November 2019

Investigating Among-Individual Growth Heterogeneity in Longleaf Pine: Advancing Dendrochronological Approaches

Jamie E. Munn
University of South Florida

Follow this and additional works at: https://scholarcommons.usf.edu/etd

Part of the Biology Commons, and the Ecology and Evolutionary Biology Commons

Scholar Commons Citation

This Dissertation is brought to you for free and open access by the Graduate School at Scholar Commons. It has been accepted for inclusion in Graduate Theses and Dissertations by an authorized administrator of Scholar Commons. For more information, please contact scholarcommons@usf.edu.
Investigating Among-Individual Growth Heterogeneity in Longleaf Pine: Advancing Dendrochronological Approaches

by

Jamie E. Gluvna Munn

A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Biology with a concentration in Ecology and Evolution
Department of Integrative Biology
College of Arts and Sciences
University of South Florida

Co-Major Professor: Gordon A. Fox, Ph.D.
Co-Major Professor: Luanna Prevost, Ph.D.
    Earl McCoy, Ph.D.
    Christina Richards, Ph.D.
    Marc Lajeunesse, Ph.D.
    Eric Menges, Ph.D.

Date of Approval:
August 26, 2019

Keywords: Tree-rings, mixed models, growth rate, fire history

Copyright © 2019, Jamie E. Gluvna Munn
ACKNOWLEDGMENTS

I am grateful to Dr. Gordon A. Fox for his unequivocal support and patience; I am a better thinker and scientist thanks to his guidance. Thank you to Dr. Luanna Prevost for her thoughtful attention and support, especially to my writing endeavors. I also thank my committee members, Drs. Earl McCoy, Christina Richards, Marc Lajeunesse, and Eric Menges for their detailed insight and expertise. I thank my lab mates and fellow graduate students for their assistance and moral support. I appreciate the help I received in the field from undergraduate volunteers. I am grateful to Christine Brubaker for her consistent kindness and helpfulness.

Thank you to my funding sources. Financial support was provided by the Department of Integrative Biology, the Fern Garden Club of Odessa, the USF Student Government Conference Grant Program, and the National Science Foundation (NSF grant DEB-1120330).
DEDICATION

To my mom, Dina Snyder; you are an endless source of optimism, support, kindness, and advice. Thank you for being an example of resilience for me to follow. To my dad, Jack Gluvna; thank you for your early lessons in plant science and research. To my grandparents, John and Germaine Gluvna; your support allowed me the opportunity to have this privileged education. To Tucker; you are a ray of sunshine during difficult times. To my husband, Jonathan Munn; thank you for believing in me.
# TABLE OF CONTENTS

LIST OF TABLES ........................................................................................................ iii

LIST OF FIGURES ..................................................................................................... iv

ABSTRACT: ..................................................................................................................... vii

CHAPTER 1: DENDROCHRONOLOGY OF PINUS PALUSTRIS IN CENTRAL FLORIDA ................................................................. 1
   Introduction ............................................................................................................. 1
   Materials and Methods ...................................................................................... 5
      Study site ......................................................................................................... 5
      Sampling ......................................................................................................... 7
      Method for measuring tree rings ................................................................. 9
      Calculation of the growth rate ................................................................. 10
      Chronology methods .................................................................................... 10
   Results ............................................................................................................. 13
      Statistical results ....................................................................................... 13
      Other analyses ......................................................................................... 18
      Model results ............................................................................................ 19
   Discussion ...................................................................................................... 21
   Citations .......................................................................................................... 25

CHAPTER 2: MIXED MODELS, DENDROECOLOGY, AND HETEROGENEITY ...... 30
   Introduction ...................................................................................................... 30
   Materials and Methods .................................................................................. 36
      Study site ....................................................................................................... 36
      Sampling ....................................................................................................... 37
      Method for measuring tree rings ............................................................. 38
      Calculation of Growth Rate .................................................................... 39
      Model building ......................................................................................... 39
      Model selection ......................................................................................... 42
   Results ........................................................................................................... 44
      Ring widths and general growth patterns .................................................. 44
      Models ......................................................................................................... 46
      Random effects .......................................................................................... 62
   Discussion ...................................................................................................... 68
      Elevation ..................................................................................................... 69
      Diameter and diameter x age ................................................................. 71
LIST OF TABLES

Table 1: Descriptive statistics from COFECHA for the USFFP burn plots. .......................... 13

Table 2: Stepwise-selected model of best fit using temperature and precipitation residuals. ................................................................................................................. 20

Table 3: Mixed model results.................................................................................................................. 20

Table 4: Detailed description of the fire category main effect................................................................. 41

Table 5: Age-based models....................................................................................................................... 47

Table 6: Size-based models...................................................................................................................... 48

Table 7: Size- and age-based models...................................................................................................... 51

Table 8: Comparison of best-fitting models which are size-only, age-only, or include size and age. ................................................................................................................................... 51

Table 9: Age-size models including fire. .................................................................................................. 52

Table 10: Select main effects and interactions, pre-burn and burned periods. ................................. 53
LIST OF FIGURES

Figure 1: Map of the USF Forest Preserve burn plots with elevation contour......................... 6
Figure 2: Map of the USF Forest Preserve burn plots showing two replicates each of five different prescribed burn frequency.................................................................................. 6
Figure 3: History of prescribed fire in the USF Forest Preserve. Red boxes indicate that a prescribed burn occurred that year................................................................. 8
Figure 4: Chronology for the USF Forest Preserve, detrended using a spline ..................... 13
Figure 5: Standardized site chronology (all plots, pooled), shown with 95% confidence intervals. ...................................................................................................................... 14
Figure 6: Standardized chronology for individual plots......................................................... 15
Figure 7: Chronology traces for each of the 10 plots, with the pooled trace shown in black................................................................................................................................. 16
Figure 8: Individual plot chronologies (black traces) with recent burn history (Fire Category) shown during the burn period only ............................................................. 17
Figure 9: Temperature and precipitation at the Preserve, 1939-on ...................................... 18
Figure 10: Plot-wise correlations and comparison to the Preserve chronology (USF), total annual precipitation in mm, and average annual temperature in Celsius....... 18
Figure 11: Log growth rate (GR) compared to age (scaled and centered) ......................... 45
Figure 12: Log(GR) declines as trees grow larger .................................................................. 45
Figure 13: Comparison of diameter variance as a function of age..................................... 46
Figure 14: Concept diagram for age-based models ................................................................. 47
Figure 15: Concept diagram for size-based models ................................................................. 48
Figure 16: Concept diagram for models including first-order interactions, only .................. 49
Figure 17: Coefficients for each predictor against the response; pre-burn ............................ 50
Figure 18: Coefficients for each predictor against the response; burned period .................. 50
Figure 19: Concept diagram for models including fire ......................................................... 52
Figure 20: Concept diagram for models including first-order interactions, only .................. 53
Figure 21: Parameter estimates for the best-fitting model for the pre-burn period, shown with confidence intervals ......................................................................................... 54
Figure 22: Selected parameter estimates for the best-fitting model for the burned period, shown with confidence intervals ......................................................................................... 55
Figure 23: Pre-burn period: Average effect of diameter×age interaction over time ............ 56
Figure 24: Burned period: Average effect of diameter×age interaction over time .............. 56
Figure 25: Pre-burn period: Average effect of age×elevation interaction over time ............ 57
Figure 26: Burned period: Average effect of age×elevation interaction over time ............ 58
Figure 27: Interaction plot showing the pre-burn three-way interaction between tree diameter, age, and elevation, all of which were studentized .................................................. 58
Figure 28: Interaction plot showing the burned period three-way interaction between tree diameter, age, and elevation, all of which were studentized ........................................ 59
Figure 29: Plot showing the interaction of diameter and elevation, both studentized, pre-burn period ............................................................................................................... 60
Figure 30: Plot showing the interaction of diameter and elevation, both studentized, burned period ................................................................................................................. 60
Figure 31: Parameter estimates for fire category with standard error ........................................ 61

Figure 32: The interaction between fire category and studentized elevation ......................... 62

Figure 33: Random effects (variance) for the pre-burn and burned periods. ....................... 62

Figure 34: Individual Random effects, pre-burn .................................................................... 64

Figure 35: Random effects for year, pre-burn period .............................................................. 65

Figure 36: Random effects for individual, burned period ....................................................... 66

Figure 37: Random effects of year, burned period ................................................................. 67

Figure 38: One chronology shown with two different spline lengths ................................. 87

Figure 39: Comparing the standardized chronology (black) with the parameter estimates for the random effect of year from the GLMM (red) .................................................. 91

Figure 40: Density plots showing a breakdown for the effects of year (top) and individual (bottom), .................................................................................................................................. 92

Figure 41: Values for the effect of year, visualized by plot .................................................. 93
ABSTRACT:

Within a population, individuals frequently differ in the rate at which they grow, and this rate can be impacted by both genetic differences and abiotic factors. Often, dendrochronology is used to elucidate growth trends based on climate or other factors. This dissertation explores new statistical approaches to dendrochronological research.

First, I created a chronology for a population of longleaf pine (*Pinus palustris* P. Mill.) individuals in a southwest Florida sandhill community. I then used generalized linear mixed models to investigate the effects of fire frequency, year, tree age and size, and elevation on variation in radial growth heterogeneity. I then compared the chronology results to the model results.

Whereas classical dendrochronological approaches typically focus on a single signal of interest, I present an approach using linear mixed models incorporating multiple parameters that may impact growth. These models also indicated that individual tree growth variation tripled after a period of prescribed burns compared to a prior period with no prescribed fire. Growth rate variation has been shown to have important impacts on population dynamics and extinction risk; this dissertation provides evidence that fire may increase this variation. Further, the model estimates for yearly growth correlate with the chronology ring width indices, forming a statistically-based chronology while also explicitly accounting for multiple parameters at once.

Tree-ring data were collected from pines in experimental plots, each with one of four levels of prescribed fire-return interval. The fire-return intervals approximated 1-, 2-, 5-, and 7-
year fire frequencies, or the plot was left unburned, for a total of five treatments. Prescribed
burns were ongoing from 1976 - 2004. Tree age and basal area increment were calculated from
radial tree-ring growth measurements in order to compare these factors with year and burn
frequency.

In building the chronology, the trees were systematically sampled across burn plots, size,
age, and elevation within the site, then detrended individually using a spline. The chronology
showed more variation when trees were young, and there were some marker years consistent
among plots. I built models to determine how weather (precipitation or temperature) impacts
residual tree growth, and they indicated that wetter than average springs or summers had the
strongest impact on growth. I created a generalized linear mixed model containing year and a
term for fire, but the impact of fire was small. Overall, I was unable to clearly detect burn years
by looking at the growth trace or using statistical models on the chronology growth residuals.

I examined the periods before 1976 and after 1976 in separate analyses using linear
mixed effects models. For both periods, I included burn frequency, tree size and age, and
elevation as fixed effects. Individual tree and year were included in the model as random effects
in order to quantify the amount of variation in these parameters. Some key results included: the
relationship between diameter and elevation has varied and complicated impacts on growth rate;
all levels of recent fire history impact growth rate negatively, with back-to-back burns resulting
in extremely varied growth rates; individual tree core growth variance tripled within burned plots
compared to unburned plots, indicating that longleaf pines exhibit some persistent heterogeneous
growth when fire is incorporated into the plots. Importantly, the use of GLMMs provided
flexibility to incorporate statistical sampling methods instead of targeted sampling methods, and
explicitly addresses age or other factors without dismissing them as “noise”. Because other
factors can be addressed, this type of approach can also answer a wider variety of questions instead of focusing on a single, overarching signal of interest.

In the period after prescribed burns began, estimated individual tree growth variances were three times larger than variance estimates for between years. This indicates that longleaf pines exhibit some individual-level, persistent heterogeneous growth when fire is incorporated into the plots, and less heterogeneous growth when fire is excluded. This leads to hypotheses regarding how fire may increase between-individual tree growth variance. Due to the heterogeneous nature of fire, each tree often experiences it differently, and growth may change accordingly. Also, fire commonly reduces competition, which could make pine growth heterogeneity more distinct by underscoring the importance of other factors, like genetics or microhabitats.

In Chapter 4, I compared the classical chronology to the statistically-based chronology created in Chapter 3. I showed that the random effect estimates for year and the ring width index from the chronology were correlated, and showed that the random effect estimates for year form a statistically-based chronology. While the model results closely resemble traditional chronological results, the model approach allows us to more explicitly describe changing tree growth due to factors like fire or water availability. Further, GLMMs provide the opportunity to measure individual variation; demographic heterogeneity has important consequences for populations and is not typically addressed when filtering out noise to produce a signal within a classical dendrochronological approach. While more exploration of these model types is in order, GLMMs are an important new tool for dendrochronologists.
CHAPTER 1:

DENDROCHRONOLOGY OF PINUS PALUSTRIS IN CENTRAL FLORIDA

Introduction

Dendrochronology is a field of research that uses tree-rings to place events in time or to evaluate environmental effects (Speer, 2010), because tree growth is partly a response to weather. Dendrochronology can be used to investigate climate, insect outbreaks, fire history, and extreme weather events like hurricanes (Gentry, Lewis, & Speer, 2010; Henderson & Grissino-Mayer, 2009; Speer, Clay, Bishop, & Creech, 2010; Stambaugh, Guyette, & Marschall, 2011) and has archeological applications as well (Čufar, 2009).

Dendrochronological studies typically (but not always) focus on trees that reliably produce one ring per year. In trees, radial growth (or width) initiates within the vascular cambium. The cells in the vascular cambium differentiate into mainly water- and nutrient-carrying xylem cells or phloem, which carries products synthesized in the plant through photosynthesis (Stokes & Smiley, 1996). The xylem cells can vary in size and cell-wall width over the course of a season, can be used to delineate a single tree ring. Temperate seasonality typically results in changing growth conditions that temporarily stop radial tree growth, resulting in an annual tree ring (Rathgeber, Cuny, & Fonti, 2016). When growth begins again in the next growing season, another ring is created. In conifers, the cells at the beginning of the growing season are typically wide, open, and thin-walled, and become thicker-walled and flatter as the
growing season commences. When the growing season returns, the rings become wide and open again, resulting in what appears to be a line that demarcates one year of growth (Speer, 2010). I can use trees which produce annual rings to make inferences about what the tree experienced in a particular year, as evidenced in the ring width or quality.

Tree rings allow past radial growth rates of an individual to be measured and linked to other factors such as rainfall or elevation, as well as other factors like age and size. Because trees rely on the environment for nutrients, water, and sunlight, variations in these factors from year to year result in changing tree-ring width. By measuring the tree-rings, one can make inferences on changing environmental or climate variables. The impacts of fire, ice, or insects can be noted by documenting damage to a particular tree ring. For example, a tree sample taken in 2004 shows a fire scar 12 tree-rings back from the bark. From this information one can determine that a fire occurred in 1992. In another example, if all of the trees in a sample experienced minimal growth in a particular year, one can infer there is an environmental reason for this like drought or cold. If only one tree or a small number of trees exhibit a particular growth pattern or unusual growth in a specific year, one can infer a more local cause, like competition or microsite. Longleaf pines are well-documented to produce annual growth rings (e.g., (Foster & Brooks, 2001; Henderson & Grissino-Mayer, 2009; Stambaugh et al., 2011)).

Trees respond differently as environmental factors change over time, but also because they are unique individuals; further, factors like size, competition, and microsite create differences between trees as well. Tree ring width therefore represents a sum of influences. By choosing to study one factor’s impact on a population of trees, I must account for or filter out the other effects. The aggregate tree growth model describes ring growth

\[ R_i = B_i + P + C + O + e \quad (1) \]
where $R_i$ is ring width of tree $i$, $B_i$ is biological component for tree $i$, $C$ is stand or regional climate, $O$ is regional disturbance, $e$ is an error term incorporating factors not otherwise included, like local disturbance or individual heterogeneity (Van Deusen, 1989). By accounting for variables like the growth trends, and disturbances, one can isolate an effect of climate, for example. Differences in growth patterns which are not linked to climate (or the environmental factor in question) are often factored out as “noise” in traditional dendrochronological applications. I will explain the idea of noise, and its applications and limitations, below.

Classical dendrochronological approaches involve investigating tree-ring growth; the desired “signal” may be climate- or ecologically-based, while any variation which has not been accounted for mathematically is classified as “noise” (Fritts & Swetnam, 1989). Noise is produced by a variety of factors such as precipitation, temperature, fire (and more) and compounded by the fact that trees are biological individuals, biochemically and physiologically distinct (Speer, 2010). Raw ring width is generally standardized. Standardization serves two purposes; it helps to adjust the ring width values to accommodate geometrical constraints of adding wood to the outer layer as a tree ages (Fritts, 1976) and it helps eliminate noise and maximize the signal of interest. Typically during standardization ring width is divided by some kind of growth curve (the modified negative exponential and splines are two common options) for each year, accounting for growth-related trends (Fritts, 1976). Deterministic standardization using the modified negative exponential tends to work best for open growth forest with few disturbances (Cook & Peters, 1997); other standardization options are empirical (Speer, 2010).

The process of isolating a signal of interest begins by sampling trees to build a chronology. Often, targeted sampling is done deliberately as to maximize chronology length (tree age) and target the most sensitive trees. Trees can be considered sensitive or complacent.
Sensitive trees are strongly limited by the environmental variables of interest, and thus have more variation in their year-to-year growth. Complacent trees may not respond strongly to changes in the environment. For example, most trees in a desert (precipitation-limited) population may show a response to precipitation, whereas the individual trees which exist very near a water source may be complacent with regard to precipitation, since water is not typically restricted (Speer, 2010). While informative, targeted sampling of old or sensitive individuals can overestimate forest climate sensitivity. Representative sampling can introduce more variation but may better represent the gradient response of the population (Klesse et al., 2018).

In order to create a chronology, multiple trees from one stand or site must be included. This allows growth to be averaged amongst the samples, producing a stand-level signal and removing some individual variation. It also allows one to crossdate the trees. This process of replication is critical to creating a chronology (Speer, 2010). After multiple trees are sampled from a site, the next step is crossdating. Crossdating is the process by which I match ‘marker years’—years for which growth was relatively high or very low within an individual tree—across the individuals in the sample. Crossdating allows one to be sure a ring is present for each year, or pinpoint the location of any missing rings. After crossdating, the rings are measured and the chronology can be created.

In Florida, and particularly in our study site, trees ring variation is most likely responsive to climate (specifically water availability), and disturbances like fire, freezing events, and other extreme weather events. Longleaf pine (*Pinus palustris*) creates the necessary characteristic annual growth rings in the cell structure of the wood, which makes it suitable for dendrochronological studies. In this chapter, I used stratified random sampling (as opposed to targeted sampling) of longleaf pine in an area with partially known site history, which includes a
known prescribed fire-history spanning 26 years. Our goal was to use tree-ring measurements to build a chronology and determine general growth trends in a stand of longleaf pines (1910-2014; average age ~45 yo). Using a standard chronology approach with a stratified sample, I examine how much chronologies can tell us about major factors impacting growth (precipitation, temperature, and fire) and identify any areas where I can know more. I will use simple known weather and fire data to investigate how much this chronology can tell us about longleaf pine growth response. Rather than looking for an explicit fire or climate signal by filtering out or accounting for most other factors, the objectives were (1) develop a chronology for *Pinus palustris* in central Florida, (2), if possible, determine which factors influence longleaf pine growth by detecting any growth patterns relating to these factors, and (3) discuss possibilities for expanding tree-ring analyses.

**Materials and Methods**

**Study site**

The University of South Florida Forest Preserve is a 200 ha tract of Florida vegetation located in west central Florida, within the city of Tampa in Hillsborough County, FL (27°857’N, 82°832’W). The Preserve varies in plant communities—lowland communities like floodplain forest, hydric hammock and wet flatwoods comprise 65% of the area, and upland plant communities like sandhill, mesic flatwoods, and xeric hammock comprise the remaining 35% (Schmidt, 2005). The study plots, nested within the Preserve, are primarily sandhill, with a progression to mesic flatwoods at the northern edges of the plots (Schmidt, 2005). The canopy is generally open and dominated by longleaf pines (*Pinus palustris*), typical for pine sandhill (Florida Natural Areas Inventory, 2010). Co-occurring vegetation includes a sub- to mid-canopy of deciduous oak species, and an herbaceous layer dominated by grasses and forbs (Schmidt
There is an elevation gradient from approximately 17 m asl to 10 m asl (Figure 1) and the environment shifts from xeric sandhill to mesic flatwoods along this elevation gradient due to depth of the sandy soils and location of the water table. The soils at the highest elevations are primarily Candler fine sand and Pomello, resulting in an excessively fast-draining xeric sandhill with deep soil (Foster & Brooks, 2001).

**Figure 1:** Map of the USF Forest Preserve burn plots with elevation contour.

**Figure 2:** Map of the USF Forest Preserve burn plots showing two replicates each of five different prescribed burn frequency.
Prescribed burns within the study site began in 1976, with four levels of prescribed fire-return interval, approximating 1-, 2-, 5-, and 7-year fire frequencies. There are two replicates per fire frequency, as well as two plots that have remained unburned (Figure 2).

**Sampling**

Classical dendrochronological studies seek to maximize tree age signal by choosing the oldest trees or those most likely to respond to the signal in question. I sampled the longleaf pine population using a stratified random sample, stratified by size class, elevation, and burn plot. I measured diameter at breast height (DBH) and classified trees into size classes with 2.5 cm increments beginning at 10 cm dbh. I collected two samples from each size class, per burn plot. In the event that a burn plot only had one or no individuals within a certain size class, I collected one or zero samples accordingly. The beginning sample pool totaled 276 trees, with sampling occurring during 2013-2016. The samples were stratified by relative elevation within plot.

Within each plot, I chose a tree at a low elevation and high elevation within each size class. This method ensured representation of high and low elevation within a particular burn frequency.

I used an increment borer (Haglof, Sweden) to collect two samples from each tree at approximately breast height. I collected the samples at 90° angles (north-south and east-west) except when the land contour necessitated adjusting in order to properly sample compression and tension wood, inconsistencies in wood density that arise when trees grow on a slope. Each core was dried, mounted, and then I sanded each sample with a series of progressively finer sandpaper grits starting at 80 and working up to 400. I hand-sanded as needed.
Next, I removed any samples that were too damaged for measurement. Some of these cores were damaged due to heart rot, missing pieces, or multiple breaks in the sample upon removal from the tree. Commonly, both samples from a single tree exhibited the same damage, so if one core was damaged, I removed the tree from the sample. After I removed damaged cores, I randomly removed some trees from any plots that had more than 25 trees in order to prevent overrepresentation; in this case, 1 to 7 trees were removed from all plots except for 1W and 5W, which began with fewer than 25 trees. Of the original 276 sampled trees, 26 were removed before crossdating. Once crossdating began, if I detected a problem with a core, it was corrected if possible, otherwise it (and the other core from that tree) was removed. I attempted to crossdate the remaining 250 trees, and I removed 24 trees that could not be crossdated.
Method for measuring tree rings

Because the sampling date for the trees was known, samples were first dated, then crossdated using the list method (Yamaguchi, 1991), and later using the memorization method (Douglass, 1941; Speer, 2010). The list method is suitable for samples for which the date of the outermost ring in the sample is known, as opposed to “floating” wood—samples for which the dates for the innermost and outermost rings are unknown. This method consists of identifying (by listing on paper) narrow rings by calendar date within a sample, then using the lists to determine which years’ rings are consistently narrow amongst samples. The memorization method builds on this, by allowing me to quickly check new cores for known marker rings which were indicated by the list method, ensuring that dating is still accurate (Speer, 2010).

Annual growth was measured using a tree-ring measuring system which included a SZ-40 Olympus boom stereoscope (40x) using a unislide stage encoded to 0.001 mm (Velmex, Bloomfield, N.Y., USA) connected to a Metronics Quick-Chek. Measuring began at the bark-cambium interface, which was considered the most recent known year. The year nearest the pith was considered the first year of growth. Trees were crossdated statistically using COFECHA, which creates a master chronology using all trees and compares each tree to this chronology individually (Grissino-Mayer, 2001; Holmes, 1983). Because the samples were typically less than 100 years old, cores were analyzed using 22-year segments with an 11-year overlap. If a series did not crossdate well, it was corrected if possible. Samples which could not be reliably crossdated, or which exhibited low or negative correlations to the master were removed from the sample if issues could not be resolved. The samples which remained after crossdating in COFECHA typically had a series intercorrelation above 0.5 within each plot.
The series intercorrelation threshold for keeping a series in the chronology sample was 0.3 within its respective plot, and if either or both of the series within a tree did not reach this threshold, they were both removed from the chronology. 48 trees did not meet the 0.3 within-plot series intercorrelation threshold and were removed from the sample. Series which were not retained in the chronology due to low series intercorrelation remained part of the larger sample [used in chapter 3]. After removing any damaged or poorly-intercorrelated series, all trees were re-run through the COFECHA software in order to obtain an overall USFFP chronology. The final number of trees in the chronology was 151.

**Calculation of the growth rate**

Generally, the calculation of growth rate relies on the logarithmic ratio of some measure of growth from one point to another. The growth equation

\[ GR = \ln \left( \frac{x'}{x} \right) \quad (2) \]

utilizes size this year and size last year (represented by \( x' \) and \( x \), respectively). For this study, I used ring width measurements to estimate \( r \), where \( r \) equals the radius of the tree in a given year. I then calculated the basal area for each year using \( \pi r^2 \). Then, the growth rate was calculated using equation 2. I used the natural log of this ratio in order to maintain results that are understandable as approximately proportional to original values (Gelman and Hill 2007).

**Chronology methods**

I built one chronology for the site (all ten burn plots) but also built chronologies for the individual plots.

To build the chronologies, I used the Dendrochronology Program Library in R (dplR) (Bunn et al., 2018). The first step is standardization, a process which maximizes a signal of
interest while minimizing tree-specific trends like size- or age-related growth patterns (Speer, 2010). In order to standardize our samples, I detrended using a spline which usually provides a good fit for interior forests (Cook & Peters, 1981). The USFFP chronology was detrended using a spline and graphed using dplR (Bunn et al., 2018). For the purpose of this chronology, the signal of interest is ring width index (RWI), which I can use in order to determine any particularly “bad” or “good” years, or any patterns of higher or lower than average growth. RWI is a unitless measure of actual ring width compared to expected ring width based on the method of detrending. In order to compare individual plots to one another, I also calculated Pearson’s correlation coefficient.

I used bootstrapping on the ring widths to create what I refer to as a ‘pseudochronology’, so-named because of the way bootstrapping operates: by resampling the data, with replacement, to create pseudo-datasets. During bootstrapping, individual trees are randomly removed from the chronology one at a time, then the chronology is recalculated. I bootstrapped all chronologies using 10,000 bootstrap replicates in order to estimate 95% confidence intervals around the chronology; this seems especially important going back in time, especially as sample size decreases.

Monthly mean temperature and monthly precipitation were obtained for Hillsborough County, Florida through the National Climatic Data Center, Asheville, NC (www.ncdc.noaa.gov/). Measurements were recorded at Tampa International Airport beginning in 1939. Because tree sample size was small prior to that time, analyses including weather used ring data from 1939 – 2014.

Using the tree ring measurements, I calculated a linear regression to predict annual radial growth residuals based on temperature and precipitation. In order to do this, I included annual
average temperature and annual total precipitation, as well as seasonal total precipitation and seasonal average temperature. I calculated annual tree growth residuals by taking the difference between the individual series and the annual mean. I studentized all temperature and precipitation measurements. I also calculated seasonal average temperature and total precipitation residuals by taking the difference between seasonal average temperature or total precipitation and annual average temperature or total precipitation. To more closely match Florida climate, I used three seasons—spring (months 2-5), summer (months 6-9), and winter months (10, 11, 12, and 1 from the next year) (Foster & Brooks, 2001). I then calculated a linear regression to predict this residual annual tree growth based on temperature and precipitation. I began with a full model, then used the stepAIC function from the ‘MASS’ package in R (Venables & Ripley, 2002) in R to check all possible parameters and choose the model with the lowest AIC.

In order to test for an impact of fire, I built two linear mixed effects models using the lme function (using optimizer “bobyqa”) in the lme4 package in R (Bates et al., 2018; R Core Team 2018). The models contained either recent fire history (FireCat) or a binary term for fire. Year was included in the model as both a fixed (continuous) and random effect (factor), which is a standard approach for repeated measures analyses (Bolker, 2015). Including year in the model as a fixed effect is necessary; I have taken repeated measurements per individual, in the form of tree rings which allowed me to quantify growth changes from year to year. Including year as a random effect as well allowed me to quantify the variation among years (Gelman & Hill, 2007).
Results

Statistical results

The final sample size was 151 trees (302 series) spanning 105 years with an average age (series length) of 43.5 years (Table 1).

*Table 1: Descriptive statistics from COFECHA for the USFFP burn plots.*

<table>
<thead>
<tr>
<th>Statistic</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of trees</td>
<td>151</td>
</tr>
<tr>
<td>Number of dated series</td>
<td>302</td>
</tr>
<tr>
<td>Master series time span (yrs)</td>
<td>105</td>
</tr>
<tr>
<td>Total rings</td>
<td>13124</td>
</tr>
<tr>
<td>Interseries correlation</td>
<td>0.503</td>
</tr>
<tr>
<td>Mean sensitivity</td>
<td>0.346</td>
</tr>
<tr>
<td>Chronology start date</td>
<td>1910</td>
</tr>
<tr>
<td>Mean series length (yrs)</td>
<td>43.5</td>
</tr>
</tbody>
</table>

Site: Chronology

*Figure 4: Chronology for the USF Forest Preserve, detrended using a spline; Red line is an 11-year spline used for visualization. Gray background indicates series sample size.*

The chronology is most variable when sample size is low; the signal seems to stabilize around 1950. There was a notable decrease in RWI in the year 2000, followed by an increase in 2004 (Figure 4).
Site: Bootstrap

Bootstrapping shows narrow confidence intervals throughout, becoming even smaller from the 1950s until the end of sampling in the 2010s. Prior to this, confidence intervals are wider, possibly partly due to sample size (Figure 5). The year 2000 was the strongest marker year found within the samples.

![Graph showing standardized site chronology with 95% confidence intervals](image)

**Figure 5**: Standardized site chronology (all plots, pooled), shown with 95% confidence intervals. CIs were calculated by bootstrapping the chronology using 10,000 replicates, omitting a single tree at time. The smallest confidence interval is found in the year 2000. CIs shown for years where the number of individuals is at least 5.

While each of the plot traces was unique, showing different patterns throughout time, there were some details that were similar across plots. In all plots, the beginning of the growth trace is highly variable, likely due to small sample size and young trees (Figure 6). All plots exhibited a noticeable decrease in growth for the year 2000, and all plots experienced increased
growth in 2003 and 2004. The plot growth patterns are similar from 2000 on, but the plots were less similar 1975-2000 (Figure 7).

**Plots: Chronology**

![Plots Chronology](image)

*Figure 6: Standardized chronology for individual plots. Pooled chronology trace shown in black. Dashed line provides a reference for RWI = 1.*

When examining the plot chronology traces with recent fire history (Figure 8), I saw a slight pattern of decreased growth the year of a fire, with a slight rebound the following year if there was not a subsequent burn. There were some prominent peaks and valleys that did not appear to result from fire history. I tested this with a model later in this section.
Figure 7: Chronology traces for each of the 10 plots, with the pooled trace shown in black. Dashed line as in Figure 6.
Figure 8: Individual plot chronologies (black traces) with recent burn history (Fire Category) shown during the burn period only. 0 indicates no burns in year x nor year x-1. 1 indicates burned in year x. 2 indicates burned in year x-1, and 3 indicates burned in year x and year x-1.
Other analyses

Figure 9: Temperature and precipitation at the Preserve, 1939-on. Note the increase in average annual temperature while the precipitation pattern stays relatively consistent.

Figure 10: Plot-wise correlations and comparison to the Preserve chronology (USF), total annual precipitation in mm, and average annual temperature in Celsius. Darkness of color and increasing pie shape indicates higher correlation.
Plot 2W was most highly correlated with the Preserve chronology (0.849), followed by the two unburned plots (UE 0.840; UW 0.835). Because the Preserve is divided into east and west sides, I also looked at the correlation between the east-west pairs of plots per burn frequency. While I expected the east-west pairs to be more highly correlated due to similarities in burn history, this was not the case. Between east-west pairs, correlations were highest for the unburned plots (0.74) and lowest for the 5-year plots (0.23). All plots were more highly correlated with the Preserve chronology than their east or west match. The Preserve chronology was more highly correlated with annual precipitation (0.33) than annual temperature (0.01) (Figure 10), but this relationship may be complicated by changing average temperature across the time frame (Figure 9). Plot elevations may also impact moisture availability or response to precipitation depending on elevation (Figure 1) as well as the natural heterogeneity of fire itself.

Model results

After calculating the linear regression predicting residual annual tree growth based on temperature or precipitation, the stepwise-selected model retained spring and summer precipitation residuals. This indicated that wetter than normal springs or summers were the best predictors of increased annual growth (Table 2). All variables were studentized. For each SD unit increase in residual spring rain, tree growth increases by 0.30 units (SE 0.11). For each SD unit in residual summer rain, tree growth increases by 0.22 units (SE 0.11).

I looked at all the possible models to determine if any others were well-supported by AIC. Two models were within 3 ΔAIC but both retained spring and summer precipitation residuals; the stronger of these two models also retained winter temperature residuals, and the other model retained winter temperature residuals and summer temperature residuals. When
winter or summer temperature residuals were retained, cooler than average temperatures resulted in decreased growth. All models within 8 ΔAIC retained spring and summer precipitation.

Table 2: Stepwise-selected model of best fit using temperature and precipitation residuals.

<table>
<thead>
<tr>
<th></th>
<th>Df</th>
<th>Sum Sq</th>
<th>Mean Sq</th>
<th>F value</th>
<th>Pr(&gt;F)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring total precip, residual</td>
<td>1</td>
<td>6.99</td>
<td>6.99</td>
<td>7.92</td>
<td>0.01</td>
</tr>
<tr>
<td>Summer total precip, residual</td>
<td>1</td>
<td>3.37</td>
<td>3.37</td>
<td>3.82</td>
<td>0.05</td>
</tr>
<tr>
<td>Residuals</td>
<td>71</td>
<td>62.64</td>
<td>0.88</td>
<td>NA</td>
<td>NA</td>
</tr>
</tbody>
</table>

I checked for any outstanding patterns due to fire in the growth residuals by building a mixed model containing year and fire category (FireCat) or a binary term (fire_binary1) for fire as fixed effects and year and plot as random effects. The impact of fire was very small in both models (Table 3). The plot-wise growth residuals are very small and average near zero, indicating that growth in different plots, despite prescribed burn regime, has been accounted for in the chronology.

Table 3: Mixed model results. A: Model results for the mixed model containing fire category (FireCat). Fire category was 0, 1, 2, or 3. 0 indicates no burns in year x nor year x-1. 1 indicates burned in year x. 2 indicates burned in year x-1, and 3 indicates burned in year x and year x-1. B: model results for the mixed model including a binary fire term (fire_binary1) as a fixed effect.

A:

<table>
<thead>
<tr>
<th>Estimator</th>
<th>Estimate</th>
<th>Std. Error</th>
<th>t value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-0.554</td>
<td>0.656</td>
<td>-0.845</td>
</tr>
<tr>
<td>FireCat1</td>
<td>-0.050</td>
<td>0.029</td>
<td>-1.700</td>
</tr>
<tr>
<td>FireCat2</td>
<td>-0.019</td>
<td>0.031</td>
<td>-0.621</td>
</tr>
<tr>
<td>FireCat3</td>
<td>-0.012</td>
<td>0.029</td>
<td>-0.418</td>
</tr>
<tr>
<td>Year</td>
<td>0.000</td>
<td>0.000</td>
<td>0.849</td>
</tr>
</tbody>
</table>

B:

<table>
<thead>
<tr>
<th>Estimator</th>
<th>Estimate</th>
<th>Std. Error</th>
<th>t value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-0.505</td>
<td>0.644</td>
<td>-0.785</td>
</tr>
<tr>
<td>fire_binary1</td>
<td>-0.028</td>
<td>0.021</td>
<td>-1.323</td>
</tr>
<tr>
<td>Year</td>
<td>0.000</td>
<td>0.000</td>
<td>0.789</td>
</tr>
</tbody>
</table>
Discussion

The chronology for the Preserve showed more variation further back in time. When trees are young, they tend to have more variation in growth rate, and the variation in the chronologies is compounded by sample depth as well. In 1940, sample depth reaches 25 trees and from then on, I can detect some interesting patterns. Often I see less growth in a burn year, followed by a slight uptick in growth the following year if there is not a burn (Figure 8). This finding is consistent with prior research (Ford, Minor, & Fox, 2010). It is thought that recovery between fires may be due to the deep rooting structure of these trees which allows for access to water (Ford, Mitchell, & Teskey, 2008) combined with stored carbon reserves (Varner et al., 2009). While I was only able to detect this impact graphically, it is possible that one could construct a model that incorporates other environmental data to confirm an impact of fire. Including complementary data to tree-ring data can improve predictions (Evans et al., 2017).

Visual comparison of the plot chronologies all showed a deep valley for the year 2000, but otherwise showed different patterns (Figure 7). Some plot pairs are poorly correlated (1W/5W, 7W/7E, 5W/5E), and other pairs are highly correlated (UW/5E, 7W/1E, UE/UW) (Figure 10). Overall, while I did not explicitly test for spatial correlation, it does not appear that plots that are near to one another exhibit especially similar growth patterns in longleaf pine. The opposite applies—plots far away from each other are not especially different. Some other factors that may impact plot similarities include changing interspecies (i.e. oak encroachment) competition across the plots (see Schmidt, 2005), or difficulty obtaining accurate ring measurements when trees are exhibiting strong compression wood despite our efforts to avoid this. Elevation changes across the plots (Figure 1)
which likely changes moisture availability (Foster, 2014) and fire behavior (Behm, Duryea, Long, & Zipperer, 2004). While matching burn regime does not seem to make the plots themselves grow more similarly, the two unburned plots are more highly correlated than any other pair with the same burn regime (Figure 10). This shows that the relationships among fire, moisture, and other ecological factors are complicated; further complexity is added when I account for individual heterogeneity.

Understanding the peaks and valleys in our chronologies may be particularly complicated because I have spatially unbiased samples, which can result in a reduced climate signal (Klesse et al., 2018); further, hurricanes and fires (both factors experienced by our study site) are both spatially heterogeneous. Hurricanes produce wind and rain which interact with the topography of the land and produce heterogeneous impacts on land and vegetation in the hurricane’s path (Boose, Foster, & Fluet, 2011). Fires tend to be inherently patchy, with amount of burned area and burn temperature changing across the landscape (Turner, Romme, Gardner, & Hargrove, 1997). Fire heterogeneity can further impact population and community dynamics (Menges, 2007).

The linear regression predicting growth response to weather indicated that wetter than average springs or summers had the strongest impact on growth. The mixed model containing year and a term for fire detected a small impact of fire. Overall, the plot-wise growth residuals were very small, averaging near zero, which indicated that growth in different plots has been accounted for in the chronology.

I was unable to clearly detect burn years by looking at the growth trace or using statistical models on growth residuals. I suggest that this is for three broad reasons. First, because I used
annual growth residuals calculated from the chronology, the chronology has already accounted for a huge proportion of the variance within tree growth.

Second, this might be due to the complex interaction of multiple factors existing within these types of disturbance. For example, hurricanes bring water but also cause foliar damage. Trees may experience decreased growth due to crown repair in the three years following a hurricane (Tucker, 2015) but the growth response is further is confounded by storm frequency and annual precipitation in those years that follow. For example, southwest Florida experienced flooding in 1997 followed by drought in 1998 – 2000, which possibly explains a visible growth downturn in 2000. In 2001 precipitation rebounded (Verdi, Tomlinson, & Marella, 2006; also Figure 9) but in 2004 the Tampa Bay area experienced four hurricanes. There is a peak in growth for 2004 and 2005 followed by the second biggest single year dip across the century. 2002-2003 may have had generally high growth due to rebounding water and the decline in 2005 was likely a delayed reaction from the 2004 hurricanes. A particular storm may or may not show up in our sample because of the opposing growth responses to increased water and increased damage resulting from a severe weather event, but the consecutive storms seem to have decreased growth visibly.

Third, sampling scheme, data analysis, and the conclusions I draw are interconnected. Recalling the aggregate tree growth model, tree growth relies on several factors, including age, size, climate, and endogenous and exogenous disturbance, and some amount of error (Van Deusen, 1989). Dendrochronology relies on isolating a signal of interest through detrending methods and splines. Classically, these studies rely on targeting sensitive, old trees—trees most likely to be responding to the signal of interest. When I use representative or statistical sampling with the goal of elucidating any general patterns or assessing the impact of known disturbances, as I did in my study, it is possible that the results become much less clear due to the complexity
and number of factors impacting growth. Classical dendrochronological studies, by their procedure, typically do not use individual factors like size or age as growth predictors. There is growing interest in understanding individual tree differences in dendrochronology (Trouillier et al., 2018) instead of looking solely at population-level growth means. We are also learning how targeted selection compares with representative or statistical sampling schemes (Klesse et al., 2018). I suggest a modelling approach may provide more detailed information about our growth patterns given our sampling method, though this approach can certainly be done with targeted sampling schemes as well.

Dendrochronology has increasingly been used to address large-scale responses to climate change (Charney et al., 2016) and climate change is expected to change the spatial range or distribution of forest biomes (and their composition) through a multitude of factors (Bonan, 2008). Changing climate can elicit heterogeneous growth and survival by further altering the factors which influence tree growth. Climate change can influence disturbance rate, type, and frequency, indirectly impacting forests (Dale et al., 2000). Climate change is expected to bring about changes to hurricane frequency and intensity through increased ocean heating, though the details of these processes are not widely understood (Lugo, 2000).

Climate change is also impacting forest fires by increasing fire number, fire intensity, and area burned (Flannigan, Stocks, & Wotton, 2000). Climate change may impact forest fire ignition rates due to increased cloud-to-ground lightning resulting from increased global temperatures (Flannigan et al., 2000; Price & Rind, 1994). Lightning is an important ignition source for longleaf pine, and while lightning often strikes and kills the largest trees in the stand, it also produces gaps and natural forest fires, affecting the ecosystem as a whole (Outcalt, 2008) and changing growth responses of nearby trees. Longleaf pines depend on medium-frequency,
low-intensity fires to reduce hardwood growth, but increased fire frequency or severity may have
extreme results (Dale et al., 2000) and result in decreased growth. Further, increased temperature
can result in increased evaporation, increasing drought stress (Dale et al., 2001). I recognize the
important role dendrochronology will have in seeking out to understand how forests will respond
to climate change at different scales.

Growth in trees relies on many biotic and abiotic factors which can be recorded in tree-rings. These factors can produce demographic heterogeneity, which can have important
consequences for populations (Kendall, Nogeire, Fox, & Fujiwara, 2011; Pfister & Stevens,
2003; Vindenes et al., 2008; Zuidema, Brienen, During, & Güneralp, 2009). The standard
method of chronology-building seeks to minimize some variation while highlighting or targeting
a specific signal of interest but does not address heterogeneity. I suggest advancing the
dendrochronology field by incorporating the use of other models which can explicitly include
demographic variables like size or age, or environmental factors like competition, microsite qualities, or fire.

Citations

Package “lme4.” Retrieved from

understory species in pine flatwood and hardwood hammock ecosystems and implications
https://doi.org/10.1071/WF03075

Bolker, B. M. (2015). Linear and generalized linear mixed models. In G. A. Fox, S. Negrete-
Yankelevich, & V. J. Sosa (Eds.), Ecological Statistics: Contemporary theory and
application (pp. 309–334). Oxford University Press.


Forest Landscapes, 64(4), 369–400. https://doi.org/10.1111/mcn.12137


Schmidt, A. C. (2005). A vascular plant inventory and description of the twelve plant community types found in the University of South Florida ecological research area, Hillsborough County, Florida. *Graduate Theses and Dissertations*. https://doi.org/10.1203/PDR.0b013e31818702a2


Florida’s Hydrology and Landscape: Circular 1295, 34.


CHAPTER 2:
MIXED MODELS, DENDROECOLOGY, AND HETEROGENEITY

Introduction

Growth in organisms relies on many intrinsic and environmental factors, and the latter vary both spatially and temporally. Variation in growth rate may differ among individuals, as a result of age, genetics, or size. Genetic variation may introduce growth heterogeneity directly or indirectly; different genotypes may produce naturally different growth rates in an environment, or genetic variation may introduce growth heterogeneity indirectly by creating differential tolerance to pathogens, for example. External factors impacting growth may be biotic or abiotic and interact. Biotic factors that impact individual growth rates (or the degree to which growth rates change) include ‘malentities’ such as parasites, diseases, herbivory, and competition. For example, in response to disease, demographic heterogeneity may result in heterogeneous survival, which can increase the long term population growth rate through cohort selection by removing susceptible (or frail) individuals from the population first (Kendall, Nogeire, Fox, & Fujiwara, 2011). Broadly, these factors produce demographic heterogeneity, which can have important consequences for populations (Kendall et al., 2011; Pfister & Stevens, 2003; Vindenes et al., 2008; Zuidema, Brienen, During, & Güneralp, 2009). Abiotic factors like microsite and fire are also linked to growth and can interact with each other. For example, soil moisture can affect presence or absence of fire, as well as fire speed, movement, and residence time, with moister soils sometimes creating long-burning smoldering duff in otherwise cool fires. Further,
the natural heterogeneity of fire itself introduces growth rate variation by (e.g.) unevenly burning trees and other plants, which impacts the trees and alters microsite qualities.

Spatial and temporal heterogeneity impacts growth rate as well: consider topography and seasonality. Growth may vary temporally by season—and the effects of topography may be amplified or mitigated at different times. For example, areas on top of a hill may be the first areas to experience drought conditions during dry seasons, but areas of different elevations may experience similar moisture levels during wet seasons. While topography or season may be informative on their own, the interaction is important.

Environmental variables and tree growth are correlated. Classical dendrochronological approaches involve investigating tree-ring growth; the desired “signal” may be climate- or ecologically-based, while the variation present from all other sources is classified as “noise” (Fritts & Swetnam, 1989). Noise is produced by variation in factors such as precipitation, temperature, microsite, fire (and more) and compounded by the fact that trees are biological individuals, biochemically and physiologically distinct (Speer, 2010). Dendroclimatography is a common type of tree-ring analysis that is used to determine long-term regional patterns in growth in relation to climate. These analyses rely on the use of standardization to eliminate “noise” from the signal detected within a group of trees. I take a different approach: in this study I looked more deeply at the factors often considered “noise” in classical studies, by estimating parameters of interest, as well as variation among some factors. Dendrochronological studies typically look at the patterns of growth of a group, which I did, while I expanded on this by investigating individual growth rate. The sources of variation and the magnitude thereof can contribute to our knowledge of tree growth and how it changes, and ideally, inform management practices with respect to fire, conservation, and other issues.
To investigate the sources and magnitude of growth rate variation, I used generalized linear mixed effects models (GLMMs), which allow the incorporation of both fixed-effects terms and random-effects terms (Bates, 2010). In GLMMs, random effects are named not because they are chosen or sampled at random; random effects are categorical variables for which one wants to quantify among-level variation. Continuous predictors for the response variables are included in the model as fixed effects (Bolker, 2015). GLMMs describe the relationship between a response variable and some predictors, at least one of which is categorical, and represents experimental/observational units in the data set (Bates, 2010). GLMMs allow us to investigate the impact of tree size and age (continuous predictors—fixed effects) while also quantifying the among-individual or among-plot variance (categorical predictors—random effects). The model also accommodates our data structure, with multiple measurements per year and multiple years per individual.

While longleaf pine ecosystems previously dominated much of the Southeast, they have declined by approximately 95% (Frost, 1993) and are associated with approximately 230 rare plant and animal species (Hardin & White, 1989; Walker, 1993). Longleaf occurs in a wide range of ecosystems in the Southeast, from wet flatwoods to xeric sandhills, and to mid-elevation mountain slopes (Frost, 1993; Outcalt & Sheffield, 1996; Outcalt, 2000). For this study, I investigated the growth of longleaf pine (*Pinus palustris*) within the University of South Florida Forest Preserve (USFP or the Preserve), a 200 ha tract of land located in west central Florida.

The study site within the Preserve contains typical longleaf forest, with a xeric sandhill, fairly infertile soil, and fire-adapted vegetation (Outcalt & Sheffield, 1996). The species composition and over-/under-story structure are typical for sandhill environments. The vegetation is fire-adapted, and characterized by longleaf pine, wiregrass (*Aristida stricta*), and
scattered oaks (*Quercus laevis* and *Q. geminata*) (Myers & Ewel, 1990). Longleaf pine is dominant in the upper canopy; oaks comprise part of the midstory, but sometimes become co-dominant with longleaf pine in less-frequently burned areas. The understory is heavily wiregrass, with *Sabal palmetto* is scattered throughout (Schmidt, 2005). There is an elevation gradient from approximately 17 m asl to 11 m asl, and the environment shifts from xeric sandhill to mesic flatwoods at the edges of this elevation gradient due to depth of the sandy soils and location of the water table (Foster & Brooks, 2001). Further, the trees I used were within 10 experimental prescribed burn plots, which were burned multiple times from 1976-2001. The plots were assigned one of four levels of prescribed fire-return interval, approximating 1-, 2-, 5-, and 7-year fire frequencies. There were two replicates per fire frequency, as well as two plots that remained unburned (Figure 3). Generally, burns occurred on schedule, but for various reasons, some years no burns took place. Thus, I consider shorter treatments (1- and 2-year frequencies) as “more frequent” intervals and longer treatments (5- and 7-year frequencies) as “less frequent” intervals. Importantly, the trees I studied in the Preserve are nearing the southern-most range limit of the species; because they are growing near the edge of their ecological amplitude, they are good candidates for producing sensitive growth (Speer, 2010).

The factors which I focused on include fire, elevation, age, and size. I relied on individual growth rates to elucidate trends in the age-size relationship in longleaf pine within a population and facilitate the investigation of other factors as sources of heterogeneity. In longleaf pine, there are typically three general phases of growth; growth is highest when the tree is young (bolting), then the tree experiences a long decline in growth rate as it matures. Near senescence, growth nearly stops (Platt, Evans, & Rathbun, 1988). I predict that the population at the USF Forest
Preserve will show mainly the first two of these, because the trees in this population are generally too young to be undergoing senescence.

Variation in elevation is expected to produce heterogeneity in individual longleaf growth because elevation is a proxy for distance to the water table. Longleaf pine production decreases as depth to the water table increases (Ford, Mitchell, & Teskey, 2008). Cedro and Lamentowicz (2011), used tree-ring analysis to measure the responses of Scots pine to anthropogenic forces and found similar patterns; they found that tree-ring growth narrowed as distance to the water table increased, but they also found that partial root inundation suppressed growth. There are two potential patterns of growth which may occur in the Forest Preserve that may be influenced by elevation. First, based on water table levels alone, juveniles at lower elevations may experience increased growth rates as water is less likely to be a limiting factor. At low elevations, adults (with deeper roots), may show a sharper growth rate decline as they age due to roots reaching the water table and becoming partially or seasonally inundated. Seasonal root inundation has been shown to be negatively correlated with growth in Pinus elliottii (Foster & Brooks, 2001). In higher elevations, the inverse may be expected: juveniles struggle to add aboveground biomass if the roots are unable to reach the water table but large adults can continue growing at a faster rate. Water impacts the behavior of fire directly and indirectly. Fire will be patchier if there are moist spots, and soil moisture can impact fire residence time. For example, in one longleaf pine restoration, decreased duff moisture was correlated with increased pine mortality (Varner et al., 2007) likely due to duff consumption and root heating, and crown scorch was significant only in dry burns (Varner et al., 2009). Water can also indirectly impact fire behavior by changing the vegetation structure and composition, with some plants being more flammable or consumable than others (Behm, Duryea, Long, & Zipperer, 2004). Changing moisture conditions may also
impact the effects of competition, levels and variation of tissue damage, and rates of nutrient
cycling, and other scenarios which impact growth rate and increase growth rate heterogeneity.

The relationship between growth rate and fire is complex and dynamic depending on the
burn history of the site and tree size (Ryan, Peterson, & Reinhardt, 1988; Wade & Johansen,
1986). Tree growth is reduced in fire years, but longer fire intervals result in less growth during
fire years. When fire returns after a long interval, the period of depressed growth also lasts longer
(Ford, Minor, & Fox, 2010). In ecosystems maintained by frequent fire, mortality decreases with
increasing DBH (Ryan et al., 1988). Because mortality increases with percentage of crown
killed, and decreases as bark thickness increases, larger, older trees with higher crowns and
thicker bark experience less mortality (Ryan & Reinhardt, 1988; Wade & Johansen, 1986).
However, in restoration fires, large trees can experience more mortality because of increased
needle litter and high fire residence time (Kush, Meldahl, & Avery, 2004), or there can be similar
mortality among small and large trees (Varner, Kush, & Meldahl, 2000) forming a bimodal
response, with the intermediate trees more likely to survive. Overall, fire damage impacts growth
rate, tree mortality, competitive effects, and soil resource availability (McHugh & Kolb, 2003;
Powers, Palik, Bradford, Fraver, & Webster, 2010).

Given the general fire patterns above, I predict that trees that are most frequently burned
will exhibit the pattern shown by Ford et al., (2010), with fire years resulting in decreased
growth, but the least frequently burned trees may show a different fire response than frequently
burned trees (Kush et al., 2004). Whereas others have tended to investigate the impact of fire on
mortality, I focused on growth rate and its variability. I used either fire frequency (burn plot) or
recent fire history, as convenient, to understand how fire dynamics alter growth heterogeneity.
Overall, the objectives were (1) use individual growth rates to elucidate trends in the growth patterns of longleaf pine with a focus on fire, elevation, age and size, (2) use GLMMs to estimate the impacts of these factors on longleaf pine growth rates, and (3) identify sources of individual growth rate variation using GLMMs.

Materials and Methods

Study site

The University of South Florida Forest Preserve is a 200 ha tract of Florida vegetation located in west central Florida, within the city of Tampa in Hillsborough County, FL (27°857′N, 82°832′W). The Preserve varies in plant communities—lowland communities like floodplain forest, hydric hammock and wet flatwoods comprise 65% of the area, and upland plant communities like sandhill, mesic flatwoods, and xeric hammock comprise the remaining 35% (Schmidt, 2005). The study plots, nested within the Preserve, are primarily sandhill, with a progression to mesic flatwoods at the northern edges of the plots (Schmidt, 2005). The canopy is generally open and dominated by longleaf pines (*Pinus palustris*), typical for pine sandhill (Florida Natural Areas Inventory, 2010). Co-occurring vegetation includes a sub- to mid-canopy of deciduous oak species, and an herbaceous layer dominated by grasses and forbs (Schmidt 2005). There is an elevation gradient from approximately 17 m asl to 10 m asl (Figure 1) and the environment shifts from xeric sandhill to mesic flatwoods along this elevation gradient due to depth of the sandy soils and location of the water table. The soils at the highest elevations are primarily Candler fine sand and Pomello, resulting in an excessively fast-draining xeric sandhill with deep soil (Foster & Brooks, 2001).
Prescribed burns within the study site began in 1976, with four levels of prescribed fire-return interval, approximating 1-, 2-, 5-, and 7-year fire frequencies. There are two replicates per fire frequency, as well as two plots that have remained unburned (Figure 2).

**Sampling**

I sampled the longleaf pine population using a stratified random sample, stratified by size class, elevation, and burn plot. Size classes were 2.5 cm increments beginning at 10 cm dbh. I collected two samples from each size class, per burn plot. In the event that a burn plot only had one or no individuals within a certain size class, I collected one or zero samples accordingly. The beginning sample pool totaled 276 trees, with sampling occurring during 2013-2016. The samples were stratified by relative elevation within plot. Within each plot, I chose a tree at a low elevation and high elevation within each size class. This stratified random sampling method ensured representation of high and low elevation within a particular burn frequency.

I used an increment borer (Haglof, Sweden) to collect two samples from each tree at approximately breast height. I collected the samples at 90° angles (north-south and east-west) except when the land contour necessitated adjusting in order to properly sample compression and tension wood, inconsistencies in wood density that arise when trees grow on a slope. Each core was dried, mounted, and then I sanded each sample with a series of progressively finer sandpaper grits starting at 80 and working up to 400. I hand-sanded as needed.

Next, I removed any samples that were too damaged for measurement. Some of these cores were damaged due to heart rot, missing pieces, or multiple breaks in the sample upon removal from the tree. Commonly, both samples from a single tree exhibited the same damage, so if one core was damaged, I removed the tree from the sample. After I removed damaged
cores, I randomly removed some trees from any plots that had more than 25 trees in order to prevent overrepresentation; in this case, 1 to 7 trees were removed from all plots except for 1W and 5W, which began with fewer than 25 trees. Once cross-dating began, if I detected a problem with a core, it was corrected if possible, otherwise it (and the other core from that tree) was removed. The final sample size was 223 trees.

For all sampled trees, I measured diameter at breast height (DBH) and noted its location using GPS using a DeLorme Earthmate PN-40 GPS unit. Precision was typically 0.5m. I obtained GPS measurements in order to infer tree elevation using an elevational contour map.

**Method for measuring tree rings**

Because the sampling date for the trees was known, samples were first dated, then crossdated using the list method (Yamaguchi 1991), and later using the memorization method (Douglass, 1941; Speer, 2010). The list method is suitable for samples for which the date of the outermost ring in the sample is known, as opposed to “floating” wood—samples for which the dates for the innermost and outermost rings are unknown. The list method consists of identifying (by listing on paper) narrow rings by calendar date within a sample, then using the lists to determine which years’ rings are consistently narrow amongst samples. The memorization method builds on this, by allowing me to quickly check new cores for narrow rings which were indicated by the list method, ensuring that dating is still accurate (Speer, 2010). Annual growth was measured using a tree-ring measuring system which included a SZ-40 Olympus boom stereoscope (40x) using a unislide stage encoded to 0.001 mm (Velmex, Bloomfield, N.Y., USA) connected to a Metronics Quick-Chek. Measuring began at the bark-cambium interface, which was considered the most recent known year. The year nearest the pith was considered the first year of growth. Trees were crossdated statistically using COFECHA, which creates a master
chronology using all trees and compares each tree to this chronology individually (Grissino, 2001; Holmes, 1983). Because the samples were typically less than 100 years old, cores were analyzed using 22-year segments with an 11-year overlap. If a series did not crossdate well, it was corrected if possible. Samples which could not be reliably crossdated, or which exhibited low or negative correlations to the master were removed from the sample if issues could not be resolved. The samples which remained after crossdating in COFECHA typically had a series intercorrelation above 0.5 within each plot.

**Calculation of Growth Rate**

Generally, the calculation of growth rate (GR) relies on the logarithmic ratio of some measure of growth from one point to another. The growth equation

$$\text{GR} = \ln \left( \frac{x'}{x} \right)$$ (2)

utilizes size this year and size last year (represented by x’ and x, respectively). For this study, I used ring width measurements to estimate r, where r equals the radius of the tree in a given year. I then calculated the basal area for each year using \( \pi r^2 \). Then, the growth rate was calculated using equation 2. I used the natural log of this ratio in order to maintain results that are understandable as approximately proportional to original values (Gelman and Hill 2007).

**Model building**

To build GLMMs, I used the lme function (using optimizer “bobyqa”) in the lme4 package in R (Bates et al., 2018; R Core Team 2018). I built the models by starting with the simplest biologically-relevant model and then building in complexity, to make the problem of understanding the models easier (Gelman & Hill, 2007). As in traditional repeated measures ANOVA, GLMMs can assess between-subject and within-subject effects. In our case, I included
fixed effects like age or size which allowed us to investigate average effects on growth over time (“between subject”), and random effects like individual or plot allow us to analyze individual change in growth over time (“within subject”).

First, I began model building with a simple null model which contained ln(GR) as the dependent variable, year as a fixed effect, and year and individual as random effects. Then, I built three separate categories of models—age-based, size-based, or age-size interaction-based. All of the models tested included individual, in order to account for and estimate variation in growth among individuals. Year was included in the model as both a fixed (continuous) and random effect (factor), which is a standard approach for repeated measures analyses (Bolker, 2015). Including year in the model as a fixed effect is necessary; I have taken repeated measurements per individual, in the form of tree rings which allowed us to quantify growth changes from year to year. Including year as a random effect as well allowed us to quantify the variation among years (Gelman & Hill, 2007). Among-year variation is expected to be substantial due to aforementioned environmental factors like moisture and fire (and others), so it is necessary and informative to account for and measure this variation. Variation may occur on other timescales as well, but cannot be estimated under this sampling design.

Fire was incorporated as a fixed effect as burn frequency, cumulative fire number, or a categorical indication of fire per year. Burn frequency aligns with the intentional burn regime of different plots—burns occurred approximately every 1, 2, 5, 7 years, or never for unburned plots. Categorical indication of fire per year (“Fire Category”) describes year-by-year presence or absence of prescribed fire within a plot. Fire category levels range from 0 to 3 (Table 4), which allows us to investigate the impact of recent fire history on growth rate by modeling ln(GR). Other variables and biologically-relevant interactions were added and retained only if model fit
was improved. I included age, size, elevation, and various interactions as fixed effects and fire frequency, year, and individual as random effects. Throughout, year was converted to relative year (0-103 instead of 1911-2014). I studentized elevation, diameter, and age. Doing so facilitates model fitting (as predictors are on a common scale) as well as model interpretation. I observed a distinctly curvilinear relationship between elevation and ln(GR) (Figure 17; Figure 18). Because of this, I used polynomial regression for elevation, up to order 3.

Table 4: Detailed description of the fire category main effect.

<table>
<thead>
<tr>
<th>Fire Category</th>
<th>Burned in year x?</th>
<th>Burned in year x-1?</th>
</tr>
</thead>
<tbody>
<tr>
<td>FireCat0</td>
<td>NO</td>
<td>NO</td>
</tr>
<tr>
<td>FireCat1</td>
<td>YES</td>
<td>NO</td>
</tr>
<tr>
<td>FireCat2</td>
<td>NO</td>
<td>YES</td>
</tr>
<tr>
<td>FireCat3</td>
<td>YES</td>
<td>YES</td>
</tr>
</tbody>
</table>

For models using both size and age, I repeated the above process, with age, size, and year as fixed effects in the initial model.

Other factors, like plot and burn frequency were also included. To determine these effects, I added to the models either “Plot” (there are 10 plots) or “burn” (there are 5 intentional burn levels). Burn was added as a fixed effect because of the low number of levels (Gelman, 2005). Plot was tested as a fixed effect and as a random effect. Adding plot as a fixed effect would enable us to test differences between plots, but adding it as a random effect allows us to quantify variability among plots. Again, these factors were retained only if they improved model fit.
Using complicated mixed models requires a large sample size. Some models could be unable to converge, likely due to data insufficiency. While it is common for dendrochronology data sets to contain as few as 15 or 20 trees, a data set of that size would not be suitable for mixed models unless the trees were extremely old—which would further inhibit the researcher’s ability to ask questions about variables like fire. Care should be taken in reading model output to avoid convergence issues.

For each model category, the trees were broken into two timeframes. The groups were considered as either pre-burn (prior to 1976) or burned (1976 to present). While the formal burn regimes began in 1979, three plots were burned in 1976 (5E, 5W, and 7W).

GLMMs are likely less adept for asking questions when less is known about the history of the wood samples. For example, sample sets with a great deal of floating wood (samples for which beginning and end dates are unknown) would present specific dating challenges that would require more classical methods to cross-date correctly, particularly if trees are more complacent. This would precede the sole use of mixed models. Further, studying the explicit impact of fire would be more difficult if fire history is not known, as the investigator would need to rely entirely on fire scars to reconstruct fire history. The samples used in this study were all taken from live wood, so the most recent growth year is known, and all trees were within prescribed burn plots of a set frequency, though it is possible that not all trees experienced a burn in the same year.

**Model selection**

For standard GLMs, likelihood ratio (LR) tests could be a reasonable way to select the best model from pairs of possible models, but likelihood ratio tests are not recommended for
GLMMs unless the total sample size is large and there are many experimental blocks (Bolker et al., 2009), and neither of those qualities applies to the data. LR tests compare nested models, but an information-theoretic (IT) approach avoids the need for nested models (Richards, 2015).

Akaike’s Information Criterion (AIC) is the commonly used IT approach to model selection. AIC is an estimate of Kullback-Leibler (K-L) distance. The K-L distance indicates the difference between the true probability distribution and the model’s predicted distribution (Richards, 2009). Thus, a low K-L distance suggests a well-fit model, and a low AIC is associated with decreased K-L distance. However, it is important to point out that independently, AICs are uninformative; it is the difference between AICs for the same data set that is meaningful. Selecting the model based on only the lowest AIC is sensible only when there are no models with similar AICs (Bolker et al., 2009). If all of the AICs are similar, other methods of model selection should be considered as well before choosing the best model. Because models with different fixed effects cannot be compared using restricted maximum likelihood (REML) (Bolker, 2015) models were first evaluated using maximum likelihood (ML) to compare models, and re-evaluated using REML to obtain final parameter estimates. ML is unbiased for the fixed effects, which allows for the comparison of models with differing fixed effects, and re-evaluation using REML provides unbiased estimates of the variance components.

After comparing models to determine which had the lowest AICs, I plotted the data residuals against the fitted data values. The best models show an unbiased, homoscedastic pattern of residuals representing constant variance among all points (Dobson, 2001). Heteroscedastic residuals may suggest that models are lacking a relevant interaction between effects and that the model should be respecified, or that I have violated an assumption of the model.
Visualization of complex model interactions was facilitated using the ‘effects’ package (J. Fox et al., 2018). The effects package allows the user to isolate particular predictors and graphically display their values. Because our models are fairly complex, with high-order interactions, this package allows us to isolate one specific interaction and view its overall effect over time. Graphing the interactions using the effects package is most useful for two- or three-way interactions that I can interpret biologically, as well.

Results

Ring widths and general growth patterns

Relative growth was greatest when the trees are youngest, and declined as they age (Figure 11). The GR-age relationship is curved somewhat due to the generally young age of the sample, but it appeared the relationship may have been beginning to stabilize in the oldest trees. The sample also showed declining growth rate as size increased, with the largest trees showing dramatically decreased growth rate (Figure 12). Variance in diameter increased in approximately the first 25 years of tree growth before stabilizing somewhat. The relationship between diameter variance and age became less predictable starting around 75 years of age, but this was likely impacted by sample depth (Figure 13).
Figure 11: Log growth rate (GR) compared to age (scaled and centered). Growth rate declines quickly when a tree is young, then declines more slowly as the tree ages. The range of age represented (-1.33 to 3.70) on the graph represents 1-103 years. A centered age of 1 indicates a tree age of 48. Color gradient represents calendar year of the measured ring.

Figure 12: Log(GR) declines as trees grow larger. An adjusted diameter of -2 correlates to approximately 13 cm diameter. Color gradient represents calendar year of the measured ring.
Figure 13: Comparison of diameter variance as a function of age. Coefficient of variation (CV) was calculated by dividing the standard deviation of diameter at age x by the mean diameter, which prevents increasing tree size from inflating variation. Dot areas are proportional to sample size used to calculate CV; the largest sample has 195 values and the smallest has 5 values. Trees limited to <88 years to keep the number of trees per age no less than 5.

Models

For both age- and size-based approaches, the full models (i.e., models including all the predictors and their interactions) exhibited the lowest AIC and the highest $\Delta H_0$, an indicator of improvement from the null model (Table 5; Table 6). For both model types (Figure 14; Figure 15), the best-fitting pre-burn models were similar in AIC, varying by less than $\Delta AIC_{10}$, though the full model still had the most support (Table 5; Table 6). Post-burn the potential models were more varied, with more support for the full model. Age-based models were generally stronger for both the pre-burn period and the burned period, as indicated by AIC.
Age based—best models

Figure 14: Concept diagram for age-based models. Rectangles represent fixed effects, ovals represent random effects, and the dependent variable is shown inside a circle. Bolded lines indicate main effects. Dashed lines and thin solid lines indicate interactions created by combining main effects. For clarity, only first-order interactions shown.

Table 5: Age-based models. Notation: Fixed and random effects: Age (A), Year (Y), Elevation (E), Individual (I). Interactions indicated by ‘*’. Non-interacting fixed effects indicated by ‘+’. AIC: Akaike’s information criterion. \( \Delta_i \): The AIC difference between the current model and the model with the lowest AIC. \( \Delta H_0 \): The AIC difference between the current model and the null hypothesis.

<table>
<thead>
<tr>
<th></th>
<th>Model</th>
<th>Fixed</th>
<th>Random</th>
<th>Df</th>
<th>AIC</th>
<th>( \Delta_i )</th>
<th>( \Delta H_0 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-burn</td>
<td>3</td>
<td>A*Y</td>
<td>Y, I</td>
<td>7</td>
<td>3793.19</td>
<td>3.2</td>
<td>-758.5</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>A*Y+E</td>
<td>Y, I</td>
<td>8</td>
<td>3792.39</td>
<td>2.4</td>
<td>-759.3</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>A<em>Y</em>E</td>
<td>Y, I</td>
<td>11</td>
<td>3789.95</td>
<td>0</td>
<td>-761.8</td>
</tr>
<tr>
<td>Post-burn</td>
<td>3</td>
<td>A*Y</td>
<td>Y, I</td>
<td>7</td>
<td>7009.38</td>
<td>123.6</td>
<td>-2182.5</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>A*Y+E</td>
<td>Y, I</td>
<td>8</td>
<td>7010.54</td>
<td>124.8</td>
<td>-2181.4</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>A<em>Y</em>E</td>
<td>Y, I</td>
<td>11</td>
<td>6885.75</td>
<td>0</td>
<td>-2306.2</td>
</tr>
</tbody>
</table>
Size based—best models

![Concept diagram for size-based models. Rectangles represent fixed effects, ovals represent random effects, and the dependent variable is shown inside a circle. Bolded lines indicate main effects. Dashed lines and thin solid lines indicate interactions created by combining main effects. For clarity, only first-order interactions shown.](image)

**Figure 15:** Concept diagram for size-based models. Rectangles represent fixed effects, ovals represent random effects, and the dependent variable is shown inside a circle. Bolded lines indicate main effects. Dashed lines and thin solid lines indicate interactions created by combining main effects. For clarity, only first-order interactions shown.

**Table 6: Size-based models.** Notation: Fixed and random effects: Size (S), Year (Y), Elevation (E), Individual (I). Interactions indicated by ‘*’. Non-interacting fixed effects indicated by ‘+’. AIC: Akaike’s information criterion. Δ: The AIC difference between the current model and the model with the lowest AIC. ΔH₀: The AIC difference between the current model and the null hypothesis.

<table>
<thead>
<tr>
<th></th>
<th>Model</th>
<th>Fixed</th>
<th>Random</th>
<th>Df</th>
<th>AIC</th>
<th>Δᵢ</th>
<th>ΔH₀</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-burn</td>
<td>3</td>
<td>S×Y</td>
<td>Y, I</td>
<td>7</td>
<td>3848.927</td>
<td>4.1</td>
<td>-702.8</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>S×Y+E</td>
<td>Y, I</td>
<td>8</td>
<td>3850.916</td>
<td>6.1</td>
<td>-700.8</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>S×Y×E</td>
<td>Y, I</td>
<td>11</td>
<td>3844.854</td>
<td>0</td>
<td>-706.9</td>
</tr>
<tr>
<td>Post-burn</td>
<td>1</td>
<td>S+Y</td>
<td>Y, I</td>
<td>6</td>
<td>7350.852</td>
<td>35.7</td>
<td>-1841.1</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>S+Y</td>
<td>Y, L, E</td>
<td>7</td>
<td>7352.852</td>
<td>37.7</td>
<td>-1839.1</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>S×Y</td>
<td>Y, I</td>
<td>7</td>
<td>7349.353</td>
<td>34.2</td>
<td>-1842.6</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>S+Y+E</td>
<td>Y, I</td>
<td>7</td>
<td>7352.726</td>
<td>37.6</td>
<td>-1839.2</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>S×Y+E</td>
<td>Y, I</td>
<td>8</td>
<td>7351.257</td>
<td>36.1</td>
<td>-1840.7</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>S×Y×E</td>
<td>Y, I</td>
<td>11</td>
<td>7315.172</td>
<td>0</td>
<td>-1876.7</td>
</tr>
</tbody>
</table>

Size- and age- based models

Models including only size (S×Y×E) or only age (A×Y×E) resulted in much higher AICs (Δᵢ 472.9 - 1007.5) than the best-fitting models including both size and age (S×Y×A×E).
particularly in the pre-burn period (Table 5; Table 6; Table 7). I identified a unique curvilinear response pattern for elevation (Figure 17; Figure 18) that informed the decision to experimentally add polynomials for elevation into the model. Including the linear, quadratic, and cubic terms for elevation helped improve the model ($S\times Y\times A\times (E^1+E^2+E^3)$), although models including only the linear term still proved better than the best size- or age-only models (Table 8). The pre-burn model AIC decreased from 3844.9 ($S\times Y\times E$) or 3790.0 ($A\times Y\times E$) to 3170.2 with the inclusion of size and age, as well as the elevation polynomials ($S\times Y\times A\times (E^1+E^2+E^3)$). The AIC for the burned period model including size, age, and elevation polynomials ($S\times Y\times A\times (E^1+E^2+E^3)$) was 6289.8, an improvement upon prior model fits with AIC of 7315.2 ($S\times Y\times E$) and 6885.6 ($S\times Y\times E$).

Figure 16: Concept diagram for models including first-order interactions, only. Rectangles represent fixed effects, ovals represent random effects, and the dependent variable is shown inside a circle. For clarity, elevation polynomials have been left off. Bolded lines indicate main effects. Dashed lines and thin solid lines indicate interactions created by combining main effects.
Figure 17: Coefficients for each predictor against the response; pre-burn. Blue line indicates the Loess-smoothed response variable, red indicates a strictly-linear model for each single predictor, and the red-shaded area represents 95% CIs.

Figure 18: Coefficients for each predictor against the response; burned period. Blue line indicates the Loess-smoothed response variable, red indicates a strictly-linear model for each single predictor, and the red-shaded area represents 95% CIs.
Table 7: Size- and age-based models. Notation: Fixed and random effects: Size (S), Age (A), Year (Y), Elevation (E), Individual (I), Plot (P), Burn Frequency (B). Interactions indicated by ‘*’. Non-interacting fixed effects indicated by ‘+’. When slopes and intercepts vary for random effects, ‘|’. Nesting indicated by ‘/’. AIC: Akaike’s information criterion. $\Delta_i$: The AIC difference between the current model and the model with the lowest AIC. Superscripts represent linear, quadratic, or cubic transformations.

<table>
<thead>
<tr>
<th>Model</th>
<th>Fixed</th>
<th>Random</th>
<th>Df</th>
<th>AIC</th>
<th>$\Delta_i$</th>
<th>$\Delta H_o$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-burn</td>
<td>7</td>
<td>S<em>Y</em>A*E+B</td>
<td>Y, I</td>
<td>23</td>
<td>3211.6</td>
<td>41.3</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>S<em>Y</em>A*E+P</td>
<td>Y, I</td>
<td>28</td>
<td>3209.1</td>
<td>38.8</td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>S<em>Y</em>A*E</td>
<td>P, Y, I</td>
<td>73</td>
<td>3205.7</td>
<td>35.5</td>
</tr>
<tr>
<td></td>
<td>12</td>
<td>S<em>Y</em>A*E</td>
<td>P/I, P/Y</td>
<td>74</td>
<td>3207.2</td>
<td>36.9</td>
</tr>
<tr>
<td>Post-burn</td>
<td>9</td>
<td>S<em>Y</em>A*(E^1+E^2+E^3)</td>
<td>Y, I</td>
<td>35</td>
<td>3170.2</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>S<em>Y</em>A*E</td>
<td>P, Y, I</td>
<td>73</td>
<td>6412.8</td>
<td>123.1</td>
</tr>
<tr>
<td></td>
<td>12</td>
<td>S<em>Y</em>A*(E^1+E^2+E^3)</td>
<td>P, Y, I</td>
<td>81</td>
<td>6307.7</td>
<td>17.9</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>S<em>Y</em>A*(E^1+E^2+E^3)</td>
<td>Y, I</td>
<td>35</td>
<td>6289.8</td>
<td>0</td>
</tr>
</tbody>
</table>

Table 8: Comparison of best-fitting models which are size-only, age-only, or include size and age. Notation: Fixed and random effects: Size (S), Year (Y), Elevation (E), Individual (I), Plot (P). Interactions indicated by ‘*’. Non-interacting fixed effects indicated by ‘+’. AIC: Akaike’s information criterion. $\Delta_i$: The AIC difference between the current model and the model with the lowest AIC. $\Delta H_o$: The AIC difference between the current model and the null hypothesis.

**Pre-burn period**

<table>
<thead>
<tr>
<th>Fixed</th>
<th>Random</th>
<th>Df</th>
<th>AIC</th>
<th>$\Delta_i$</th>
<th>$\Delta H_o$</th>
</tr>
</thead>
<tbody>
<tr>
<td>A<em>Y</em>E</td>
<td>Y, I</td>
<td>11</td>
<td>3789.953</td>
<td>619.7032</td>
<td>-761.8</td>
</tr>
<tr>
<td>S<em>Y</em>E</td>
<td>Y, I</td>
<td>11</td>
<td>3844.854</td>
<td>674.6042</td>
<td>-706.9</td>
</tr>
<tr>
<td>S<em>Y</em>A*E</td>
<td>P, Y, I</td>
<td>73</td>
<td>3205.735</td>
<td>35.48581</td>
<td>-1345.99</td>
</tr>
<tr>
<td>S<em>Y</em>A*E</td>
<td>P, I, P/Y</td>
<td>74</td>
<td>3207.198</td>
<td>36.94862</td>
<td>-1344.53</td>
</tr>
<tr>
<td>S<em>Y</em>A*(E^1+E^2+E^3)</td>
<td>Y, I</td>
<td>35</td>
<td>3170.25</td>
<td>0</td>
<td>-1381.48</td>
</tr>
</tbody>
</table>

**Burned period**

<table>
<thead>
<tr>
<th>Fixed</th>
<th>Random</th>
<th>Df</th>
<th>AIC</th>
<th>$\Delta_i$</th>
<th>$\Delta H_o$</th>
</tr>
</thead>
<tbody>
<tr>
<td>A<em>Y</em>E</td>
<td>Y, I</td>
<td>11</td>
<td>6885.755</td>
<td>595.9754</td>
<td>-2306.2</td>
</tr>
<tr>
<td>S<em>Y</em>E</td>
<td>Y, I</td>
<td>11</td>
<td>7315.172</td>
<td>1025.392</td>
<td>-1876.7</td>
</tr>
<tr>
<td>S<em>Y</em>A*E</td>
<td>P, Y, I</td>
<td>73</td>
<td>6412.846</td>
<td>123.0663</td>
<td>-2779.06</td>
</tr>
<tr>
<td>S<em>Y</em>A*(E^1+E^2)</td>
<td>P, Y, I</td>
<td>81</td>
<td>6307.669</td>
<td>17.88941</td>
<td>-2884.24</td>
</tr>
<tr>
<td>S<em>Y</em>A*(E^1+E^2+E^3)</td>
<td>Y, I</td>
<td>35</td>
<td>6289.779</td>
<td>0</td>
<td>-2902.13</td>
</tr>
</tbody>
</table>
Effects of fire

The addition of fire to the models continued to improve their fits, decreasing AIC from 6289.8 to 6175.4 (Table 9). The term for fire in these models was fire category (FireCat), which indicated recent burn history, shown in Table 4.

Table 9: Age-size models including fire. Notation: Fixed and random effects: Size(S), Age (A), Year (Y), Elevation (E), Individual (I), Plot (P), Fire (F). Interactions indicated by ‘*’. Non-interacting fixed effects indicated by ‘+’. When slopes and intercepts vary for random effects, ‘|’. AIC: Akaike’s information criterion. Δi: The AIC difference between the current model and the model with the lowest AIC. Note: No pre-burn model shown, as fire was not added to that model. Previously best-fitting model AIC: 6289.8

<table>
<thead>
<tr>
<th>Model</th>
<th>Fixed</th>
<th>Random</th>
<th>Df</th>
<th>AIC</th>
<th>Δi</th>
<th>ΔHi</th>
</tr>
</thead>
<tbody>
<tr>
<td>Burned period</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>S<em>Y</em>A*E+F</td>
<td>Y, 1</td>
<td>22</td>
<td>6449.8</td>
<td>274.4</td>
<td>-2742.1</td>
</tr>
<tr>
<td>2</td>
<td>S<em>Y</em>A*E+F</td>
<td>Y, 1</td>
<td>67</td>
<td>6387.7</td>
<td>212.3</td>
<td>-2804.2</td>
</tr>
<tr>
<td>3</td>
<td>S<em>Y</em>A*E+F</td>
<td>P</td>
<td>Y, I</td>
<td>121</td>
<td>6350.6</td>
<td>175.2</td>
</tr>
<tr>
<td>4</td>
<td>S<em>Y</em>A*(E-E^2)*F</td>
<td>P</td>
<td>Y, I</td>
<td>153</td>
<td>6258.5</td>
<td>83.1</td>
</tr>
<tr>
<td>5</td>
<td>S<em>Y</em>A*(E^1+E^2+E^3)*F</td>
<td>Y, 1</td>
<td>131</td>
<td>6211.6</td>
<td>36.2</td>
<td>-2980.3</td>
</tr>
</tbody>
</table>

Figure 19: Concept diagram for models including fire. Bolded lines indicate main effects. Dashed lines and thin solid lines indicate interactions created by combining main effects. For clarity, elevation polynomials and levels for Fire Category have been left off
Figure 20: Concept diagram for models including first-order interactions, only. For clarity, elevation polynomials and levels for Fire Category have been left off. Bolded lines indicate main effects. Dashed lines and thin solid lines indicate interactions created by combining main effects.

Fixed effects and interactions:

Table 10: Select main effects and interactions, pre-burn and burned periods. Relative year (YearR). “Poly(Elevation,3)2 and Poly(Elevation,3)3” denote quadratic and cubic elevation polynomials, respectively. Age, diameter, and elevation were studentized

<table>
<thead>
<tr>
<th></th>
<th>Pre-burn model</th>
<th>Std. Error</th>
<th>t value</th>
<th>Post-burn model</th>
<th>Std. Error</th>
<th>t value</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Intercept)</td>
<td>-2.762</td>
<td>0.256</td>
<td>-10.801</td>
<td>-2.647</td>
<td>0.271</td>
<td>-9.777</td>
</tr>
<tr>
<td>Diameter</td>
<td>4.011</td>
<td>0.217</td>
<td>18.506</td>
<td>2.594</td>
<td>0.238</td>
<td>10.879</td>
</tr>
<tr>
<td>YearR</td>
<td>0.012</td>
<td>0.005</td>
<td>2.490</td>
<td>-0.004</td>
<td>0.003</td>
<td>-1.226</td>
</tr>
<tr>
<td>Age</td>
<td>-2.433</td>
<td>0.232</td>
<td>-10.467</td>
<td>-3.082</td>
<td>0.178</td>
<td>-17.285</td>
</tr>
<tr>
<td>poly(Elevation, 3)1</td>
<td>-23.387</td>
<td>8.498</td>
<td>-2.752</td>
<td>19.756</td>
<td>11.249</td>
<td>1.756</td>
</tr>
<tr>
<td>poly(Elevation, 3)2</td>
<td>32.940</td>
<td>8.325</td>
<td>3.957</td>
<td>54.410</td>
<td>12.513</td>
<td>4.348</td>
</tr>
<tr>
<td>poly(Elevation, 3)3</td>
<td>-18.134</td>
<td>8.759</td>
<td>-2.070</td>
<td>16.051</td>
<td>12.332</td>
<td>1.281</td>
</tr>
<tr>
<td>Diameter:YearR</td>
<td>-0.081</td>
<td>0.004</td>
<td>-20.365</td>
<td>-0.028</td>
<td>0.002</td>
<td>-11.397</td>
</tr>
<tr>
<td>Diameter:Age</td>
<td>2.810</td>
<td>0.144</td>
<td>19.504</td>
<td>1.126</td>
<td>0.133</td>
<td>8.454</td>
</tr>
<tr>
<td>YearR:Age</td>
<td>0.034</td>
<td>0.004</td>
<td>8.365</td>
<td>0.020</td>
<td>0.002</td>
<td>10.841</td>
</tr>
<tr>
<td>Diameter:poly(Elevation, 3)2</td>
<td>10.792</td>
<td>10.194</td>
<td>1.059</td>
<td>-28.312</td>
<td>15.005</td>
<td>-1.887</td>
</tr>
<tr>
<td>Diameter:poly(Elevation, 3)3</td>
<td>3.122</td>
<td>9.039</td>
<td>0.345</td>
<td>-51.978</td>
<td>15.093</td>
<td>-3.444</td>
</tr>
<tr>
<td>YearR:poly(Elevation, 3)1</td>
<td>0.455</td>
<td>0.148</td>
<td>3.072</td>
<td>-0.030</td>
<td>0.121</td>
<td>1.677</td>
</tr>
<tr>
<td>YearR:poly(Elevation, 3)2</td>
<td>-0.580</td>
<td>0.151</td>
<td>-3.832</td>
<td>-0.438</td>
<td>0.132</td>
<td>-3.310</td>
</tr>
<tr>
<td>YearR:poly(Elevation, 3)3</td>
<td>0.394</td>
<td>0.162</td>
<td>2.435</td>
<td>-0.116</td>
<td>0.132</td>
<td>-0.884</td>
</tr>
<tr>
<td>Age:poly(Elevation, 3)1</td>
<td>-22.934</td>
<td>9.549</td>
<td>-2.402</td>
<td>27.728</td>
<td>10.841</td>
<td>2.558</td>
</tr>
<tr>
<td>Age:poly(Elevation, 3)2</td>
<td>24.690</td>
<td>10.226</td>
<td>2.414</td>
<td>38.107</td>
<td>12.422</td>
<td>3.068</td>
</tr>
<tr>
<td>Age:poly(Elevation, 3)3</td>
<td>-18.858</td>
<td>11.222</td>
<td>-1.680</td>
<td>59.953</td>
<td>12.556</td>
<td>4.775</td>
</tr>
<tr>
<td>Diameter:YearR:Age</td>
<td>-0.049</td>
<td>0.003</td>
<td>-18.705</td>
<td>-0.007</td>
<td>0.001</td>
<td>-5.031</td>
</tr>
<tr>
<td>Diameter:YearR:poly(Elevation, 3)1</td>
<td>0.166</td>
<td>0.148</td>
<td>1.125</td>
<td>0.347</td>
<td>0.148</td>
<td>2.336</td>
</tr>
<tr>
<td>Diameter:YearR:poly(Elevation, 3)2</td>
<td>0.049</td>
<td>0.172</td>
<td>0.282</td>
<td>-0.060</td>
<td>0.154</td>
<td>-0.388</td>
</tr>
<tr>
<td>Diameter:YearR:poly(Elevation, 3)3</td>
<td>-0.127</td>
<td>0.159</td>
<td>-0.799</td>
<td>0.531</td>
<td>0.155</td>
<td>3.433</td>
</tr>
<tr>
<td>Diameter:Age:poly(Elevation, 3)1</td>
<td>-10.025</td>
<td>5.765</td>
<td>-1.739</td>
<td>4.756</td>
<td>9.027</td>
<td>0.527</td>
</tr>
<tr>
<td>Diameter:Age:poly(Elevation, 3)2</td>
<td>7.288</td>
<td>6.447</td>
<td>1.130</td>
<td>-20.914</td>
<td>9.118</td>
<td>-2.294</td>
</tr>
<tr>
<td>Diameter:Age:poly(Elevation, 3)3</td>
<td>0.497</td>
<td>5.693</td>
<td>0.087</td>
<td>-13.834</td>
<td>9.257</td>
<td>-1.494</td>
</tr>
</tbody>
</table>
Figure 21: Parameter estimates for the best-fitting model for the pre-burn period, shown with confidence intervals. Relative year is shown as “YearR” and “Poly(Elevation,3)1”, “Poly(Elevation,3)2”, Poly(Elevation,3)3 denote linear, quadratic, and cubic elevation polynomials, respectively.
**Diameter×Age**

Pre-burn, the interaction of diameter and age indicated that at higher age, growth increased with size. Young, large trees grew more slowly than young small trees. The relationship between the diameter×age interaction and growth rate varied little when trees were young. The relationship was most variable when trees are old but small (Figure 23). For the burned period, the pattern was largely the same, but the impact of the diameter×age interaction on growth rate was much stronger (Figure 24). During this time, old small-diameter trees grew
slowly, but holding age steady while tree diameter increased resulted in a much faster growth rate. These relationships were also slightly less variable than the pre-burn data.

**Figure 23**: Pre-burn period: Average effect of diameter×age interaction over time. Diameter and age were studentized. Shaded area represents 95% confidence intervals throughout interaction plots.

**Figure 24**: Burned period: Average effect of diameter×age interaction over time. Diameter and age were studentized. Shaded area represents 95% confidence intervals throughout interaction plots.
**AgElevation**

Pre-fire, the age×elevation interaction had a slight negative effect on GR. Generally, large trees grew slower at any given elevation. The key change is the variation—older trees at high OR low elevations were most variable in growth rate (Figure 25). The pattern of variation was preserved during the burned period, but I also saw that high elevation/high age resulted in higher GR, and low elevation/high age resulted in moderated growth compared to intermediate elevations (Figure 26).

![Figure 25: Pre-burn period: Average effect of age×elevation interaction over time. Age and elevation were studentized. Shaded area represents 95% confidence intervals throughout interaction plots.](image)

At the youngest ages, growth was not impacted by diameter or elevation. For the ages that were relatively central, I started to see a pattern; at the lowest elevations, small trees grew more slowly and more variably. At the highest elevations, the smallest trees grew faster, but there was also variation in this relationship. This pattern continued and became most pronounced at the highest ages. There was no notable change between pre-burn and burned period models (Figure 27; Figure 28).
Figure 26: Burned period: Average effect of age x elevation interaction over time. Age and elevation were studentized. Note: change in x-axis scale from previous figure. Shaded area represents 95% confidence intervals throughout interaction plots.

Figure 27: Interaction plot showing the pre-burn three-way interaction between tree diameter, age, and elevation, all of which were studentized. Small, low, old trees grow slowly, and this pattern changes as the trees get larger. Old, high, small trees grow quickly, but as they get larger they grow more slowly. The relationships here are most varied when trees are small and at elevational extremes. Shaded area represents 95% confidence intervals throughout interaction plots.
Figure 28: Interaction plot showing the burned period three-way interaction between tree diameter, age, and elevation, all of which were studentized Old, small trees grow slowly, with the exception of high, old, small trees, which grow fastest. The diameterxagexelevation relationship varies most when trees are old and at elevational extremes. Shaded area represents 95% confidence intervals throughout interaction plots.

Pre-burn growth rate was lowest for small, low elevation trees, with an increase in growth rate as size increased. In the intermediate elevations, growth had a very shallow slope, indicating that trees grew about the same independent of size. At the highest elevations, larger trees grew slightly faster. Variation in these relationships was highest for small trees at the highest and lowest elevations. During the burned period, at lowest and highest elevations, small trees grew fastest. (Figure 29, Figure 30). Overall, the fastest growing trees were small trees at high elevation, but growth rate declined quickly as size increases. In intermediate elevations, large trees had increased growth rates.

Fire reduced ln(GR), regardless of recent fire history (Figure 31). The largest parameter estimate was for fire category 2 (-1.07; SE 0.41), but fire category 3 had the largest standard error (-0.93 SE 0.82), at least double the error for the other two burn categories. This high value for error indicated that consecutive burns introduced the most variation in growth rate. However,
the overall parameter estimates for fire category were small but variable; in some cases (FireCat1/burned this year and FireCat3/burned this year and last year), recent burn history may increase growth rate by a small amount. The model specifications were such that FireCat0 (no burns in the current year or the year prior) is set to zero.

Figure 29: Plot showing the interaction of diameter and elevation, both studentized, pre-burn period. Shaded area represents 95% confidence intervals throughout interaction plots.

Figure 30: Plot showing the interaction of diameter and elevation, both studentized, burned period. Shaded area represents 95% confidence intervals throughout interaction plots.
Growth was slightly negative in lowest elevations and slightly positive in higher elevations for FireCat0 (Figure 32). The relationship also had very little variation, which is likely a result of our sampling method. Because prescribed burns only occurred for 25 years, there are far more instances in which trees experienced zero fire; as such, fire category 0 helps to serve as a baseline for comparing the other three fire categories. Fire category and elevation interact such that trees at higher elevations always experience increased growth compared to those at lower elevations. That said, trees experiencing back-to-back burns (FireCat3) grew fastest at high elevations, even faster than trees experiencing no burns (Figure 32). The changing slopes of the interactions indicate elevations lower than the mean experienced slight increases in growth. The average effects of elevation for growth rate in fire categories 1 and 2 were very similar.

Figure 31: Parameter estimates for fire category with standard error. FireCat1: Burned this year; FireCat2: Burned last year; FireCat3: Burned this year and last year.
Figure 32: The interaction between fire category and studentized elevation. FireCat 0: No burns this year or last year. FireCat1: Burn this year. FireCat2: Burn last year. FireCat3: Burn this year and last year. Shaded area represents 95% confidence intervals throughout interaction plots.

Random effects

Figure 33: Random effects (variance) for the pre-burn and burned periods.
Variance among individuals in the burned period was about three times as large as in the years pre-burn. The variance for year was considerably smaller than individual variance, but increased by a third from pre-burn to the burned period. Residual variance declined during the burned period.

These random effects estimates demonstrate that some individuals tend to have greater GRs than others, across time. Some individuals performed more consistently than others, but overall, best linear unbiased predictors (BLUPs) indicate that pre-burn individual growth falls within wide prediction intervals (PIs) (Figure 34). Not surprisingly, some years are better than others for growth. Random effects for Year for the pre-burn models were strongly negatively impacted by small sample size (N), with years prior to approximately 1935 showing very wide PIs (Figure 35). The values for the random effect of year seem to cluster near 0 pre-burn, indicating the effect of year is weaker than it is during burned period years (Figure 35; Figure 37). Compared to the pre-burn period, during the burned period the effect of both year and individual became less variable (as indicated by smaller PIs) (Figure 34; Figure 35; Figure 36; Figure 37). Post-burn, some years were clearly stronger for growth than others (Figure 37). Years 1999 and 2000 were the ‘worst’ years for tree growth. Good years and bad years tended to be grouped into multiples, with 2-5 consecutive years showing consistently positive or negative BLUPs.
Figure 34: Individual Random effects, pre-burn. Each point indicates one individual. Red indicates negative BLUP; gray indicates positive BLUP.
Figure 35: Random effects for year, pre-burn period. Year is shown on the y-axis. Red indicates negative BLUP; gray indicates positive BLUP.
Figure 36: Random effects for individual, burned period. Each point represents one individual. Red indicates negative BLUP; gray indicates positive BLUP.
Figure 37: Random effects of year, burned period. Year is shown on the y-axis. Red indicates negative BLUP; gray indicates positive BLUP.
Discussion

This study demonstrates the interaction of age, size, and certain ecological effects on growth rate. I found that longleaf pine growth rate is best predicted using age and size together. The relationship between diameter and elevation has varied and complicated impacts on growth rate. Growth is highest at the elevational extremes within the study site, especially during periods of regular fire, with smaller trees demonstrating higher growth rates than large trees. Elevation interacts with age to decrease the growth rate for oldest trees at high or low elevation but while also increasing growth rate variation substantially. All levels of recent fire history impact growth rate negatively, with back-to-back burns resulting in extremely varied growth rates. Within the three fire categories examined here, growth is slowest the year after a burn, but burns within the last two years all resulted in decreased growth relative to no burns in the current or prior year. Using age or size alone in the model structure may be sufficient, but using both together improves the model substantially, as evidenced by a large decrease in AIC. This decrease in AIC indicates that using size and age together is better for predicting growth rate than either alone, and that size, age, and their interaction have important impacts on tree growth. Because the variation in the age-size relationship in longleaf pine is well-documented (Platt et al., 1988) and further, tree size impacts the outcome of fire (Kush et al., 2004; Ryan et al., 1988; Varner, Kush, & Meldahl, 2000), this research demonstrates that understanding longleaf growth rate requires using both age and size. The importance of using both size and age is congruent with prior and current research (Caswell, de Vries, Hartemink, Roth, & van Daalen, 2018; Chu & Adler, 2014; Coleman, McConnaughay, & Ackerly, 1994; Platt et al., 1988) that also emphasize the need for both when investigating growth. Age-size effects are linked to population growth mortality,
evolution, and span studies involving animals, plants, and theoretical populations (Caswell et al., 2018; Clutton-Brock & Sheldon, 2010; Vindenes et al., 2008; Zuidema et al., 2009 and others).

Understanding the way size and age interact enhances the possibilities for dendrochronological studies. Because dendrochronological studies usually rely on sampling the oldest trees in order to encompass a long span of time, our work contributes two things. First, it allows flexibility for researchers to include younger trees or systematic sampling methods, since a model can be built which addresses age or other factors without dismissing them as “noise”. Second, using a model-based approach can help answer questions that go beyond a single, overarching signal of interest.

**Elevation**

The elevational gradient in the sampled plots is small (approximately 6 meters) compared to typical ecological discussion of elevation. However, the topography of Florida is fairly flat which allows small changes to have increased impacts in some cases. In other Florida species, elevation can serve as a good proxy for depth to the water table, impacting drought sensitivity or plant distribution over small elevational changes (Foster, 2014). This study found that the physiological function of sand live oak changes over an elevational gradient of 1.2 meters. Further, the distribution of three co-occurring Florida scrub oak species changed across this gradient; specifically, increased elevation was associated with increased oak cover. Elevation may be impacting moisture by proxy and therefore burn conditions, and vegetation structure and composition also changes with moisture and fire conditions.

In our study, the relationship between growth rate and elevation is more complicated than the GR-age or GR-size relationships. Pre-burn, growth rate was highest at elevational extremes
(Figure 17) with a slight increase in growth rate around average elevation. In the burned period, this relationship was exaggerated further (Figure 18), with the lowest GRs occurring at the middle elevations, with either extreme continuing to show high GR. This pattern of high/low elevations resulting in faster growth rates may be due partly to changing fire behavior due to changing moisture conditions or altered vegetation structure and composition. Low elevations may experience moister soils, with fires being especially short-lived or cool, resulting in less stress on trees and maintaining a higher growth rate. At high elevation, increased growth rate may be due to the likelihood of fires moving faster and burning more shallowly where the fuel is drier. The three plots with the highest elevations consist of one unburned plot, one 7-year plot, and one 2-year plot. The highest elevation plots being of different burn regimes further supports the notion fire-return interval alone may not be eliciting this response and that that elevation (and by proxy, moisture) may be involved.

In another study, elevational changes of 3m resulted in substantial changes in species composition as distance to the water table changed in scrub habitat (Boughton, Quintana-Ascencio, Menges, & Boughton, 2006). In the burn plots, the more-frequently burned areas tend to be more open-canopied, and the lesser-burned areas have denser sub-canopies with more oak encroachment (Schmidt, 2005). Taken together, the relationship between elevation and burn history in the Preserve is complicated; oak cover may increase at higher elevations, increasing competition; frequent burning may remove oaks and in turn, decrease competition. Further, changing elevation (and the changing the relative position of the water table) also impacts soil qualities like organic matter accumulation or leaching (Schmalzer, Hensley, & Dunlevy, 2001), and changing fire frequency and moisture both have important impacts on longleaf seed germination (Loudermilk, Cropper, Mitchell, & Lee, 2011; O’Hare & Dalrymple, 2006).
In order for a tree to become very large, it must survive through all of the smaller size classes. That is, not all small trees represented in the sample are likely to survive to become the largest trees. I consider the possibility that elevation increases individual demographic heterogeneity, with some trees simply growing at faster rates, which may have led to increased survival when the prescribed burns began by moving the canopy upward and thickening the bark. An increase in individual heterogeneity may be due to microsite; longleaf pines tend to tolerate very dry, well-drained soils better than they do poorly-drained soils (Gonzalez-Benecke, Martin, & Cropper, 2011), which might help explain the high GRs I see at high elevation in this study.

**Diameter and diameter×age**

Diameter increases over the lifetime of a tree, but the rate of increase changes depending on the current size and age of the tree. Generally, growth rate peaks when a tree is young, then growth stabilizes somewhat as a tree reaches approximately 80 years old. Growth rate declines as trees grow large and plateaus near senescence (Platt et al. 1988). I see similar patterns in our data, while acknowledging that the data do not contain trees experiencing senescence. However, our pre-burn model shows that the effect of diameter on growth rate is very large (4.04 SE 0.22), greater than what was expected. The effect of increased diameter resulting in higher growth rate is smaller but still positive once burns are considered (4.04 vs 2.60). This effect may be due to the data structure; because all trees in the pre-burn period also exist in the burned period, the burned period trees have older maximum ages and sizes. However, when I are able to de-couple age and size by using these models, trees that are already large continue to have high GR. It has been shown that longleaf pine growth rate tends to decrease then remain steadily low beginning around 30 cm DBH (Platt et al., 1988); our data indicate this limitation on growth rate is due mainly to size.
Given that these trees produce rings (increasing diameter) nearly every year (increasing age), the diameter×age interaction is important. Pre-burn the diameter×age interaction was smaller, but still positive (2.83 SE 0.14), indicating that larger, older trees tended to grow fastest (Figure 23), contrary to what was expected. This effect was maintained in the burned period (Figure 24), despite what I saw in the parameter estimate (0.020 SE 0.002). The large impact of diameter alone allowed younger, large trees to maintain a relatively fast growth rate despite being above-average size-at-age.

I expected that high values for both age and size would contribute to a lower growth rate in trees, but here, in all parameter estimates, increasing size in larger trees results in a higher GR. It is only when scrutinizing the interaction effects plots that I see the real pattern: young, large trees have the slowest growth rates.

**Diameter×Elevation**

Ln(GR) exhibited the most curvilinear response to elevation which necessitated using elevation polynomials in the model and in all elevation interactions. Figure 29-30 suggest that the pattern of growth similar across periods when elevation interacts with diameter, but that the strength of the effect is stronger during the burned period; small trees grow faster at higher elevations, and larger trees grow faster at lower elevations. This is further supported by looking at the magnitude of the parameter estimates for the diameter×elevation interaction, which are considerably larger for all elevation polynomials during the burned period (-24.82 – 14.52 across elevation polynomials pre-burn vs. -95.75 – 182.68 during the burned period). This appears to be directly contrary to what I expected, with large trees possibly suffering root inundation at low elevation, and smaller trees suffering from decreased water accessibility at high elevation.
However, while the largest trees grow fastest at lowest elevations, growth is generally very low throughout elevations which are lower than average.

Because of longleaf pine’s unique ability to remain in the grass stage until both the taproot development and environmental conditions are suitable for bolting, it is possible that the smaller, fast-growing trees at higher elevations were able to successfully grow a taproot deep enough to reliably reach the water table, possibly remaining in the grass stage long to build up the carbohydrate stores in the root as well, making them well-suited to the higher elevation. It is also plausible that larger trees do relatively more poorly at higher elevations simply due to higher water requirements in general.

**AgexElevation interaction**

Pre-burn, the overall impact of the agexelevation interaction was generally negative (Figure 25). This indicates that growth rate is negatively impacted by the combination of being old and at a higher elevation. This was an unexpected result—generally, I expected older trees at higher elevation to experience at least average growth due to deep roots providing plenty of access to water. Longleaf pine production generally decreases as depth to the water table increases (Ford et al., 2008) up to a point, but it is most reasonable that the oldest trees would have had the most time to invest in deep roots and therefore experience the least decline in growth rate due to elevation. However, when I look at the agexelevation effect plot (Figure 25), I see that only the highest and lowest elevations have considerable variation. The lowest elevations may have at times experienced partial root inundation which has been shown to decrease tree-ring growth in Scots pine (Cedro and Lamentowicz, 2011). At ‘medium’ elevations, there is essentially zero impact on growth rate—age seems to be the driving factor. Older trees do slightly better at the highest elevation (possibly an indication of roots that have met the water
table). Post-burn the direction of the age×elevation interaction for only the highest elevation was positive but the pattern is essentially the same before and after burns (Figure 26), albeit stronger. In both cases I see that older trees generally grow slower when accounting for elevation, but the only time impact of this effect is positive is during the burned period, within the highest elevations. It is possible that increased growth rate for old/high elevation individuals during the burned period is due to cohort selection, with more “frail” individuals failing to survive the burned period, which influences population dynamics (Kendall, Fox, Nogeire & Fujiwara, 2011). The general conclusion that older trees are larger trees, which are better able to survive fire due to thickened bark and increased crown height (Myers, 1990) may support the possibility of cohort selection.

**Fire and its interactions**

Given the positive impact of high elevation on growth rate during the burned period, it is important to consider how fire interacts with elevation. The three fire categories (FireCat1: burned this year, FireCat2: burned last year, FireCat3: burned this year and last year) interact differently with elevation (Figure 32). The parameter estimates for all three levels indicate that burns affect growth rate, similarly, in negative but very small ways (FireCat1: -0.2SE 0.39, FireCat2: -1.06 SE 0.41, FireCat3: -0.92, SE 0.82). This is different than prior research that shows that growth is reduced only during burn years with growth rebounding in non-burn years (Ford et al., 2010). Our results show that being burned one year ago (FireCat2) is most detrimental to growth rate, but that back-to-back burning (FireCat3) results in slightly higher, though more variable growth rate. Importantly, the model used in our research accounts for many other factors not used in Ford’s study. Thus, it is necessary to look at the interactions.
Elevation positively impacts growth rate in the burned period, possibly because of the interaction of moisture and fuel loads. Sandhill pine populations respond more positively to frequent, variable burns (every 1 – 3 years), while flatwoods pine populations respond better to slightly less frequent burns (2 – 4 years) with extremely frequent fires resulting in decreased plant diversity (Myers & Ewel, 1990). Because sandhills and flatwoods populations tend to experience different fire responses, it is possible that elevation is working not simply as a proxy for moisture or distance to the water table, but also as a vegetation gradient from mesic flatwoods to sandhill. The majority of the burn plots present as sandhill, but the lower elevation plots border mesic flatwoods (Schmidt, 2005). Elevation and fire category interact in an interesting way; high elevation trees which are burned most frequently experience the fastest growth rates (Figure 32). Further, while the presence of any fire regime increases variance, the relationship with fire and elevation is highly variable, with frequent fires most increasing growth heterogeneity.

Individual tree core growth variance tripled within burned plots compared to unburned plots, indicating that longleaf pines exhibit some persistent heterogeneous growth when fire is incorporated into the plots, and less heterogeneous growth when fire is excluded. Due to the heterogeneous nature of fire (Loudermilk et al., 2012), each tree likely experienced it differently, and growth may have changed accordingly. Also, fire can reduce competition, which could create one or more scenarios. For example, reduced competition may make pine growth heterogeneity more distinct by underscoring the importance of other factors, like genetics or microhabitats (Grace & Platt, 1995), or, reduced competition between trees and surrounding vegetation could change the patterns in the growth heterogeneity/fire relationship (Mitchell, Hiers, O’Brien, Jack, & Engstrom, 2006).
Conclusions

Traditionally, tree ring growth utilizes a dendrochronological approach in order to isolate a signal of interest—frequently, but not always, climate. Using our unique approach offers flexibility in the type of questions that can be asked. GLMMs allow for the estimation of variance between years, rather than only a qualitative determination of “good years” or “bad years”. Estimating variance via GLMM is valuable given the numerous number of studies linking variance and demographic heterogeneity to extinction risk, population structure, and more (G. A. Fox, Kendall, & Schwinning, 2010; Kendall et al., 2011; Stover, Kendall, & Fox, 2012; Vindenes et al., 2008). There is interest in understanding individual tree differences in dendrochronology (Trouillier et al., 2018) instead of looking at population-level growth means. In order to detect a climate signal, for example, there are factors which may impact all trees similarly, like precipitation and temperature, but there are factors like microsite, competition, or individual characteristics of the tree that also feed into that signal. Environmental factors can combine to produce a variety of different impacts on tree growth (Trouillier et al., 2018), but GLMMs allow us to begin to understand how these factors come together to produce an overall signal of some kind. Without this explicit consideration of individuals, dendrochronological studies which draw broad conclusions based on many highly-sensitive, old trees have been shown to overestimate climate change risk (Klesse et al., 2018).

Standard dendrochronological studies usually rely on sampling sensitive trees—trees which have rings that vary due to their ecological position, as opposed to complacent trees, in which ring width is generally consistent. While any study using tree rings to investigate an ecological signal will require at least some degree of tree sensitivity, mixed effects models are more powerful in the event that trees are more complacent. A model-based approach allows us to
explicitly investigate factors producing individual heterogeneity such as age and size, while also examining the growth response.

**Citations**


https://doi.org/10.1016/0169-5347(94)90086-8


Foster, T. E. (2014). Water Availability as the Driving Factor of Growth and Physiological Function of Co-occurring Scrub Species in Central Florida. *Graduate Theses and Dissertations*, (May), 142. Retrieved from https://scholarcommons.usf.edu/etd/5020%0A%0A


Schmidt, A. C. (2005). A vascular plant inventory and description of the twelve plant community types found in the University of South Florida ecological research area, Hillsborough County, Florida. Graduate Theses and Dissertations. https://doi.org/10.1203/PDR.0b013e31818702a2


Trouillier, M., van der Maaten-Theunissen, M., Harvey, J. E., Würth, D., Schnittler, M., &


CHAPTER 3:

METHODS FOR STUDYING GROWTH VARIATION IN TREES AND THEIR CONSEQUENCES

Introduction:

Dendrochronology has a long history. While scientists started looking at rings several hundred years ago, it was Douglass, beginning in 1904, who was the first to use crossdating extensively (Studhalter, 1956) which became foundational to the field. Later, technological advances led to the creation of computer software in the 1960s and ‘70s, much of which is still used today. For example, COFECHA, the software which allows researchers to check their crossdating quality, was developed in 1983 (Holmes, 1983). Classical dendrochronological methods are useful for asking long-term questions about variables impacting a population or group of trees, or for investigating specific events by comparing one group of trees to the regional signal.

Generally, dendrochronology seeks to link time and environmental variability. Depending on the variables being investigated, dendrochronology can be used to answer a variety of questions. These questions frequently involve climate and its fluctuations, and the tree rings within a group of trees are the data upon which these inferences can be made. Dendrochronology can be used to investigate an enormous variety of ecological, demographic, and climate-response questions which span a variety of subfields For example, dendroclimatology often links tree growth to climate (Henderson & Grissino-Mayer, 2009). Some examples of dendroecological work include using tree rings to investigate specific tree
growth responses like drought tolerance (Eilmann & Rigling, 2012), competition (Evans et al., 2017), recruitment (Pederson, Varner, & Palik, 2008), mortality (Palik & Michener, 1999), fire (Henderson, 2006), and more. It has also been used to compare interspecific responses to ecological factors (Cook et al., 2001; Foster & Brooks, 2001; Foster, Schmalzer, & Fox, 2015). Dendrochronological methods can also be used to determine dates and patterns of meteorological events like frost or storms (subfield: dendrotempestology; Henderson, 2006; Tucker, 2015). Other subfields include dendroarchaeology, which involves using wood samples from archaeological structures to study human behavior; dendrogeomorphology, which uses tree rings to investigate land movement or geologic phenomena like landslides and volcanic events; and dendrochemistry, which seeks to understand how chemicals in the environment deposit into wood (Speer, 2010). As the discipline grows, there has been increased understanding that investigating noise in a tree-ring signal can uncover additional biological information (Speer, 2010).

In recent years, there has been an increasing drive to include covariate data (age, height, microsite information and more) while investigating tree rings (Trouillier et al., 2018), and newer approaches (like generalized linear mixed effects models, GLMMs) seek to incorporate this information. Whereas traditional approaches frequently average tree-ring measurements across individuals, it is possible that aggregate tree growth would be best assessed per individual in order to account for individual heterogeneity arising from age, size, microsite or more (Trouillier et al., 2018; Wilmking, Juday, Barber, & Zald, 2004).

Dendrochronological studies rely on five steps—sampling, processing, dating, measuring, and crossdating. There are a variety of ways to sample depending on the goals of the study. Processing, or preparing a fresh tree sample for dating by drying and sanding is always the next step. There are some technological advances that can aid in measuring and crossdating after the
initial dating has been completed, but regardless of the details, these five steps are always completed. One purpose of this chapter is to discuss the use of generalized linear mixed models (GLMMs) using the tree-ring data obtained through this process. Because any study wishing to utilize tree-ring data will need to include these steps, I explore an additional tool to understand tree growth. In this chapter, I first discuss the pros and cons of traditional dendrochronological analyses and then discuss how I may extend the use of the tree-ring data using generalized linear mixed models. Finally, I give some examples from prior work (see chapter 3).

**Classical dendrochronology**

Classical approaches begin by recognizing that tree ring width represents a sum of influences. In order to detect a signal of interest, other effects must be accounted for or filtered out. Recall the aggregate tree growth model for a tree-ring series describes ring growth

\[ R_i = B_i + P + C + O + e \] (2)

where \( R_i \) is ring width of tree \( i \), \( B_i \) is biological component for tree \( i \), \( P \) is stand-level perturbation, \( C \) is stand or regional climate, \( O \) is regional disturbance, \( e \) is an error term incorporating factors not otherwise included, like local disturbance or individual heterogeneity (Van Deusen, 1989). Age- or size-related growth trends can be accounted for using standardization; negative exponential curves and cubic smoothing splines are two common options. Long term trends in climate can be detected by standardizing tree ring data using a regional curve standardization method. Choosing an appropriate standardization method is key to a strong dendrochronological analysis.

Classical dendrochronology relies on the “Principle of Limiting Factors” which posits that the factor which is most limited will control tree growth (Speer, 2010). Then, a site is chosen
according to the “Principle of Site Selection”, which suggests that the site for sampled trees should be limited by the factor that the researcher is interested in reconstructing. For example, if moisture is expected to be the limiting factor, the site should experience some degree of moisture limitation. This targeted sampling seeks out what may be the best-responding trees. This depends on making some assumptions that can be difficult to uphold. One assumption is that the environment has been stationary throughout the trees’ growth: it varies from year to year, but always from the same statistical distribution. Some studies have shown that during certain periods, growth patterns can change, or the driving factor (temperature versus water) can change over time (Stahle & Cleaveland, 1994; Wilmking et al., 2004). Tree growth is aggregate, influenced by a variety of factors (Cook, 1987), and it can be difficult to ascertain which factor is the one that most controls growth, and especially challenging to be certain that a single limiting factor has been the only one throughout a tree’s lifetime. Further, the trees one targets for sampling in one decade may not have been suitable for targeting in a prior decade (Carrer, 2011), as the environment and climate may have changed, especially over long time periods. This limiting-factor approach can produce generally good results regarding the limiting factor or factor of interest (Schweingruber, 1988), but here I suggest new methods to enhance the understanding of tree growth variation.

In classical dendrochronology, trees are frequently selected so as to represent the longest amount of time possible, which results in older trees being differentially sampled, especially for climate reconstructions. While this helps account for the increased growth variability in younger trees, this targeted sampling presents certain challenges. Detrending is used to remove age-related size trends. There are a variety of widely-discussed detrending methods (Biondi & Qeadan, 2008; Bunn, Sharac, & Graumlich, 2009; Cook & Peters, 1997), but changing
Detrending methods can produce different results. For example, Sullivan, Pattison, Brownlee, Cahoon, & Hollingsworth (2016) investigated growth trends following the Industrial Revolution in black spruce and white spruce in Alaska. Long-term growth trends were strongly positive with single-curve regional curve standardization (RCS) and basal area increment (BAI), but the horizontal-line method of detrending showed negative growth trends. Different detrending methods can also suit different environments. Cubic smoothing splines, for example, are thought to best accommodate chronologies formed using trees from closed-canopy forests because they are impacted more strongly by factors around them (competition, light, etc) than open-canopy forests (Cook & Peters, 1981). Cubic smoothing splines can be adjusted to determine the amount of variation removed from the growth trend (Grissino-Mayer, 2001) and can be somewhat subjective (Figure 38). Chronology length can also impact what detrending method is chosen; very long chronologies looking for low-frequency variability are best suited to RCS instead of negative exponential curve standardization (Bunn et al., 2009).

Typical dendrochronological analyses (like simple climate response analyses) require less time to complete than the preparatory core processing and crossdating. One advantage to building a simple chronology is that oftentimes sample size need not be especially large; generally, 30 living trees can be used for climate reconstruction (Speer, 2010).
Figure 38: One chronology shown with two different spline lengths; top spline length = 10, bottom spline length = 40. The spline length indicates the point at which half the variance is retained. For example, a 40 year spline length retains 50% of the variance at 40 years, 99% at 12.67 years, and 1% at 126.17 years (Speer, 2010).

A Model-based Approach

Generalized linear mixed models (GLMMs) describe the relationship between a response variable and some predictors, at least one of which is categorical, and represents experimental/observational units in the data set (Bates, 2010). This type of model allowed us to investigate the impact of tree size and age (continuous predictors—fixed effects) while also quantifying the among-individual or among-plot variance (categorical predictors—random effects), in chapter 3. Random effects can account for variation within individuals when there are multiple measurements per individual (Bolker et al., 2009), as is the case with multiple tree-ring measurements per tree sample. Random effects can also be used to quantify the amount of variation between study blocks or observational units (Bates, 2010), or in the case, plots. Compared to simple dendrochronological analyses, GLMMs allow for more robust testing of
specific variables. Instead of creating one average chronology, this type of model allow us to parse specific pieces of covariate data which are contributing to the chronology. I can ask questions that are more direct—“What is the impact of elevation?” instead of “Can I biologically infer that elevation is impacting the chronology?” Further, these models allow us to investigate the impact of fixed effects like age or size while also quantifying the among-individual or among-plot variance by including these as random factors. Instead of removing variation among individuals as unwanted noise in the data, this approach allows us to estimate variation and model some of the causes of among-individual variation. We are interested in the signals that are isolated from tree-rings through chronology-building, but GLMMs give us the opportunity to build on this by modelling many other levels and types of predictors like plot, elevation, competition, and more.

Being able to test specific variables more readily also means that I can incorporate more types of data; this can be complimentary covariate data I record in the field such as canopy position, height, or measurements of competition, or it can include microsite information like moisture, soil type, or elevation. Recall the aggregate tree growth model (Equation 1), which includes a term for regional disturbance and local disturbance. GLMMs help us explicitly incorporate measurements which could reasonably contribute to tree-ring growth. By accounting for more variables in the tree growth model, I reduce the error term and strengthen the conclusions. Incorporation of complementary data from forest inventories has potential to strengthen models of forest dynamics under changing climate scenarios (Evans et al., 2017).

Assumption of a single limiting factor can make environmental reconstructions more difficult, as the limiting factor can change from year to year, and that more than one factor may be limiting at once (Speer, 2010). The Principle of Limiting Factors is based on Liebig’s Law of
the Minimum (LM), which I know may apply differentially depending on location or throughout a season (Stine, 2019), and may change depending on scale (Danger, Daufresne, Lucas, Pissard, & Lacroix, 2008). Because trees are influenced by within-stand and beyond-stand influences, a method like GLMM which explicitly incorporates data for these influences is likely to prove useful in tree-ring studies. Using the prior chapter as an example: water availability is very reasonably a limiting factor for longleaf pine at the site. I also tested fire as a limiting factor and the model was able to accommodate both factors, as well as their interaction (Chapter 3; Figure 20).

Because I can use model-based approaches for a variety of factors impacting tree growth by the use of GLMM, I can avoid marginal site selection and targeted sampling if desired. Targeted sampling and/or marginal site selection (as opposed to representative or random sampling) can overestimate forest climate sensitivity and introduce bias into measurements of tree response to environmental change (Klesse et al., 2018; Nehrbass-Ahles et al., 2014), and assimilation of forest inventory data can strengthen dendrochronological conclusions (Evans et al., 2017). Targeting old trees on marginal sites can overestimate the impacts of climate change (Klesse et al., 2018). Sampling dominant trees only has been shown to bias absolute growth rates by over 400% (Nehrbass-Ahles et al., 2014). When I use representative or statistical sampling to understand known disturbances, as I did in chapter 2, the results become much less clear due to the complexity and number of factors impacting growth. While classical chronologies do not require targeted sampling, they are often designed this way to overcome noisiness and to distill a signal of interest. Using GLMMs provides the opportunity to avoid sampling bias while managing noise.
In order to gather tree-ring measurements for a mixed model, the standard prep work applies; no extra steps are needed. Detrending follows crossdating—but detrending methods can impact overall chronology results. Using tree-ring measurements in a mixed model does not require a detrending step.

Model-based approaches do have some drawbacks. As more data are included in the model, the risk of creating spurious models increases. It is critical that the researcher consider which hypotheses will be investigated before forming the model and choosing interactions, as it is possible to create models which make statistical sense but are biologically unlikely or unreasonable. Model selection requires researcher input rather than relying on stepwise-model selection functions. Further, there are cases where more data may be needed, requiring more trees to include in the sample. For example, as GLMMs quickly become complicated, they can fail to converge if there are not enough remaining degrees of freedom. In a prior chapter, I encountered this when comparing the pre-burn period to the burned period using separate models. The pre-burn period had a smaller sample size and fewer data-years and would not converge using a fuller model. Convergence errors can be complicated to understand and solve, and it requires the researcher to have a thorough understanding of how to resolve them should they arise.

When choosing hypotheses to be tested using model-based approaches like GLMMs, one should use caution if the chronology is very long because the variables being tested and the trees’ environment may have changed. For example, the number of neighbors near any single tree changes over time, and these changes can impact competition for nutrients and light, while also impacting a tree’s experience of fire or wind. Certainly, climate change is another consideration; if the average tree age is extremely old, I know to account for any known changes in climate. It
is especially important to consider the ways tree density, forest type or composition, or soils may have changed over time. The forest environment experienced by the first tree could vary more than the environment which is experienced by all the present-day trees. Given what I know about limiting factors (see above), GLMMs can be extremely useful to make inferences over time, but this is limited by what I can reasonably say about the covariates and site history going back in time.

**Synthesis and Conclusions**

In the two prior chapters, I have investigated longleaf pine growth two ways—first, by building a chronology, and second, by creating a generalized linear mixed model (GLMM). The chronology results gave us a composite trace showing average growth over time, but the GLMM expanded on this by including covariates. I tested for the effects of size, age, elevation, recent burn history, year, and quantified individual and year-to-year variation. In order to compare the results, I used the random effects of year and compared them to the chronology. The correlation between the standardized chronology and the random effect of year estimates was 0.63.

![Figure 39: Comparing the standardized chronology (black) with the parameter estimates for the random effect of year from the GLMM (red)](image-url)

91
While there are some differences, the random effect of year estimates form an estimated chronology. Interestingly, the two methods can provide similar results although the classical chronology relied on tree-rings and detrending only, rather than explicit factors impacting tree growth (Figure 39). For example, elevation was tested for and retained in the final model as a proxy for water availability, but I do not have a straightforward way to understand the impact of elevation on tree growth from the simple chronology. GLMMs add valuable depth to the understanding of peaks and valleys in the chronology trace. I can also further parse the effects of year or individual. Using the year estimates, I can see that average years (estimate = 0) are not common during the burned period, likely due to the prescribed burns that occurred during this time. Pre-burn the values center closer to zero, indicating that growth response per year is more homogenous when there are few or no fires. For individual trees, burned period variation is much higher, and the estimates for above-average individuals extends very far to the right (Figure 40).

Figure 40: Density plots showing a breakdown for the effects of year (top) and individual (bottom). Data were separated into pre-burn (prior to 1976) and burned (1976- 2014) time periods. Pre-burn densities are shown in gray, and burned densities are shown in red.
It seemed likely that the bimodal appears for the year effect during the burned period was caused by burn regime, but when I separated the results by plot (and therefore, burn frequency), no obvious pattern emerges (Figure 41). Again, I see that burned period growth was more variable, and all plots but 1e and 7w experienced the biggest increases in growth due to year at some point during the burned period. Though growth can decline during a burn year, this may be explained by resilient growth following a fire (Ford, Minor, & Fox, 2010) which can compensate overall but requires increased growth in the year following a burn. In contrast, only plots 5e and 7e experienced the largest growth decreases during the pre-burn period. I was unable to test for differences in the unburned plots compared to the burned plots using these complex GLMMs because of lack of data (Chapter 3). I did not see any distinct patterns in the unburned plots graphically (Figure 41).

Figure 41: Values for the effect of year, visualized by plot. Data were separated into pre-burn (prior to 1976) and burned (1976-2014) time periods. Pre-burn densities are shown in gray, and burned densities are shown in red.
Dendrochronology has been used to answer questions in hundreds of studies spanning a broad variety of topics. GLMMs represent a new statistical advancement for dendrochronology and rely on the same core sampling and processing that would be done for a traditional dendrochronological study. GLMMs (and other model-based approaches) allow researchers to incorporate tree covariates (e.g., age, size, microsite information) which has been shown to have important consequences when drawing conclusions about tree growth (Evans et al., 2017).

GLMMs can also quantify among-individual or among-site variation, and although dendrochronology typically filters out noise in favor of a desired signal, individual or site variation can have important consequences (Trouillier et al., 2018; see chapter 3). In the example above, model results closely resemble traditional chronological results, but the model approach allows us to more explicitly describe changing tree growth due to factors like fire or water availability. Further, GLMMs give us the opportunity to measure individual variation; demographic heterogeneity has important consequences for populations (Kendall, Nogeire, Fox, & Fujiwara, 2011; Pfister & Stevens, 2003; Vindenes, Engen, & Sæther, 2008; Zuidema, Brienen, During, & Güneralp, 2009) and is not typically addressed when filtering out noise to produce a signal. While more exploration of these model types is in order, GLMMs are an important new tool for dendrochronologists.

Citations


