

VARIATION IN PHYSIOLOGICAL RESPONSES OF FOREST TREES TO DISTURBANCE:
IMPLICATIONS FOR FUTURE FOREST CARBON AND MANAGEMENT

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Submitted to the Department of Ecology and Evolutionary Biology
and the Graduate Faculty of the University of Kansas
in partial fulfillment of the requirements
for the degree of Doctor of Philosophy

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ABSTRACT

Rapid environmental change in recent decades has challenged Ecologists to focus on understanding ecosystem response and physiological functioning in the face of increased disturbances. Understanding physiological responses of trees to disturbance and climatic variability can enable researchers to manage ecosystems to ensure continued ecological functioning in the future. In this dissertation, I use classic dendroecology, tree physiology theory, original stable isotope methodology, and a novel analytical model to explore the impacts of disturbance and climate variability on *Quercus* species in forested ecosystems in the Midwestern U.S. Anthropogenic land use changes along with increased occurrence of pathogen, pest, and climatic disturbance events are impacting forest ecosystems. A tree's susceptibility to decline following disturbance events must be assessed to understand changes to forest ecosystem function and distribution, especially at species boundaries, with predicted future increases in the frequency of disturbances such as drought in the Midwestern U.S. The oak ecosystems of eastern Kansas and the mixed oak-hickory forests of northwest Arkansas have experienced high levels of climatic variability in the past 5 decades, which have influenced differential physiological responses of co-occurring species. In Chapter 1, I investigate differential physiological response to pest and drought disturbances in co-occurring *Quercus rubra*. By examining growth, stable carbon, oxygen and nitrogen isotopes in tree-rings, and contemporary leaf nitrogen dynamics, I show that differential stable carbon and oxygen isotope relationships in tree-rings, along with leaf nitrogen relationships, suggest varied susceptibility to disturbance among well-interspersed, co-occurring trees.

The differential responses of co-occurring species may provide insight into future forest composition under the prediction of increased disturbance events. In Chapter 2, I use two co-occurring species to explore the impacts of climate variability on physiological responses. I investigate climate relationships through growth, stable isotopes in tree-rings, and contemporary leaf data in an effort to understand the future of these species at their western range boundaries at the prairie-forest ecotone of North America. I suggest that a typically drought-vulnerable species exhibits stable carbon and oxygen isotopic values suggestive of greater water stress relative to a less drought-prone oak species and find evidence hinting at differences in factors influencing carbon source:sink dynamics related to response to vapor pressure deficit (VPD) and photosynthetic regulation. Comparing these data to the C source:sink dynamics of the more drought-tolerant, co-occurring oak leads me to explore nitrogen dynamics in an effort to understand the impacts of climate variability on these species' growth. The dynamics studied in this forest-prairie ecotone at the University of Kansas Field Station provide insight into the changing forest dynamics in coming decades under predicted increases in drought disturbance events.

Nonlinear patterns in ecological systems can provide insight into capacity of a system to deal with variability. In Chapter 3, I use simplex and s-map forecasting models to assess nonlinearity in growth between healthy and dying trees to determine if nonlinear growth dynamics may relate to a tree's vulnerability to mortality following disturbance events for two forested regions in northwestern and west-central Arkansas, USA. By applying nonlinear

forecasting models in a novel manner, I investigate the utility of discerning non-linear vs. linear dynamics in growth for understanding forest ecosystem dynamics and predictions of adaptability of trees to climatic variability. I also explore data concatenation, or stringing together of time series to increase statistical power, of tree-ring data sets to assess the presence of nonlinearity pre- and post-drought disturbance events, and the potential use of concatenation with nonlinear forecasting models as a tool for exploring the future of forest ecosystems with predicted increases in disturbance events. I suggest that nonlinear growth dynamics are linked to increased capacity to adapt to variability for trees, and discuss why this may be the case.

Disturbance events are predicted to increase in frequency and duration under future climate change. Maintaining forest ecosystems, and their ability to cope with stress, is thus an increasing concern for forest managers. In Chapter 4, I explore forest management policy and its impacts on forest decline events in northwest Arkansas. I review the management policies of our nation's forests, and suggest adaptive management strategies and monitoring tools for decreasing the vulnerability of forests to future disturbance events. I suggest that management policies should address local goals for increasing biodiversity and adaptability of forests in the future and recommend ecosystem monitoring tools for forest managers.

The results of this dissertation suggest that increasing frequency of forest disturbances will have significant ramifications for forest ecosystems through impacts on forest ecophysiological function, species distribution, and carbon and nutrient cycling. Detection of disturbance vulnerability may help in managers develop strategies for increasing forest adaptability to disturbances such as droughts and pest infestations.

ACKNOWLEDGEMENTS

The great support system of colleagues, mentors, and close friends has helped me through my time at KU. I want to express my deep gratitude to my advisor, Sharon Billings. Her professional grace and broad research scope drew me into academia, and I am grateful for her insight, brilliance, and drive for making me strive for my best. Her encouraging ways made me a better researcher overall, and she has been the best resource for my research endeavors. Along with the influence of my committee members Joy Ward, Bryan Foster, Val Smith, and Nate Brunsell, I have gained helpful feedback and insight into my research undertakings. Also of great help were Joane Nagel of KU, Fred Stephen of University of Arkansas, and Jesse Nippert of Kansas State University, by supporting my research and providing resources.

My research was conducted at the Kansas Field Station with the help of Bill Busby, Craig Freeman, Dean Kettle, my great field assistants and, of course, my advisor Sharon Billings. Field

collection in the Boston and Ouachita Mountains was undertaken by Fred Stephen's lab at the University of Arkansas with much help from Laurel Haavik. I greatly appreciate my undergraduate field and lab assistants Anna Tartarko, Nameer Baker, and Alison King; my former fellow-PhD student Lisa Tiemann; and the important work by Laurel Haavik and Fred Stephen in Arkansas forests. Funding from the Department of Energy, the U.S. Department of Agriculture's National Forest Service, the Mary Harkey Hall Award in Plant Biology, the KU Field Station Small Grants Program, and the National Science Foundation IGERT C-CHANGE program enabled me to conduct my research and to present my research at national conferences.

My family, Alicia, Scott, Max and Judy Reed, have been incredibly important on my graduate journey. My fiancé, Brad Boone, has offered much stress relief and a supportive shoulder on which to lean. The endless support and understanding of my family has greatly helped me throughout my studies.

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GENERAL INTRODUCTION

Disturbance events are part of the natural ecological process governing ecosystems, but predicted increases in duration and frequency of disturbances in the future can negatively impact forest ecosystems (Dale et al. 2001). We define disturbance as a sporadic interruption in substrate integrity or resource availability, or deviation in environmental conditions, that impacts the ecological functioning of an ecosystem, as defined in White and Pickett (year). Disturbance events are not foreign to forest ecosystems and can play a natural and important ecological role, but increases can also have major negative implications for ecosystem structure and function (Overpeck et al. 1990, Dale et al. 2001).

Natural cycles such as windthrow events and natural and anthropogenic fires drive gap dynamics, thinning of tree stock, and nutrient release cycles that can improve some tree species performance (Guyette and Spetich 2004, Spetich 2004). For example, fires can reduce standing stock and release surviving trees from light limitation (Guyette and Spetich 2004). Cycles of disturbance were altered following European settlement in North America, and subsequent changes in management and land use resulted in forest structure, species composition, and system complexity different from historic forests. Harvesting and fire suppression following European settlement contributed to a change in forest ecosystem dynamics (Strauberg and Hough 1997, Spetich 2004), but forest ecosystems are currently experiencing disturbances at spatial extents and rates that are unmatched since Earth's last glaciation event (Overpeck et al. 1990, Nave et al. 2011). Rising global temperatures are expected with changes in climate in the future, and an increase in extreme events such as drought, which act as disturbance events negatively impacting water and nutrient resources in forest ecosystems, are expected to accompany global climate change (Overpeck et al. 1990, IPCC 2007).

The increased disturbance frequency predicted with future climate change is expected to impact forest ecosystems— evidenced by recent climate change-associated droughts resulting in widespread mortality of tree species in the American southwest (Adams et al. 2009). Also, increasingly warm temperatures have been theorized to have influenced major infestations of forest pests – evidenced by wide-spread pine mortality resulting from pine bark beetle outbreaks associated with warmer temperatures in recent decades (Bentz et al. 2010). Tree mortality and changes in forest carbon and nutrient cycling associated with disturbances could have major ramifications for global carbon cycles along with ecosystem services such as recreation, habitat, water quality, and timber resources on which local communities rely (Anderson et al. 1976). Oak decline is occurring with increasing frequency in North American and European forests (Tainter et al. 1990, Oak et al. 1996, Vettraino et al. 2002), and appears linked to climatic change (Starkey et al. 2000). Understanding the impacts of such climate-related disturbances on forest function and on forest management strategies is a key concern for climate change scientists and forest managers alike.

In this dissertation, I examine the impacts of disturbance on forest ecosystems at different spatial scales (local and regional), at different levels of ecological organization (individual and species), and use different analytical techniques (tree-rings, stable isotopes, and forecast modeling). In Chapter 1, I use tree-ring growth, contemporary leaves, and stable carbon ($\delta^{13}\text{C}$), oxygen ($\delta^{18}\text{O}$), and nitrogen ($\delta^{15}\text{N}$) isotope ratios, and N dynamics to investigate differential growth and mortality resulting from drought and insect infestation on co-occurring northern red oak (*Quercus rubra*). In Chapter 2, I examine co-occurring *Q. rubra* and *Q. macrocarpa* (bur oak) responses to climatic variability utilizing past physiological responses to droughts to understand species-specific abilities to cope with changes in moisture availability. In Chapter 3, I

utilize a forecast modeling in a novel application to investigate underlying growth dynamics from trees in two regions in Arkansas, USA, to understand the impacts of disturbance on growth and to determine if underlying growth dynamics relate to trees' abilities to cope with disturbance. In Chapter 4, I explore past forest policy management implications for recent decline events witnessed in the 21st century, and suggest policy strategies and monitoring tools associated with forecast modeling that could assist in increasing forest abilities to cope with disturbance events in the future. In all the research in this dissertation, I employ established ecological and dendrochronological (tree-ring) theory to develop and test hypotheses of species' responses to climate variability and disturbance. Below I briefly outline the climate change motivation of each of my research goals and the underlying theoretical motivation, along with a concise summary of my main results.

Chapter 1: Tree-ring and contemporary leaf stable isotopes as indicators of tree growth strategies and susceptibility to disturbance

Forest response to variability has been a focus of dendrochronology since the earliest days of the science. Fritts and Cook (year) analyzed patterns of tree-ring growth and found impacts of climate, site, and aspect on growth responses. Historic climate and atmospheric variability can be reconstructed through evidence derived from tree-ring growth and chemical composition. Reconstructing historic climate over centuries is founded in the theory of uniformitarianism, proposed by 18th century geologist James Hutton, which suggests that the natural processes that govern tree-ring development have been consistent through time. While tree-rings can act as a record of past disturbance or variability, they may also provide tools to predict the future of forest ecosystem dynamics.

Understanding how tree growth strategies may influence tree susceptibility to disturbance is an important goal, given projected increases in forest disturbances this century. In Chapter 1, I invoke a region-wide forest disturbance event in an oak-dominated forest in Arkansas, U.S. contrasting healthy trees' responses with co-occurring dying trees' responses to disturbance. In apparently healthy and dying co-occurring *Q. rubra* trees, I assess physiological responses to climate through tree-ring stable isotopic signatures of carbon ($\delta^{13}\text{C}$), oxygen ($\delta^{18}\text{O}$), and nitrogen ($\delta^{15}\text{N}$) along with $\delta^{13}\text{C}$, $\delta^{15}\text{N}$ and nitrogen (N) dynamics in contemporary leaves. We contrast healthy and dying trees to assess N status as a potential driver of tree carbon (C) dynamics. My goal is to explore the mechanisms driving differential responses to disturbance events to understand resilience in apparently healthy trees, while neighboring trees experienced decline and mortality in response to the same environmental forcings.

Environmental stress associated with decreased moisture availability can interrupt tree carbon (C) and water relations (reviewed in Billings and Phillips 2011), production and storage of sugars, and mineral transport (Houston 1987), generating increased susceptibility to opportunistic parasites and secondary stresses (McDowell et al. 2008, Anderegg et al. 2012). Decreased tree radial growth is predicted with decreased moisture availability, with greatest reduction expected in tree species that are sensitive to drought (Orwig and Abrams 1997, Kolb and Adams 2004). Isotopic theory suggests that $\delta^{13}\text{C}$ values of vegetation reflect the ratio of internal to atmospheric $[\text{CO}_2]$ (c_i/c_a), which depends upon photosynthetic capacity (A_{max}) and stomatal conductance (g_s) response to moisture availability (Francey and Farquhar 1982, Farquhar et al. 1982, Farquhar et al. 1989). Variations in $\delta^{13}\text{C}$ of tree-ring α -cellulose is associated with g_s and A_{max} , thus $\delta^{13}\text{C}$ is often linked to measures of water availability (Leavitt and Long 1989, Hubick and Gibson 1993, Saurer et al. 1995) and, less frequently, nitrogen (N)

availability which can govern A_{max} (Gebauer and Schulze 1991). $\delta^{18}\text{O}$ of tree-ring α -cellulose reflects the isotopic signature of source water, internal exchange of O during organic compound formation, evaporative isotopic enrichment of water remaining in the leaf during transpiration, and the concurrent isotopic depletion of leaf water as ^{18}O -deplete xylem water is transported to the stomate (the Peclet effect, Yakir 1992, Farquhar and Lloyd 1993, Barbour et al. 2002, Barbour 2007). Simultaneous analysis of tree-ring $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ suggests the importance of CO_2 source strength (i.e. stomatal conductance, g_s) relative to C sink strength (i.e. photosynthetic rate, A_{max}) as limitations to growth (Barbour and Farquhar 2000, Barbour et al. 2002, Cabrera-Bosquet et al. 2010). $\delta^{13}\text{C}$, but not $\delta^{18}\text{O}$, can vary with A_{max} , and both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ can vary with changes in g_s in response to conditions. Thus, models predict a positive relationship between vegetation $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ with changing g_s , holding all other variables constant (Scheidegger et al. 2000, Barbour et al. 2002). Based on these isotopic theories, decreased moisture availability is predicted to result in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ enrichment of plant organic matter (Barbour et al 2002, Leavitt and Long 1989).

$\delta^{15}\text{N}$ of plant organic matter provides insight into changes in the local N cycle (Robinson 2001). Tree-ring $\delta^{15}\text{N}$ has been applied in studies of ecosystem N loss and retention (McLauchlan et al. 2007), tree sources of N (Poulson et al. 1995), and the impacts of N deposition (Guerrieri et al. 2010) and fertilization (Balster et al. 2010) on tree growth. The influence of N availability on A_{max} (Evans 1989, Reich et al. 1999) and the association between A_{max} and tree-ring $\delta^{13}\text{C}$ (Farquhar et al. 1982, Dawson and Ehleringer 1993) suggest that integrating $\delta^{15}\text{N}$ and N data from tree-rings and leaves with growth patterns and $\delta^{13}\text{C}$ may provide insight into tree responses to past and contemporary environments.

In Chapter 1, I build on previous research of a recent oak decline event (i.e. Stephen et al. 2003, Haavik et al. 2008), and expand our understanding of disturbance impacts by incorporating tree-ring $\delta^{18}\text{O}$ and N status, and contemporary leaf N dynamics. I predicted a greater impact of drought and insect disturbance on dying trees' growth rates relative to healthy trees and greater $\delta^{13}\text{C}$ enrichment of organic matter in dying trees. I also predicted that N would be a factor influencing the C dynamics of these co-occurring *Q. rubra*. Dying trees exhibited divergent, reduced growth following a severe drought and infestation in the mid-1970s. Tree-ring $\delta^{13}\text{C}$ exhibited a decline across time in both healthy and dying trees. When examined in conjunction with tree-ring $\delta^{18}\text{O}$, I found a significant correlation between these variables ($P < 0.05$), consistent with great sensitivity to vapor pressure deficit (VPD) and potentially associated with increased stomatal control of C dynamics in dying trees. I find support for a differential C dynamics in healthy trees, potentially associated with a greater influence of photosynthetic capacity, via a significant, positive relationship ($P < 0.05$) between contemporary leaf $\delta^{13}\text{C}$ and N_{mass} . Though contemporary leaf data are confounded by the extent of insect infestation in dying trees, in conjunction with the significantly greater [N] in tree-rings of dying trees, these data indicate that N dynamics differed between these tree health classes for decades prior to the insect outbreak, and that N is a strong driver of biomass $\delta^{13}\text{C}$ in healthy trees. The differential growth, isotopic, and N responses in these co-occurring *Q. rubra* is consistent with differential resilience to disturbance events and may provide insight into future management of oak ecosystems, economically important species prevalent in the central US.

Chapter 2: Distinct ecophysiological responses of co-occurring oak species to climatic variation: using tree-rings and leaf nitrogen status to understand tree carbon dynamics

Differential responses to climate variability among co-occurring species can influence changes in forest species composition and distribution. Studies of co-occurring tree species have demonstrated differential growth and isotopic trends that shed light on potential changes in distributions and physiological responses to climate (Adams and Kolb 2005, Gebrekirstos et al. 2009). Trees at the edge of their distributions are expected to express environmental stress to a greater degree in their tree-rings (Fritts 1976). As droughts are predicted to increase in frequency and duration in the future in many regions, understanding the impacts of decreased moisture availability on co-occurring species is needed to understand potential forest range restrictions or changes in ecosystem function in the future.

In Chapter 2, I examine physiological responses to climate variability in *Q. rubra* and *Q. macrocarpa* at the University of Kansas Field Station, located at the prairie-forest ecotone of the Midwest U.S. *Q. rubra* typically occurs on mesic sites, while *Q. macrocarpa* appear to be more drought tolerant (Abrams 1990). I use growth data along with contemporary leaf $\delta^{13}\text{C}$, N status, and tree-ring $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ to understand C dynamics in co-occurring tree species. I predicted that *Q. rubra* would experience greater reduction in radial growth and greater $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ enrichment of tree-rings in response to decreased moisture availability. Differential physiological responses of tree species at the forest boundary may have ramifications for the prairie-forest ecotone, and determining the factors that govern C dynamics in these species provides insight into their ability to adapt to variable conditions in the future

I observed greater dependence of *Q. macrocarpa* growth on precipitation-derived moisture availability relative to *Q. rubra*, contrary to my predictions, which suggests that *Q. macrocarpa* will be more sensitive to such climactic changes. I found a positive relationship between tree-ring $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in *Q. macrocarpa*, a strong indication that the dominant driver

of this species' C dynamics is stomatal regulation of water loss and, concurrently, availability of CO₂ for fixation within the leaf. In contrast, *Q. rubra* exhibited weaker relationships between growth and climate measures, and no relationship between tree-ring $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, suggesting that factors other than stomatal response to water availability is a dominant driver of its C dynamics. Indeed, we observed a significant, negative relationship between leaf $\delta^{13}\text{C}$ and C:N in this species, suggesting that *Q. rubra* leaf $\delta^{13}\text{C}$ and, presumably, tree-ring $\delta^{13}\text{C}$ as well, is linked to N availability in a different manner than in *Q. macrocarpa*, which exhibited a counter-intuitive significant, positive relationship between leaf $\delta^{13}\text{C}$ and C:N. The species-specific physiological responses to climate in these co-occurring oak species suggest that increasing drought frequency and duration in the future in the region may have great impacts on *Q. macrocarpa* C dynamics relative to *Q. rubra*, a finding that has implications for oak range restriction and changes in the species composition of the prairie-forest ecotone in the future.

Chapter 3: Forest response to disturbance: exploring tree-ring growth patterns with nonlinear dynamic models

Tree rings, as a singular recorder of multiple environmental and anthropological variables impacting growth, may be useful tools for assessing a forest's resilience to disturbance (Schweingruber 1996). I base my predictions on the assumption of stable climate-growth relationships over time, which is central to historic climate reconstruction from tree growth chronologies (Fritts 1976). Tree-ring studies are often founded on the principle of uniformitarianism, proposed by 18th century geologist James Hutton, to justify the use of growth-climate relationships to reconstruct past climate conditions (Fritts 1976, Carrer and Urbanati 2006). Typically, multivariate regressions or correlations are used to explore growth-climate

interactions under the assumption of linear relationships (Fritts 1976, Carrer and Urbanati 2001). However, nonlinear growth responses of trees to precipitation and temperature are suggested by some dendrochronological research (Graumlich and Brubaker 1986, Graumlich 1991, Driscoll et al. 2005). Shifting correlation analyses have challenged assumptions of stable growth-climate relationships by revealing varying climate-growth correlation strengths over time (Carrer and Urbanati 2006, Reynolds-Henne et al. 2007), but often these analyses consider only a single climate variable and are inadequate for revealing nonlinear responses (Graumlich and Brubaker 1986, Carrer and Urbanati 2001).

Forecasting models, invoked in multiple systems ranging from biological (Hsieh et al. 2005; Sugihara et al. 1996, Glaser et al. 2011) and astronomic (Kilcik et al. 2009) to economic (Schittenkopf 2000), are useful for detecting nonlinear dynamics in time series data sets. In Chapter 3, I apply forecasting model techniques in a novel manner to tree-ring time series to explore the underlying dynamics of *Q. rubra* growth from two regions in Arkansas experiencing differential disturbance impacts from drought and insect infestation. Forecast models use time lagged growth trajectories to project future growth and validate model accuracy through series data excluded from the model (Sugihara et al. 1994). I use two models: i) simplex models which determine the dimensionality of a time-series and ii) S-maps projections which use simplex dimensionality as model inputs to detect nonlinear dynamics in time series.

I predicted that *Q. rubra* remaining healthy through disturbance events would exhibit linear growth dynamics, while neighboring trees that experienced mortality will exhibit nonlinear growth dynamics. I also explore the impacts of changing time series input length on detection of nonlinear dynamics in an effort to increase the applicability of forecast modeling in tree-ring studies. In contrast to predictions, I find that healthy *Q. rubra* are more likely to exhibit

nonlinear growth dynamics relative to dying trees, consistent with nonlinear dynamics, perhaps suggesting that nonlinearity represents an important ability to cope with environmental variability. Evidence supports similar regional ecosystem dynamics among the two study regions. I also find evidence that tree-ring series shorter than 30 years limit our ability to detect nonlinear dynamics in time series, even when invoking concatenation as a tool, an important consideration for use of these models in the tree-ring community. I suggest forecast modeling as a potential tool for monitoring tree vulnerability to disturbance in Chapter 4 of this dissertation.

Chapter 4: Forest management in the Boston Mountains of Arkansas, U.S.: forest management adapting to climate change

Disturbance is a natural component of forest ecosystems, but an increased frequency and severity in disturbances predicted in the future could negatively impact forests. Implementing forest management policies to increase the adaptive abilities of forests to resist and recover from disturbance events is an important undertaking. Adaptive management is founded in learning from management decisions and using management opportunities as long-term experiments from which we can learn how to improve management strategies as conditions change (Holling 1973, 1978). Current disturbance impacts in forest ecosystems can be used as learning opportunities and incorporated into policies to increase ecosystem resilience and resistance to disturbance in order to maintain forest function in the future. Resilience is the quick return to pre-disturbance structure and condition in a system following disturbance, while resistance is a system's ability to absorb the impacts of disturbance with little change in forest structure or function (Holling 1973).

In Chapter 4 of this dissertation, I use a framework of past forest management to demonstrate the need for a change in management strategies applicable to forested lands throughout North America. I employ a case study of oak decline linked to climatic disturbance in the Ozark National Forest of northwest Arkansas to demonstrate the link between past management and forest decline. I propose that the challenge of future forest management policies is meeting local economic timber needs while promoting forest function in the face of climate change uncertainty, which is a common concern between state, federal, and private lands. Primary conclusions of this chapter promote 1) developing adaptive management strategies with local goal-setting, 2) employing tree growth monitoring to assess tree vulnerability to disturbance, and 3) reconciling local timber demands with increased forest resilience and resistance in the future.

CHAPTER 1: Tree-ring and contemporary leaf stable isotopes as indicators of tree growth strategies and susceptibility to disturbance

Abstract

Understanding how tree growth strategies may influence tree susceptibility to disturbance is an important goal given projected increases in forest disturbances this century. We invoke a region-wide forest disturbance event in an oak-dominated forest in Arkansas, USA to explore these issues. In apparently healthy and dying co-occurring *Quercus rubra* trees, we assess historic growth responses to climate, relationships between stable isotopic signatures of carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) in tree-rings, and wood nitrogen (N) and $\delta^{15}\text{N}$. We also use contemporary leaves of healthy and dying trees to assess N status as a potential driver of tree carbon (C) dynamics. Our goal was to explore the mechanisms driving differential responses to disturbance events to understand resilience in apparently healthy tree while neighboring trees experienced decline and mortality in response to the same environmental forcings. Dying trees exhibited divergent, reduced growth following a severe drought and infestation in the mid-1970s. Tree-ring $\delta^{13}\text{C}$ exhibited a decline across time in both healthy and dying trees. The relationship between tree-ring $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ was significantly positive ($P < 0.05$) in dying trees, but was not expressed in healthy trees, suggesting that dying trees' C dynamics were controlled to a greater extent by response to vapor pressure deficit (VPD) and potentially stomatal regulation than by photosynthetic capacity. In contrast, we observed a significant, positive relationship ($P < 0.05$) between contemporary leaf $\delta^{13}\text{C}$ and N_{mass} in healthy trees, but not in dying trees. This implies that C dynamics in healthy trees is more strongly linked to N status and, perhaps, C sink strength compared to dying trees. The differential growth responses to past climate, isotopic patterns, and indices of N status observed in these co-occurring *Q. rubra* coincide with divergent

resilience to disturbance events and may provide clues for how to predict responses to disturbances of oak-dominated forests. Monitoring tree-ring patterns of growth and isotopic relationships may help us understand the mechanisms driving tree decline and persistence in the future, when disturbance events are predicted to increase.

INTRODUCTION

In the coming decades, climate change has the potential to impact North American forests by increasing the frequency of disturbance events (McKenney et al. 2007, Woodall et al. 2009). Here, a disturbance is defined as an interruption in substrate integrity or resource availability, or deviation in environmental conditions, that impacts the ecological functioning of an ecosystem (White and Pickett 1985). We focus on two disturbance factors contributing to or inciting forest decline (Manion 1991): drought and associated insect outbreaks. Such disturbances can result in forest decline and wide-spread mortality (Stephen et al. 2003; Adams et al. 2009). Understanding how oak species (*Quercus*) respond to such events is important, given the genus' wide range (Abrams 1996, Vettrano et al. 2002) and its dominant status in many North American forests (Abrams 1992).

Multiple oak decline events have been observed in recent decades throughout the U.S. and Europe (Vettrano et al. 2002, Voelker et al. 2008, Fan et al. 2008). Oak mortality during decline events is often associated with increased susceptibility of trees to secondary factors, including fungal root infection (Bruhn et al. 2000, Balci et al. 2003) and insect infestations (Fan et al. 2008, Fierke et al. 2005), but climatic events like drought (Houston 1987) are often viewed as the underlying mechanism that initiates declines (Tainter et al. 1990, Jenkins and Pallady 1995). Environmental stresses imposed by climate can interrupt tree carbon (C) and water

relations (Billings and Phillips 2011), production and storage of sugars, and mineral transport (Houston 1987), generating increased susceptibility to opportunistic parasites and secondary stresses (McDowell et al. 2008, Anderegg et al. 2012). The specific mechanisms driving climate-associated oak decline are not well understood, but appear related to tree C source and sink strengths (Manion 1991), as has been suggested for climate-related decline of other tree species (McDowell et al. 2008).

Dendroecological studies can guide our understanding of tree responses to environmental cues, and hence the potential drivers of oak decline. For example, growth indices have provided evidence of differential drought responses among co-occurring species (Adams et al. 2009) and individuals of the same species (Haavik et al. 2008, Levanic et al. 2011), changes in growth rates over time (Johnson and Abrams 2009), and are linked to oak decline susceptibility (Voelker et al. 2008). Recent work further emphasizes how a dendroecological approach can help us understand historical responses of trees to disturbances such as insect outbreaks (Muzika and Liebhold 1999, Girardin et al. 2002, Simard et al. 2008) and elucidate climatic factors that appear to increase susceptibility of some trees to insect-related disturbance (Haavik et al. 2008). Such an approach is particularly useful when coupled with stable isotopic analyses of tree-rings.

Stable isotopic signatures of C ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) of tree-rings (typically the α -cellulose extracted from rings; McCarroll and Loader 2004) can augment the knowledge gained from growth patterns by highlighting the drivers of tree C dynamics (Barbour et al. 2001). Isotopic theory suggests that the ratio of internal to atmospheric $[\text{CO}_2]$ (c_i/c_a) is reflected in the $\delta^{13}\text{C}$ values of vegetation, which in turn depends upon photosynthetic capacity (A_{max}) and the response of stomatal conductance (g_s) to moisture availability (Francey and Farquhar 1982, Farquhar et al. 1982, Farquhar et al. 1989). Because fluctuations of $\delta^{13}\text{C}$ in tree-ring α -cellulose

are associated with g_s and A_{max} , $\delta^{13}\text{C}$ is often linked to measures of water availability (Leavitt and Long 1989, Hubick and Gibson 1993, Saurer et al. 1995) and, less frequently, nitrogen (N) availability which can govern A_{max} (Gebauer and Schulze 1991).

$\delta^{18}\text{O}$ of tree-ring α -cellulose reflects the isotopic signature of source water, internal exchange of O during organic compound formation, and atmospheric demand for water, which results in evaporative isotopic enrichment of water remaining in the leaf during transpiration (Yakir 1992, Farquhar and Lloyd 1993, Barbour et al. 2002, Barbour 2007). Because of the linkages between $\delta^{18}\text{O}$ of vegetation and source water, vegetation $\delta^{18}\text{O}$ can reflect rooting depth, given that deep water sources are often $\delta^{18}\text{O}$ -depleted relative to shallower water sources (Roden et al. 2005, Pataki et al. 2008). In contrast with $\delta^{13}\text{C}$, $\delta^{18}\text{O}$ of vegetation is not associated with A_{max} , and hence does not appear linked to plant nutrient status (Scheidegger et al. 2000, Barbour et al. 2001, Barbour 2007).

Recent work demonstrates how simultaneous analysis of tree-ring $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ can suggest the importance of CO_2 source strength (i.e. stomatal conductance, g_s) relative to C sink strength (i.e. photosynthetic rate, A_{max}) as limitations to growth (Barbour and Farquhar 2000, Barbour et al. 2002, Cabrera-Bosquet et al. 2010). Because $\delta^{13}\text{C}$, but not $\delta^{18}\text{O}$, can vary with A_{max} , and both $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ can vary with stomatal responses to the environment, models predict a positive relationship between vegetation $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ with changing g_s , holding all other variables constant (Scheidegger et al. 2000, Barbour et al. 2002). In contrast, models predict no relationship between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ if A_{max} changes and all other parameters remain constant (Scheidegger et al. 2000, Barbour et al. 2002, Hiltunen and Berninger 2010). Such analyses thus can reveal the relative extent to which g_s vs. A_{max} govern variation in $\delta^{13}\text{C}$ of tree-ring α -cellulose, and hence the relative degree to which these parameters drive C dynamics and

related growth performance. This is a particularly useful approach among co-occurring trees with similar access to light, given the importance of light as a driver of A_{max} and thus $\delta^{13}\text{C}$ (Yakir and Israeli 1995).

Integrating the stable isotopic signature of nitrogen (N, $\delta^{15}\text{N}$) of tree-rings into a dendroecological approach can further elucidate the drivers of tree responses to variation in climate and resource availability across time (Poulson et al. 1995, Amundson et al. 2003, Guerrieri et al. 2010). Biomass $\delta^{15}\text{N}$ provides insight into changes in the local N cycle (Robinson 2001). Although N translocation after wood formation can confound tree-ring [N] and $\delta^{15}\text{N}$ (Poulson et al. 1995), tree-ring $\delta^{15}\text{N}$ has been applied in studies of ecosystem N loss and retention (McLauchlan et al. 2007), tree sources of N (Poulson et al. 1995), and the impacts of N deposition (Guerrieri et al. 2010) and fertilization (Balster et al. 2010) on tree growth. Further, linkages between N availability and A_{max} (Evans 1989, Reich et al. 1999), and A_{max} and tree-ring $\delta^{13}\text{C}$ (Farquhar et al. 1982, Dawson and Ehleringer 1993) suggest that integrating tree-ring and leaf $\delta^{15}\text{N}$ and [N] data with both tree-ring growth patterns and $\delta^{13}\text{C}$ likely can further clarify tree responses to past and contemporary environments.

We use dendroecological and stable isotopic approaches, in conjunction with contemporary leaf N status, to develop a greater understanding of the ecophysiological mechanisms influencing oak susceptibility to drought and subsequent insect outbreak disturbance. We focus on a recent oak decline event associated with rapid population increases of a native wood boring insect, the red oak borer (*Enaphalodes rufulus* (Haldeman) (Coleoptera: Cerambycidae)), to elucidate how variation in past and contemporary tree responses to multiple environmental cues may relate to susceptibility to disturbance. This decline event, centered in the Boston Mountains of Arkansas, USA followed five decades of cyclical droughts, historically

high wood-boring insect infestations from the mid-1970's through the early 2000's, and resulted in high mortality rates of northern red oak (*Quercus rubra* L. (Fagaceae)) on a landscape scale (Stephen et al. 2003, Muzika and Guyette 2004, Fierke et al. 2005, Fierke et al. 2007, Haavik et al. 2011). Many forest stands experiencing high oak mortality contained multiple, apparently healthy trees immediately adjacent to trees experiencing severe crown dieback and subsequent mortality. Poor site quality and even-aged stands may have been contributing factors to the decline (Oak et al. 1996), but several studies implicate cyclical drought beginning decades prior to observable decline in the region as a key factor determining susceptibility at these sites (Tainter et al. 1990, Jenkins and Pallardy 1995, Haavik et al. 2008, Haavik et al. 2010). Indeed, tree-ring growth patterns at these sites suggest that antecedent drought was an important factor governing tree susceptibility to insect infestation and eventual mortality (Haavik et al. 2008; Haavik et al. 2011). However, $\delta^{13}\text{C}$ values of α -cellulose from tree-rings of more susceptible trees did not exhibit the increases one might predict with drought stress from isotopic theory (Haavik et al. 2008). Thus, although drought likely played an important role in governing tree response to this oak decline event, the mechanisms governing the variable susceptibility of co-occurring trees remain unclear.

Working at the same sites described in Haavik et al. (2008) on an expanded number of trees, we explore the role of antecedent climate as a potential driver of tree susceptibility to disturbance, and how tree growth strategies may have influenced susceptibility vs. survival. Because drought has been implicated as a driver of this decline event (Haavik et al. 2008; Haavik et al. 2010), we might anticipate that declining trees' tree-rings may reveal evidence of different water-related growth strategies compared to their surviving neighbors. We use tree-ring growth patterns, as well as $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of tree-ring α -cellulose to assess the historic, relative

importance of g_s vs. A_{max} as drivers of $\delta^{13}\text{C}$ (Barbour and Farquhar 2000, Barbour et al. 2002). We also infer how tree N status may have influenced tree survival or mortality during this oak decline event. To our knowledge, this is the first study to incorporate $\delta^{13}\text{C}$, $\delta^{18}\text{O}$, and $\delta^{15}\text{N}$ and [N] of tree-rings, as well as contemporary leaf N status, to explore tree growth strategies and susceptibility to disturbance. We address three questions relevant for understanding tree responses to this oak decline event and, more broadly, oak-dominated forest strategies for coping with disturbance: i) Do trees that remained apparently healthy throughout this disturbance exhibit different growth responses to antecedent temperature and precipitation than those that suffer mortality? ii) Do surviving trees exhibit patterns of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in tree-ring α -cellulose reflective of different drivers of C dynamics compared to their dying neighbors? iii) Do tree-rings or contemporary leaves reveal differences in N dynamics between surviving and dying trees, suggestive of different growth strategies between these co-occurring populations?

METHODS

Sites

We sampled healthy and dying oaks at three pre-established study sites in the Ozark National Forest in northwest Arkansas (UTM Zone 15-S NAD83) (Fierke et al. 2005). The three sites, Oark, Fly Gap, and White Rock, were selected on the basis of red oak borer presence. Sampling focused on trees sampled from ridge locations, where differences between dying and apparently healthy trees were most evident. Details of site conditions can be obtained in Fierke et al. (2007). Briefly, the three sampling sites are oak-hickory dominated (USDA Forest Service 1999), support similarly aged oaks (~60 y) on acidic, clay-rich soils with low organic matter content (Sander 1965), and are all within 50 km of each other. Regional climate is temperate

with warm summers and mild winters; mean annual temperature is 16 °C. Mean annual precipitation totals 124 cm and falls mostly during spring, summer, and fall. Bedrock composition is comprised of limestone, shale, and sandstone, with cliff elevations reaching up to 750 m (Adamaski et al. 1995).

Climate data

Climate records were obtained from the NOAA website (<http://www1.ncdc.noaa.gov/pubdata/cirs>) for the climate regions of interest. Total annual precipitation for the years of interest was calculated using average precipitation for the calendar year across the four NOAA regions encompassed by the sampling area. Seasonal precipitation was calculated from May-August as growing season values. We also calculated precipitation for January to June and for July to December, to assess the influence of moisture availability during different periods of growth. Seven periods of interest were determined using NOAA Palmer Drought Severity Index (PDSI; Palmer 1965) from regional data (<http://www1.ncdc.noaa.gov/pub/data/cirs>), consisting of alternating periods of extreme wet and dry periods. Time periods examined and their relative wet or dry status were 1952-56 (dry), 1957-59 (wet), 1962-67 (dry), 1972-75 (wet), 1979-81 (dry), 1992-95 (wet), and 1998-2001 (dry). Cumulative precipitation values were also averaged from each of the seven periods of interest to gain a single climate parameter value for correlation analyses with stable isotope data (described below). Indices of annual, growing season and winter values for temperature and PDSI, an index of moisture availability derived from water balance equations (Palmer 1965), were developed in the same manner.

Sampling procedure and cellulose extraction

At each site we sampled trees experiencing moderate to heavy levels of red oak borer infestation, as well as their apparently healthy neighbors. Tree health was assessed based on the number of borer emergence holes and percent crown cover (Fierke et al. 2007), and we created categorical groups of apparently healthy trees (referred to throughout as healthy trees), trees exhibiting initial stages of canopy decline (moderately infested trees), and trees experiencing severe crown dieback (dying trees). All trees, regardless of health status, were well-interspersed at each sampling site. In 2002, 2003 and 2007, we felled oaks with similar diameter at breast height (DBH) and canopy co-dominance positions (Stephen, unpublished data, Haavik et al. 2008). Six healthy trees from Fly Gap were sampled during 2002 and 2003. At each of three sites in 2007, we sampled 2 trees categorized as healthy (6 total), 3 moderately infested (9 total) and 3 dying trees (9 total) for a total of 24 trees. Along with the six trees felled in 2002-2003, these trees comprised our $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ data set ($n=30$). We scanned cookies cut from tree boles sampled in 2002, 2003, and 2007 into Adobe Acrobat 8 Professional, and we measured and dated ring widths using event year markers as outlined in Haavik et al. (2008). Most trees exhibited ring width series from 1930 to date of felling; in two trees from Fly Gap ring widths prior to 1930 were unavailable due to stand clearcutting in prior decades. We cross-dated the tree-rings using COFECHA software (Holmes 1983), which ensures proper dating through event-year comparisons. We measured tree-ring widths to the nearest 0.01cm for each sample on a total of three radii per cookie, and averaged these widths to determine ring width in each year. Though growth patterns were assessed throughout each tree's life, we isolated tree-rings only from the seven periods of climate extremes for isotopic analyses, to maximize the climate signals captured.

We generated 1 to 2g of whole-wood sawdust using a Dremel tool (Bosch Tool Corporation, Chicago, IL) from each cookie for each of the seven time periods, being careful to avoid the earlywood visible at the start of each time period to limit the inclusion of C fixed prior to the period of interest (McCaroll and Loader 2004). Sawdust was placed in fiber filter bags (ANKOM, Fairport, NY) and heat sealed for α -cellulose extraction as per a procedure modified from Leavitt and Danzer (1993). We placed the filter bags into a Soxhlet apparatus, where they boiled for 24 hours in a 2:1 mixture of toluene:ethanol, followed by another similar treatment with replaced extractant. After drying, samples were boiled for two successive 24 h periods with 95% ethanol. Bags were dried and then boiled for 1 h in a 6 g sodium chlorite, 1 mL glacial acetic acid mixture, and 700 mL DI water mixture to extract soluble sugars and low molecular mass polysaccharides. This procedure was performed three times, rinsing samples completely between cycles. Samples were then washed with sodium hydroxide and glacial acetic acid and subjected to a final rinsing period. The remaining α -cellulose was then oven dried for 24 hours at 70°C.

In 2007, we collected 5 clusters of full-sun leaves from the top of each felled tree (n=24). This sampling scheme ultimately generated leaf samples from 5 healthy trees, 9 trees experiencing moderate infestation, and 8 dying trees, reflecting leaf samples later deemed unusable during processing. We stored all leaves in coolers until return to the laboratory, where they were frozen in flattened, air-tight bags for later analysis. We subsequently scanned leaves in Adobe Photoshop and calculated leaf area using Image-J software (NIH, Bethesda, MD). Leaves were then dried at 65°C for >48 h, weighed and ground to produce homogenized samples.

Analysis of stable carbon, oxygen and nitrogen isotope ratios

We weighed α -cellulose (0.09-0.11 mg) and whole wood sawdust samples (15-20 mg) and placed them into tin capsules for analysis of $\delta^{13}\text{C}$ (α -cellulose) and $\delta^{15}\text{N}$ and %N (sawdust). Tin capsules were combusted with excess O_2 in an elemental analyzer (EA-1100, Carlo Erba, Milano, Italy) connected through an open split interface (Conflo II, Finnigan MAT) to an IRMS (Delta-S Finnigan MAT, Bremen, Germany) at the University of Kansas KPESIL. Following procedures for non-resinous trees like northern red oak (Bukata and Keyser 2005), we did not wash sawdust with distilled water prior to N analyses (Doucet et al. 2010). We loaded approximately 1 mg of tree-ring α -cellulose into silver capsules for $\delta^{18}\text{O}$ analysis via pyrolysis to CO on an elemental analyzer (EA-1110, Carlo Erba, Milano, Italy) coupled with a continuous flow mass spectrometer (Delta Plus- Finnigan MAT, Bremen, Germany) at the University of Kansas KPESIL. All leaf samples were analyzed for [C], [N], $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ an elemental analyzer coupled to an Isotope Ratio Mass Spectrometer (Delta Plus IRMS, Thermofinnigan, San Jose, CA) at Kansas State University. Isotopic values are reported as delta values (in per mil, ‰) relative to deviations for international standards (V-PDB for $\delta^{13}\text{C}$, V-SMOW for $\delta^{18}\text{O}$, and atmospheric N_2 for $\delta^{15}\text{N}$).

Data Analysis

We calculated basal area increments for all trees from measurements of ring width and DBH measurements using the following formula:

$$BAI = \pi(R_n^2 - R_{n-1}^2) \quad (1)$$

where R_n represents the radius at the time of felling and R_{n-1} the radius of the previous year, with the assumption that stem growth approximates the area of a circle (Fritts 1976). Raw ring-width

measurements were standardized to zero to produce ring width indices (RWI) for each individual tree. We calculated both BAI and RWI because of their respective utilities for examining growth trends across time (BAI) and the influence of climate on growth (RWI; Johnson and Abrams 2009). BAI is generally used in the field of dendroecology to reflect growth over time as a standardized measure with juvenile trends removed, while RWI is more typically used for examining physiological responses to growth (Esper et al. 2002, Johnson and Abrams 2009).

At each of the three sites, we used regression analyses to assess relationships between these two indices of growth and three climate variables: PDSI, precipitation, and temperature. We calculated four measures of each climate variable, representing annual and seasonal averages, the average value for January to December (annual), January to June, July to December and June to August to investigate seasonal influences of these variables on tree growth. We did not adjust for multiple comparisons since we used these climate-growth relations in a qualitative manner, to assess differential strengths of these relationships with health status. We assessed potential lags in growth responses to climate, but we present here only current year growth-climate relationships, which were stronger. For some analyses, specified in our results and discussion, we analyzed the influence of PDSI on growth using PDSI values less than two, given our interest in strong drought conditions. PDSI values of less than two are recognized as representing relatively dry conditions (Palmer 1965, Adams and Kolb 2005).

We used these same climate-related variables to test for their influence on tree-ring stable isotopic and [N] data as well. We employed ANOVA to test for the influence of relatively wet vs. dry conditions in our seven time periods of interest on $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ of tree-ring α -cellulose and on $\delta^{15}\text{N}$ and N content of tree-ring whole wood (PROC ANOVA, SAS 9.1.3, Cary, NC). We also tested for the influence of site and tree health class on BAI, with BAI adjusted to center

values around the site-averaged BAI to provide for robust analysis (Aiken and West 1991). We also used repeated measures ANOVA (PROC MIXED, SAS 9.1.3, Cary, NC) to assess the influence of site, health status, time, and their interactions on tree-ring α -cellulose $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ and tree-ring wood $\delta^{15}\text{N}$ and [N]. When site was not a significant driver of the response variable, we removed it from subsequent tests. Further, we used correlation analyses to test for differences between tree health status in relationships between tree-ring α -cellulose $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$.

We also analyzed contemporary leaf data, focusing on healthy (n=6) and dying (n=9) trees. We tested for the influence of site, health status, and their interaction on 2007 leaf sample [C], [N], $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ using ANOVA. We used correlation analysis to assess relationships between these isotopic signatures and three different measures of leaf N: N_{mass} (mg N $\text{g}_{\text{leaf-1}}$), N_{area} (mg N $\text{m}_{\text{leaf-2}}$), and leaf C:N ratios (by mass). For all analyses, we determined statistical significance at $P < 0.05$, and report all instances of $P < 0.10$. All errors presented are one standard error of the mean.

RESULTS

Ring-width and Climate Data

Ring width indices (RWI) at all sites exhibited more significant relationships with a greater diversity of climate variables than BAI (Table 1). Ring width indices were significantly and positively related to indices of precipitation, with climate and growth variables expressed as averages across multiple time periods in healthy trees. Similarly, the relationship between RWI and PDSI in multiple time periods exhibited significance in healthy trees at all three sites, but fewer such significant relationships were found in dying trees. Indices of temperature exhibited

a negative association with RWI. In contrast to RWI, and with only one exception, BAI exhibited significant relationships only with measures of temperature; these instances of statistically significant correlations exhibited generally lower Pearson correlation coefficients than with RWI. Significant correlations between growth and temperature were not observed with monthly averages during the first half of each year (January to June), but were evident with average temperatures from June to August and average temperatures from July to December. At Fly Gap, dying trees exhibited far fewer significant relationships between BAI and climate variables. When we consider all relationships between growth indices and the tested climate-related variables, healthy trees exhibited 12 more significant relationships than dying trees, and these significant growth-climate relationships in healthy trees were of greater significance than in dying trees (eight vs. three at $P < 0.001$, eight vs. seven at $P < 0.01$, and 16 vs. ten at $P < 0.05$, Table 1).

In normal to relatively dry conditions ($PDSI < 2$, Palmer 1965), we observed significant, positive relationships between BAI and PDSI in healthy trees at all sites (Figure 1), although PDSI explained only a small fraction of variation in BAI at all sites (White Rock $P < 0.10$, $R^2 = 0.02$; Fly Gap $P < 0.02$, $R^2 = 0.03$; Oark $P < 0.02$, $R^2 = 0.04$). Similar relationships were observed between BAI and PDSI in dying trees at White Rock and Oark ($P < 0.04$, $R^2 = 0.005$ and $P < 0.04$, $R^2 = 0.003$, respectively) but not at Fly Gap. Basal area increment, but not RWI, diverged between healthy and dying trees decades prior to mortality ($P < 0.05$; Figure 2).

$\delta^{13}C$ and $\delta^{18}O$ of tree-ring α -cellulose

Values of $\delta^{13}C$ for tree-ring α -cellulose in all trees varied from -27.3 to -23.0‰. We observed no significant difference in $\delta^{13}C$ values between healthy and dying trees. $\delta^{13}C$ values

declined significantly across time at all sites ($P < 0.05$) regardless of the relative availability of moisture (Figure 3). $\delta^{13}\text{C}$ values exhibited a significant, negative relationship with temperatures from June through August when data from trees at all sites were analyzed. No significant relationships were found between $\delta^{13}\text{C}$ and PDSI or precipitation. $\delta^{18}\text{O}$ of tree-ring α -cellulose varied from 27.5 to 31.8‰ and exhibited a significant, positive relationship with temperature ($P < 0.001$), and significant, negative relationships with precipitation ($P < 0.05$) and PDSI ($P < 0.05$) were found when examined for all trees at all sites. An interaction between year, site and mortality was a significant determinant of $\delta^{18}\text{O}$. $\delta^{18}\text{O}$ in tree-rings from Oark were lower in healthy trees, exhibiting an ecologically small but significant 0.6‰ difference (29.2 ± 0.2 vs. 28.6 ± 0.2 ‰, respectively; $P < 0.05$; Figure 4). Average $\delta^{18}\text{O}$ of tree-ring α -cellulose among both healthy and dying trees was significantly depleted at Oark (28.8 ± 0.1 ‰) compared to White Rock and Fly Gap (29.3 ± 0.1 ‰, $P < 0.01$; 29.2 ± 0.1 ‰, $P < 0.05$, respectively). Dying trees exhibited a significant, positive relationship between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ ($P < 0.0005$, $R^2 = 0.15$; Figure 5). The correlation between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ for healthy trees revealed no significant trend.

Tree-ring and Leaf Nitrogen Dynamics

We observed a significant difference in tree-ring [N] between dying and healthy trees (Figure 6). Tree-ring [N] exhibited relatively slight variation across time until the final sampling period (1998-2001), when those in healthy trees increased 34.8% from their lowest point to 0.115 mg g^{-1} , and those in dying trees increased 45.6% from their lowest point to 0.143 mg g^{-1} . There were no differences in tree-ring $\delta^{15}\text{N}$ between sites or tree health status. We observed a positive relationship between wood $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in α -cellulose. Both whole-wood $\delta^{15}\text{N}$ and α -

cellulose $\delta^{13}\text{C}$ exhibit negative relationships across time, so the positive relationship between these variable is likely an artifact of the shared trend across time.

We observed no significant relationship between leaf $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, at any site or for any health status, but we observed a significant, positive relationship between leaf $\delta^{13}\text{C}$ and leaf N_{mass} of healthy trees ($P < 0.05$, $R^2 = 0.77$; Figure 7). Dying trees and moderately infested trees exhibited no relationship between leaf $\delta^{13}\text{C}$ and leaf N_{mass} . Leaf $\delta^{15}\text{N}$ was significantly, negatively related to leaf C:N ratios across all sites ($P < 0.05$, $R^2 = 0.19$) with no interaction with tree health status. Nitrogen concentrations in leaves sampled in 2007 ranged from 1.99 to 3.53 mg g^{-1} (mass basis, N_{mass}). We observed no significant differences in leaf N_{mass} , N_{area} , or C:N between tree health classes. We did not observe any site effects on leaf N_{area} , but on a mass basis, we found significant differences in leaf N_{mass} between Fly Gap and Oark ($P < 0.005$; 2.89 ± 0.12 and 2.28 ± 0.08 mg g^{-1} , respectively) and between White Rock and Oark ($P < 0.05$; 2.44 ± 0.12 and 2.28 ± 0.08 mg g^{-1} , respectively).

DISCUSSION

Our data suggest that tree susceptibility to disturbance, represented here by cyclical drought and wood-boring insect infestation, is linked to divergent tree responses to antecedent climatic conditions driving moisture availability and demand, and to tree N status. We observed significant relationships between multiple measures of temperature, precipitation, and PDSI data and growth indices more frequently for healthy trees than for their dying counterparts.

Relationships between tree-ring α -cellulose $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ suggest that healthy and dying trees likely experienced different drivers of C dynamics and associated $\delta^{13}\text{C}$ values for decades prior to the disturbance. Differences between healthy and dying tree-ring N are consistent with this

hypothesis. Divergent relationships between contemporary leaf $\delta^{13}\text{C}$ and N_{area} in healthy and dying trees imply, but are not conclusive of, different drivers of C dynamics between these populations of co-occurring healthy and dying neighbors. Below, we examine the concepts of climate-growth and N influences on tree C dynamics in more detail.

Growth patterns

Basal area increment in healthy and dying trees diverged following a severe drought that began in 1979 (Figure 2). These data are consistent with the data reported in Haavik et al. (2008), a study taking place at the same sites but examining fewer trees, and indicate that drought disturbance decades prior to this oak decline event may have influenced tree susceptibility to mortality during the later disturbance (Manion 1991). Decreased growth has been associated with oak decline events in America and Europe (Pedersen 1998, Levanič et al. 2011) and has been linked to drought (Figure 1; Manion 1991, Klos et al. 2009). Growth suppression in declining oaks a decade prior to mortality and divergent growth rates when comparing growth patterns in early life stages of declining vs. healthy trees have been observed in other studies (Drobyshev et al. 2007). Though we observed decreased growth accrual later in life for dying trees, DBH was similar among health classes. This counter-intuitive phenomenon may result if dying trees experienced faster growth in earlier decades, as has been observed at this site (Haavik et al. 2010) and as a more general phenomenon among trees with relatively short lifespans (Black et al. 2008, Johnson and Abrams 2009).

Relationships between growth indices and climate-related variables confirm that moisture availability and air temperature are both important drivers of growth patterns in these forests. Other studies of oak-dominated forests have emphasized the importance of both precipitation and

temperature as drivers of growth (Pan et al. 1997, Friedrichs et al. 2009, Hiltunen and Berninger 2010). Healthy trees' growth indices, particularly RWI, were more frequently related to climate measures than were growth indices of dying trees. The growth rates of healthy trees showed recovery following drought relative to dying trees, consistent with greater ability to cope with drought stress in healthy trees (Eilmann and Rigling 2012). The greater number of highly significant relationships between growth indices and climate variables in healthy trees compared to dying trees suggests that dying trees' growth was less responsive to environmental conditions potentially due to C limitations. The negative impacts of drought would not manifest until stored C reserves declined, consistent with declining growth observed in dying trees if C stores were depleted (Sala et al. 2012). The mechanisms behind these differences in climatic influence on growth between tree health classes remain unclear, as C reserves were not examined in the scope of our study, but stable isotopic and N-related data suggest that healthy and dying trees employed different growth strategies.

Patterns of tree-ring α -cellulose $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$

Growth patterns and tree-ring $\delta^{13}\text{C}$ data in isolation from other data sets do little to help us understand divergent susceptibilities of neighboring oaks to disturbance in these forests. If drought was indeed an important factor, as suggested by growth patterns, we might expect trees susceptible to this disturbance to exhibit elevated $\delta^{13}\text{C}$ values, relative to their healthy neighbors, prior to their obvious crown dieback and eventual mortality. However, expanding the number of trees sampled did not alter the earlier conclusions of Haavik et al. (2008), who observed no variation in tree-ring α -cellulose $\delta^{13}\text{C}$ at these sites with health status. Further, like Haavik et al. (2008), we observed little variation in $\delta^{13}\text{C}$ with climate parameters typically associated with

vegetation $\delta^{13}\text{C}$ signatures (Figure 3). Although stable isotope theory predicts that tree-ring α -cellulose becomes ^{13}C -enriched with moisture stress (Farquhar and Lloyd 1993), we did not observe such responses after the 1979 drought (Figure 4), a phenomenon sometimes reported in the literature (Ramesh et al. 1986, Cullen et al. 2007, Haavik et al. 2008).

Incorporating $\delta^{18}\text{O}$ of tree-ring α -cellulose into our analyses can provide clues about the mechanisms driving the decades-long, markedly lower growth trajectory of trees destined to die during this oak decline event, and about these trees' growth strategies (Figure 4). We observed a positive relationship between tree-ring α -cellulose $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in dying trees, but no such relationship in apparently healthy trees (Figure 5). These data suggest that C source-sink dynamics in trees that remained healthy during this disturbance were governed less by water status than by other factors, presumably those that influence A_{max} given that this term is the other key driver of vegetation $\delta^{13}\text{C}$ signatures (Farquhar et al. 1989, Barbour and Farquhar 2000). In contrast, the significant, positive relationship between tree-ring $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in dying trees suggests that C source-sink dynamics in these trees were governed to a greater extent by stomatal responses to their environment, given that both isotopic signatures are positively influenced by stomatal aperture (Barbour et al. 2002).

Antecedent and contemporary tree nitrogen status

Given the importance of N as a driver of A_{max} (Evans 1989) and, accordingly, of growth (Raison et al. 1990) and vegetation $\delta^{13}\text{C}$ (Korol et al. 1999, Balster et al. 2009, Guerrieri et al. 2011, Brooks and Mitchell 2011), integrating N dynamics into these analyses may help us understand these trees' responses to their environment and susceptibilities to disturbance. Tree N status may also help us understand why tree-ring $\delta^{13}\text{C}$ in these forests did not vary with moisture

availability after a severe drought in 1979 (Figure 6). Tree-ring N data can be confounded by mobility of nitrogenous compounds across tree-rings after wood formation (Poulson et al. 1995), but multiple studies have successfully used tree-ring N data to observe changes across time in tree N status, particularly when environmental perturbations are sufficiently great to generate a strong signal (Sauer et al. 2004, McLauchlan et al. 2007, Balster et al. 2009, Guerrieri et al. 2010).

The enhanced tree-ring N of dying relative to healthy trees during and following the 1979 drought provides a clue about these trees' response to their environments, and their eventual susceptibility to later disturbance. Given the co-occurring, interspersed nature of healthy and dying individuals and their co-dominant canopy status at each site, it is unlikely that these two populations experienced differences their environment that drove differences in wood N concentration. Nor do tree-ring $\delta^{15}\text{N}$ data imply that healthy and dying trees obtained N from different sources. We infer that trees dying in the early 2000s either allocated more N to their bole wood or took up more available N from the soil after the 1979 drought, compared to their healthier neighbors. Given that allocation of limiting resources to bole wood is a relatively low priority for trees, particularly those under stress (Waring and Schlesinger 1985), these data suggest that dying trees were less limited in their N than healthier ones.

It is unclear if tree-ring N does, in fact, reflect different N limitations of these trees, but tree-ring N has been linked to N availability in other studies (McLauchlan et al. 2007). If tree-ring [N] data are reflective of different N statuses in dying vs. healthy trees, we might expect to find other evidence consistent with lower N availability in healthy trees. Our data provide two such pieces of evidence. First, the lack of a relationship between tree-ring α -cellulose $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in healthy trees is suggestive of A_{max} being a relatively more important driver of those trees'

C dynamics than g_s (Barbour et al. 2002). We might expect such a feature of trees for which N is more limiting, given that N can be a key limitation on A_{max} (Ripullone et al. 2003). Second, we observed a significant, positive relationship between leaf $\delta^{13}\text{C}$ and N_{mass} in healthy, but not in dying, trees (Figure 7). Such a relationship is consistent with isotopic theory; an increase in N can prompt increases in A_{max} , which, all else equal, is linked to increases in leaf $\delta^{13}\text{C}$ (Barbour et al. 2002, Ripullone et al. 2003). We cannot know if the relationship between leaf $\delta^{13}\text{C}$ and [N] in healthy trees existed in past years. We did not observe such a relationship between tree-ring α -cellulose $\delta^{13}\text{C}$ and tree-ring wood [N], but these analyses likely were confounded by declining $\delta^{13}\text{C}$ values and increasing [N] in tree-rings of all trees over time. The significant relationship observed in contemporary leaves in healthy trees, however, hints that N is more of a key factor of C source-sink dynamics in these trees compared to their dying neighbors. Alternatively, the oak decline event may have altered the physiology of dying trees such that the influence of N on C source-sink dynamics was diminished. Although insect infestation may have masked relationships between leaf $\delta^{13}\text{C}$ and [N] in dying trees, the observed relationship in healthy tree leaves is consistent with those trees' lack of significant relationship between tree-ring α -cellulose $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ and their apparent greater N limitation. Together, these data sets imply that something other than g_s – perhaps N – was a more dominant driver of tree-ring α -cellulose $\delta^{13}\text{C}$ values and C dynamics in healthy trees.

The mechanisms linking N availability and tree health status are not clear. Reduced nutrient availability typically is linked to increased tree susceptibility to disturbance when C reserves are not limited (Matson and Waring 1984). Nitrogen availability is an important feature of tree resistance to disturbance, and enhanced N availability may increase recovery rates in surviving trees following an insect infestation (Waring and Pitman 1985). However, tree C

allocation strategies can change with stress, and C reserves allocated to defense compounds and hydraulic transport can depend on individual tree reserves, allocation strategies and nutrient status (Waring and Pitman 1985, Waring 1987, Sala et al. 2012). Differences in allocation patterns have been hypothesized as an influential factor driving susceptibility of oaks to disturbance at these sites (Haavik et al. 2011). Low C reserves in the presence of excess of N can increase tree susceptibility to disturbance-associated mortality (Matson and Waring 1984), which may help explain the linkages we observed between N and tree health status. Further, root pathogens such as *Armillaria* that negatively impact tree growth are active in these forests, and although no differences in infection rates of this pathogen have been observed between healthy and dying trees in recent events (Kelley et al. 2009), past infections may have impacted C reserves differently among these co-occurring oaks. Though we remain uncertain of the linkages between tree N and health status in our study, differential C allocation strategies driven by varying degrees of N limitation may have played a role in governing eventual disturbance susceptibility.

Conclusion

These data provide insight into several features of tree responses to disturbance, the utility of a multi-isotope approach for understanding the drivers of tree C dynamics, and linkages between vegetation N status and variation in vegetation $\delta^{13}\text{C}$ values:

- 1) Trees that eventually died during this forest disturbance experienced slower growth rates for decades prior to mortality (Figure 2) and exhibited weaker growth- climate relationships than their healthier neighbors.

- 2) Relationships between tree-ring α -cellulose $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ suggest that C dynamics of healthy trees were dominated more so by leaf C sink strength, A_{max} , than by g_s (Figure 5). Correspondingly, contemporary leaf $\delta^{13}\text{C}$ and [N] data imply that healthy trees' leaf $\delta^{13}\text{C}$ values were governed to a larger degree by vegetation N status than in dying trees (Figure 7).
- 3) Although it remains unclear why healthy trees' growth was more frequently related to climate variables, stable isotope and N data suggest that linkages between climate and N availability were more important for healthy trees, which appeared to be more N limited than dying trees, than the association of climate and moisture availability.
- 4) Tree-ring $\delta^{13}\text{C}$ values do not always vary as predicted with moisture availability, a feature that creates challenges for dendroecologists attempting to understand past tree responses to their environment. Our data suggest that N may have been an important driver of biomass $\delta^{13}\text{C}$ in healthy trees. Although isotopic theory predicts that both moisture and N can drive biomass $\delta^{13}\text{C}$, linkages between $\delta^{13}\text{C}$ and N availability are discussed relatively infrequently in the literature, and rarely in the context of tree-ring studies.
- 5) Assessing relationships between tree-ring α -cellulose $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ can provide a useful tool for predicting eventual oak susceptibility to oak decline, but the mechanisms driving such relationships, or their absence, need further study. Experiments in which trees' g_s , A_{max} , and tissue N concentrations are manipulated via N fertilization, and biomass $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ measured, will be an important means of achieving this goal.

As disturbance impacts on forests increase in the future, determining the response of trees and potential indices to predict decline events will become increasingly important. Our study highlights how examining past responses of trees to their environment can provide a greater understanding of future forest decline events and disturbance responses among co-occurring species.

TABLES AND FIGURES

Table 1. Pearson correlation coefficients between ring width indices (RWI) and basal area increment (BAI) for *Quercus rubra* trees and climate parameters at three sites in northwest Arkansas, USA: Fly Gap (FG), White Rock (WR), and Oark (O). H= Healthy, D=Dying.

	RWI						BAI					
	O, H	O, D	FG, H	FG, D	WR, H	WR, D	O, H	O, D	FG, H	FG, D	WR, H	WR, D
PDSI	0.24*	NS	0.32**	NS	0.25*	0.27**	NS	NS	NS	NS	NS	NS
PDSI, JJ	NS	NS	NS	NS	NS	0.25*	NS	NS	NS	NS	NS	NS
PDSI, MA	0.29**	0.23*	0.34***	NS	0.34**	0.27**	NS	NS	NS	NS	NS	NS
PDSI, JD	0.24*	0.22*	0.39***	NS	0.25*	0.24*	NS	NS	NS	NS	NS	NS
Precip.	NS	NS	0.22*	NS	NS	NS	NS	NS	NS	NS	NS	NS
Precip, JJ	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Precip, MA	0.24*	NS	0.28**	NS	0.24*	NS	NS	NS	NS	NS	NS	NS
Precip, JD	NS	NS	0.22*	NS	NS	NS	NS	NS	0.22*	NS	NS	NS
Temp.	NS	-0.31**	-0.33***	NS	-0.47***	-0.33***	-0.26*	-0.30*	-0.22*	NS	-0.33**	-0.33**
Temp, JJ	NS	-0.23*	NS	NS	-0.26*	NS	NS	NS	NS	NS	NS	NS
Temp, MA	-0.24*	-0.31**	-0.32**	NS	-0.47***	-0.32**	-0.28*	-0.30**	-0.23*	-0.23*	-0.3**	-0.21*
Temp, JD	NS	-0.25*	-0.34***	NS	-0.47***	-0.34***	-0.31**	-0.30**	-0.25*	NS	-0.34***	-0.34***

*p<0.05, **p<0.01, ***p<0.001. Annual averages represented by the generic terms, followed by the monthly values averaged together for each year for groups of months: JJ=January – June averages; MA = May – August averages; and JD= July – December. NS = non-significant relationships.

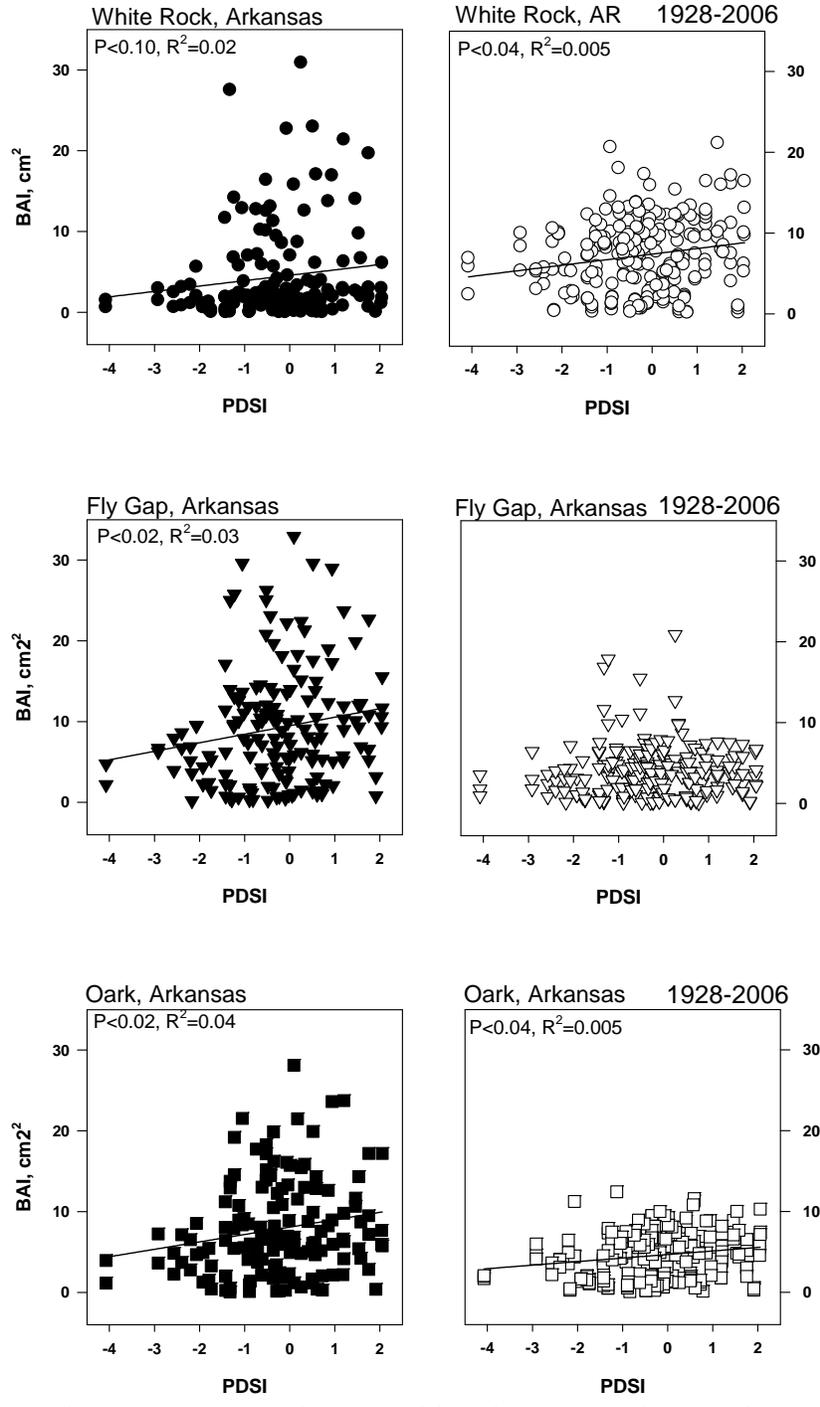


Figure 1. Basal area increment (BAI) changes with Palmer Drought Severity Index (PDSI) during relatively dry periods (PDSI<2) in three forests in Arkansas, USA. White Rock (healthy n=2, dying n=3), Fly Gap (healthy n=2, dying n=3), and Oark (healthy n=2, dying n=3) all exhibit significant (P<0.05), positive BAI trends for healthy trees and dying trees at White Rock and Oark exhibited similar significant trends. Healthy trees are represented by filled symbols and dying trees by open symbols. Trend lines represent linear regressions for healthy trees.

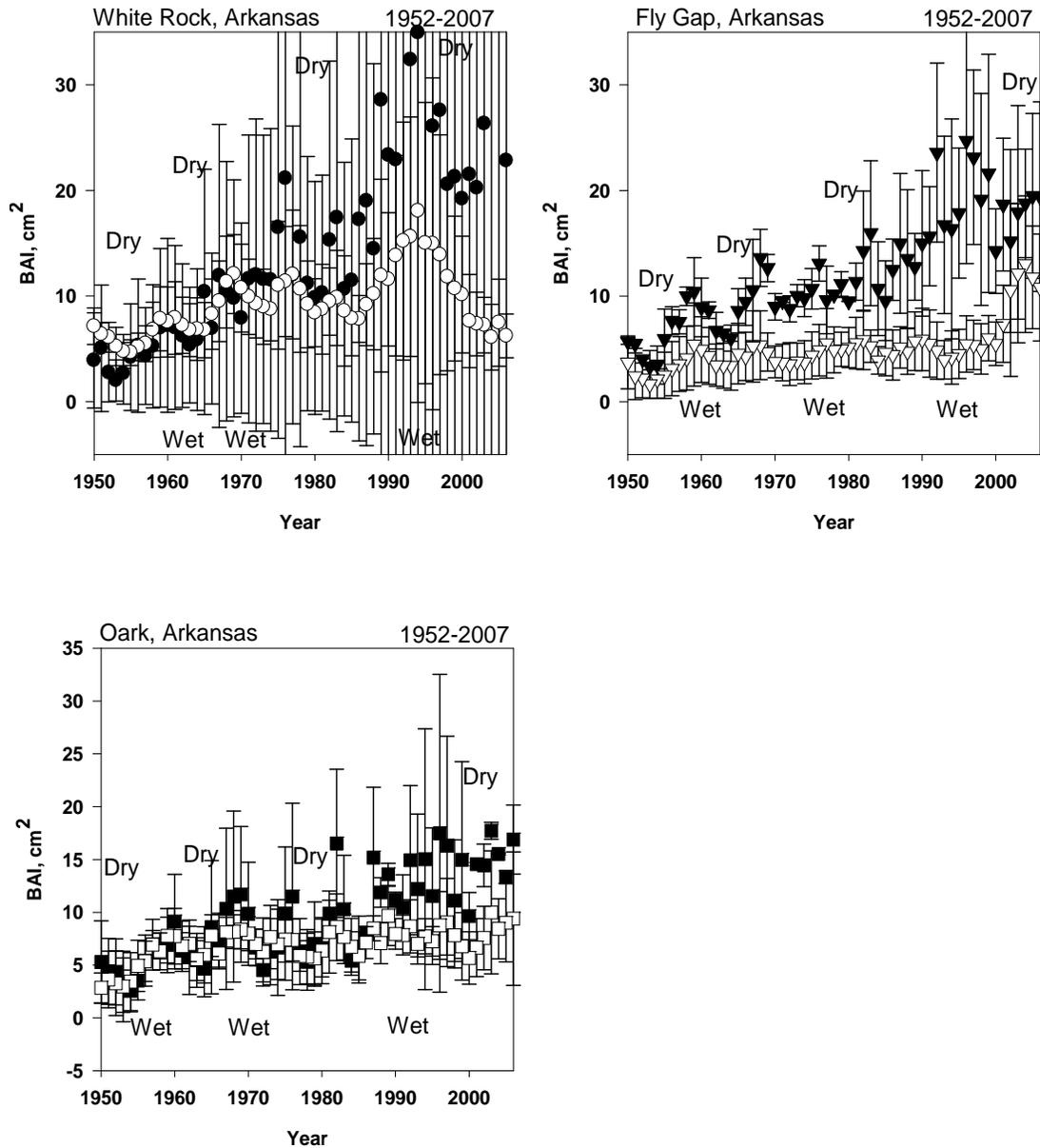


Figure 2. Basal area increment (BAI) trends across time at three forested sites in northwest Arkansas, USA. Symbols represent healthy (shaded) and dying (open) trees. Error bars are one standard error of the mean. Relatively wet and dry time periods are specified in each panel (see text for details on condition definitions).

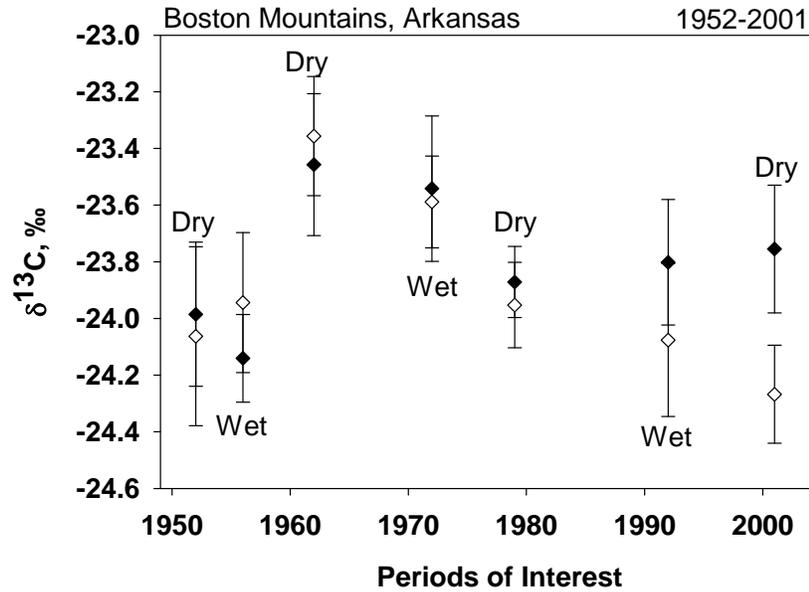


Figure 3. $\delta^{13}\text{C}$ of tree-ring α -cellulose across time from healthy ($n=9$, shaded) and dying ($n=12$, dying) trees at three forested sites in northwest Arkansas, USA. Relatively wet and dry time periods are specified in each panel (see text for details on condition definitions). $\delta^{13}\text{C}$ declines significantly for both healthy and dying populations. Error bars are one standard error of the mean.

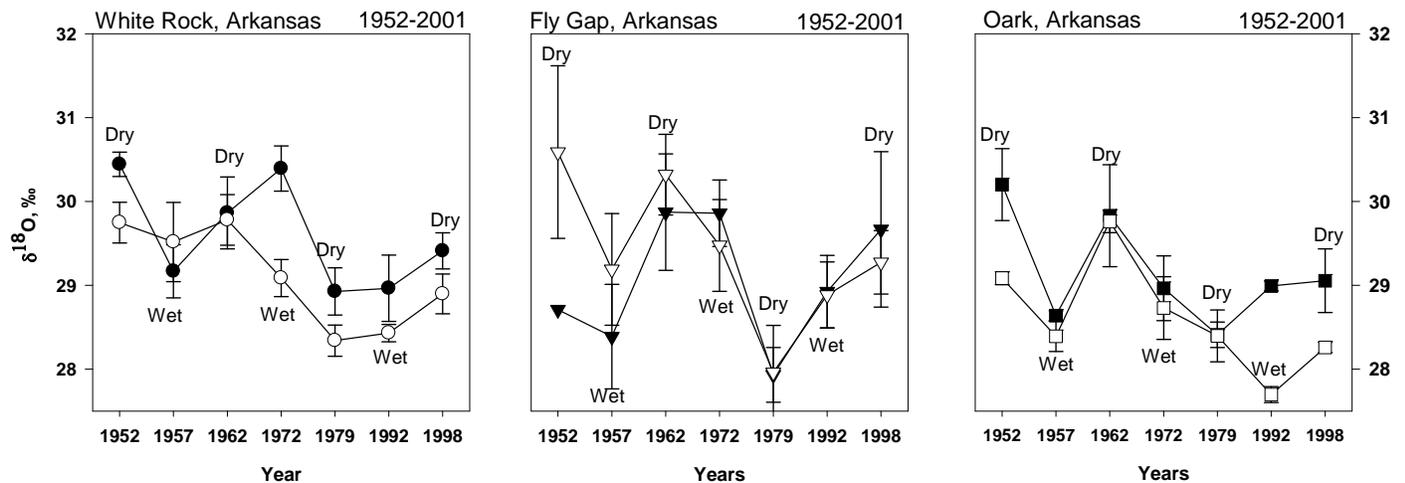


Figure 4. $\delta^{18}\text{O}$ of tree-ring α -cellulose from healthy (filled symbol) and dying (open symbol) trees from 1952-2000 at three forested sites in Arkansas, USA. Each point represents the mean of 2 healthy or 3 dying trees, except at Fly Gap which has 5 healthy and 6 dying trees represented in the 5 latter time periods. Error bars are one standard error of the mean.

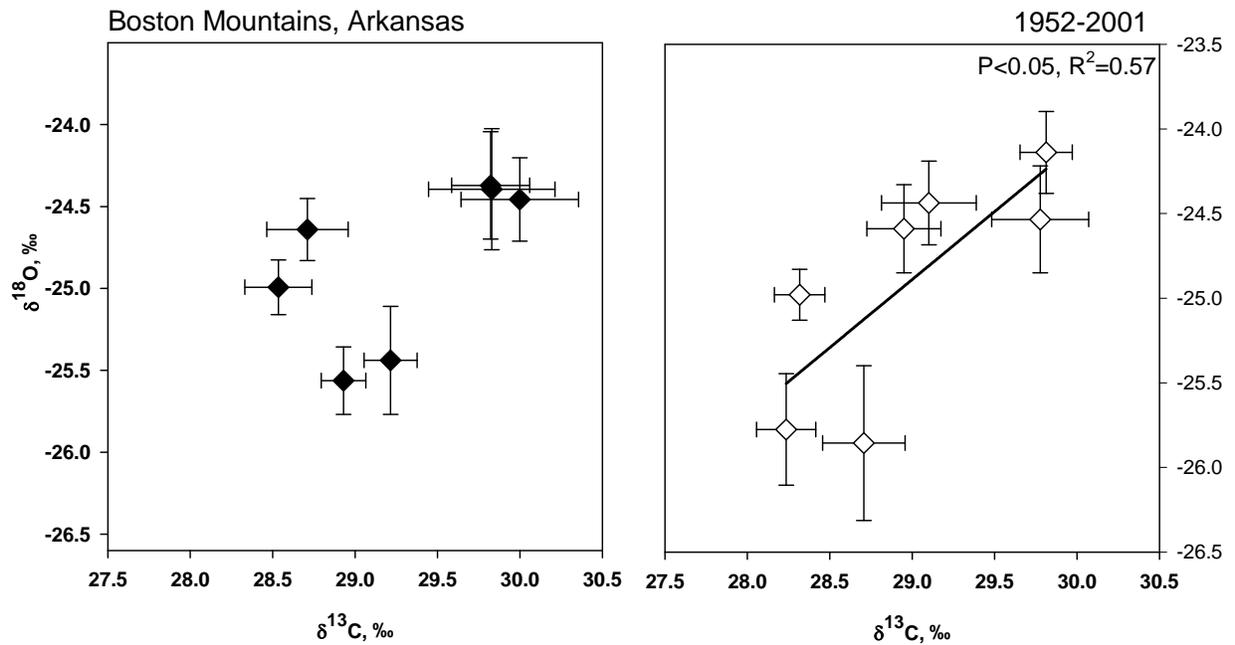


Figure 5. Relationship between averaged $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of tree-ring α -cellulose for seven wet and dry period within the specified years in healthy (n=6; filled) and dying (n=9; open) trees in three forested sites in Arkansas. Relationship for dying trees is significant ($P < 0.05$, $R^2 = 0.57$), and represented by the regression line. Healthy trees exhibit no significant trend. Error bars are one standard error of the mean.

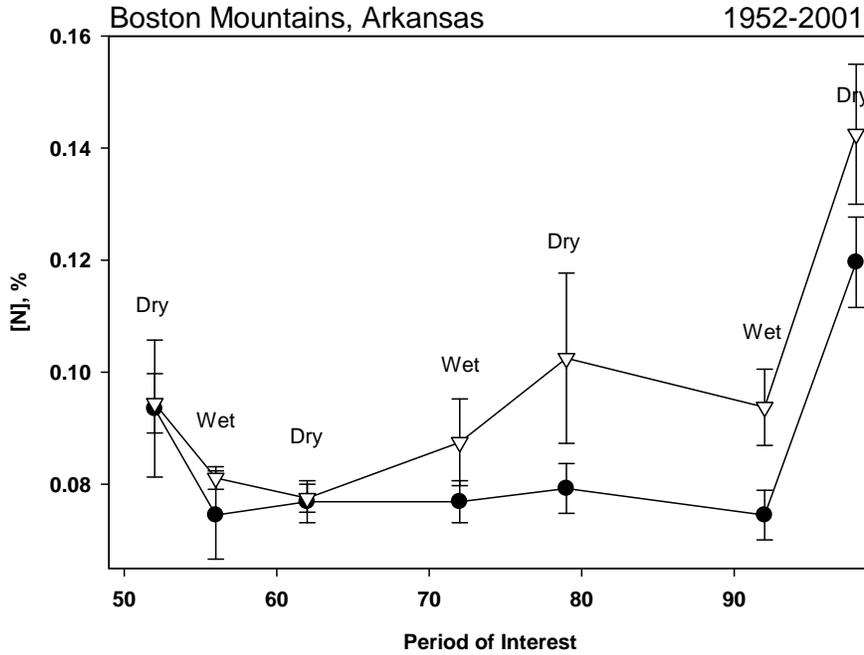


Figure 6. Tree-ring [N] in mg g-1 across time periods specified for healthy (n=5, filled symbols) and dying (n=9; open symbols) trees from three forested stands in Arkansas. Error bars represent one standard error of the mean.

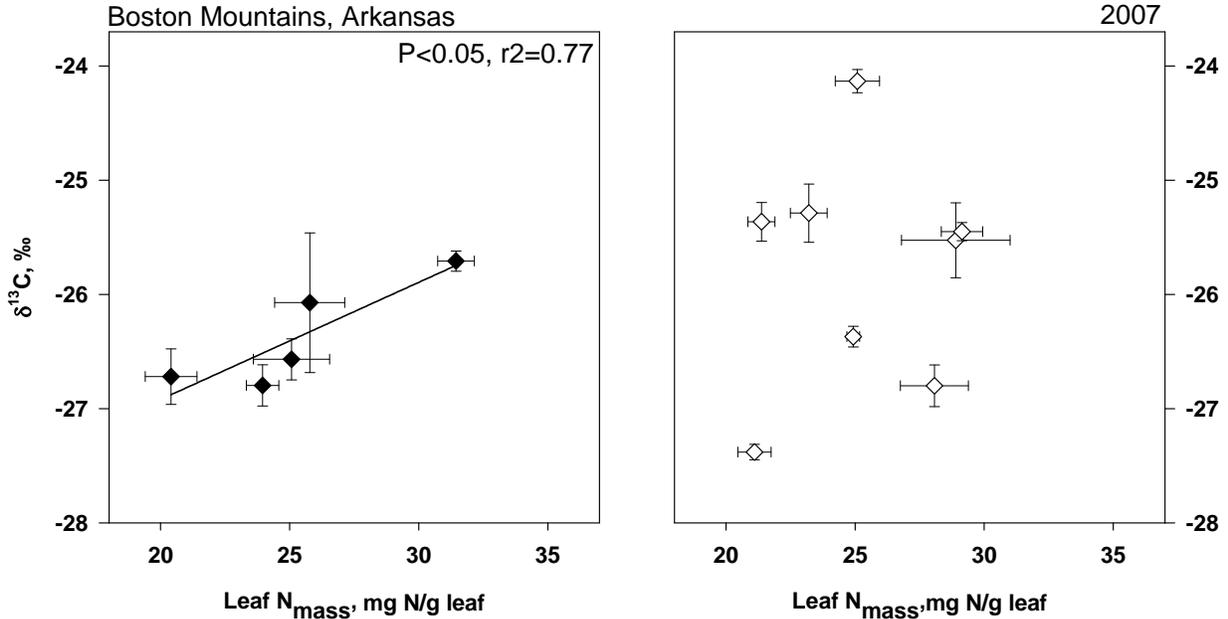


Figure 7. Relationship between $\delta^{13}C$ and N_{mass} in healthy ($P < 0.05$, $R^2 = 0.77$; shaded; n=5) and dying (open; n=8) trees at three forests in northwest Arkansas, USA. Points represent the average values for each period of interest per health class. Error bars represent one standard error of the mean.

CHAPTER 2: Distinct ecophysiological responses of co-occurring oak species to climatic variation: using tree-rings and leaf nitrogen status to understand tree carbon dynamics

Abstract

Future global climate projections suggest increased frequency and duration of extreme climate events such as drought. Understanding the impacts of decreased moisture availability on the differential responses of co-occurring species may provide insight into future forest responses to the increased disturbance events likely to accompany increases in drought conditions. Differential physiological responses to climate variability can influence changes in forest species composition and distribution. I use co-occurring *Quercus rubra* and *Q. macrocarpa* tree-rings and contemporary leaves to understand responses of these species to climate at the western edge of their distribution, at the prairie-forest ecotone in North America. I predicted greater influence of decreased moisture availability on growth patterns and stable carbon ($\delta^{13}\text{C}$) isotopic enrichment of tree-rings in *Q. rubra*, a species typically restricted to relatively mesic sites, relative to *Q. macrocarpa*, a species known to tolerate drought conditions. We also hypothesized that $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of tree-rings would suggest that stomatal conductance (g_s) governs carbon (C) dynamics in *Q. rubra*, given that species' moisture sensitivity, to a greater extent than in *Q. macrocarpa*. Contrary to my hypothesis, growth of *Q. rubra* was not as sensitive to moisture-related climate variables, or to temperature, as *Q. macrocarpa*, which exhibited significant, negative growth responses to temperature and positive responses to moisture availability. Further, I found $\delta^{13}\text{C}$ enrichment of tree-rings in *Q. rubra* relative to *Q. macrocarpa* across time, suggesting greater moisture stress experienced by *Q. rubra*. A significant, positive relationship between $\delta^{13}\text{C}$ and stable oxygen ($\delta^{18}\text{O}$) isotopes in tree-rings of *Q. macrocarpa* suggests a greater influence of g_s on C dynamics in that species relative to *Q.*

rubra, which exhibited no such relationship. *Q. rubra* tree-ring data suggests that variables driving photosynthetic capacity influence tree C dynamics more than variables linked to g_s . Correspondingly, seasonal leaf $\delta^{13}\text{C}$ was positively linked to leaf N in *Q. rubra*, consistent with isotopic theory and suggesting that enhanced tree-ring $\delta^{13}\text{C}$ in *Q. rubra* was driven, at least in part, by N availability in that species. Thus, tree-rings of *Q. macrocarpa* suggest that this species' C dynamics respond negatively to temperature and are more strongly driven by stomatal responses to moisture limitation than *Q. rubra*, and contemporary leaf samples suggest that this species is less able to capitalize on N availability relative to *Q. rubra*.

INTRODUCTION

Differential responses to moisture limitation among co-occurring forest tree species (Adams 2005, Ciasis et al. 2005, Allen et al. 2010, Dietze et al. 2011) suggest that ecophysiological vulnerability to disturbance events such as drought differ among species and are likely influences on species boundaries. Climate change and associated droughts are predicted to increasingly impact North American forests through changes in species distribution and composition (Allen and Breshears 1998, McKenney et al. 2007), and forest boundaries are expected to shift in response to climate change at a rapid rate (DeSantis et al. 2011). The prairie-forest boundary of the Midwest U.S. has shifted to the northeast with past climate change, allowing for prairie expansion, and similar shifts in forest boundaries are predicted in response to anthropogenic climate change, patterns of land use, and disturbance events (Frelich and Reich 2009). With predictions of increases of 3-9°C in summer high temperatures in the central U.S. during the 21st century (IPCC 2007), a major factor influencing future forest distributions will be

drought related changes in mortality related to increased background stress on forest species (Breshears 2005).

Assessing the responses of co-occurring tree species to recent climatic variation may help us project those species' abilities to cope with future climate change (Graumlich 1992, Gebrekistos 2009, Adams et al. 2009). Stem growth, although a relatively low priority for tree carbon (C) allocation, is a sensitive recorder of stresses that can change a tree's C allocation strategy and thus patterns of growth (Waring and Pitman 1985, Pedersen 1998). As such, tree-ring widths, and the growth indices derived from them (Fritts 1974, Johnson and Abrams 2009), can provide valuable information describing how tree species respond to climatic variation. Positive increases in growth in North American trees are typically correlated with increased moisture availability, while drought and high temperatures often correspond with decreased radial growth (Fritts 1974). For example, positive growth responses to precipitation are recorded in tree ring growth of *Quercus rubra*, which seems especially sensitive to climatic variation during the early growing season (Tardif et al. 2006). Radial tree growth is expected to be less sensitive to climatic variability in *Quercus macrocarpa*, a relatively drought-tolerant species compared to co-occurring *Q. rubra*, which is typically restricted to mesic sites and appears more sensitive to water stress (Dickson and Tomlinson 1996, Abrams 1990).

More refined measures of tree physiological responses to drought can also be key indicators of tree response to climate and, more specifically, the moisture limitations that climate often imposes. Two distinct drought survival strategies are theorized for trees. Increased stomatal regulation decreases cavitation risks by decreasing water loss, but limits C uptake (the C-starvation hypothesis, McDowell et al. 2008). Alternatively, relative lack of stomatal regulation can increase cavitation risk (the cavitation hypothesis; McDowell 2008). These

theories have been linked to tree drought mortality in the American southwest (Adams et al. 2009), with differential responses noted among co-occurring species. Though real-time measurements of tree physiological responses to environmental conditions are valuable for assessing the degree to which different tree species regulate their stomatal responses to water demand (Franks et al. 1997, Bond and Kavanaugh 1999, Ward et al. 2002), we often are interested in developing long-term data sets describing past tree responses to known climatic conditions. For such analyses, we can use $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ signatures of tree-rings, or tree-ring α -cellulose, to assess tree physiological responses to past drought (McCarroll and Loader 2004, Marshall and Monserud 2006). Variation in biomass $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ is linked to vegetation responses to the environment during tissue formation in ways that make these values important features of understanding tree strategies for coping with water limitation.

$\delta^{18}\text{O}$ in tree-ring α -cellulose is influenced by the $\delta^{18}\text{O}$ value of source water, evaporative demand at the stomatal aperture, the extent to which relatively ^{18}O -enriched water at the stomatal aperture is mixed with ^{18}O -deplete xylem water during transpiration (the Péclet effect; Farquhar and Lloyd 1993, Barbour et al. 2000), and biochemical fractionation within the tree during cellulose formation (Farquhar and Lloyd 1993, Roden et al. 2000a). $\delta^{18}\text{O}$ of source water is dependent on $\delta^{18}\text{O}$ values of input precipitation, evaporative demand on source water, and the depth of water source in the soil profile (Roden et al. 2005). Variation in $\delta^{18}\text{O}$ in precipitation results from Rayleigh distillation processes (Dansgaard 1964), and is more directly linked to $\delta^{18}\text{O}$ values of cellulose if the tree is accessing surface water. $\delta^{18}\text{O}$ of vegetation biomass tends to increase with evaporation, and the discrimination against ^{18}O that occurs during that process (Shu et al. 2005). Because of the ^{18}O enrichment that occurs in leaf water with transpiration, $\delta^{18}\text{O}$ of organic matter is correlated with humidity (Edward and Fritz 1986, DeNiro and Cooper

1989, Robertson et al. 2001), temperature (Burk and Stuiver 1981), transpiration rates (Barbour et al. 2000), water balance (White et al. 1994) and vapor pressure deficit (Farquhar and Lloyd 1993, Roden et al. 2000b) – all features linked to or driving evaporative demand. The relative importance of the Peclet effect may be similar in scale to biochemical fractionation (Barbour 2000), which occurs during the incorporation of oxygen into cellulose and may dampen the evaporative signal captured by leaf water $\delta^{18}\text{O}$ (Saurer et al. 1997a). $\delta^{13}\text{C}$ of tree-ring cellulose is influenced by the $\delta^{13}\text{C}$ of atmospheric CO_2 and the diffusional and enzymatic discrimination against ^{13}C during CO_2 flow into the leaf and photosynthesis, respectively (Farquhar et al. 1989, Warren 2001). $\delta^{13}\text{C}$ of tree-rings is expected to increase with water stress due to enhanced stomatal resistance, associated restricted CO_2 availability inside the leaf (c_i), and resulting decreased discrimination against ^{13}C during C assimilation. As a result, tree-ring $\delta^{13}\text{C}$ values are expected to reflect greater ^{13}C incorporation at drier sites (Saurer et al. 1997b). Other environmental factors like temperature, solar irradiation, and nutrient availability also can influence $\delta^{13}\text{C}$ due to their effect on photosynthetic capacity and resulting c_i (Francey and Farquhar 1982).

Given that both $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ of vegetation are linked to stomatal regulation, theory predicts strong correlations between tree-ring ^{13}C and ^{18}O if stomatal regulation is a dominant feature driving C relations within a tree (Barbour et al. 2000, Barbour et al. 2004). This concept has been used in multiple studies assessing the degree to which C source:sink dynamics are governed by stomatal conductance (g_s) and how leaf c_i/c_a , the ratio of internal to external CO_2 concentrations, relates to changing relative humidity (Scheidegger et al. 2000, Barbour 2002). If vegetation $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ are not related, or exhibit a negative relationship, it suggests that A_{max} , or drivers of this factor, play a greater role in C dynamics than g_s (Barbour 2002).

In addition to tree-ring $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$, biomass nitrogen (N) concentrations and stable isotopic signatures can aid us in understanding the drivers of tree responses to climate. Nitrogen availability is a critical influence on A_{max} (Gebauer and Schulze 1991, Warren and Adams 2001) and as such, can also influence $\delta^{13}\text{C}$ signatures of tree-rings (Guerrieri et al. 2010). Typically N is a limiting nutrient in North American forests (Vitousek and Howarth 1991), and perturbations to N dynamics can play a large role in forest productivity although their influence on C source:sink dynamics (Aber 1992, Norby 1998). For example, Guerrieri et al. (2010) linked N deposition to enriched $\delta^{13}\text{C}$ of tree rings via a greater change in A_{max} compared to g_s . Leaf N concentration can provide information related to the ability of a tree to generate the photosynthetic enzyme Rubisco (Field and Mooney 1986) and thus can be a valuable feature of studies assessing vegetation $\delta^{13}\text{C}$. More generally, integrative measures of vegetation N dynamics and N sources such as foliar $\delta^{15}\text{N}$ (Robinson 2001) can indicate differences in N dynamics between individuals that might help us understand variation in vegetation $\delta^{13}\text{C}$.

We combine these approaches to examine the responses of co-occurring *Quercus macrocarpa* (bur oak) and *Quercus rubra* (northern red oak) in the Midwest of North America to recent climatic variability. We use these responses to understand how these two species may differ in their strategies for dealing with moisture limitation, which is predicted to increase in the region in the coming decades. The *Quercus* genus is globally distributed, and though their growth is evidently promoted with increasing moisture availability, they typically can prosper in spite of periodic drought conditions (Hanson et al 2005). *Quercus* spp. in the Midwest, and specifically at the tallgrass prairie-forest ecotone, thus are ideal for exploring species' responses to drought, to project changes in function and ultimately in distribution under predicted future increases in drought conditions (IPCC 2007).

Using tree-rings from these co-occurring species, we assessed species' differences in radial growth responses to precipitation, temperature and the Palmer Drought Severity Index (PDSI), three indicators of environmental conditions during the past several decades. We then use tree-ring $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ to infer these species' ecophysiological responses to past moisture availability, and data describing contemporary leaf N status to investigate the degree to which responses to moisture availability vs. N dynamics govern tree C dynamics. We use these data as a means of projecting these two species' growth performance in a future warmer and more drought-prone climate. Because *Q. rubra* typically occurs on relatively mesic sites (Abrams 1990), we hypothesized 1) that dry conditions would be associated with greater declines in radial growth for *Q. rubra* than for *Q. macrocarpa*. Accordingly, we hypothesized 2) that *Q. rubra* would exhibit relative ^{13}C -enrichment in its tree-rings, with that enrichment more pronounced during drought years. Given the relative drought sensitivity of *Q. rubra* compared to *Q. macrocarpa*, we further hypothesized 3) *Q. rubra* would exhibit a more robust positive relationship between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ than *Q. macrocarpa*, indicative of g_s serving as a relatively strong influence on *Q. rubra* C source:sink dynamics, and that *Q. macrocarpa* C dynamics would be driven to a greater extent by N availability, given strong linkages between leaf N and A_{max} .

METHODS

Site selection

We sampled three *Q. macrocarpa* and three *Q. rubra* at the University of Kansas Field Station's Briedenthal Tract (95°17'W, 38°75'N), a forested stand of mixed hardwoods at the prairie-forest ecotone. Species composition of trees and understory plants suggest this is a high quality, relatively old forest that has never been logged (Fitch and Kettle 1988). We selected co-

occurring trees of similar diameter at breast height (DBH), all within 500m of each other. All trees serve as co-dominant contributors to the closed canopy forest, and presumably experience the same light conditions as a result (Table 1). The climate is continental with warm summers and periodically cold winters. Average annual precipitation is 1003 mm, with most precipitation falling in spring and fall with relatively little winter snowfall (Kettle and Whitemore 1991). Potential evapotranspiration averages 1200mm annually (Abrams et al. 1986). Soils are loam with high clay content (Oxyaquic Vertic Argiudolls, Soil Survey Staff).

Tree core sampling and development of growth indices

Increment borer cores were sampled at breast height (1.7m) in May 2007. Four cores (12 mm diameter) per tree were taken from each cardinal direction per tree. Tree cores were mounted, sanded and scanned into Adobe Photoshop. We used Image-J software to measure ring widths (NIH, Bethesda, MD). Tree-rings were dated using event years, and cross-dated using COFECHA (Holmes 1983). Ring widths for *Q. macrocarpa* (n=3; 1953-2007) and *Q. rubra* (n=3; 1960-2007) were standardized in ARSTAN software (Cook 1985) to remove non-climatic signals from the tree ring series (Pan et al. 1997) and produce a ring width index (RWI) with standardized variance (Cook 1985). *Q. rubra* ring widths exhibit a negative exponential form over time (Pan et al. 1997), supporting the use of the negative exponential regression performed in ARSTAN to standardize the oak chronologies; we assumed a similar function was appropriate for *Q. macrocarpa*. We observed stronger climate-growth relationships using RWI in comparison to basal area increment (Visser 1995), thus we present RWI as our growth index of interest.

Tree-ring isotopic analyses

We selected seven time periods of particular interest for isotopic analyses, representing four dry periods and three wetter periods according to PDSI estimates for the sites (Table 2; Haavik et al. 2008). Each period lasted approximately three years. Tree-rings were separated using a razor blade to extract the years of interest. Because earlywood can be derived from C fixed during the previous growing season (Hill et al. 1995), we were careful to exclude earlywood at the beginning of each ring series of interest. We generated 1 to 2 g of sawdust for each period of interest using a Dremel tool (Bosch Tool Corporation, Chicago, IL).

For $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ analyses, we extracted α -cellulose from sawdust samples following procedures from Leavitt and Danzer (1993) and McCarroll and Loader (2004). Briefly, samples were soaked and rinsed in a Soxhlet apparatus with toluene:ethanol solution, then soaked and rinsed in ethanol to remove lipids and resins. To remove lignin components, NaClO_2 (6-8 g) was added to 1 mL of CH_3COOH and then 700 mL of DI water was added. Samples were washed in NaOH solution to remove holocellulose. Samples were washed multiple times in DI water to remove NaOH, and isolated α -cellulose was then dried at 60°C for 24 h. Approximately 0.10 mg α -cellulose was weighed into tin capsules for $\delta^{13}\text{C}$ analysis, and approximately 1 mg of α -cellulose was loaded into silver capsules for $\delta^{18}\text{O}$ analysis at the University of Kansas Stable Isotope Laboratory. Samples were analyzed for $\delta^{13}\text{C}$ on a Carlo Erba elemental analyzer (1110 CHN Combustion Analyzer, Carlo Erba Strumentazione, Milan, Italy) linked to a ThermoFinnigan Delta Plus mass spectrometer (Finnigan MAT, Germany, precision +/- 0.13‰) and are expressed as deviations from PDB standard (Craig 1957, Farquhar et al 1982). $\delta^{18}\text{O}$ analysis via TC/EA-IRMS provided values expressed as deviations from V-SMOW. Isotopic values are presented using the conventional δ (delta) notation.

Contemporary leaf and soil sampling

Full sun leaves were collected via shot gun sampling in July and September of 2010. Leaves were immediately sealed flat in plastic bags and placed in a cooler. Upon return to the lab, we weighed and scanned leaves for area in Image J software (NIH, Maryland, US). After scanning, leaves were dried at 60°C for 48 hours and crushed to a fine powder. Leaf material from five leaves from each tree, except *Q. rubra* tree three during September which is represented by only two leaves, was weighed into tin capsules for $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, [C], and [N] analyses on the instrumentation used for tree-ring α -cellulose $\delta^{13}\text{C}$ analyses.

Climate Data

We obtained average annual temperature, precipitation and PDSI records from the National Oceanic and Atmospheric Administration website (<http://www1.ncdc.noaa.gov/pubdata/cirs>) for the appropriate region in Kansas. Both precipitation and temperature, along with potential evapotranspiration, runoff and soil moisture, are incorporated into a meteorological drought measure in PDSI (Palmer 1965, Oladipo 1985). PDSI is appealing because it represents a combination of factors that correspond to the degree of drought severity (Alley 1984). We also developed more refined, seasonal climate indices to assess the influence of climate in specified months on radial growth throughout the growing season. We summed precipitation from May to September as growing season values, April to May as pre-growing season, April to August as pre-growing in addition to growing season, August to September as late growing season, and October to April as winter precipitation for each of our seven periods of interest, in addition to using annual sums. Indices of annual and various growing season values for temperature and PDSI were developed in the same manner.

Statistical Analysis

We corrected tree ring $\delta^{13}\text{C}$ values by an annual correction value of -0.025‰ to account for ^{13}C -deplete additions of CO_2 to the atmosphere via fossil fuel emissions since 1950 (Francey et al. 1999). We assessed the strength of relationships between climate indices and tree radial growth with tree growth data ranging 1953 to 2007 for most, but not all, trees (Table 1) using Pearson product-moment correlation coefficients. Lag responses between growth indices and the previous year's environmental data (antecedent climate) were also assessed. Correlations were examined between $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of tree-ring α -cellulose and also between leaf $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ on tree ring $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$. We tested for the influence of moisture availability on radial growth and $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ using ANOVA (PROC ANOVA, SAS 9.1.3, Cary, NC). Repeated measures ANOVA (PROC MIXED, SAS 9.1.3, Cary, NC) was used to assess the influence of species, time, and their interactions on tree-ring α -cellulose $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$. We assessed correlation relationships between leaf isotopic signatures and three different measures of leaf N: N_{mass} ($\text{mg N g}_{\text{leaf-1}}$), N_{area} ($\text{mg N m}_{\text{leaf-2}}$), and leaf C:N ratios (by mass). N_{mass} captures the mg of N per g leaf weight and N_{area} captures mg of N per leaf meter. ANOVA was also used to test for the influence of leaf N and $\delta^{15}\text{N}$ on leaf $\delta^{13}\text{C}$. Because individual leaf data were not independent of each other, we averaged individual leaf data on a per-tree basis, and performed statistical analyses on these averaged data. This resulted in a reduction in statistical power ($n=3$). In relevant plots, we display individual leaf data as well to demonstrate the general trends and spread of the entire data set. We determined statistical significance at $P < 0.05$, and report all instances of $P < 0.10$.

RESULTS

Radial growth responses to climate

Relationships between RWI and the two climate variables most closely related to moisture availability, precipitation and PDSI, exhibited more frequent and stronger degrees of significance for *Q. macrocarpa* than for *Q. rubra* (Table 3). Averaged RWI for *Q. macrocarpa* and *Q. rubra* exhibited no significant trends across time, but exhibited significant, positive relationships with average annual PDSI ($R^2=0.52$, $P<0.0005$, $n=3$ and $R^2=0.36$, $P<0.05$, $n=3$, respectively). Precipitation also exhibited significant, positive relationships with RWI in *Q. macrocarpa* and *Q. rubra* (Table 3). Temperature was a significant, negative influence on *Q. macrocarpa* RWI, but not *Q. rubra*. Linear regressions revealed similar slopes for RWI with precipitation, PDSI, and temperature for both species. *Quercus rubra* radial growth responses to relatively dry conditions did not significantly differ from *Q. macrocarpa*.

Tree-ring α -cellulose $\delta^{13}C$ and $\delta^{18}O$

Quercus macrocarpa consistently displayed significantly lower $\delta^{13}C$ values compared to *Q. rubra* (-25.3 ± 0.4 and $-24.1\pm 0.1\%$, respectively; $n=3$; Figure 1a). As with $\delta^{13}C$ values, *Q. macrocarpa* exhibited consistent ^{18}O -depletion in tree-ring α -cellulose relative to *Q. rubra*, (28.0 ± 0.3 and $29.9\pm 0.4\%$, respectively; $n=3$, Figure 1b). Tree ring α -cellulose $\delta^{13}C$ and $\delta^{18}O$ exhibited no significant relationships with annual or seasonal measures of precipitation, PDSI or temperatures in either species (Figure 1a and 1b). A significant, positive relationship was found between $\delta^{13}C$ and $\delta^{18}O$ in *Q. macrocarpa* ($R^2=0.78$, $P<0.001$; Figure 2).

Contemporary leaf data

We observed declines in tree-averaged leaf N concentration across the 2010 growing season, reflected as increases in leaf C:N ratios (Fig. 3). Leaf C:N varied from July minimums to September maximums in both *Q. macrocarpa* and *Q. rubra* (12.97 to 20.47 and 14.05 to 20.63, respectively). July leaf C:N was significantly different between *Q. macrocarpa* and *Q. rubra* ($P < 0.005$; 14.4 ± 1.1 and 15.4 ± 0.60 , respectively), but leaf C:N was not significantly different between species in September. Across both species, the seasonal shift in leaf C:N was associated with a concurrent change in leaf $\delta^{13}\text{C}$ (Fig. 4). In September, we observed a significant, positive relationship between *Q. macrocarpa* leaf $\delta^{13}\text{C}$ and C:N ratio ($R^2 = 0.99$, $P < 0.05$; Figure 4a) and a significant, negative relationship between *Q. rubra* leaf $\delta^{13}\text{C}$ and C:N ratio ($R^2 = 0.98$, $P < 0.07$; Figure 4b). We observed no significant relationships for either species in July. The [C] of *Q. macrocarpa* leaves was significantly lower than *Q. rubra*, with an average offset of 1.6 mg C $\text{g}_{\text{leaf}}^{-1}$ in July and 2.0 mg C $\text{g}_{\text{leaf}}^{-1}$ in September. Leaf N_{mass} declined significantly between July and September in *Q. macrocarpa* and *Q. rubra* (3.3 ± 0.1 to $2.5 \pm 0.0\%$ and 3.1 ± 0.0 to 2.6 ± 0.1 mg N $\text{g}_{\text{leaf}}^{-1}$, respectively). $\delta^{13}\text{C}$ values exhibited more enriched values in July than in September in *Q. macrocarpa* and *Q. rubra* (-28.2 ± 0.2 and $-30.1 \pm 0.2\%$; -27.8 ± 0.3 and $-29.0 \pm 0.4\%$ respectively; Figure 4).

Leaf $\delta^{15}\text{N}$ ranged from 1.9 to -2.0% (mean of $-0.7 \pm 0.3\%$) in July and 0.3 to -2.3% (mean of $-0.6 \pm 0.2\%$) in September in *Q. macrocarpa*, and from 1.4 to -1.3% (mean of $0.2 \pm 0.2\%$) in July and 1.7 to -0.7 (mean of $0.6 \pm 0.2\%$) in September in *Q. rubra*. $\delta^{15}\text{N}$ did not differ significantly between July and September in either species, but was significantly greater for *Q. rubra*. *Q. macrocarpa* and *Q. rubra* both exhibited near significant relationships between $\delta^{15}\text{N}$ and C:N in September ($P < 0.01$, $R^2 = 0.98$ and $P < 0.10$, $R^2 = 0.96$, respectively; Fig. 5).

DISCUSSION

Tree-ring growth patterns and stable isotopes

Tree-rings of species at the edge of their range typically exhibit great sensitivity to climate (Fritts 1976, LaMarche 1978, Jump et al. 2006), and bole growth exhibits positive responses to moisture where this factor is relatively limiting (Fritts 1976, Tardif and Bergeron 1997). *Quercus rubra* typically is found on relatively mesic sites (Abrams 1986), and the *Q. rubra* used in this study occur at the very western edge of their distribution (Sander 1965), where annual precipitation is relatively low. Given these features and the propensity for *Q. macrocarpa* to access relatively deep water sources (Struve 2006) we expected greater growth sensitivity during wetter periods and more sharply decreased radial growth during dry conditions in *Q. rubra* relative to *Q. macrocarpa*. We did not observe these trends over the ~5 decades of growth assessed in this study.

Relatively deep water within soil profiles frequently exhibits ^{18}O -depletion (Allison 1983, Barnes and Allison 1983, Kendall and Caldwell 1998). Though we do not know the $\delta^{18}\text{O}$ of shallow vs. deep water sources in these forests, the observed ^{18}O -depletion of *Q. macrocarpa* tree-ring α -cellulose is consistent with more deeply rooted *Q. macrocarpa* (Fig. 1b). To the extent that biomass $\delta^{13}\text{C}$ reflects integrated tree water relations (Leavitt and Long 1989, Ehleringer et al. 2000), tree-ring $\delta^{13}\text{C}$ values further imply that *Q. macrocarpa* trees experienced less moisture stress than *Q. rubra* (Fig. 1a). Further, the significant correlation between tree-ring $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in *Q. macrocarpa* implies that C dynamics in these trees were governed to a large extent by stomatal regulation, and less so by drivers of A_{max} (Barbour et al. 2002); such a correlation was not observed in *Q. rubra* (Fig. 2). This, combined with the weaker growth response of *Q. rubra* to moisture-related climate parameters (Table 2) suggests that growth of

these *Q. rubra* individuals was influenced by factors other than water relations and associated stomatal regulation to a greater degree than neighboring *Q. macrocarpa*.

Linking contemporary leaf samples to tree-ring data

Given the influence of leaf photosynthetic sink strength on biomass $\delta^{13}\text{C}$ (Farquhar et al. 1982) and the importance of N as a driver of that sink (Evans 1983, Evans 1989, Reich and Walters 1994), exploring N dynamics in these trees may provide a means of elucidating the relative importance of drivers of growth other than stomatal regulation. Working with N in tree-rings can be problematic due to its low concentrations and apparent mobility after ring formation (Cutter and Guyette 1993, Poulson 1995) but we can employ contemporary leaf samples from these trees to help us understand the relative degree to which N dynamics, vs. stomatal regulation of water relations, govern biomass $\delta^{13}\text{C}$ values and, more specifically, C dynamics of these species. We can use these data to infer what may have driven past differences in growth dynamics and stable isotopic signatures, now reflected in tree-ring data.

The decrease in leaf C:N over time with season was concurrent with an increase in leaf $\delta^{13}\text{C}$ (Fig. 4). Tree resorption of multiple compounds may have begun in anticipation of leaf senescence by our sampling date in September, possibly driving the higher C:N ratios at that time (Killingbeck 1996). However, mobilization and resorption of C-rich compounds would likely result in ^{13}C -enrichment of leaves, not the ^{13}C -depletion observed (Gessler et al. 2009, Bruggemann et al. 2011). The negative relationship between *Q. rubra* leaf $\delta^{13}\text{C}$ and C:N in September (Figure 4b) thus implies that these leaves experienced ^{13}C -enrichment with greater N concentrations. Given the positive influence of leaf N on C fixation rates (Evans 1983, Evan 1989, Reich et al. 1991), such data are consistent with the idea that discrimination against ^{13}C -

CO₂ during fixation declines as C sink strength increases. In contrast, we observed a non-significant trend of a positive relationship between *Q. macrocarpa* leaf $\delta^{13}\text{C}$ and C:N in September (Figure 4a). This counter-intuitive pattern suggests that a factor other than N availability is driving biomass $\delta^{13}\text{C}$ and associated C dynamics. Congruent with this idea is the positive relationship between tree-ring $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ observed in this species, and the associated implication that stomatal regulation is more of a driver of C dynamics than drivers of A_{max} .

Nitrogen dynamics also appear to differ between these two species when we explore leaf $\delta^{15}\text{N}$. Both species exhibited a decline in leaf $\delta^{15}\text{N}$ with increasing C:N in September, but not in July (Figure 5). Studies in semi-arid systems have linked low values of biomass C:N to high $\delta^{15}\text{N}$ (Pataki et al. 2008), with changing slopes of this relationship across seasons (Goedhardt et al. 2010). Data in the current study suggest that such a relationship does not emerge in these tree species until late in the growing season. If the relationships exhibited in September were driven by resorption of nitrogenous compounds prior to senescence, we would expect ^{15}N -enrichment as leaf C:N increased. Regardless, in *Q. rubra*, leaf $\delta^{15}\text{N}$ does not appear linked to resorption processes (Kolb and Evans 2002). Instead, the data imply that trees successful at obtaining relatively more N in September acquired N from ^{15}N -enriched sources (Pataki et al. 2008). Soil $\delta^{15}\text{N}$ values typically increase with depth in forest soil profiles (Billings and Richter 2006, Hobbie and Ouimette 2009), as we observed at this site (data not shown). We might predict, given the propensity of *Q. macrocarpa* for deep rooting (Abrams 1990, Struve 2006) and its generally ^{18}O -depletion in tree-ring α -cellulose, that its $\delta^{15}\text{N}$ would also reflect N sources from deeper in the soil profile. However, we observed the opposite trend; *Q. rubra* leaf $\delta^{15}\text{N}$ was significantly greater than *Q. macrocarpa*. Mycorrhizal symbionts also likely are relevant to these trees' $\delta^{15}\text{N}$ values given mycorrhizal transfer of ^{15}N -deplete compounds to their hosts

(Hogberg et al. 1997, Hobbie et al. 2006), but we know of no study suggesting a different propensity for such symbioses between these species. Species can experience differences in the degree to which nitrate is assimilated in the root vs. the shoot (Gebauer and Schultze 1997), which in turn can influence foliar $\delta^{15}\text{N}$ (Kolb and Evans 2002); it is feasible that *Q. rubra* may assimilate proportionately less nitrate in its roots, resulting in more ^{15}N -enriched nitrate being assimilated in its leaves. This would result, all else equal, in *Q. rubra* leaf ^{15}N -enrichment. Though these oaks' leaf $\delta^{15}\text{N}$ values imply different N dynamics between these species, it remains unclear why leaf N status of these species' was linked in divergent ways to leaf $\delta^{13}\text{C}$.

Contemporary leaf data certainly are not a conclusive means of assessing past drivers of tree growth. However, in spite of our inability to elucidate drivers of different N dynamics between these species, the leaf data in conjunction with tree-ring data are suggestive of some important differences in drivers of C dynamics in these co-occurring oaks. The September values of *Q. rubra* leaf $\delta^{13}\text{C}$ are linked to leaf N in ways predicted by isotopic theory, and suggest that enhanced biomass $\delta^{13}\text{C}$ is driven, in part, by greater N availability. These data provide one line of evidence that biomass $\delta^{13}\text{C}$ in *Q. rubra* is significantly governed by at least one factor governing C sink strength. This concept corresponds with tree-ring data, which for this species suggest that variables driving A_{max} are likely more tightly linked to tree C dynamics than variables linked to g_s . In contrast, *Q. macrocarpa* tree-ring data suggest that g_s is a strong driver of biomass $\delta^{13}\text{C}$ and associated C dynamics; correspondingly, *Q. macrocarpa* leaf data indicate no relationship between biomass $\delta^{13}\text{C}$ and N predicted by isotopic theory.

Linking past oak performance to future climate change

The distinct drivers of C dynamics between these two oak species suggested by these data have important implications for their ability to persist in this region in a changing climate. Climate projections suggest increase frequency of extreme events, elevated maximum temperatures, and increased frequency and duration of drought in the Midwest (IPCC 2007). The greater dependence of *Q. macrocarpa* growth on precipitation-derived moisture availability relative to *Q. rubra*, contrary to our predictions, as well as the negative response of *Q. macrocarpa* to temperature, suggests that this species will be more sensitive to such climatic changes. In particular, the positive relationship between tree-ring $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in this species is a strong indication that the dominant driver of this species' C dynamics is stomatal regulation of water loss and, concurrently, CO_2 availability. In contrast, *Q. rubra* exhibited weaker relationships between RWI and climate parameters. Further, *Q. rubra* exhibited no relationship between tree-ring $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, suggesting that factors other than stomatal response to water availability was a dominant driver of its C dynamics. Indeed, we observed a significant, negative relationship between leaf $\delta^{13}\text{C}$ and C:N in this species, suggesting that *Q. rubra* leaf $\delta^{13}\text{C}$ and, presumably, tree-ring $\delta^{13}\text{C}$ as well, is linked to N availability in a different manner than in *Q. macrocarpa*, which exhibited a significant, positive relationship between leaf $\delta^{13}\text{C}$ and C:N not predicted by isotopic theory. We suggest that further research on C source:sink dynamics, as elucidated via relationships between biomass $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, and $\delta^{13}\text{C}$ and N status, can help us predict drivers of tree species success in an altered climate.

TABLES AND FIGURES

Site	Age	Oldest Tree ring	DBH (cm)	Height (m)
Quru1	49	1958	38.6	17.0
Quru2	41	1966	63.5	15.2
Quru3	44	1963	58.9	16.6
Quma1	49	1958	87.6	14.6
Quma2	55	1952	81.54	17.5
Quma3	55	1952	79.2	12.1

Table 1. Diameter at breast height (DBH), height, approximate age of each of the *Q. rubra* (Quru) and *Q. macrocarpa* (Quma) trees from the University of Kansas Field Station, Kansas, USA.

Time Period	Drought or Wet	Most extreme PDSI	Mean monthly PDSI±SE
1952 - 1956	Drought	-5.51	-2.57±0.09
1957 - 1959	Wet	4.71	1.77±0.14
1962 - 1967	Drought	-5.39	-1.52±0.10
1972 - 1975	Wet	5.58	2.68±0.09
1979 - 1981	Drought	-4.11	-2.09±0.15
1992 - 1995	Wet	3.75	1.52±0.11
1998 - 2001	Drought	-3.44	-1.16±0.09

Table 2. Palmer Drought Severity Index (PDSI) for selected periods of interest (drought; negative PDSI and wet; positive) derived from National Oceanic and Atmospheric Administration climate records. Values represent monthly values averaged for the specified periods (~3 years) for the single climate region encompassing sampling locations at the University of Kansas Field Station, Kansas, USA.

Table 3: Pair-wise correlation matrix of Pearson correlation coefficients for ring width indices (RWI) from 1951-2001 with seasonal and annual environmental data for *Quercus macrocarpa* (Quinn, n=3) and *Q. rubra* (Quru, n=3) at the University of Kansas Field Station, Kansas, USA.

	Seasonal Climate						Annual Climate							
	Precipitation			PDSI			Temperature							
	Grow	Pre	Pre+G	Late	Grow	Pre	Pre+G	Late	Grow	Pre	Pre+G	Late	Pp	Temp
Quinn	0.44***	0.29*	0.49*	NS	0.53 ^s	0.43**	0.52 ^s	0.49 ^s	-0.01*	NS	-0.28*	-0.28*	0.52 ^s	0.47 ^s
Quru	0.28	NS	0.31*	NS	0.33*	0.26	0.34*	0.35**	NS	NS	NS	NS	0.36*	0.3*

Coefficients of correlation; p-values represented by p<0.10 have no asterisk, p<0.05*, p<0.005**, p<0.001***, and p<0.0005^s. G=growing season averaged (May- September) per year, Pre= pre-growing seasonal (April-May), PG = pre-growing season in addition to growing season climate averaged (April - August) per year, and LG = late growing season from August - September averaged for each year. Pp= precipitation, PDSI= Palmer drought severity index, and Temp = temperature.

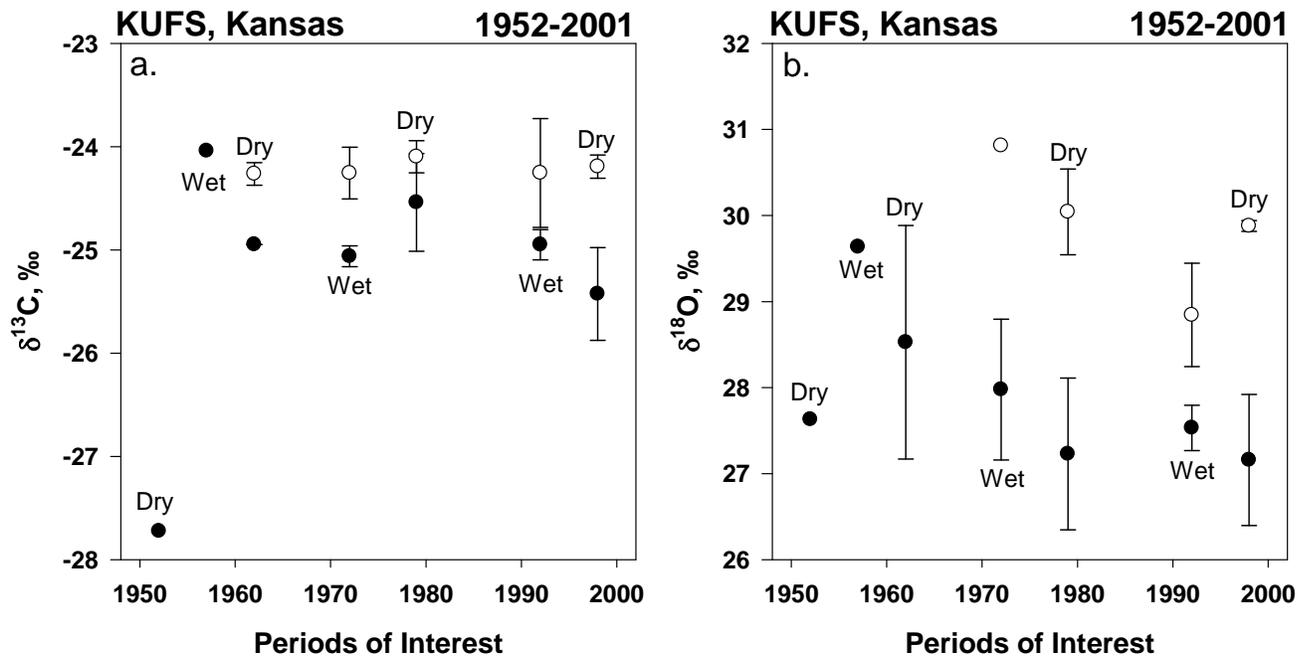


Figure 1. *Quercus rubra* and *Q. macrocarpa* $\delta^{13}\text{C}$ (a) and $\delta^{18}\text{O}$ (b) of α -cellulose over time at a forested site at the University of Kansas Field Station, Kansas, US. *Quma* averaged values are represented by filled circles and *Quru* by open circles. Error bars are one standard error of the mean.

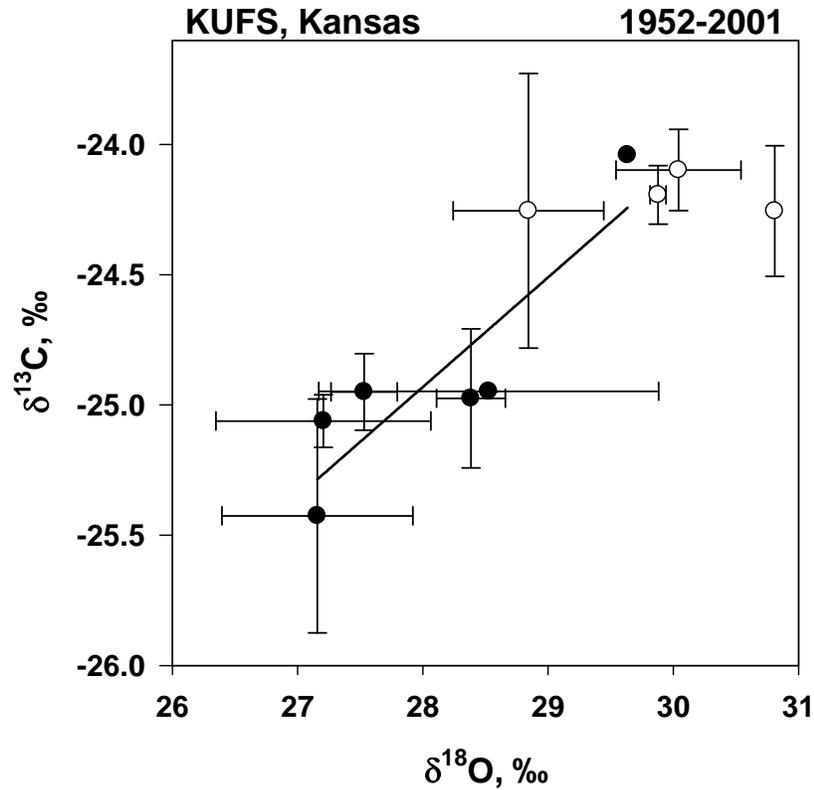


Figure 2. Relationship between tree-ring α -cellulose $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ from *Quercus macrocarpa* (*Quma*, filled circles, $n=3$) and *Quercus rubra* (*Quru*, open circles, $n=3$) at a forested site at the University of Kansas Field Station, Kansas, US. Significant linear regression for *Quma* is represented by black line ($R^2=0.78$, $P<0.001$); *Quru* does not exhibit a significant relationship. Error bars are one standard error of the mean.

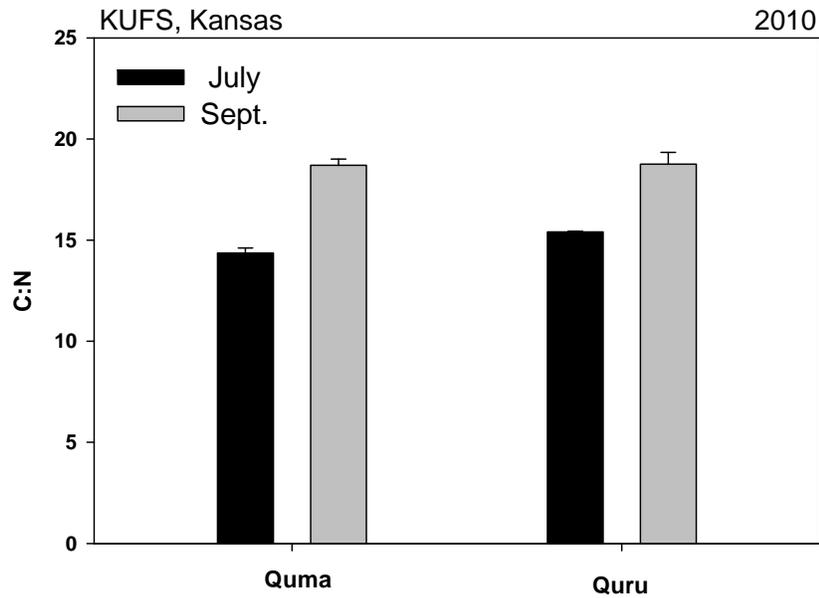


Figure 3: Leaf C:N (mass basis) for *Q. macrocarpa* (Quma, n=3) and *Q. rubra* (Quru, n=3) leaves collected in July and September 2010 at a forested site at the University of Kansas Field Station, Kansas, US. Significant differences were found between *Quma* and *Quru* C:N in July ($P < 0.005$), but no difference between species in September. Both species exhibited higher C:N in September ($P < 0.05$) relative to July. Error bars are one standard error of the mean.

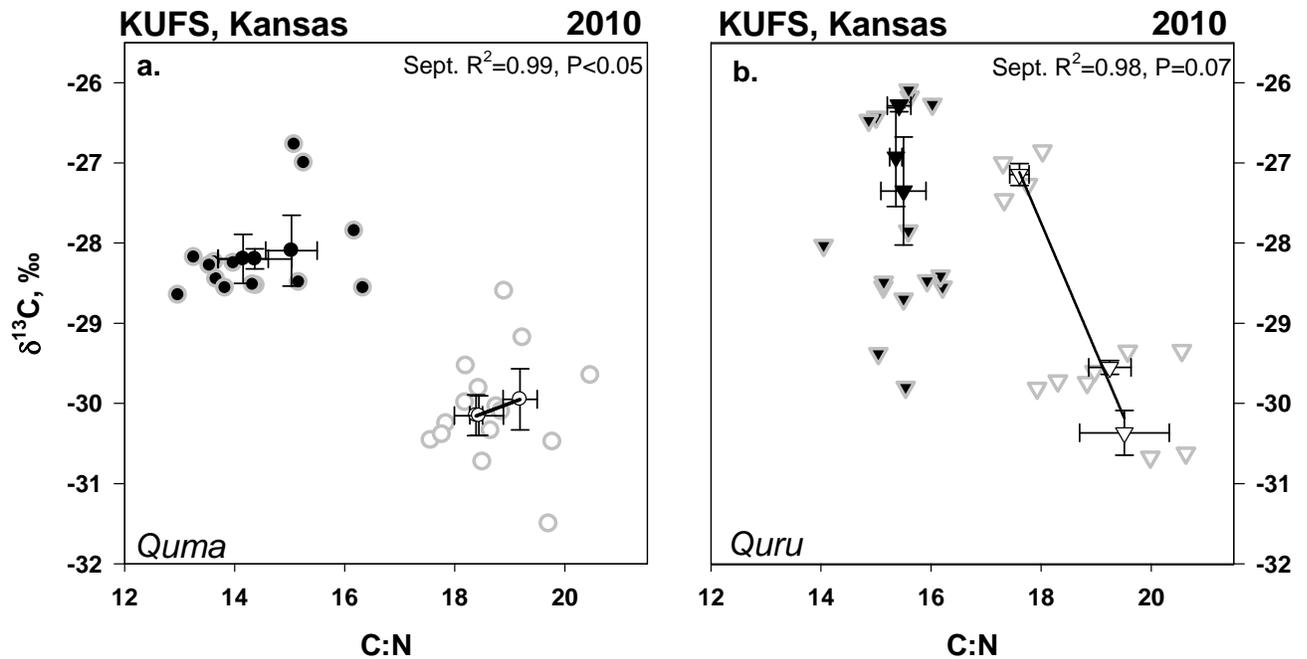


Figure 4. Relationship between leaf $\delta^{13}\text{C}$ and C:N for *Q. macrocarpa* (*Quma*, $n=3$) and *Q. rubra* (*Quru*, $n=3$) from a forested site at the University of Kansas Field Station, Kansas, US. Filled symbols represent July and open symbols represent September. Black edged symbols with error bars represent individual trees, and gray edged symbols represent individual leaves (5 per tree, except for *Quru* tree 3 in September represented by 2 leaves). Significant linear regressions of tree-level data are represented by black lines. Error bars are one standard error of the mean.

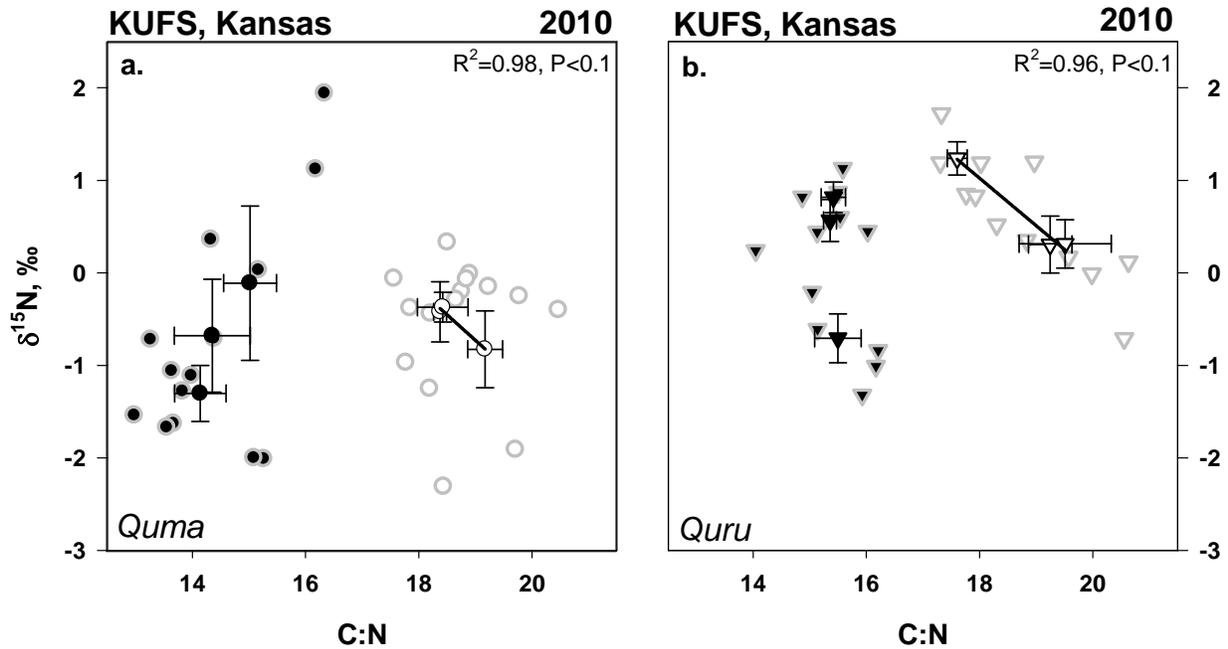


Figure 5: Relationship between leaf $\delta^{15}\text{N}$ and C:N for *Q. macrocarpa* (Quma, n=3) (a) and *Q. rubra* (Quru, n=3) (b) from a forested site at the University of Kansas Field Station, Kansas, US. *Quma* leaf data are represented by circles and *Quru* leaf data is represented by triangles. Filled symbols represent July and open symbols represent September. Black edged symbols with error bars represent individual trees, and gray edged symbols represent individual leaves. Significant linear regressions of tree-level data are represented by black lines. Error bars are one standard error of the mean.

CHAPTER 3: Forest response to disturbance: exploring tree-ring growth patterns with nonlinear dynamic models

Abstract

Disturbance events are predicted to increase in the future and can impact forest ecosystem distribution and function. Tree rings, as a singular recorder of multiple environmental and anthropological variables impacting growth, may be useful tools for assessing a forest's resilience to disturbance. I base my predictions on the assumption of stable climate-growth relationships over time founded on the principle of uniformitarianism, proposed by 18th century geologist James Hutton. This principle is central to historic climate reconstruction from tree growth chronologies. Nonlinear growth responses of trees to precipitation and temperature and shifting correlation analyses are suggested by some dendrochronological research and have challenged assumptions of stable growth-climate relationships over time. The multivariate regressions or correlations typically used to explore growth-climate interactions assume a linear relationship, but often these analyses consider only a single climate variable and are inadequate for revealing nonlinear growth dynamics that may be associated with disturbance impacts in forests. I use two models to assess linear vs. nonlinear growth dynamics of northern red oak trees (*Quercus rubra*) in two forests experiencing a mortality-inducing disturbance event: i) simplex models which determine the dimensionality of a time-series and ii) S-maps projections which use simplex dimensionality as model inputs to detect nonlinear dynamics in time series.

I predicted that *Q. rubra* remaining healthy through the disturbance event would exhibit linear growth dynamics, while neighboring trees that experienced mortality would exhibit nonlinear growth dynamics. I also predicted that dying trees would exhibit a shift in their growth dynamics from linear to non-linear after the disturbance event. I explored the impacts of changing time series length, a key feature of time series models, on detection of nonlinear

dynamics in an effort to increase the applicability of forecast modeling in tree-ring studies. In contrast with my hypotheses, I found that healthy *Q. rubra* are more likely to exhibit nonlinear growth dynamics relative to dying trees, whose growth patterns were consistently nonlinear throughout their lives. I also find evidence that tree-ring series shorter than 30 years limit the ability to detect nonlinear dynamics in time series, an important consideration for use of these models in the tree-ring community. Nonlinear dynamics in time series of healthy trees may represent a greater ability to cope with variability, and thus an ability to capitalize on resource pulses, relative to the linear dynamics expressed by dying trees. I suggest that nonlinear time series modeling represents a way forward for dendrochronologists exploring how past patterns of tree growth can help us predict forest responses to disturbance events, which are projected to increase in frequency and severity in the future. However, further application of these models in forest ecosystem research is needed to increase their applicability in understanding the vulnerability of trees to disturbance impacts.

INTRODUCTION

Forest ecosystems can exhibit strong responses to disturbance events, which may result in wide-spread mortality or, more subtly, altered primary productivity of tree species (Breshears et al. 2005, Ciais et al. 2005). Enhancing the ability of an ecosystem to resist change and maintain function in response to variable conditions is the goal of adaptive management (Scheffer et al. 2009), which is especially important with projected increases in the frequency of disturbance events in the coming decades in many forested regions (IPCC 2007). Disturbance events may be broadly defined as periodic interference in the availability of resources, substrate or environmental conditions that impact ecological functioning of an ecosystem (White and Pickett

1985). Clear-cutting and fires represent large-scale disturbances that impacted entire forest stands particularly during 19th century European settlement of North America (Nave et al. 2011). Disturbance events impacting forests are increasing in frequency in North America (Dale et al. 2001), and appear related to land use change, pollution, and more natural events like pest infestations, windthrow, and droughts (Hanson and Weltzin 2000, Haavik et al. 2008, Ulanova 2000, Dale et al. 2001). A forest is considered resilient to disturbance if it is able to endure disturbance events while maintaining a stable state (Holling 1973), or is able to absorb disturbance events with little change in function (Folke et al. 2004).

Tree ring chronologies may be useful tools for assessing a forest's resilience to disturbance. Tree-rings have often been employed to understand tree population dynamics, as a singular recorder of multiple environmental and anthropological variables impacting growth. Tree radial growth is an integrated measure of many factors influencing the carbon (C) source/sink dynamics of a tree on an annual basis (Schweingruber 1996), and is particularly useful as a measure of the impacts of disturbance and climate factors such as drought, temperature and precipitation. The assumption of stable climate-growth relationships over time is central to historic climate reconstruction from tree growth chronologies (Fritts 1976). Tree-ring research often uses the principle of uniformitarianism, founded by geologist James Hutton, to justify the use of growth-climate relationships to reconstruct past climate conditions (Fritts 1976, Carrer and Urbanati 2006). Typically, growth-climate relationships are explored as linear relationships through multivariate regressions or correlations (Fritts 1976, Carrer and Urbanati 2001). Some dendrochronological studies find evidence of nonlinear growth responses of trees to precipitation and temperature, however (Graumlich and Brubaker 1986, Graumlich 1991, Driscoll et al. 2005). The assumption of stable growth-climate relationships has also been

challenged through the use of shifting correlation analyses that have revealed varying climate-growth correlation strengths over time (Carrer and Urbanati 2006, Reynolds-Henne et al. 2007), but often these analyses are associated with a single climate variable and are inadequate for revealing nonlinear responses (Graumlich and Brubaker 1986, Carrer and Urbanatic 2001).

Forecasting models, invoked in multiple systems ranging from biological (Hsieh et al. 2005; Sugihara et al. 1996, Glaser et al. 2011) and astronomic (Kilcik et al. 2009) to economic (Schittenkopf 2000), are useful for detecting nonlinear dynamics in time series data sets. To our knowledge, these models have not been applied to patterns of tree growth over time in spite of their successful application in multiple systems for elucidating distinct patterns of functioning between populations. Forecasting models often require large quantities of data, which can limit the number and type of systems in which they are applied. Tree-ring studies, however, are often characterized by relatively lengthy chronologies of growth measurements, ranging from multiple decades to centuries. Concatenation of tree-ring data sets can further increase the statistical power of model output, and permits application of forecast modeling even to relatively short tree-ring time series (Sugihara 1994; Hsieh et al. 2008).

We explore disturbance impacts on temporal dynamics of tree growth, and forest resilience to disturbance, using a recent, regional scale oak decline event in northwest and west-central Arkansas, U.S. The decline and eventual mortality of a significant fraction of northern red oaks (*Quercus rubra*) in these forests was linked to cyclical droughts during the previous decades and a subsequent, wood-boring insect outbreak (Stephen et al. 2003, Haavik et al. 2008, Haavik et al. 2011, Reed et al. in review). After a severe drought period, wood-boring insect infestations increased in the mid-1970s and tree growth rates declined in severely infested trees. These trees eventually experienced mortality in the early 21st century (Stephen et al. 2003).

Previous work at one of these sites demonstrates different degrees of influence of stomatal control and nitrogen status on the C dynamics of dying and apparently healthy trees across multiple decades, implying that these trees employed distinct strategies for growth (Reed et al. in review).

We attempt to relate the impacts of this disturbance event – increased prevalence of infestation – on patterns of *Q. rubra* growth dynamics. We present forecast modeling as a useful tool for understanding tree-ring growth patterns in response to forest disturbance, assess the degree to which disturbance signals can be captured as linear vs. nonlinear growth dynamics among co-occurring *Q. rubra*, and determine if trees apparently resilient to these disturbances exhibited distinct growth patterns from those that eventually died. Given the foundational tree-ring assumption of stable climate-growth relationships over time (Fritts 1976), we hypothesized that, if disturbance signals could be captured using forecast modeling, the dynamics of trees that remained apparently healthy during the drought and insect infestation would exhibit linear dynamics – representing a predictable growth response to environmental conditions – relative to neighboring trees which experienced decline. We also hypothesized that declining or dying trees would exhibit a shift to non-linear dynamics after infestation levels increased substantially in the 1970s.

METHODS

Ecological data

We developed ring width indices (RWI) for *Q. rubra* sampled from two forested regions in Arkansas, USA: the Boston Mountains (Region 1; n=24) and the Ouachita Mountains (Region 2; n=46). Detailed site information is available in Fierke et al. (2005). Briefly, both regions experienced hot summers and mild winters with mean annual temperature is 16°C, and wet spring and fall seasons result in 124 cm total precipitation in the Boston Mountains and 150 cm in the Ouachita Mountains (National Climatic Data Center 2009). Soils are fine sandy loam in Region 1 and Clebit loam soils in Region 2 (Soil Survey 2012).

We measured ring widths for four radii derived from each of 24 tree cookies from a 2007 felling in the Boston Mountains, and from two tree cores extracted from 46 trees in the Ouachita Mountains, sampled in 2009. Radii for trees from the Boston Mountains were located along each of the four cardinal directions, and cores from Ouachita Mountain trees were extracted from east and west directions with adjustments made to avoid reaction wood when needed. We assigned each tree a health status classification. In the Boston Mountains the classification integrated percent crown dieback and abundance of wood-boring insect scars (Fierke et al. 2005); in the Ouachita Mountains, tree health was classified using percent crown cover. We defined class, or health status, of studied trees as healthy in trees with percent crown dieback <1% or percent crown cover >99% (class one); declining in trees experiencing moderate levels of wood-boring insect infestation and crown dieback or percent crown cover of 33-66% (class two); and dying in trees experiencing high levels of boring insect infestations and crown dieback >66% or percent crown cover < 44% (class three; Fierke et al. 2005).

We measured annual raw ring width using Image-J software (U.S. NIH, Bethesda, MD) and standardized these raw measures (mean = one) to generate a ring width index (RWI) for each tree. We analyzed six healthy, nine declining, and nine dying well-interspersed, neighboring trees from the Boston Mountains. Time series for these trees were developed from RWI representing the average of the four radii. For Ouachita Mountain trees, RWI represented the average of two cores derived for each of 24 healthy, nine declining, and 13 dying well-interspersed, neighboring trees. Our tree-ring growth series all represented at least 50 years of growth, but no more than 100 years, due to clear-cutting of the region during 19th century timber harvests (Soucy et al. 2005).

Analytical Methods

Nonlinear models

Nonlinear forecasting models estimate system dimensionality (simplex models; Sugihara and May 1990) and detect nonlinear dynamics (s-maps; Sugihara 1994) using out-of-sample, cross-validation forecasting algorithms. Employing forecasting models avoided the structural uncertainty associated with incorrectly specified models which could decrease our ability to detect trends (Charles 1998). However, this approach did not, strictly speaking, test the mechanisms involved in state changes, preventing its use for defining the drivers of changes in ecosystem stable state dynamics (Scheffer et al. 2009). Rather, we applied this approach to test for relationships between dynamic signatures in time series (i.e., linear vs. nonlinear dynamics) and health status of trees. We analyzed standardized (mean=0, standard deviation =1) first differenced time series (difference in $x_{t-1}-x_t$, where x is the RWI, t is a specified time point, and $t-1$ is the time point prior to t). The use of first differences removed secular trends and increased

the density of data points, which enabled greater ability to detect attractors (Sugihara and May 1990). In this instance, attractors represented the major factors impacting tree population dynamics. The use of attractors was based on the concept that, in this case, the pattern of RWI in an E -dimensional space will exhibit a trend around a point (the attractor) over a sufficient time period, and this trend can be used to forecast the trajectory of tree growth (Lorenz 1963).

We employed two nonlinear forecasting models to examine dynamics in individual trees: simplex projection, which determines dimensionality (Sugihara and May 1990), and sequential, locally weighted, global linear maps, or S-maps, which detect nonlinear dynamics of a time series (Sugihara 1994). Both simplex projection and S-maps use shadow attractors (Takens 1981, Sugihara 1994, Hsieh et al. 2008) to explore signals in one variable, in this instance the time series of RWI, to address questions relevant to forest dynamics. Shadow attractors are representations of real attractors and represent a few factors, narrowed down from the vast number of factors that can influence a population (Hsieh et al. 2008). We constructed shadow attractors from the lags of time series, and plotted them to produce a trajectory of a population to detect underlying dynamics (Glaser et al. 2011). The use of attractors is a key difference between these models and autoregressive models. Simplex projection and S-maps models are both cross-validated using out-of-sample forecasting. In other words, the process builds a model using a portion of our time series, and then forecasts the excluded portion, or prediction vector (Sugihara and May 1990). Optimal models were selected based on criteria introduced below. In addition to our method overview, model elaborations are available in Hsieh et al. 2005 and Glaser et al. 2011; here we summarize the models.

Simplex projection models

The reconstructed attractors from individual tree growth series reflected repeating patterns underlying tree growth dynamics. The length of the library vector was directly reflected in the number of time lags associated with the series, and the number of time lags was defined as E , the embedding dimension. Typical representation of standardized tree-ring growth across time produced a one-dimensional display of growth dynamics across a coordinate space represented by time (x_t). When series were represented in multiple dimensions, the geometry of repeating patterns was detected in a coordinate plot ($E=2$; x_{t-1} , x_t ; Fig 1a). Attractors, or the major factors influencing underlying population dynamics, were detected in data sets based on multi-dimensional lagged-coordinate plots with coherent geometry. The geometry around attractors provided our forecasts, and the forecasting skill associated with each model allowed us to select E (for example: $E=3$; x_{t-2} , x_{t-1} , x_t ; Fig. 1b). Repeating patterns are often observed in nature (Glaser et al. 2011), and tree-rings were no exception.

Simplex projection calculates the degrees of freedom of the time series and reduces a system into dimensions E which define the shape of the attractor (Hsieh et al. 2008). Low E typically means a system can be explained by a simple model because fewer variables influence system dynamics (Hsieh et al. 2008). Increasing E represented increasing complexity of a system and typically implies greater amounts of data are required for reconstructing the underlying geometry around attractors relative to lower E (Ruelle 1989, Hsieh et al. 2008). A nearest neighbor algorithm using Euclidean distances is employed to determine trajectories around a shadow attractor. The trajectory of the $E+1$ nearest neighbors (circles around the triangle in Fig1a) is used to produce a forecast. The more complex a system (higher E), the more difficult it would be to develop a model and therefore produce robust predictions for the system.

A prediction vector is held out of the model data set and used to cross-validate model projections; this vector is not model output. We performed iterative tests of E ($E=1$ through 10) and use the selection criteria of ρ , the Pearson correlation coefficient found between the observed and forecast values of the time series, and the mean absolute error (MAE), found from the difference between observed and forecast values. High ρ and low MAE are used for model selection in both simplex projections and S-maps. We used the first difference, the derivative, to run these models. The highest values of ρ and lowest MAE were used as criterion for selecting E values, which were input for our S-maps. In most cases these values corresponded within the same model, but if the highest ρ did not correspond to the lowest MAE for the same model, we used ρ as the most weighted model selection criteria. We employed t-tests to test for significant differences ($P<0.05$) in the E values between health classes and between regions 1 and 2 (SAS Institute Inc. 2004).

S-maps

S-maps quantified the degree of nonlinearity in a time series (Casdagli 1992, Sugihara 1994). Nonlinear dynamics of a time series were detected if out-of-sample forecasts were better modeled by nonlinear rather than linear models as the model adjusted to an increasingly nonlinear structure with each iteration. In S-maps, the library vectors (circles in Fig. 1a) were weighted depending on their distance from the prediction vector (triangle). The exponential weighting on the S-maps, the nonlinear tuning parameter θ , classified dynamics; when $\theta=0$, the data were best modeled with a global linear model, and $\theta>0$ indicated the data were best modeled with a local nonlinear model. The S-maps weighting function ($w(d)$) was applied as

$$w(d)=e^{-\theta d/\text{mean } d} \quad (2.1)$$

where d was Euclidean distance between the neighboring vector and prediction vector, and \bar{d} was the mean distance between neighbors (Sugihara 1994). When $\theta=0$, all neighbors in the area around the prediction vectors were equally weighted and when $\theta>0$, the weighting was given by equation 2.1. The time series was deconstructed into vectors of length E , derived from the simplex model, and the geometry of all vectors was used simultaneously to produce one-year-ahead forecasts. The forecasted trajectories of the data were used to cross-validate and select the best form of the model.

The highest value of ρ , the Pearson correlation coefficient, or lowest mean absolute error (MAE) were used as selection criteria for the best model. The degree of nonlinearity in the system corresponded to the increase in correlation ($\Delta\rho$) or decrease in MAE (ΔMAE) associated with the forecast: $\Delta\rho_\theta = \rho_{\theta=\text{best}} - \rho_{\theta=0}$ and $\Delta\text{MAE}_\theta = |\text{MAE}_{\theta=\text{best}} - \text{MAE}_{\theta=0}|$, where ρ was the Pearson correlation coefficient, and the improvement in ρ was used to detect nonlinear dynamics. $\Delta\rho$ represented the degree of nonlinearity. MAE_{\min} was the lowest mean absolute error used for model selection, ΔMAE_{\min} was a measure of nonlinear dynamics, and ΔMAE_{\min} P -value was the significance of the improvement in the error between linear and nonlinear models (Hsieh et al. 2008, Glaser et al. 2011). $\Delta\rho_\theta$ was tested using Fisher's Z-test (Kleinbaum et al. 1998) but could contain high autocorrelation bias. We calculated a test ΔMAE_θ for each time series, then randomize the time series and recalculate ΔMAE_θ for 500 iterations to develop a null distribution. We tested significance using a bootstrapping procedure and used $P<0.1$ as our classification of nonlinearity (Hsieh and Ohman 2006). ΔMAE and associated P -values were considered to determine the degree of nonlinearity found by the models in our study. The nonlinear dynamics detected by S-maps helped us determine if differences exist among Region 1 and 2 and between

health classes, and we used logistic regression to test for relationships between presence of nonlinear dynamics and tree health class.

Linking growth dynamics to tree resilience: tree-level dynamics linked to ecosystem response

We used the classification of linear vs. nonlinear derived from S-maps as a dependent variable in a series of logistic regressions. If we determined significant ΔMAE_{θ} in the randomization test, series were classified as nonlinear. We employed a logistic regression model to test for statistical relationships between nonlinear dynamics and health class at the scale of each individual tree from each region. Logistic regressions examined the dynamic signal at the whole-tree scale and permitted us to link a tree's health status with linear or nonlinear dynamics exhibited in its growth. We created a variable to represent classification (0=linear, 1=nonlinear) and predicted classification membership through our logistic model. We analyzed data from the Boston and Ouachita Mountains separately and also combined in logistic models, with health classes analyzed separately and also with declining and dying trees combined. The generally negative response of declining and dying trees to insect infestation, regardless of infestation level, justified our merging of these classes for some tests. When analyzing regions together, we used the equation:

$$\text{Nonlinearity} = \text{class} + \text{region} + \text{region} * \text{class} \quad (2.2)$$

with the dependent variable of nonlinearity referring to the dynamics of a single tree and the independent variables of region (1 and 2) and class as tree health class (SAS 2008). Recall that S-maps, using information obtained from simplex projection, are used to produce the measure ρ , with which we judged model forecasting skill. We did not include trees generating statistically non-significant forecast models (ρ not significant at $\alpha=0.05$) in the logistic regression. To control

for time series length, we created a variable (ts_L) that counts the number of valid data points that each tree has, and found that ts_L was not a significant predictor of nonlinearity, suggesting that our findings are robust regardless of time series length. Chi-square statistics were generated, with non-significance of the test statistic suggesting that model predictions and observations do not differ.

We also tested for shifts in growth dynamics pre- and post-insect infestation by dividing our time series into pre-1979 and post-1981, when infestation levels increased in trees eventually declining or dying in the early 2000s. We created strings of RWI series for each health class, separated by region for series prior to 1979 and then for series post-1981, excluding years 1979 through 1981. Splitting of the time series reduced the length of our data sets. For example, we had only 25 years of growth in our post-insect infestation time series. As a result, we concatenated our data to increase our statistical power and thus our ability to detect trends in data (Hsieh, Anderson and Sugihara 2008). We assumed that the dynamics observed at the scale of individual trees were governed by identical dynamic processes in co-occurring trees to justify concatenation approaches (Sugihara 1994). The concatenation resulted in functionally lengthened time series with selected time series placed end-to-end. Simplex projections and S-maps were reran with end-to-end time series input, which allowed us to examine pre- and post-insect infestation dynamics and to test the effect of examining a given time period on the classification of the dynamics. The time series were split between library vectors and completely out-of-sample prediction vectors such that half of the trees were part of the library while the other half would comprise the prediction set. The library and prediction sets were randomized 200 times and mean values were calculated. The disturbance dynamics of wood-boring insects

may differ between regions (Haavik et al. 2010), so concatenation within each region was applied separately, with tree health classes tested from cross-prediction abilities.

Dewdrop regression allowed us to determine if trees within a health class and within a region exhibited roughly the same trajectory around an attractor, which would signify co-predictability (Hsieh et al. 2008). The embedding of multiple, short time series (<25 years with our data set) provided a view of the attractor; each embedding produced points on the surfaces of the attractor, referred to as dewdrops, and a greater number of series provided more clarity to our attractor (Hsieh et al. 2008). S-maps pairwise predictions between tree health classes are used to establish the shape of the attractor developed from dewdrop regression. The S-maps used with concatenated data series permitted us to assess ecosystem-level dynamics derived from individual tree level dynamics. Similar trajectories, judged by low error values, meant high cross-predictability between tree health classes. In our study systems, the underlying influences of site dynamics and climate were the same on a regional scale for each the Boston Mountains and the Ouachita Mountains samples, supported by cross-predictability of trees within each site.

RESULTS

Nonlinear classifications

We found significantly lower mean E values in the Ouachita Mountains relative to the Boston Mountains (Fig. 2). In the Boston Mountains, healthy trees were best represented by significantly lower system complexity (lower E) relative to dying trees exhibiting linear dynamics ($P < 0.05$; Table 1). Contrary to our hypotheses, S-maps revealed that healthy trees at both the Boston Mountain and Ouachita Mountain sites were more likely to exhibit nonlinear dynamics than declining or dying trees (Table 1 and 2; Fig. 3). The majority of healthy trees

(n=6) from the Boston Mountains exhibited nonlinear dynamics (66%; Table 1; Fig. 3). In the Ouachita Mountains 46% of healthy trees (n=24) exhibited nonlinear dynamics, proportionately higher than the 11% of declining and 15% of dying trees exhibiting nonlinear dynamics at Ouachita (Table 2; Fig. 3). Significantly higher dimensionality was found in healthy trees exhibiting linear dynamics in the Ouachita Mountains relative to declining classes ($P<0.005$) and between dying trees relative to and declining trees exhibiting nonlinear dynamics ($P<0.05$, Table 2). Higher forecasting skill was found in Ouachita relative to Boston Mountain trees (Table 3).

Logistic regression

Our logistic regressions revealed that healthy trees were more likely to exhibit nonlinear dynamics relative to a merged group of declining and dying trees (Table 3). We also ran analyses with declining and dying trees in separate groups and found similar results. Data further suggest that Ouachita trees, regardless of health status, are more likely to be linear than those in the Boston Mountains. Logistic regression revealed no dynamic patterns associated with health class when Boston Mountain trees were run in isolation from Ouachita Mountain trees. Through combination of dying and declining tree health classes, we created a more robust data set for comparison and found the combined dying and declining classes were statistically more likely to be exhibit linear dynamics relative to healthy trees.

The combination of declining and dying trees was supported by the cross-predictability exhibited by the two classes – each were able to predict tree time series of the other class ($P_{\text{rho}} < 0.05$). The co-predictability between trees across regions supported that the dynamics observed at individual tree scale are governed by identical processes at the regional scale in these forested ecosystems. Concatenation of data revealed no evidence supporting shifts in tree-ring growth

dynamics pre- and post-disturbance. In our logistic regressions, we found that ts_L was not a significant predictor of nonlinearity, suggesting that our findings were not an artifact of having more or less data in some trees. The regression coefficients of declining and dying trees were similar in magnitude and in the same direction, further supporting the robustness of our results.

DISCUSSION

Dendrochronology typically attempts to reveal the few, key variables that influence the dynamic processes that govern individual tree growth within regions. For example, we know that the strongest growth-climate relationships in *Q. rubra* at Region 1 occur when using monthly May and June precipitation and summer temperatures (Haavik et al. 2011). A multitude of factors including aspect, light availability, inter- and intra-species competition (Fritts 1976) and moisture availability (Orwig and Abrams 1997) all may influence growth patterns, and these are often explored through linear regressions and correlation analyses. The methods typically used to explore tree growth responses fail to detect nonlinear dynamics because they are imposed under the assumption of linearity (Fritts 1976, Briffa 1995, Carrer and Urbanati 2001). The great complexity of interactions that influence tree growth (Fritts 1976) makes nonlinear modeling a useful tool in reducing the dimensionality down a few factors (E) and in detecting underlying patterns.

Forecast modeling

Contrary to our hypotheses, healthy trees exhibited nonlinear growth dynamics and declining and dying trees experienced linear growth dynamics throughout their lives. Nonlinear dynamics observed in natural systems have been linked to an increased ability to adapt to variable conditions while linear trends may represent decreased adaptive coping abilities) and

destabilized population dynamics (Sugihara et al. 1996, Hsieh et al. 2005). For example, linear trends have been linked to a decreased ability to respond to changing conditions in infant heart rates (Sugihara et al. 1996). Nonlinear dynamics in fishery populations have been linked to human exploitation and destabilization of population dynamics (Hsieh et al. 2006). Greater variation in tree radial growth in response to drought has been associated with higher likelihood of experiencing drought-related tree mortality (Ogle et al. 2000), which may relate to the nonlinear growth dynamics in dying and declining trees observed in our study. While nonlinear growth dynamics need to be further explored to understand their implications for a tree's ability to cope with environmental variability, the differential dynamics we found here between healthy trees and dying and declining trees further supports previous research that has found differences between trees of different health classes in growth patterns (Haavik et al. 2011) and in C source:sink dynamics (Reed et al. in review).

The number of embedding dimensions (E) might help explain the complexity of the system (Casdagli 1992). For example, an E of five would represent two to four major variables governing ecosystem dynamics (Casdagli 1992; Sugihara 1994). The dimensionality of our study regions sheds light on the factors that may govern tree C source:sink dynamics, with higher dimensionality implying that more variables controlling C dynamics (Table 1; Table 2). Lower complexity in underlying growth dynamics in dying and declining trees would be consistent with the idea of a few, major drivers (i.e. drought, insect infestation) of radial growth responses in trees that experienced the greatest negative growth response to disturbance, as observed in Ouachita Mountain trees (Table 2). Drought has been a major driver of growth in trees that later experienced drought-related mortality (Bigler 2007, 2009). We do not know why the differences in E across health classes were not the same at both sites, differences in climate and productivity

are likely at these sites, so it is likely that these trees experience different drivers of and limits to growth. We know the drivers of the insect infestation are different to some extent (Haavik et al. 2011), so the differences in trends in E with health class might be explained by differences in site-specific stresses influencing tree-ring growth.

The differential growth dynamics among classes are consistent with different dynamics governing the C dynamics of these trees, as explored by Reed et al. (in review) at the Boston Mountain sites. That study demonstrates a stronger influence of leaf nitrogen availability and, presumably, associated photosynthetic capacity, on leaf C dynamics in healthy trees. Dying trees exhibited isotopic patterns in their tree-rings suggesting a stronger influence of stomatal regulation of C supply on tree C dynamics than in healthy trees (Reed et al. in review). Though nonlinear forecast models cannot elucidate the mechanisms driving distinct, linear vs. nonlinear growth dynamics in these trees, the observed differences in growth dynamics between health classes are consistent with healthy trees being able to capitalize on some environmental resource – perhaps nitrogen. Soil nitrogen (N) pulse events following precipitation are important for resource availability in N-limited ecosystems (Gebauer et al. 2002). If healthy trees are better adapted to variable moisture availability, then they may also be able to capitalize on variable N availability to a greater degree than co-occurring, dying and declining trees. In contrast, increased vulnerability to mortality following drought and subsequent insect infestation disturbance may result from strictly adhered to, more stable growth strategies that permit little capacity for a tree to capitalize on resource pulses. Further application of forecast modeling on tree-ring growth series is required to explore the interaction of nonlinear growth dynamics and vulnerability to disturbance impacts. Such model results are best coupled with empirical studies that help us understand the mechanisms driving observed differences in growth dynamics.

Growth series dynamics exhibited no shifts when examined for pre-and post-infestation dynamics, contrary to our second hypothesis. We explored concatenated data sets to i) detect potential changes in nonlinear dynamics in our time series resulting from disturbance events pre- and post- insect infestation and ii) provide a separate analysis of the class dynamics (combining all trees of a given class and testing their ability to predict other classes and providing insight into the co-predictive abilities of time series). In this instance, concatenation of our data was not helpful in distinguishing a change in growth dynamics, potentially because our time series were 25 years in length while 30 years is typically the minimum to detect differences in dynamics between time series. However, concatenation of tree-ring time series represents a new technique generally applicable for nonlinear forecasting in tree-ring studies. Detection of nonlinear patterns in ecological studies is constrained by the need for long time series (Hsieh et al. 2008), but concatenation, or compositing of data sets, may enhance the utility of many tree-ring data sets for forecast modeling.

Conclusion

Simplex projections and S-maps helped us discern different growth dynamics among declining and dying vs. healthy trees, such that the latter exhibited radial growth suggestive of non-linear growth dynamics. The linear growth dynamics exhibited by declining and dying trees suggests that these trees are perhaps less able to respond to environmental variability, and the resource pulses that accompany such variability, compared to their healthy counterparts in these forest ecosystems (Sugihara et al. 1996). Our logistic regression approach detected a general enhancement in linear behavior in dying trees at the individual tree level. Although we did not find evidence supporting any shifts in growth dynamics pre- and post-infestation in any tree healthy class, time-series concatenation may nonetheless be useful for exploring growth

dynamics in tree-ring series otherwise too short to consider using with nonlinear models. Overall our study explores new methodologies in tree-ring research that may shed light on detection of tree growth dynamics in response to disturbance. Further research is needed to develop forecast modeling as a tool for understanding vulnerability and resilience of trees to disturbance impacts in the future, and to understand the long-term implications of and mechanisms behind linear vs. nonlinear dynamics in tree growth trends.

TABLES AND FIGURES

Table 1. Boston Mountain S-map forecast modeling results (n=26) summarized for each health class for a forested stand in northwest Arkansas, U.S. Dynamics reflect S-map forecasts. Series N represents the number of forecasts made by the model, related to the length of the time series and dimensionality. E is dimensionality as determined by simplex projection. ρ is the Pearson correlation coefficient, and the improvement in ρ is used to detect nonlinearity dynamics. $\Delta\rho$ represents the degree of nonlinearity. MAE_{min} is the lowest mean absolute error used for model selection. $|\Delta MAE_{min}|$ is a measure of nonlinear dynamics and ΔMAE_{min} P-value is the significance of the improvement in the error between linear and nonlinear models. % nonlinear is the percent of each health class exhibiting nonlinear dynamics. Standard errors are shown for averages of models grouped by class and nonlinear dynamics. No significant P-values for $\Delta\rho$ were found.

Health Class	Dynamics	Series N	E	ρ_{max}	$\Delta\rho$	MAE_{min}	$ \Delta MAE_{min} $	ΔMAE_{min} P-value	% nonlinear
Healthy N=6	Linear	81±9	3±0.5	0.21±0.10	0.05±0.04	0.72±0.05	0.002±0.002	NS	46%
	Nonlinear	74±2	4±0.6	0.36±0.03	0.06±0.03	0.71±0.02	0.029±0.01	<0.05	
Declining N=9	Linear	75±4	4±1.1	0.33±0.04	0.01±0.01	0.75±0.02	0.004±0.002	NS	11%
	Nonlinear	65±6	5±0.9	0.26±0.07	0.26±0.09	0.77±0.03	0.028±0.003	<0.05	
Dying N=8	Linear	70±6	6±5.7	0.16±0.08	0.01±0.01	0.77±0.04	0.002±0.002	NS	8%
	Nonlinear	70±4	4±3.5	0.26±0.18	0.16±0.07	0.73±0.03	0.030±0.008	<0.05	

Table 2. Ouachita Mountain S-map forecast modeling results (n=46) summarized for each health class for a forested stand in west-central Arkansas, U.S. Dynamics reflect S-map forecasts. Series N represents the number of forecasts made by the model, related to the length of the time series and dimensionality. E is dimensionality as determined by simplex projection. ρ is the Pearson correlation coefficient, and the improvement in ρ is used to detect nonlinearity dynamics. $\Delta\rho$ represents the degree of nonlinearity. MAE_{\min} is the lowest mean absolute error used for model selection, ΔMAE_{\min} is a measure of nonlinear dynamics and ΔMAE_{\min} P-value is the significance of the improvement in the error between linear and nonlinear models. % nonlinear is the percent of each health class exhibiting nonlinear dynamics. Standard errors are shown for averages of 10 model forecasts per tree and grouped by class and nonlinear dynamics. No significant P-values for $\Delta\rho$ were found.

Health Class	Dynamics	Series N	E	ρ_{\max}	$\Delta\rho$	MAE_{\min}	$ \Delta MAE_{\min} $	ΔMAE P-value	% nonlinear
Healthy N=24	Linear	65±4	5±0.74	0.57±0.02	0.01±0.005	0.64±0.01	0.003±0.002	NS	46%
	Nonlinear	60±4	5±0.50	0.64±0.02	0.06±0.01	0.60±0.01	0.05±0.01	<0.05	
Declining N=9	Linear	52±8	3±0.25	0.54±0.04	0.06±0.04	0.064±0.02	0.01±0.004	NS	11%
	Nonlinear	70	1	0.65	0.07	0.58	0.02	<0.10	
Dying N=13	Linear	57±6	4±0.43	0.57±0.02	0.01±0.004	0.64±0.01	0.006±0.002	NS	15%
	Nonlinear	62±5	3	0.610.01	0.03±0.006	0.59±0.01	0.03±0.005	<0.05	

Table 3. Logistic regression analysis of the Boston Mountains (region 1; n=24) and Ouachita Mountains (region 2; n=46) in Arkansas, U.S. Declining and dying trees were combined and analyzed with healthy trees; analyses were also performed without combining declining and dying trees and results were similar. Regions were analyzed together thus two model variables of class along with region were included in our logistic regressions. The estimate of the independent variable, whose real value is either 0 or 1, is shown as an average for each model variable.

Region	Model variables	Estimate	SE	Chi-square	Pr> ChiSq
1	Class	0.75	0.62	1.47	0.23
2	Class	0.75	0.37	5.09	0.02
1+2	Class	0.88	0.37	5.66	0.02
	Region	1.16	0.60	3.70	0.05

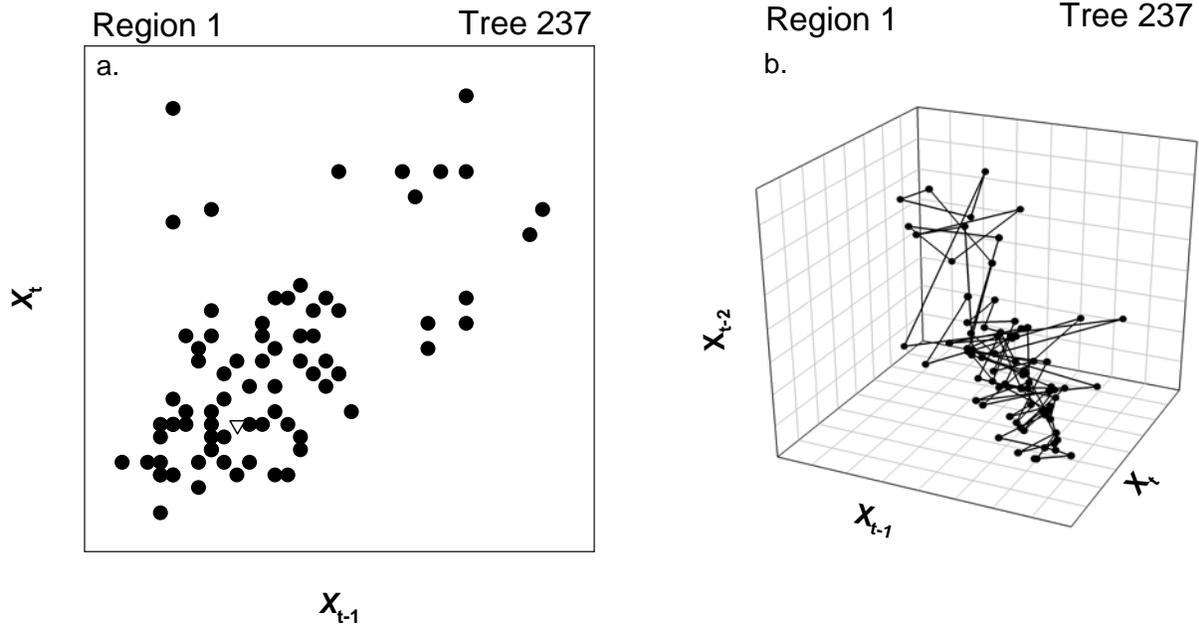


Figure 1: Simplex projection (a) Two-dimensional embedding ($E=2$) of time lags of a sample tree's growth data from a forested region in northwest Arkansas, U.S. (b) Three-dimensional embedding ($E=3$) of time lags of a sample tree's growth data from a forested region in northwest Arkansas, U.S. reveals the geometric pattern forming around an attractor. Simplex projections and s-maps output a forecast based on the library vectors (represented by circles). A prediction vector (represented by the triangle in 1a) is used to judge the forecast skill of the simplex projections and used to weight library vectors (neighbors) in S-maps.

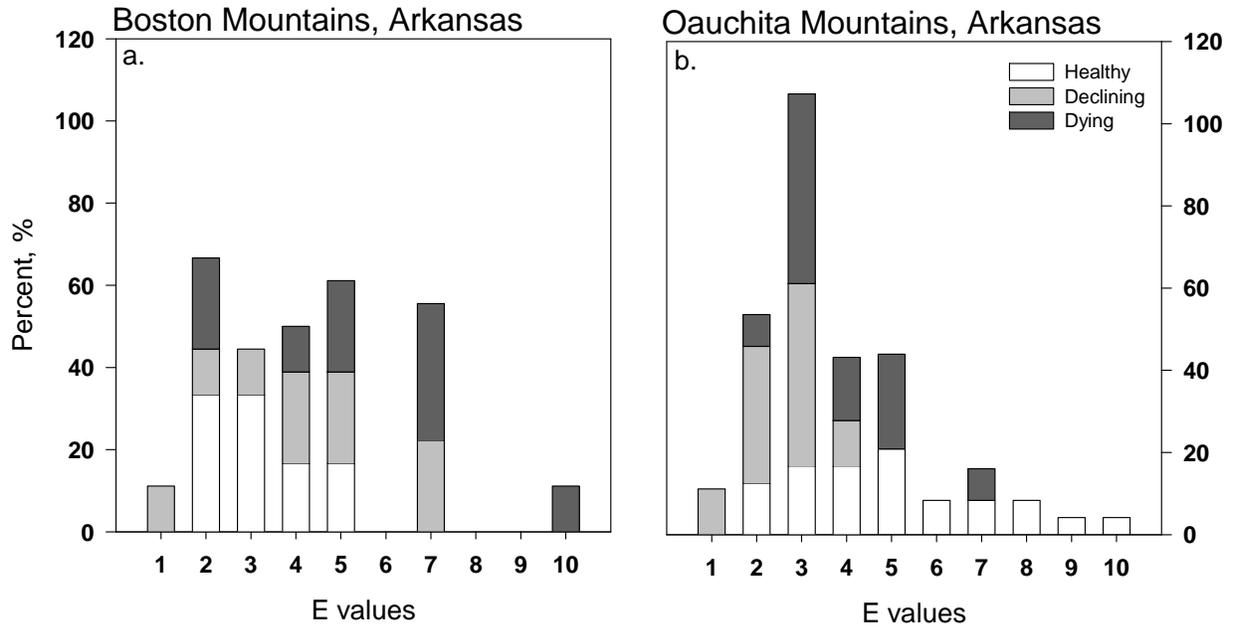


Figure 2. Embedding dimension (E) for trees from the Boston Mountains ($n=24$; a) and from the Ouachita Mountains ($n=46$; b) in Arkansas, U.S. Percent on Y-axis represents the distribution of each value of E value across a tree health class, and thus sums may be greater than 100% if the E was common among several classes. White bars represent class one trees (healthy), light gray bars represent class two (declining), and dark gray bars represent class three tree (dying). A t-test revealed significant differences ($P<0.05$) in the distribution of E between region 2 and region 1.

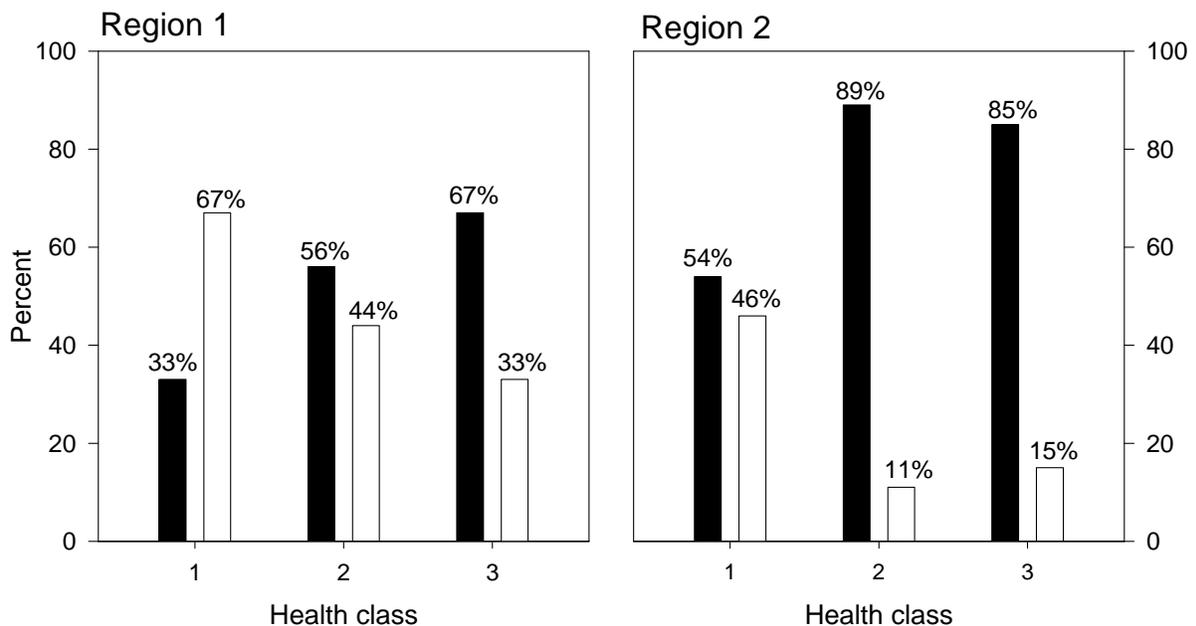


Figure 3. S-map-classified dynamics from healthy (class 1), declining (class 2) and dying trees (class 3) from the Boston Mountains ($n=24$) and from the Ouachita Mountains ($n=46$) in Arkansas, U.S. Black bars represent linear dynamics ($\theta=0$) and white bars represent nonlinear dynamics ($\theta > 0$).

CHAPTER 4: Forest management in the Boston Mountains of Arkansas, US: Forest management adapting to climate change

Abstract

Climate change is anticipated to impact North American forests through shifts in species distribution and composition in coming decades, as well as through the increased frequency, severity, and duration of natural disturbance events. Disturbance is a natural component of forest ecosystems, but an increased frequency and severity in disturbances predicted in the future could negatively impact forests. Implementing forest management policies to increase the adaptive abilities of forests to resist and recover from disturbance events is an important undertaking in public and private forest lands. Adaptive management strategies to maintain forest ecosystem health use disturbance impacts as learning opportunities and incorporate ecosystem resilience into policy. Such strategies are needed to maintain forest function in the future. In this chapter, I discuss the impacts of past forest management on a national scale and local scale in a case study to demonstrate the need for a change in management strategies applicable to forested lands throughout the Nation. I use a case study of oak decline linked to climatic disturbance in the Ozark National Forest of northwest Arkansas to demonstrate the link between past management and forest decline. The true challenge of future forest management policies is meeting local economic timber needs while promoting forest function in the face of climate change uncertainty, which is a common concern between state, federal and private lands. Adaptive management strategies and forest monitoring tools examining tree growth and ecosystem health are recommended for forest managers and researchers to detect tree vulnerability to disturbance. A goal of this work is to highlight the need for forest management

in the face of climate change uncertainties with emphasis placed on local goal-setting related to maintaining carbon stocks, biodiversity and monitoring tools.

INTRODUCTION

Looming shifts in species composition and forest distribution predicted with future climate change and increases in disturbance event frequency make adaptive management of forests a priority (Hanson et al. 2000, Dale et al. 2001, IPCC 2007, McKenney et al. 2007). Disturbance events are naturally occurring in ecosystems, but the predicted increase in frequency and duration of disturbance events in the future will impact forest ecosystems to a greater extent than in the past (Waring and Schlesinger 1985, Attwalli 1994, Dale 2001). The history of US forest management fails to incorporate uncertainty in conditions or goals related to ecosystem adaptability, which will be highlighted in a regional forest decline event. Adaptive management uses policy decisions as learning opportunities – at each step in the management process, changes in environmental conditions and their impacts on forest ecosystems can be incorporated into management strategies (Stankey et al. 2003). The need for local-scale forest management policy that incorporates climate change uncertainty is critical to the future of forests and tool are needed assist with detection of tree susceptibility to disturbance.

Increasing resilience and resistance of forest ecosystems to future climate change and disturbance impacts, which may often be rapid in nature, can be a goal of adaptive management (Bolte et al. 2009). Adaptive management is intended to decrease the biological and physical impacts of climate change on forest ecosystems (Millar et al. 2007) and incorporates uncertainties such as disturbance events into the development of management strategies (Millar et al. 2007, Lawler et al. 2010). Potential management actions that could increase ecosystem

resistance to disturbance – its ability to absorb disturbance impacts and maintain function and structure (Holling 1973) – include increasing biodiversity of tree species and focusing on maintaining ecosystem function while selecting trees adapted to hotter, drier conditions in many areas (Millar et al. 2007). Management could also increase ecosystem resilience- its ability to recover and quickly achieve pre-disturbance conditions- through increased system complexity or species composition (Holling 1973).

Ecosystem management that incorporates disturbance impacts on ecosystem dynamics creates a complex challenge. Forest ecosystems are comprised of living and abiotic components that interact to create complex structure and function. These systems are vital for North American carbon (C) storage and economic use, and are valued by many for their recreational qualities (Tansley 1935, Goodale et al. 2002). Current ecosystem management that considers changing climate impacts typically addresses two major goals: 1) increasing forest C stocks in an effort to mitigate the impacts of climate change and associated disturbance, and 2) promote complexity in structure and biodiversity to increase adaptation to variability (D'Amato et al. 2011). While C sequestration rates associated with forests cannot increase at a pace matching rising atmospheric CO₂ levels (McKinley et al. 2011), increased resilience and resistance of forest ecosystems can help to decrease negative climate change impacts on forests while helping ensure forest function in the future (Millar et al. 2007, D'Amato et al. 2011).

Adaptive management invoking scientific findings may provide insight for achieving these goals. If ecosystem adaptability is not considered in the development of forest management policies, ecosystem structure may experience increased vulnerability to disturbance. For example, if forest ecosystem management is undertaken with a single goal of increasing C stocks, biodiversity decreases and thus adaptability of the ecosystem decreases (D'Amato et al.

2011). Prioritizing adaptive forest management goals with a focus on increasing structural complexity, biodiversity and maintaining forest C stores in the future is needed to prepare forest ecosystems in the central U.S. for the potentially detrimental impacts of climate change. There may be exceptions to the benefits of structural complexity in forest ecosystems in terms of increasing resistance or resilience of forest systems to disturbance. For example, pine-grassland restoration in Arkansas simplified forest structure through thinning, fire reintroduction and hardwood midstory reduction but made forest stands more resistant to wildfires and to insect attacks (Guldin et al. 2004, Hedrick et al. 2007). Even-aged versus uneven-aged stands and simple versus complex ecosystem structure should be addressed at the local scale depending on the types of wildlife and the types of disturbance events common in the area. Most research on climate change impacts focuses upon regional consequences (IPCC 2007), but there is still uncertainty in the impacts of climate change at any scale (Lawler et al. 2010). Local adaptive management strategies can utilize regional predictions and learn from disturbance impacts to implement strategies that are unique for the circumstances encountered in the future (i.e. Stankey et al. 2003, Hedrick et al. 2007). Local management efforts are likely the strongest tools for forest management in the face of future uncertainty in conditions (Roe 1997).

European settlement in North America led to high-grading, or selective cutting of the most desirable timber, across the landscape that resulted in heavily cutover conditions where most of the trees in the dominant canopy were cut and genetically poor tree stock often remained (Strausberg and Hough 1997). The poor conditions for growth and the susceptibility of these stands to fire in the late 19th and early 20th centuries resulted in public outcries for conservation of soil, water and wildlife resources (Hirt 1994). In the early 20th century, national forests were initially set aside to safe guard water resources, help overexploited forests recover, and provide

recreational and timber harvesting opportunities (Hirt 1994). During this time period, The Ozark National Forest was established in northwest Arkansas (Strausberg and Hough 1997). The goals of fire suppression and reestablishing forest timber stocks led to older, even-aged stands and denser timber stocks than were historically observed in the Ozark National Forest and forests throughout the eastern US.

High stocking density and progressive aging of stands manifested in a forest decline event in the early 21st century (Soucy et al. 2004). Forest decline events are typically influenced by complex abiotic and biotic factors that result in a loss in vigor and sometimes mortality, and may be influenced by background stress (Manion 1991, Van Mantgem et al. 2009). Shifts in forest management in recent decades among federal and state agencies (as well as with conservation organizations) highlight how management may be used to promote conservation in response to disturbance events (Littell et al. 2012). Proceeds from timber sales can often be used to help defray the cost of restoration work needed to help forests be more resilient to climate change (Thill et al. 2004). Mature markets for forest products provide the revenue needed to support restoration work and highlights the importance of balancing timber industry interests and increasing forest resilience in the face of climate change.

Modeling of forest ecosystems may provide useful tools for understanding the impacts of management regimes, and allow for uncertainty to be accounted for to some degrees. Forecast modeling may also be a useful tool for managers to detect underlying trends in tree ring growth patterns related to tree vulnerability to disturbance. The goals of this paper are to i) provide a brief history of forest management policies impacting North American forests with emphasis on northwest Arkansas forests, ii) link implications of past management regimes to recently

observed decline events in the Ozark National Forest, and iii) focus on adaptive management strategies tools to address predicted increased in disturbance events in the future.

DISCUSSION

History of Ozark National Forest management

The mid- to late-1800s represented a period of exploitation of forest resources in the United States. Large corporate ownership and unsustainable harvesting of private forests led to disruption of prevailing forest ecosystems in many parts of the nation (Hirt 1994). Unregulated harvesting caused instabilities in local economies throughout the U.S. and created boom-and-bust cycles in the Ozark Plateau forests of northern Arkansas, with wide-spread timber harvesting followed by exploitation and industry departure once resources were depleted (Anderson 1999; Foti 2004). Concerns over clean water, wildlife, and recreational space following forest clear-cutting raised public awareness of over-harvesting issues (DuPuy 1938, Thompson 1980).

Although conservation of natural resources in national forests was a greater focus in the early 20th century, increased preventative measures to combat forest fire irrevocably changed the landscape (Guyette and Spetich 2003, Hirt 1994). Large stocks of debris resulting from logging had accumulated following the introduction of industrial harvesting into the virgin forests of North America, and this fuel-rich environment was a concern in rural communities. Increased intensity of forest fires following harvesting marked a considerable change in these ecosystems, and the prevention of fires was needed to promote rural stability (Guyette and Spetich 2003, Engbring et al. 2008).

From the inception of publically owned federal lands in 1891, later called national forests, conflicting goals have been set forth for the lands (Hirt 1994). The Organic Act of 1897 resulted from concerns over degradation of soils and watersheds and set forth the goals of securing water reserves, preserving forests, and ensuring timber supplies (Strausber and Hough 1997). The U.S. Congress established reserves to buffer national resources from privatization of all natural resources and to ensure that public lands had protection from market interests (Du Puy 1938, Thompson 1980). The USFS promoted the multiple-use goals of timber production and protection of natural resources for public use through reestablishment of forests and fire suppression (DuPuy 1938, Sedjo 2008). The prioritizing of management goals regarding ecosystem health and timber harvesting interests, which can at times contribute to management goals together but may also counter each other, is a historic challenged faced in forest management.

The USFS fire suppression policies became common practice in the Ozark National Forest around 1910 and had major influences on forest ecosystem processes (Spetich 2004a). Suppression of fires led to changes in species composition, tree densities, and understory dynamics that further influenced the need for informed management goals to maintain ecosystem function (Kabrick et al. 2008, Voelker et al. 2008). During early forest management in Arkansas, fire suppression was a priority along with reestablishment of shortleaf pine forests to provide needed saw timber to communities (Strausberg and Hough 1997). The even-aged stands that regenerated on formerly harvested lands were denser than historic forests. Regular fire intervals of three to ten years existed in these forests from earliest European observations (1680) through 1930, after which fire suppression was enforced and fire intervals increased to 80 years (Spetich 2004). High grading and industrial intensification placed a strain on sustainable management of

many forests (Strausberg and Hough 1997, Hirt 1994). The principle of sustainable yield implemented during the 1930s (Hirt 1994) transformed the forest products industry into a permanent fixture that could persist in a region with the proper management of resources instead of a cycle of boom and bust harvesting in the rural landscape.

Forest management following WWII

Post-war prosperity led to increased demands for housing and timber products and resulted in increases in allowable harvests on public lands (Hirt 1994). Clear cut harvesting was used to increase timber volume and decrease expenses; the shift from high grade harvesting allowed for increased turnover of timber products through increased efficiency (Sedjo 2008). Intensive management efforts in many forests focused on increasing wood production and often resulting in even-aged plantation stands typically composed of a single species, often pine in the Ozark highlands (Hirt 1994, Strausberg and Hough 1997).

Intensive harvesting efforts peaked in the 1960s, but USFS policies of the 1960s and 1970s attempted to focus priority on forest conservation. The Multiple-Use and Sustainable Yield Act of 1964 tried to refocus agency goals and balance timber demands with the protection of water and soil resources, but had little effect on harvesting quantities or practices (Haynes 2007). The National Environmental Policy Act of 1969 incorporated public and scientific input into policy, and the Endangered Species Act of 1973 established protocol for protecting habitats (Hirt 1994). The balancing act between timber and other forest resource protection continues through the 1980s, with no significant change in funding allocations within the USFS that would signify a shift away from having timber production as a top priority (Sedjo 2008). Decreases in

the harvesting rates in the 1990s took timber production from national forests back to pre-WWII harvesting levels.

Different priorities are often set forth for the USFS with each new presidential administration, making it a challenge to maintain long-term goals (Sedjo 2008). USFS Chief Jack Ward Thomas, who served from 1993 to 1996, stated that the fundamental problem for policy action within the USFS was the existence of too many laws directing the agency to do too many things with no clear establishment of priorities (Sedjo 2008). This lack of prioritization, essentially a historic issue caused by the conflicting goals that have plagued the USFS since its inception, becomes more problematic with predicted climate change. Future changes to forest ecosystems may enhance the historical struggle to balance socio-economic and environmental goals within timber-oriented management policies in federal, state, and private forests alike.

Setting the stage for Arkansas oak decline

Pre-European settlement, Arkansas was 96% forested, but today is only 54% forested (Engbring et al. 2008). Changing composition and structure resulting from management and natural, successive processes are apparent in the mixed oak-hickory forests of the Ozark National Forest. Early European settlers in the Ozark National Forest region likely encountered oak savannah ecosystems interspersed with conifers and prairie with open canopies resulting from fires (Spetich 2004). In the early part of the 20th century, mild temperatures and moisture conditions enabled even-aged stands of northern red oak (*Quercus rubra*) to become established on sites with lower soil water holding capacity (Engbring et al. 2008, Foti 2004). As even-aged stands advanced in aged and tree density was not controlled, forests became vulnerable to oak

decline. Oak decline is a decadal process that has impacted oak ecosystems globally with often varied influential factors (Wargo et al. 1983, Vettrano et al. 2002, Voelker 2008).

Oak decline events have been reported for the past 150 years in the United States throughout the mixed oak-hickory forests of Missouri, Arkansas, and the Southeast region (Starkey et al. 1989, Starkey et al. 2000, Stephen et al. 2003), as well as in Europe (Vettrano et al. 2002). Cyclical droughts from the 1950s through the early 21st century threatened oak forests. Trees that utilized stored carbohydrates from their root systems to endure early droughts may have experienced decreased abilities to survive future drought events, related to the carbon starvation hypothesis (McDowell 2008). Drought stress on *Q. rubra* likely influenced their resource allocation to defensive chemicals and reduced their ability to fight off insects and pathogens (Haavik et al. 2011, Kelley et al. 2009). In general, disturbance stresses such as drought or warming have been linked to increased mortality events in forest ecosystems, and are likely to increase in the future (Van Mantgen 2009).

Climatic variability was a contributing factor to the current decline of oak forests (Woodall et al. 2008). Stressed trees may have experienced increased vulnerability due to poor site quality and even-aged, densely stocked forest conditions (Oak et al. 1996). Beginning in the mid-1980s, increased activity of the red oak borer was also noted (Stephen et al. 2003). The above mentioned factors resulted in a cycle of decreasing vitality that led to large die-offs of northern red oak (*Quercus rubra*) at the start of the 21st century in Ozark highland forests (Stephen et al. 2003, Starkey et al. 2000). Potential adaptive management strategies may be able to increase forest structural complexity, decrease tree density, and reinstate fire to the ecosystem (Dey et al. 2008)

Because droughts are predicted to increase in frequency as precipitation events become increasingly intense and the periods between precipitation events extends (IPCC 2007), the use of management techniques for decreasing competition stress within forest stands will be needed to mitigate the negative effects of climate change upon forested ecosystems (Dey et al. 2008). Dwyer et al. (2007) found that experimental thinning of tree stands did not prevent oak decline, but thinning may decrease competition between individuals, mitigating competition stresses (Brooks and Mitchell 2011). While thinning may not be a management practice that can increase the health and vigor of declining stands, it may be preventative measure to decrease competition stress during drought periods (Voelker et al. 2008, Dwyer et al. 2007), perhaps thus preventing future decline events.

Accounting for climate change uncertainty

The forests of today are major players in the climate cycle. For example, Northern Hemisphere forests are able to sequester approximately 12% of human global carbon emissions annually (Schimel et al. 2001), or approximately 0.6-0.7 Pt g/yr (Goodale 2002). Carbon storage and sequestration abilities in North American forests are vital management issues in influencing global climate, but also in being greatly impacted by climate change (Hicke et al. 2012). Current forest declines and widespread tree mortality events have been observed in the U.S. in response to disturbances such as drought and pest infestations (Adams et al. 2009, Hicke et al. 2012), and such disturbances can have a major impact on the forest C stocks in the U.S. (Hicke et al. 2012).

Forest ecosystems may act as C sinks during normal climate conditions, but North American and European forests have seen C losses due to drought-associated mortality events (Huang et al. 2010, Ciais et al. 2005). While forest mortality and conversion to transient sources

of C may occur during drought periods, decreasing drought and competition stress through management may help in preserving future forest C stocks. An important consideration may be selection of tree species that are more drought resistant (Millar et al. 2007).

For improved policy efforts, direct interaction between policy makers, federal and state agencies, non-governmental organizations, and scientists may provide the most improvement for moving forward on forest management policy that prioritizes adaptive abilities along with C storage (Seavy and Howell 2010). For example, the current joint efforts between the USFS, The Nature Conservancy, and other conservation organizations in the Ozark National Forest has resulted in proposals for forest landscape restoration that promote biodiversity and ecosystem adaptability goals (USFS 2005). The role of forests as a method of carbon sequestration has gained acceptance through such efforts as the Kyoto Protocol, and forest management to maximize carbon storage will grow in importance in the future (Thurig and Kaugman 2010). However, it remains unclear how adaptive forest management strategies will cope with the potentially changing role of North American forest C dynamics in a changing climate.

Region-wide and nation-wide forest management policies often lack the ability to quickly change in response to alterations in conditions (Millar et al. 2007). Also, lessons from local management are applicable on a smaller scale (Littell et al. 2010). With the uncertainty and variability surrounding the impacts of climate change, the ability for forest managers and policy to adapt quickly to change will be critical. Difficulty in addressing management of forests often arises from uncertainty in climate change predictions for these ecosystems (Lawler et al. 2010). Extreme events are expected to increase in frequency in many regions. For example, climate projections for Northwestern Arkansas suggest decreased frequency of precipitation and increased storm intensity, leading to increased duration of drought in the future (IPCC 2007).

Drought is seen as a factor in oak decline events (Wargo 1996), and management of species composition and stand densities may decrease the negative impacts of drought on forest ecosystems (Kabrick et al. 2008). Along with stand management to address uncertainty in ecosystem response, some tools for managers could consist of ecosystem modeling, tree growth modeling, and predict analysis of past tree response climate.

Modeling efforts have been used successfully to assess forest health and determine optimal ecosystem management strategies. For example, modeling the impacts of differing fire regimes can help determine vulnerability of sites to decline events, and thus indicate areas in which management regimes such as thinning or changes in fire intervals should be focused (Spetich and He 2008). Process modeling has been proposed as a potential management tool to predict the response of tree species to climate change impacts (Johnsen et al. 2001). Understanding the underlying dynamics governing tree growth can provide further insight into the response of forest ecosystems to climate variability. Forecast models, for example, can detect nonlinear dynamics in tree-ring growth series, and thus may highlight growth strategies linked to resilience to disturbance and ability of trees to cope with variable conditions (Reed et al. in prep.). Detection of linear dynamics in forest stands can help identify areas that may be vulnerable to disturbance associated with predicted climate change in the future (Reed et al. in prep.).

CONCLUSION

Difficult choices are required by decision makers to face the challenges predicted with increased climatic variability and drought in the future (IPCC 2007, Lawler et al. 2010). The historical management regimes of US forests are reflected in Arkansas's struggle to balance a healthy timber industry and climate change uncertainties. Historic forest management policy in

the Ozark National Forest set the stage for oak decline events observed in the early 21th century (Stephen et al. 2003, Fierke et al. 2005). Though this paper focuses on the Ozark National Forest as a case study, it is clear that implementing a multiple-use mandate in all U.S. forests, no matter their location will be made significantly more complex in the face of climate change. Given the demands on US forests, forest adaptive management policy must be developed on a local basis with goals focused on maintaining forest resistance and resilience, forest C stock, and timber resources for communities. Reconciling adaptive management and economic demands will be vital for determining the fate of national forests in the U.S. under climate change and disturbance impacts in the future.

GENERAL CONCLUSIONS

This dissertation explores the impacts of disturbance events on forest tree functioning. Each chapter is rooted in tree physiology and modeling theory, with research motivated by future predictions of novel disturbance conditions in forest ecosystems. The incorporation of tree-rings, contemporary leaves, and novel model application provided the means of understanding how variation in physiological strategies may be linked to survival during such disturbance events. In Chapter 1, differential C dynamics in response to disturbance are derived from tree-ring records of tree physiological responses as well as contemporary leaves. In Chapter 2, I expand on concepts of differential C dynamics by increasing the scope of species in my study. In Chapter 3, I use nonlinear dynamic modeling in a novel application to explore underlying radial growth dynamics as potential indicators of disturbance susceptibility. Adaptive, local forest management policies along with nonlinear growth dynamics as tool for managers are proposed in Chapter 4 as a means of maintaining forest functioning under future increases in disturbance. Overall, my data indicate that differential C dynamics relate to differential responses to disturbance events within and among tree species, and these differential responses are important considerations for the future of forest composition and distribution.

My first chapter finds that trees susceptible to disturbance exhibit greater stomatal control over C dynamics, while N appears to play a larger role in the C dynamics of trees that remained healthy. The importance of differential controls on C dynamics of co-occurring trees is further evidenced by my second chapter, in which *Q. macrocarpa* exhibited greater sensitivity to decrease moisture availability and greater stomatal control over C dynamics relative to co-occurring *Q. rubra* (Chapter 2). Utilizing a conceptual model of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ helped to support findings in both of the above mentioned studies, relating a significant, positive slope in the

relationship to greater stomatal influence on C dynamics. These chapters are founded in tree physiological theory, and inconsistencies provide opportunities to further our understandings of tree physiological responses to environmental variability. In Chapter 3, forecast modeling of tree-ring time series enabled detection of underlying nonlinear dynamics in tree growth, consistent with divergent dynamics in trees that are susceptible relative to trees that are resistant to disturbance. Forecast modeling is potentially useful for forest managers and researchers in detecting susceptibility to disturbance in forest communities and is incorporated into Chapter 4. My final chapter also proposes local-scale adaptive management strategies to counter uncertainty related to disturbance impacts on forest ecosystems in future. I highlight a case study of forest decline related to past management and ecosystem-level disturbances to emphasize the importance of local goal setting to incorporate community timber demands along with ecosystem resilience and resistance in the face of predicted increases in disturbance in the future.

Several major conclusions can be taken away from this research. First, approaches that employ multiple techniques to detect physiological responses in trees are needed to understand the impacts of disturbances on forest ecosystems. Growth dynamics can provide evidence of differential C allocation strategies (Chapter 1) and underlying dynamics related to disturbance responses (Chapter 3), but further insight into differential responses is gained through stable isotopic analysis of wood and leaf material (Chapters 1 and 2). Decreased growth in trees dying after a disturbance event provides little insight into the C dynamics and mechanisms influencing differential responses in healthy, neighboring trees. The employment of tree-ring and leaf stable isotopes and N dynamics enables detection of differential factors governing C dynamics in co-occurring trees and species.

Secondly, human management of forests has major implications for forest function (Chapter 1 and 4), and must incorporate disturbance uncertainties to ensure ecosystem structure and function in the future (Chapter 4). My work suggests that densely managed stands of even-aged trees predisposed *Q. rubra* to the negative disturbance impacts associated with a cycle of droughts and subsequent wood-boring insect infestation. With increasing environmental stress predicted with increased disturbance in the future, managing forests must incorporate adaptation, uncertainty, and monitoring tools to maintain future forest structure and function.

Finally, increases in disturbance may have major global implications for future tree range, forest C cycling or productivity in North America. Decreased productivity has already been linked to disturbance impacts in forest ecosystems, evidenced by decreased growth rates (Chapter 1). Changes in species range and forest composition can decrease forest structural complexity, which has been linked to increased disturbance vulnerability in some systems (Chapter 4), and could impact timber and water resources at the local scale. Understanding disturbance impacts, which will increase in the future, and incorporating our understanding into management efforts, is needed to counter potential negative impacts of disturbance (Chapter 4).

Overall, I hope the findings of this dissertation, and the tools and recommendations I develop, demonstrate the important role disturbance plays in forest ecosystems now, and the likelihood of those impacts in the future. My dissertation can help guide future research, monitoring, and management to further understand the implications of future disturbances for forest ecosystems. Forest ecosystem function under climate change relies upon ecological understanding of the underlying mechanisms that govern tree response to disturbance.

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