

forest ecology

Applicability of Predictive Models of Drought-Induced Tree Mortality between the Midwest and Northeast United States

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Regression models developed in the upper Midwest (United States) to predict drought-induced tree mortality from measures of drought (Palmer Drought Severity Index) were tested in the northeastern United States and found inadequate. The most likely cause of this result is that long drought events were rare in the Northeast during the period when inventory data were available. Therefore, new predictive models of drought mortality for the Northeast were built using USDA Forest Service inventory data and national climate data from 1969 to 2007. The Standardized Precipitation Index was better correlated with tree mortality in the Northeast than the Palmer Drought Severity Index, and new models were estimated. The reliability of the northeast models varied considerably by drought-sensitivity class, with the model for drought-intolerant species being particularly suspect. I argue that the Midwest models may nevertheless have some value in the Northeast because my tests were unable to cover the range of drought conditions under which the models were developed, there is no obvious reason why the same species should respond differently in a very similar ecological province, and some northeast models are very weak.

Keywords: drought stress, climate change, forest biomass, Northeastern Mixed Forest Province, Laurentian mixed forest province

An important impact of climate change in temperate forests will probably be an increase in drought conditions (Allen and Breshears 1998). Moisture stress can kill trees directly or make trees more susceptible to pests, pathogens, or other stressors (Hanson and Weltzin 2000). In some forested ecosystems, such as those at the northern prairie-forest border of central North America, an increase in drought conditions may dramatically alter forest composition, perhaps resulting in the conversion of forest to savanna (Frelich and Reich 2010) or prairie (Hogg and Hurdle 1995). Although precipitation in the northeastern United States is expected to rise during the current century, drought stress is nevertheless expected to increase because of higher evapotranspirative demand caused by elevated temperatures (Ollinger et al. 2007).

Gustafson and Sturtevant (2013) developed regression and simulation models to predict the impact of changes in the drought regime on tree mortality and forest dynamics in the upper Midwest. They found that a single measure of drought (mean length of drought events [annual Palmer Drought Severity Index <[0.5]]) could be used to predict the tree biomass lost to mortality of tree

species in the Laurentian Mixed Forest Province (No. 212) (Cleland et al. 2007) in Minnesota, Wisconsin, and Michigan (Figure 1). The authors suggested that their models may be applicable in similar ecological provinces but cautioned that they should be tested first.

The primary objective of this study was to conduct such a test in the similar Northeastern Mixed Forest Province (No. 211) in the northeast states of Pennsylvania, New York, Vermont, New Hampshire, Massachusetts, and Maine. Should the models perform poorly, the secondary objective was to determine whether reliable predictive models of drought-induced mortality can be estimated for forests of the Northeast using different indices of drought or other model formulations.

Methods

I tested models that were constructed in Province 212 for their validity in the portion of Province 211 that is located in the northeast United States (Figure 1), including the mountainous subprovince (M211). I explored the possibility that the orographic effects of

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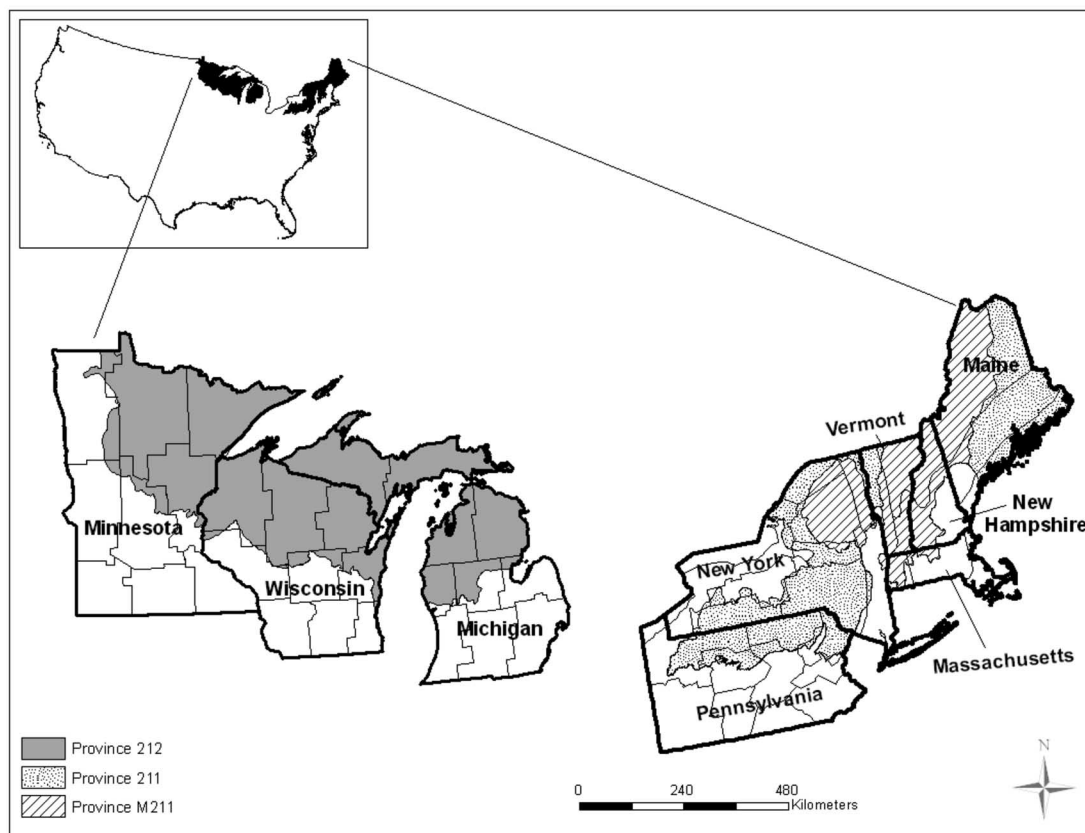


Figure 1. Map of US ecological provinces used for the study area (Cleland et al. 2007). State boundaries are thick lines, and National Climate Data Center (NCDC) climate division boundaries are shown as medium lines.

Table 1. Species assignments to the four drought sensitivity classes (as in Gustafson and Sturtevant 2013).

Drought-sensitivity class	Common name	Scientific name
Intolerant	Quaking aspen, big-toothed aspen, paper birch, black ash	<i>Populus tremuloides</i> (Michx.), <i>Populus grandidentata</i> (Michx.), <i>Betula papyrifera</i> (Marsh.), <i>Fraxinus nigra</i> (Marsh.)
Somewhat intolerant	Eastern hemlock, White spruce, Northern white cedar, yellow birch, balsam fir, American beech	<i>Tsuga canadensis</i> (L.), <i>Picea glauca</i> (Voss), <i>Thuja occidentalis</i> (L.), <i>Betula alleghaniensis</i> (Britton), <i>Abies balsamea</i> (L.), <i>Fagus grandifolia</i> (Ehrh.)
Somewhat tolerant	Red maple, sugar maple, black cherry, white ash, basswood, American larch, black spruce	<i>Acer rubrum</i> (L.), <i>Acer saccharum</i> (Marsh.), <i>Prunus serotinus</i> (Ehrh.), <i>Fraxinus americana</i> (L.), <i>Tilia americana</i> (L.), <i>Larix laricina</i> (K Koch), <i>Picea mariana</i> (Mill.)
Tolerant	Red pine, white pine, jack pine, red oak, white oak	<i>Pinus resinosa</i> (Ait.), <i>Pinus strobus</i> (L.), <i>Pinus banksiana</i> (Lamb.), <i>Quercus rubra</i> (L.), <i>Quercus alba</i> (L.)

the mountains might obscure the drought mortality signal, but concluded that Province M211 need not be omitted.

Testing the Midwest Models

Following the methods of Gustafson and Sturtevant (2013), I used USDA Forest Service Forest Inventory and Analysis (FIA) data to assemble a data set of tree mortality on FIA plots (Woudenberg et al. 2010) within Province 211 and combined it with climate records (by climate zone) obtained from the National Climate Data Center (NCDC). I used the drought-sensitivity classes defined by Gustafson and Sturtevant (2013), adding American beech to the somewhat drought-intolerant class (Table 1). Tree mortality was estimated using FIA data obtained from the FIA Data Mart website (USDA Forest Service 2012). The observations were inventory plots within counties falling at least partially within Province 211 (Figure 1) that were classified as timberland for each inventory period. Measurements taken of the trees on each plot included species, dbh,

height, form, and living or dead status, and the volume of each tree was calculated by FIA using allometric equations (Woudenberg et al. 2010). The mortality rate for each drought-sensitivity class was calculated as the biomass lost to mortality on each FIA plot during the inventory period. The annual proportion of biomass lost to mortality (pm) was calculated using Equation 7 of Sheil et al. (1995): $pm = 1 - [1 - (N_0 - N_1) N_0]^{1/t}$, where, in this study, N_0 is the biomass of live trees (of a given drought-sensitivity class) in the previous inventory, N_1 is the biomass of live trees at the end of the inventory period, and t is the number of years between inventories. This equation corrects for time bias of mortality rates where instantaneous mortality rates are not equivalent to periodic rates. Plots with fewer than six trees in a given class or those in which $>10\%$ of the trees were harvested since the previous inventory were omitted. Inventory periods used were 1978–1989 and 1990–2004 for Pennsylvania, 1980–1993 and 1994–2007 for New York, 1973–1983, 1984–1997, and 1998–2007 for Vermont, 1973–1983,

Table 2. Prediction equations developed for the Midwest by Gustafson and Sturtevant (2013).

Drought-sensitivity class	Intercept (γ)	SE (γ)	Slope (β)	SE (β)	Predictor variable (x)
Intolerant	-5.499	0.028	0.576	0.015	Mean drought length ¹
Somewhat intolerant	-4.426	0.037	0.235	0.019	Mean drought length ¹
Somewhat tolerant	-5.668	0.031	0.258	0.016	Mean drought length ¹
Tolerant ²	NA	NA	NA	NA	NA

Predicted annual proportion of biomass lost to mortality (pm) is calculated (back-transformed) using $pm = \exp(\gamma + \beta x)$. NA, not applicable.

¹ Mean length (years) of drought events (successive years where mean annual PDSI ≤ -0.5).

² No valid predictive model for drought-tolerant species was found. No relationship was assumed.

1984–1997, and 1998–2007 for New Hampshire, 1972–1985, 1986–1998, and 1999–2007 for Massachusetts, and 1982–1995 and 1996–2003 for Maine, with the last inventory in each state including all “annual plots” measured after 1998. Climate data were from a national data set of time-bias-corrected monthly divisional temperature-precipitation-drought index values from the NCDC (National Oceanic and Atmospheric Administration 2012) for the years 1969–2010. Additional details about data preparation are found in Gustafson and Sturtevant (2013).

Using the regression equations of Gustafson and Sturtevant (2013) for each drought-sensitivity class (Table 2), I calculated the predicted loss of tree biomass to drought-induced mortality for each class on each FIA plot and statistically compared observed versus predicted mortality rates. I regressed observed mortality on FIA plots against mortality rates predicted using the equations of Gustafson and Sturtevant (2013) and used the SAS v9.3 (SAS Institute, Inc. 2011) TEST statement in Proc REG to test the joint hypotheses that the intercept was equal to 0.0 and that the slope was equal to 1.0 (Dent and Blackie 1979, p. 103) with $\alpha = 0.1$.

Building New Models

As described in the Results, the Midwest models did not pass these statistical tests, so I estimated new models. Using the climate data described above, I linked five monthly drought variables to the FIA data by climate zone: the Palmer Drought Severity Index (PDSI) (Palmer 1965), the Palmer Modified Drought Severity Index (PMDI) (Heddinghaus and Sabol 1991), and three estimates of the Standardized Precipitation Index (SPI) calculated using precipitation amounts during the prior 3, 12, or 24 months, respectively (McKee et al. 1995). From temperature and precipitation data, I also calculated a measure of available moisture for plants (precipitation minus potential evapotranspiration [P-PET]) (Gustafson et al. 2003) from temperature ($^{\circ}$ C) and precipitation (cm) records annually and for the growing season (May through September) using the Thornthwaite (1948) method, correcting for latitude (Dunne and Leopold 1978, p. 138).

I computed Pearson correlation coefficients between pm on each FIA plot and each of the six drought indices (Table 3). It should be noted that the correlations were generally quite weak, and, in some cases, the sign of the correlation was opposite the biologically expected sign (i.e., mortality rate decreased as conditions got drier [drought index value decreased]), suggesting that the correlations may be spurious. Mean annual SPI-12 had the highest correlation coefficient (Table 3), so all further analysis was conducted using this index. I built generalized linear mixed models to predict pm using a 70% random subset of the FIA data set, reserving the remainder of the data set for model testing purposes. I used the Shapiro-Wilks test and visual examination of stem and leaf plots (UNIVARIATE procedure) to determine the distribution of pm and used an exponential distribution with a log link via Proc GLIMMIX in SAS to estimate

Table 3. Pearson correlation coefficients between proportion of biomass lost to mortality (pm) and various indices of drought in the Northeast.

Drought index ¹	N	r	$Pr > r $
Mean annual PDSI	10,065	-0.008	0.4103
Mean annual PMDI	10,065	-0.009	0.3639
Mean annual SPI-03	10,065	-0.103	<0.001
Mean annual SPI-12	10,065	-0.127	<0.001
Mean annual SPI-24	10,065	-0.124	<0.001
Mean annual P-PET	10,065	0.064 ²	<0.001
Mean growing season P-PET	10,065	0.018 ²	0.075
Drainage class ³	9,545	0.092 ²	<0.001

¹ See text for full variable names.

² The sign of the correlation coefficient (r) was counter to biological expectation.

³ Integer values range from 1 to 3, xeric to hydric.

Table 4. Candidate prediction models, in which drought stress predictor variables predict tree mortality rate (as in Gustafson and Sturtevant 2013).

Model no.	Drought stress predictor variables
1	Mean annual drought index value
2	Most severe annual drought index value
3	Cumulative length of all drought events (normalized per decade)
4	Mean severity of drought events
5	Mean length of drought events
6	Length of longest drought event (years)
7	Mean severity of drought events, mean length of drought events (years)

The drought index value used here was SPI-12, and drought was defined as mean annual SPI-12 ≤ -0.5 .

the seven candidate models used by Gustafson and Sturtevant (2013) (Table 4), choosing the best model using a weight-of-evidence approach (Burnham and Anderson 2002, p. 49–97). Drought conditions referenced in the candidate models were defined as mean annual SPI-12 values ≤ -0.5 . Using the remaining 30% of the observations in the data set, I tested the most plausible models by regressing observed against predicted mortality rates and again tested the joint hypotheses that the intercept was equal to 0.0 and the slope was equal to 1.0.

Results

Testing the Midwest Models

None of the models developed in Province 212 passed observed versus predicted statistical tests of their predictive ability in Province 211 (Table 5). Given these results, I attempted to build new models using data from the Northeast.

Building New Models

The Akaike weights for the candidate models of each drought sensitivity class (Table 4) indicated a high relative plausibility for several models that had a sign of the slope coefficient that was

Table 5. Model test results showing the regression of predicted mortality rate against observed rate (expected slope = 1.0).

Drought-sensitivity class	<i>N</i>	Intercept (SE)	Slope (SE)	Pr > <i>F</i>
Intolerant	1,939	0.02 (0.001)	-1.12 (0.12)	<0.001
Somewhat intolerant	1,195	0.06 (0.010)	-2.60 (0.63)	<0.001
Somewhat tolerant	2,414	0.01 (0.003)	-1.46 (0.52)	<0.001
Tolerant ¹	1,020	NA	NA	

Models were estimated using data from Lakes States forests (Gustafson and Sturtevant 2013), and predictions were generated for the Northeast. *N* indicates the number of FIA plots used to test the models. *P* > 0.1 suggests that the joint hypotheses that the intercept = 0.0 and the slope = 1.0 could not be rejected. NA, not applicable.

¹ No valid predictive model was found for this class in the Midwest (Gustafson and Sturtevant 2013).

variable was usually a measure of drought severity. However, when the northeast models are compared with the models estimated for the Midwest (Figure 3), suspicions about their reliability arise. In the Midwest, the mortality probability curves progressively flatten from the most drought-intolerant class to the most tolerant class (the relationship is flat, not shown), as one would expect. However, the curves estimated for the Northeast do not fully exhibit such a pattern. Given that the curve for the tolerant class is also flat (no relationship found, not shown), the pattern mostly holds except that the curve for the intolerant class (Figure 3B) is dramatically flatter than that expected both on theoretical grounds and on a comparison with the Midwest curves. Furthermore, the fact that the most plausible models did not test well supports the idea that the models may

Table 6. Akaike weights for candidate models of each drought-sensitivity class.

Drought-sensitivity class	<i>N</i>	Akaike weights for model						
		1	2	3	4	5	6	7
.....(%).....								
Intolerant	1,447	0.0 ¹	0.0 ¹	0.0 ¹	0.0 ²	0.0 ¹	100.0 ^{1,2}	0.0 ¹
Somewhat intolerant	898	0.0 ²	0.0 ¹	0.0	0.0 ²	0.0 ¹	0.0 ¹	100.0 ^{1,2}
Somewhat tolerant	1,915	0.0 ²	0.0 ¹	0.0	0.0 ²	0.0 ¹	0.0 ¹	100.0 ^{1,2}
Tolerant	770	91.0 ²	0.0	9.0 ²	0.0	0.0	0.0	0.0

Higher weight indicates greater plausibility for a model. *N* indicates the number of FIA plots used to fit the models.

¹ Models in which at least one sign of a slope coefficient was counter to expectation.

² Models actually used to generate and test predictions.

Table 7. Model test results showing the regression of predicted biomass lost to drought-induced mortality against observed biomass lost.

Drought-sensitivity class	<i>N</i>	Model no.	Intercept (SE)	Slope (SE)	Pr > <i>F</i>	<i>R</i> ²
Intolerant	645	4	-0.00 (0.01)	1.06 (0.45)	0.602	0.008
Intolerant	645	6 ²	0.01 (0.00)	0.46 (0.07)	<0.001	0.068
Somewhat intolerant	409	1	-0.00 (0.01)	0.91 (0.45)	0.463	0.010
Somewhat intolerant	409	4	0.01 (0.02)	0.36 (1.18)	0.393 ¹	0.000
Somewhat intolerant	409	7 ²	0.01 (0.00)	0.12 (0.25)	0.001	0.000
Somewhat tolerant	837	1	-0.00 (0.00)	1.69 (0.73)	0.036	0.006
Somewhat tolerant	837	4	-0.01 (0.00)	2.82 (0.81)	0.005	0.014
Somewhat tolerant	837	7 ²	-0.00 (0.00)	1.06 (0.21)	0.061 ³	0.028
Tolerant	354	1	0.00 (0.00)	0.44 (0.21)	0.002	0.012
Tolerant	354	3	0.00 (0.00)	0.36 (0.20)	0.000	0.010

Models were fit using a subset of FIA data from the Northeast and tested using the remaining data. *N* indicates the number of FIA plots used to test the models. *P* > 0.1 suggests that the joint hypotheses that the intercept = 0.0 and the slope = 1.0 could not be rejected.

¹ True significance is unlikely; statistical significance is the result of high variability.

² The sign of at least one predictive model coefficient is counter to biological expectation.

³ True significance is actually likely; the SE of the intercept term was slightly larger than that for the parameter estimate, resulting in an insignificant test statistic score.

counter to biological expectation (i.e., mortality went down as conditions got drier; shown by footnote 1 in Table 6). These models may be spurious. For each drought-sensitivity class, I tested the most plausible model, but when the sign of the coefficient was counter to biological expectation, I also tested other models having the expected sign. A single valid model was found for each class with the exception of the drought-tolerant class (Table 7), similar to the results for the Midwest. However, the valid model was never the same as the most plausible model except for the somewhat drought-tolerant class. Model 7 for the somewhat tolerant class was deemed a valid model despite the statistical test. In this case, the error of the test regression intercept term was so low that an intercept estimate of virtually zero was nevertheless not statistically equal to zero. Coefficients for the best model for each drought-sensitivity class in the Northeast are given in Table 8.

The predictor variable in the Midwest was always the mean length of drought events, whereas in the Northeast the predictor

be somewhat spurious in the Northeast.

Discussion

I used the same assumptions for this study that were made by Gustafson and Sturtevant (2013). I assumed that a drought-induced mortality signal might be weak and difficult to detect amid the noise of many other proximate and ultimate mortality factors but that it could nevertheless be detected by using a large number of observations. It should be noted that there were far fewer FIA plots suitable for this analysis in the northeast (*N* = 10,065) than in the Midwest (*N* = 43,665). In the Midwest, the models for all drought-susceptibility groups were consistent in terms of the best predictor variable, and they predicted that drought-induced mortality decreased steadily from the least drought-tolerant class to the most drought-tolerant class as one would expect, suggesting that this assumption was valid (Gustafson and Sturtevant 2013). However, in the Northeast, the models were less consistent. This could occur because the

Table 8. Prediction equations developed for the Northeast.

Drought-sensitivity class	Intercept (y)	SE (y)	Slope (b_1)	SE (b_1)	Predictor variable (x_1)	Slope (b_2)	SE (b_2)	Predictor variable (x_2)
Intolerant	-4.526	0.096	-0.351	0.114	Avg drought severity ¹	NA	NA	NA
Somewhat intolerant	-3.955	0.033	-0.629	0.110	Mean SPI-12 ²	NA	NA	NA
Somewhat tolerant	-5.270	0.044	-1.476	0.093	Avg drought severity ¹	-1.011	0.052	Avg. drought length ³
Tolerant ⁴	NA	NA	NA	NA	NA	NA	NA	NA

Predicted annual proportion of biomass lost to mortality (pm) is calculated (back-transformed) using $pm = \exp(y + b_1x_1 + b_2x_2)$. Avg, average; NA, not applicable.

¹ Mean severity of drought events (successive years where mean annual SPI-12 ≤ -0.5).

² Mean annual SPI-12 index value between tree inventories.

³ Mean length of drought events (successive years where mean annual SPI-12 ≤ -0.5).

⁴ No valid predictive model for drought-tolerant species was found. No relationship was assumed.

sample size was inadequate, or the drought-induced mortality signal was too weak during the time period analyzed, or both. I also did not use a zero-inflation model to build the predictive models (following Gustafson and Sturtevant 2013) because there is no a priori expectation that observations of zero mortality reflect a different process than observations where mortality occurred. Zero mortality is a reasonable outcome when drought conditions do not occur or are mild.

The Province 212 models did not reliably predict drought-induced mortality in Province 211. Consequently, new models were estimated for Province 211, although their generality and reliability for making predictions is perhaps questionable. There are three potential explanations for the poor performance of the Midwest models in the Northeast. First, the measure of drought used in the Midwest study (PDSI) for some reason is not a good indicator of drought conditions in the Northeast, whereas another measure is better suited to northeast forests. Second, drought events were uncommon or weak in the Northeast during the period tested, and drought-induced mortality was therefore relatively rare. Third, there are stressors in the Northeast that are not found in the upper Midwest (e.g., hemlock woolly adelgid and balsam woolly adelgid) or are more pronounced (e.g., sugar maple decline and acidic deposition). These explanations will be discussed in turn.

At first glance, it does appear that the problem with the Midwest models in the Northeast was either the drought index used or the predictor variable (length of drought events) because I was able to build statistically viable models for the Northeast using a different drought index and different predictor variables. However, I have already enumerated concerns about the generality and reliability of these new models. Furthermore, it is not clear why the SPI-12 index should be fundamentally superior to the PDSI in the Northeast. The difficulty in building consistent predictive models for the Northeast suggests that the drought signal is extremely weak in this data set and/or the sample size is inadequate, and the new models may therefore be spurious.

Although the ecological provinces are similar and most of the tree species are the same, Province 211 may experience fewer and less severe drought events because of the closer proximity of a major moisture source (Atlantic Ocean). The distribution of mean annual PDSI values shows that the Northeast does, in fact, have fewer of the lowest (driest) values compared with the Midwest (Figure 2). Hanson and Weltzin (2000) delineated drought regimes in the United States and showed that droughts in the upper Midwest are fairly common, whereas droughts are limited in duration and spatial extent in the Northeast. The SPI drought index is not a useful index to compare absolute wetness between locations because it is calculated relative to median conditions at a location. I therefore used P-PET to compare the moisture regimes between the Northeast and the

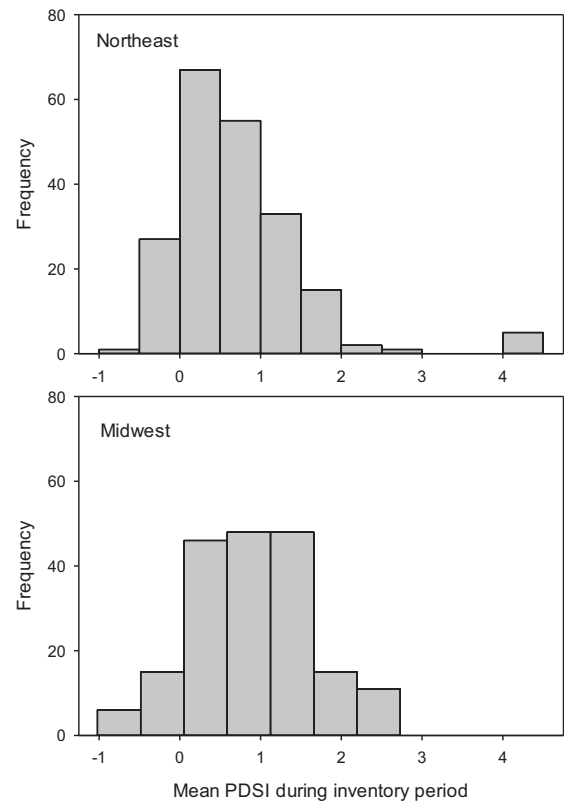


Figure 2. Frequency distribution of mean annual PDSI in the Northeast (1970–2007) and Midwest (1963–2009). The unit of analysis is FIA inventory periods in each NCDC climate division within each study area.

upper Midwest and found that the decadal mean number (n) and intensity of droughts in the Northeast during the time period studied (1969–2007) were less than those that occurred in the Midwest during the time period studied by Gustafson and Sturtevant (2013) (1963–2009) ($n = 0.13$, mean P-PET = -11.5 and $n = 0.21$, mean P-PET = -14.1 , respectively). To determine whether the incidence of drought in the Northeast during the study period may have been lower than normal by chance, I compared the mean P-PET values between the study period and the period of the NCDC record (1895–2010). The mean P-PET in the Northeast over the last century was 45.94 ± 19.3 inches (minimum = -18.78), whereas during the study period it was 52.46 ± 19.3 inches (minimum = 0.74), suggesting that the study period was somewhat wetter than usual, although the difference was not statistically significant because of high variability ($t = -0.18$, $P = 0.86$). Furthermore, long-term conditions in the Northeast were significantly wetter ($t = 1.98$, $P = 0.05$) than those in the Midwest (mean

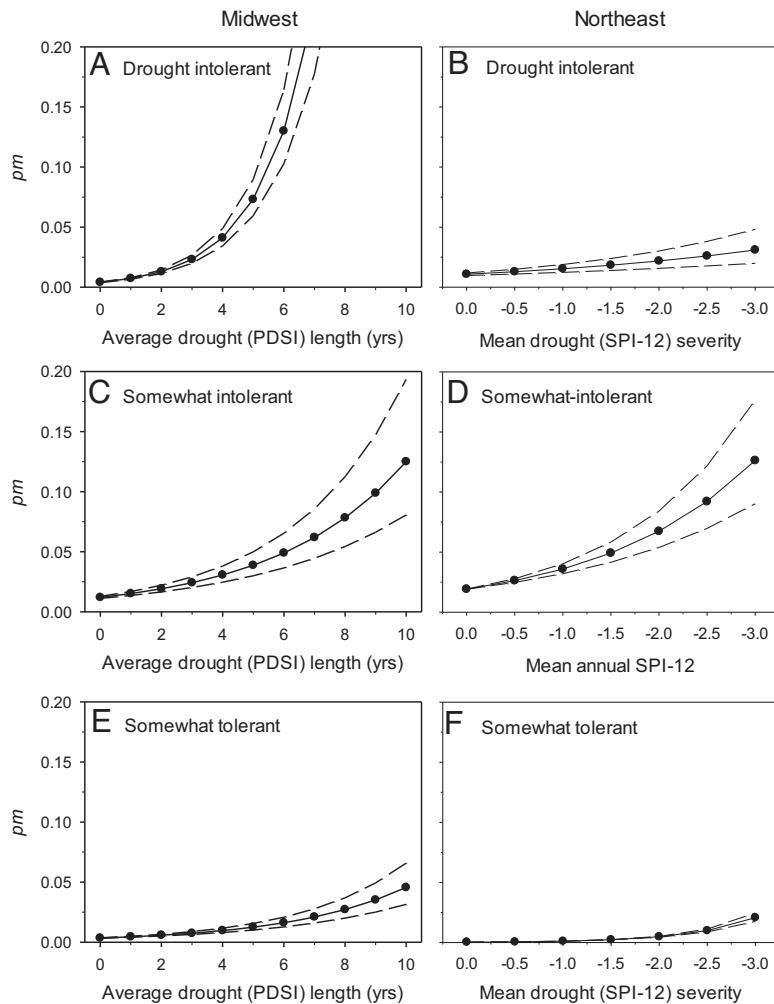


Figure 3. Comparison of the best prediction equations between the Midwest (A, C, and E) (Gustafson and Sturtevant 2013) and the Northeast (B, D, and F). Dashed lines represent 1 SE. Panel F represents a two-factor model and the graph depicts the response when mean length of drought events was fixed at 3 years. There was no relationship between measures of drought and mortality for drought-tolerant species in the Midwest or the Northeast.

P-PET [1895–2010] = 45.94 ± 19.3 inches (minimum = -18.78) and 10.61 ± 13.9 inches (minimum = -45.4), respectively). Thus, it appears that my study period was somewhat wetter than usual in the Northeast and that the Northeast is on average considerably wetter than the Midwest.

It is well known that drought can stress trees and make them more susceptible to being killed by other stressors (Dale et al. 2001). Although there are many such stressors in the Midwest, there are others in the Northeast that are not found in the Midwest. For example, there are adelgids in the Northeast that attack hemlock and balsam fir, potentially making those somewhat drought-intolerant species even more vulnerable to drought in the Northeast. Sugar maple is susceptible to decline in the Northeast, and drought is one of several factors listed as possible contributors (Hendershot and Jones 1989, Horsley et al. 2002). Drought may also exacerbate the effects of other stressors such as acidic deposition (Johnson et al. 1986). In addition, trees experience different types of selection pressures when water is and is not limiting. For example, populations of some pathogens can be higher when it is wet (Frankel et al. 2012), and it is possible that the counterintuitive sign in some of the models is related to such effects.

Although I was able to estimate predictive models for the North-

east (Table 8), I am nevertheless hesitant to advocate for their use because of concerns about their reliability, particularly the model for drought-intolerant species (Figure 3B). Based on my observations above, I submit that perhaps the Midwest prediction equations should work in the Northeast when long droughts occur, but because long droughts happened to be relatively rare in the Northeast during the test period (when FIA inventories were available), the predictions of drought-induced mortality by the models were not numerically high enough to be distinguished from similar levels of random background mortality. The median length of drought (defined by PDSI) in the Northeast during the study period (when FIA inventories were available) was only 1.0 years and the 90% quantile was 2.0, whereas in the Midwest study the median was 1.5 years and the 90% quantile was 3.0.

It is unfortunate that FIA inventories do not include the major northeast drought of the 1960s. It is possible that the 1960s drought did generate enough drought-induced mortality to be detectable. To evaluate this idea, I searched for data sets in which tree mortality was tallied on plots from the 1950s to the present to see whether there was any indication that mortality was higher during the drought of the 1960s. I identified two candidate data sets, but the only one that reliably recorded mortality was from the Penobscot

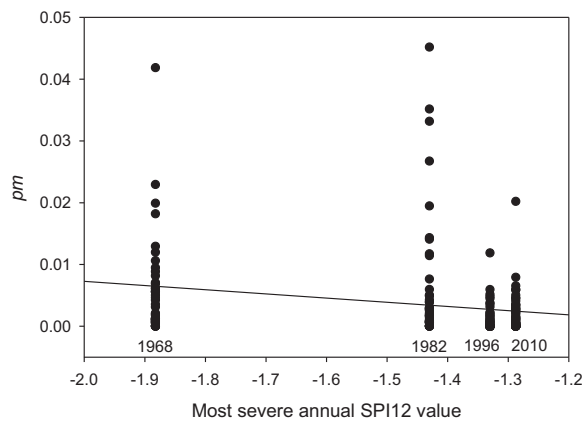


Figure 4. Annual proportion of biomass lost to mortality (pm) on Penobscot Experimental Forest inventory plots as a function of the most significantly related drought index between inventories beginning in 1955. Annotations give the end year of each inventory represented by the points above. The slope of the regression is -0.007 ($t = -3.17$, $P > |t| = 0.024$, $df = 189$).

Experimental Forest in central Maine, where plots were established to study tree response to harvesting treatments (Sendak et al. 2003). I used plots from uncut reference areas ($N = 20$) and from a treatment that involved very light cutting ($N = 33$), calculating mortality and climate using the same methods as for FIA plots. Inventories were conducted on each plot approximately every 5 years. Cumulative mortality on each plot was tabulated for climatic periods chosen to reflect distinct wet and dry periods: 1955–1968, 1969–1982, 1983–1996, and 1997–2010. There were insufficient observations by drought-sensitivity classes to definitively test the Midwest models, but I plotted annual mortality (all species combined) against the most significantly related drought variable (most severe annual drought index value) to see whether the 1960s drought produced a higher mortality rate than other periods (Figure 4). Unfortunately, the 1960s drought in central Maine did not produce longer or more severe droughts than those found in the FIA data set, but it does provide an independent observation of another relatively dry period. As expected, the data are noisy because of multiple causes of mortality, and the wettest periods occurred as the trees aged and became more prone to other mortality factors. Nevertheless, the regression line represents a putative drought signal. The slope is significantly different from zero despite a relatively small sample size. The second most significant variable was length of drought (not shown), and it too was significantly different from zero. These results provide some additional support for the notion that the Midwest models tested poorly because the length of droughts in the Northeast was limited during the time period studied. It is interesting to note that in this particular data set the length of drought events was more related to mortality than the severity of those drought events, which is consistent with the results from the Midwest (Gustafson and Sturtevant 2013).

There is not a large body of literature on the effect of drought on trees in the Northeast. This may be another indicator that drought has not been a large factor for forest dynamics there. In the Northeast, most forest ecosystems have probably been structured by disturbances other than drought. Outbreaks of spruce budworms can kill certain coniferous species across large areas (Williams and Liebhold 2000) and repeated outbreaks of gypsy moths can similarly cause mortality of certain deciduous species (Gansner et al. 1993).

Wind events such as hurricanes can cause forest damage, but the extent of severe damage declines with distance from the coast (Boose et al. 2001). On the other hand, large stand-replacing wildfires are extremely rare compared with those of other regions (National Interagency Fire Center 2008).

Drought has the potential to kill many trees relatively quickly over a very large area (Breshears et al. 2005), so drought has the potential to dramatically alter normal forest dynamics if the drought regime is altered by climate change. Based on results from the Midwest, longer drought periods would increase mortality of drought-sensitive trees in the Northeast and alter normal forest dynamics as suggested for other regions (Allen et al. 2010). There are similar potential changes in carbon budgets and pools if drought were to become more common (Breshears and Allen 2002). Exploring the future role of drought in structuring forests in the Northeast is an important arena for future research.

Conclusions

Despite presenting considerable evidence against using the Midwest models of Gustafson and Sturtevant (2013) in the Northeast, they may nevertheless have some value to predict mortality response to droughts in the Northeast, especially for species for which the Northeast models do not inspire confidence (i.e., drought-intolerant species; Figure 3B). My tests did not cover the range of drought conditions under which the models were developed because it happens that lengthy drought events were rare in the Northeast during the period of FIA record (Figure 2), and given the noisiness of the drought mortality signal, it should not be surprising that the tests were equivocal under such conditions. There is no obvious ecological or mechanistic reason why species should respond differently in an adjacent, very similar, ecological province. For applications in the Northeast, it may be prudent to use a combination of Northeast and Midwest models, for example, substituting the Midwest drought-intolerant model for the Northeast one. Accepting the Midwest models for the Northeast presumes that the failure of the Midwest models in the Northeast (Table 5) was caused primarily by low rates of drought-induced mortality because drought events were rare, short, and weak. Nevertheless, given that this presumption is uncertain, I concede that they should be used only with caution and transparency.

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