Tree mortality from an exceptional drought spanning mesic to semiarid ecoregions

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Abstract. Significant areas of the southern USA periodically experience intense drought that can lead to episodic tree mortality events. Because drought tolerance varies among species and size of trees, such events can alter the structure and function of terrestrial ecosystem in ways that are difficult to detect with local data sets or solely with remote-sensing platforms. We investigated a widespread tree mortality event that resulted from the worst 1-year drought on record for the state of Texas, USA. The drought affected ecoregions spanning mesic to semiarid climate zones and provided a unique opportunity to test hypotheses related to how trees of varying genus and size were affected. The study was based on an extensive set of 599 distributed plots, each 0.16 ha, surveyed in the summer following the drought. In each plot, dead trees larger than 12.7 cm in diameter were counted, sized, and identified to the genus level. Estimates of total mortality were obtained for each of 10 regions using a combination of design-based estimators and calibrated remote sensing using MODIS 1-yr change in normalized difference vegetation index products developed by the U.S. Forest Service. As compared with most of the publicized extreme die-off events, this study documents relatively low rates of mortality occurring over a very large area. However, statewide, regional tree mortality was massive, with an estimated 6.2% of the live trees perishing, nearly nine times greater than normal annual mortality. Dead tree diameters averaged larger than the live trees for most ecoregions, and this trend was most pronounced in the wetter climate zones, suggesting a potential re-ordering of species dominance and downward trend in tree size that was specific to climatic regions. The net effect on carbon storage was estimated to be a redistribution of 24–30 Tg C from the live tree to dead tree carbon pool. The dead tree survey documented drought mortality in more than 29 genera across all regions, and surprisingly, drought resistant and sensitive species fared similarly in some regions. Both angiosperms and gymnosperms were affected. These results highlight that drought-driven mortality alters forest structure differently across climatic regions and genera.

Key words: acute drought impact; Central North America; dead carbon pool; forest structure; Texas, USA; tree death.

Introduction

Large-scale tree die-off events represent a major disruption to ecosystem function and services (Woodward and Lomas 2004, Breshears et al. 2011). Under future climate scenarios, drought-related disturbance could become an increasingly important factor in global carbon estimates. More frequent and severe droughts are likely to shift tree species composition (Coops and Waring 2011), modify terrestrial energy balance (Royer et al. 2011), and cause permanent community change, as ecosystems recovering from die-off events may follow different successional trajectories (Kane et al. 2011). Most of these forest changes, however, are difficult to quantify at the regional scale

because dead trees are widely dispersed or die gradually, with some exceptions (Swetnam and Betancourt 1998, Allen et al. 2010).

Tree species can vary in their susceptibility to drought. However, fundamental questions remain as to whether drought hardiness ultimately leads to greater survival (Ryan 2011). In the widely-studied Arizona pinyon-juniper dieoff (Mueller et al. 2005), pinyon pines were six times more likely to die than the more drought-hardy junipers; however, insect attack was a major factor in the loss of pinyon pines. Also, larger pine trees (>10 cm) were more likely to die, as were trees that were reproductively mature. Trees weakened by drought are generally more vulnerable to pathogens (Desprez-Loustau et al. 2006), and yet, previous exposure to chronic drought might predispose trees toward survival under extreme drought (McNulty et al. 2014). This provokes questions about whether future climate scenarios will fundamentally shift

forest composition. Which species will win out? For instance, a common assumption as to why gymnosperms occur more widely in drier regions relates to their ability to maintain larger hydraulic safety margins than angiosperms; however, whether this trait enhances survival during extreme drought remains uncertain (Choat et al. 2012). Investigating droughts that kill a greater variety of species is critical to improving our predictions of future drought responses and inform dynamic global vegetation models. The relatively few detailed case studies that do exist (see Allen et al. 2010) have been too limited in geographic range and number of species considered to provide much guidance on the development of general drought mortality models, even for models of regional scope.

Susceptibility to drought mortality also varies with tree size and age. A growing body of evidence suggests large old trees are most vulnerable (Lindenmayer et al. 2012), which could escalate decline of forests under more frequent drought scenarios. Large trees typically have more exposed canopies than surrounding vegetation. Further, older trees may be weakened by prior disturbances. Drought disproportionately affected large pinyon pine in the 1996 and 2002 droughts that occurred in northern Arizona, USA (Mueller et al. 2005). Likewise in Amazonia, large tropical trees and lianas died in greater numbers than smaller trees (Nepstad et al. 2007). Given that similar findings span from semi-arid to tropical regions, the trend appears to be global in scope. It remains to be determined whether climate is a factor in the size of trees most susceptible to drought mortality.

We investigated the exceptional drought that occurred in Texas, USA, in 2011, which caused widespread tree mortality to numerous species. That year was the driest on record for the state, with many areas reporting less than 25% of their normal 12-month precipitation (Hoerling et al. 2013). Average temperatures for June–August 2011 were over 1.1°C above the previous record and were close to the warmest statewide summer temperatures ever recorded in the USA. By August 2011, trees were showing signs of stress in many different areas of the state, senescing months earlier than normal. According to the Palmer Drought Severity Index, by spring of the following year, winter rains had lessened the drought in many forested areas of the state and ended it in others.

This event provided a unique opportunity to test hypotheses related to type and size of trees affected and ecosystem-climate feedbacks. Texas forestland encompasses 25 million ha (36% of the land area) and spans several distinct ecoregions, each with unique assemblages of woody plants that follow a pronounced east to west precipitation gradient and a north to south temperature gradient. To document the extent of mortality as soon as possible after the disturbance event itself, the primary objective of this study was to estimate the number of dead trees across all of Texas forestlands the following summer. Specific hypotheses tested were: (1) greater mortality occurred in eastern regions with greater abundance of mesic species; (2) greater proportions of angiosperms were killed compared with gymnosperms; and (3) greater mortality occurred in larger sized trees.

METHODS

The state was divided into 10 regions: the Panhandle, Trans Pecos, North, Central, South, Brazos Valley, Southeast East, Southwest East, Northeast East, and Northwest East (Fig. 1). Within each region, two-stage unequal probability sampling with replacement was conducted (Lohr 1999). A 10 × 10 km grid was overlaid on a forest distribution map (Wilson et al. 2012) creating a list of primary sample units (PSUs) of known forest area (Fig. 1). We used forest area in an unequal probability sample design to select PSUs. In each sampled PSU, seven secondary sample units (SSUs) consisting of 0.16-ha circular plots were selected at random. This produced an initial set of 700 plots distributed across 100 PSUs throughout the state of Texas. Sampling efforts began in the four eastern regions where forest coverage is greatest and then shifted westward as time and personnel permitted. Because access to private land was expected to reduce plot coverage in some regions, we estimated regional mortality two ways depending on the region. Design-based estimation was selected for the four eastern regions where plot densities were higher and forest cover relatively continuous. Calibrated remote sensing was selected for the other six regions to accommodate uneven and sparse coverage of plots in areas with less even forest cover.

Field protocols called for tallying dead trees ≥12.7 cm in diameter, recording size (diameter), and identifying them to at least the genus level. Mortality from insects and disease was observed and noted, as were any other causes besides drought, if known. Because mortality from Hypoxylon canker (common in *Quercus*) and Ips beetles (common in *Pinus*) is accelerated during drought, trees thus diagnosed were considered drought-killed. Some of the species considered dead can resprout from the root crown (Cox and Leslie 1988). Trees whose aboveground portions were dead but were sprouting below the root crown were tallied as dead. Those sprouts, if they survive, will create a new tree. Trees whose aboveground portions were now dead but were sprouting above the root crown were evaluated based on the vigor and amount of sprouting. These individuals could have been tallied as imminent mortality or not tallied if expected to recover.

Design-based estimates of regional mortality were calculated using estimators provide in Lohr (1999),

$$\hat{t}_\psi = \frac{1}{n} \sum_{i=1}^{N} \sum_{j=1}^{Q_i} \frac{\hat{t}_{ij}}{\psi_i}$$

$$\hat{V}\left(\hat{t}_\psi\right) = \frac{1}{n} \sum_{i=1}^{N} \sum_{j=1}^{Q_i} \frac{\left(\frac{\hat{t}_{ij}}{\psi_i} - \hat{t}_\psi\right)^2}{n-1}$$

where $\hat{t}_\psi$ is the estimated population total and $\hat{V}(\hat{t}_\psi)$ is the variance of the estimator of the population total. N is
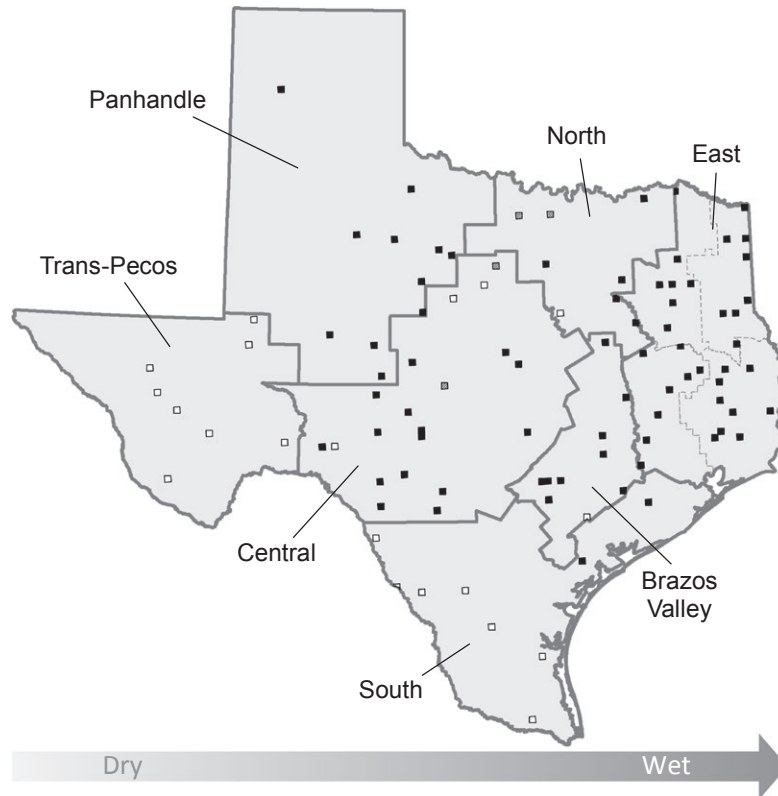
Fig. 1. Locations of study regions and primary sampling units (PSUs). Seven plots were selected within each PSU. Black boxes are PSUs with seven plots measured, gray boxes are PSUs that had one to six plots measured, and PSUs unshaded did not have any plots measured.

the number of PSUs in the population, Q_i is the number of times PSU $_i$ occurs in the sample, $\hat{t}_{ij}$ is the jth estimate of PSU i total, ψ_i is the probability of selection of PSU i, and n is the number of PSUs sampled in the population.

Estimates of PSU totals were calculated using simple random sample estimators. Estimates for multi-region areas are estimated by adding the population stratum totals (i.e., region totals). The variance of the estimate is the sum of the variances of the population stratum totals as sampling was done independently by region.

Western plots and those on the western fringe of the eastern regions were calibrated and scaled to forestland extent using remotely sensed data developed for the U.S. Forest Service forest threats program (Hargrove et al. 2009). The field mortality data were calibrated to a 1-yr change in normalized difference vegetation index (ΔNDVI = May 2012 NDVI−May 2011 NDVI) product that was derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) satellite sensor (*data available online*).[5] We chose ΔNDVI because the datasets were already processed and available and therefore consistent with project timelines. Overlays of observed mortality in the plots and corresponding NDVI change at that location revealed an exponential relationship; i.e., areas with lower
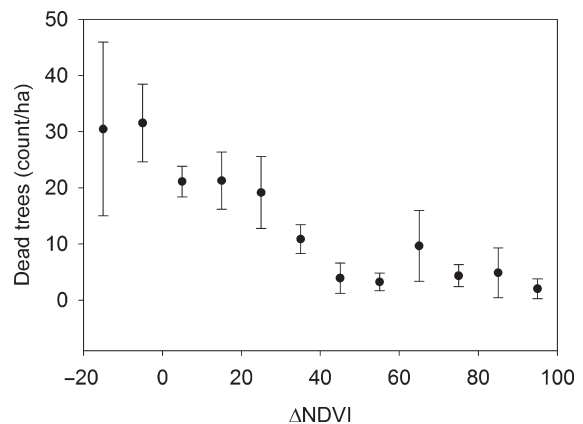
[5] http://forwarn.forestthreats.org/fcav

Fig. 2. The MODIS NDVI difference between May 2011 and May 2012 relates to counts of dead trees in the survey plots contained within that MODIS pixel. The mean number of dead trees aggregated for multiple plots within each of twelve ranges of NDVI change ($n = 436$ total) is shown with standard errors.

NDVI change values between the two dates correlated with areas with larger numbers of dead trees/ha (Fig. 2). The resulting exponential model specific to all western regions used to predict the total number dead trees in the remainder of forestland was validated using a 20% subset
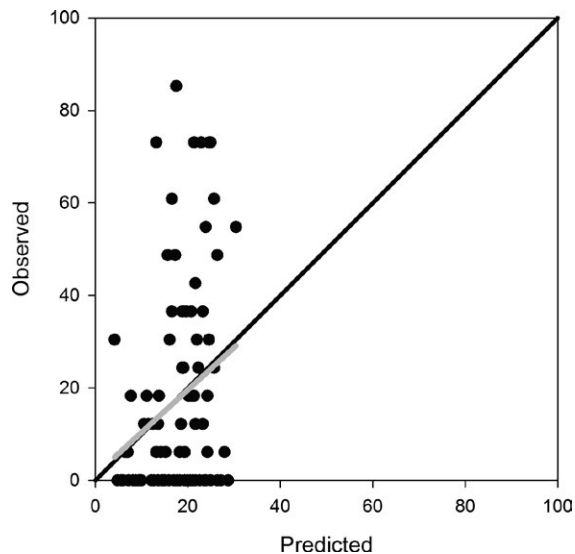
Fig. 3. Comparison of observed and predicted tree mortality derived from the exponential model: dead/ha = $24.914 \times e^{-0.018 \times \Delta NDVI}$. The 87 plots used for validation had a total of 1541 dead trees. The regression (gray line) approaches the 1:1 relationship. The sum of predicted − observed = 20, indicating no apparent bias.

of plots (Fig. 3; $P < 0.001$). It is important to point out that we did not aim to generate a spatial map of mortality, only regional-level estimates.

Estimates of dead trees were compared to estimates of live trees prior to the drought using the USFS Forest Inventory and Analysis (FIA) dataset (Bechtold and Patterson 2005). Note that FIA plots have not yet been remeasured in the western regions of the state. For each region, we compared mortality among common genera (at least four per region). The analysis of genus-level mortality was based on the assumption that the proportion of dead trees found in a given genus should equal the known proportions of live trees in that genus. Admittedly, this is overly simplistic given that mortality rates may inherently differ among species, and ultimately populations are driven by recruitment, growth, and death rates. This was not possible for less common genera because of insufficient sample size in both dead and live categories. We did, however, note a few cases where significant numbers of rarer species were found. While dead proportions prior to the drought were also known from FIA data for the eastern regions of the state, these data were unavailable for the six western regions where plots have yet to be remeasured and year of death of standing dead trees are not known.

Dead tree diameters collected in 2012 and the long term FIA data were used to determine whether drought mortality affected trees larger or smaller than the average size (excluding trees smaller than 12.7 cm for both measures). Proportional differences between live and dead trees were developed for diameters measured both at breast height (DBH; 1.37 m) and trees measured at the root collar (DRC). The size difference was weighted by the number of dead

trees measured across measurement types and genera. In using design-based estimation of dead basal area in regions where coverage was not complete, weight-class adjustment was used (Lohr 1999). In addition, we derived estimates of carbon stock contained in the dead trees (in teragrams per region) using the FIA carbon stock estimation procedure that uses allometric equations for biomass based on diameter and volume equations (Heath et al. 2009). For eastern Texas, estimates of total live biomass were based on FIA data collected from 2006 to 2010 and in all other regions, estimates were derived from 2004 to 2010. Since annual biomass remained stable over this period, multi-year means were used. Because of uncertainties in dead tree estimates, we report estimates of dead carbon stock two ways: (1) by multiplying the estimated percentage of dead trees lost in the drought by the mean pre-drought biomass and (2) by multiplying the percentage of biomass lost in the drought by the mean pre-drought biomass.

Results

The number of plots measured totaled 599, or 85.5% of the number targeted (700). Plot coverage was complete in the four eastern regions and the Panhandle. Coverage was good, although not complete, in the Brazos Valley ($n = 63$), North ($n = 39$), and Central ($n = 117$) regions. Coverage was sparse in the South ($n = 14$) and West ($n = 51$) regions.

Within the plots, a total of 1385 dead trees were surveyed and measured; 53% of plots contained no dead trees. Plot-level observations of mortality by region are presented in Table 1 for only the most common genera, which comprised 89% of surveyed trees. Depending on region, these include *Pinus, Quercus, Liquidambar, Ulmus, Fraxinus, Prosopis, Juniperus,* and *Celtis.* All total, the dead tree survey documented mortality in more than 29 genera across all regions. Plots contained an average of 2.80 ± 0.53 dead trees. Assuming no bias in the sampling, the total dead tree observations in the plots represent an estimated 8.3% of the population sampled.

Drought-related tree mortality occurred virtually everywhere in Texas, affecting a wide diversity of species and habitats. Yet some forested areas suffered more damage than others. Table 2 presents regional-scale estimates of mortality. On a percentage basis, the centrally located Brazos Valley region lost the most trees, almost 10% (13% of stand basal area). North Texas suffered a similar fate, losing 8.3% of trees (10% of stand basal area). Trees in southeast East Texas seemed to fare the best with just 1.3% of trees succumbing to the drought and associated insect pests and disease. Similarly, just 3.9% died in northeast East Texas. Consequently, we did not find evidence to support our first hypothesis that mortality would be higher in eastern regions. Despite the wide range of ecosystem types across a strong mesic-to-arid climate gradient, mortality did not differ by more than a few percentage points between regions. In the regions with the best plot coverage, the relative proportion of live gymnosperms and

TABLE 1. Regional mortality for the most common genera by rank.

Region		Pinus	Quercus	Liquidambar	Ulmus	Fraxinus	Prosopis	Juniperus	Celtis	Nyssa	All trees
Southeast-East	Rank	1	2	3						4	
Mortality in	No. dead	29	11	3						0	48
15/70 plots	Diam.	8.5 ± 0.6	16.0 ± 2.0	14.5 ± 3.9						NA	10.7 ± 0.8
Southeast-West	Rank	1	2	3	4	8		9	7		
Mortality in	No. dead	70	60	8	15	3		1	8		182
34/56 plots	Diam.	11.6 ± 0.6	11.1 ± 0.8	8.1 ± 0.8	13.8 ± 1.2	14.7 ± 6.2		5	9.4 ± 1.2		11.1 ± 0.4
Northeast-East	Rank	1	2	3	4	8					
Mortality in	No. dead	28	46	15	7	4					121
30/63 plots	Diam.	10.0 ± 0.7	13.3 ± 1.0	7.8 ± 0.5	9.3 ± 1.2	10.1 ± 1.3					10.4 ± 0.5
Northeast-West	Rank	1	2	3	4	5		6	8		
Mortality in	No. dead	11	94	27	23	7		5	1		206
33/49 plots	Diam.	12.2 ± 2.2	11.2 ± 0.5	10.8 ± 0.9	9.4 ± 0.9	11.9 ± 0.4		7.5 ± 0.9	5.3		10.5 ± 0.3
North	Rank		1		3	6	2	5	4		
Mortality in	No. dead		73		29	19	18	5	8		170
27/39 plots	Diam.		9.0 ± 0.5		8.1 ± 0.4	8.7 ± 1.0	10.4 ± 1.2	8.6 ± 0.8	12.9 ± 3.4		9.2 ± 0.3
Brazos Valley	Rank		1		3		2	4	5		
Mortality in	No. dead		68		84		56	44	3		279
45/63 plots	Diam.		12.8 ± 0.7		9.1 ± 0.4		8.8 ± 0.4	10.7 ± 0.5	6.0 ± 0.6		10.2 ± 0.3
Central	Rank		2		4	8	3	1	5		
Mortality in	No. dead		66		5	6	11	186	1		301
47/117 plots	Diam.		7.0 ± 0.2		9.6 ± 1.1	7.0 ± 0.6	7.9 ± 0.6	9.1 ± 0.3	6.5		8.5 ± 0.2
Panhandle	Rank		4		5		1	2	3		
Mortality in	No. dead		1		2		60	7	1		78
20/77 plots	Diam.		36.5		12.0 ± 4.0		8.5 ± 0.3	9.0 ± 1.9	7		9.1 ± 0.5

Notes: Observations for the four top-ranked genera (out of 30 total genera observed in the survey) and for all dead trees are reported for the plots containing at least one drought-killed tree. Some additional cases where numerous dead trees were found of a less-common genus are noted. Also shown are mean diameters in cm.

TABLE 2. Texas forestland tree inventory and carbon stocks for live trees prior to the drought of 2011 and dead trees following the drought reported for 10 regions.

Region	Prior to the drought				Drought-related mortality			
	Forestland area (×10⁶ ha)	Live trees (×10⁶)	Live basal area (×10⁶ m²)	Live carbon (Tg)	Dead trees (×10⁶; %)	Dead basal area (×10⁶ m²; %)	Num-based dead carbon (Tg)	Basal area-based dead carbon (Tg)
SE East	1.8	597.1	26.3	77.3	7.5; 1.3%	0.5; 2.1%	1.0	1.6
SW East	1.0	289.7	15.6	48.6	18.8; 6.5%	1.5; 9.3%	3.2	4.5
NE East	1.2	356.0	17.4	53.0	13.9; 3.9%	1.0; 5.6%	2.1	3.0
NW East	1.0	309.4	14.4	39.7	25.3; 8.2%	1.7; 12.1%	3.2	4.8
North	1.7	370.5	16.4	34.0	30.9; 8.3%	1.7; 10.2%	2.8	3.5
Brazos Valley	1.1	256.4	12.2	26.3	24.9; 9.7%	1.6; 12.9%	2.6	3.4
South	3.2	431.2	19.2	31.2	31.7; 7.4%	1.4; 7.4%	2.3	2.3
Central	7.3	1540.0	65.0	76.1	102.3; 6.6%	4.5; 7.0%	5.1	5.3
Panhandle	4.6	556.3	22.4	18.8	33.1; 6.0%	1.7; 7.6%	1.1	1.4
Trans-Pecos	2.5	163.4	5.5	3.0	12.2; 7.5%	0.4; 7.5%	0.2	0.2
Total	25.3	4869.9	214.3	407.9	300.6; 6.2%	16.0; 7.5%	23.5	30.0

Notes: Estimates of dead carbon stock are reported two ways: (1) numbers-based estimates of dead carbon stocks are the percentage of dead trees lost in the drought multiplied by the mean pre-drought biomass, and (2) basal area-based estimates of dead carbon stocks are the percentage of biomass lost in the drought multiplied by the mean pre-drought biomass.

angiosperms is 44% and 56%, respectively, but the proportion of dead gymnosperms and angiosperms in our plots was 30% and 70% indicating generally higher survival in gymnosperms. This generally supports our second hypothesis, but it is important to note that gymnosperm species differ between eastern and western regions (Table 1). The two dominant gymnosperms, *Juniperus* and *Pinus*, were only 19% and 10% of the dead tree tally, given their live proportion of 25% and 18%, respectively. Between them, *Pinus* is dominant in the wetter eastern regions and *Juniperus* is increasingly common moving west toward drier regions (Fig. 4). In general, *Pinus* fared well while *Juniperus* mortality was more varied. *P. taeda* largely occurs in managed plantations at young rotational ages. Oaks (*Quercus*), the most diverse and ubiquitous tree genus across Texas, suffered disproportionate dieback through most of their range. A greater than expected number of elms (*Ulmus*) died in the Brazos Valley region, with rates of mortality that far exceeded their proportion on the landscape. For example, only 11% of Brazos Valley trees are elms, but dead elms amounted to 32% of all dead trees.

Comparing mortality across regions, greater proportions of *Ulmus* and *Quercus* died in the western, drier regions of the state (Fig. 4). However, there was an apparent threshold where higher mortality gave way to survival. In the case of *Quercus*, this shift occurred at the transition between dominant species: *Q. nigra* in the east (although many other oak species are present) and *Q. fusiformis* and *Q. stellata* in the west (most common oaks in the Central and Brazos Valley regions, respectively). *Quercus* composed 25% of live trees in the NE East region, but was a much higher proportion (46%) of the dead; whereas, in Brazos Valley, *Quercus* composed 48% of live and only 26% of dead. Likewise the shift occurred in the Central region where *Ulmus crassifolia* becomes the predominant

Ulmus species. *Ulmus* composed 11% of live trees in the Brazos Valley, but was a much higher proportion (32%) of the dead; whereas, in Central Texas, *Ulmus* composed 4% of live and 2% of dead.

Proportionally greater mortality than other genera was observed in the drought hardy *Prosopis* and *Juniperus* in two regions (Fig. 4). In the Panhandle, where 56% of live trees were *Prosopis*, nearly 77% of the dead trees belonged to that genus (a quantity equivalent to 9% of their total). By contrast, *Juniperus* genera, which constituted 38% of live trees in the Panhandle, comprised only 9% of the dead trees. The vast majority of junipers in Texas are *J. ashei*, *J. virginiana*, and *J. pinchotii* with the latter being the only species among them that resprouts. Notably, the two regions with high occurrence of *J. pinchotii*, North and Panhandle, saw disproportionately low mortality for the genus. In Central Texas, *Juniperus* mortality (mostly *J. ashei*) exceeded that of oaks. Less common genera were too rare among the dead trees tallied to draw conclusions about their proportional abundance.

We found strong evidence in support of our third hypothesis that drought affected larger trees more than smaller trees across regions (Fig. 5). Overall, dead angiosperms were 17.4% larger than the average live angiosperm before the drought, and the gymnosperms were 19.3% larger than the average live gymnosperm. The largest discrepancy between live and dead tree sizes was observed in mesic climate regions and declined linearly in progressively drier regions ($r^2 = 0.74$; $P < 0.01$; Fig. 5).

At the time of our survey, the drought had killed an estimated 301 million trees statewide or about one in 16 trees (Table 2). With larger trees more susceptible to drought, the statewide death of 6.2% of trees amounted to a loss of 7.5% of the forest stand basal area from living biomass. In East Texas forests, 4.2% dead amounted to
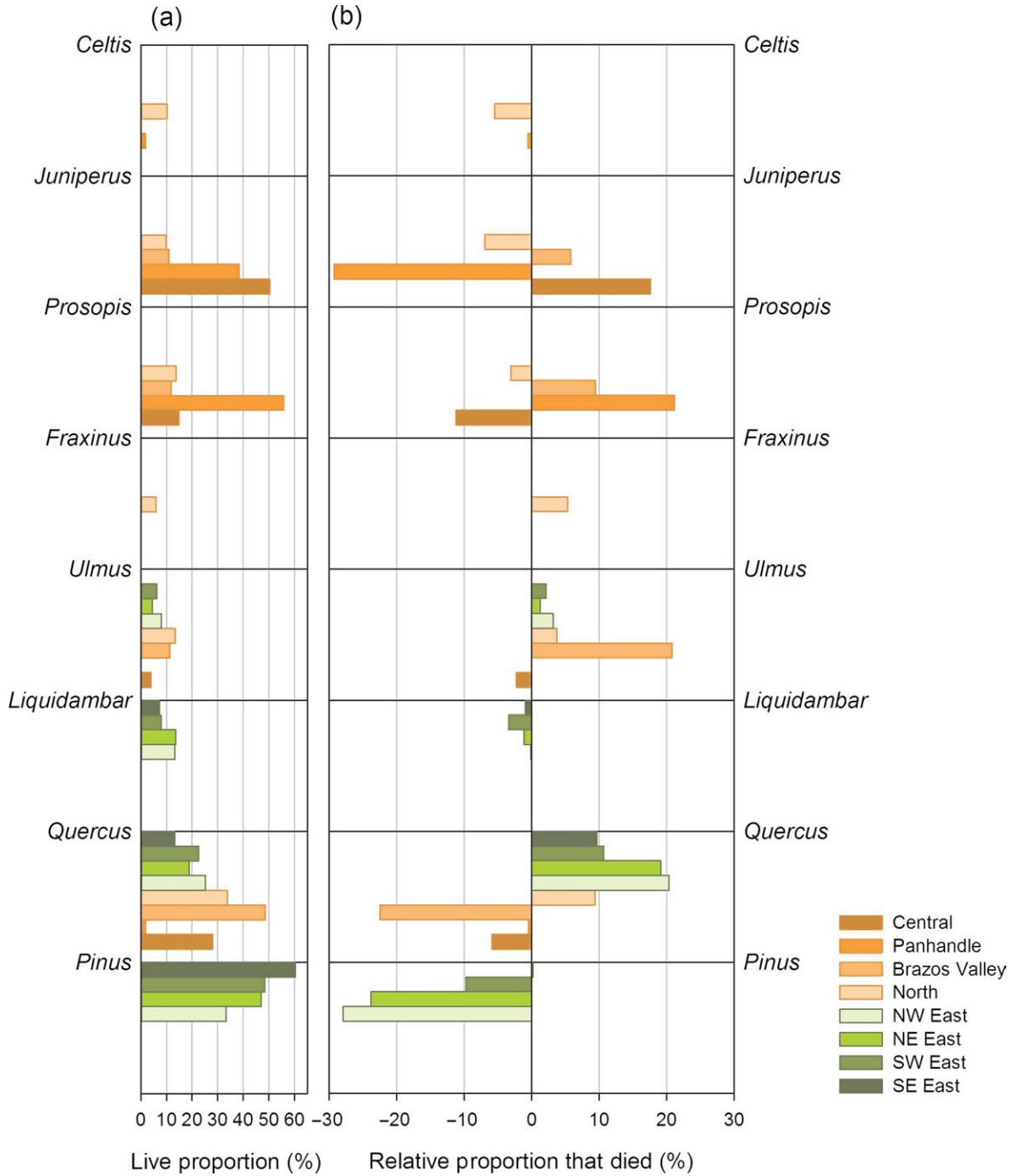
Fig. 4. Regional trends of tree mortality across Texas among common genera, given (a) the proportion of live trees for each genus in that region from USFS Forest Inventory Analysis (FIA) data, and (b) the relative proportion of trees that died in the survey plots (percentage of surveyed dead trees minus the expected mortality, which we assumed was equal to the percentage of live trees from FIA data). Positive values indicate greater than expected mortality. The four most common genera are reported for each region, plus those who deviated >5% from expected mortality.

6.4% of the basal area. For the entire state, the newly dead trees amounted to a loss of between 24 and 30 Tg C of live tree biomass, which equates to 5.8–7.4% of predrought live tree carbon storage in state forestlands (Table 2).

DISCUSSION

This study contributes to the growing body of evidence that drought can significantly alter the structure and function of a wide-range of forest ecosystems (e.g., Breshears
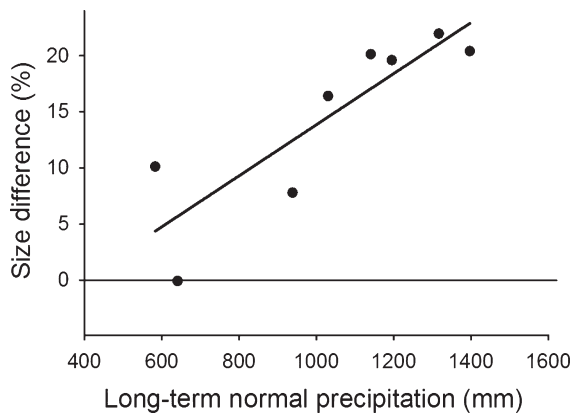
FIG. 5. The size of dead trees relative to live trees (%) varies with long-term precipitation (mm). Each point represents all dead trees measured within an area in 2012 relative to the long-term average size of live trees as estimated by USFS Forest Inventory Analysis (FIA) data.

et al. 2005, McDowell et al. 2008, Allen et al. 2010, Anderegg et al. 2012). Unique to this study was that the drought's extent covered vastly different climate zones, ecoregions, and tree species within a very limited time-frame of only about 1 year (Hoerling et al. 2013). This feature allowed for robust genus-level and size comparisons across climate gradients. This mortality represented a nearly ninefold increase over the normal background tree mortality rate of 0.7% that is estimated from USFS Forest Inventory and Analysis (FIA) data for East Texas forests. Standing dead trees numbered 272 million prior to the drought, so the drought more than doubled the number of standing dead trees and the dead tree carbon stock. Even though mortality rates were nine times above normal, occurrences were diffusely distributed within the live forest matrix, rather than patchy in nature. For these reasons, this event posed great challenges for producing large-scale estimates of mortality using moderate-resolution calibrated remote-sensing approaches. Although the field plots were randomly located within each primary sample unit (PSU), simple upscaling from plot to region without the aid of remote sensing was not possible beyond eastern forests. For the sake of comparison, if we assume live tree densities in the plots mirrored that of region-wide averages, it is possible to derive separate estimates of mortality (dead per hectare/live per hectare) from plot averages of 4.6% East, 12.2% North, 11.8% Brazos Valley, 7.7% Central, and 5.2% Panhandle that are similar to values in Table 2. Bearing in mind the above limitations in our estimates, mortality rates were surprisingly similar from region to region, despite that duration and severity of the drought differed among regions (Hoerling et al. 2013). This was unexpected, given how vastly these regions differ in climatic norms and relative species composition.

We expected past knowledge of life history strategy and drought resistance among major plant groups would help predict which genera would fare better or worse.

However, not only was the distinction between drought resistant and sensitive species difficult to discern among the dead trees tallied, some trends emerged that were contrary to expectations. While neither *Ulmus* nor *Quercus* are considered particularly drought resistant, *Prosopis* and *Juniperus* are known for their ability to survive in extremely dry conditions, which would have led to predictions of higher survival (Willson et al. 2008). Both are woody encroachers into grasslands whose competitive advantage is attributed in part to superior drought resistance (Van Auken 2000, Volder et al. 2013). Part of the advantage of these genera in droughty environments may be the ability for some species to resprout. Although every effort was made to exclude trees that were resprouting from the dead tree tally, our assessment could have missed a few survivors with delayed onset of resprouting.

The mesic-to-semiarid regional climate gradient revealed new insights into population-level survival patterns. The vast majority of *Prosopis* in Texas are honey mesquite (*Prosopis glandulosa*), a deep-rooted, drought-adapted species prolific in semiarid regions of the state. Its deep taproot may explain the very high survival of *Prosopis* in the Panhandle region where soils tend to be deeper by comparison. Another notable comparison occurred in the North region where *Celtis* fared better than *Fraxinus. Fraxinus* is common in only the mesic eastern half of the North region and eastward; whereas, *Celtis* extends its range into the Panhandle and West region (Cox and Leslie 1988), suggesting greater drought hardiness. In a few cases where regional composition was dominated by one species within a genus, it was possible to infer species-level trends in drought tolerance across the mesic-to-semiarid climate gradient. In the case of two elms, the species common to mesic regions, *U. alata*, had the greatest mortality on the western fringe of its range; markedly less *Ulmus* mortality occurred in semiarid regions where the more drought-hardy *U. crassifolia* is common. Also, in regions where resprouting juniper species were common, juniper survival was greater (Fig. 4).

Although our finding that larger trees were more likely to die from drought has been previously demonstrated for other droughts (Lindenmayer et al. 2012), we found that the effect was greater in the eastern (mesic) portion of our study area. This trend has never before been reported and merits further investigation into the mechanisms. This could reflect differences in size distribution across climatic regions, where drier regions have a more uniform tree size distribution because of lower inherent tree densities and a lack of inter-tree competition. The degree of inter-tree competition has been found to correlate with tree mortality under drought conditions (Klos et al. 2009). Another likely factor is that the canopies of taller trees are more exposed in the eastern regions and are more vulnerable to extremes in high temperatures and associated vapor pressure deficits. Finally, variation in regional hydrology might have been a factor in the size distribution of tree mortality; trees growing in wetter regions with more extensive floodplain networks likely experienced dramatic

drops in the water table. Higher mortality was noted in mature floodplain forests (Brian Pope, Texas A&M Forest Service, Personal Communication), apparently caused when water tables fell below the root zone.

Because this mortality event affected larger trees, we estimate that it also had a disproportionately large effect on live tree biomass and ecosystem carbon cycling. Less certain are effects of carbon release from decomposing snags and coarse woody debris in altering net primary production. The dead carbon pool created from the Texas drought was massive, equaling about half as much carbon as emitted from U.S. wildfires (McKinley et al. 2011) and about a quarter as much as Canadian wildfires (Amiro et al. 2001) in an average year. Our estimates of dead trees and their biomass excluded fire-damaged areas, which in 2011 amounted to 1.6 million ha burned. The timing of carbon released as trees decay is uncertain as wood decomposition is relatively poorly constrained for standing dead trees. Further, wood decomposition in this region can be dominated by subterranean termites, which both dramatically increase decomposition rates and can be a significant source of methane. Finally, the potential losses of net primary production will depend on whether or when the remaining live vegetation can compensate. Recovery may take some time as larger trees can contribute proportionally more to forest net primary production than smaller trees (Stephenson et al. 2014). Ultimately, the long-term implications of this drought for carbon cycling will depend on future climate, decomposition, and the rate and trajectory of vegetation recovery.

Surprisingly little is known about the threshold conditions that trigger tree death (Ryan 2011). These data are crucial for future predictions of drought impacts and underscore the importance of observational data to support models of drought mortality (Quillet et al. 2010). Because the survey plots are so dispersed (Fig. 1) and limited to genera, which encompass different species in different areas, more intensive and detailed scientific studies are needed to validate trends, investigate patterns of mortality at finer scales, and determine underlying mechanisms (McDowell et al. 2013).

The greatest uncertainties in the mortality estimates from this study occur for the South and West regions because of the challenges in identifying landowners and obtaining permissions (South), or in identifying remotely whether a location was forested (West). A decision was made part way through the field collection to concentrate resources in other regions (Brazos Valley, North, and Central) to ensure complete sampling in more heavily forested areas (Fig. 1). The sparseness of coverage in the South and West was deemed not especially problematic, since the South is dominated by mesquite, a drought hardy tree, and the West is not heavily forested. In the four eastern regions where plot coverage was complete, we were able to calculate variances of estimates. An estimated 65.6 million trees died in the East and the standard error on the estimate is 7.3 million (11.2% sampling error). In East Texas, sampling errors on the four most abundant genera (*Pinus*, *Liquidambar*, *Quercus*, and

Ulmus) ranged between 15.6% and 35.7%. Achieving complete plot coverage in the Panhandle enabled comparison of design-based and calibrated remote sensing estimates for the region. A difference of 14.5% was observed for the two methods in that region.

The consequences of the exceptional 2011 Texas Drought are significant well beyond Texas, as other regions of the USA, and the world, experience similar tree mortality events. These results highlight how drought-driven mortality alters forest structure and function in ways that are currently difficult to predict. Dynamic vegetation models are well parameterized to predict community changes based on gradual temperature and precipitation shifts, but they are generally not parameterized to predict sudden drought-related die-off events and their aftermaths (Gustafson and Sturtevant 2013), and this deficit has been identified as a major research priority for the development of earth system models for a drier climate (Bonan 2008, Ostle et al. 2009, Fisher et al. 2010, Quillet et al. 2010). Forest managers will also require such predictions to decide how best to adapt to future climate change scenarios, for example, by shifting ranges for plantation forests (Chmura et al. 2011). This is already happening in the western USA where foresters are engaging in a bet-hedging strategy on a grand scale by redrawing ranges for lodgepole pine (Wang et al. 2010).

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