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Interactive comment on "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" *by* L. Gu et al.

Anonymous Referee #1

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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.

I do, however, think that several major issues need to be addressed before the study is suitable for publication.

1) 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.

2) 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).

3) 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.

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).

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.

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).

L29: "ideotypes" should be replaced with a different word here and elsewhere

P1288 L21-23: Not sure what this sentence is trying to say.

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.

1289 L3: stomatal regulation capacities?

1291 L10: Please list sample sizes for each species water potential measurements

L12: How were samples collected from canopy trees?

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).

1292 L17: This is a very good point and one often underappreciated.

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.

1294 L26: Williams et al. 2013 in Nature Climate Change is a key citation here.

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.

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.

The authors should also state what statistical software the analyses were conducted in.

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.

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.

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.

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.

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.

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.

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.

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.

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.

Interactive comment on Biogeosciences Discuss., 12, 1285, 2015.