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ECOSYSTEMS

Modeling Forest Mortality Caused by Drought Stress: Implications for Climate Change

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ABSTRACT

Climate change is expected to affect forest landscape dynamics in many ways, but it is possible that the most important direct impact of climate change will be drought stress. We combined data from weather stations and forest inventory plots (FIA) across the upper Great Lakes region (USA) to study the relationship between measures of drought stress and mortality for four drought sensitivity species groups using a weight-of-evidence approach. For all groups, the model that predicted mortality as a function of mean drought length had the greatest plausibility. Model tests confirmed that the models for all groups except the most drought tolerant had predictive value. We assumed that no relationship exists between drought and mortality for the drought-tolerant group. We used these empirical models to develop a drought extension for the forest landscape disturbance and succession model LANDIS-II, and applied the model in Oconto county, Wisconsin (USA) to assess the influence of drought on forest dynamics relative to other factors such as stand-replacing disturbance and site characteristics. The simulations showed that drought stress does affect species composition and total biomass, but effects on age classes, spatial pattern, and productivity were insignificant. We conclude that (for the upper Midwest) (1) a drought-induced tree mortality signal can be detected using FIA data, (2) tree species respond primarily to the length of drought events rather than their severity, (3) the differences in drought tolerance of tree species can be quantified, (4) future increases in drought can potentially change forest composition, and (5) drought is a potentially important factor to include in forest dynamics simulations because it affects forest composition and carbon storage.

Key words: drought stress; climate change; tree mortality; forest landscape disturbance and succession model; LANDIS-II; forest biomass.

INTRODUCTION

Climate change is expected to affect forest dynamics at landscape scales through effects on growth rates of trees, the ability of new tree cohorts to become established, and altered disturbance regimes (Scheller and Mladenoff 2005). These changes will come in response to alterations in mean and extremes of temperature, precipitation, and cumulative solar irradiation (Allen and others

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2010). However, some authors suggest that the most important direct impact of climate change will likely be drought (for example, Allen and Breshears 1998). Frelich and Reich (2010, p. 372) make the claim that ''For the continued existence of a given forest, all else being equal, trees must survive the longest summer dry period that occurs at a multidecadal scale.'' Frelich and Reich (2010) also suggest that in some forested ecosystems, such as those at the northern prairie-forest border of central North America, the projected future climate (particularly drought) may dramatically alter forest composition, perhaps resulting in the conversion of forest to savanna. They offer several lines of evidence based on well-known ecological processes and their theoretic relationships to forest succession, drawing conclusions about the cumulative impacts of multiple drivers of forest dynamics.

There are a number of published studies that relate mortality rates of individual species (or forest types) to droughts of various intensity and duration in a way that could allow predictions of the landscape-scale effects of the droughts expected in the future under altered climate. A majority of these have been conducted in arid (for example, Allen and Breshears 1998), temperate (for example, Elliott and Swank1994; Pedersen 1998), or tropical ecosystems (for example, Condit and others 1995). McEwan and others (2011) associated drought reconstructions with forest composition change in the Midwest and concluded that drought-induced tree mortality was an important driver. Fewer studies have been done in the northern prairie-forest ecotone of North America, although one such study suggests that CO_2 fertilization may reduce drought sensitivity of established bur oak trees enough to delay the loss of forests at the prairie-forest ecotone in Minnesota, perhaps indefinitely (Wyckoff and Bowers 2010).

Although these studies provide quantitative estimates of drought-induced mortality rates, none has been integrated into a forest landscape model to study how change in drought regimes might impact forest composition and successional dynamics. Frelich and Reich (2010) propose a process-based model of these dynamics, but it is conceptual. A process-based simulation model that integrates the multiple drivers of forest dynamics, including drought, would provide a more robust basis for drawing conclusions.

Landscape-level impacts on forest composition and spatial pattern of altered disturbance regimes and climate are often projected by landscape-scale disturbance and succession models (LDSM) (for example, Gustafson and others 2010; Scheller and Mladenoff 2008). Drought effects are seldom explicitly modeled other than by modifying mean precipitation rates as they affect fire regimes and forest succession and growth (but see McMahon and others 2009). The effects of drought as a disturbance that causes mortality of trees are compatible with most LDSMs, but have not yet been widely implemented, presumably because of a paucity of empirical studies.

The relationship between drought stress and tree mortality can be studied empirically using the network of weather stations and the network of the US Forest Service Forest Inventory and Analysis (FIA) plots. Although the FIA inventory reliably measures mortality, it is usually difficult to determine the ultimate cause of the mortality, given that drought stress can result in death by a number of other proximal causes. Consequently, the FIA dataset includes mortality by all causes, resulting in a drought-induced mortality signal that is degraded by the noise of mortality by other ultimate causes. However, because FIA data exist at high spatial density and over a long time period (>50 years), the large number of plot observations through time should allow the drought signal to be detected. Empirical relationships derived from such analyses could be incorporated into an LDSM to improve forecasts of the response of forests to climate change.

LANDIS-II (Scheller and others 2007) is a forest LDSM that simulates forest growth processes of establishment, growth, competition and the forest regression processes of senescence and disturbances such as fire, wind, insect outbreaks, and timber harvesting at large spatial scales ($>100{,}000$ ha) and long temporal scales (centuries). The model tracks living and dead biomass within cohorts of species, and has several parameters that represent aboveground productivity and mortality. The model provides a way to formalize multiple processes that are known at the site or tree scale and project them to the landscape scale to discover potential dynamics of forest productivity, composition, and spatial pattern. LANDIS-II was designed to allow easy addition of new disturbance processes in the form of extensions (Scheller and others 2010). Such extensions simulate the mortality of species' age cohorts by simulating the ecological or physical processes that cause cohort death. Mortality caused by drought should be readily encapsulated in a new LANDIS-II extension.

Our objectives for this study were to (1) determine the relative plausibility of relationships between measures of drought stress and tree mortality for the major tree species in the upper Great Lakes region, (2) generate predictive models of drought-induced mortality as a function of drought measures, (3) develop a drought extension for LANDIS-II, and (4) assess the landscape effects of drought-induced mortality on forest composition and spatial pattern in the region using LANDIS-II.

METHODS

Following Frelich and Reich (2010), we hypothesized that tree mortality during a given time period (for example, decade) is related to the severity and duration of dry conditions that may occur during the period. We generated seven candidate prediction models of the relationship between measures of drought and tree mortality (Table 1). Five of these models reference drought events, which we defined as a period in which the mean annual PDSI was ≤ -0.5. The study area included all counties in Minnesota, Wisconsin, and Michigan that at least partially fall within the ecological Laurentian Mixed Forest Province (#212, Cleland and others 2007). This area encompasses most of the predominantly forested parts of those states (Figure 1). The climate is generally cold continental, with mean annual precipitation ranging from 51 to 94 cm and mean annual temperature ranging from 2 to 8°C (Cleland and others 2007). The topographic relief is generally flat or gently rolling, and the Great Lakes influence the climate near their shores.

Predictor Variables

To quantify drought stress, we obtained a national dataset of time bias corrected (for systematic, nonclimatic changes that bias temperature trend), monthly, divisional temperature-precipitation-drought index values from the National Climate Data Center (http://www1.ncdc.noaa.gov/pub/data/cirs/). The dataset included the calculated monthly values for the Palmer Drought Severity Index (PDSI) (Palmer 1965), the Modified Palmer Drought Severity Index (Heddinghause and Sabol 1991), and three estimates of the Standardized Precipitation Index calculated using precipitation amounts during the prior 3, 12, or 24 months (McKee and others 1995). We also calculated a measure of moisture deficit (precipitation minus potential evapotranspiration (Gustafson and others 2003) from temperature and precipitation records using the Thornthwaite method (Thornthwaite 1948).

We used this dataset to estimate drought stress for the time period between each FIA inventory (varies by state) such that tree mortality observed on an FIA plot occurred during the time period for which drought stress measures were calculated. The spatial units for the climate data were the NCDC climate divisions within each state, which more or less follow county boundaries (Figure 1). There are up to 10 climate divisions in each state. We identified the climate division in which most of a county falls, and linked all FIA plots in the county to that climate division.

Because topographic position and soil texture affect how long precipitation remains available to plants, we also considered a soil moisture predictor variable based on physiographic class data (PHYSCLCD) collected on FIA plots (Woudenberg et al. 2010). We aggregated the FIA codes into three classes ranging from 1 (xeric) to 3 (hydric).

Table 1. Candidate Prediction Models Using Drought Stress Predictor Variables to Predict Tree Mortality Rate

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 was the Palmer drought severity index (PDSI), and drought was defined as mean annual PDSI ≤ -0.5.

Response Variable

Our ultimate objective was to incorporate drought effects into the process-based LANDIS-II model, simulating the loss of biomass from species cohorts as a function of drought. Ideally, we would estimate how drought affects tree growth (aboveground net primary productivity), simulating mortality when growth falls below a critical threshold. Unfortunately, growth estimates are available for only a small percentage of FIA plots. However, biomass estimates of live and dead (since the previous inventory) trees are calculated by FIA on most plots. To quantify mortality rate, we calculated the biomass lost to mortality for each species on each FIA plot within the study area that was classified as timberland for each inventory period (~13 years). The annual proportion of biomass lost to mortality (pm) was calculated using Eq. 7 of Sheil and others (1995); $pm = 1 - [1 - (N_0 - N_1)/N_0]^{1/t}$, where, in

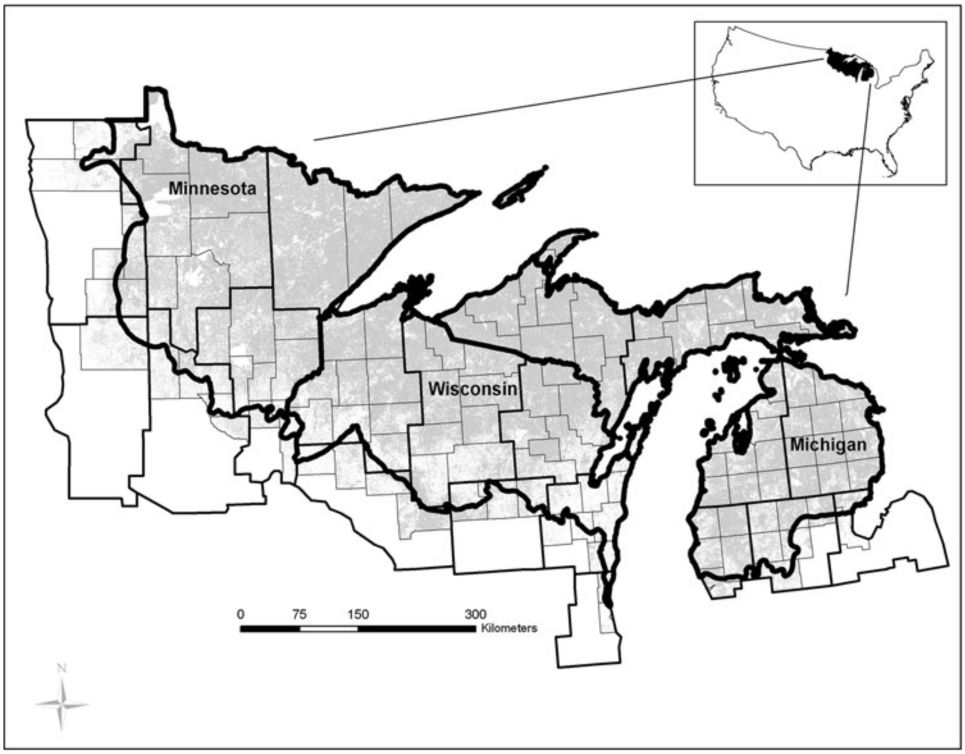

Fig. 1. Map of the study area showing the counties falling at least partly within the Laurentian Mixed Forest Province (#212). *Shading* indicates forest cover. The *heaviest lines* indicate ecological Province and state boundaries, the *intermediate lines* indicate NCDC climate division boundaries, and the *light lines* are county boundaries

our case, N_0 is the biomass of live trees (of a given species) 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 periodic mortality rates. The inventory dates used were as follows: Minnesota (1977, 1990, 2003), Wisconsin (1983, 1996, 2009), and Michigan (1980, 1993, 2004). Undisturbed plots from 1990s inventories on which growth and mortality were modeled rather than measured were omitted. Observations with less than a total of six trees of a species were also omitted. Observations in which more than 10% of the trees were harvested since the previous inventory were excluded from the analysis because it was not known if those trees were alive or dead when harvested. On plots with less than 10% cut trees, the cut trees were not included in the live or dead totals (that is, ignored). In an attempt to reduce data noise of mortality caused by factors unrelated to moisture stress, we omitted plots that were consistently wet during the inventory cycle (that is, mean PDSI $> +1.5$ and minimum PDSI > -0.5). Similarly, we omitted plots where the relative density of trees was greater than 0.6, assuming that much of the mortality on such plots was caused by self-thinning processes (Woodall and others 2005). These constraints yielded 43,665 plots suitable for the analysis.

Analysis

We computed Pearson correlation coefficients between *pm* (all species combined) on FIA plots and each of the six drought indices and the soil variable and selected the drought index with the consistently strongest correlation across states and FIA inventory cycles (PDSI). The soil variable was poorly correlated with mortality (Kendall's tau = 0.007) and was counter intuitively lowest on xeric soil; so, it was dropped from further consideration. For each FIA inventory period and NCDC climate division, we calculated (1) mean annual PDSI value, (2) minimum annual PDSI value during the period, (3) total number of years (normalized per decade) in drought status, (4) average annual severity (PDSI) of drought events, (5) average length (y) of drought events, and (6) length of the longest drought event. Because drought-induced mortality in an inventory cycle may reflect drought conditions just prior to the inventory period (Bigler and others 2007; Clinton and others 1993), we included the 2 years prior to the beginning of an FIA inventory cycle when calculating drought measures. These variables were included in the candidate models evaluated (Table 1).

We built generalized linear mixed models to predict *pm* using a 70% random subset of the FIA dataset, reserving the remainder of the dataset for

Table 2. Species Assignments to the Four Drought Sensitivity Classes

Drought-sensitivity class	Common name	Scientific name
Intolerant	Quaking aspen, big-toothed aspen, paper birch, black ash	*Populus tremuloides, P. grandidentata, Betula papyrifera, Fraxinus nigra*
Somewhat intolerant	Eastern hemlock, White spruce, Northern white cedar, yellow birch, balsam fir	*Tsuga canadensis, Picea glauca, Thuja occidentalis, Betula alleghaniensis, Abies balsamea*
Somewhat tolerant	Red maple, sugar maple, black cherry, white ash, basswood, American larch, black spruce	*Acer rubrum, A. saccharum, Prunus serotinus, Fraxinus americana, Tilia americana, Larix laricina, Picea mariana*
Tolerant	Red pine, white pine, jack pine, red oak, white oak	*Pinus rubra, P. strobus, P. banksiana, Quercus rubra, Q. alba*

model testing purposes. Based on the distribution of *pm*, we used an exponential distribution with a log link function via PROC GLIMMIX in SAS v9.3 (SAS Institute Inc 2011) to estimate the seven candidate models, choosing the best model using a weight-of-evidence approach (Burnham and Anderson 2002). All variables in the candidate models were considered fixed effects with a random intercept. We initially attempted to model each species separately, but sample sizes were too low for most species to generate satisfactory estimates, given the noisiness of the drought signal. We therefore assigned each species to one of four categories of drought sensitivity (Table 2) based on the literature (for example, Burns and Honkala 1990), expert opinion, and relationships seen in the model-building subset of the dataset, and built models for these four classes. Using the testing dataset, we regressed observed against predicted *pm* values, and used the SAS (SAS Institute Inc 2011) TEST statement in Proc REG to test ($\alpha = 0.10$) the joint hypotheses that the intercept was equal to 0.0 and that the slope was equal to 1.0 (Dent and Blackie 1979).

LANDIS-II Drought Extension

We developed a drought disturbance extension for LANDIS-II (Scheller and others 2007) that simulates loss of living biomass from cohorts by species as a result of drought-induced mortality. The extension is designed to work with a succession extension that simulates live aboveground biomass for each tree species cohort (for example, Scheller and Mladenoff 2004), allowing partial disturbance (that is, mortality that transfers live biomass to the dead biomass pool) of any given tree species cohort. At each time step, a measure of drought is drawn from a user-specified distribution. If the value of this drought variable exceeds a user-defined minimum threshold for drought effects to cause mortality, the 95% confidence interval (CI) of the predicted annual proportion of biomass lost is calculated for each species based on regression coefficients (and standard error) input by the user (see Figure 2 for examples). When the drought variable exceeds a user-defined maximum threshold, the drought variable is set equal to the maximum threshold. This feature is used to constrain the regression equation from making predictions beyond the range of the predictor variable to which the model was fit (that is, extrapolation). For each active cell on the landscape, and for each species on the cell, a value of *pm* is selected from the confidence interval using the age of the oldest cohort (calculated as a percent of the species longevity) as an index to specify a location between the lower and upper bounds of the CI. Thus, cells with the oldest cohorts nearer to longevity age will have a *pm* value found in the upper part of the CI, whereas cells with younger oldest cohorts will have a *pm* value found in lower portions. This is consistent with the observation that cohorts older than 50% of longevity (approximately) are more weakened by drought and are more susceptible to tree-killing agents such as insects and disease (Ganey and Vojta 2011; Mark Theisen, pers comm). Because the regression coefficients were estimated using non-linear link functions, back-transformation is completed after the *pm* value is selected from the CI. The extension can optionally remove the intercept term from the predicted values of *pm*. Often, the intercept represents background mortality and it may be useful to remove this background mortality to simulate only drought-related mortality. The amount of biomass removed by drought-related mortality is total species biomass times *pm*, and biomass is removed from cohorts (beginning with oldest cohort) until that amount is reached. Because drought often kills entire cohorts, in cases where the amount to be removed is at least 90% of the biomass of the oldest cohort, all of the biomass of the oldest cohort is removed. Additionally, the probability of establishment (P_{est})

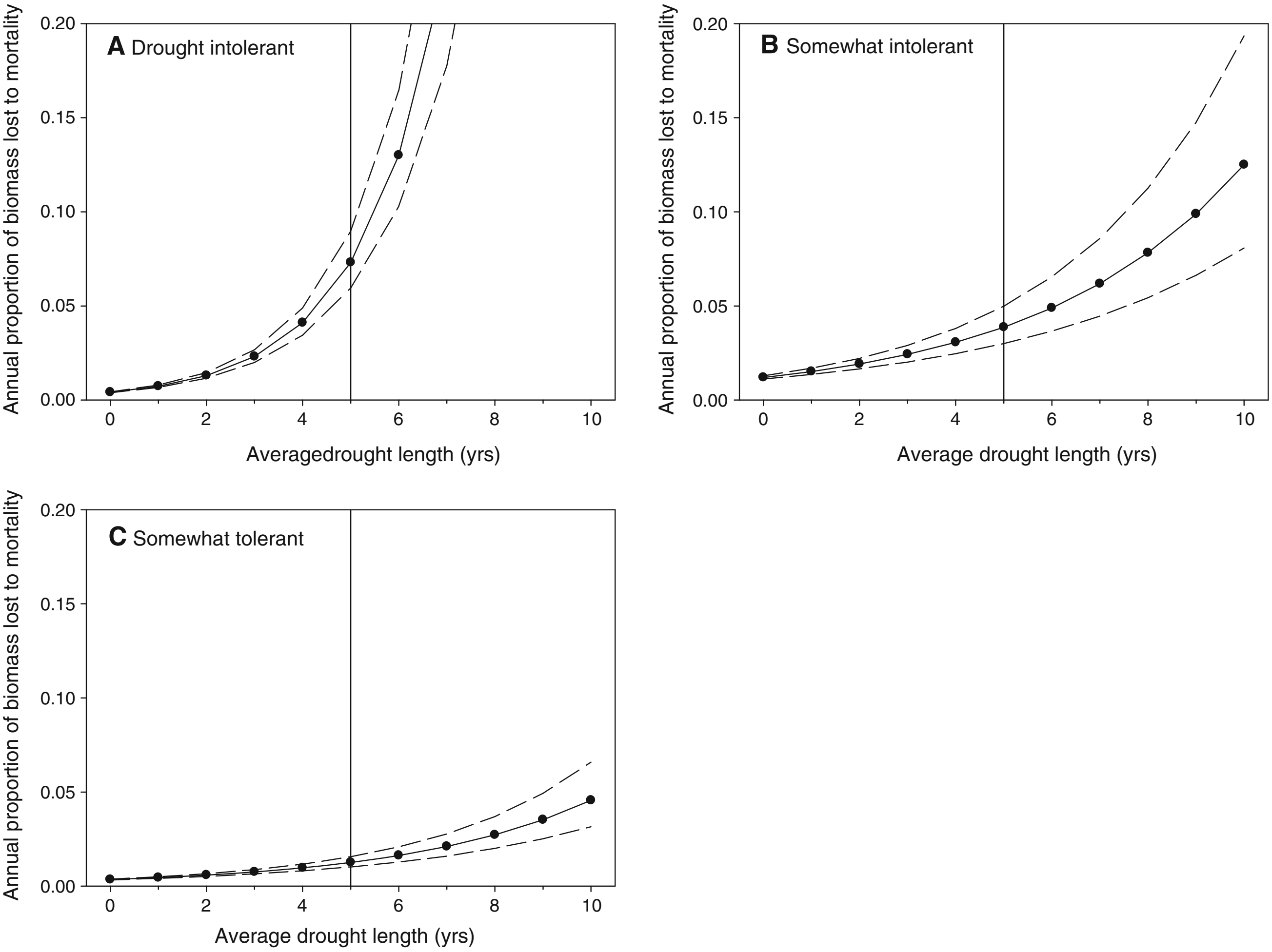

Fig. 2. Back-transformed prediction equations (Model 5) and 95% confidence intervals for the four drought tolerance classes. The model for the drought tolerant class (not shown) failed the validation test, and it was assumed that drought has no effect on mortality for that class. Average drought length values above 5.0 years (reference line) were assigned a value of 5 in the simulations to minimize extrapolation beyond the data used to fit the models

for the species is modified (for the current time step only) to 0.0 if the species has seedlings relatively sensitive to drought, and modified by half if seedlings are moderately sensitive to drought (Mark Theisen, pers comm., Hanson and Weltzin 2000). P_{est} is unchanged for species relatively insensitive to drought. This simulates the loss of seedlings to drought stress. All biomass removed from the cohorts is moved to the dead biomass pool. A log file is updated at each time step with details about the amount of biomass removed from the cohorts, and a map is generated that shows the spatial distribution of biomass removed.

Simulations

We used the drought extension to heuristically explore the effects of drought on forest composition and spatial pattern on a 65,733 ha study area centered on the Lakewood sub-district of the Chequamegon-Nicolet National Forest, located in northeastern Wisconsin, USA (Figure 3), near the prairie-forest ecotone. Forested ecosystems in the study area are strongly influenced by glacial landforms that create a sharp soil moisture gradient from west (mesic and nutrient-rich) to east (xeric and nutrient-poor). Initial conditions (cell size = 0.09 ha) were generated by Sturtevant and others (2009), and included four ''land types'' reflecting biophysical units with similar presettlement fire-return (FR) intervals determined primarily by soil conditions (Cleland and others 2004). Species parameters followed those used in other studies in the region (Table 3). We used land type-specific species growth rate values [maximum aboveground net primary productivity (MaxANPP),

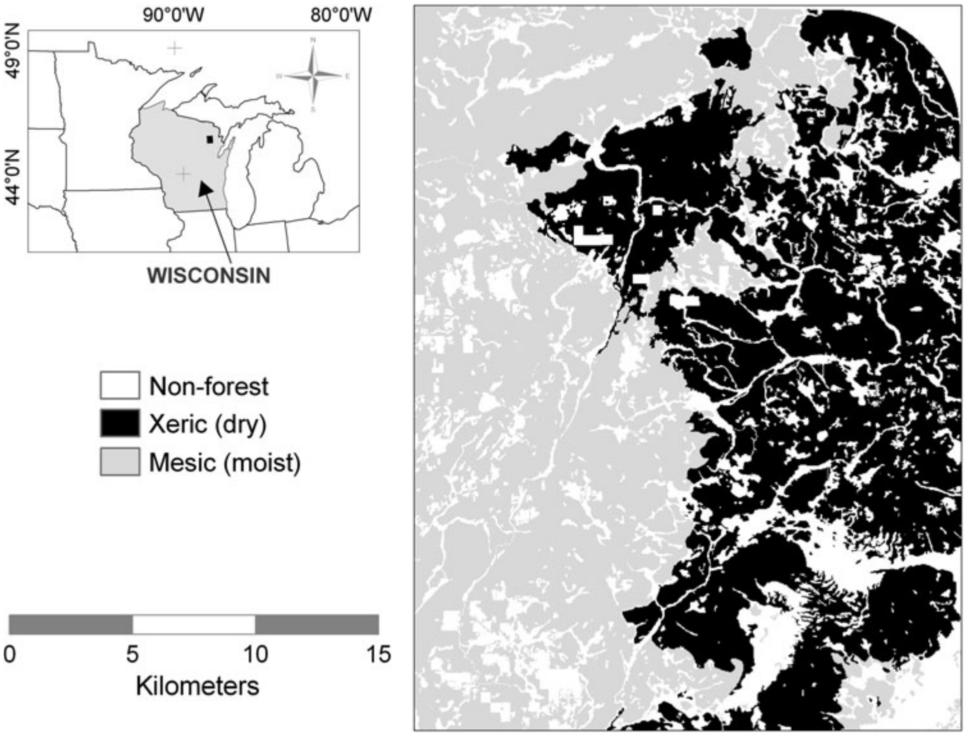

Fig. 3. Map of simulation study area in Oconto County, Wisconsin (USA)

Appendix in Supplementary Materials] from Scheller and Mladenoff (2005), selecting their ecoregions that coincided with our land type classes. We used the P_{est} values of Sturtevant and others (2009) because they were developed specifically for our study area (Appendix in Supplementary Materials).

Parameters to describe the distribution of the drought variable (average length of droughts) were estimated from the NCDC dataset described above, using data from 1900 to 2010. We conducted a two factor simulation experiment with drought and stand-replacing disturbance as main effects, with each factor either present or absent. To allow additional exploration of the importance of physiography on drought effects, a third factor (land type) was included by assigning each cell in the output maps to one of two land types (Xeric = FR1 and FR2; Mesic = FR3 and FR4, Figure 3), and evaluating land type as a fixed treatment effect. We used version 6.0 (Scheller and others 2007) of LANDIS-II and the Biomass Succession v3 (Scheller and Mladenoff 2004) and Biomass Harvest (Gustafson and others 2000) (to simulate harvest) extensions, with harvesting simulated before drought. Harvesting was simulated by removing all cohorts of all species from 5% of stands each decade, half of those stands being mature aspen/birch and the other half randomly selected. All extensions used a 10-year time step and all simulations were run for 300 years with three replicates.

Response variables were forest composition (% of each species group) (Table 4), age class composition (% of each age class), total biomass on the landscape, and mean cell ANPP. In addition, we calculated the Aggregation Index (He and others 2000) as a measure of fragmentation, where higher values indicate that pixels of the same class tend to be found adjacent to each other, and lower values indicate that adjacent pixels tend to be of a different class. We analyzed the values of response variables at the end of the simulations (year 300) with drought, disturbance, and land type (xeric or mesic) as the main fixed effects using generalized linear mixed models via PROC GLIMMIX. We included the drought × land type interaction to determine if physiography modifies any drought effect. The Kolmogorov–Smirnov test and visual examination of stem and leaf plots (UNIVARIATE procedure) were used to determine the distribution of each response variable. We used a gamma distribution and log link for all species composition response variables, an exponential distribution and log link for the age class variables and a normal distribution and identity link for all others. We evaluated the relative influence of main effects using LSMEANS and Tukey's comparisons.

Table 3. Selected LANDIS-II Species Parameter Values Used in the Simulations

Species	Seedling drought sensitivity[1]	Longevity (y)	Sexual maturity (y)	Shade tolerance[2]	Effective seed dispersal distance (m)[3]	Maximum seed dispersal distance (m)[4]
Aspen	2	90	15	1	500	5000
White ash	2	200	30	4	70	140
Black ash	3	150	20	2	100	200
Basswood	2	250	15	4	30	200
Black cherry	2	200	20	2	30	3000
Paper birch	2	100	20	2	200	5000
Cedar	3	350	30	3	45	60
Hemlock	3	450	60	5	30	100
Jack pine	2	120	10	1	30	100
Larch	2	175	35	1	50	200
Red pine	2	250	25	2	12	275
White pine	2	350	15	3	100	250
Red maple	2	150	10	3	100	200
Red oak	2	200	25	3	30	3000
Black spruce	2	200	30	3	80	200
White spruce	2	200	25	3	30	200
Balsam fir	2	150	25	4	30	160
Sugar maple	2	250	40	5	100	200
White oak	2	250	40	1	30	3000
Pin oak[5]	2	200	35	2	30	3000
Yellow birch	3	300	40	4	100	400

Drought regression parameters used were from Model 5 (Table 7).
[1] *Seedlings relatively insensitive to drought = 1, moderately sensitive = 2, sensitive = 3.*
[2] *Index of ability to establish under shade. Least shade tolerant = 1, most shade tolerant = 5.*
[3] *95% of propagules disperse within this distance.*
[4] *100% of propagules disperse within this distance.*
[5] *Pin oak was uncommon in our FIA dataset and was not used to build the drought models. It did occur on the Oconto county study site, and was assigned to the ''tolerant'' drought class.*

Table 4. Species Group Definitions Used for LANDIS-II Output

Species group	Common name(s)	Scientific name(s)
Aspen-birch	Quaking aspen, big-toothed aspen, paper birch	*Populus tremuloides, P. grandidentata, Betula papyrifera*
Northern hardwoods	Sugar maple, yellow birch, red oak, black cherry, white ash, basswood	*Acer saccharum, Betula alleghaniensis, Quercus rubra, Prunus serotinus, Fraxinus americana, Tilia americana*
Pines	Jack pine, red pine, white pine	*Pinus banksiana, P. rubra, P. strobus*
Oaks	White oak, northern pin oak	*Quercus alba, Q. ellipsoidalis*
Red maple	Red maple	*Acer rubrum*
Hemlock	Eastern hemlock	*Tsuga canadensis*
Spruce-fir	White spruce, balsam fir	*Picea glauca, Abies balsamea*
Larch	American larch	*Larix laricina*
Cedar	Northern white cedar	*Thuja occidentalis*
Wetland species	Black spruce, black ash	*Picea mariana, Fraxinus nigra*

RESULTS

Candidate model 7 was dropped from further consideration when it was discovered that collinearity between the two predictor variables caused untenable predictions (that is, mortality decreased as drought increased). For all four drought sensitivity classes, the Akaike weights showed extremely high plausibility for model 5 (Table 5). The model

Table 5. Akaike Weights (%) for Candidate Models (Table 1) of Each Species Group

Drought-sensitivity class	*N*	**Model**					
		1	2	3	4	5	6
Intolerant	13489	0.0	0.0	0.0	0.0	100.0	0.0
Somewhat intolerant	6249	0.0	0.15	0.0	0.0	99.85	0.0
Somewhat tolerant	9699	0.0	0.0	0.0	0.0	100.0	0.0
Tolerant	3892	0.0	0.0	0.0	0.0	100.0	0.0

Higher weight indicates greater plausibility for a model. Model #7 was dropped from consideration because of high collinearity between the two predictor variables. N indicates the number of FIA plots used to fit the models.

Table 6. Model Test Results Showing the Regression of Predicted Mortality Rate Against Observed Rate

Drought-sensitivity class	*N*	**Model 5**		
		Intercept (se)	Slope (se)	Prob $> F$
Intolerant	5700	0.001 (0.002)	1.041 (0.176)	**0.44**
Somewhat intolerant	2678	−0.000 (0.008)	0.994 (0.395)	**0.95**
Somewhat tolerant	4170	−0.003 (0.003)	1.37 (0.509)	**0.47**
Tolerant	1689	0.005 (0.004)	0.081 (0.522)	0.07

N indicates the number of FIA plots used to test the models. P values indicate the probability that that the joint hypotheses that the intercept = 0.0 and the slope = 1.0 could not be rejected, and bold values indicate that the model passed this test ($\alpha = 0.1$).

tests showed that all models except one passed the statistical test of model predictive ability (Table 6). The slope of the regression of observed against predicted *pm* values for drought-tolerant species was a value quite close to zero, and the test of the joint hypothesis failed ($\alpha = 0.1$).

When back-transformed, the prediction equations produced curves that show progressively less mortality from drought-intolerant species to somewhat drought-intolerant species (Figure 2). The curve for the most drought-tolerant species (not shown) was paradoxically intermediate between the drought-intolerant and somewhat drought-intolerant species, but that equation failed the model test (Table 6). We concluded that because GLIMMIX fit a spurious, insignificant curve to the data for this species group, a drought-induced mortality signal could not be reliably detected and can safely be ignored for this species group. Note that the intercept is noticeably higher for the somewhat drought-intolerant group (Figure 2B). This is likely caused by high background mortality of balsam fir, which constituted nearly half of the plots used to fit this model.

Given these results, we parameterized the drought extension using Model 5 (Table 7). The empirical distribution of the drought variable (average length of droughts) in the study area

Table 7. Univariate Predictive Models for Each Drought Sensitivity Class Based on a Measure of Drought Between FIA Inventories

Drought-sensitivity class	**Model 5**				
	Intcpt. (y)	Std error (y)	Slope (β)	Std error (β)	Predictor variable (x)
Intolerant	−5.499	0.028	0.576	0.015	Mean drt length[1]
Somewhat intolerant	−4.426	0.037	0.235	0.019	Mean drt length[1]
Somewhat tolerant	−5.668	0.031	0.258	0.016	Mean drt length[1]
Tolerant[2]	N/A	N/A	N/A	N/A	N/A

Predicted annual proportion of biomass lost to mortality (pm) is calculated (back-transformed) using $pm = EXP(y + \beta x)$.

[1] *Mean length (years) of drought events (mean annual PDSI ≤ -0.5).*

[2] *No valid predictive for drought-tolerant species was found. Assumed there was no relationship.*

during the last century was approximately lognormal with $\mu = 0.3$, $\sigma = 0.7$. We set the minimum threshold for the drought variable to 1.0. The longest mean drought length in our model-building dataset was 4.0 years, so we set the maximum threshold to 5.0 years (see Figure 2), allowing extrapolation of the mortality function by only one year. Droughts exceeding 5 years were rare over the last century. We activated the removal of the background mortality option. Drought mortality was not simulated for the drought-tolerant species.

Simulation Results

The DROUGHT treatment was significant for four of the species groups (Table 8). Aspen-birch was more abundant under drought conditions, whereas northern hardwoods were negatively impacted, and the change in abundance caused by drought appears to accelerate over time (Figure 4). The drought-tolerant pines did marginally better and the oaks (white and pin oak) significantly better under drought conditions, although their abundance was very low by the end of the simulations. The somewhat drought-tolerant red maple also did significantly better under drought conditions. The DROUGHT treatment tended to reduce the oldest age class and increase younger ones as expected, but the tendency was not significant (Table 8). DROUGHT did not significantly affect the aggregation of age classes. DROUGHT significantly reduced live biomass on the landscape, and slightly increased mean aboveground productivity, but not significantly so (Table 8; Figure 5).

DISTURBANCE generally had an intuitive effect on species composition and age class, positively affecting species favored by disturbance and increasing the abundance of younger age classes at the expense of the oldest age classes (Table 8). DISTURBANCE also reduced aggregation and significantly reduced biomass on the landscape and ANPP.

The LAND TYPE treatment generally had a significant and intuitive effect on northern hardwoods, pine, and oaks. The other species were more common on more droughty land types, but they were also more common there at the start of the simulations. The LAND TYPE treatment also significantly impacted two age classes and the aggregation measures, although there is no clear mechanism to expect there to be such an effect. This may also be an artifact of the initial conditions because most of the differences are similar to those seen at time step = 0. The mesic LAND TYPE treatment produced significantly higher amounts of biomass and ANPP than the xeric. The DROUGHT-LAND TYPE interaction was significant for only % aspen-birch, % oaks, % spruce-fir, AI-species, and total biomass.

DISCUSSION

Assumptions

Several important assumptions were made for this study. (1) We assumed that a drought-induced mortality signal could be detected in the presence of many other mortality factors by the large number of observations in the FIA dataset. The fact that the same model was the most plausible for all drought tolerance classes, and that the resulting equations predicted greater mortality as putative drought tolerance decreased, suggests that this assumption was valid. (2) By pooling all FIA plots across the region, we assumed that drought and mortality relationships are similar across major portions of each species' range. We did not test this assumption, but signal noise may have been greater because of it. (3) In our LANDIS-II drought extension, we assumed that the oldest trees are the most susceptible to drought-induced mortality, and therefore our model removes biomass starting with the oldest cohort and working toward progressively younger cohorts. This assumption was based primarily on expert opinion and may not hold in other ecosystems.

Insights

Our results produced several important insights. (1) Average dryness (mean or min. PDSI) is not as important as the characteristics of drought events to predict tree mortality. This is seen in the lack of plausibility for Models 1 and 2 (Table 5). (2) Severity of drought (Model 4) is not as important as length of drought (Model 5). We suspect that the various drought length measures are perhaps interchangeable as predictive variables because many of them are highly correlated. (3) The relationship between length of drought and biomass loss to mortality is non-linear, where mortality increases at an ever faster rate as the length of a drought increases. (4) Although the DROUGHT treatment was significant, the magnitude of the effect was relatively low. The largest effect was on the abundance of northern hardwoods, where DROUGHT reduced abundance by 7% over 300 years. The significant effect of DROUGHT on total biomass was stable through simulated time (Figure 5). The insignificant positive effect of DROUGHT on ANPP (Table 8; Figure 5) is likely

Table 8. GLIMMIX Results for Selected Response Variables at the End of the Simulations (year 300)

Response variable	DROUGHT			DISTURBANCE			LAND TYPE			Inter-action
	Present (LSmean, se)	Absent (LSmean, se)	Pr > *F*	Present (LSmean, se)	Absent (LSmean, se)	Pr > *F*	Mesic (LSmean, se)	Xeric (LSmean, se)	Pr > *F*	Pr > *F*
% Aspen-birch	1.01 (0.09)	0.68 (0.06)	0.006	49.91 (1.52)	0.01 (0.00)	≤ 0.001	0.65 (0.06)	1.06 (0.10)	≤ 0.001	0.04
% Northern hardwood	23.65 (0.53)	30.65 (0.68)	≤ 0.001	20.81 (0.46)	34.82 (0.78)	≤ 0.001	54.57 (1.22)	13.28 (0.30)	≤ 0.001	0.46
% Pines	28.19 (1.79)	24.77 (1.57)	0.166	17.55 (1.12)	39.78 (2.55)	≤ 0.001	18.50 (1.18)	37.73 (2.41)	≤ 0.001	0.11
% Oaks	0.19 (0.02)	0.12 (0.01)	0.001	0.42 (0.04)	0.05 (0.00)	≤ 0.001	0.03 (0.00)	0.76 (0.06)	≤ 0.001	< 0.01
% Spruce-fir	2.53 (0.19)	2.31 (0.17)	0.387	1.70 (0.13)	3.43 (0.26)	≤ 0.001	1.21 (0.09)	4.81 (0.36)	≤ 0.001	< 0.01
% Hemlock	0.02 (0.00)	0.02 (0.00)	0.474	0.02 (0.00)	0.03 (0.00)	≤ 0.001	0.01 (0.00)	0.05 (0.00)	≤ 0.001	0.47
% Red maple	3.76 (0.42)	2.20 (0.25)	0.003	4.23 (0.49)	1.96 (0.23)	≤ 0.001	1.12 (0.13)	7.38 (0.86)	≤ 0.001	0.54
% (1–40 years)	0.44 (0.13)	0.44 (0.13)	0.987	19.31 (5.58)	0.01 (0.00)	≤ 0.001	0.42 (0.12)	0.46 (0.13)	0.841	0.95
% (41–100 years)	2.91 (0.86)	1.51 (0.45)	0.141	22.56 (6.79)	0.20 (0.06)	≤ 0.001	1.27 (0.37)	3.47 (1.02)	0.029	0.46
% (101–140 years)	12.22 (3.55)	6.76 (1.96)	0.168	25.94 (8.00)	3.18 (0.98)	≤ 0.001	4.69 (1.44)	17.60 (5.39)	0.009	0.92
% (141–180 years)	10.73 (3.11)	7.88 (2.28)	0.461	8.54 (2.56)	9.90 (2.96)	0.740	6.24 (1.86)	13.54 (4.03)	0.090	0.74
% (> 180 years)	42.60 (12.30)	51.19 (14.78)	0.658	26.71 (7.73)	81.64 (23.64)	0.014	59.98 (17.36)	36.36 (10.52)	0.238	0.93
AI-species[1]	0.169 (0.006)	0.184 (0.006)	0.082	0.133 (0.006)	0.220 (0.006)	≤ 0.001	0.209 (0.006)	0.143 (0.006)	≤ 0.001	0.02
AI-age class[2]	0.191 (0.010)	0.215 (0.010)	0.115	0.136 (0.010)	0.271 (0.010)	≤ 0.001	0.251 (0.010)	0.155 (0.010)	0.878	0.88
Total biomass (Mg/ha)[3]	334.3 (1.22)	353.7 (1.22)	≤ 0.001	327.2 (1.22)	360.8 (1.22)	≤ 0.001	387.3 (1.22)	300.6 (1.22)	≤ 0.001	< 0.01
ANPP (g/m^2/years)[4]	1003.9 (9.50)	996.0 (9.50)	0.567	964.3 (9.50)	1035.6 (9.50)	≤ 0.001	1047.5 (9.50)	952.4 (9.50)	≤ 0.001	0.62

Columns contain back-transformed least squares means and associated standard errors for the levels of the main treatment effects via Tukey adjustments. The significance of the Drought x Land type interaction is given in the last column.

[1] *Aggregation Index calculated from species maps. Unitless value ranging from 0.0 (pixels never adjacent to a similar pixel) to 1.0 (pixels always adjacent to a similar pixel).*

[2] *Aggregation Index calculated from maps of oldest age cohort on each cell.*

[3] *Mean total biomass of map cells.*

[4] *Mean total aboveground net primary productivity of map cells.*

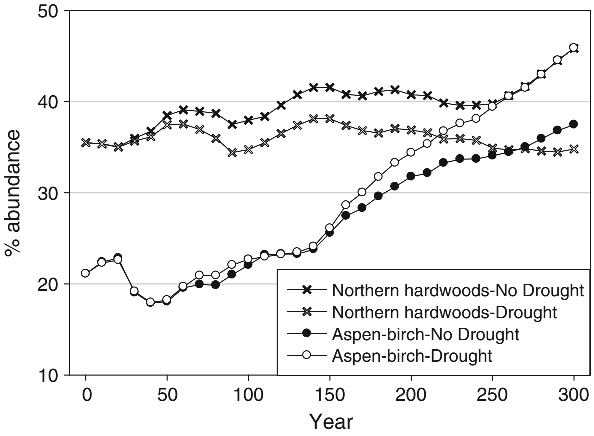

Fig. 4. Effect of DROUGHT on the relative abundance of northern hardwoods and aspen-birch through simulated time, on mesic soil and with harvesting. Lines represent the mean of three replicates, and standard deviations were generally less than the width of the symbols

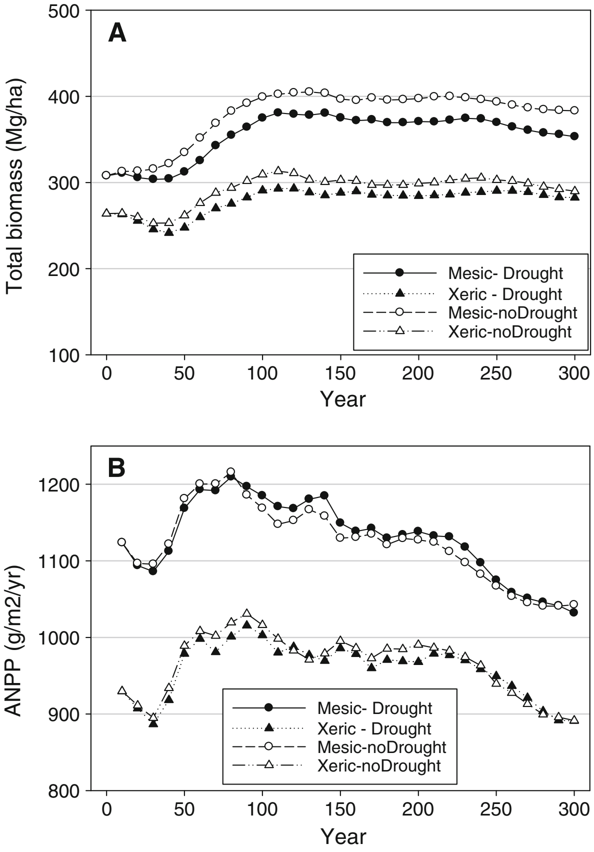

Fig. 5. Effect of DROUGHT and LAND TYPE on **a** total biomass and **b** ANPP through simulated time, with harvesting simulated. *Symbols* represent the mean of three replicates, and standard deviations were less than the width of the symbols

related to mortality in the oldest age class and concurrent increases in more productive younger age classes. Despite these modest effects, our study suggests that where drought increases in the future, forest composition and biomass may gradually change because of relative differences in drought tolerance among species. (5) The lack of correlation between soil drainage class and drought-induced tree mortality suggests that trees tend to be adapted to the soils on which they occur. However, we did not explore this in depth, and this may warrant further study.

Simulation Results

In terms of species, DROUGHT negatively affected northern hardwoods, which include some drought-intolerant species (Table 2). However, it positively affected the drought-intolerant aspen-birch, likely because these species regenerate after being killed by all but the most severe of droughts (Burns and Honkala 1990; Worrall and others 2010) and colonize other sites opened up by drought mortality. The drought-tolerant oaks and pines were either unaffected or positively related to drought, and the somewhat tolerant red maple was positively related to drought, as expected. The somewhat drought-intolerant hemlock was surprisingly not affected by drought, but its abundance may have been too low for an effect to be detected. DISTURBANCE affected all species groups, positively affecting pioneer species and negatively affecting disturbance-sensitive species. The exception may be the pines, but the three species of pines in this class each had a different shade tolerance. The LAND TYPE treatment had the expected effect on northern hardwoods, pines, and oaks. The other species groups were more abundant on xeric land types than expected at the end of 300 years; but, compared to the initial conditions map, only aspen-birch and pines increased in abundance there. The drought by land type interaction was significant for several species groups, suggesting that land type indeed may play an exacerbating or ameliorating role in the response of species to drought by affecting the competitive interactions among species.

DROUGHT and DISTURBANCE tended to decrease aggregation (that is, lower AI values). Aggregation was lower on xeric land types, but it was also lower in the initial conditions map. Drought mortality was simulated independently on each cell (spatially random), so it is not surprising that it tended to disaggregate the landscape. DISTURBANCE decreased landscape biomass and ANPP by killing live, productive biomass. Total biomass and ANPP were higher on mesic soils, reflecting the higher growth rates of most species on these soils.

Our simulations were not designed to test the Frelich and Reich (2010) hypothesis that forests in the region may convert to savanna under future climate. We did not include important processes such as fire. However, our results provide support for the idea that drought is an important process to include in forest landscape models because drought sensitivity significantly varies by species and therefore affects forest composition. We also did not include the capability to vary drought effects spatially in our drought extension (for example, across climate divisions or landforms), but such a capability can easily be added.

Comparison to Other Studies

There are several studies in other ecosystems that document tree mortality rates that presumably were drought induced, but there seem to be few data from temperate mixed forests to compare to our results. Mortality rates of southeastern oak species after a severe drought in Georgia were only modestly higher than those our models predicted for white and northern red oak (Elliott and Swank 1994). Koepke and others (2010) also found that drought effects vary by species in northern Arizona. Similar to our findings, Guarin and Taylor (2005) found that extended drought length (2–5 years) was necessary to trigger tree mortality in Yosemite National Park (California, USA). Contrary to our findings, Hogg and others (2008) found that drought-induced aspen mortality in western Canada was primarily related to drought severity. Pedersen (1998) also found drought severity to be the most important factor related to drought-induced mortality in oak forests of the southern Midwest. Fensham and others (2012) related forest biomass mortality to drought in mulga forests of eastern Australia and not only found mean rainfall to be the most important predictor, but also found the effect of soils to be minor.

Remaining Uncertainties

Predicting drought-induced mortality is inherently difficult (Breshears and others 2009). Trees rarely die directly of moisture deprivation, but drought stress makes them susceptible to death by other agents (Manion 1981; Raffa and others 2008; Ganey and Vojta 2011). Genetic factors also play a role (Cobb and others 1994). Consequently, there is a great deal of stochasticity in drought-induced mortality. Furthermore, our study examined drought at the scale of FIA inventory cycles (~ 13 years) and was unable to link mortality to drought events that may have occurred much earlier (Pedersen 1998). Similarly, the years we studied did not include exceptionally severe or prolonged droughts, so our models may not perform well under such conditions. Our models presumably detected the drought-induced mortality signal from the noise of all the other factors that kill trees, but it is unreasonable to expect that model predictions will perform well for individual forest stands during individual drought events because they predict mean responses. However, for the purpose of stochastically modeling drought mortality over large areas and long time periods, the models should have good utility. Our results are directly applicable to the forests of Province 212 in the upper Midwest. They may also be applicable in similar Provinces (for example, #211 in the northeast US), but this should be tested. Certainly, our methods can readily be extended to other regions. Our results suggest that predictions of the effects of changing climate can be improved by accounting for the effects of drought stress.

Although our analysis indicated that each drought tolerance class has a unique susceptibility to drought as evidenced by unique regression coefficients, the uncertainty in those parameter estimates is high. Furthermore, we cannot rule out the possibility that all species respond in the same way, although this seems unlikely given what we know about the ecology of these species. The tests of each regression model are also somewhat uncertain because of high variability. We believe that most of this uncertainty is caused by the fact that mortality from many causes is included in the FIA data. Nevertheless, the relative susceptibility to drought of these species is consistent with that from other sources [for example, silvics manual (Burns and Honkala 1990)]. It should be noted that the drought extension of LANDIS-II allows the use of regression equations based on theoretic considerations. For example, the curves in Figure 2 could easily be replaced with generic curves that produce a different transition from a high mortality effect (for example, Figure 2A) to a low mortality effect (Figure 2C).

Our study suggests several questions needing further study. (1) How (and when) does soil drainage class modify the probability of mortality from drought? (2) Do the relationships we found in the upper Midwest hold elsewhere? (3) Will this approach work in other biomes? (4) Can the noisiness of the drought signal in FIA data be reduced further?

CONCLUSIONS

From our study, we can conclude that (for the upper Midwest) (1) a drought-induced tree mortality signal can be detected using FIA data, (2) tree species respond primarily to the length of drought events rather than their severity, (3) the differences in drought tolerance of tree species can be quantified, (4) where climate change results in more drought in the future, forest composition has the potential to gradually change because of these differences in drought tolerance among species, and (5) drought is a potentially important factor to include in forest dynamics simulations because it affects species' composition and, potentially, forest spatial pattern. (6) This study represents an important first step to add drought-induced mortality to forest landscape models. Because LANDIS-II extensions are open source, refinements can readily be made as our understanding improves.

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