

SITE FACTORS INFLUENCING TREE MORTALITY DURING DROUGHT IN
TEXAS

By

Sarah E. Crouchet, B.S.

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Committee Members:

Susan Schwinning, Chair

Jennifer Jensen

Benjamin Schwartz

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ABSTRACT

Climate models predict an increase in the frequency of severe weather events, including prolonged drought conditions coupled with exceptionally high temperatures. These so called “global-change-type” drought events have been linked to numerous forest dieback events worldwide. Texas experienced such an event in 2011, which reportedly killed 6% of all trees in the state. The purpose of my research was to identify site factors that modified local rates of tree mortality. In 2014, I censused 64 plots across the state, of which, 40 were included in the final analysis focusing on Central Texas. Over 6000 trees were included, mostly in the genera *Juniperus* (n=3487), *Quercus* (n=1054), *Ilex* (n=745), *Ulmus* (n=347) and *Diospyros* (n=308). Each tree above 10 cm circumference was identified to the species level, its basal circumference was measured and its health status recorded in one of seven categories between dead with no sign of resprouting to < 25% crown die-back. For each plot, I also collected site variables describing community composition, elevation, slope, aspect, solar insolation, water storage capacity, soil texture and depth, as well as climate factors, including annual precipitation from 2008 to 2011 and daily temperatures in 2011. I used binary logistic regression in a multivariate model selection analysis for individual species and in some cases, pooled samples of two closely related species, to determine which factors produced the most efficient model for the prediction of crown dieback and tree mortality.

The number of days in which trees were exposed to temperatures over 35 or 38°C in 2011 had significantly positive effects on tree mortality in three out of nine models.

Heat exposure had independent effects on crown dieback and on the odds of resprouting. Precipitation in 2011 had significant effects in eight out of nine models, but they were positive for some species and negative for others. Topographic effects (e.g., slope and aspect) were significant for four out of nine models. Collective stand density was not as good a predictor of mortality as species-specific densities. For example, the mortality odds of *Juniperus ashei* on the Edwards Plateau were more closely related to intraspecific density, suggesting self-limiting. Although *J. ashei* was by far the most common species, *Quercus fusiformis* was not negatively affected by *J. ashei* density, but instead by its own intraspecific density and the density of *Diospyros texana*.

I conclude that studies of drought-related tree mortality focusing on purely abiotic factors such as climate, topography and soil are incomplete, because they omit the influence of species interactions in multispecies communities. My study exposed some of the complexities associated with linking climate events to vegetation changes, in particular, the effects of landscape variation, vegetation composition and management history.

I. INTRODUCTION

Climate change and the global phenomenon of tree die-off

Tree die-off events associated with drought and heat have been reported to occur on all wooded continents.¹ A die-off event is defined as a level of mortality significantly above the normal baseline. While infrequent tree die-offs may have always been an aspect of wooded ecosystems, an increased occurrence of such events is expected to change normal ecosystem function and services. For example, frequent tree deaths could create domino effects on other species in the ecosystem with widespread and possibly irreversible effects on community composition, including the prevalence of invasive species², aridification³, and disruptions of the food web leading to local extinctions.⁴

While it is still unclear whether the occurrences of tree die-off events have already increased in the past decades, the link between tree die-off and high temperature has been well established and suggests that such events could occur with greater frequency in the near future due to climate change.⁵ Global climate models generally

¹ Craig D. Allen and others, "A Global Overview of Drought and Heat-Induced Tree Mortality Reveals Emerging Climate Change Risks for Forests," *Forest Ecology and Management* 259, no. 4 (2010); Christof Bigler and others, "Drought as an Inciting Mortality Factor in Scots Pine Stands of the Valais, Switzerland," *Ecosystems* 9, no. 3 (2006); Nathalie Bréda and others, "Temperate Forest Trees and Stands under Severe Drought: A Review of Ecophysiological Responses, Adaptation Processes and Long-Term Consequences," *Ann. For. Sci.* 63, no. 6 (2006); J. Peñuelas, F. Lloret, and R. Montoya, "Severe Drought Effects on Mediterranean Woody Flora in Spain," *Forest Science* 47, no. 2 (2001); Phillip J. van Mantgem and others, "Widespread Increase of Tree Mortality Rates in the Western United States," *Science* 323, no. 5913 (2009).

² Allen and others; Devin P. Bendixsen, Stephen W. Hallgren, and Amy E. Frazier, "Stress Factors Associated with Forest Decline in Xeric Oak Forests of South-Central United States," *Forest Ecology and Management* 347, (2015).

³ Jedediah Brodie, Eric Post, and William F. Laurance, "Climate Change and Tropical Biodiversity: A New Focus," *Trends in Ecology & Evolution* 27, no. 3 (2012).

⁴ Anthony D. Barnosky and others, "Approaching a State Shift in Earth's Biosphere," *Nature* 486, no. 7401 (2012).

⁵ Jens Hesselbjerg Christensen and Ole Bøssing Christensen, "A Summary of the Prudence Model Projections of Changes in European Climate by the End of This Century," *Climatic Change* 81, no. 1 (2007).

predict an increase in global temperature and some predict a greater occurrence of extreme heat waves, even up to 50°C in some areas, by the end of this century.⁶ Since it is extreme temperature in combination with drought, rather than drought alone, which appears to be causing climate related tree die-off events, this prediction is particularly important in the context of woodland and forest dynamics and calls for further research into understanding how drought, heat, and stand factors might interact to modify tree mortality.

In North America, some of the most highly publicized tree mortality events have occurred in the pinon-juniper woodlands of the Southwest⁷ and western montane conifer forests.⁸ These cases involved conifer mortality and were often associated with bark beetle outbreaks concurrent with drought and heat.⁹ However, there are also studies documenting drought-related die-off events in broadleaf central and eastern forests, including Texas, in which the involvement of insect pests has not been noted as particularly important to causing or expediting tree death.¹⁰

⁶ Andreas Sterl and others, "When Can We Expect Extremely High Surface Temperatures?," *Geophysical Research Letters* 35, no. 14 (2008).

⁷ M. Lisa Floyd and others, "Structural and Regenerative Changes in Old-Growth Pinon-Juniper Woodlands Following Drought-Induced Mortality," *Forest Ecology and Management* 341, (2015); David L. Greenwood and Peter J. Weisberg, "Density-Dependent Tree Mortality in Pinyon-Juniper Woodlands," *Forest Ecology and Management* 255, no. 7 (2008); Robert E. Pangle and others, "Prolonged Experimental Drought Reduces Plant Hydraulic Conductance and Transpiration and Increases Mortality in a Pinon-Juniper Woodland," *Ecology and Evolution* 5, no. 8 (2015).

⁸ Lafe G. Conner, Michael C. Bunnell, and Richard A. Gill, "Forest Diversity as a Factor Influencing Engelmann Spruce Resistance to Beetle Outbreaks," *Canadian Journal of Forest Research* 44, no. 11 (2014); Nicholas C. Coops and Richard H. Waring, "Estimating the Vulnerability of Fifteen Tree Species under Changing Climate in Northwest North America," *Ecological Modelling* 222, no. 13 (2011).

⁹ Barbara J Bentz and others, "Climate Change and Bark Beetles of the Western United States and Canada: Direct and Indirect Effects," *Bioscience* 60, no. 8 (2010); Greenwood and Weisberg.

¹⁰ Bendixsen, Hallgren, and Frazier; William A. Hoffmann and others, "Hydraulic Failure and Tree Dieback Are Associated with High Wood Density in a Temperate Forest under Extreme Drought," *Global Change Biology* 17, no. 8 (2011).

The 2011 Texas Drought

The state of Texas experienced an extreme drought event in 2011; extreme in terms of both spatial extent and duration.¹¹ (Nielsen-Gammon 2012) In addition to the record low precipitation, the state also experienced significantly warmer than normal temperatures. High temperature records were exceeded across the state and the average temperature was 2.1°C higher than normal.¹²

Texas is a large state with 10 distinct vegetation zones or ecoregions ranging from semi-arid scrublands in the West to southern prairies and woodlands in the East.¹³ Average annual precipitation varies east to west from 137 cm to < 35 cm, respectively. Average annual temperature varies north to south from 13°C to 23°C. Thus, the 2011 drought in Texas was a natural experiment well suited to investigating tree mortality across an exceptionally wide biogeographic range with multiple climate zones. Across the entire state, 301 million trees died as a result of the drought, an estimated 6% mortality rate statewide.¹⁴ Moore et al.¹⁵ (2015) used a combination of ground-level observations by the Texas Forest Service and NDVI data to quantify geographic and biological patterns of tree mortality, using a sampling design that focused on tallying dead trees in observation plots. Even though plot-level mortality rates were not assessed, dead tree counts could be set in relation to live tree inventories for eight geographical subdivisions of Texas. Their key findings were that 1) drought mortality affected almost

¹¹ John William Nielsen-Gammon, "The 2011 Texas Drought," *Texas Water Journal* 3, no. 1 (2012).

¹² NCDC, "North American Drought Monitor, September 2011 ", National Climatic Data Center (accessed February 3 2016).

¹³ FW Gould, GO Hoffman, and CA Rechenhain, "Vegetational Areas of Texas: Texas Agriculture Experimental Station Leaflet 492: College Station," *Texas A&M University*, (1960); TPWD, "Gould Ecoregions of Texas", Texas Parks and Wildlife Department (accessed February 3 2016).

¹⁴ Georgianne W. Moore and others, "Tree Mortality from an Exceptional Drought Spanning Mesic to Semiarid Ecoregions," *Ecological Applications*, (2015).

¹⁵ Ibid.

all woody plant species of Texas, i.e., dead trees were found in 29 of 30 genera; 2) there was complex geographic variation in the occurrence of dead trees, attributed in part to species turn-over along biogeographical and climate gradients, and; 3) in most genera, dead trees were larger than live trees on average, suggesting that tree size is a significant risk factor during drought. There were other notable patterns. For example, more angiosperms than gymnosperms died (70% versus 30% in the total sample of 1385 dead trees), which might be expected based on the greater resistance of gymnosperm wood to embolism. In the regions where *Prosopis* and *Juniperus* had the highest proportions in the live tree inventories, in the Panhandle and in central Texas respectively, they tallied in disproportionately high numbers among the dead trees. In central Texas, 62% of all dead trees were in the genus *Juniperus*; in the Panhandle, 77% of all dead trees were in the genus *Prosopis*. Species in both genera are considered woody plant encroachers into grasslands. These findings suggest that drought events take a greater toll on species capable of rapid population expansion. *Quercus* tallied more dead trees in North and East Texas than would be expected based on live tree inventories, and less than expected in the Brazos Valley and central Texas. By contrast, in the Brazos Valley, 32% of all dead trees were in the genus *Ulmus*, although only 11% of all trees in this region are in this genus. Overall, these patterns suggest complex effects of biology (as represented by genus), community and climate zone on drought-induced tree mortality, but they are ultimately difficult to interpret, as the underlying data lack resolution beyond the genus level. More importantly, lacking resolution below the regional scale, they also do not have much to say about drivers of mortality risks at the landscape level.

An additional challenge in assessing “tree mortality” is that different studies apply different criteria for assessing “death”. For example, in the study by Moore et al.¹⁶ (2015), a tree was considered dead when it had 100% crown die-back, although it is well known that many tree species have the ability to resprout from the root collar. Arguably, from a forestry point of view, a resprouting tree is a new tree, although ecologically, resprouting from the root collar is very different compared to regeneration from seed. In studies using proxies such as spectral vegetation indices (e.g., NDVI), mortality rates apply to the scale of tree branches more aptly than to the scale of whole trees, thus also document a different ecological phenomenon. In linking climatic and edaphic factors to tree mortality, it is important to distinguish what kind of damage drought causes in forests and woodlands, whether it causes merely crown die-back but no tree death, and whether or not it interferes with the ability of damaged trees to re-sprout. These alternatives have all been subsumed under the term “tree die-back”, but they could have very different consequences on rates of recovery and ultimately on community response to climate change.

Causes of crown die-back and death

Hydraulic failure is the mechanism leading to branch dieback. The disruption of all or a part of the plant’s hydraulic transport pathway leads to lethal tissue desiccation, first of small distal branches, and then progressively towards the larger branches near the central trunk. Hydraulic failure by drought is driven by low water potentials.¹⁷ The first

¹⁶ Ibid.

¹⁷ Melvin T. Tyree and M. H. Zimmermann, "Xylem Structure and the Ascent of Sap," in *Xylem Structure and the Ascent of Sap*, Springer Series in Wood Science (Springer-Verlag New York Inc., 175 Fifth Avenue,

stage towards hydraulic failure is the spontaneous formation of air bubbles inside xylem conduits or the entry of outside air through xylem pits, which establishes atmospheric pressure inside a xylem conduit. Air may initially enter the outermost xylem through mechanical damage. Once air is inside one conduit, it can spread due to the pressure differential between air-filled and a water-filled conduits by “air seeding” or meniscal failure inside the pit structures connecting xylem conduits. In this way, the embolism of the xylem can spread, initially only to larger conduits with larger pits (for example “early wood”), which have less negative water potential thresholds for air seeding. Thus, initially, there is only partial loss of hydraulic conductivity. If drought conditions intensify, further lowering xylem water potentials, more xylem conduits become embolized leading to a progressive loss of hydraulic conductivity. Eventually, a process of runaway cavitation may be triggered by crossing a critical water potential threshold. This will cause a total loss of transport capacity or “hydraulic failure.”¹⁸

Every type of wood has a critical xylem water potential beyond which runaway cavitation occurs.¹⁹ This critical value depends on wood structure and within angiosperms (which have xylem vessels) and gymnosperms (which do not) wood density generally correlates with greater tolerance for low water potentials.²⁰ Thus, more drought tolerant species have denser wood with more and narrower conduits and thicker walls.²¹ The relationships between tolerance for low water potentials and wood density is different for

New York, NY, 10010-7858, USA; Springer-Verlag GmbH & Co. KG, Heidelberger Platz 3, D-14197, Berlin, Germany, 2002).

¹⁸ Uwe G. Hacke and John S. Sperry, "Functional and Ecological Xylem Anatomy," *Perspectives in Plant Ecology Evolution and Systematics* 4, no. 2 (2001); W. F. Pickard, "The Ascent of Sap in Plants," *Progress in Biophysics and Molecular Biology* 37, no. 3 (1981); Tyree and Zimmermann.

¹⁹ Hacke and Sperry.

²⁰ Uwe G. Hacke and others, "Trends in Wood Density and Structure Are Linked to Prevention of Xylem Implosion by Negative Pressure," *Oecologia* 126, no. 4 (2001).

²¹ *Ibid.*

angiosperms and gymnosperms, specifically, gymnosperm wood is more cavitation resistant at the same wood density.

Hydraulic failure, however, is not a death sentence, as parts or all of the hydraulic transport system reach this point every year at the end of the growing season, but recover transport capacity by refilling conduits or growing new conduits at the start of the next growing season.²² For branches and whole trees to die from drought, further physiological damage must occur that kills living tissues and prevents recovery.²³ Tissue death can result from exceeding critical temperature thresholds, but many have argued that acute carbon deficit can also kill branches to whole trees.²⁴ Carbon deficit is the imbalance between carbon demand and supply. For a branch to recover transport function after hydraulic failure, its surviving tissues must be supplied with carbohydrates for repair (either for xylem refilling or growth). Carbohydrates are supplied from storage organs by translocation via the living phloem. It has been argued that prolonged drought either critically depletes carbon reserves or damages the phloem transport system. Regardless, carbon deficits would ultimately result in a self-reinforcing feedback involving incomplete recovery of the hydraulic transport system, which would limit photosynthesis and thereby further diminish carbon storage leading to chronic carbon deficit. The resulting physiological decline can be amplified by diminishing resources towards defense against parasites and pathogens.²⁵ Hydraulic failure and carbon deficit

²² Henry H. Dixon and J. Joly, "On the Ascent of Sap," *Philosophical Transactions of the Royal Society of London. B* 186, (1895); Hacke and Sperry, "Functional and Ecological Xylem Anatomy."

²³ William R. L. Anderegg, Joseph A. Berry, and Christopher B. Field, "Linking Definitions, Mechanisms, and Modeling of Drought-Induced Tree Death," *Trends in Plant Science* 17, no. 12 (2012).

²⁴ Henry D. Adams and others, "Temperature Sensitivity of Drought-Induced Tree Mortality Portends Increased Regional Die-Off under Global-Change-Type Drought," *Proceedings of the National Academy of Sciences* 106, no. 17 (2009).

²⁵ Paul D Manion, *Tree Disease Concepts* (Prentice-Hall, Inc., 1981); Paul D Manion and Denis Lachance, *Forest Decline Concepts* (American Phytopathological Society (APS), 1992).

are probably closely linked processes, both necessary components leading to the eventual death of trees.²⁶

Technically, drought kills trees in the same way, as discussed above, but there are still large species differences in tolerance to drought conditions, thus potentially large differences in rates of mortality during any given drought event. Tree species fall along a continuum of hydraulic strategies from high tolerance for low xylem water potentials, enabling drought tolerance, to low tolerance for low xylem water potentials, requiring drought avoidance. Drought avoiders tend to close stomata during the day to maintain higher water potentials. This strategy has been called “isohydry”. Because of frequent stomatal closure at times of drought, these plants have limited time for photosynthesis and should be more carbon-limited but more protected from hydraulic failure during severe drought. By contrast, drought tolerators keep stomata open for longer during drought, thereby allowing their water potentials to drop with declining soil water potentials. This has been called “anisohydry”. These species can maintain photosynthetic activities for longer during drought, but may be at a higher risk of runaway cavitation.²⁷

²⁶ Nate G. McDowell and others, "The Interdependence of Mechanisms Underlying Climate-Driven Vegetation Mortality," *Trends in Ecology & Evolution* 26, no. 10 (2011); Nathan G. McDowell, "Mechanisms Linking Drought, Hydraulics, Carbon Metabolism, and Vegetation Mortality," *Plant Physiology* 155, no. 3 (2011).

²⁷ MJ Linton, JS Sperry, and DG Williams, "Limits to Water Transport in *Juniperus Osteosperma* and *Pinus Edulis*: Implications for Drought Tolerance and Regulation of Transpiration," *Functional Ecology* 12, no. 6 (1998); Nate McDowell and others, "Mechanisms of Plant Survival and Mortality During Drought: Why Do Some Plants Survive While Others Succumb to Drought?," 2008; Nir Sade, Alem Gebremedhin, and Menachem Moshelion, "Risk-Taking Plants: Anisohydric Behavior as a Stress-Resistance Trait," *Plant Signaling & Behavior* 7, no. 7 (2012); Nir Sade and others, "Improving Plant Stress Tolerance and Yield Production: Is the Tonoplast Aquaporin Sltp2; 2 a Key to Isohydric to Anisohydric Conversion?," *New Phytologist* 181, no. 3 (2009).

Multiple factors modify drought mortality rates

The circumstances surrounding tree mortality have been discussed in terms of predisposing, inciting, and contributing factors.²⁸ Predisposing factors are persistent site factors that could intensify stress levels experienced by plants during drought or other disturbances, such as high tree density, south-facing slopes and shallow soil depth. Inciting factors are the events that cause acute stress conditions, such as droughts and heat waves. Contributing factors are additional factors, acting on an individual level that tip may the scale between life and death, such as age, prior injury, or infection.²⁹

Predisposing factors. During drought, trees access to water declines. Eventually, no water may be available for uptake. The rate of water loss in the root zone is affected in part by physical site factors, such as slope and aspect, which influence soil temperature and evaporation rate, and in part by biological factors, such as stand density and species composition, which control water loss by transpiration. Drought induced mortality has been reported to be greater where stand density is higher,³⁰ though additional studies have indicated hot droughts may kill trees irrespective of stand density.³¹

The length of time over which no water is available can also be influenced by the amount of water stored at the onset of the drought. This could vary by the amount of runoff produced by a site, for example steeper slopes have more runoff, but also by the

²⁸ Manion, *Tree Disease Concepts*; W. J. Mattson and R. A. Haack, "The Role of Drought in Outbreaks of Plant-Eating Insects," *Bioscience* 37, no. 2 (1987); McDowell and others, "The Interdependence of Mechanisms Underlying Climate-Driven Vegetation Mortality."; McDowell, "Mechanisms Linking Drought, Hydraulics, Carbon Metabolism, and Vegetation Mortality."; Gaëlle Rouault and others, "Effects of Drought and Heat on Forest Insect Populations in Relation to the 2003 Drought in Western Europe," *Ann. For. Sci.* 63, no. 6 (2006); James J. Worrall and others, "Rapid Mortality of *Populus Tremuloides* in Southwestern Colorado, USA," *Forest Ecology and Management* 255, no. 3–4 (2008).

²⁹ Manion, *Tree Disease Concepts*.

³⁰ Greenwood and Weisberg; Gillis J Horner and others, "Mortality of Developing Floodplain Forests Subjected to a Drying Climate and Water Extraction," *Global Change Biology* 15, no. 9 (2009).

³¹ M. Lisa Floyd and others, "Relationship of Stand Characteristics to Drought-Induced Mortality in Three Southwestern Pinon-Juniper Woodlands," *Ecological Applications* 19, no. 5 (2009); Moore and others.

storage capacity of the root zone. Soil texture, rockiness and depth to bedrock determine storage capacity and thus can make a difference to tree mortality.³²

Inciting factors. It is well documented that tree mortality is linked to hot droughts,³³ and it is becoming increasingly recognized that drought alone rarely kills trees, but rather high temperatures at a time of water scarcity.³⁴ Thus, high temperature can be considered an important inciting factor. High temperatures increase water vapor deficits in the air causing trees to transpire more than at lower temperatures. Maintenance respiration is also increased at higher temperatures, intensifying carbon deficits.³⁵

Contributing factors. Differences between the traits of species and the age or size of individuals can be considered contributing factors. Even though the continuum of adaptations to water shortage is well known, it is not easy to make predictions about drought mortality rates solely on the basis of trait differences. For example, we may expect that trees with denser wood have greater drought survivorship.³⁶ Contrary to this, across species, trees with higher wood density can experience greater crown dieback during drought.³⁷ Hoffman et al.³⁸ attributed this unexpected result to the type of drought

³² S. C. Gupta and W. E. Larson, "Estimating Soil-Water Retention Characteristics from Particle-Size Distribution, Organic-Matter Percent, and Bulk-Density," *Water Resources Research* 15, no. 6 (1979).

³³ Allen and others.

³⁴ Nadine K. Ruehr and others, "Water Availability as Dominant Control of Heat Stress Responses in Two Contrasting Tree Species," *Tree Physiology* 36, no. 2 (2016).

³⁵ Adams and others; Allen and others; William R. L. Anderegg, Jeffrey M. Kane, and Leander D. L. Anderegg, "Consequences of Widespread Tree Mortality Triggered by Drought and Temperature Stress," *Nature Clim. Change* 3, no. 1 (2013); David D. Breshears and others, "Regional Vegetation Die-Off in Response to Global-Change-Type Drought," *Proceedings of the National Academy of Sciences of the United States of America* 102, no. 42 (2005); McDowell and others, "The Interdependence of Mechanisms Underlying Climate-Driven Vegetation Mortality."; McDowell and others, "Mechanisms of Plant Survival and Mortality During Drought: Why Do Some Plants Survive While Others Succumb to Drought?."; A. P. Williams and others, "Temperature as a Potent Driver of Regional Forest Drought Stress and Tree Mortality," *Nature Climate Change* 3, no. 3 (2013).

³⁶ Manuela Ruiz Diaz Britez and others, "Wood Density Proxies of Adaptive Traits Linked with Resistance to Drought in Douglas Fir (*Pseudotsuga Menziesii* (Mirb.) Franco)," *Trees (Berlin)* 28, no. 5 (2014).

³⁷ Hoffmann and others.

³⁸ *Ibid.*

event, which was in this case both long and intense, which could have increased risks for anisohydric trees with higher wood density.³⁹ Compounding this, their lower stem water storage capacity⁴⁰ could have reduced safety margins for reaching and exceeding critical water potentials in the late stages of the drought.

Higher wood density and more drought tolerance is typically correlated with environments in which short-term seasonal drought is expected.⁴¹ Generally, woodland communities on drier sites or in drier climates will have relatively more anisohydric tree species. Thus, when severe drought conditions occur over a large regional scale, such as the 2011 drought in Texas, we may observe no change in mortality in more drought tolerant taxons at the drier end of the climate gradient than in less tolerant taxons in more mesic locations. For example, the higher abundance of deciduous, isohydric trees in East Texas could have buffered tree mortality rates in mesic eastern forests compared to more xeric western woodlands, as observed by Moore et al.⁴² (2015) Furthermore, on the Edwards Plateau in Central Texas, where soils are typically shallow and predominantly occupied by dense stands of *Juniperus ashei*, tree mortality rates were relatively high, even though juniper is one of the most drought-tolerant tree species of Texas.⁴³

Tree size may also be a significant contributing factor to drought related mortality. Larger trees are expected to have more developed root systems, which may

³⁹ David Ackerly, "Functional Strategies of Chaparral Shrubs in Relation to Seasonal Water Deficit and Disturbance," *Ecological Monographs* 74, no. 1 (2004); S. J. Bucci and others, "Functional Convergence in Hydraulic Architecture and Water Relations of Tropical Savanna Trees: From Leaf to Whole Plant," *Tree Physiology* 24, no. 8 (2004); Hoffmann and others; Frederick C. Meinzer and others, "Coordination of Leaf and Stem Water Transport Properties in Tropical Forest Trees," *Oecologia* 156, no. 1 (2008).

⁴⁰ Hoffmann and others.

⁴¹ Hacke and others, "Trends in Wood Density and Structure Are Linked to Prevention of Xylem Implosion by Negative Pressure."; Hoffmann and others; Anna L. Jacobsen and others, "Cavitation Resistance and Seasonal Hydraulics Differ among Three Arid Californian Plant Communities," *Plant, Cell & Environment* 30, no. 12 (2007).

⁴² Moore and others.

⁴³ Ibid.

enable them to reach water sources below ground unavailable to smaller trees with smaller root systems. Thus, larger trees may have a higher probability of surviving drought. On the other hand, larger trees also have bigger crowns and evaporative demands, which may deplete water resources in the rhizosphere sooner and increase mortality risk. Also, larger trees may be older and reaching the limit of their life expectancy and are therefore more susceptible to any kind of stress condition. A few studies published after recent extensive droughts have found that larger trees within a species or genus were generally more susceptible to drought induced mortality.⁴⁴ On the other hand, in species comparisons, smaller, subdominant tree species tended to be more susceptible to drought induced mortality.⁴⁵

Purpose of the study

The purpose of the study was to take advantage of the unusually large geographic extent of the 2011 Texas Drought by examining how drought conditions and site factors influenced local rates of tree mortality across several different vegetation zones. In this way, I was hoping to document the influence and regional variation in inciting, contributing, and predisposing factors on local tree mortality. Specifically, my analysis was guided by the following questions:

1. What are the drivers of tree mortality for different species?
 - a. Was spatial variability in precipitation and temperature large enough to cause significant effects on local tree mortality?

⁴⁴ Floyd and others, "Relationship of Stand Characteristics to Drought-Induced Mortality in Three Southwestern Pinon-Juniper Woodlands."; Moore and others.

⁴⁵ K. J. Elliott and W. T. Swank, "Impacts of Drought on Tree Mortality and Growth in a Mixed Hardwood Forest," *Journal of Vegetation Science* 5, no. 2 (1994).

- b. Was soil depth or soil water storage capacity a significant predictor of drought mortality?
 - c. Was heat load, based on slope and aspect, a significant predictor of drought mortality?
2. Did tree size and/or stand density impact tree mortality and was intraspecific stand density more detrimental than interspecific stand density?
 3. Among trees that experienced 100% crown dieback, were there factors that were significantly correlated with resprouting?

II. METHODS

Site selection

Across the state of Texas, I censused 64 plots, 58 on privately owned land, three in state parks, and three plots owned or managed by Texas State University (the Freeman Ranch and the Pollard Property). Sites included the mesquite-juniper savannas of the High Plains, mesquite-juniper woodlands of the Rolling Plains, the creosote bush-mesquite shrub vegetation of the Trans-Pecos region, Post oak savanna, loblolly-shortleaf pine forests, and dense oak-juniper woodlands.

Not all plots were included in the statistical analysis. First, stands affected by infestation or showing burn marks were excluded. Several bioregions were underrepresented and also could not be used in the final analysis. In the end, I only included 40 plots that fell along an East-West gradient across central Texas, specifically in the regions of the Edwards Plateau, the East Central Texas Prairie, the Cross Timbers and the Blackland Prairie (Figure 1). Plots were located between latitudes 29.62592 and 30.91915, longitudes -98.16294 and -100.58144, and elevations between 52.7546 m and 681.5294 m above sea level (Table 2). Within this range, key factors varied to differing degrees, for example, annual precipitation from 2008 to 2011 showed a coefficient of variation from about 18 to 32%, whereas the number of days above 35 °C in 2011(DA35) varied by 7.5%.

Plot surveys

At each property, areas of interest were selected based on an initial perusal of stand structure and tree mortality from visual inspection of Google Earth imagery.

Because the purpose of the study was to correlate tree mortality with site factors, my aim was to sample a broad range of site conditions and mortality rates; ideally between zero and 100%, rather than to conduct “representative” (i.e., random) sampling. Therefore, on each property, several sampling sites with contrasting characteristics were chosen for survey plot locations. For some sites with especially low tree density, additional plots were surveyed to bring the total tree count to at least 90 trees.

At each location, 30 m x 30 m plots were randomly placed within the general areas of interest and delineated by surveyor tape. Within a region of interest, the exact plot location was chosen at random. Trees at or above a 10 cm circumference were counted and identified by species, basal circumferences were measured, and crown status was assessed and ranked according to four categories (>75% alive (LP), 25-75% (L), <25% (LM) and dead (D)). Dead trees were recorded only if, based on their appearance, they had died recently, likely in or as a consequence of the 2011 drought. The criterion was based on the amount of terminal branch breakage, loss of bark, and degree of decomposition. Trees with substantial signs of decay were not recorded. There were three additional categories for trees that experienced 100% crown death, but had survived and sprouted back. I distinguished whether these trees sprouted back from the base (SB), from the trunk (ST) or from the branches (SBR).

Electronic data extraction

For each site, local climate data was obtained from the PRISM tool⁴⁶ for the period January 1, 2008 – December 31, 2011. From these data, I calculated the climate indicators provided in Table 1.

⁴⁶ Prism Climate Group, (Oregon State University, <http://prism.oregonstate.edu>, created 27 April 2016.).

Plot characteristics were extracted from multiple GIS databases. Soil water capacity was extracted from the USDA Gridded Soil Survey Geographic Database for Texas.⁴⁷ Sand, silt, and clay fraction, and depth to bedrock were extracted from the Soil Information for Environmental Modeling and Ecosystem Management soil database.⁴⁸ Slope, aspect, and elevation were extracted for the plot level with 30 m Digital Elevation Models (DEM) from the National Elevation Dataset produced by the United States Geological Survey.⁴⁹

Solar radiation was calculated using the Spatial Analyst tool in ArcGIS⁵⁰ based on slope, aspect and elevation derived from the DEM. Slope was calculated as degree. Aspect was calculated by first converting the aspect grid to radians. Next, I performed a cosine transformation to the aspect grid radians, producing a Northness and Eastness index, and extracted the values based on plot locations. Stand tree density was calculated in two ways: as stems per plot (Nplot) and stem basal area per plot (Aplot).

Statistical methods

I restricted the analysis of tree mortality to species that were represented in at least eight plots, which reduced the number of target species to nine. Among these nine, two pairs of species are considered very closely related, can co-occur, and are difficult to distinguish in the field. For these species I first examined pooled data sets and tested for significant differences between species. If they were insignificant, I continued to analyze

⁴⁷ Gridded Soil Survey Geographic (Gssurgo) Database for Texas, ed. Soil Survey Staff <http://datagateway.nrcs.usda.gov/> (accessed November 04, 2015).

⁴⁸ D.A. Miller and R.A. White, "A Conterminous United States Multi-Layer Soil Characteristics Data Set for Regional Climate and Hydrology Modeling" <http://EarthInteractions.org> (accessed April 1, 2016 2).

⁴⁹ U.S. Geological Survey, "National Elevation Dataset (Ned)," ed. U.S. Geological Survey (USGS) (Sioux Falls, SD: 2009).

⁵⁰ ESRI, Arcgis Desktop (Redlands, CA: Environmental Systems Research Institute.).

the pooled data. Species handled in this way were *Quercus fusiformis*/*Quercus virginiana* (Escarpment live oak/Southern live oak) and *Ulmus alata*/*Ulmus crassifolia* (Winged elm/Cedar elm). Thus, the final number of regression models I derived was seven, for nine species.

I used the GLM procedure in SPSS (Version 22) with binary distribution and log-link function for the prediction of tree mortality. For the initial analysis, I considered trees dead only if there was no evidence of resprouting (i.e. in the category “d”).

Because I initially selected multiple alternative indicators for one hypothesized driver (e.g., total precipitation in 2011 and largest consecutive number of days with precipitation < 5 mm), as well as some potentially meaningful two-factor interactions (e.g., precipitation in 2011 x Storage Capacity; Table 1), my first task was to reduce this long list of variables or interactions to a short list that proved most effective as candidate variables in predicting tree mortality. I did this by species, since the variables that best correlated with tree mortality could be different for different species. In this step, I tested the individual effects of all factors one by one, retaining those with $p < 0.1$ (summarized in Table 2). I used this less conservative criterion anticipating that some factors with marginally significant effects in a single factor regression analysis could rise to significance at the $p < 0.05$ level in a multivariate regression model. Next I quantified collinearity between all remaining variable pairs. If any two variables were correlated by more than a Pearson correlation coefficient of 0.6(Connor et al 2014),⁵¹ I removed the variable with the higher p-value in the previous regression analysis. This procedure removed alternative variables meant to represent the same putative driver (for example,

⁵¹ Conner, Bunnell, and Gill.

longest consecutive number of days without rain or annual rainfall). In some cases, it also revealed unexpected collinearities, such as between stem area density (Aplot) and precipitation, but still, one of the collinear variables was removed. Finally, all variables that survived the second selection procedure were combined in one model to predict tree mortality. More often than not, all remaining variables for each species maintained their significant influence on mortality in the full model and the removal of any factor increased the AIC_C value. In some cases, not all factors remained significant in the multivariate model, and in this case I tested different combinations of variables to identify the model with the lowest AIC_C value.

To test if tree size and heat exposure had different effects on crown die-back and actual tree death (i.e., no resprouting), I conducted two additional binomial linear regression analyses. In the first model, I distinguished between trees with < 100% crown dieback (i.e., categories LM, L, LP) and trees with 100% crown die-back (i.e., SB, ST, SBR, D). Then I constructed a data set containing only trees with 100% crown die-back and distinguished those trees in the set that had actually died (D).

For the comparison of inter- and intraspecific density effects on tree mortality, I focused on the Edwards Plateau, because it had the most plots and relatively narrow species distribution. For the prairie bioregions of the East Central Texas Plains, the Blackland Prairies, and the Cross Timbers, relatively low plot numbers with relatively high species diversity resulted in data sets that did not have sufficient power to tease apart effects of intra- and interspecific competition. For the plots on the Edwards Plateau, I calculated the component densities for the three most abundant species, *J. ashei*, *D. texana* and the species pair *Q. fusiformis*/*Q. virginiana*. All other species were grouped

into one joint density. As before, I used a binomial linear regression with a logit link function to examine the effects of heterospecific and homospecific density on mortality for each species.

III. RESULTS

Data summary

In the original sample, including all 64 plots, tree densities ranged from 18 to 339 trees per plot (equivalent to 178 to 3767 trees ha⁻¹) and stand mortality was between 0 and 36% (Table 4). The sixteen most common tree species are shown in Figure 2. Together they represent 98% of all censused trees. Across these 6640 trees, 80% were living, 17% had died, and 3% resprouted. *Quercus havardii* (Shin oak) had the highest overall mortality at 27% and *Sophora secundiflora* (Mountain laurel) the lowest at 3%, while the mortalities of the most common species, *Juniperus ashei* (Ashe juniper) and *Ilex vomitoria* (Yaupon holly), were 18% and 20%, respectively. Mortality rates were significantly different between species ($p < 0.001$).

Correlates of tree mortality by species

The top models for the respective species or species pairs are summarized in Table 3. For *J. ashei*, which is a species closely associated with the Edwards Plateau, precipitation effects were significant, not only precipitation in 2011 (ConsNo_P), but also in the previous drought year of 2008. For both years, wetter conditions favored survivorship. However, precipitation in 2010, in interaction with water storage capacity, increased mortality odds. The number of days $> 35^{\circ}\text{C}$ in 2011 increased mortality odds. In addition to these mostly climatic effects, one other site factor was significant: depth to bedrock. Higher mortality rates were associated with deeper soils. Finally, greater basal stem area decreased mortality odds.

The second most abundant species, *I. vomitoria*, which is an understory species, had an opposite response to ConsNo_P than *J. ashei*. With an increase in aridity, *I. vomitoria* mortality odds decreased. Additionally, *I. vomitoria* mortality odds responded to topography: Hotter, more westward facing aspects and drier, steeper slopes increased mortality odds.

In *Juniperus virginiana* (Red cedar), which a close relative of *J. ashei* but largely excluded from the Edwards Plateau, mortality odds were increased by Cons_NoP and heat exposure (Days > 35°C). This was the same for *J. ashei*. But in contrast to *J. ashei*, mortality odds increased with stem area density (Aplot) and larger trees had a higher risk of dying (Figure 3).

The species pair *Q. fusiformis*/*Q. virginiana* responded negatively to precipitation in 2011: As precipitation increased, trees were more likely to die. Higher Aplot significantly decreased mortality odds. As with *I. vomitoria*, westerly aspect increased mortality. The trends with respect to precipitation and stem area density are illustrated in Figure 4. The precipitation trend, although significant in the analysis, seemed unconvincing, as both high and low mortality rates could be observed within a narrow range of precipitation values. These trends might thus be spurious. On the other hand, the trend with stem area density appears sound.

Diospyros texana, another understory species, like *J. virginiana*, exhibited a decrease in mortality odds with increasing stem area density. In addition, it exhibited sensitivity to high temperatures. However, unlike all other species, *D. texana* was most significantly affected by number of days > 38°C.

For the species pair *U. alata/U. crassifolia*, mortality odds increased with precipitation in 2009 and 2011, both drought years, but these trends had only marginal support and were kept as factors in the model only because they produced a substantially lower AIC_c value. Unique among species, *U. alata/U. crassifolia* mortality increased in plots with a northerly facing aspect, associated with colder temperatures. Trees in sites with a Northness index less than 0.5 radians all had zero mortality, while plot mortalities above 0.5 radians were 0 (2 plots), 0.02, 0.15, 0.22 and 0.4.

U. americana was the least common species in the analysis, and only two marginally significant factors could be identified. *U. americana* increased mortality odds with stem density (Nplot) and decreased mortality odds with an increase in Cons_NoP, another precipitation effect opposite of expectation.

Resprouting

Overall, resprouting occurred rarely. Of the 20% of trees that experienced 100% crown death, only 15% resprouted (Table 5). Resprouting was unevenly distributed across species ($p < 0.001$), for example, the species with the highest resprout percentages were *Prosopis glandulosa* (Honey mesquite) and *Q. virginiana*, those with the lowest, *J. ashei*, *J. virginiana* and *Quercus texana* (Texas oak). For some species, the re-sprout probability was significantly affected by basal stem area. For *J. ashei* and *Q. havardii*, larger trees were more likely to re-sprout ($p = 0.021$ and $p = 0.051$, respectively), but for *Q. texana*, smaller trees were more likely to re-sprout ($p = 0.022$).

Heat exposure in 2011 also had effects on resprouting (Figure 5). Although heat exposure did not always have a significant effect on crown death and tree death, when it

did, the effect was positive. For *D. texana*, more days of exposure to extreme temperatures increased crown death to as much as 20%. At the lower end of exposure, a relatively small proportion of trees died, whereas at the higher end, close to 80% of the trees with crown death died. For *I. vomitoria*, *J. ashei* and *J. virginiana*, the probability of tree death was high for any tree that experienced crown death (>80%) and for *I. vomitoria* and *J. ashei*, heat exposure significantly increased the mortality rate from 80 to 100%. For *J. virginiana*, trees died only at the very highest levels of heat exposure, but then mortality was almost 100%. For *Q. fusiformis*, heat exposure had a significant effect on crown death with percentages reaching up to 80%, whereas for *Q. virginiana*, crown death rate fluctuated around 30%, irrespective of the number of hot days experienced. Therefore, the heat effect on crown death for *Q. virginiana* was not significant, although the heat effect on tree death was marginally significant.

Intra- versus interspecific effects on tree mortality

On the Edwards Plateau, mortality of *J. ashei* and *Q. fusiformis/Q. virginiana* was primarily affected by members of their own species; the higher the intraspecific tree density on a plot, the greater the mortality (Table 6; Figure 9). No other tree densities affected *J. ashei*. However, *D. texana* had a positive effect on *Q. fusiformis/Q. virginiana* mortality, while “Other” species had a significant negative effect on mortality. For *D. texana*, “Other” tree density also had a significantly negative effect on mortality. Notably, *J. ashei* density did not significantly affect *Q. fusiformis/Q. virginiana* or *D. texana* mortality even though it was by far the most abundant species on the Edwards Plateau.

IV. DISCUSSION

Strengths and weaknesses of the data

The examination of regional mortality data is challenging, as it is not possible to maximize precision and scope at the same time. There is only one other study that attempted to conduct a regional analysis of tree mortality,⁵² (Moore et al. 2016) which opted to maximize scope, sacrificing precision. Working with the Texas Forest Service survey data that counted dead trees on long-term observation plots, Moore et al.⁵³ (2016) surveyed 117 plots of 0.16 ha each in Central Texas. By comparison, my study encompassed 40 plots of 0.09 ha each, thus it was much smaller in scope. However, I collected more detailed data at the plot scale. In Moore et al.'s study,⁵⁴(2016) the total count of dead juniper trees for Central Texas was 186 (in my study: 634) and for oak 66 trees (in my study: 57). Thus, while my study is not representative of mortality rates in Central Texas, it does provide a good basis for examining local drivers of tree mortality.

I surveyed over 6600 trees on the Edwards Plateau, a far greater number than in any other ecoregion. Therefore, I have higher confidence in the analyses of species common on the Edwards Plateau and somewhat less confidence for species occurring only outside the Edwards Plateau. For example, the most common species that were dominant outside the Edwards Plateau were *J. virginiana* and *Quercus stellata* (Post oak), and they were represented by 391 and 264 trees in 9 and 12 plots, respectively. On the Edwards Plateau, the most common dominant species were *J. ashei* and *Q. fusiformis*,

⁵² Moore and others.

⁵³ Ibid.

⁵⁴ Ibid.

represented by 3535 and 79 trees in 31 and 9 plots, respectively. Some species were found across ecoregions, such as the understory species *D. texana* and *I. vomitoria*, with 303 and 742 trees in 16 and 8 plots, respectively. Thus, some species responses were specific to ecoregion, while others were responses to a wider range of conditions across ecoregions.

Drivers of tree mortality by species

Indicators of precipitation in drought years significantly affected six out of the seven species groups, including Cons_NoP and Precipitation in 2008, 2009 and 2011. However, the effects of more precipitation on mortality were not always positive. By contrast, indicators of heat exposure in 2011 had consistently negative effects on the survivorship of three species: *J. ashei*, *J. virginiana*, and *D. texana*, with particularly strong effects on *J. virginiana* (Figure 5). *J. ashei* and *J. virginiana* were also negatively affected by ConsNo_P, while *D. texana* was not affected by precipitation at all. The *Juniper* genus is considered a drought tolerant, anisohydric genus with dense wood, though *D. texana* is considered much less so.⁵⁵ In average drought years, these species may operate close to their critical water potentials, but exceed critical levels when long drought periods are coupled with high temperature. With less water storage capacity, due to dense wood, the extreme heat during a severe drought year could have depleted stem water storage at an accelerated pace and killed the tree.

⁵⁵ H. González Rodríguez and others, "Plant Water Relations of Thornscrub Shrub Species, North-Eastern Mexico," *Journal of Arid Environments* 58, no. 4 (2004); Linton, Sperry, and Williams; H. Stienen and others, "Ecophysiology of 8 Woody Multipurpose Species from Semiarid Northeastern Mexico," *Annales des Sciences Forestières (Paris)* 46, no. SUPPL (1989).

This result supports the leading hypothesis of tree die-off⁵⁶ (Allen et al. 2010) that “hot drought” triggers elevated mortality rates and that anisohydric trees are especially susceptible to such events.⁵⁷ However, some species responded to the contrary. In the three elm species, which are winter-deciduous, and *I. vomitoria*, an evergreen understory species, precipitation in a drought year (either 2009 or 2011) appeared to increase mortality odds, while heat exposure had no significant effect. These species do not lack in drought tolerance. Precipitation in a non-drought year, did not affect these species negatively, suggesting perhaps that the timing of precipitation in a drought year can have a negative effect on survivorship. Further analysis of the distribution of precipitation variation in 2011 may shed more light on this phenomenon.

Effects of topography, which influences insolation, were comparatively minor, with largely predictable effects on *J. ashei*, *I. vomitoria* and *Q. fusiformis/virginiana*, indicating that higher exposure to radiation increased mortality odds. However, *U. alata/U. crassifolia* responded negatively to northern exposure, which suggests negative effects of winter-low temperatures, rather than summer-high temperatures, perhaps in association with drought.

The comparison of *J. ashei* and *J. virginiana* also demonstrated that members of the same genus can respond differently to drivers of mortality, while having similar mortality rates. Between *J. ashei* and *J. virginiana*, this was probably driven by the two species occupying different ecoregions. For example, in *J. ashei*, which grows predominantly on the Edwards Plateau, depth to bedrock and the interaction of

⁵⁶ Allen and others.

⁵⁷ McDowell and others, "Mechanisms of Plant Survival and Mortality During Drought: Why Do Some Plants Survive While Others Succumb to Drought?."

precipitation in 2010 and water storage capacity significantly affected mortality odds. These factors were not significant to *J. virginiana*, because on the deep prairie soils where *J. virginiana* was growing, there was no shallow bedrock and little variation in water storage capacity. Surprisingly, *J. ashei* had increased mortality odds where conditions for growth were presumably better: in deeper soil and/or with more potential for water storage. Tree densities were higher on these sites, which could have intensified water stress in an extreme drought year. *J. ashei* is a woody encroacher on the Edwards Plateau and has established very high densities in places where it has been historically absent. It is believed that before European arrival, *J. ashei* populations were found mostly on rocky slopes,⁵⁸ where in our study, mortality was comparatively low. This suggests that recently encroached landscape elements have elevated levels of tree mortality, specifically for the woody encroacher.

Effects of tree size and density

I initially hypothesized that tree density would be a driver of mortality. In addition, Moore et al.'s⁵⁹ (2016) study, as well as other studies,⁶⁰ indicated that larger trees have higher mortality rates. My study showed that measures of tree density or other measures correlated with tree density, such as depth to bedrock, had inconsistent effects on mortality odds, for some species increasing, in others decreasing the odds and in still

⁵⁸ O. W. Van Auken, "Shrub Invasions of North American Semiarid Grasslands," *Annual Review of Ecology and Systematics* 31, (2000).

⁵⁹ Moore and others.

⁶⁰ Morgane Merlin and others, "Effects of Stand Composition and Tree Size on Resistance and Resilience to Drought in Sessile Oak and Scots Pine," *Forest Ecology and Management* 339, (2014); Rebecca C. Mueller and others, "Differential Tree Mortality in Response to Severe Drought: Evidence for Long-Term Vegetation Shifts," *Journal of Ecology* 93, no. 6 (2005).

other species having no significant effects at all. This illustrates that community-integrated stem density or stem-area density is a poor predictor of tree mortality.

Further, tree size was not significantly associated with mortality in most species, except in *J. ashei* and *J. virginiana*, where tree size had opposite effects, increasing the mortality odds for *J. virginiana* and decreasing them for *J. ashei* (Figure 3). This result is not too surprising, considering that *J. ashei*, as a woody encroacher, commonly occurs in dense stands of trees with low basal areas. For species experiencing a high degree of intraspecific competition, being a larger individual is rarely a risk, on the contrary.⁶¹ However, few tree species experience strong intraspecific competition and size may affect survivorship differently for species experiencing diffuse competition from heterospecific trees. In my study, the highest number of *J. ashei* trees in a plot was 270, whereas the highest number of *J. virginiana* trees was 112.

Intraspecific density effects on mortality were significant in *J. ashei* and *Q. fusiformis/virginiana*. The effect of *Q. fusiformis/Q. virginiana* on itself was surprising because the density of these species is much lower than that of *J. ashei*. However, Quercus trees are known to be deep-rooted⁶² and they may also be quite old, being far more likely to regenerate vegetatively from root sprouts than sexually from seeds.⁶³ Thus, oak trees could have very extensive root systems that may be able to interact over large inter-individual distances. The apparently positive effect of “Other” trees on *Q. fusiformis/Q. virginiana* is probably indirect: Plots that had few “Other” trees were

⁶¹ Jacob Weiner, "Asymmetric Competition in Plant Populations," *Trends in Ecology & Evolution* 5, no. 11 (1990).

⁶² R. B. Jackson and others, "Ecosystem Rooting Depth Determined with Caves and DNA," *Proceedings of the National Academy of Sciences* 96, no. 20 (1999).

⁶³ F. Leland Russell and Norma L. Fowler, "Rarity of Oak Saplings in Savannas and Woodlands of the Eastern Edwards Plateau, Texas," *The Southwestern Naturalist* 44, no. 1 (1999).

dominated by *Q. fusiformis/virginiana*, *D. texana* and *J. ashei*, which together had a negative effect.

Q. fusiformis/Q. virginiana was also negatively affected by *D. texana* density. I observed that *D. texana* often forms dense understories below large trees, including oak trees. This suggests that a nurse-plant relationship between *Quercus* and *D. texana* could develop into a risk factor for the canopy species in a drought year. Very little is known about the root structure of *D. texana*. Only one study suggests that it is shallow-rooted,⁶⁴ but this seems unlikely given its negative effect on *Quercus* during drought.

D. texana itself responded positively to the density of trees other than *J. ashei* and *Q. fusiformis/vi. D. texana* was also the only species negatively affected only by temperatures > 38°C, which may signify greater protection from heat exposure by growing in the shade of larger trees.

Contrary to common belief, *J. ashei*, the most common species on the Edwards Plateau, did not significantly affect *Q. fusiformis* mortality. There is a common perception that *J. ashei* competes with *Q. fusiformis* for water, thus killing off *Q. fusiformis* in a drought year. This perception was not supported by my study. But it provides further evidence that the rooting systems of *J. ashei* and *Q. fusiformis* are well separated⁶⁵ and that the species avoid below-ground competition, explaining their frequent coexistence in Edwards Plateau woodlands.

⁶⁴ Jim A Nelson, Paul W Barnes, and Steve Archer, "Leaf Demography and Growth Responses to Altered Resource Availability in Woody Plants of Contrasting Leaf Habit in a Subtropical Savanna," *Plant Ecology* 160, no. 2 (2002).

⁶⁵ Marcy E Litvak, Susan Schwinning, and James L Heilman, "Woody Plant Rooting Depth and Ecosystem Function of Savannas: A Case Study from the Edwards Plateau Karst, Texas," *Ecosystem Function in Savannas*, (2011).

Resprouting

Resprouting is rarely considered in studies of tree mortality. Usually, as in Moore et al.'s⁶⁶(2016) study, trees with 100% crown dieback are considered “dead”. From a forestry viewpoint, this may be reasonable, since a new tree stem grows back from a root stock. However, from the viewpoint of vegetation dynamics, this is problematic, because regeneration from sprouts ensures that a forest gap continues to be occupied by the same individual and species. Furthermore, the growth and survivorship of sprouts should be much greater than those of seedlings. Thus, it is important to ask, how often crown dieback is associated with the true death of an individual.

There are tree species for which 100% crown dieback is highly associated with tree death. In *I. vomitoria*, *J. ashei*, and *J. virginiana*, trees that lost their entire crown had an 80-100% risk of dying. Juniper trees are not commonly considered “sprouters” but we did observe small resprout percentages specifically in *J. ashei*. In *Q. fusiformis* and *Q. virginiana* resprouting was more common, although a majority of trees did not resprout. Although we examined only 36 trees in *P. glandulosa*, more individuals resprouted than died after crown loss.

Both crown loss and death were positively associated with heat exposure (Figure 5). For some species, temperature affected the odds of resprouting more strongly than the odds of crown die-back. For example, in *D. texana*, tree death was strongly associated with the inability to resprout under high temperature. Complex interactions could have contributed here. For example, high temperature exposure could have killed the crown of

⁶⁶ Moore and others.

D. texana's nurse trees, which would have abruptly changed for the worse the micro-environment of *D. texana* during recovery.

Conclusion

Despite the relatively limited spatial extent of my study, I was able to identify a small set of important drivers of tree mortality from among many potential drivers examined. The data supported well-known drivers, such as high temperature exposure, but also less obvious complexities affecting mortality patterns. The most compelling results were found for *J. ashei*, by far the most numerous species in our study. I found that this woody encroacher exhibited strong intraspecific density-dependent mortality during a drought year, but had no effect on the mortality of other species. It is possible that the mortality rates observed locally increased with site productivity (i.e. deeper soils), because stem densities recover faster between droughts where trees can grow faster.

By contrast, frequently ignored species, such as the understory species *D. texana* did have negative effects on other species' survivorship. In the short term, it exploited canopy species by profiting from their abundance, but in the longer term, *D. texana*'s negative effect on their survivorship may have decreased its chance of resprouting.

Tree mortality is an important component to climate change adaptation, as it opens space for species to turn over. Studies should also be conducted to examine what happens in spaces where trees have died to determine the consequences of tree mortality events during "climate-change type" droughts on the future of plant communities.

V. SIGNIFICANCE

My study is among the few studies in North America so far that have examined drought mortality among multiple species and communities and evaluated the contributions of multiple landscape factors. I examined the influence of several contributing, inciting and predisposing factors on mortality odds. In general, my study showed that species tend to respond idiosyncratically to these factors and that there may be complex interactions between species traits, community dynamics and drought-related mortality. This information is important to the management of forest resources and the development of vegetation models aimed at representing climate-vegetation interactions.⁶⁷ Tree mortality paves the way for the establishment of new trees, a first step in the process of community change and shifts in ecosystem function.⁶⁸ Among these changes, could also be the accelerated spread of invasive species.⁶⁹

⁶⁷ Céline Boisvenue and Steven W Running, "Impacts of Climate Change on Natural Forest Productivity—Evidence since the Middle of the 20th Century," *Global Change Biology* 12, no. 5 (2006); Gordon B Bonan, "Forests and Climate Change: Forcings, Feedbacks, and the Climate Benefits of Forests," *Science* 320, no. 5882 (2008).

⁶⁸ Craig D. Allen and David D. Breshears, "Drought-Induced Shift of a Forest–Woodland Ecotone: Rapid Landscape Response to Climate Variation," *Proceedings of the National Academy of Sciences* 95, no. 25 (1998); Jerry F. Franklin, H. H. Shugart, and Mark E. Harmon, "Tree Death as an Ecological Process," *Bioscience* 37, no. 8 (1987); María L. Suarez and Thomas Kitzberger, "Recruitment Patterns Following a Severe Drought: Long-Term Compositional Shifts in Patagonian Forests," *Canadian Journal of Forest Research* 38, no. 12 (2008); Gian-Reto Walther, Silje Berger, and Martin T Sykes, "An Ecological 'Footprint' of Climate Change," *Proceedings of the Royal Society of London B: Biological Sciences* 272, no. 1571 (2005).

⁶⁹ Gian-Reto Walther, "Community and Ecosystem Responses to Recent Climate Change," *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 365, no. 1549 (2010).

TABLES

Table 1. Covariates used in the regression analysis.

Abbrev.	Definition	Range	Unit
CLIMATE			
P2008	Total precipitation in 2008	320 - 1034	mm
P2009	Total precipitation in 2009	405 – 1176	mm
P2010	Total precipitation in 2010	464 – 1050	mm
P2011	Total precipitation in 2011	280 – 578	mm
ConsNo_P	Longest consecutive number of days with precipitation < 5 mm in 2001	62 – 116	days
DA30	Total number of days above 30°C in 2011	163 - 183	days
DA35	Total number of days above 35°C in 2011	92 – 117	days
DA38	Total number of days above 38°C in 2011	9 – 63	days
ELEV	Elevation above sea level	53 - 682	m
SOIL			
CLAY	Percent clay in soil	9.5 – 39.0	%
BRD	Depth to bedrock (for deep soils, the maximal depth is set to 152 cm)	37 - 152	cm
WS	Water storage in the top 150 cm	1.47 – 9.22	
TOPOGRAPHY			
SLOPE	Average slope at plot coordinates	0.7 – 22.7	degrees
EAST	Sine of Eastern Aspect	-1 – 1	radians
NORTH	Cosine of Northern Aspect	-1 – 1	radians
INSOL	Annual insolation	1.22 – 1.53	
COMMUNITY			
NPLOT	Number of stems > 10 cm basal circumference in plot	18 – 339	dimensionless
APLOT	Total basal stem area of stems > 10 cm basal circumference in plot	1.15- 5.80	m ²
NJUAS	Number of <i>J. ashei</i> stems > 10 cm basal circumference (Edwards Plateau only)	4 – 270	dimensionless
NQU	Number of <i>Q. fusiformis</i> and <i>Q. virginiana</i> stems > 10 cm basal circumference (Edwards Plateau only)	0 – 39	dimensionless
NDITE	Number of <i>D. texana</i> stems > 10 cm basal circumference (Edwards Plateau only)	0 – 69	dimensionless
INDIVIDUAL			
STEM	Basal stem area	6.5 – 7170.4	cm ²

Table 2. Physical plot summary

Variable	N	Median	Minimum	Maximum	Range
Latitude	40	30.151725	29.62592	30.91915	1.29323
Longitude	40	-98.16294	-100.58144	-96.14155	4.43989
NPLOT	40	171	18	339	321
APLOT	40	37468.95345	11539.9021	57955.4331	46415.531
Cons_noP	40	163	116	281	165
DA35	40	52	19	73	54
DA38	40	11	3	26	23
P2008	40	388.1	320.4	1034.12	713.72
P2009	40	813.055	404.91	1176.34	771.43
P2011	40	446.1	279.8	578.92	299.12
ELEV	40	334.8182	52.7546	681.5294	628.7748
SLOPE	40	3.1255	0.7378	22.6505	21.9127
EAST	40	-0.1926	-0.9972	0.9997	1.9969
NORTH	40	0.24035	-0.9936	0.9997	1.9933
INSOL	40	1.43625	1.2247	1.5273	0.3026
BRD	40	91	37	152	115
WS	40	3.415	1.47	9.22	7.75
CLAY	40	36.5952	9.6	56.25	46.65

Table 3. Results of the site factor analysis using binomial linear regression after standardizing covariates. The statistic Exp(B) is the odds ratio for the event of death to occur. Thus, values > 1 indicate that the factor is positively associated with tree death and values < 1 indicate the opposite.

Co-variates	Juas		Ilvo		Juvi		Qufu/Quvi		Dite		Ulal/Ulcr		Ulam	
	N = 3487		N = 742		N = 439		N = 352		N = 303		N = 225		N = 122	
	Plots = 30		Plots = 8		Plots = 10		Plots = 25		Plots = 16		Plots = 11		Plots = 8	
	Overall mortality 18%		Overall mortality 20%		Overall mortality 13%		Overall mortality 15%		Overall mortality 8.6%		Overall mortality 7%		Overall mortality 7%	
	Nagelkerke R2 = 0.099		Nagelkerke R2 = 0.127		Nagelkerke R2 = 0.321		Nagelkerke R2 = 0.141		Nagelkerke R2 = 0.161		Nagelkerke R2 = 0.316		Nagelkerke R2 = 0.422	
	p-value	Exp(B)	p-value	Exp(B)	p-value	Exp(B)	p-value	Exp(B)	p-value	Exp(B)	p-value	Exp(B)	p-value	Exp(B)
Cons-No P	0.000	1.430	0.000	0.565	0.021	3.357							0.067	0.632
APLOT					0.026	1.389	0.000	0.374	0.015	0.573				
EAST			0.000	0.535			0.001	0.552						
DA35	0.001	1.221			0.005	17.135								
P2011							0.001	2.008			0.050	1.897		
NORTH											0.014	52.667		
DA38									0.001	3.020				
BRD	0.000	1.566												
NPLOT													0.053	36.038
P2008	0.000	0.151												
P2009											0.096	12.904		
P2010 x WS	0.010	1.244												
SLOPE			0.001	1.375										
STEM AREA (tree size)	0.000	0.408			0.071	1.338								
INSOL	0.000	1.219												

Table 4. Plot summary

Plot Number	Bioregion	Most common tree	Number of trees in 30 x 30 m plot	Plot Mortality Rate (%)
1	Bioregion	Juas	203	6.9
2	Edwards Plateau	Juas	177	9.0
3	Edwards Plateau	Juvi	166	16.3
4	East Central Texas Plains	Qust	104	16.3
5	East Central Texas Plains	Qust	38	34.2
6	East Central Texas Plains	Juvi	203	18.7
7	East Central Texas Plains	Ulal	117	5.1
8	East Central Texas Plains	Juvi	203	25.1
9	East Central Texas Plains	Juas	171	5.3
10	Edwards Plateau	Juas	228	16.2
11	Edwards Plateau	Juas	284	11.6
12	Edwards Plateau	Juas	208	22.1
13	Edwards Plateau	Juas	171	20.5
14	Edwards Plateau	Juas	223	18.4
15	Edwards Plateau	Juas	129	2.3
16	Edwards Plateau	Juas	105	2.9
17	Edwards Plateau	Juas	208	20.2
18	Edwards Plateau	Quha	246	24.0
19	Cross Timbers	Quha	310	15.5
20	Cross Timbers	Juas	131	30.5
21	Edwards Plateau	Juas	163	22.7
22	Edwards Plateau	Juas	116	12.9
23	Edwards Plateau	Juas	53	11.3
24	Edwards Plateau	Juas	61	3.3
25	Edwards Plateau	Juas	144	32.6
26	Edwards Plateau	Dite	149	18.1
27	Edwards Plateau	Juas	285	29.5
28	Edwards Plateau	Ilvo	241	18.3
29	East Central Texas Plains	Ilvo	247	4.5
30	East Central Texas Plains	Juvi	222	10.8
31	Blackland Prairie	Quvi	38	31.6
32	Edwards Plateau	Quvi	18	0.0
33	Edwards Plateau	Quvi	54	1.9
34	Edwards Plateau	Juas	69	17.4
35	Edwards Plateau	Juas	111	7.2
36	Edwards Plateau	Juas	145	15.9
37	Edwards Plateau	Sose	226	10.6
38	Edwards Plateau	Ilvo	339	19.8
39	East Central Texas Plains	Juas	196	36.2
40	Edwards Plateau	Juas	280	14.3
Average			170	16.0
Range			18 - 339	0-36.2

Table 5. Most common species in the plot census. %Dead is the percentage of all trees with 100% crown death that no sign of resprouting. % Resprout is the percentage of all trees of that species with crown death that resprouted. % Live is the percentage of all trees with surviving crowns.

Species abbreviation	Scientific Name	Common Name	Total Count	Number of plots	% Resprout	% Dead	% Live
Juas	<i>Juniperus ashei</i>	Ashe juniper	3487	30	2	18	80
Quvi	<i>Quercus virginiana</i>	Southern live oak	273	17	9	13	78
Dite	<i>Diospyros texana</i>	Texas persimmon	303	16	6	9	85
Qust	<i>Quercus stellata</i>	Post oak	264	12	2	17	81
Ulal	<i>Ulmus alata</i>	Winged elm	137	10	1	8	91
Juvi	<i>Juniperus virginiana</i>	Red cedar	439	10	0	13	87
Qufu	<i>Quercus fusiformis</i>	Escarpment live oak	79	9	5	20	75
Ilvo	<i>Ilex vomitoria</i>	Yaupon holly	742	8	3	20	78
Ulam	<i>Ulmus Americana</i>	American elm	122	8	2	7	91
Quha	<i>Quercus havardii</i>	Shin oak	381	7	6	27	67
Prgl	<i>Prosopis glandulosa</i>	Honey mesquite	36	7	14	8	78
Sose	<i>Sophora secundiflora</i>	Mountain laurel	173	6	9	3	87
Ulcr	<i>Ulmus crassifolia</i>	Cedar elm	88	6	3	5	92
Qute	<i>Quercus texana</i>	Texas oak	30	6	0	7	93
Ceoc	<i>Celtis occidentalis</i>	Common hackberry	33	3	3	21	76
Vaar	<i>Vaccinium arboreum</i>	Farkleberry	54	1	15	24	61
Total			6640	40	3	17	80

Table 6. Intra- and interspecific density effect on tree mortality on the Edwards Plateau.

	Effect on Juas mortality		Effect on Dite mortality		Effect on Qufu/vi mortality	
	P	Exp(B)	P	Exp(B)	P	Exp(B)
Juas	<0.001	1.003	0.035	0.990	0.711	0.999
Dite	0.066	1.005	0.294	0.989	<0.001	1.034
Qufuvi	0.801	1.001	0.444	0.983	0.038	1.032
Other	0.001	0.994	0.044	0.987	0.009	0.932

FIGURES

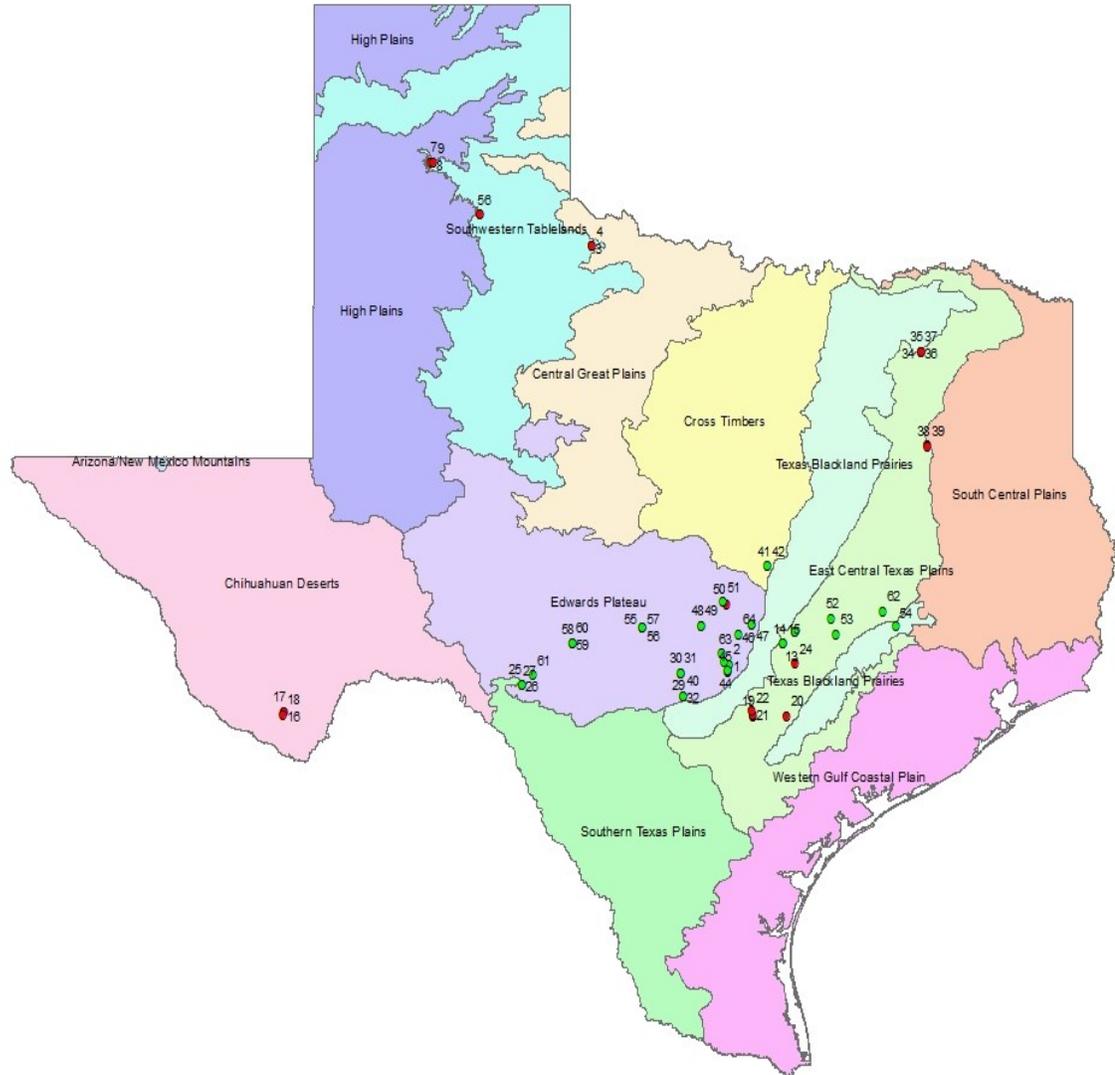


Figure 1. Map of site locations. Green symbols for plots included in the analysis. Ecoregions layer (Omernik III) provided by the U.S. Environmental Protection Agency.⁷⁰

⁷⁰ G.E. Griffith, Bryce, S.A., Omernik, J.M., Comstock, J.A., Rogers, A.C., Harrison, B., Hatch, S.L., and Bezanson, D., "Ecoregions of Texas," (Reston, Virginia: U.S. Geological Survey (map scale 1:2,500,000), 2004).

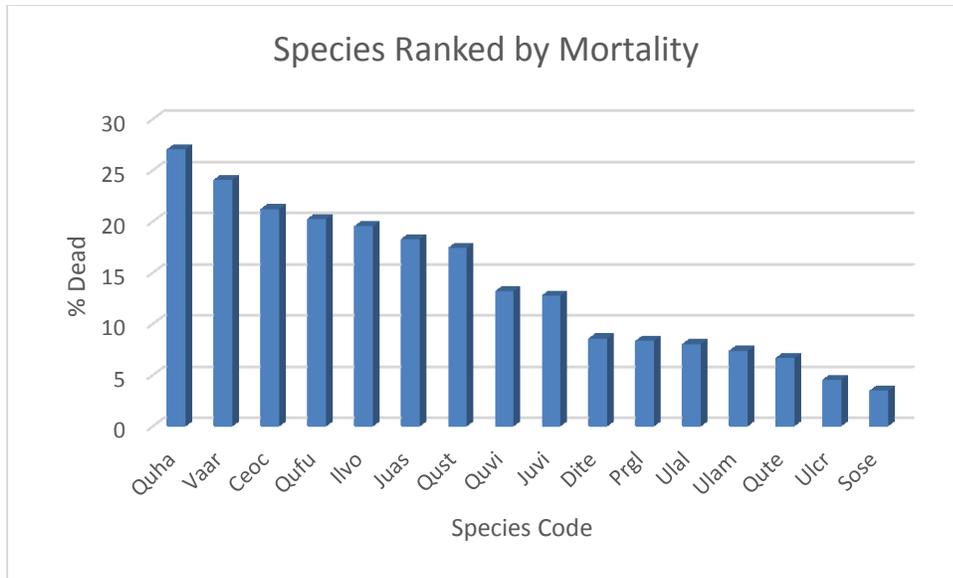


Figure 2. Species ranked by level of mortality.

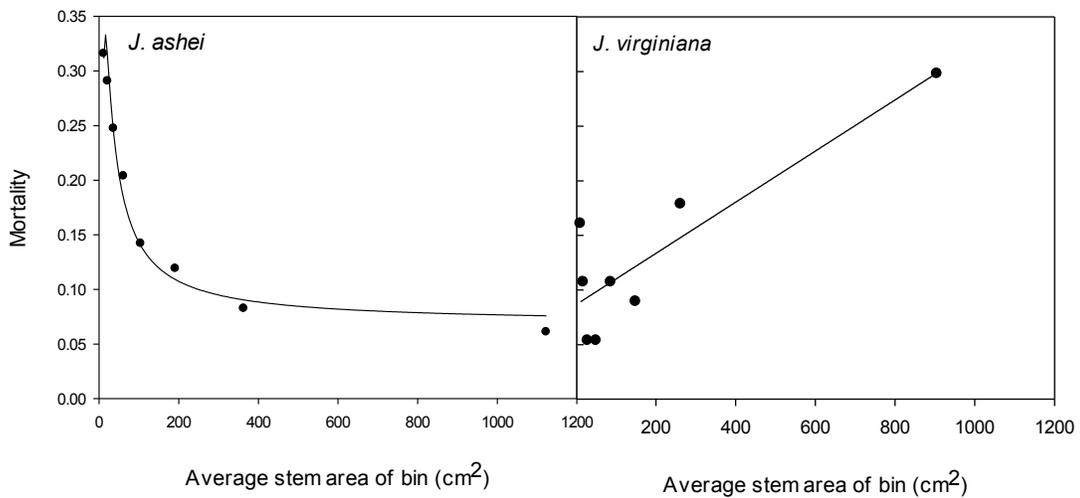


Figure 3. Comparison of Juas and Juvi mortality rate in plots by basal stem area. Stem areas were distributed into eight bins between the lowest and the highest stem area. The range of each bin was determined by equalizing membership per bin. Bins are represented by the average stem area of bin members. The lines represent the best fit of a four-parameter logistic model.

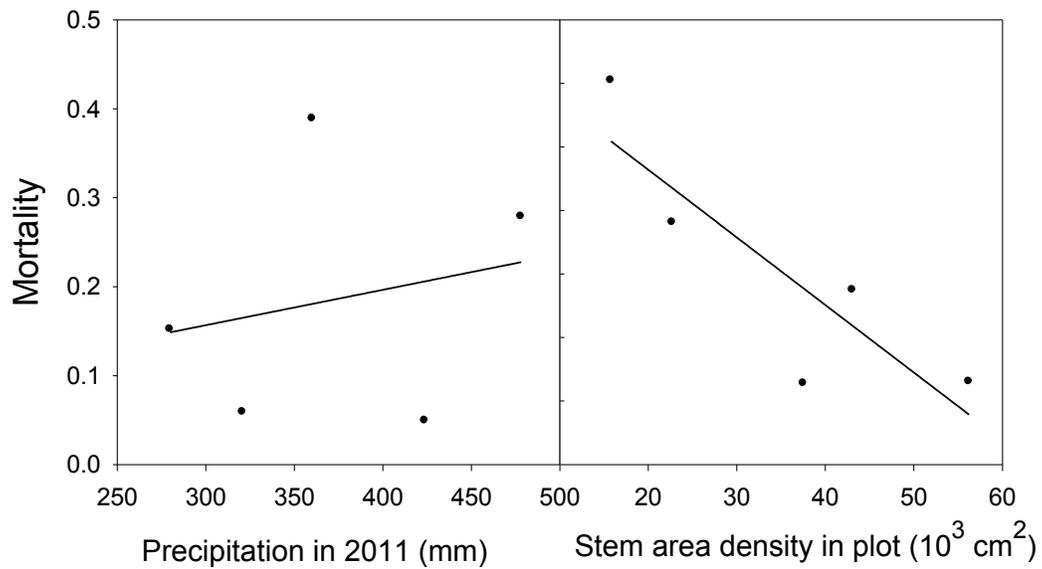


Figure 4. The effects 2011 precipitation and Stem area density on Qufu/Quvi mortality. Mortalities were calculated for precipitation and density bins. The range of precipitation and density were divided into bins of equal width. The values on the x-axis correspond to bin averages weighted by tree number. The lines are linear regression lines to aid visualization of the data trends.

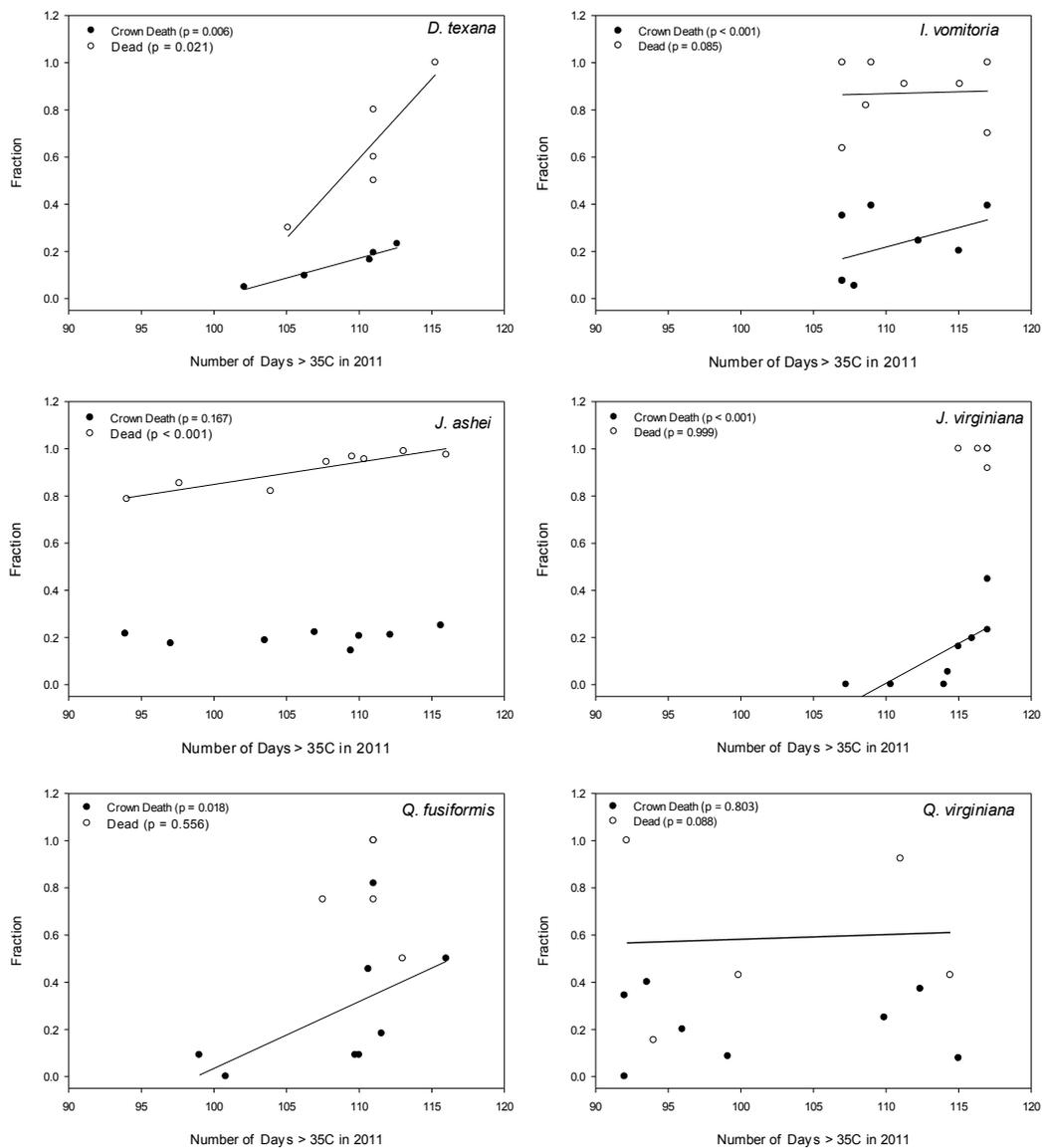


Figure 5. Temperature effects on die-back and resprouting. The effect of days in 2011 with temperatures > 35°C (days>35) on the fraction of trees that experienced to total canopy dieback (closed circles) and among the latter, the fraction of trees that did not resprout (open circles). Samples were divided into 8 or 5 bins according to days>35 values. The range of each bin was determined by equalizing samples per bin. Species with smaller sample sizes were divided into 5 bins, all others into 8 bins. Bins are represented by their average values for days>35. The regression lines are drawn for visualization and only for cases in which the temperature regime had a significant effect. P-values represent the result of binomial linear regression.

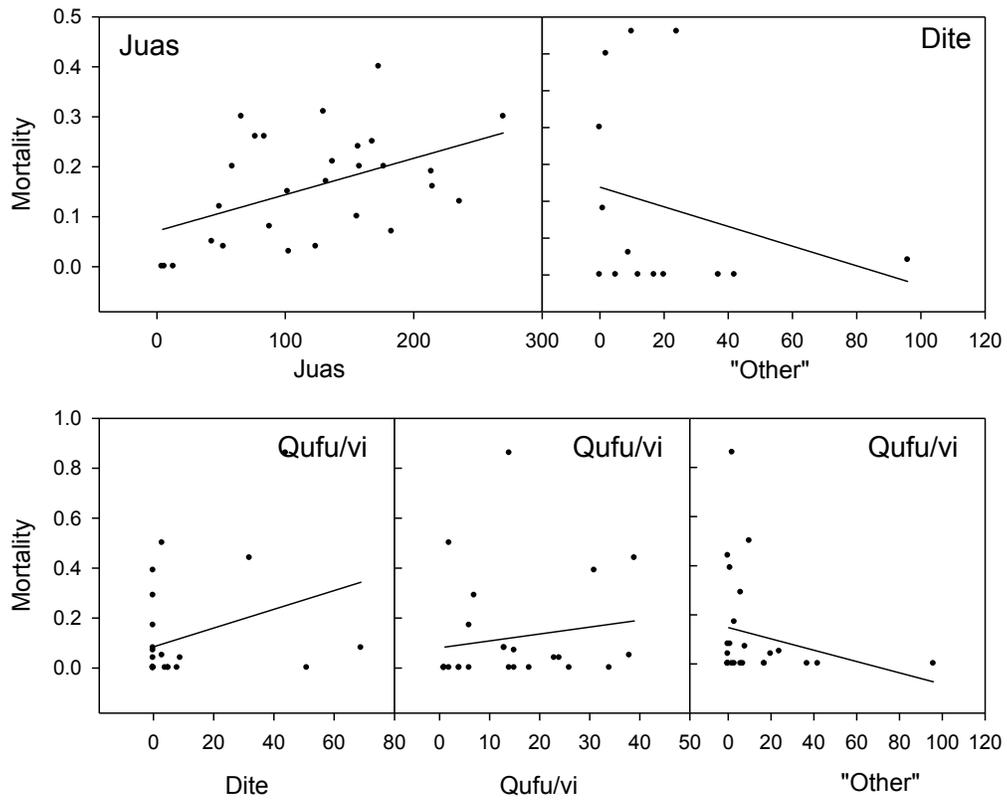


Figure 6. Significant intra- and interspecific effects of tree density on the Edwards Plateau. Plot-level mortality is shown as a function of tree number per plot for the respective species. "Other" refers to all trees other than Juas, Dite, Qufu and Quvi. Results of the binomial regression analysis are shown in Table 7. Regression lines are drawn for visualization only.

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