UNEVEN-AGED MANAGEMENT IN THE MISSOURI OZARKS: EFFECTS OF SITE CONDITIONS, STAND DENSITY, AND PRIOR POPULATIONS ON OAK REGENERATION

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by
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The undersigned, appointed by the dean of the Graduate School, have examined the thesis entitled

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ON OAK REGENERATION

presented by Trystan Harpold,

a candidate for the degree of Master of Science,

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Dedication

This thesis is dedicated to both my wife Trianna and the multitude of amazing professors and educators that I have had the immense privilege and pleasure of working with during my education. My wife Trianna has been my rock throughout most of my undergraduate and graduate education and has been there through thick and thin, never wavering in her support of my goals and ambitions, even when it required moving a thousand miles from home. I can only hope to be as supporting and loving to her as she has been to me over the past 6 years. I would also like to dedicate this thesis to the many passionate and dedicated educators that have mentored me and guided me to this point. There are too many outstanding educators that have helped and inspired me since the beginning of my education to list here, however just a few include Dr. Ben Knapp, Dr. Sara Fuentes-Soriano, Mr. Zachary Rogers, Dr. Kristen Waring, and Dr. Donovan Bailey. Without these and other individuals, I would not be where I am today, and I will carry their lessons with me for the rest of my life. I am eternally grateful to you all.

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Abstract

While studies have shown the importance of site characteristics and overstory density on the success of white oak regeneration under uneven-aged management, few studies have analyzed the effects of these variables over time in the Missouri Ozarks. Here, we quantify the effects of site variables, stand density, and prior populations of reproduction on temporal patterns of white oak reproduction establishment and recruitment following decades of uneven-aged management.

The results of this study indicate that while site characteristics, stand density, and prior populations are all important for white oak regeneration, this is not the case for every site characteristic or stage of regeneration. While xeric conditions often improve white oak regeneration, some xeric site characteristics, such as low available water capacity, reduce white oak regeneration. This study found that stand density reduction is also important for increasing future white oak recruitment; however, it was not important for increasing white oak seedling establishment. Further, under uneven-aged management stand density was not closely related to understory sunlight levels. Finally, prior populations of regeneration are vital to future recruitment, and it is necessary to have prior populations established many years in advance of desired recruitment.

Chapter 1: Literature Review

Oak Forests

Oak (*Quercus* spp.) forests are an important ecosystem type that covers roughly 140 million acres of land in the eastern United States (Oswalt *et al.*, 2019). These forests often vary in their composition, with oaks comprising a relatively minor component (roughly 10% of the overstory in New England and the Lake States) in the Northern Hardwoods Region and a major component in areas such as the Central Hardwoods Region, where they can make up, on average, 50% of the trees in a stand and up to 78% in some sections like the Ozark Highlands Section (Hanberry and Nowacki, 2016; Johnson *et al.*, 2009). Within the Ozarks, oak dominated ecosystems vary widely in their structure, ranging from oak savannas with low densities (23-45 trees/acre), low canopy cover (38-60%), and low stocking (16-30%) to closed oak forests with high densities (78-129 trees/acre), extremely high canopy cover (83-94%), and extremely high stocking (76->105%) (Hanberry *et al.*, 2014). In addition to being a common tree in oak forests, oaks also provide many important ecosystem services/benefits including cultural, provisioning, and ecological/support services.

Oaks provide many important cultural and provisioning ecosystem services including recreation, aesthetics, food, fuel, and lumber. Oak forests are valued for aesthetic and recreation opportunities, including hunting, fishing, camping, sightseeing, and tourism, for millions of people each year (Clark and Hutchinson, 1989; Schwilling *et al.*, 1999). Oaks have long been a direct and indirect source of food, providing acorns to produce flour meal and fodder for livestock, and wood that is used in the production of whiskey and wine barrels, railroad ties, veneer, plywood, dimension lumber, hardwood flooring, fuel, and charcoal (Johnson *et al.*, 2009). These products make oaks an extremely valuable economic commodity, with the United States exporting over $1 billion of oak products in just 2017 (Bumgardner, 2019).

Oaks are an ecologically important foundation species that play a role in providing food and habitat for a wide range of animals, improving wildlife biodiversity, and regulating water and nutrient availability, among other important ecological roles (Hanberry and Nowacki, 2016). As a foundation species, oaks contribute greatly to the abundance of wildlife in oak forests by providing forage through acorn masts and foliage production, and habitat such as cavities for squirrels and canopy cover for many bird species (Dickson, 2004; Fralish, 2004; Hardin and Evans, 1977). Oaks are an important overstory species for promoting herbaceous biodiversity due to their regulatory effect on understory sunlight levels (Fralish, 2004). They also have an important role in regulating soil conditions and are often important in regulating nutrient and water availability within oak forests (Alexander and Arthur, 2010).

The Oak Regeneration Problem

Because of the ecological and economic importance of oaks, and the difficulty and time associated with establishing oak regeneration, many researchers and forest managers have been concerned with what has been termed the “oak regeneration problem”, a perceived lack of oak reproduction and recruitment in the forests of the eastern United States (Cook *et al.*, 1998; Johnson, 1997; Sander, 1977). At many sites, there is a lack of advanced oak reproduction and when adequate reproduction is present, it is often out-competed by shade-tolerant, non-oak species (Dey, 2014; Larsen and Johnson, 1998). Throughout much of the eastern United States, oaks, particularly red oaks, have declined in overstory importance since the early to mid-1900s (McEwan *et al.*, 2011). This decline in importance is often accompanied by a composition shift to other species such as red and sugar maple (*Acer rubrum* L.*; A. saccharum* Marshall) (Abrams, 2003, 1998; Fei and Steiner, 2007). In part, these shifts in composition are attributed to declines in oak reproduction establishment and recruitment populations that appear insufficient to replace and maintain oaks in the overstory on many sites (Vickers *et al.*, 2019). It can take years or decades to develop oak advance reproduction on sites where it is not already present and even longer to grow that regeneration into the overstory (Dey, 2014; Sander, 1972).

Researchers have proposed many causes for the decline in oak regeneration, including the removal of frequent fires from the landscape, changes in forest management, increased deer populations, and mesophication of ecosystems. The historical abundance of oaks in oak forests was the result of a culmination of intense timber harvesting, frequent, low to moderate intensity disturbances, such as the annual use of fire to improve livestock forage, the loss of the American chestnut, and overharvesting of wildlife (Dey, 2014). In the past 100 years, these factors have changed dramatically. Since the 1930s and 1940s, deer populations have increased above carrying capacity in some areas due to changes in hunting laws, resulting in heavy herbivory that contributes to the failure of oak regeneration (Abrams, 2003; Dey, 2014; Rooney and Waller, 2003). Prior to the 1960s, oak forests were more frequently high graded or managed using single-tree selection rather than the intense timber harvesting characteristic of agricultural conversion (Dey, 2014). By the 1960s, forest managers began to realize that single-tree selection and high grading could not successfully regenerate oaks in most cases (Roach and Gingrich, 1968; Sander and Clark, 1971). Finally, beginning in the early 20th century forest fires were suppressed across much of the United States further putting oak regeneration at a disadvantage as fire-sensitive and often-shade tolerant species gained dominance in forest understories (Abrams, 2003; Lorimer, 1993).

Oak Regeneration Ecology

The process of oak regeneration includes two primary stages, the establishment of reproduction and the recruitment of those trees into larger size classes. Authors frequently define oak reproduction as seedling germination, survival, and growth into saplings and define oak recruitment as the growth of saplings into the overstory (Dey, 2014). Generally, under even-aged management, oak recruitment occurs during stem exclusion and understory re-initiation while oak reproduction occurs during the stand initiation phase of stand dynamics (Dey, 2014; Oliver and Larson, 1996). Under uneven-aged management, recruitment and reproduction establishment both occur continuously across the life of the stand (Oliver and Larson, 1996). Due to much of the past literature not distinguishing between seedling growth and sapling growth, and due to limitations of this study, we will consider recruitment to include both sapling abundance and sapling growth into the overstory, while reproduction includes only seedling abundance.

Sources of oak reproduction establishment include true seedlings, advance reproduction, and stump sprouts (Johnson *et al.*, 2009). True seedlings are seedlings that have originated from acorns and have not resprouted from the root system and thus have roots and stems of the same age (McQuilkin, 1976). In the eastern United States, true seedlings are typically the slowest growing of all the reproduction types and do not persist long in mature forests before transitioning to advance reproduction or dying (Dey *et al.*, 1996; Liming and Johnston, 1944; Sander, 1971). It is generally thought that they do not contribute significantly to the overall regeneration of oaks and that successful regeneration depends on advance reproduction and stump sprouts (Beck, 1970; Loftis, 1990a; McQuilkin, 1976; Sander and Clark, 1971). Over time, true seedlings that are able to develop tap roots large enough to resprout will often be top killed repeatedly but still persist in the understory and thus become advance reproduction (seedlings with root systems older than the above ground stem) (Liming and Johnston, 1944; Merz and Boyce, 1956). Advance reproduction is often the most abundant form of regeneration for oaks (Johnson *et al.*, 2009; Liming and Johnston, 1944). They generally grow more rapidly and have better survival than true seedlings and are often considered the most important form of regeneration for oaks in the central states (Beck, 1970; Loftis, 1990a; McQuilkin, 1976; Sander and Clark, 1971). Stump sprouts are oak reproduction produced from the stumps of damaged and/or harvested overstory trees (Johnson *et al.*, 2009; McQuilkin, 1976). Researchers have found that, while stump sprouts tend to grow more quickly and have a better chance of survival than advance reproduction, they are often not present in sufficient numbers to fully regenerate a stand (Dey, 2014).

The differentiation of these 3 types of reproduction is the result of the unique competitor/stress-tolerator life history of oaks whereby oaks are relatively long-lived, slow growing, and able to withstand frequent stressors (Wonkka *et al.*, 2013). These traits also extend to oak reproduction. Oaks start out as acorns, which are relatively large compared to seeds of other species due to storage of large amounts of nutrients that germinants use for growth and survival in their first year (Hewitt, 1998; Johnson *et al.*, 2009; Wonkka *et al.*, 2013). These nutrients allow oak seedlings to become established under intermediately shaded conditions and to persist longer than shade intolerant species in the absence of canopy openings (Hewitt, 1998; Johnson *et al.*, 2009). After germination, oaks prioritize root system growth over stem growth (Johnson *et al.*, 2009). Because of this, seedlings are able persist under low light conditions for extensive periods of time (up to 30 or 40 years), even resprouting from the root collar after being top killed by shade, fire, herbivory, or other disturbances (Liming and Johnston, 1944; Merz and Boyce, 1956). Another benefit of prioritizing tap root growth is that oak seedlings with larger tap roots can grow rapidly following canopy release events due to well-developed belowground structures (McQuilkin, 1976).

Most oaks are considered moderately to highly shade intolerant and grow poorly under dense canopy cover. However, not all oak species have the same level of shade tolerance, and the shade tolerance of individual species can change over the course of their lives (Burns and Honkala, 1990; Johnson *et al.*, 2009). White oak (*Quercus alba* L.) is the most shade tolerant of the common upland oaks, and black oak (*Q. velutina* Lam.) is considered slightly more shade tolerant than scarlet oak (*Q. coccinea* Muenchh.) (Johnson *et al.*, 2009). Oaks tend to become less shade tolerant over the course of their lives (Burns and Honkala, 1990).

The life history of oaks and their moderate to low shade tolerance make them more competitive when frequent ecosystem disturbances occur. Many authors have postulated that the reduction in oak importance and regeneration in oak forests is the result of changing disturbance regimes, from frequent fires and agricultural clearcutting that made oaks dominant in the late 1800s and early 1900s to disturbance regimes that encourage non-oak reproduction and recruitment in the absence of fire, including single-tree selection and windthrow (Abrams, 2003; Fei *et al.*, 2011; Lorimer, 1993). These more recent disturbances create small gaps that favor shade-tolerant non-oaks such as sugar maples, particularly when fire is excluded from the landscape (Abrams, 2003, 1998; Dey, 2014).

Despite being generally associated with frequent disturbances, the competitive success of oak regeneration is also influenced by site productivity. On more xeric sites where understory sunlight levels are greater, frequent disturbance is less important for providing oaks with a competitive advantage as oaks can persist longer than many shade-tolerant non oaks by using their large root systems as energy reserves when disturbances are infrequent (Dey, 2014; Johnson *et al.*, 2009). When non-oak reproduction is reduced in these conditions, oak advance reproduction and resprouts are not shaded out after moderate overstory disturbance and are often more competitive than much of the non-oak competition that is present on these sites (Fan et al., 2015; Iverson et al., 2017; Izbicki et al., 2020). On more productive sites, oaks require frequent understory disturbance to remain competitive as non-oak competition increases (Fan et al., 2015; Iverson et al., 2017; Izbicki et al., 2020). On these sites, the oak's ability to resprout repeatedly after being top killed by understory disturbance allows oaks to accumulate greater advance reproduction abundance than species that are not able to repeatedly resprout and must rely on true seedlings to regenerate (Johnson *et al.*, 2009). On productive sites without frequent disturbance, oak advance reproduction is often out competed by shade tolerant non-oaks and thus are not released by subsequent overstory disturbance (Johnson *et al.*, 2009).

Given the role of site productivity in moderating oak regeneration, topography and soil characteristics are often associated with oak reproduction abundance and recruitment (Carvell and Tryon, 1961; Chadwell and Buckley, 2003; Fei and Steiner, 2008; Kabrick *et al.*, 2014; Larsen and Johnson, 1998). Topographic characteristics shown to be correlated with oak reproduction abundance include slope aspect, slope steepness, slope position, slope shape, and elevation (Carvell and Tryon, 1961, 1959; Fei and Steiner, 2008; Kabrick *et al.*, 2014). Slope aspect and slope position have also been correlated with the rate of oak seedling growth (Chadwell and Buckley, 2003; Vickers *et al.*, 2019). Both Kabrick *et al.* (2014) and Fei and Steiner (2008) found that both oak seedling abundance and recruitment are correlated with soil characteristics. In particular, Kabrick *et al.* (2014) observed that nutrient availability (measured by soil acidity (pH) and base saturation) and plant available water capacity are negatively correlated with oak seedling abundance. Several studies have reported that oak recruitment and seedling growth are correlated with these characteristics but less strongly than oak seedling abundance (Iverson *et al.*, 2017; Kabrick *et al.*, 2014; Musselman and Gatherum, 1969; Phares, 1971).

The amount of sunlight reaching the understory is understood to be one of the strongest limiting factors for oak seedling and sapling growth and survival. Because of the difficulty and cost associated with obtaining direct sunlight measurements and the need for easily manipulated variables to change understory sunlight levels, overstory density (stand stocking and basal area) is often used as a surrogate to estimate understory sunlight levels (Blizzard *et al.*, 2013; Buckley *et al.*, 1999; Larsen *et al.*, 1997). Both direct measures of understory sunlight levels and overstory density have been correlated with oak reproduction abundance and recruitment (Brose and Rebbeck, 2017; Carvell and Tryon, 1961; Green, 2008; Iverson *et al.*, 2017; Larsen *et al.*, 1997; Vickers *et al.*, 2014). Vickers *et al.* (2014) determined that overstory density is important in predicting oak periodic annual height increment, particularly in the 90th quartile of saplings. Larsen *et al.*, (1997) recognized that, while it was difficult to correlate oak reproduction abundance with changes in overstory density, as overstory density decreases, there is an increased probability of having sufficient reproduction abundance.

Oak Silviculture

Research has suggested that, because of the oaks' need for moderate to high severity overstory disturbance, reproduction and recruitment are best maintained by using even-aged silviculture (Burns and Honkala, 1990; Roach and Gingrich, 1968; Sander and Clark, 1971). Since the 19760s, it has been suggested that clearcutting is the best method for regenerating oak forests when large advance reproduction was abundant, and shelterwood systems are used to develop competitive advance reproduction when it was lacking (Loftis, 1990b; Roach and Gingrich, 1968; Sander and Clark, 1971; Schlesinger *et al.*, 1993). The successful use of the shelterwood system frequently includes variations such as incorporating understory treatments (prescribed fire and herbicides), and altering residual tree density (Loftis, 1990b; Schlesinger *et al.*, 1993). Despite the success of even-aged management, there has been increasing interest in the use of uneven-aged management for sustaining oaks.

Research has demonstrated that uneven-aged group-selection can successfully maintain oak stand structure and composition (Hannah, 1987; Lhotka *et al.*, 2018). In the Missouri Ozarks, Loewenstein (1996) and Loewenstein *et al.* (2000) demonstrated that it might be possible to successfully maintain oak stand structure and composition using single-tree selection. Unfortunately, outside of the Ozarks, uneven-aged, single-tree selection cannot successfully maintain oaks, even with supplemental understory treatments such as herbicide use (Della-Bianca and Beck, 1985; Keyser and Loftis, 2013; Schuler *et al.*, 2017).

While single-tree selection may be capable of maintaining stand structure and composition in the Ozarks, the effect of single-tree selection on oak regeneration has shown mixed results. Loewenstein *et al.* (2000) documented three age classes in a forest managed with single-tree selection but did not quantify regeneration through time. Past research has suggested that single-tree selection significantly reduces the growth and survival of oak stump sprouts, true seedlings, and advance reproduction when compared to group selection and clearcutting (Dey *et al.*, 2008; Jensen and Kabrick, 2008). In contrast, Larsen *et al.* (1999, 1997) indicated that single-tree selection can successfully regenerate oaks, so long as overstory density is reduced to approximately 50 ft^2/acre of basal area every twenty years. This fits with past research that has suggested that, regardless of treatment, the success of oak regeneration is highly dependent on the intensity of harvesting, with more intense harvests promoting more oak reproduction and recruitment (Fan *et al.*, 2015; Heitzman and Stephens, 2006; Vickers *et al.*, 2014).

Oaks in the Missouri Ozarks

The mesic-xeric conditions experienced in the Ozark Highlands are a function of the location, topography, soils, and climate of the region. The Ozark Highlands extends across much of Missouri south of the Missouri River except for the western quarter and southeastern corner of the state, down to northern Arkansas (Natural Resources

Conservation Service (NRCS), 2022). Topographically, the Ozark Highlands range in elevation from 300 to 1600ft and range from unglaciated, deeply dissected hillslopes, steep ridges, and broad, flat ridge tops to flat plateaus (NRCS, 2022). The soils of the Ozark Highlands are mostly Ultisols and Alfisols derived from hillslope sediments, residuum, loess, and/or gravelly alluvium (Meinert *et al.*, 1997). Soils range from shallow to very deep (Meinert *et al.*, 1997). The climate of the region has average annual maximum temperatures around 68F, average annual minimum temperatures around 68F, and annual precipitation averaging 45.5in (NRCS, 2022).

These conditions favor oak reproduction and recruitment by inhibiting the growth and survival of non-oak competition. Oaks are generally more shade-intolerant than their non-oak competition in the Ozarks and are thus at a competitive disadvantage when heavily shaded, such as under the closed canopy of an uneven-aged forest (Larsen *et al.*, 1999; Larsen and Johnson, 1998). In xeric forests such as the Missouri Ozarks, oaks can compensate for their low shade-tolerance by using physiological adaptations that allow them to grow better on xeric sites than their competitors (Hodges and Gardner, 1993; Larsen and Johnson, 1998).

Chapter 2: Introduction

Over the past two decades, foresters at Pioneer Forest, a large private forest in southeastern Missouri purchased by Leo Drey and now owned by the L-A-D Foundation, have become concerned with the sustainability of the forest due to a significant decrease in the abundance of oak reproduction and a lack of oak recruitment. While past research seems to indicate that uneven-aged management can successfully regenerate oaks, there is a knowledge gap that creates uncertainty as to whether it is working in practice. In addition, Pioneer Forest has set operational density targets and a 20-year cutting cycle, however these targets may not always be met, further creating uncertainty. Here we sought to address these concerns by identifying temporal patterns and associated factors affecting key regeneration populations for sustaining uneven-aged oak forests, including seedlings, saplings, and ingrowth into the overstory. Because oak regeneration is a process rather than a discrete event, it is necessary to analyze regeneration at various points within the process and analyze the effects of explanatory variables on each of these points. The continuous forest inventory (CFI) at Pioneer Forest provides an excellent opportunity to do this due to the longitudinal nature of the CFI, spanning over 70 years, and the regeneration measurements taken during the CFI, which include seedlings, saplings, and overstory trees.

Because past research has demonstrated significant differences between the characteristics of oak reproduction establishment and recruitment, we anticipate that each of these three groups will be influenced in different ways by each site factor (Figure 1) and that the interconnectedness between different forms of reproduction will result in cascading effects of site and stand characteristics, where effects on the abundance of younger regeneration will have cascading effects on the abundance of older regeneration. For example, we expect that soil characteristics will have a different effect on seedling abundance than on either sapling abundance or ingrowth into the overstory. We also expect that any reduction or paucity in seedling abundance will result in a reduction in sapling abundance on the same site in future years.

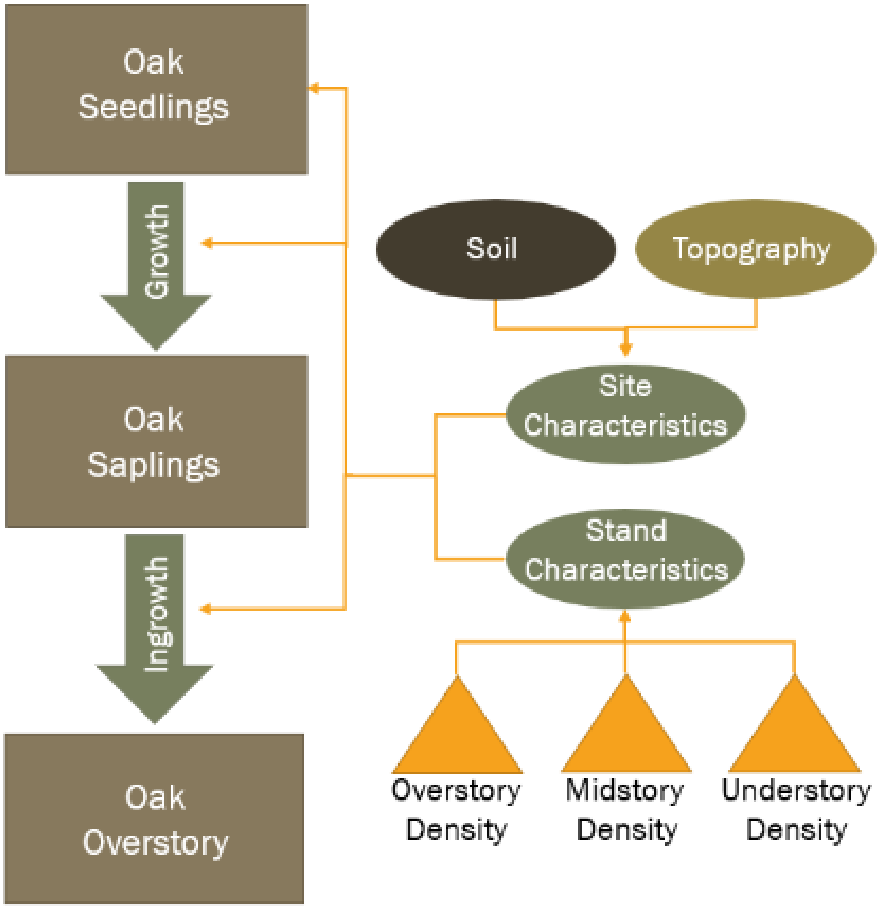

Figure 1. Diagram of the relationships of interest between various forms of regeneration, and site characteristics and stand density.

In this study, we used data from the CFI at Pioneer Forest to determine the relationship between white oak reproduction and recruitment, and stand characteristics including soil, topography, and stand density. In addition, we studied the relationship between stand structure and understory sunlight levels. We determined if soil and topographic characteristics are drivers of white oak reproduction establishment and recruitment and quantified temporal effects resulting from these characteristics. We also determined the relationship between overstory density and white oak reproduction establishment and recruitment and determined if this relationship is related to changes in understory sunlight levels. Finally, we determined the relationship between past white oak regeneration abundance and regeneration abundance in subsequent years.

Objectives and Hypotheses

- Objective 1: Determine if understory sunlight levels are correlated with stand stocking, basal area, and midstory density.
    a. H_0- Understory sunlight levels are not correlated with stand stocking.
    H_a- Understory sunlight levels have a negative correlation with stand stocking.
    b. H_0- Understory sunlight levels are not correlated with overstory basal area.
    H_a- Understory sunlight levels are negatively correlated with overstory basal area.
    c. H_0- Understory sunlight levels are not correlated with midstory density.
    H_a- Understory sunlight levels are negatively correlated with midstory density.
- Objective 2: Determine the effects of topo-edaphic characteristics on temporal trends in white oak regeneration abundance in xeric/mesic-xeric oak-hickory forests.
    a. H_o-Topographic characteristics including aspect, topographic position index (TPI), and slope gradient do not have a significant effect on trends in white oak regeneration abundance.

H_a-Topographic characteristics resulting in more xeric conditions (e.g., exposed south and west aspects) have significantly higher trends in white oak regeneration abundance than more mesic topographic characteristics.

b. H_0-Edaphic characteristics including available water capacity (AWC), soil pH, and depth to restriction do not have a significant effect on trends in white oak regeneration abundance.

   H_a-Edaphic characteristics resulting in more xeric conditions (e.g., lower AWC, lower pH, or shallower soil depth) have significantly higher trends in white oak regeneration abundance than more mesic edaphic characteristics.

- Objective 3: Determine and compare the effects of (concurrent) stand stocking and lagged stand stocking on trends in white oak reproduction and recruitment abundance in xeric/mesic-xeric oak-hickory forests.

  a. H_0-There is no significant difference between the effects of concurrent and lagged stand stocking on trends in white oak regeneration abundance.

     H_a-Lagged stand stocking has a significantly stronger effect on trends in white oak regeneration abundance than concurrent stand stocking and as the number of lagged years increases the strength of the effect on trends in white oak regeneration abundance increases.

  b. H_0-Neither concurrent nor lagged stand stocking have a significant effect on trends in white oak regeneration abundance.

     H_a-Increasing concurrent and lagged stand stocking result in decreasing white oak regeneration abundance.

- Objective 4: Determine and compare the effects of concurrent and lagged prior populations on trends in white oak regeneration abundance.
    a. H_0-Neither concurrent nor lagged prior populations of white oak regeneration a significant effect on trends in white oak regeneration abundance.

       H_a-Increasing concurrent and lagged prior populations of white oak regeneration result in increases in trends of white oak regeneration abundance.
    b. H_0-There is no significant difference between the effects of concurrent and lagged prior populations of white oak regeneration on trends in white oak regeneration abundance.

       H_a-Lagged prior population abundance has a significantly stronger effect on trends in white oak regeneration abundance than concurrent prior population abundance and as the number of lagged years increases the strength of the effect on trends in white oak regeneration abundance increases.

Chapter 3: Methods

Study Site

The study site for this work was Pioneer Forest, an approximately 150,000-acre, private forest located in southeastern Missouri. Pioneer Forest was originally purchased by Leo Drey from National Distillers in 1951 under an agreement whereby National Distillers could have unrestricted harvests for the first 5 years of Drey's ownership. In 1952, the continuous forest inventory (CFI) plots used in this study were established on the forest. Under the ownership of Leo Drey, Pioneer Forest has since been managed using uneven-aged, single-tree selection.

Pioneer Forest is located in the Current River Hills subsection of the Ozark Highlands (NRCS, 2022). The topography encompasses unglaciated, deeply dissected hillslopes, steep ridges, and broad flat ridge tops (NRCS, 2022; Meinert *et al.*, 1997). Soils are rocky, droughty, and generally composed of gravelly silt loam, with an occasional top layer made up of decayed plant material (Web Soil Survey, 2022). Soils are generally derived from slope alluvium over residuum weathered from either cherty dolomite or cherty limestone, with some soils derived from loess over pedisediment over dolomite or limestone residuum (Web Soil Survey, 2022; Hammer, 1997). Soils usually have a low to very low available water capacity that ranges from 0.04 in/in to 0.18 in/in, a pH between 4.5 and 7.8, and a depth to restriction ranging from 10.6 in and 79 in (Web Soil Survey, 2022). Commonly associated plant communities are dry chert and dry sandstone woodlands (Nelson, 2005). Dominant plant species include white oak, black oak (*Quercus velutina* Lam.), shortleaf pine (*Pinus echinata* Mill.), and black hickory (*Carya texana* Buckley) in the overstory and fragrant sumac (*Rhus aromatica* Aiton), lowbush blueberry (*Vaccinium pallidum* Aiton), and service berry (*Amelanchier arborea* (F. Michx.) Fernald) in the understory (Nelson, 2005).

Data Collection

This study uses longitudinal data collected from the overstory, midstory, and understory at Pioneer Forest. Overstory data consists of a CFI started in 1952 shortly after the acquisition of the forest. The inventory began with 132, 0.2-acre circular plots measured every 5 years. In 1957, 60 additional plots were added and a plot was added 5 chains north of all established plots, bringing the total number of plots to 383 (including plots added and lost through land acquisitions and sales). The first 200 plots were placed within each full section owned by Pioneer Forest, in the center of a randomly selected 40-acre quarter-quarter section. Plots 401 through 498 were placed in the center of the sixteenth 40-acre parcel of ownership. All subsequent plots are placed randomly within each section. As of 2017, the total number of plots was 448. Within these plots, all trees ≥ 5 in DBH are numbered and have their species recorded. These trees are measured for DBH, total height, soundness, cause of mortality (if relevant), and other operational metrics.

Beginning in 1992, Pioneer Forest began sampling midstory trees on the 0.2-acre overstory plots and understory trees on 0.02-acre sampling plots nested within the overstory plots. Within all overstory plots, midstory stems (all woody plants between 1.5 and 4.9 in DBH) were measured for DBH and height, with species recorded. Understory plots were 0.02-acre, circular plots placed at the center of 100 CFI plots selected using a stratified design based on aspect, slope, soil depth, and soil quality. Within these plots, all woody plants under 1.5 in DBH were tallied and measured for species, DBH (if applicable), diameter at root collar, and height.

Sunlight levels were quantified from a subsample of CFI plots during the summer of 2021. These plots were stratified on stocking percent and site index. Stocking percent from the 2017 data was grouped into 6 bins by increments of 10 from 40% to 100%. Site index was estimated for black oak at base age 50 and was grouped into 3 bins, in increments of 10 from 50ft to 80ft. Site index data were from Larsen (1980) and in some cases converted from white oak or scarlet oak site index to black oak site index using the equations of McQuilkin (1974). For each combination of stocking percent and site index, 3 plots were randomly selected for light measurements, for a total of 54 observations. Sunlight levels were measured using hemispherical photography and the program HemiView (Delta-T Devices, Cambridge, UK), following the classification instructions in the HemiView users-manual (Delta-T Devices, 1999). Photos were taken with a Canon EOS 70D camera (Canon Corporation, Tokyo, Japan) and a Sigma EX DC 4.5mm Fisheye Lens (Sigma Corporation, Tokyo, Japan) on a tripod. These photos were taken under either overcast skies with direct sunlight obscured or during dusk after the sun had set. The camera was placed directly over plot center, leveled, and raised to approximately 4.5ft on the tripod. Any foliage above the camera was removed up to head height to eliminate any bias from leaves close to the lens. A marker placed on the edge of the camera lens was aligned to magnetic north with a compass. Because four years had passed between the last inventory and the sunlight photographs, all trees at or above 5 in DBH were re-measured to determine current stand structure.

To determine soil and topographic characteristics for plots at Pioneer Forest, polygon shapefiles of plot boundaries were created in ArcMap and imported into the Web Soil Survey provided by the NRCS (2022). Soil data were exported from the Web Soil Survey and transferred to ArcMap using Microsoft Access and Soil Data Viewer (NRCS, 2022), where shapefiles of depth to any restriction, soil pH (1 to 1 water), and Available Water Capacity (AWC) were created (Table 1). For all soil characteristics, all soil layers were used, aggregation was done with a weighted average, and no cut-off was used. The default lower tie break rule was selected for depth to restriction while the program default higher tie break rule was used for soil pH and AWC. These soil shapefiles were then joined to a plot coordinate point shapefile using the spatial join tool in ArcMap, and the table of the plot coordinate shapefile was exported to Excel for analysis. Topographic data including slope gradient, slope position (calculated as topographic position index (TPI) (Weiss, 2001)) and slope aspect were calculated using QGIS by importing 32ft derived digital elevation model rasters for the study area from the Missouri Spatial Data Information Service (Missouri Spatial Data Information System (MSDIS), 2021) (Table 1). These rasters were analyzed using the Aspect, Position, and TPI tools in the raster analysis toolbox. Data from the resulting rasters were then joined to the GPS coordinates for the Pioneer Forest plots using the Sample Raster Tool in QGIS.

Table 1. Means, standard deviations, and ranges of site characteristics of interest at Pioneer Forest.

Variable	Mean	Standard Deviation	Range
Slope Gradient	21.20%	11.90%	0.53 to 57.07%
TPI	0.01	0.27	1.26 to 1.11
Soil AWC	0.09in/in	0.02in/in	0.04 to 0.18in/in
Soil pH	5.2	0.49	4.5-7.8
Soil Depth	29.9in	14.1in	10.6-79.1in

Data Analyses

The data in this study were analyzed using multiple regressions and generalized linear mixed models (GLMMs). GLMMs were used because of their compatibility with non-normal data, both categorical and quantitative data, and the ability of GLMMs to analyze repeated measures, while multiple regressions are easily interpreted and provide a simple method of prediction.

To determine the effect of site characteristics on understory sunlight levels, we used the indirect site factor (ISF) and direct site factor (DSF) calculated in HemiView to determine the Gap Light Index (GLI) (Canham, 1988) of each plot ($GLI = [(T_{diffuse} P_{diffuse}) + (T_{beam} P_{beam})]*100$), where ISF is $T_{diffuse}$ and DSF is T_{beam} (Delta-T Devices, 1999) and both $P_{diffuse}$ and P_{beam} are 0.5 (Battaglia *et al.*, 2003; Knapp *et al.*, 2016). GLI has been found to be a better representation of light availability than the components of GLI by themselves (Canham, 1988). Using the current stand structure determined when sunlight photographs were captured, basal area and stocking percent (Gingrich, 1967) were calculated. Midstory abundance estimates were taken from measurements done in 2017 and included all trees in the midstory. Analysis of this data was done by constructing both simple and multiple regression models that compare the Gap Light Index to stocking percent, basal area, the number of trees in the midstory, and the site index measured by Larsen (1980) using linear and non-linear regression. Goodness of fit was determined by the highest R-Square value (Objective 1).

We defined recruitment as the number of trees that grew into the overstory (ingrowth) in a plot between measurements. Recruitment trees were determined by giving each tree in the CFI plots a unique identifier and determining the first year of occurrence for that identifier. Because it is not possible to determine which trees were recruited each year without data from the prior year, all plots without a prior measurement were excluded from the data. In many cases we noticed that there were ingrowth trees with impossibly large increases in diameter when growing into the overstory (e.g., an ingrowth tree of 10 in DBH when the overstory starts at 5 in DBH). To rectify these errors, we determined the diameter increment of each tree the measurement after growing into the overstory and used the 3rd standard deviation plus the average of these values to exclude possible outliers. This excludes any ingrowth trees that were above 7.2 in DBH. Overstory oak abundance and midstory and understory oak and non-oak abundance were calculated from the CFI, midstory, and understory plots measured by Pioneer Forest. AWC, pH, depth to restriction, TPI, slope aspect, and slope gradient values were taken from plot GPS points and exported to excel for analysis. We noticed a large amount of error in the plot GPS points. We determined that this error impacted the accuracy of the TPI, slope aspect, and slope gradient (topographic) data but had less of an effect on the AWC, pH, and depth to restriction data by recording more accurate coordinates on roughly 20 plots and using a confusion matrix and standard deviations to compare these more accurate coordinates to the less accurate coordinates. During this analysis, we found that much of the GPS error for soil characteristics was similar to the error already inherent in soil maps used to generate them and thus they did not substantially alter the calculated soil characteristic. On the other hand, the GPS error for topographic characteristics frequently had substantially different results, largely due to sudden changes in topography (e.g., a plot near the top of the northern aspect of a ridge only takes a small amount of error to be recorded as a southern aspect plot). The topographic data were retained to determine if further investigation with less error was warranted, and we attempted to collect more accurate coordinates using a high precision GPS. Unfortunately, only approximately 40 plot coordinates could be rectified due to time constraints.

Relationships between the topographic, soil, and stand density variables (Objectives 2 and 3) and the response variables (seedling abundance, sapling abundance, ingrowth) were modeled with GLMMs. The model used for oak ingrowth and sapling abundance was seedlings was of the following form:

$$\log_e \mu_i = \alpha + \beta_1 X_{site} + \beta_2 X_{Year} + \beta_3 X_{site} X_{Year} + Z_1 \upsilon_{Year} + Z_2 \upsilon_{Plot} + Z_3 \upsilon_{Pair} + \epsilon$$

With β_x and Z_x being the incidence matrix corresponding to fixed and random effects, respectively, and X_x and υ_x being the vector of fixed and random effects, respectively. In this model, $\log_e \mu_i$ is the log link function for the type 1 negative binomial distribution, α is the intercept of the model, and ϵ is the vector of random residuals. The same model was used to analyze seedling abundance, except the $Z_1 \upsilon_{Year}$ and $Z_3 \upsilon_{Pair}$ random effects were replaced by a first-order autoregressive structure with a year by pair random effect without an intercept for year, as recommended by Kristensen and McGillycuddy (2021). Post-hoc model diagnostics were conducted using a residual qq plot and inference was conducted using estimated marginal means (EMM) contrasts and type III analysis of variance.

We were also interested in the relationship between smaller size classes and larger size classes to test the assumption that the population of saplings in a stand are correlated with the population of seedlings in a stand and that the amount of ingrowth in a stand is correlated with the number of saplings in a stand (also referred to as prior populations) (Objective 4). We tested this assumption by building models with sapling and seedling abundance as explanatory variables for ingrowth and sapling abundance, respectively.

To further discern the effect of time on the relationship between both stocking and prior populations on oak regeneration, we created lagged measures of these variables. Lagged measures refer to the measure of an explanatory variable a certain amount of time prior to a response variable (Objectives 3 and 4). For example, 5-year lagged stocking is the stand stocking 5 years prior to a response variable of interest such as ingrowth (e.g., Stocking in 1992 is compared to ingrowth in 1997, stocking in 1997 is compared to ingrowth in 2002, etc.). The concurrent (non-lagged) and lagged seedling, sapling, and stocking models were analyzed using the following GLMM using only data from 2017:

$$\log_e \mu_i = \alpha + \beta_1 X_{density} + Z_1 \upsilon_{Pair} + \epsilon$$

These models were compared using the highest marginal r-square values. The lag with the highest marginal r-square was further analyzed using the same models as those for the sapling and ingrowth abundance topographic and edaphic characteristics with all years included.

Chapter 4: Results

General Results

Over the past 20 years white oak sapling abundance has declined from an average of 143 stems/acre in 1992 to 34 stems/acre in 2017, and white oak seedling abundance has declined from an average of 1000 seedlings/acre in 1992 to 522 seedlings/acre in 2017 (Figure 2). Over that same period, average stand stocking has increased from 54.9% to 73.6%. From 1957 to 2017, overstory ingrowth declined from 0.97 trees/acre/year to 0.67 trees/acre/year, while average stand stocking increased from 32.0% to 70.6%.

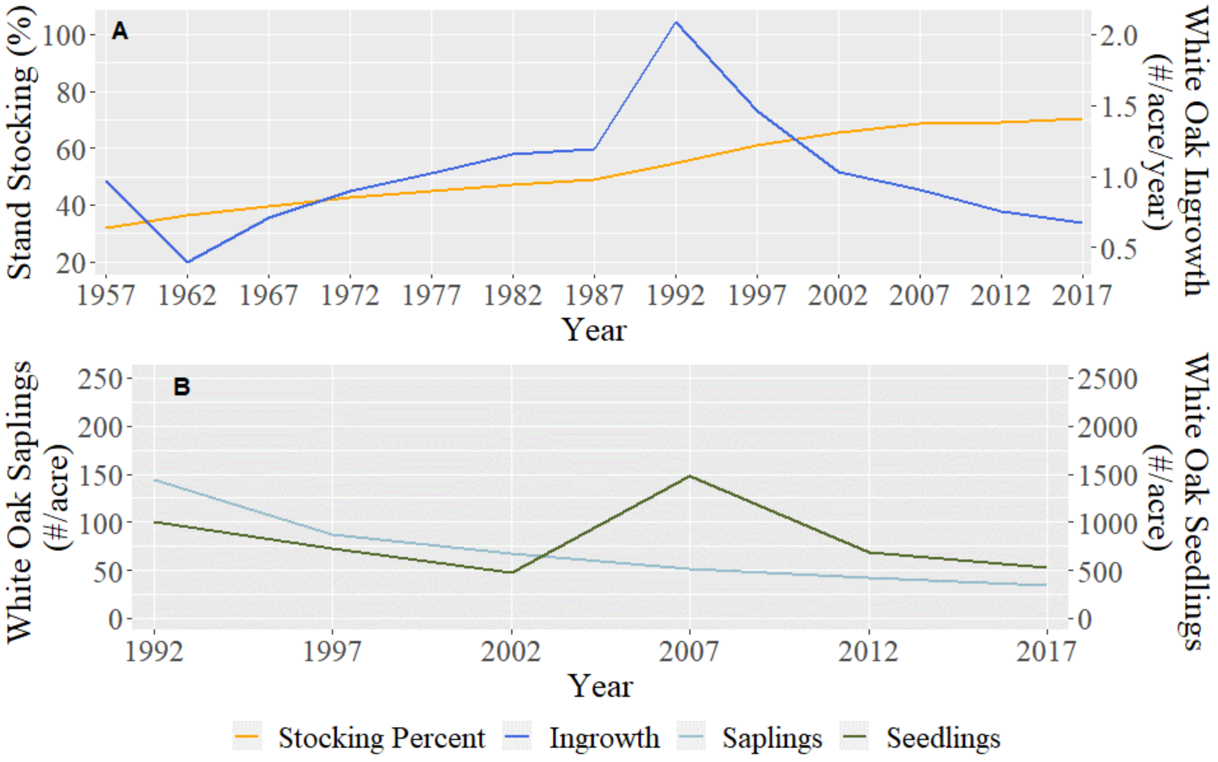

Figure 2. Temporal trends in average stand stocking and white oak ingrowth (A), and average white oak seedling and sapling abundance (B) at Pioneer Forest.

Density and Understory Sunlight

GLI was not significantly correlated with stocking percent but was significantly correlated with both basal area and trees per acre. Basal area had the strongest correlation with GLI when compared to stocking percent and trees per acre (Table 2). There was a positive relationship between GLI and both basal area and TPA (Figure 3). All species sapling abundance was significantly correlated with GLI and greatly improved the fit of the model when included with basal area.

Table 2. Results of simple and multiple regression models analyzing the relationship between understory sunlight and stand density metrics.

Model	Term	Estimates	P-value	Adjusted R-square
Stocking Percent (SP)	SP	-0.11	0.704	-0.02
Basal Area (BA)	BA	0.07	0.006	0.12
Trees Per Acre (TPA)	TPA	0.03	0.028	0.07
Sapling Abundance (SA)	SA	-0.02	0.007	0.11
Basal Area (BA) + Sapling Abundance (SA)	BA	0.06	0.01	0.21
	SA	-0.01	0.013	
Basal Area*Sapling Abundance	BA	0.06	0.27	0.19
	SA	-0.01	0.587	
	BA*SA	-0.0001	0.986	

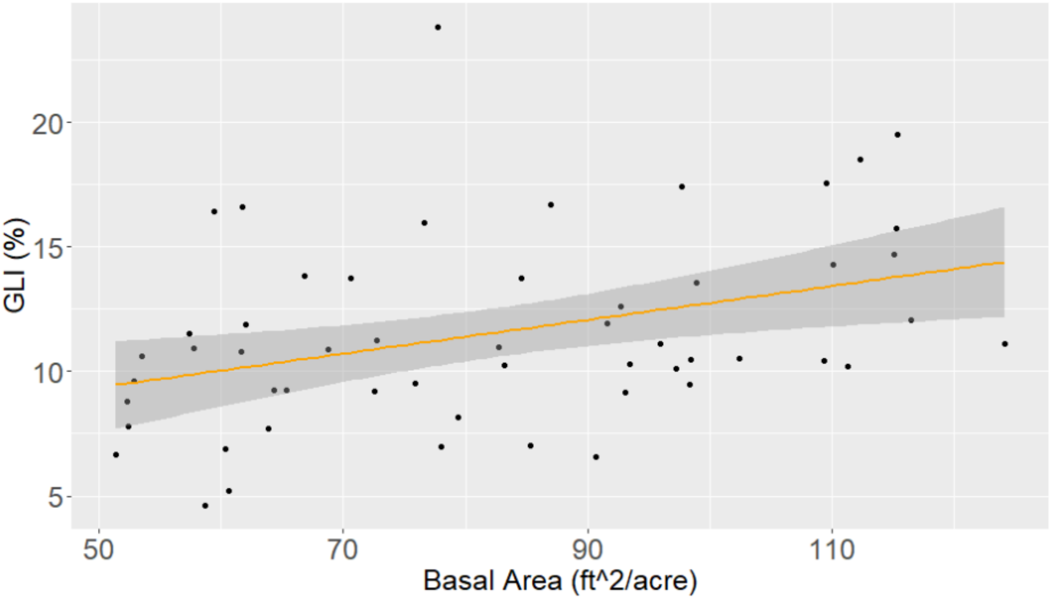

Figure 2. An estimate of the mean and standard error of the GLI across different stand basal areas (ft^2/acre) under uneven-aged management at Pioneer Forest.

Topo-edaphic Characteristics

For the white oak seedling population, there were significant interactions between the site variable and year for aspect class, slope gradient, AWC, and soil depth to restriction (Table 3). There was also a main effect for aspect class and year in the aspect class model. There were no significant main effects or interactions with year for pH or TPI class.

Table 3. ANOVA results of GLMMs estimating the relationship between white oak seedling abundance and site characteristics, including aspect class, slopes gradient, TPI class, AWC, soil pH, and soil depth to restriction, over time. Each model includes the site variable, year, and an interaction between them as fixed effects.

Model	Effect	Chi-square	df	P-value
Aspect Class*Year	Aspect	8.20	3	0.042
	Year	21.47	5	<0.001
	Aspect*Year	31.36	15	0.008
Slope Gradient*Year	Gradient	2.88	1	0.090
	Year	27.37	5	<0.001
	Gradient*Year	12.20	5	0.032
TPI Class*Year	TPI	6.88	5	0.230
	Year	6.99	5	0.221
	TPI*Year	36.10	25	0.070
AWC*Year	AWC	2.58	1	0.108
	Year	24.39	5	<0.001
	AWC*Year	30.77	5	<0.001
Soil pH*Year	pH	1.21	1	0.271
	Year	4.79	5	0.441
	pH*Year	5.04	5	0.412
Soil Depth to Restriction*Year	Depth	0.06	1	0.806
	Year	29.65	5	<0.001
	Depth*Year	11.92	5	0.036

Although variable through time, white oak seedlings were generally more abundant on south and west facing slopes than on north and east facing slopes (Figure 4). East slopes had significantly fewer seedlings than west slopes in 1992 (p = 0.039) and 2012 (p = 0.003) and fewer seedlings than south facing slopes in 2012 (p = 0.038). North slopes had significantly fewer seedlings than west slopes in 2002 (p = 0.016), 2012 (p = 0.010), and 2017 (p = 0.001) and fewer seedlings than south facing slopes in 2017 (p = 0.002). On east facing slopes, there were significantly fewer seedlings in 1997 than in 2012 (p=0.004) and in 1997 than in 2017 (p=0.004). On north facing slopes, there were significantly fewer seedlings in 1992 than in any other years except 1997 and 2007 (p<0.006), in 1997 than in 2017 (p=0.003), and in 2007 than in both 2012 and 2017 (p=0.046 and <0.001). There were also significantly more seedlings in 2002 than in 2007 (p=0.004). There were no statistically significant changes over time on south and west facing slopes.

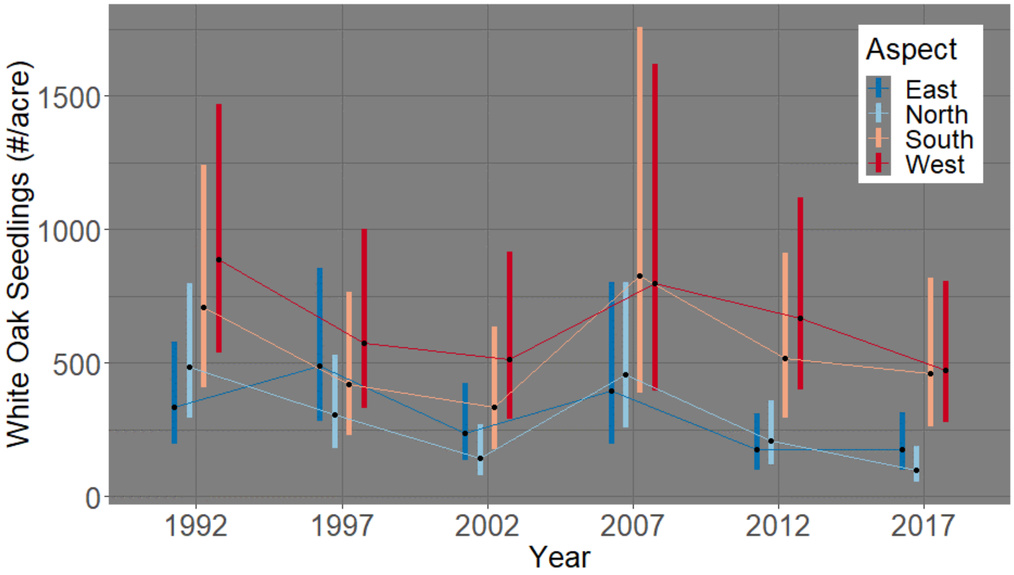

Figure 3. Estimated means and standard errors for white oak seedling abundance through time by slope aspect under uneven-aged management at Pioneer Forest.

There was a negative relationship between slope gradient and seedling abundance in all years. The only significant difference in the slope coefficients among years was for the pairwise comparison of 1992 and 2007 ($p=0.011$). White oak seedling population density was much higher on sites with low slope gradients; however, this relationship was only strong in 2007 (Figure 5A). For AWC, there were significant differences between the slope in 2007 and all other years ($p<0.003$). In all years the relationship between AWC and seedling abundance was positive (Figure 5B). While the only significantly different slope occurred in 2007, the predicted white oak seedling values in 2007 were unreasonably large (e.g., 3000 seedlings per acre at 0.11in/in AWC). This may have been the result of outliers and a small sample size in that year at high AWC values. Because of this, we decided to exclude results for 2007 from our graphs and discussion. In 1992, 2012, and 2017, the relationship between depth to restriction and seedling abundance was positive, however in 1997, 2002, and 2007 the relationship was negative (Figure 5C).

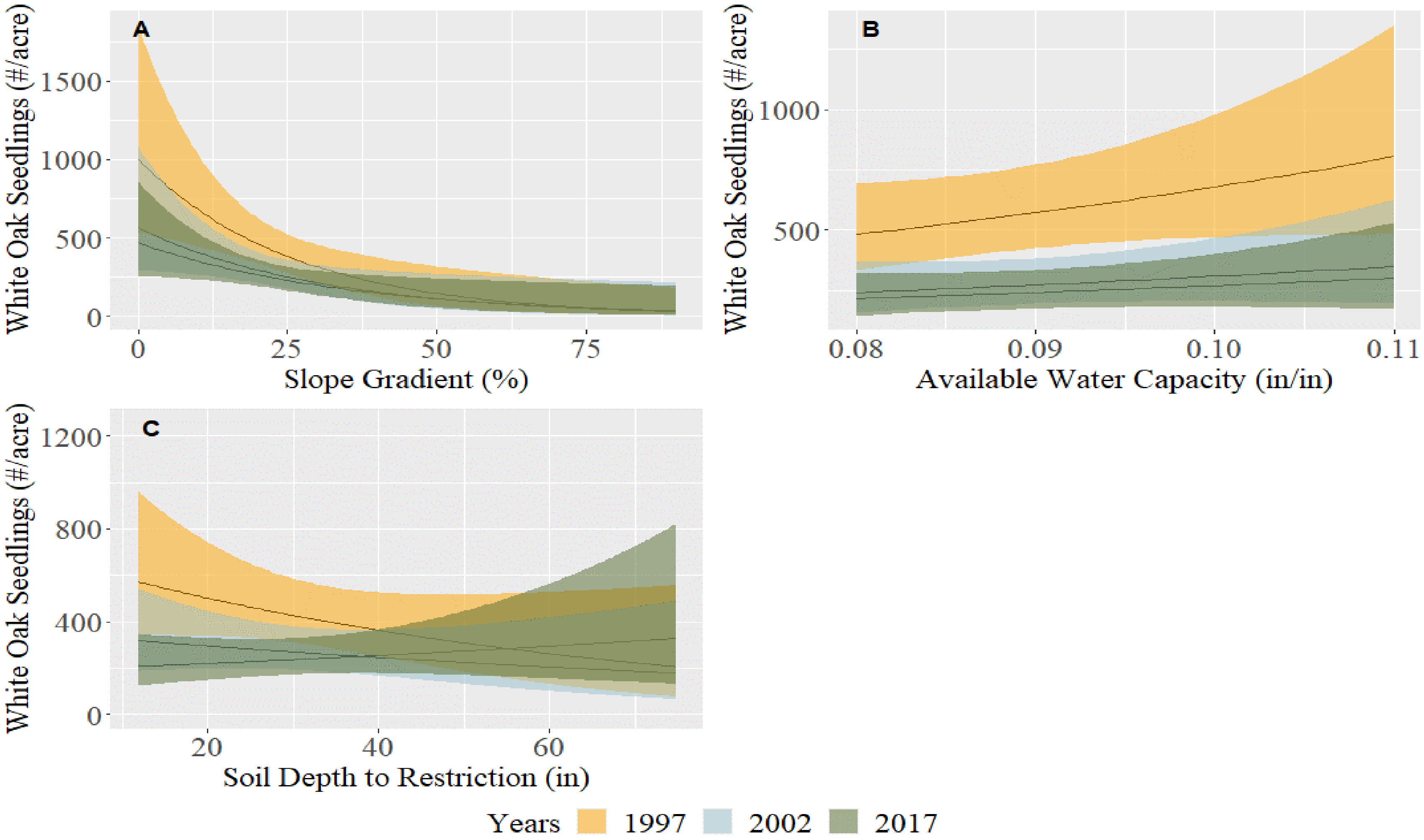

Figure 4. Estimated marginal mean and standard errors of white oak seedling abundance across different site characteristics, including slope gradient (A), soil available water capacity (B), and soil depth to restriction (C), in 1997, 2002, and 2017 under uneven-aged management at Pioneer Forest.

For white oak sapling abundance, there were significant main effects as well as interactions for slope aspect and soil depth to restriction (Table 4). There were significant interactions but no significant main effect for TPI class and soil acidity. There were no significant main effects or interactions for AWC and slope gradient.

Table 4. ANOVA results of GLMMs estimating the relationship between white oak sapling abundance and site characteristics. Each model includes the site variable, year, and an interaction between them as fixed effects.

Model	Effect	Chi-square	df	P-value
Aspect Class*Year	Aspect	14.53	3	0.002
	Year	385.64	5	<0.001
	Aspect*Year	63.84	15	<0.001
Slope Gradient*Year	Gradient	0.58	1	0.448
	Year	136.74	5	<0.001
	Gradient*Year	10.04	5	0.074
TPI Class*Year	TPI	6.21	5	0.286
	Year	23.35	5	<0.001
	TPI*Year	41.63	25	0.020
AWC*Year	AWC	2.07	1	0.151
	Year	13.19	5	0.022
	AWC*Year	3.85	5	0.571
Soil pH*Year	pH	1.00	1	0.317
	Year	28.14	5	<0.001
	pH*Year	49.44	5	<0.001
Soil Depth to Restriction*Year	Depth	21.47	1	<0.001
	Year	37.44	5	<0.001
	Depth*Year	93.69	5	<0.001

For aspect class and sapling abundance, west facing slopes had significantly more saplings than east facing slopes in 2007 and 2012 (p = 0.015 and 0.041, respectively) and west facing slopes had significantly more saplings than north facing slopes in 2017 (p = 0.036) (Figure 6A). There were also significantly more saplings on east facing slopes than on north, south, or west facing aspects in 1992 (p = 0.014, 0.016, and 0.012, respectively). Over time, there were significant declines in sapling abundance on all slopes and between most years. All pairwise comparisons between years were significant except comparisons between 2007 and 2012, and 2012 and 2017 on east facing slopes (p<0.035). On north facing slopes the only non-significant comparisons were between 1997 and 2002, and 2007 and 2012 (p<0.030). On south facing slopes all comparisons were significant except comparisons between 1992 and 1997, between 2002 and 2007, and between 2012 and 2017 (p<0.043). On west facing slopes all pairwise comparisons were significant except between 1992 and 1997, 1992 and 2002, 1997 and 2002, 2002 and 2007, 2007 and 2012, and 2012 and 2017 (p<0.001).

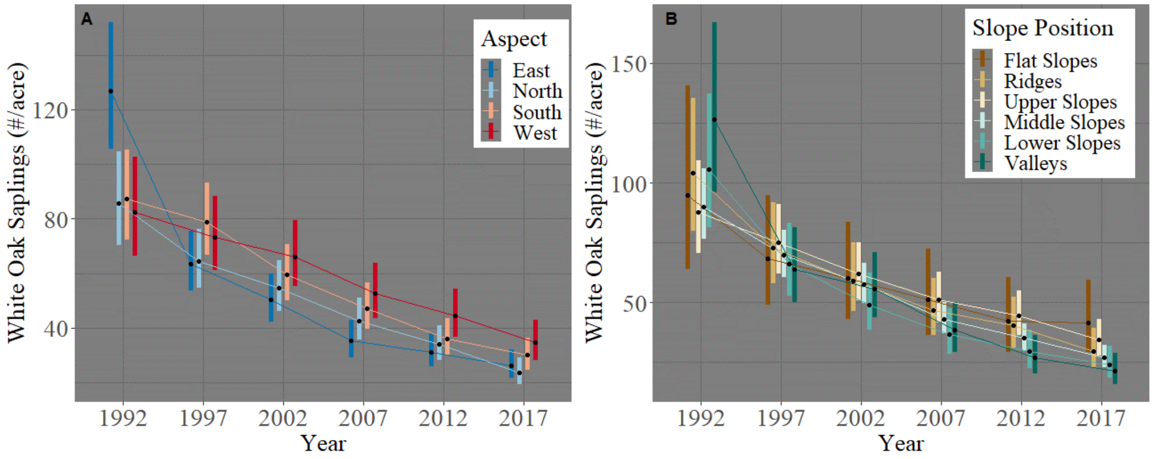

Figure 5. Estimated means and standard errors of oak sapling abundance on different slope aspects (A) and slope positions (B) over time under uneven-aged management at Pioneer Forest.

For saplings, the only significant difference between TPI classes was in 2012 when upper slopes had significantly more saplings than valleys (p = 0.050). There were significantly fewer saplings on all TPI classes in 2017 than in 1992, with the largest differences being on lower slopes and valleys (Figure 6B). Pairwise comparisons between years within TPI classes showed mixed results with some being significant and some not. On flat slopes, the only significant pairwise comparisons were between 1992 and 2007, 1992 and 2012, 1992 and 2017, and 1997 and 2017 (p<0.046). On ridges and upper slopes all pairwise comparisons were significant except between 1997 and 2002, 2002 and 2007, 2007 and 2012, and 2012 and 2017 (p<0.033). There was also a non-significant comparison between 1992 and 1997 on upper slopes. On middle slopes all pairwise comparisons were significant except between 2007 and 2012 (p<0.021). On lower slopes all pairwise comparisons were significant except between 1997 and 2002, 2002 and 2007, 2007 and 2012, and 2012 and 2017 (p<0.043). Finally, on valleys, all pairwise comparisons were significant except between 1997 and 2002, and 2007 and 2012 (p<0.047).

For soil pH there was a negative relationship with sapling abundance in all years except 1992 (Figure 7A). The difference between the slope in 1992 and all other years was statistically significant (p<0.001 for all comparisons). None of the other slopes were statistically different from one another. For soil depth to restriction, there was a negative relationship with sapling abundance in all years except 1992, with 1992 being significantly different than all other years (p<0.001) (Figure 7B). None of the other pairwise comparisons were significant.

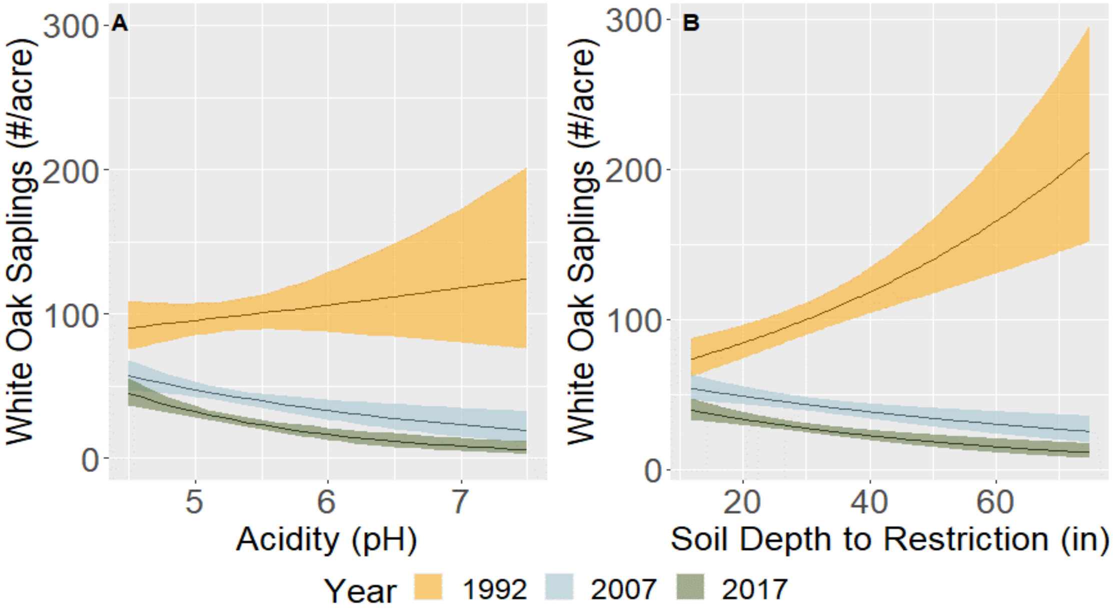

Figure 6. Estimated means and standard errors of white oak sapling abundance across gradients of soil characteristics, including soil pH (A) and soil depth to restriction (B), in 1992, 2007, and 2017 under uneven-aged management at Pioneer Forest.

For ingrowth abundance, slope aspect and soil pH all had significant main effects, however only soil pH had a significant interaction with year (Table 5). While the type III ANOVA found significant main effects for slope aspect, the EMM analysis did not find any significant pairwise comparisons between aspects. This may be due to the different between the marginal means used in the EMM analysis and the non-marginal means used in the ANOVA. Soil depth to restriction did not have a statistically significant main effect, however it did have a significant interaction with year. There were no significant effects of TPI, AWC, and slope gradient.

Table 5. ANOVA results of GLMMs estimating the relationship between white oak ingrowth abundance site characteristics, including aspect class, slopes gradient, TPI class, AWC, soil pH, and soil depth to restriction, over time. Each model includes the site variable, year, and an interaction between them as fixed effects.

Model	Term	Chi-square	df	P-value
Aspect Class*Year	Aspect	9.74	3	0.021
	Year	114.95	12	< 0.001
	Aspect*Year	42.07	36	0.225
Slope Gradient*Year	Gradient	0.01	1	0.942
	Year	90.59	12	<0.001
	Gradient*Year	14.84	12	0.250
TPI Class*Year	TPI	10.36	5	0.066
	Year	22.39	12	0.033
	TPI*Year	70.61	60	0.164
AWC*Year	AWC	0.11	1	0.740
	Year	11.09	12	0.521
	AWC*Year	4.21	12	0.979
Soil pH*Year	pH	32.05	1	<0.001
	Year	96.32	12	<0.001
	pH*Year	84.53	12	<0.001
Soil Depth to Restriction*Year	Depth	3.38	1	0.066
	Year	190.79	12	<0.001
	Depth*Year	61.21	12	<0.001

For ingrowth, the slope coefficients of the relationship between soil pH and ingrowth abundance were negative in all years except 1957 and 1962 (Figure 8A). The only significant contrasts were between the slope in 1957 and all other years except 1962 ($p<0.020$), and between the slope in 1962 and all other years except 1967 and 1972 ($p<0.003$) For soil depth to restriction, the slope coefficients of the relationship between depth to restriction and ingrowth abundance were only significantly different in 1962 and 1967, where they differed from all other years except each other and the slope coefficient in 1972 ($p<0.020$ and 0.031, respectively). Before 1977, the relationship between depth to restriction and ingrowth appeared to be positive, however during and after 1977, the relationship was negative (Figure 8B). It is important to note that there is a large gap in sampling between 40 and 75in soil depth and the data in that range may not be representative of actual conditions.

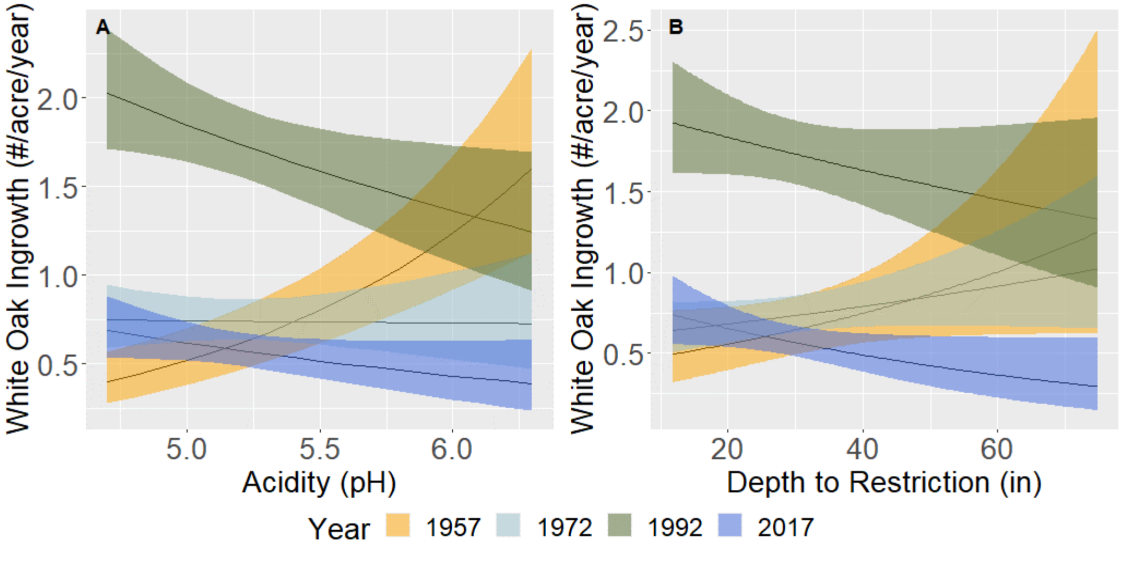

Figure 7. Estimated means and standard errors of white oak ingrowth abundance on different soil characteristics, including soil pH (A) and soil depth to restriction (B), in 1957, 1972, 1992, and 2017 under uneven-aged management at Pioneer Forest.

Stand Density

Neither concurrent nor lagged stand stocking had a significant effect on white oak seedling abundance. For saplings, only the 30-year lagged stocking model was significant, and it had an r-square of 0.014 (Table 6). For white oak ingrowth, only the 5-year lagged stocking was significant with an r-square of 0.017 (Table 7). When 30-year lagged stocking was analyzed in the full model, the r-square increased from 0.014 to 0.266 (Table 8). There was a negative relationship between 30-year lagged stocking and sapling abundance in the full model (Figure 9A). In the full 5-year lagged stocking model for white oak ingrowth, year and the interaction were significant (Table 9). Ingrowth was negatively correlated with lagged stocking in all years except 1962 and 1967 (Figure 9B). The relationship was also non-negative in 1957, however this was not a statistically significant difference from other years and the slope was nearly zero.

Table 6. ANOVA results of GLMMs estimating the relationship between concurrent and lagged stand stocking, and white oak sapling abundance in 2017. All models consisted of a GLMM with a negative binomial distribution and only plot pair as a random effect.

Term	Chi-square	df	P-value	R-squared
Stocking	0.75	1	0.387	
5-year Stocking	1.13	1	0.288	
10-year Stocking	1.05	1	0.305	
15-year Stocking	1.14	1	0.284	
20-year Stocking	2.13	1	0.145	
25-year Stocking	2.27	1	0.132	
30-year Stocking	5.71	1	0.017	0.014

Table 7. ANOVA results for concurrent and lagged stand stocking. All models consisted of a GLMM with a negative binomial distribution and plot pair as a random effect.

Term	Chi-square	df	P-value	R-squared
Stocking	0.30	1	0.587	
5-year Stocking	4.20	1	0.040	0.017
10-year Stocking	0.47	1	0.491	
15-year Stocking	0.09	1	0.761	
20-year Stocking	0.01	1	0.933	
25-year Stocking	0.003	1	0.957	
30-year Stocking	0.03	1	0.860	

Table 8. ANOVA results of the full GLMM estimating the relationship between 30-year lagged stocking and white oak sapling abundance over time. Includes all random effects and a year interaction.

Term	Chi-square	df	P-value	R-squared
30-year Lagged Stocking	6.23	1	0.013	0.266
Year	102.09	5	<0.001	
30-year Lagged Stocking*Year	1.05	5	0.958	

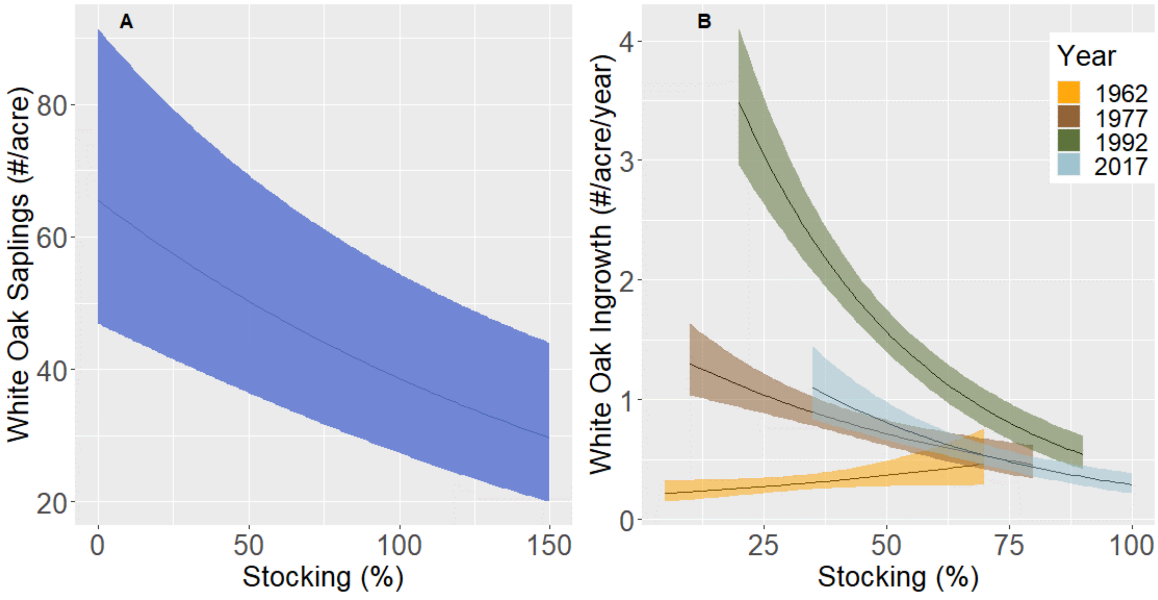

Figure 8. Estimated means and standard errors of white oak sapling (A) and ingrowth (B) abundance across a gradient of 30-year (A) and 5-year (B) lagged stand stocking over time under uneven-aged management at Pioneer Forest.

Table 9. ANOVA results of the full GLMM estimating temporal trends in the effect of 5-year lagged seedling abundance on ingrowth abundance. Model includes all random effects.

Term	Chi-square	df	P-value	R-squared
5-year Lagged Stocking	0.03	1	0.086	0.238
Year	292.16	12	<0.001	
5-year Lagged Stocking*Year	73.49	12	<0.001	

Prior Populations

Of the models analyzing the effect of seedling abundance on sapling abundance in 2017, only the 10-year lag was not statistically significant. The best fitting lag was the 20-year lag with an r-square of 0.151 (Table 10). In the full model, the main effect was not significant, however both year and the interaction between year and 20-year lagged seedling abundance were significant (Table 11). The relationship between 20-year lagged seedling abundance and sapling abundance was positive with sapling abundance increasing as seedling abundance increases (Figure 10A).

Table 10. ANOVA results for the analysis of the effect of various lags in seedling abundance on sapling abundance in 2017. Models were GLMMs with a negative binomial distribution with only plot pair as a random effect.

Term	Chi-square	df	P-value	R-squared
Seedlings	4.25	1	0.039	0.037
5-year Seedlings	3.94	1	0.047	0.050
10-year Seedlings	1.53	1	0.216	
15-year Seedlings	5.74	1	0.017	0.060
20-year Seedlings	16.37	1	<0.001	0.151

Table 11. ANOVA results of the full GLMM estimating temporal trends in the effect of 20-year lagged seedling abundance on sapling abundance. Model includes all random effects.

Term	Chi-square	df	P-value	R-squared
20-year Lagged Seedlings	0.001	1	0.982	0.272
Year	42.17	5	<0.001	
20-year Lagged Seedlings *Year	11.17	5	0.048	

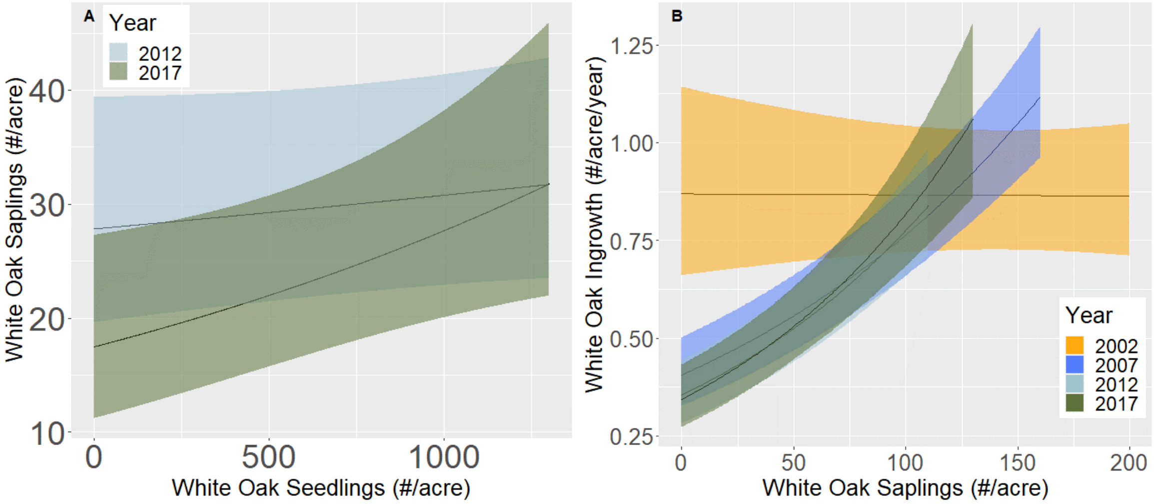

Figure 9. Estimated means and standard errors of white oak ingrowth (A) and sapling (B) abundance across a gradient of 20-year lagged sapling (A) and 10-year lagged seedling (B) abundance over time under uneven-aged management at Pioneer Forest.

All of the models comparing ingrowth in 2017 to concurrent and lagged sapling abundance were statistically significant (Table 12). The best fitting model was the 10-year lagged sapling abundance model with an r-square of 0.154. In the full model for 10-year lagged sapling abundance, only year and the interaction between year and 10-year lagged sapling abundance were significant (Table 13). In the full model, the relationship between 10-year lagged sapling abundance and ingrowth abundance was positive for all years except 2002 (Figure 10B).

Table 12. ANOVA results for GLMMs estimating the effect of various lags in sapling abundance on ingrowth abundance in 2017. Models had a negative binomial distribution with only plot pair as a random effect.

Term	Chi-square	df	P-value	R-squared
Saplings	65.14	1	<0.001	0.121
5-year Saplings	65.70	1	<0.001	0.116
10-year Saplings	69.88	1	<0.001	0.154
15-year Saplings	75.32	1	<0.001	0.148
20-year Saplings	36.91	1	<0.001	0.075

Table 13. Results of the full GLMM estimating temporal trends in the effect of 20-year lagged seedling abundance on sapling abundance. Model includes all random effects.

Term	Chi-square	df	P-value	R-squared
10-year Lagged Saplings	0.002	1	0.966	0.153
Year	34.48	3	<0.001	
10-year Lagged Saplings *Year	60.88	3	<0.001	

Chapter 5: Discussion

Density and Understory Sunlight

There was a positive relationship between basal area and GLI, while there was a negative relationship between midstory TPA and GLI. These relationships were not as strong as those found in past studies under even-aged management (Battaglia *et al.*, 2003; Blizzard *et al.*, 2013). In addition, it was surprising that stocking percent was not significantly correlated at all with understory sunlight levels as past research has frequently found such a relationship (Battaglia *et al.*, 2003; Blizzard *et al.*, 2013). We are not certain why this is the case; however, it may be linked to both stand dynamics under uneven-aged management and the harvesting conducted by Pioneer Forest. After a harvest is conducted it may take time for the understory and midstory to fill in the newly opened growing space and the same is true of the canopy and canopy closure (Oliver and Larson, 1996). Because of this, sunlight and midstory measurements collected too soon after a harvest may be confounded and not represent the true relationship between sunlight levels, and midstory and overstory density.

The poor fit of overstory density metrics may also be due to seedlings and saplings being excluded from overstory density calculations. Under uneven-aged management, overstory density may be reduced to increase understory sunlight levels. However, density reduction also releases oaks and non-oaks in the midstory and understory. These newly released saplings and seedlings may be subsequently reducing understory sunlight levels and thus confounding the relationship between overstory density and sunlight levels. The basal area/sapling model may have a better fit to the data when more recent sapling abundance data is used (sunlight measurements were collected in 2021 while sapling data was collected in 2017) and when collections are not conducted during canopy closure.

Topo-edaphic Characteristics

Past studies have indicated that oak reproduction and recruitment are more abundant on harsh, xeric sites and have been associated with a variety of topographic and soil characteristics (Carvell and Tryon, 1961; Chadwell and Buckley, 2003; Fei and Steiner, 2008; Kabrick *et al.*, 2014; Larsen and Johnson, 1998). Our results generally support the idea that more abundant oak populations occurred on more xeric sites, although we observed variation in the importance of individual topographic and soil factors tested. Additionally, the importance of individual factors differed among the seedling, sapling, and ingrowth populations. For example, we found that topography may not strongly influence white oak recruitment; however, it is a strong driver of white oak seedling abundance. In addition, while soil characteristics were important contributors to both recruitment and reproduction abundance, the drivers were not the same, as soil pH and depth were important drivers of recruitment but not reproduction abundance, while soil AWC had a strong influence on reproduction abundance but not recruitment. Further, we found some cases where reproduction and recruitment were more abundant on sites with mesic characteristics than xeric characteristics.

One of the strongest drivers of white oak seedling abundance in this study was slope aspect, where xeric south- and west-facing slopes had significantly more seedlings than north- and east-facing slopes. Past research has been somewhat inconsistent when determining the relationship between white oak reproduction and slope aspect. Many studies have looked at all oaks combined, rather than red and white oaks separately, and observed that more xeric slopes have more reproduction abundance than mesic slopes (Carvell and Tryon, 1961; Fan *et al.*, 2015; Groninger and Long, 2008; Kabrick *et al.*, 2014). However, when studies examined white oaks separately from red oaks, contradictory results were found. Kabrick *et al.* (2014), for example, determined that white oak reproduction was slightly more abundant on northeastern (mesic) slopes. In contrast, other studies have indicated that white oak reproduction is significantly more abundant on southwest facing slopes (Fei and Steiner, 2008; Groninger and Long, 2008; Jensen and Kabrick, 2008). Our results support the latter, as we found significantly more white oak reproduction on south and west facing slopes in most years.

Slope gradient was another significant topographic driver of white oak seedling abundance; however, surprisingly, the relationship was negative. We anticipated that increasing slope gradient would create harsher site conditions that would be better suited for white oak seedling survival and competition, however we found that white oak seedlings were less abundant on steep slopes than on gradual slopes. Fei and Steiner (2008) observed similar results with a negative correlation between slope gradient and oak reproduction. This may be the result of increased acorn dispersal distance on steep slopes, which may cause acorns to roll to the bottom of a slope when slope gradients are steep, rather than stopping mid-slope (Ohsawa *et al.*, 2007). In addition, site index is generally higher on backslopes than on summits and shoulders, which generally have slopes that are less steep than backslopes. These higher site indices may be increasing competition on steep backslopes, thus decreasing oak seedling abundance.

Soil characteristics generally did not strongly influence white oak seedling abundance in our study. Soil pH was not significantly correlated with seedling abundance. While soil depth to restriction initially appeared to be correlated with seedling abundance, the nature of the relationship alternated from positive to negative over time indicating that soil depth to restriction may still not have a meaningful effect on white oak seedling abundance. Soil AWC was the only soil characteristic meaningfully correlated with white oak seedling abundance and we were surprised to find that it was a positive correlation. Past studies on the effect of plant available water on oak reproduction have found that it usually decreases as AWC increases (Kabrick *et al.*, 2014). It is possible that our results differ from those of Kabrick *et al.* (2014) due to methodological differences including the method used to calculate AWC, the size of the study area, and the fact that this study includes seedlings much smaller than those used by Kabrick *et al.* (2014). Burns and Honkala (1990) indicate that soil moisture may not be a common limiting factor for white oak germination except under extremely dry conditions such as those found in the Ozarks. Our results indicate that low AWC may be inhibiting acorn germination, reducing the population of true seedlings on dry sites and obscuring the effect of AWC on advance reproduction.

In contrast to past studies, we did not find oak reproduction most abundant on mid-slopes and upper slopes and did not find a negative relationship with soil pH (Carvell and Tryon, 1961; 1959; Kabrick *et al.*, 2014). Our differing results may be due to gaps or short comings in the range of pH we were able to analyze.

Most of the site variables for seedlings had some minor variability over time; however, many of them were only between 1 or 2 years and were not in recent years, thus they may not represent current trends in the relationship between these variables and regeneration. There were minor temporal variations in the seedling models for slope gradient and AWC, however in both cases variations only occurred in a single year prior to 2012. These aberrations may be the result of measurement errors or the natural stochasticity inherent in seedling data. Major temporal variations were present in the slope aspect-seedling abundance model, where xeric slopes were only significantly different from mesic slopes in 2017, 2012, 2002, and 1992. It is possible that these temporal variations are the result of changes in seedling population size resulting from mast years as at least 1 non-significant year (2007) corresponds with a large increase in seedling abundance across the whole forest and follows 2 moderately heavy mast years (2005 and 2006) (Olson *et al.*, 1993). Heavy masts may obscure the effect of slope aspect on seedling abundance as masts will initially create large populations of true seedlings on both xeric and mesic aspects with acorns providing them enough nutrients to survive their first year under a wide range of conditions (Johnson, 2009).

Past studies have shown topography to be an important driver of oak recruitment success following even-aged management; however, results from this study suggest that topographic characteristics do not strongly contribute to white oak recruitment abundance under uneven-aged management. While relatively little research has been done on the effects of topography on oak recruitment, Groninger and Long (2008) and Morrissey *et al.* (2008) determined that 15-26 years after clearcutting, oaks made up a larger proportion of new stands and were more competitive on upper and middle slopes and on exposed aspects. Our results do not match those of either Groninger and Long (2008) or Morrissey *et al.* (2008) as we observed that none of the topographic characteristics were significant contributors to white oak ingrowth and while both slope aspect and TPI class were statistically significant factors influencing white oak sapling abundance, TPI class was not a meaningful driver of sapling abundance and slope aspect only weakly contributed to sapling abundance.

These results may differ from past research due to silvicultural differences between even- and uneven-aged management, and differences in methodology. For example, our study analyzed recruitment abundance while both Groninger and Long (2008) and Morrissey *et al.* (2008) studied competitive success and recruitment growth. Both Groninger and Long (2008) and Morrissey *et al.* (2008) conducted their studies on even-aged management following clearcutting, under which oak reproduction is given much more sunlight during and following release than under uneven-aged management. Under these high sunlight conditions, oak reproduction may be unable to out compete non-oak competition that is more abundant on productive topography.

Soil characteristics were somewhat stronger drivers of recruitment abundance than topographic characteristics. Past research has indicated that soil characteristics are also important drivers of oak recruitment competitive success. Researchers have found that oak recruitment competitive success increases with increasingly xeric conditions including shallow soil depths and low water availability (Morrissey *et al.*, 2008). Kabrick *et al.* (2014) determined that advance reproduction abundance was correlated with soil pH, however they did not study recruitment abundance and thus our results for recruitment may differ from theirs. Both soil pH and soil depth to restriction were significant drivers of white oak sapling abundance, however only soil pH was a significant driver of white oak ingrowth abundance. We observed a negative relationship between both soil characteristics and white oak recruitment that matched those observed in past research. Morrissey *et al.* (2008) noted that shallower soils will have lower total available water than deeper soils and this might explain the negative relationship we found between soil depth and recruitment abundance. Lower total available water (total available water = AWC*soil depth) may make the soil susceptible to drying, particularly during droughts and thus may favor the more drought tolerant oaks over less drought tolerant non-oaks (Morrissey *et al.* 2008).

Soil pH may be an important driver of oak recruitment as pH is closely linked to the availability of macronutrients Ca, Mg, and K in the soil and subsequently the abundance of competing plants on a site (Brady and Weil, 1999). Generally, macronutrients, including N and P, are most readily available around a pH of 6.5 and as pH decreases from there, macronutrients become less available (Brady and Weil, 1999; Hammer, 1997; Neina, 2019). Oaks generally require less nutrients and can accumulate more easily than their competitors on low pH sites where nutrients are less available (Fei and Steiner, 2008; Johnson *et al.,* 2009; Kabrick *et al.,* 2014). Our results indicating that oak recruitment is negatively correlated with soil pH support this inference.

There were also temporal variations in the relationship between site variables and recruitment, however the only meaningful temporal variations were between saplings and slope aspect. There were some minor temporal variations in the correlation between soil pH, soil depth, and sapling abundance, and soil pH, soil depth, and ingrowth abundance, however these were generally only single years that may result from typical stochasticity in ingrowth and sapling data or from measurement error. These variations are ephemeral and do not significantly alter the overall trends in the data. The only major temporal variations were between sapling abundance and slope aspect, where only 4 out of 6 years had significant results and 1 of the 4 years had contrary results to the other 3.

The weak, temporally variable results we observed for many of these site characteristics may be the result of a few factors including high GPS error on many plots, low resolution in the elevation rasters used to calculate topographic characteristics, and the stochasticity inherent in oak seedlings. While we attempted to collect more accurate plot coordinates using a more powerful, modern GPS unit, many of the plot locations were not recollected and may have an average error of up to 27m. This error is large enough to significantly change the recorded aspect of a plot, particularly near ridge tops and valleys. The elevation rasters taken from the MSDIS (2022) had a resolution of 10m which could have added some additional, minor error to our analyses.

Stand Density

Past research has frequently shown that both oak reproduction abundance and recruitment are influenced by understory sunlight levels and overstory density. Many authors have indicated that intermediate to high understory sunlight levels are vital for maintaining oak survival and growth (Gottschalk, 1987; 1994; Phares, 1971; Brose and Reddeck, 2017). Unfortunately, understory sunlight levels are difficult to measure operationally and thus many authors have attempted to and succeeded in linking understory sunlight levels with common metrics of stand structure including stand stocking and stand density (Battaglia *et al.*, 2003; Blizzard *et al.*, 2013; Lhotka and Loewenstein, 2006). Because of this link, researchers have found that overstory density is indirectly correlated with both white oak recruitment and reproduction establishment (Larson *et al.*, 1997; Iverson *et al.*, 2017; Green, 2008; Brose and Reddeck, 2017; Vickers *et al.*, 2014; Carvell and Tryon, 1961). Most of these studies, however, were conducted under even-aged management and little research has looked at the effect of overstory density on understory sunlight levels in uneven-aged stands.

Surprisingly, our analyses indicated that overstory density was not a significant factor affecting seedling abundance. Larson *et al.* (1997) indicated that the probability of having more advance reproduction on a site increased as overstory density decreased, however seedling abundance is highly stochastic, and their models are not predictive of individual stands. We believe that our results are the product of the high stochasticity mentioned by Larsen *et al.* (1997). This may be particularly true for our analyses as we were using relatively complex models with a temporal component compared to the simple logistic regression models of Larsen *et al.* (1997). Another possible explanation for the lack of a relationship here is once again the difference between true seedlings and advance reproduction, where understory sunlight levels may not be limiting for true seedlings through their first year (Johnson, 2009). Because sunlight levels are not limiting for true seedlings during their first year, seedlings can develop regardless of how heavily a stand density is reduced. True seedling populations are also greatly affected by mast years which may be creating temporal stochasticity in the data.

We found that while lagged stand stocking was important for both ingrowth and sapling abundance, the optimal lag length for them differed. For ingrowth, the optimal lag length was 5 years, while the optimal lag length for saplings was 30 years. The 30-year lagged stocking model being the best fit for sapling abundance was contrary to our expectations when considering the fact that it should only take seedlings 15 to 20 years to reach the size of a sapling due to their growth rate of 1.2 in DBH per decade and our sapling class starting at 1.5 in DBH (Shifley and Smith, 1982). We were somewhat surprised that the 5-year lagged stocking model was the best fitting model for ingrowth as we expected it to be closer to the lag for the sapling abundance model as it takes many years for saplings to grow to the size of an overstory tree given the slow growth rates of white oaks (Shifley and Smith, 1982). This may be due to the fact that saplings do tend to grow in diameter slightly faster than seedlings and the fact that saplings range from 1.5in DBH to 5in DBH and thus some of them will reach the overstory much quicker than 20 years, however this does not entirely explain the difference between the models for saplings and ingrowth. In addition, past research has suggested that oaks must be in a dominant or co-dominant position to successfully out-compete non-oak competition. Once they are dominant (e.g., saplings), their growth is much greater than those that are not dominant or co-dominant, thus allowing saplings to reach the overstory much more rapidly than oak seedlings, which may or may not be dominant, reach the sapling class after release (Vickers *et al.*, 2014; Vickers *et al.*, 2019). Thus, the sapling class used in our research may be biased towards oaks that are already highly competitive and grow more rapidly.

There were only meaningful temporal variations between 5-year lagged stocking and ingrowth abundance. Prior to and during 1967, the effect of 5-year lagged stocking on ingrowth was positive while it was negative after 1972. This may be the result of a very small range of plot stocking percents in early years due to the heavy cutting that occurred at Pioneer Forest the first 5 years of ownership. This might imply that these models are only accurate or applicable when the full range of possible stocking percents are present in the model.

Prior Populations

We determined that the abundance of prior populations is important for the process of regenerating oaks. As common sense would dictate, there cannot be sufficient ingrowth without sufficient numbers of saplings already in place. Similarly, there cannot be sufficient sapling abundance in the future without sufficient seedlings already in place. This is important for uneven-aged management of oaks as reproduction establishment and recruitment must be occurring continuously to regenerate overstory oaks. This was particularly noticeable with saplings, with insufficient saplings in our data frequently resulting in insufficient ingrowth into the overstory.

We found that lagged measures of prior populations were more important for regeneration success than concurrent measures of prior populations. This supports the well accepted idea that reproduction must be established well in advance of desired recruitment. This has often been phrased as advance reproduction being necessary prior to a significant harvest or disturbance under even-aged management; however, our results indicate that this is also the case for uneven-aged management where discrete events do not reinitiate stand development in the same way they do under even-aged management. We also found that the optimal lag is different for ingrowth and saplings. This outcome is logical considering seedlings and saplings have different growth rates (Shifley and Smith, 1982). The 10-year growth of a sapling is between 1.4 and 1.8 in and the size class for saplings spanned 3.5 in (1.5 to 5 in) DBH (Shifley and Smith, 1982). If we consider that roughly half of the saplings in our dataset were already halfway to 5 in DBH, it makes sense that at that growth rate it would only take approximately 10 years for a statistically significant number of saplings to reach the overstory. In contrast, the optimal lagged prior populations for seedlings does not match the growth rate and size classes for seedlings. The growth rate for seedlings is roughly 1.2 in DBH every 10 years and the size class only spanned 1.5 in, thus we would expect it to take only approximately 10 years to become a sapling. We found that the optimal lag was 20-years instead of 10. This might be explained by the fact that many seedlings persist in the understory as advance reproduction for long periods of time before being released by overstory disturbances. The extra 10 years we observed in optimal lag time may be due to insufficient disturbance to achieve expected growth rates.

Chapter 6: Conclusions

The results found during this study highlight the importance of treating oak regeneration as a process with two distinct phases rather than a discrete event. This is particularly important under uneven-aged management because both reproduction establishment and recruitment must be continuously occurring and thriving throughout the stand rather than occurring independently at distinct times as in even-aged management. Many factors are important for maintaining and encouraging continuous regeneration including topographic, site, and stand characteristics; however, we also found that these factors have varying effects on the different stages of the regeneration process.

Topo-edaphic characteristics are a good example of how the effects of various factors may change based on the stage of the regeneration process. Both white oak reproduction establishment and recruitment were affected by topo-edaphic characteristics, but there were substantial differences in the effects of individual factors on each form of regeneration and there was a large amount of temporal variability. Topographic characteristics were stronger drivers of reproduction abundance than were edaphic characteristics; however, both had significant temporal variation. Topographic characteristics were generally not strong drivers of recruitment, but edaphic characteristics were. In contrast, topographic characteristics were stronger drivers of seedling abundance than edaphic characteristics. In addition, there was substantially less temporal variation in these characteristics for saplings and ingrowth than there was for seedlings.

We anticipated that xeric conditions would increase reproduction and recruitment abundance in all cases. Instead, we found that the relationship was highly dependent on both the metric measured and the stage of regeneration. For example, oak seedling abundance was higher on xeric aspects but was lower on steep slopes and soils with low available water capacity. In contrast, recruitment responded well to xeric conditions in all cases where the explanatory variable was significant. These findings suggest that in many, but not all cases, oak regeneration will be more successful on xeric sites and thus these sites may require less intensive management than more mesic sites.

From these results, we can recommend that management decisions should consider individual site characteristics and their combined effect rather than relying on broad mesic-xeric classifications. In addition, more intensive management may be necessary to regenerate oaks when certain site factors are mesic. This more intensive management can include heavier, more frequent harvesting that drops stand stocking below 50% as recommended by Gingrich (1967) and keeps the stand below 50% more consistently. In addition, targeted midstory thinning can also be considered to remove non-oak competition and make oaks more competitive.

Stand density was not as strong of a driver of oak regeneration as we anticipated, however our results further support the accepted recommendation that successful oak regeneration requires density reduction below the B-line of the Gingrich stocking chart. While stand density was not a driver of white oak seedling abundance, it was a significant driver of oak recruitment. Past research has repeatedly recommended reducing stocking below the B-line of the Gingrich stocking chart to successfully regenerate oaks (Larsen *et al.*, 1997; Larsen and Johnson, 1998). Our research further supports this idea as the reduction in ingrowth drops sharply around 50%, just below the B-line. Further, it appears that overstory density becomes more important for regeneration in larger size classes as stocking was more important for ingrowth than for saplings. Finally, while overstory density is important for oak regeneration, our results showing that overstory density is not as strongly correlated with understory sunlight levels as we anticipated, supports one of the conclusions of Fan *et al.* (2017) that successful regeneration in the Missouri Ozarks may require midstory density reduction as well as overstory density reduction.

Our findings support long held beliefs that establishment and recruitment of oaks is a long-term process that requires proactive rather than reactive management (Dey, 2014; Larsen and Johnson, 1998). Lagged measures of stand density were stronger predictors of white oak recruitment than concurrent stand density and that the strongest relationship depends on the type of recruitment of interest. Generally, our results imply that it takes longer for seedlings to grow into the sapling size class than it does for saplings to grow into the overstory and that this will affect management recommendations and decisions such as how far in advance should harvests take place. For oaks to become successfully established, persist, and grow enough into the overstory, forest managers must prepare up to 30-years in advance of the desired ingrowth period.

As we expected, prior populations are vital to the process of oak regeneration. We found that the abundance of oak saplings is greatly affected by the abundance of oak seedlings and similarly without sufficient oak saplings it is difficult to obtain sufficient ingrowth into the overstory. We also found that, like stand density, lagged prior populations had a stronger effect on regeneration than concurrent populations. As with stand density, these findings support conventional knowledge that regeneration is a long-term process that must be initiated many years prior to the desired ingrowth period. As previously stated, management must be proactive rather than reactive and it may be necessary to take management to 30 years prior to the desired ingrowth period for successful regeneration.

Across Pioneer Forest, we found that there has been a sustained decline in all phases of regeneration that may lead to continued regeneration deficits when coupled with current management intensities. Since the 1990s, both white oak ingrowth and sapling abundance have experienced a continuous decline, while white oak seedling abundance has experienced a more erratic decline. Over the same period of time, stand stocking percent has had a continuous increase past recommended stocking levels of roughly 60% (Larsen *et al.*, 1999). While Loewenstein *et al.* (2000) found that appropriate stand composition and structure was being maintained at Pioneer Forest under uneven-aged management, recruitment at that time was at or above levels recommended by Larsen *et al.* (1997). We found that not only is current recruitment far below levels recommended by Larsen *et al.* (1997), regeneration abundance continues to decline and management goals of <60% stand stocking are no longer being met due to operational extension of the target cutting cycle (20-years) to a 30-year cutting cycle. These levels of recruitment and density management may not be able to sustain the stand structure and composition reported by Loewenstein *et al.* (2000).

Overall, the findings of this study highlight the need for management and research that incorporates temporality as well as finer grained, species-specific metrics of site productivity and harshness. Often times, management and research decisions are made using overarching descriptions of a site, which broadly define site productivity and harshness (e.g., exposed vs protected backslope), under current conditions rather than using finer grained metrics of soil and topography, and historical conditions. Our findings indicate that managers and researchers must incorporate both facets into decision making to successfully regenerate white oaks.

While we propose that less intensive management may be sufficient to regenerate oaks on more xeric sites (relative to the Ozarks), we were not able to directly analyze the interaction between site characteristics and different forms of management (e.g., overstory density, changes in density, or harvesting). Future research should seek to determine if there is a difference in regeneration abundance on xeric and mesic sites under either different management regimes or under various stocking levels. In addition, future research could improve upon the results seen here by conducting similar analyses using more accurate GPS coordinates and more fine-grained soil maps and digital elevation models or on the ground soil and topography measurements.

Unlike results from past research in even-aged stands, stand density was not strongly related to the availability of understory sunlight in uneven-aged upland oak stands of southeastern MO. While this may be the result of sunlight obstruction due to the multi-aged midstory present in uneven-aged stands, this is not entirely borne out by our midstory density results. Because past research indicates that light and the reduction of overstory density are vital for regeneration success, future research should seek to elucidate the cause of the contradictory results we found under uneven-aged management and find alternative operational measures to predict understory sunlight availability in uneven-aged oak forests (Brose and Rebbeck, 2017; Iverson et al., 2017). In addition, future research should focus on more accurately measuring midstory density and understory sunlight levels and take harvesting and stand dynamics into account in the study design.

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