Environ. 37: 2667-78; Choat et al. (2015) New Phytol. 205: 1095–1105; Cochard et al. (2015) Plant, Cell Environ. 38: 201-206; Torres-Ruiz et al (2015) Plant Physiol. 167: 40-43; Jansen et al. (2015) New Phytol. 205: 961-964). The nature of the potential artifact may involve induction of embolism during stem excision under water that is proportional to the tension in the xylem upon excision. As a result, loss of hydraulic function may be overestimated, and more so as tensions in the xylem increase. For example, applications of NMR and x-ray tomography imaging techniques have shown that xylem of <u>Laurus nobilis</u> (Cochard et al. 2015) and <u>Vitis</u> (Choat et al., 2011) may be substantially more resistant to cavitation than have been obtained with conventional techniques. This potential artifact also may be responsible for the apparent refilling of xylem because normal diel recovery of water potential in the afternoon and after would reduce the tension-induced artifact and result in apparent recovery of hydraulic conductivity. While imaging techniques may show some refilling of elements under well-watered or mild stress (>~0.5 MPa), drought-exposed plants may not (e.g., Betula spp. Suuronen et al., 2013); Sequoia sempervirens Choat et al., 2015). It also is pertinent to our paper to note that, even if one accepts the literature's positive assertions about novel refilling, it is considered only to be significant under mild to moderate water stress (Secchi and Zwieniecki, 2010; Brodersen and McElrone, 2013; Rockwell et al., 2014) and not the frequent severe stress encountered in our study. In revision, we have carefully defined the nature of our results and their limitations.

Author Point 3

One reviewer had an issue with use of predawn leaf water potentials as an indirect indicator of k. Our data analysis and assertions rely only on SPAC principles and do not depend on measurements of hydraulic conductivity per se. Hence we would assert that the uniformly prompt recovery of predawn water potentials after numerous droughts of widely varying severity across almost a decade of observations does support the possibility that hydraulic disconnection (sensu stricto, as above) is not a direct agent of* *mortality in our observations. We have been careful to word our revision language within these constraints. We have also revised the text to note that associations of increased PLC with mortality have been reported previously (albeit within the limits of correlational studies and the potential artifact effects noted above). We realize the methodological issues involved here might elicit strong opinions from the community and hope our approach will merit forbearance to publish our interpretation and let readers and time decide.*

**The soil-to-leaf component of the SPAC equation:* $E= - k_{soil\text{-}to\text{-}leaf} * [psi_{leaf}\text{-}psi_{soil}]$ *predicts that if hydraulic failure occurs, k should be drastically reduced and after a soaking rain psi* $_{leaf}$ *should not quickly return to the vicinity of psi* $_{soil}$ *at predawn (where E (transpiration) =0).*

Comment: The authors should further highlight in the introduction and especially in the Discussion/ Conclusion that 2012 was a very important case because the severity of the drought overwhelmed all of the species isohydric/anisohydric tendencies. This is a very important finding. It is not well appreciated in the literature but the authors can clearly show that isohydry is really only true under certain levels of water stress, so that drought severity can even drive relatively isohydric trees' water potentials to be highly negative. ***Response:*** *We agree with the importance of the loss of differential capacity to maintain higher predawn psi under extreme drought, but have reframed this phenomenon in general drought tolerance terms.*

Comment: Figures: Water potential and mortality figures are excellent, but regression figures (Fig 7-10) should be simplified when statistics are revised (e.g. not necessary to show all variables). ***Response:*** *We adopted this suggestion.*

Comment: Specific comments Pg 1287 L4: Neither the Phillips et al nor the Allen et al studies can demonstrate increasing tree mortality rates. I would recommend moving the Allen et al citation to the previous sentence to replace that reference and cutting the Phillips reference here. ***Response:*** *We adopted this suggestion.*

Comment: L15-16: This is simply not true. It has indeed been established in mortality of mature trees and shrubs (e.g. Hoffmann et al. 2010 Global Change Biol; Anderegg et al. 2012 PNAS; Nardini et al. 2013 New Phyt; Anderegg et al. 2014 Oecologia). ***Response:*** *See comments above.*

Comment: L29: "ideotypes" should be replaced with a different word here and elsewhere. ***Response:*** *We changed "ideotypes" to "idealized types".*

Comment: P1288 L21-23: Not sure what this sentence is trying to say. ***Response:*** *We rephrased this sentence.*

<u>Comment:</u>L23-28: It's not clear that these must be non-linear, but mortality mechanisms will certainly depend on drought characteristics. Some relevant discussion of drought characteristics and mortality in a 2013 review paper, in Tree Physiology if I recall. ***<u>Response:</u>*** *We revised this material by reframing the issues in terms of drought tolerance, rather than the strict isohydric-anisophydric paradigm.*

<u>Comment:</u> 1289 L3: stomatal regulation capacities? ***<u>Response:</u>*** *We rephrased this sentence to emphasize stomatal and other regulations.*

<u>Comment:</u> 1291 L10: Please list sample sizes for each species water potential measurements. ***<u>Response:</u>*** *Suggestion adopted.*

<u>Comment:</u> L12: How were samples collected from canopy trees? ***<u>Response:</u>*** *This wording was added to the relevant section:*
Leaves or leaflets (all Quercus, Carya and Fraxinus) or shoots (A. saccharum and J. virginiana) were sampled from lower branches (<2 m height) thus rendering any gravitational component negligible. After excision with a razor blade samples were immediately placed in humidified bags in a chest cooler until measurement promptly after sample collection was complete.

<u>Comment:</u> L15: Worth citing here Hoffmann et al. 2010 Global Change Biol and Nardini et al. 2013 New Phyt who look at predictors of mortality across a number of species. In fact, the Hoffmann paper should be referenced earlier in the introduction as well, as it is very relevant (temperate forests, examining drought-induced mortality of different iso and anisohydric species). ***<u>Response:</u>*** *Suggestion adopted.*

<u>Comment:</u>1292 L17: This is a very good point and one often underappreciated. ***<u>Response:</u>*** *Thanks.*

<u>Comment:</u> L20-23: This is not necessarily true. It rests on the assumption that overnight refilling under tension is not possible. While there is a lot of controversy in the literature about whether this occurs, there is some amount of evidence for it occurring (see Broderson & co-author 2013 review paper in Plant Physiology). I suggest removing this statement. ***<u>Response:</u>*** *We believe the reviewer meant a paper in Frontiers of Plant Science which gathered literature both supporting the concept (many papers) and not (a few). However, the paper did not address the recent concerns about refilling as an artifact. The methodological problems discussed above and their potential impact on reports of diurnal-scale refilling remain. We also note again that refilling, if it occurs, has been considered relevant only in mild-to-moderate stress situations. Nevertheless we have retained conditionality in our statement to reflect this concern.*

<u>Comment:</u> 1294 L26: Williams et al. 2013 in Nature Climate Change is a key citation here. ***<u>Response:</u>*** *Suggestion adopted.*

<u>Comment:</u> 1296 L4-7: This makes sense, but the authors should also briefly mention if any (or how much) precipitation falls as snow and might enter the soil at the start of the growing season from snowmelt. In other systems, snowmelt is a critical input for soil moisture that might be relevant to tree mortality, though I suspect it is much less critical in this ecosystem. ***Response:*** *Persistence of snow cover at this site is limited to a few weeks at most in mid-winter and by late April (~day 120) all snow has long melted.*

Comment: 1297 More details and methods are needed here on the statistical analyses. Were these linear regressions? The frequent problem with mortality data is that they are often non-normal and so other methods (e.g. count-based regressions; non-parametric regressions, or transformations) are often needed. In fact, some form of model selection using multi-variate regression and then stepwise model selection with AIC (the "stepAIC" function in R's MASS package works quite well) would be valuable here. I would recommend first testing for correlations among the predictor variables (perhaps using variance inflation factors), then doing this model selection algorithm. This will help determine 1) how correlated the predictor variables were and 2) which variables best explained mortality and 3) the most parsimonious model of predictor variables. ***Response:*** *See comments earlier. Multivariate and some other regression methods generally work the best when there is a large amount of data, which is a luxury for long-term mortality time series. There is not much that can be done statistically when there are only 10 points. But then again this study does not depend on statistical inference to draw conclusions. We already know the various predictors are correlated to various degrees (which is demonstrated in another paper under review and which limits the effectiveness of multivariate regression). But because some predictors (e.g. predawn leaf water potential integral) are more difficult to obtain than others, we feel it is necessary to present alternative indices that can be used to predict mortality.*

Comment: The authors should also state what statistical software the analyses were conducted in. ***Response:*** *This information is now given.*

Comment: 1301 L14-16: This analysis should be more rigorously done to test 1) whether linear regression is appropriate for these data (are assumptions of normality met) and 2) doing model selection with AIC (preferably AICc, which is corrected for sample size). Variance explained (r-squared) is not a robust way to do predictor variable selection. ***Response:*** *Suggestion adopted (see response above). Just to clarify, we don't attempt to select the best predictor variable because the time series of mortality is too short for such a task. What we do do is to demonstrate the potentials of different predictors and hopefully as the dataset grows, we will be able to do what this referee suggests here.*

Comment: L20-22: Again, in an AIC framework, models with different lags can be compared against each other statistically and statements made about whether including 1 and 2 year lags led to significantly better models. ***Response:*** *See responses above.*

Comment:1304 L8-12: A lag between drought stress and mortality is actually probably quite common (e.g. Bigler et al. 2007; Worrall et al. 2008 Forest Ecol & Mngement; Phillips et al. 2010 New Phytol; Anderegg et al. 2013 Global Change Biol) and has been explored before in the context of hydraulic failure. Multiple feedback mechanisms have been formulated and tested through which a drought can kill a mature tree hydraulically after the drought (Anderegg et al. 2013 Global Change Biol). These feedbacks can include changes in the hydraulic vulnerability, such as cavitation fatigue, that could lead trees to die in the years after drought stress from drought-triggered hydraulic damage. ***Response:*** *We have acknowledged the first sentence in revision. One of the things we have added with our work is a meaningful physiological indicator that predicts the level of mortality after the lag. See general Author Point1 and Author Point 2 above for what we're talking about here (i.e., catastrophic hydraulic disconnection, not partial loss of hydraulic function) and questions surrounding methodology underlying assertions of partial hydraulic "failure."*.

Comment: L13-17: Why is this the case? Cavitation fatigue has to do with damage during the *next* drought, not the recovery after the initial drought. Recovery after rainfall could be entirely possible, but cavitation fatigue would lead to more vulnerability during the next drought (i.e. 2013 or 2014 in the authors' case). Because the authors have not measured the appropriate mechanism directly (hydraulic conductivity) and only have water potential (and no presented evidence of hydraulic vulnerability curves for what levels of water potential are dangerous), this speculation on mechanisms is going far beyond what their data can say. ***Response:*** *There were "next droughts" during the study period, and within the same growing season (e.g., 2006, 2011, 2013). Predawns always recovered promptly after rainfall. We still have the presumed refilling possibility (but see above comments). Hence a carefully worded statement seems reasonable. Also, the cavitation fatigue concept must undergo reconsideration in the light of methodology issues raised in the general comments.*

Comment: L20-22: The authors have no direct evidence of this and their indirect evidence is very weak (e.g. multiple papers in the literature have measured this directly and found hydraulic failure in similar circumstances). It's not clear what these "indirect" methods could be (as the McDowell paper is terribly uninsightful), but many physiological processes of how drought can trigger mortality after drought (having to do with cavitation fatigue, lower growth, root mortality, and biotic agent feedbacks) have been proposed and in some cases tested. ***Response:*** *We note general Author Point 1 and 2. Our assertions of a lack of hydraulic disconnection do not preclude effects of water stress on important plant processes that, in concert with or exacerbating other stressors, eventually end in tree death, just that shoots weren't isolated from the rhizosphere by catastrophic hydraulic disconnection.*

Comment: 1305 L8-10: Again, hydraulic failure is not simply something that can be "observed" by looking for wilting. It must be measured through measurements of hydraulic conductivity. I recommend the authors remove much of the claims about mechanism. The paper is a very interesting set of data and analysis on its own without going beyond what the data can say and speculating about mechanisms that were not measured. ***Response:*** *See Author Point 1 and Author Point 2. However, because we don't want to overshadow other parts of the paper we have removed "mechanism" verbiage and carefully constrained our observations.*

Comment: Final paragraph: It’s not clear that this non-monotonic relationship “resolves” these studies contradictions at all. As the authors correctly note, iso- and anisohydry are largely relative measures and so relevant for a species compared to the other species around them. Thus, comparing their results to these other studies is difficult (as no one knows where all of these species would fall on a plot together). More importantly, the details and differences of soils and drought characteristics probably matter immensely and complicate the predictive ability of the isohydric spectrum. Rather than suggesting this parabolic curve resolves all previous discrepencies, which it most likely does not, I recommend a simple discussion of the previous studies and why they suggested they found the patterns they did. ***Response:*** *The paper has been reframed away from the strict anisohydric-isihydric paradigm to one of more general drought tolerance concepts.*

Comment: Discussion in general The authors should devote more discussion to the interesting insight that during 2012, ALL of the tree species had similar water potentials. In short, the severity of the 2012 drought seems to overwhelm the isohydric and anisohydric continuum, such that all trees were stressed. This is a very important finding and not one that is well appreciated in the literature. ***Response:*** *Suggestion adopted in concept in the revision.*

Comment: Figure 11 It’s not clear that a nonlinear relationship is necessarily better based on the sample size. A non-linear and linear model should be compared with AIC. ***Response:*** *Suggestion adopted.*

Response to Dr. Renee Marchin

<u>Comment:</u> This study explores drought-induced tree mortality over a 10-year timespan in a temperate forest in the central US. Measurements of predawn leaf water potential and tree mortality were collected for six tree species throughout the growing season, so it is a unique, long-term dataset that spans years of moderate to severe drought. ***<u>Response:</u>*** *We appreciate Dr. Marchin's careful reading of our manuscript and detailed comments and suggestions. Many thanks for the support. Our revision has benefitted greatly from Dr. Marchin's review.*

<u>Comment:</u> There were no direct measurements of mechanisms of tree mortality during drought (such as native embolism or changes in non-structural carbohydrates), however, so it would be appropriate to reduce mention of "mechanisms" throughout the discussion (and in the title). ***<u>Response:</u>*** *Suggestion adopted.*

<u>Comment:</u> I recommend removing some of the figures that are repetitive (e.g. Figures 9-11) and developing other points in the discussion (Figure 5). The authors have an excellent dataset for further developing an analysis of differential effects of moderate versus severe drought. The study found that stem mortality lagged 1-2 years after drought, and species intermediate along the anisohydric-isohydric continuum had higher survival over the decade of moderate to severe droughts. ***<u>Response:</u>*** *We have revised the manuscript along these lines but reframed it under more general drought tolerance concepts.*

<u>Comment:</u> Well-written, good summary of drought strategies in trees. ***<u>Response:</u>*** *Thanks!*

<u>Comment:</u> This paper focuses on a current hot topic in research (mechanisms of mortality during drought), and the background information in the Introduction could be updated: P1287, line 14-17 states that loss of conductivity "has not been clearly established as a direct agent of mortality in mature plants." This is incorrect (as mentioned in the discussion). Hydraulic failure is nearly universally high during drought mortality events and has been implicated as the mechanism of tree mortality in mature aspens in Colorado (see Anderegg et al. 2012, reference provided below). ***<u>Response:</u>*** *See Author Point 1 and 2, but we have now more carefully constrained our assertions and interpretation.*

<u>Comment:</u> McDowell et al. 2013 (reference below) also found an interdependency of carbon and water during drought mortality and could be cited in P1287, line 21. ***<u>Response:</u>*** *Suggestion considered but see Author Point 1 and Author Point 2*

<u>Comment:</u> P1287, line 14-17: Besides biotic agents such as insects and pathogens, fire can also interact with drought to cause tree mortality (see Pratt et al. 2014, reference provided below). ***<u>Response:</u>*** *Suggestion adopted.*

<u>Comment:</u> Materials and Methods

Gu et al. (2015) has been cited frequently in the methods of this paper, yet it is listed as "under review". These citations should be removed, unless it is accepted for publication in the near future. Then cite as "Gu et al. (in press)".). ***Response:*** *We are still waiting for the review process of that cited manuscript to be done at this moment so we removed that citation.*

Comment: Wordy in places, could be condensed:
P1289, line 15-17 could be reworded to "The study was conducted at the Missouri Ozark AmeriFlux (MOFLUX) site, previously described in Gu et al. (in press)." Or if Gu et al. (in press) is not accepted before press of this paper, delete its mention entirely. ***Response:*** *Suggestion adopted.*

Comment: P1290, line 11 could be reworded to "Measurements of precipitation, temperature, and relative humidity were made at the top of the 30 m flux tower. . ." and then delete these statements from lines 15-16. ***Response:*** *Suggestion adopted.*

Comment: P1291, line 23-24 should be deleted and "mean daily precipitation rate" should be listed with other predictors in line 20. ***Response:*** *Suggestion adopted.*

Comment: P1292, line 21 delete "if happens". ***Response:*** *See Author Point 2.*

Comment: P1291, line 7: Were samples collected at ground-level for all trees? Any samples collected from high in the canopy? ***Response:*** *Greater detail is now provided in the methods. All samples were from near ground level.*

Comment: P1291, line 2: How "frequent" were visits to the site to monitor tree mortality? ? ***Response:*** *Clarification is provided.*

Comment: How is the PLWPI calculated? The description is vague in P1292, line 1-2. Based on the units in Figure 4, it looks like a summation of seasonal water potentials, rather than an average. Please include an equation with units for repeatability. Should the units be MPa day-1 instead of MPa day? ***Response:*** *Clarification is provided.*

Comment: P1295: The description for PTAI and VPDI is also vague. Figure 8 shows annual values, but over what time interval were these values calculated? (I see this information is given later; perhaps state earlier?) Are there gaps in the MOFLUX tower meteorological data? If a lot of data was missing, couldn't this affect the values since they are summations? How were gaps handled? ***Response:*** *Details are now provided.*

Comment: In general, it is better to simply state results and reference the figure, as in P1297, line 21 "Potential abiotic factors of tree mortality varied widely. . . (Figure 1)". Avoid phrases like, "Figure 1 documents that from. . .". ***Response:*** *Suggestion adopted.*

Comment: Be careful to only state results in the Results section, and leave interpretation for the Discussion: P1299, line 11-15: Leave classification of species as anisohydric or isohydric for the discussion. P1300, line 1-3: Remove from results, put in discussion.

P1301, line 17-18 and 23-24: Remove from results, put in discussion. ***Response:*** *Revised along previously stated comments.*

Comment: P1297, line 24-25: Could you include a general description of drought severity? Were the droughts in 2007 and 2012 classified as severe? Were other years (2011, 2013) classified as moderate drought years? ***Response:*** *Suggestion adopted in the next section when results of predawn leaf water potential are presented.*

Comment: Figures 2-3 should be combined into one figure, since they show the same relationship for different study years. Perhaps just use "Figure 2 continued on next page" if necessary. ***Response:*** *In this case, some journals actually prefer separate figures because they make click-link easier in digital format.*

Comment: Figure 5: Very interesting! Check units of PLWPI, should it be MPa day-1? Include a description of how community PLWPI was calculated in the caption? ***Response:*** *Thanks. Clarification is provided.*

Comment: P1300, line 5-18: Long, could be condensed. Delete lines 7-14? ***Response:*** *Fig 6 is a complicated figure and shows that species mortality is not proportional to species abundance with oaks, which are traditionally considered drought tolerant species, suffering unusually high mortality. This information is important to the paper and needs to be described.*

Comment: Figure 6: It is not clear from the caption what is represented on the Y-axis. Is it tree diameter? I would recommend adding labels and units, perhaps replace the labels 1-10 with actual size classes (such as <6 cm, 6-12 cm, etc.). ***Response:*** *Clarification is provided.*

Comment: Figures 9-10 might be better placed in the Supplement. There is little mention of them in the Results, and the community patterns are already illustrated in Figure 8. If a linear relationship is used in Figure 11, is there still an improved prediction relative to Figure 8d? It is not a fair comparison if different prediction equations are used, plus it is not overly convincing as an exponential relationship. Regardless, Figure 11 does not need to be included. It would be enough to state that using a composite MEPI5 improved prediction of community stem mortality from R2=0.84 to R2=0.93 (if true). ***Response:*** *Fig. 11 is now placed in the supplementary material. Because the community pattern is dominated by oaks, we keep Fig. 9 and 10 in the main text to emphasize PLWPI and MEPI5, two very promising predictors, can also work for individual species.*

Comment: Figure 12: Interesting! The caption has a typo: "diving" should be "dividing". ***Response:*** *Thanks. Typo corrected.*

Comment: P1302, line 6-15: Could be deleted, because Figure 12 is a better illustration of this pattern. ***Response:*** *We feel it is important to point out that variations of PLWPI in time and across species do not mean the same thing. We therefore kept this paragraph.*

Comment: P1303, line 24-25: This is an excellent dataset to examine the importance of drought severity on stem mortality. It would be worth developing this point more, examining the different impact of a severe versus moderate drought on plant physiology. ***Response:*** *Suggestion adopted.*

Comment: P1304, line 7: It is difficult to state that hydraulic failure was not a factor in this forest, as native embolism or PLC was not measured. There were likely losses of conductivity, at least in 2012 when observations of leaf scorch were made. ***Response:*** *See Author Point 1 and Author Point 2 above.*

Comment: P1305, line 17-29: Description of previous studies could be improved to highlight the contradiction amongst studies, relative to ecosystem type (since anisohydric species can only be compared relative to isohydric species within an ecosystem). For instance, "Anisohydric species have shown higher dieback during severe drought, relative to more isohydric species, in Australia and the eastern US (Rice et al. 2004, Hoffmann et al. 2011). In contrast, an isohydric species had much higher drought-influenced mortality than a co-occurring anisohydric species in the southwestern US." Also clarify your findings in P1306, line 1-3: "Our results reveal that both anisohydric and isohydric species have higher stem mortality than species that fall intermediately between the two extremes." ***Response:***. *Species comparisons now reframed in terms of ecological distribution and drought tolerance attributes, see below*.

Comment: P1306, line 4-10: Very interesting! Might be a good ending point. ***Response:*** *Suggestion emphasized.*

Comment: P1307, line 13-14: Hydraulic failure has been determined to cause dieback or mortality in multiple species. Change wording from "postulated" to reflect this fact. ***Response:*** *See Author Point 1 and Author Point 2 above*

Comment: P1307, line 15: "death" not "depth". ***Response:*** *Typo corrected.*

Response to Referee #3

Comment: This study investigates long-term trends in tree mortality (2004-2014) observed in a central hardwood forest that experience a range of hydrologic condition during the study period, including two severe droughts in 2007 and 2012. The 2012 drought was particularly severe not only in this site, but also in many other parts of the U.S. The mortality trends are linked to a similarly long time series of pre-dawn leaf water potential, and various other proxies for variability in hydrologic stress. The principal findings are that mortality of all species tended to increase in years following a drought event, and that oaks experienced mortality at a higher rate than other species. The latter result is especially interesting given that oaks are generally believed to be more drought tolerant than other canopy co-dominants (see, for example, Abrams 1990). Linking mortality to the long-term pre-dawn leaf water potential is also a novel feature of this manuscript; and the effort necessary to collect those data for a decade is substantial and should be applauded. I am sure that researchers from a wide range of fields will find these data interesting, as they have the potential to advance our understanding of drought-induced tree mortality in forests like the Missouri Ozarks flux site that lie on the transition between water-limited and energy-limited systems. This is particularly true in the case of the oak species. ***Response:*** *Thanks. We appreciate this reviewer's insights and suggestions and have revised the manuscript accordingly.*

Comment: However, I have some significant concerns about the way the data are interpreted. Principally, I disagree that pre-dawn leaf water potential a reliable metric with which to classify species as isohydric or anisohydric. The authors are correct in defining isohydric species as those that regulate leaf water potential closely, and in defining anisohydric species as those that allow leaf water potential to drop during periods of hydrologic stress (with an associated higher risk of xylem cavitation). However, classification of species along this continuum should reflect the trends in leaf water potential during periods when gas-exchange is occurring (i.e. mid-day), and not during periods of relatively little water flow through the stem (i.e. pre-dawn). The recent work by Martinez-Vilalta et al. (2014), for example, uses variation in mid-day as compared to pre-dawn leaf water potential as the principal diagnostic for isohydric-to-anisohydric behavior; the slope of that relationship is relatively shallow for isohydric species, and relatively steep for anisohydric species. The pre-dawn value alone is insufficient alone to permit a classification of plant water use strategy using this framework. ***Response:*** *The referee has a point here, although greater capacity to access deep soil water (which is reflected in comparative values of predawn leaf water potentials) is commonly one attribute of isohydric species. Given the current entanglement of the isohydric-anisohyric paradigm with other concepts (e.g., assignment of mortality causation to hydraulic "failure" vs. carbon starvation, itself now complicated by issues raised in Author Point 2) we have chosen to reframe our species comparisons in the context of established ecological distribution patterns and physiological attributes related to drought tolerance.*

Comment: I also disagree that pre-dawn leaf water potential is sufficient to diagnose the occurrence of xylem cavitation. Stem water flow is usually represented with an Ohm's law analogy:

Water flux = K(PSI_soil – SPI_leaf – pgh)

where K is the hydraulic conductivity, PSI_soil and PSI_leaf are soil and leaf water potentials, and pgh represents gravity headlosses. If the water flux approaches zero (as is often assumed to be the case in pre-dawn periods), then that implies that PSI_soil and (PSI_leaf+pgh) are equivalent. The value of K is irrelevant if the water flux is zero. In this idealized scenario, the main determinants of species-specific differences in PSI_leaf will be differences in the effect PSI_soil relevant for each tree (i.e. rooting depth), as well as differences in tree height across species. The latter is not addressed in this manuscript, and tree height data are not presented. ***Response:*** *The actual situation is slightly different than the referee suggests. What we have is a soil-plant system that has gone from a drought condition where both plant and soil are at low water potential (and low flux), to one where the soil is substantially moistened, bringing an upper soil layer to approximately field capacity (i.e., water potential =~ -0.03 MPa). All plants are rooted in this layer. This being so, there is an immediate gradient for water flow from the soil into the plant and it is not a zero-flux system. Whether and how fast that water will flow depends on K. Our point is that even after severe drought, rapid recovery in pre-dawn leaf water potentials indicated that K wasn't limiting rehydration substantially in any species (i.e., there was no catastrophic disconnection).*

*The pgh term is now discussed in the revision. Leaf samples were taken from ground. For a height difference of 1 m, ignoring height would only result in an error 1000*9.8*1 Pa = 0.0098MPa. For comparison, in the summer of 2012, the predawn leaf water potential was in the order of -4.5MPa. The height differences in our leaf samples were typically less than 1 m. Thus it is justifiable to ignore gravity headloss in our analyses.*

Comment In the case of non-zero pre-dawn water flow, species-specific differences in PSI_leaf may incorporate information about K, but importantly these differences will also reflect: a)variations across species in nocturnal stomatal or cuticular conductance and/or temporal variation in vapor pressure deficit (which could promote a non-zero nocturnal stem flow), or b) the extent to which plants refill depleted water stores during the night, which is a widely recognized feature of plant water use for many species (e.g. Scholze et al. 2011). These processes are not addressed in the manuscript. ***Response***: *See Author Point 2 above. Also, we are not trying to make any species specific claims for relative ability to recover from peak-drought; all species showed rapid recovery. Further, nocturnal transpiration would have tended to lessen recovery in predawn leaf water potential, which we did not appreciably see.*

Comment: Ultimately, I think that the way the authors have interpreted the data, which is not consistent with recent advances in the field, detract considerably from what are really novel and interesting results on species-specific susceptibility to drought-induced mortality, and also novel and interesting results about species-specific differences in pre-dawn leaf water potential (which to a first order reflect species-specific differences in rooting depth and canopy architecture, with some caveats as listed above). ***Response***: *See Author Point 1 and 2. We reiterate that there are methodological concerns and that these concerns bring into question much of this recent work. However, in revision we have* *tried to clarify the narrowly defined, and we hope less controversial, phenomenon we are addressing in revision, as we discuss in Author Point 1 above.*

Comment: 1) It is a concern that much of the analysis is linked to Gu et al. (2015), which is under review. Has there been any change to the status of that paper? ***Response***: *Since that manuscript is still under review, we removed that citation.*

Comment: 2) In discussing future drought trends, the authors may want to consider citing the new work by Cook et al. (2015, Science Applications). ***Response***: *Suggestion adopted*

Comment: 3) Do the author's classification of species as isohydric/anisohydric agree with other relevant literature on the topic? If not, can reasons for the discrepancy be discussed? (see, for example, Thomsen et al., 2013, Forests). ***Response***: *Given the current entanglement of the isohydric-anisohyric paradigm with other concepts (e.g., assignment of mortality causation to hydraulic "failure" vs. carbon starvation, itself now complicated by issues raised in Author Point 2) we have chosen to reframe our species comparisons in the context of established ecological distribution patterns and physiological attributes related to drought tolerance.*

Comment: 4) The authors state on page 1304 that "no accepted mechanism exists for" xylem refilling in the absence of rain. Some recent work (e.g. Sala et al. 2012) suggests that NSC carbohydrates can be deployed to assist in xylem repair by affecting osmotic potential. ***Response***: *We have made relevant revision. But see Author Point 1 and 2.*

Comment: 5) It is unclear to me why some of the regressions (i.e. those Figure 8) are linear, whereas others (i.e. Fig 11) represent a non-linear function. ***Response***: *We have added the necessary details.*