Forest Ecology and Management 345 (2015) 56–64

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Long-term droughtiness and drought tolerance of eastern US forests over five decades

Matthew P. Peters [a,*], Louis R. Iverson [a], Stephen N. Matthews [a,b]

[a] Northern Research Station, USDA Forest Service, Delaware, OH, United States
[b] School of Environment and Natural Resources, The Ohio State University, Columbus, OH, United States

ARTICLE INFO

Article history:
Received 7 November 2014
Received in revised form 5 February 2015
Accepted 14 February 2015
Available online 7 March 2015

Keywords:
Cumulative drought severity index
Forest composition
Palmer Drought Severity Index
SDM

ABSTRACT

Droughts can influence forest composition directly by limiting water or indirectly by intensifying other stressors that affect establishment, growth, and mortality. Using community assemblages of eastern US tree species and drought tolerance characteristics assessed from literature, we examine recent drought conditions in relation to the spatial distribution of species and their tolerance to drought. First we calculate and compare a cumulative drought severity index (CDSI) for the conterminous US for the periods 1960–1986 and 1987–2013 using climate division Palmer Drought Severity Index (PDSI) values and a gridded self-calibrated PDSI dataset. This comparison indicates that drought conditions in the East tend to be less frequent and generally less severe than those in the West, and that the West has had a large increase in CDSI values in the latter period. Then we focus on the past and potential future role of droughtiness in eastern forests, which are relatively more diverse than western forests but have individual species that are uniquely affected by drought conditions. We found that eastern US forests tend to be relatively balanced in the composition of drought-tolerant and -intolerant species and that drought conditions are relatively uncommon in the East. Understanding the composition and distribution of drought tolerance levels within forests is crucial when managing for the impacts of drought (e.g., managing for survival), especially given the expected rise of drought in the future.

1. Introduction

The phenomenon of drought has been widely studied (Palmer, 1965; McKee et al., 1993; Paulo and Pereira, 2006), along with its impacts on forests (McKenzie et al., 2001; Breshears et al., 2005; Allen et al., 2010; Kardol et al., 2010; Pederson et al., 2014). Various studies have also sought to further our knowledge of drought tolerance levels (e.g., indications of stress and survival rates) among tree species (Niinemets and Valladares, 2006; McDowell et al., 2008; Williams et al., 2013). However, few studies have examined the relationship between spatial distributions of drought-tolerant trees and drought occurrences within the US (Hanson and Weltzin, 2000; Gustafson and Sturtevant, 2013; Russell et al., 2014).

Drought conditions in the US are often aggregated and reported at climate divisions; subdivisions of each state into 10 or fewer units, often defined by county lines (Guttman and Quayle, 1996). These climate divisions average observations among weather stations to account for missing and incomplete data, and are widely used in ecological and meteorological models. However, gridded datasets have an advantage over aggregated observations in that conditions are not averaged across large areas (Abatzoglou, 2013). Thus, by using gridded data from sources such as the PRISM Climate Group, which interpolates values among observations using a Parameter-elevation Regressions on Independent Slopes Model (PRISM) (Daly et al., 2008), drought conditions can be defined for each grid cell.

Several studies have shown differences in drought conditions when assessed at the climate division versus the station or grid cell (Wells et al., 2004; Heim, 2006; Sullivan, 2013). These differences suggest that by aggregating climate conditions to larger areas such as climate divisions, local detail is often lost or misrepresented as a regional mean. Therefore, gridded datasets should be more representative of local conditions than regionally aggregated values.

Drought indices like Palmer's provide a representative value at a particular location (i.e., climate division or grid cell) for a referenced period (i.e., weekly or monthly). Thus, analyzing conditions among locations for extended periods can require a time series analysis approach, although, there may be instances when a single integrated metric is desired. Accumulating conditions based on the frequency of occurrences for a period can provide a simplified value in which comparisons and change detection analyses can be quickly performed.

* Corresponding author.
E-mail address: matthewpeters@fs.fed.us (M.P. Peters).

http://dx.doi.org/10.1016/j.foreco.2015.02.022
0378-1127/

Droughts have occurred in nearly all US forests and tree species are adapted in diverse ways to drought conditions, which may be seasonal, annual, or multi-annual in length (Hanson and Weltzin, 2000). These periods of limited water availability can place considerable stress on individuals, which may already be under pressure from competition (native and non-native), disease, insect infestation, and pollution (Grant et al., 2013). Timber harvesting and changes in land use put additional pressure on forests. In response to these amalgamated factors, forest types of the eastern US have undergone many changes, particularly in the extent of timberland. For example, between1952 and 1997: in the North – maple-beech-birch doubled, oak-pine increased, oak-hickory and pine were stable, while aspen-birch, lowland hardwoods, and spruce-fir decreased; in the South – oak-pine and upland hardwoods increased while lowland hardwoods and pine decreased; in the eastern portion of the Great Plains – hardwoods and non-pine softwoods increased (Alig and Butler, 2004). Though the extent of forest types has changed as a result of many factors and conditions, this paper focuses on the potential influence of drought trends on forest composition over the past half century.

To examine the droughtiness and drought tolerance of eastern US forests, we first use climate divisions and a gridded PDSI dataset to calculate a cumulative drought severity index (CDSI) and identify differences among values. Second, we use gridded climate data from PRISM to parameterize a self-calibrated (sc) PDSI algorithm developed by Wells et al. (2004) to examine recent drought conditions in the eastern US. Finally, we compare the distributions of modeled suitable habitat and drought tolerance for 134 tree species to drought conditions during 1961–2012. Mapping the distribution of drought-tolerant and -intolerant species enables us to assess recent trends in drought severity and consider how the species' tolerance within the forest communities may influence impacts from drought events. This effort provides a baseline to begin to understand if the signal of drought during recent decades has influenced the composition of forests in the eastern US.

2. Methods

2.1. Palmer Drought Severity Index

The Palmer Drought Severity Index (PDSI, Palmer, 1965) describes the relative moisture supply of a location derived from precipitation and temperature data. It was originally developed using data from central Iowa and western Kansas to empirically derive values for the water balance coefficients. A recent improvement to the original PDSI equation calibrates climate variables to long-term conditions for a location of interest, or for individual grid cells across a region. This self-calibration process (scPDSI) accounts for local climate trends and generates values that can be compared among regions.

PDSI values were obtained from two sources: the National Climatic Data Center (NCDC), which reports values at climate divisions (NCDC, 2014), and the Western Regional Climate Center's WestWide Drought Tracker (WWDT), which provides a gridded dataset derived from a self-calibration process (Abatzoglou, 2013). WWDT scPDSI data are calculated using the Wells et al. (2004) algorithm and parameterized with PRISM climate data and soil available water-holding capacity from state soil survey geographic data. The gridded data have a resolution of 2.5″ (~4 km), and a calibration period as the full length of record (i.e., 1895–present).

2.2. Cumulative drought severity index for the conterminous US

We used data from both PDSI sources to calculate a cumulative drought severity index (CDSI). The frequency of monthly PDSI conditions, defined using NCDC (2014) classes for drought, where values of −2.0 to −2.99 indicate moderate, −3.0 to −3.99 are severe, and ⩽−4.0 are extreme, received a weight of 1, 2, or 3, respectively. These weighted occurrences were summed over the periods of 1960–1986 and 1987–2013 and mapped by climate divisions and ~4 km grid cells. Additionally, a mean CDSI was calculated for each climate division from the gridded data (Supplemental Table S1), and then divisional values from both datasets were aggregated to a single mean value for each state. The change in value from the 1960–1986 to the 1987–2013 periods was calculated as a percentage to examine the trend among periods and datasets.

2.3. Drought characteristics in the eastern US, 1961–2012

We calculated scPDSI values for 20 × 20 km grid cells that spatially corresponded to modeled tree species' habitat, as derived from USDA Forest Service Forest Inventory and Analysis (FIA) data (Iverson et al., 2008). The scPDSI algorithm (Wells et al., 2004) was parameterized with (1) soil available water supply to a depth of 150 cm, derived from Natural Resources Conservation Service (NRCS) county soil geographic survey data (NRCS, 2009) prepared using methods described in Peters et al. (2013); (2) latitude from the grid's centroid; (3) monthly precipitation; and (4) temperature values obtained from PRISM climate data (PRISM Climate Group, 2012) at a 4 km resolution for the period 1961–2012 (rather than the full length of record as with the WWDT data). Climate values were aggregated from the 4 km resolution by taking the mean values of precipitation and temperature that intersected the 20 km grids. Additionally, monthly mean temperatures were averaged for the 52 year period and used as a climate normal for the calibration process.

The scPDSI algorithm was designed to process data for a specific location; thus to generate gridded output, the parameters had to be updated at each location. Python code was used to extract values from raster data, update the parameter files, run the scPDSI algorithm, and copy output files. Individual output files for each grid were compiled into an eastern US dataset and the frequency, duration of longest consecutive period, and mean interval of each PDSI class were calculated from monthly values. The frequency of each PDSI class was graphed by decade and mapped for the period May–September along with duration.

2.4. Tree species drought tolerance in the eastern US

Using FIA data for the period 1980–1993, Iverson et al. (2008) modeled the distributions of potential suitable habitat in the eastern US based on importance values (IVs) derived from the relative number of stems and basal area of species reported at survey plots for 134 tree species. IVs represent a species' relative abundance and were averaged among plots contained within each 20 × 20 km cell (Iverson et al., 2008), therefore combining IVs from individual species provides a way to examine the probable composition of species within a grid cell. Potential habitat suitability (IV > 0) modeled under the 1961–1990 climate normals define the current habitat distributions of eastern tree species in this analysis.

Species' characteristics related to drought tolerance were used to develop two maps of species drought tolerance across the eastern US. Each species was scored from −3 (very drought intolerant, DIT3) to +3 (very drought tolerant, DT3) based on a literature review of its overall habitat range (Matthews et al., 2011) (Supplemental Table S2), and this score was multiplied by the IV of each species within each grid cell to derive a weighted IV. These weighted IVs were summed among species for each of the three drought tolerance and three intolerance classes within a cell to classify the underlying forest as dominantly tolerant (1,2,3), intolerant ($-3,-2,-1$), balanced, or mixed. Cells were assigned 'tolerant' if the greatest absolute value among the weighted IV sums was from the tolerant class, and likewise for 'intolerant'; 'balanced' was assigned if the sum was within ±5% of half the total sum of the weighted IVs. 'Mixed' was assigned if the maximum absolute value was shared (tied) among multiple classes. Using the dominant tolerance class, we mapped the distribution of drought tolerance for the overall forest species composition of each cell for the eastern US. In this calculation, the final class is often determined by a single or relatively few common species. For a second view of overall tolerance to drought, which better considers all species, tolerance classes were normalized to account for all species having suitable habitat within a cell by adding the weighted IV sums of each tolerance class ($-3,-2,-1,1,2,3$), and then dividing the total weighted IV sum by the unweighted IV sum of each species.

$$N_{\text{class}} = [(\text{IV}_{\text{DIT1}} * -1) + (\text{IV}_{\text{DIT2}} * -2) + (\text{IV}_{\text{DIT3}} * -3) + (\text{IV}_{\text{DT1}}) + (\text{IV}_{\text{DT2}} * 2) + (\text{IV}_{\text{DT3}} * 3)]/\text{IV}_{\text{sum}}$$

Defining the drought class based on the dominant potential habitat allows us to examine how the dominant tree species could be affected by drought conditions. Including all potential species' habitats provides information on how the forest might be affected as a community.

Drought tolerance classes for each 20 km grid were used to analyze trends related to drought conditions based on calculated scPDSI values. The frequency of PDSI-derived drought and near normal conditions was calculated and mapped. These data are summarized at the state level in Supplemental Table S3.

3. Results

3.1. Cumulative drought severity index for the conterminous US

CDSI values represent the overall droughtiness during a period, and based on CDSI values using the NCDC climate divisions and the WWDT gridded scPDSI values (Fig. 1), 35–36 states had greater CDSI values during the 1987–2013 period as compared to the 1960–1986 period (Table 1). Mean CDSI values from WWDT gridded scPDSI values were generally lower than those from NCDC data with the exception of 13 states during the 1960–1986 period and 12 states during the 1987–2013 period. A paired *t*-test of CDSI values confirmed that the mean differences between datasets and between periods were significant ($P < 0.04$). Between the two periods, based on NCDC data, 33 states experienced increases in CDSI values while 15 decreased. Based on gridded scPDSI values, 25 states had increased mean CDSI values whereas 23 decreased. The percent change among states ranged from a decrease of 83% (Massachusetts) for climate division data and 79% (Rhode Island) for gridded mean CDSI values to increases of 286% (Arizona) and 341% (South Carolina) for climate division data and gridded mean CDSI values, respectively (Table 1). Regardless of the source of data, the eastern US had lower CDSI values than the West, and between the two periods, the West has shown a much larger increase in CDSI values compared to the East (Peters et al., 2014).

3.2. Drought characteristics in the eastern US, 1961–2012

The frequency (Figs. 2 and 3), duration of the longest consecutive period (Fig. 4) and mean interval (Supplemental Table S3 and Fig. S4) of each drought severity class calculated from scPDSI values at 20 km grids indicate that, for most of the 1961–2012 period, the eastern US experienced near normal conditions. However, the frequency of near normal conditions decreased during the 1990s and continued to decrease through the end of the period of analysis (Fig. 2), at which time increases in both wet and dry conditions have been reported. Extreme drought was very rare, never occupying more than about 5% of the region (primarily during the 1960s); however, after three decades of very low levels of extreme drought (<2% of the region), the 2000s have witnessed a rise in classes both of extreme drought and of extremely moist conditions (Fig. 2). The greatest frequency of near normal conditions during the growing season (May–September) occurred within the western Great Lake states, in Iowa, and along the New England coast (Fig. 3). Frequencies of drought conditions tended to be widely dispersed across the region and localized as severity increased from moderate to extreme (Fig. 3). The duration of the longest consecutive number of months within any particular class of drought provides a glimpse of the nature of droughts in the past decades. Most are short (<6 months), though conditions lasting longer than 24 months have been distributed across the eastern US (Fig. 4). This pattern is similar to that of the conterminous US mentioned previously, in which the West has had greater CDSI values in recent decades.

3.3. Tree species drought tolerance in the eastern US

Among the 134 tree species used to examine the relationship between potential forest composition and recent drought conditions, 5, 40, and 43 species were intolerant to drought (DIT classes 3, 2, 1, respectively), while 26, 15, and 5 were tolerant to drought (DT classes 3, 2, 1, respectively) (Supplemental Table S2). Drought tolerance calculated from the dominant composition of tree species' habitat indicates that most of the eastern US falls into drought intolerant class 2 (DIT2, 45.9%), followed by Balanced (19.5%), and drought tolerant classes comprising 6, 11.5, and 12.5% (DT1, DT2, DT3, respectively) (Fig. 5A). The remaining classes of DIT1, DIT3, and Mixed cover less than 4.6% of the region. Though the classification in this map is based on multiple species within the tolerant/intolerant class contributing to the dominance, the assignment might be driven largely by a single or few species.

Accounting for the tolerance of all species with suitable habitats (i.e., IV > 0) within a weighted averaging approach greatly generalized the results, with 48% of the eastern US as having a balanced composition (Fig. 5B). Of the remaining area, most was either somewhat tolerant (DT1; ≈18%) or somewhat intolerant (DIT1; ≈29.8%). All of the more severe classes combined occupied only 4.2% of the area.

3.4. Combining drought conditions with species tolerance

Examining the recent drought conditions against the current distributions of tree species revealed that eastern forests, whether defined by the dominant class (Fig. 5A) or including all species (Fig. 5B), have all faced mainly near normal conditions (Fig. 6). Using the dominant species classification, intolerant class 2 (DIT2) represents ~46% of the eastern US, but experienced conditions similar to the other classes. Intolerant class 3 (DIT3) experienced slightly more normal conditions than the other classes (Fig. 6A). However, using all species to define drought tolerance, the DIT3 class had the smallest area of normal conditions and the largest area of moderate and severe (Fig. 6B). The source of these differences is the number of grids assigned to each class and the underlying modeled habitat. With the dominant definition, DIT2 and Balanced account for 65% of the East, whereas Balanced and DIT1 constitute 77% based on all species.

4. Discussion

Understanding the implications of long-term persistent drought conditions is important as we witness the drastic impacts that

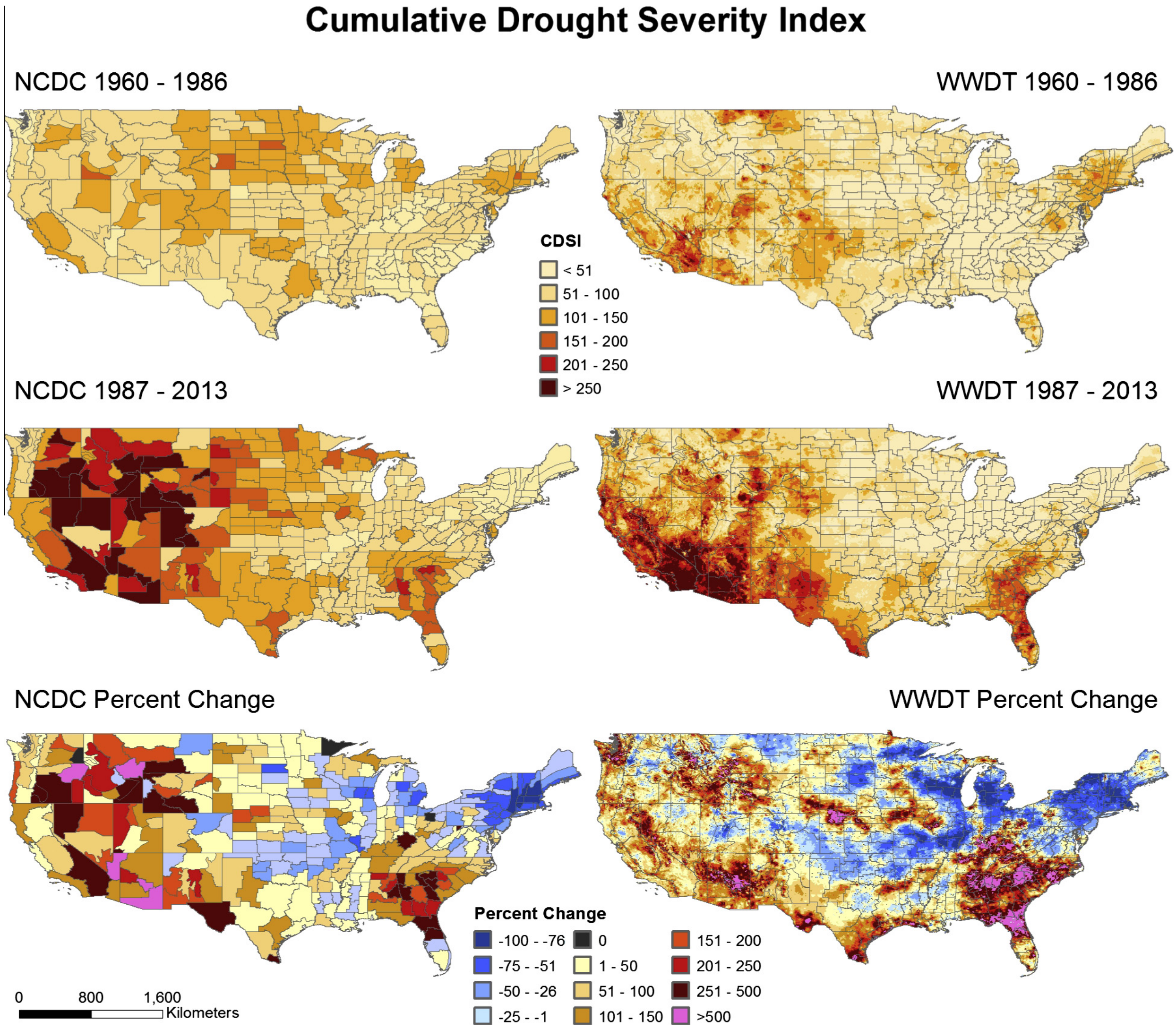

Fig. 1. A cumulative drought severity index (CDSI) for 1960–1986 and 1987–2013, calculated from Palmer Drought Severity Index (PDSI) values obtained from National Climatic Data Center (NCDC) and WestWide Drought Tracker (WWDT) self-calibrated PDSI data. The NCDC values are reported at climate divisions; WWDT values have a 2.5 arc-minutes grid with climate divisions overlaid for reference. The percentage of change from the 1960–1986 period to the 1987–2013 shows decreases (blue gradient) and increases (red gradient) as CDSI is influenced by the frequency and intensity of drought conditions. Decreases can result from more normal conditions rather than increased precipitation.

drought is having on western forest communities and strive to understand how changing drought patterns in the eastern US may emerge with projected climate change. The PDSI uses a 3-month moving window to determine the start and end of conditions, which is ideal for events occurring over multiple months. The CDSI weights the occurrence of monthly conditions for an extended period, in this case two periods of 27 years each, to assign a single value representing the overall droughtiness. Events that span many months with high intensity will have a greater impact on vegetation than might be suggested by the CDSI, but the index is useful for mapping and comparing drought conditions among multiple-year periods and among locations.

The scPDSI algorithm generates monthly values similar to the method developed by Palmer (1965). However, instead of using data from a limited region (i.e., central Iowa and western Kansas) to empirically derive values for the water balance coefficients; the algorithm uses calibration to incorporate historical patterns of climate variability within each location (in this case a 20×20 km grid cell). By accounting for local trends in the climatological record, the scPDSI values at the grid-cell level address the issue of spatial comparability (Alley, 1984; Wells et al., 2004). In this way, comparisons among fine-scale locations can be made that might not otherwise be appropriate for conditions aggregated to climate divisions, because the number and distribution of meteorological stations differ widely among divisions.

CDSI values from the two datasets (NCDC and WWDT) resulted in different spatial patterns and values when summarized at the scale of climate divisions (Fig. 1 and Supplemental Table S1). The gridded WWDT values captured more local influence within climate divisions due to calibration and the fine-scale resolution. Distinct patterns also emerged among CDSI values between the two time periods, and even more so with WWDT data: (1) the western US had higher values than the East; (2) values tended to increase from the 1960–1986 period to the 1987–2013 period; and (3) within the East, CDSI values in the more recent period were lower in the mid-Atlantic and Northeast and higher in the Southeast. Given these trends and the uncertainties of future drought predictions (Dai, 2012), it will be important for resource managers to consider how species may respond to variability in drought patterns and how forestry practices can address drought.

Table 1
Cumulative drought severity index (CDSI) calculated from climate division (NCDC) and gridded (WWDT) data for the conterminous US. Weights of 1, 2, and 3 were used for the moderate, severe, and extreme drought classes, respectively, as defined by the Palmer Drought Severity Index, and were applied to the monthly frequencies of conditions. Climate divisions were used to calculate the mean CDSI value among gridded data, and values for both datasets were averaged to the state level.

State	Cumulative drought severity index					
	1960–1986		1987–2013		Percent change	
	NCDC	WWDT	NCDC	WWDT	NCDC	WWDT
Alabama	41	28	107	81	157.7	189.4
Arizona	61	94	237	255	286.5	171.3
Arkansas	68	64	87	83	28.4	28.4
California	85	112	175	214	105.0	91.2
Colorado	133	94	183	105	37.7	12.4
Connecticut	117	121	31	42	−73.7	−65.5
Delaware	117	104	79	75	−32.9	−27.3
Florida	74	60	115	152	55.1	151.2
Georgia	46	39	161	163	247.4	313.0
Idaho	101	53	205	107	103.7	101.8
Illinois	87	46	92	34	5.7	−25.9
Indiana	64	34	77	23	20.2	−31.1
Iowa	86	38	111	55	28.4	45.9
Kansas	92	54	106	51	15.6	−4.6
Kentucky	38	17	94	45	148.3	167.8
Louisiana	84	61	90	84	7.8	37.9
Maine	71	58	36	45	−49.8	−21.7
Maryland	76	79	94	77	23.2	−2.9
Massachusetts	123	105	20	26	−83.4	−75.5
Michigan	92	53	80	29	−12.7	−46.2
Minnesota	107	49	129	48	21.1	−2.6
Mississippi	68	50	75	62	10.0	24.2
Missouri	80	55	71	42	−12.0	−23.1
Montana	86	77	210	94	142.9	21.5
Nebraska	84	33	158	64	89.4	97.4
Nevada	80	105	251	191	214.1	81.8
New Hampshire	72	75	27	24	−63.2	−67.2
New Jersey	92	113	62	76	−32.2	−33.0
New Mexico	80	92	156	168	94.7	82.7
New York	81	98	40	34	−50.6	−65.4
North Carolina	51	34	106	109	107.4	222.7
North Dakota	99	54	152	64	53.9	18.9
Ohio	65	46	67	29	4.3	−36.8
Oklahoma	104	88	86	66	−17.2	−24.6
Oregon	70	63	208	105	197.3	65.3
Pennsylvania	79	88	51	48	−35.7	−45.0
Rhode Island	81	100	20	21	−75.3	−79.4
South Carolina	44	29	138	128	213.0	341.1
South Dakota	137	65	159	63	15.9	−2.7
Tennessee	58	29	98	65	70.9	127.0
Texas	71	68	132	131	85.2	92.6
Utah	92	108	203	144	120.4	33.3
Vermont	97	81	28	21	−71.6	−73.6
Virginia	78	81	72	78	−6.7	−3.4
Washington	77	47	132	84	72.7	80.1
West Virginia	56	51	61	47	8.9	−8.0
Wisconsin	104	70	83	26	−20.5	−62.4
Wyoming	97	72	237	126	144.5	74.5

A major concern is if and when the water stress of future climates exceeds that observed over the previous 120 years, compositional shifts may occur rapidly, which is now apparent in the West (Allen and Breshears, 1998; Allen et al., 2010; Williams et al., 2013). Indeed, the North American Drought Atlas (Cook and Krusic, 2004) and further analysis (Pederson et al., 2014) indicate that 1950–2005 was one of the wettest periods since 1500 over much of the eastern US, suggesting that future drought may have relatively large impacts on eastern forests.

The scPDSI calculated for 20 × 20 km grid cells for the eastern US differs from that provided by the WestWide Drought Tracker in that the calibration period was 1961–2012 rather than 1895–present, and finer resolution soil available water supply was used (county soil surveys rather than state soil survey data). Because the number and quality of weather stations varied in the early part of the 20th century, we calibrated our PDSI values based on the 1961–2012 period, which has had a relatively stable number of stations (Menne et al., 2009). While self-calibration greatly improves the calculation of PDSI values, the influence from land use and management actions are not well represented moving away from meteorological stations. However, we assume that the temperature values interpolated to 4 km grids are representative of the average conditions and the influence from land cover change is reflected in climate observations. Calculating scPDSI values among the same grids used to model species' suitable habitat provides compatibility between data on historical drought conditions and current and potential tree habitat.

Though modeled IVs for species represent potential suitable habitat that would occur based on recent conditions, we acknowledge that species may or may not actually be present or as abundant as suggested by these data. However, the modeled habitat does provide information which landowners and managers can use to derive a list of possible species that could inhabit the landscape. Drought tolerance levels were assigned to species based on the literature, which reports general characteristics of a species that could differ among regions. Impacts on species related to recent drought conditions will vary at a fine scale: trends may or may not be captured from the local scale to the 20 × 20 km grids to the climate divisions. Site conditions (i.e., aspect, soil texture, and topography) could weaken or intensify the impacts of drought on species; thus our results should be interpreted at a macro scale.

The distribution of drought-tolerant and -intolerant species, as defined by (1) the dominant composition of species potential habitats and (2) averaged over all species' habitats, provides insight into the forest communities in the eastern US. When considering only the tolerance level of dominant species, just under half of the region is moderately intolerant to drought (DIT2). This pattern can be attributed to the tolerance level of a select few species. For example, loblolly pine (*Pinus taeda*) dominates much of the southern part of the region, and it has a moderate intolerance to drought according to the Modification Factors of Matthews et al. (2011). In the North, quaking aspen (*Populus tremuloides*) and balsam fir (*Abies balsamea*) are the dominant DIT2 species, while American elm (*Ulmus americana*) is the top contributor in the central region. Each method of defining drought tolerance provides unique information: the dominant species' habitat can be used to examine trends in forest composition, and the all-species approach is useful when evaluating the overall impact of drought on a forest.

Regardless of how cells were assigned to drought tolerance classes, the western portion of the region (Fig. 5) resembles a wedge shaped pattern, which Transeau (1935) described as the "prairie peninsula"; the transition from conifers and northern hardwoods along the north and northeastern part of the region to more open and grassy landscapes. This pattern is more prominent when the dominant class is used (Fig. 5A), where the most abundant suitable habitat corresponds to green ash (*Fraxinus pennsylvanica*), American elm (*Ulmus american*), boxelder (*Acer negundo*), hackberry (*Celtis occidentalis*), bur oak (*Quercus macrocarpa*), and post oak (*Q. stellata*).

Coupling this species-based information with drought trends over five decades indicates that species-drought classes generally experienced near normal conditions. Although most of the eastern US forests are balanced to moderately tolerant to droughts (DT1 & 2), these classes experienced drought conditions only 18.8 and 19.3% (for the dominant species classes and averaged over all species, respectively) of the period. Across the eastern US, these drought tolerance classes (including Balanced) account for 37.0 and 68.9% (dominant and all species, respectively) of the area, and their prevalence might explain why droughts have not caused dramatic shifts in species compositions in recent decades.

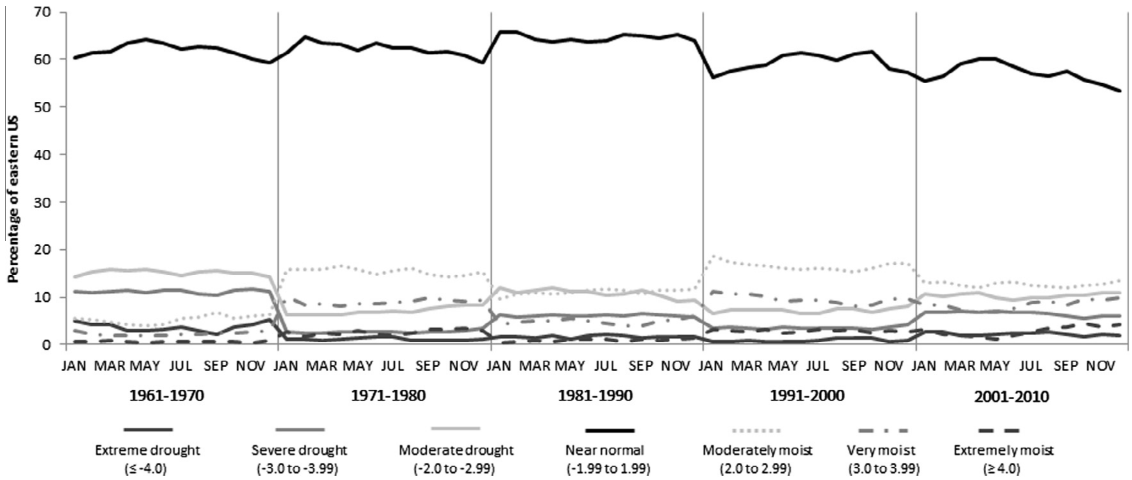

Fig. 2. Decadal frequency of self-calibrated PDSI classes presented as the percentage of 20 × 20 km grids within the eastern US.

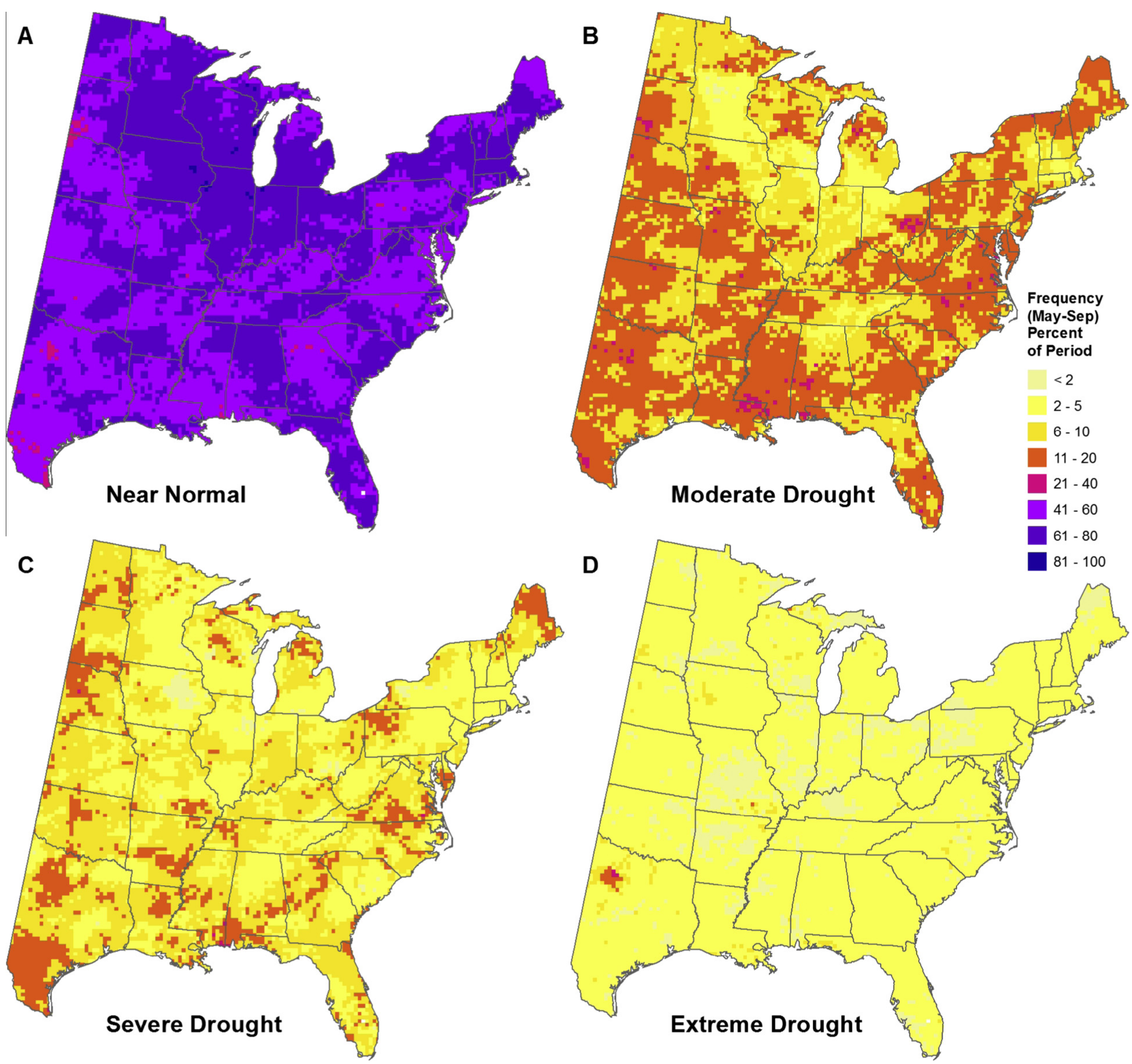

Fig. 3. Frequency of monthly drought classes (A: near normal conditions; B: moderate drought; C: severe drought; D: extreme drought) as a percentage, for the period May–September 1961–2012. The maximum potential frequency is 260 months during this period.

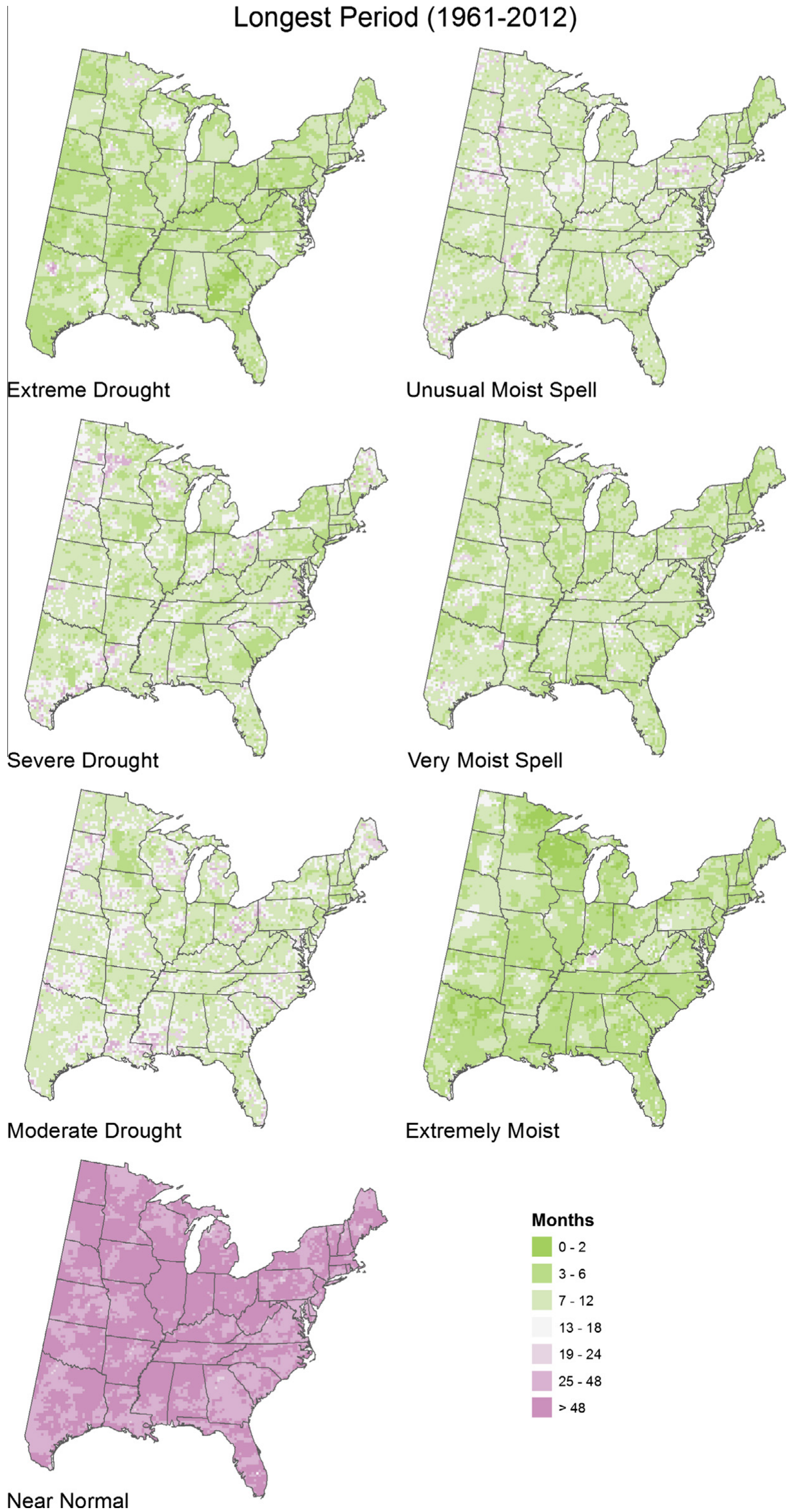

Fig. 4. Duration of longest consecutive period (monthly) for each drought class from 1961 to 2012. PDSI classes were calculated using a self-calibration algorithm, PRISM climate data, and NRCS County Soil Survey Geographic available water-holding capacity.

Additionally, the relatively short durations of droughts in the East may have allowed tree species time to recover between prolonged periods of limited water availability (Pederson et al., 2014). However, both droughts and wet conditions have increased in recent decades, and these patterns of extreme climate variability are projected to increase. Under these projected conditions, the combined stress from periods of intermingling severe droughts and very wet conditions could have the potential to initiate major changes in forest composition. Alternatively, when we define the tolerance based on habitat from all species, the different drought

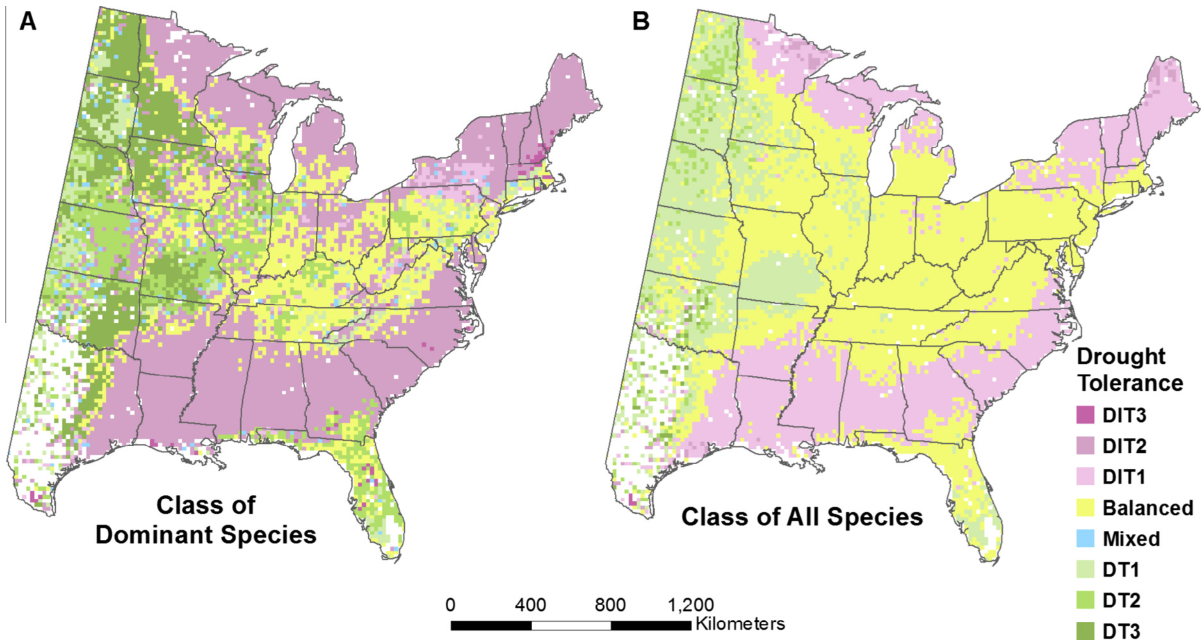

Fig. 5. Mapped distribution of drought tolerance based on (A) dominant tolerance classes among species with suitable habitat and (B) all species (mixed not used). DIT_x = drought intolerance class level, with 3 being the most intolerant; DT_x = drought tolerance level, with 3 being the most tolerant.

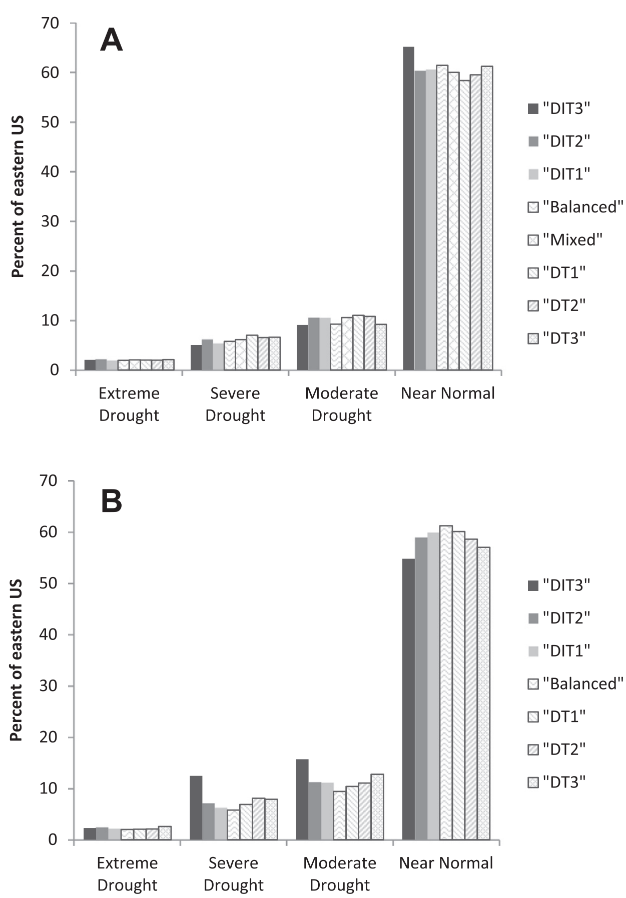

Fig. 6. Proportion of the area of drought tolerance classes of (A) the dominant species' habitat composition and (B) composition of all species' habitat experiencing drought conditions (self-calibrated) in eastern US grids, over the period 1961–2012.

tolerances contained within the community seem to suggest that eastern forests have a relatively balanced composition and as a whole, may be quite resilient to the impacts of a moderate level of drought. Should the climate models be correct, the eastern US may experience climates in the future out of the realm of that documented in this paper, with much higher temperatures and more variability in precipitation events, creating physiological drought even if overall precipitation remains the same or even increases slightly.

The results presented provide an overall depiction of the spatial distribution of 134 tree species based on modeled output and species drought tolerance from the literature. This macro-level analysis, though not precise at the forest stand level, helps further our general understanding of eastern US forests and the impacts of past and pending future drought conditions.

5. Conclusion

Drought is one of the many stress factors that affect the establishment, growth, and mortality of trees. Given that the recent trend of increasing frequency of drought conditions over much of the US is projected to continue into the future, understanding the spatial and temporal distribution of these conditions and how tree species are distributed along this gradient is important to developing and implementing management practices. Unlike the western US, which has shown large increases in the CDSI since 1986, the eastern US so far has had fewer and less intense droughts. Trees living under predominately near normal conditions, as is the case in the East, likely reflect the broader tree communities and drought tolerance classes of forests where drought occurrence has been infrequent. Our analyses of overall species tolerances indicate that, in general, the level of resilience to drought (DT1-balanced-DIT1, Fig. 5) for the eastern US forests is sufficiently balanced that dramatic compositional changes from low-level droughts between 1960 and 2013 would not be expected. However, when the analysis focuses on the numerically dominant tree species across the East, a larger proportion of both drought intolerance and tolerance appears. Nonetheless, as we move into the more variable climate that many climate projections predict, forest drought impacts will likely be amplified for specific portions of the country over short durations.

Acknowledgements

We are grateful for data provided by the National Climatic Data Center, PRISM climate group, and WestWide Drought Tracker. We thank Chris Woodall, Paul Hanson, Cynthia Moser and two anonymous reviewers who provided comments on an earlier version of this manuscript.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.02.022.

References

Abatzoglou, J.T., 2013. Development of gridded surface meteorological data for ecological applications and modelling. Int. J. Climatol. 33 (1), 121–131. http://dx.doi.org/10.1002/joc.3413.

Alig, R.J., Butler, B.J., 2004. Area changes for forest cover types in the United States, 1952 to 1997, with projections to 2050. Gen. Tech. Rep. PNW-GTR-613. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, pp. 106.

Allen, C.D., Breshears, D.D., 1998. Drought-induced shift of a forest–woodland ecotone: rapid landscape response to climate variation. Proc. Natl. Acad. Sci. 95 (25), 14839–14842.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. 259 (4), 660–684. http://dx.doi.org/10.1016/j.foreco.2009.09.001.

Alley, W.M., 1984. The palmer drought severity index: limitations and assumptions. J. Climate Appl. Meteorol. 23, 1100–1109.

Breshears, D.D., Cobb, N.S., Rich, P.M., Price, K.P., Allen, C.D., Balice, R.G., Romme, W.H., Kastens, J.H., Floyd, M.L., Belnap, J., 2005. Regional vegetation die-off in response to global-change-type drought. Proc. Natl. Acad. Sci. USA 102 (42), 15144–15148.

Cook, E.R., Krusic, P.J., 2004. The North American Drought Atlas. <http://iridl.ldeo.columbia.edu/SOURCES/.LDEO/.TRL/.NADA2004/.pdsi-atlas.html>.

Dai, A., 2012. Increasing drought under global warming in observations and models. Nat. Clim. Change 3 (1), 52–58. http://dx.doi.org/10.1038/NCLIMATE1633.

Daly, C., Halbleib, M., Smith, J.I., Gibson, W.P., Doggett, M.K., Taylor, G.H., Curtis, J., Pasteris, P.P., 2008. Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. Int. J. Climatol. 28 (15), 2031–2064.

Grant, G.E., Tague, C.L., Allen, C.D., 2013. Watering the forest for the trees: an emerging priority for managing water in forest landscapes. Front. Ecol. Environ. 11 (6), 314–321. http://dx.doi.org/10.1890/120209.

Gustafson, E.J., Sturtevant, B.R., 2013. Modeling forest mortality caused by drought stress: implications for climate change. Ecosystems 16 (1), 60–74. http://dx.doi.org/10.1007/s10021-012-9596-1.

Guttman, N.B., Quayle, R.G., 1996. A historical perspective of US climate divisions. Bull. Am. Meteorol. Soc. 77 (2), 293–303. http://dx.doi.org/10.1175/1520-0477(1996)077<0293:ahpouc>2.0.co;2.

Hanson, P.J., Weltzin, J.F., 2000. Drought disturbance from climate change: response of United States forests. Sci. Total Environ. 262 (3), 205–220. http://dx.doi.org/10.1016/S0048-9697(00)00523-4.

Heim, J., Richard R., 2006. Station-based indices for drought monitoring in the U.S. In: North American Drought Monitor Workshop, Mexico City, Mexico.

Iverson, L.R., Prasad, A.M., Matthews, S.N., Peters, M., 2008. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. For. Ecol. Manage. 254 (3), 390–406. http://dx.doi.org/10.1016/j.foreco.2007.07.023.

Kardol, P., Todd, D.E., Hanson, P.J., Mulholland, P.J., 2010. Long-term successional forest dynamics: species and community responses to climatic variability. J. Veg. Sci. 21 (4), 627–642. http://dx.doi.org/10.1111/j.1654-1103.2010.01171.x.

Matthews, S.N., Iverson, L.R., Prasad, A.M., Peters, M.P., Rodewald, P.G., 2011. Modifying climate change habitat models using tree species-specific assessments of model uncertainty and life history-factors. For. Ecol. Manage. 262 (8), 1460–1472. http://dx.doi.org/10.1016/j.foreco.2011.06.047.

McDowell, N., Pockman, W.T., Allen, C.D., Breshears, D.D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D.G., Yepez, E.A., 2008. Mechanisms of plant survival and mortality during drought: why do some plants survive while others succumb to drought? New Phytol. 178 (4), 719–739. http://dx.doi.org/10.1111/j.1469-8137.2008.02436.x.

McKee, T.B., Doesken, N.J., Kleist, J., 1993. The relationship of drought frequency and duration to time scales. In: Proceedings of the 8th Conference on Applied Climatology. American Meteorological Society, Boston, MA, pp. 179–183.

McKenzie, D., Hessl, A.E., Peterson, D.L., 2001. Recent growth of conifer species of western North America: assessing spatial patterns of radial growth trends. Can. J. For. Res. 31 (3), 526–538. http://dx.doi.org/10.1139/cjfr-31-3-526.

Menne, M.J., Williams Jr, C.N., Vose, R.S., 2009. The US historical climatology network monthly temperature data version 2. Bull. Am. Meteorol. Soc. 90 (7), 993–1007. http://dx.doi.org/10.1175/2008bams2613.1.

National Climatic Data Center, 2014. North American Drought Monitor Indices. <http://www.ncdc.noaa.gov/temp-and-precip/drought/nadm/indices.php?>.

Natural Resources Conservation Service (NRCS), 2009. Soil Survey Geographic (SSURGO) database for counties of Alabama, Arkansas, Connecticut, Delaware, District of Columbia, Florida, Georgia, Illinois, Indiana, Iowa, Kansas, Kentucky, Louisiana, Maine, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, Nebraska, New Hampshire, New Jersey, New York, North Carolina, North Dakota, Ohio, Oklahoma, Pennsylvania, Rhode Island, South Carolina, South Dakota, Tennessee, Texas, Vermont, Virginia, West Virginia, Wisconsin <http://soildatamart.nrcs.usda.gov/State.aspx> (accessed between August 2009 and November 2010).

Niinemets, Ü., Valladares, F., 2006. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. Ecol. Monogr. 76 (4), 521–547. http://dx.doi.org/10.1890/0012-9615(2006)076[0521:ttsdaw]2.0.co;2.

Palmer, W.C., 1965. Meteorological drought. In: Weather Bureau Research Paper No. 45. U.S. Department of Commerce, Washington, DC, pp. 58.

Paulo, A.A., Pereira, L.S., 2006. Drought concepts and characterization. Water Int. 31 (1), 37–49.

Pederson, N., Dyer, J.M., McEwan, R.W., Hessl, A.E., Mock, C.J., Orwig, D.A., Rieder, H.E., Cook, B.I., 2014. The legacy of episodic climatic events in shaping temperate, broadleaf forests. Ecol. Monogr. 84 (4), 599–620. http://dx.doi.org/10.1890/13-1025.1.

Peters, M.P., Iverson, L.R., Prasad, A.M., Matthews, S.N., 2013. Integrating fine-scale soil data into species distribution models: preparing Soil Survey Geographic (SSURGO) data from multiple counties. GTR NRS-122. Newtown Square, PA: US Department of Agriculture, Forest Service, Northern Research Station, pp. 70.

Peters, M.P., Iverson, L.R., Matthews, S.N., 2014. Spatio-temporal trends of drought by forest type in the conterminous United States, 1960–2013. Res. Map NRS-7. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station. (scale 1:12,000,000).

PRISM Climate Group, 2012. Oregon State University, Corvallis <http://prism.oregonstate.edu>.

Russell, M.B., Woodall, C.W., D'Amato, A.W., Domke, G.M., Saatchi, S.S., 2014. Beyond mean functional traits: influence of functional trait profiles on forest structure, production, and mortality across the eastern US. For. Ecol. Manage. 328, 1–9. http://dx.doi.org/10.1016/j.foreco.2014.05.014.

Sullivan, J.R., 2013. Characterization of drought in Texas using NLDAS soil moisture data. In: Department of Civil, Architectural and Environmental Engineering. The University of Texas at Austin, pp. 92.

Transeau, E.N., 1935. The Prairie Peninsula. Ecology 16 (3), 423–437. http://dx.doi.org/10.2307/1930078.

Wells, N., Goddard, S., Hayes, M.J., 2004. A self-calibrating palmer drought severity index. J. Clim. 17 (12), 2335–2351. http://dx.doi.org/10.1175/1520-0442(2004)017<2335:Aspdsi>2.0.Co;2.

Williams, A.P., Allen, C.D., Macalady, A.K., Griffin, D., Woodhouse, C.A., Meko, D.M., Swetnam, T.W., Rauscher, S.A., Seager, R., Grissino-Mayer, H.D., Dean, J.S., Cook, E.R., Gangodagamage, C., Cai, M., McDowell, N.G., 2013. Temperature as a potent driver of regional forest drought stress and tree mortality. Nat. Clim. Change 3 (3), 292–297. http://dx.doi.org/10.1038/nclimate1693.