WHITE OAK (*QUERCUS ALBA*) ADVANCE REPRODUCTION UNDER UNEVEN-AGED MANAGEMENT IN THE OZARK HIGHLANDS: SEEDLING DEMOGRAPHY, ESTABLISHMENT, AND GROWTH RESPONSES

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RYAN GROSS

Dr. Michael Stambaugh, Thesis Supervisor

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

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presented by Ryan Gross,

a candidate for the degree of Master of Science,

and hereby certify that, in their opinion, it is worthy of acceptance.

Dr. Michael Stambaugh

Dr. Benjamin Knapp

Dr. John Kabrick

DEDICATION

I dedicate this thesis to my loving partner, Sarah, and my grandmother, Carolyn. I would not be half the man I am today without their constant support. The compassion I receive from these amazing women inspires me every day, to be my best self and shoot for the moon. The energy that went into this thesis reflects the love and care they have given me, and I hope this work honors the pride I feel in being a part of their lives. I am forever Grateful that they are the biggest parts of me.

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NOMENCLATURE

AIC	Akaike information criterion
ANOVA	analysis of variance
BA	basal area
BDq	basal area–diameter–q-ratio method
CLA:CWT ratio	cell-lumen-area-to-cell-wall-thickness ratio
EAM	even-aged management
ELT	Ecological Land Type
EMMs	estimated marginal means
GLMM	generalized linear mixed model
GRV	growth response variable
KS	Kolmogorov-Smirnov
LDT	largest diameter tree
LMM	linear mixed model
MOFEP	Missouri Ozark Forest Ecosystem Project
MB	megabyte
OAR	oak advance reproduction
RBA	residual basal area
SD	standard deviation
STK	percent stocking
TPH	trees per hectare
UAM	uneven-aged management
wOAR	white oak advance reproduction
ZTNB	zero-truncated negative binomial
ZTP	zero-truncated Poisson
0H	control treatment
1H	one-harvest treatment
2H	two-harvest treatment

ABSTRACT

White oak (*Quercus alba* L.) remains a foundation tree species in Missouri and elsewhere across eastern U.S. forests despite ongoing regeneration problems existing for nearly a century. These issues have led to region-wide structural and compositional forest shifts with the potential to permanently displace the species in forest ecosystems. Despite these regeneration issues, white oak exhibits resilient traits such as persistent survival, a capacity to occupy broad site conditions, and adaptations to drought and fire disturbance; most notably being its ability to reinitiate stem growth, or resprout, following top kill.

Resprouting dynamics, critical to white oak's historical dominance, have been successfully promoted in even-aged management (EAM). However, a desire for uneven-aged management (UAM) has become prominent in Missouri's Ozark Highlands, where the species exists in its greatest density across its current range. Here, uneven-aged white oak forests provide a greater public acceptance of continuous canopy cover, opportunities to restore old-growth structures, and economic incentives of high-value timber products.

This study evaluated UAM's impacts on white oak advance reproduction (wOAR) in the Ozark Highlands by merging dendrochronology and quantitative wood anatomy (QWA) methods to analyze seedling stems and roots at a cellular resolution. Age data revealed long-term understory residencies with notable variability in root-to-stem age relationships, and widespread resprouting even in fire's absence. Growth was strongly related to prolonged canopy openness, emphasizing light availability as a critical factor for recruitment success. These findings inform UAM strategies that may sustain white oak's ecological resilience, economic value, social benefit, and cultural legacy.

CHAPTER 1: THE HISTORY OF WHITE OAK, THE SIGNIFICANCE OF ADVANCE REPRODUCTION, AND UNEVEN-AGED MANAGEMENT

Ecological significance and economic incentive

White oak (*Quercus alba* L.) has served as a foundation species in eastern U.S. forests, influencing ecological processes and human livelihoods for millennia (Hanberry & Nowacki, 2016; Abrams et al. 2021). White oak is also a long-lived species (often reaching ages of 200 years or older), promoting structural complexity both within forests and across the landscape (Abrams, 2003; Rentch et al., 2003a). Ecologically, white oak contributes to a great diversity of ecosystem compositions alongside co-occurring tree and other plant species, while also serving as critical habitat and a food source for numerous wildlife species, including birds, mammals, and insects (Van Dersal, 1940; Abrams, 2003; Lill & Marquis, 2003). Economically, white oak has supported industry throughout American history due to its provision of numerous forest products, including cooperage, railroad ties, firewood, charcoal, housing material, and furniture. White oak has also held cultural significance for many groups, including Indigenous Americans and early Euro-American immigrants. Both groups valued the species for its supply of essential resources and its resilience in fire-managed landscapes shaped by traditional burning practices (Abrams, 1992).

White oak has held this vast historical and contemporary influence on ecosystems and society through its longstanding dominance as an overstory species, as well as its numerous adaptations to disturbance, such as fire resistance and drought tolerance. However, the species now experiences widespread regeneration failure and successional displacement throughout its range (Johnson et al., 2019). The increasing pressure white oak faces with regeneration and recruitment dynamics now threatens the sustainability of the ecological and economic systems that have grown to rely so heavily on the species.

The historical prevalence of white oak was initiated largely due to its exploitation of disturbance regimes (Abrams, 2003; Rentch et al. 2003b). White oak's ability to reinitiate stem growth after dieback, or top kill, permitted its dominance in disturbed landscapes, particularly in the fire-adapted forests of the Midwest and Appalachians. Following European colonialization, widespread logging, fire suppression, as well as intensive agriculture and its subsequent abandonment, created settings that promoted white oak's resprouting strategy. However, drastic and sudden shifts in disturbance patterns including total fire suppression, prolonged and densified canopy closure, and increased competition from shade-tolerant species have interrupted this process. In the absence of variably frequent disturbance to forest canopies and competing species, existing white oak seedlings and saplings, or advance reproduction, struggle to persist in increasingly dense and mesic understory conditions (Nowacki & Abrams, 2008).

Ongoing structural and compositional changes in forests require management strategies that address both the ecological requirements of white oak and the complexities of altered forest dynamics. This will be essential to successful regeneration and long-term sustainability. Uneven-aged management (UAM), which maintains continuous forest cover while creating periodic canopy gaps, has shown promise in promoting white oak establishment and its competitive growth. Research in the Missouri Ozarks' relatively xeric ecosystems has shown that UAM methods can be particularly applicable on the area's drier, less productive sites. On these sites, moisture stress typically favors drought-tolerant upland oaks over many competing species (Iverson et al., 2008).

The economic incentive for uneven-aged white oak management is especially appealing in Missouri. This Midwest state holds one of the highest densities of white oak in the U.S., with most being within the Ozark Highlands (Peters et al., 2020). An obvious motivation of this incentive is the premium value of high-quality, large-diameter white oak trees that meet the stricter specifications of stave logs. Stave logs are in high demand by the cooperage industry for the production of barrels used for storing and aging bourbon, whiskey, and wine. Cooperage requires wood with specific grain, strength, and impermeability. Aside from its physical wood traits, *Quercus alba* is preferred for its unique flavor profile relative to other species in the white oak sub-genus (Leucobalanus). These characteristics have led to a high demand for white oak cooperage domestically and internationally, as well as the premium market prices for stave-quality white oak.

Given this strong, sustained demand, landowners and forest managers in Missouri are increasingly motivated to adopt UAM. This remains so despite its additional costs, such as regular stand entries, harvesting of dispersed timber, and frequent stand assessments. However, this approach offers unique economic advantages. By maintaining an assortment of tree sizes and ages within a stand, UAM facilitates periodic harvests of high-value trees as they reach stave quality. This strategy not only allows landowners to capture economic returns more frequently but also provides flexibility to capitalize on favorable market conditions, or to delay harvests during downturns. Thus, ensuring the regeneration and recruitment of white oak under UAM is not only an ecological priority but also a desirable economic strategy for land managers and the forest products industry.

Successful UAM depends on the presence of sufficient advance reproduction and the regulation of overstory tree density, understory light availability, competition from non-oak species, and disturbance (Larsen et al. 1999; Blizzard et al., 2013; Fan et al., 2015; Schweitzer et al., 2019). Therefore, this research examined the interactions among canopy disturbances, resource availability, species competition, and their effects on seedling anatomy and physiology. Particular emphasis was placed on understanding these dynamics in the Missouri Ozark Highlands using the Missouri Ozark Forest Ecosystem Project (MOFEP) in southeastern Missouri as the lone study site.

Goals and objectives

The goal of this study was to assess the advance reproduction pool of white oak and to identify the management strategies that will sustain white oak dominance in uneven aged systems. This study utilized a relatively new methodological framework for studying seedling and sapling sized trees that can be applied to a variety of species. The methods combined Quantitative Wood Anatomy (QWA), which is the science of analyzing and quantifying the variability of xylem anatomical features, with dendrochronology, or tree-ring dating. Applications of QWA included sample preparation methods of microtomy, light microscopic imaging, and micro-slide digitization. Dendrochronology techniques included normalizing and correlating tree-ring-width chronologies to determine the ages of white oak stems and roots.

The methods used in this study helped to determine if experimental treatments influenced a difference in the results from the included analyses. Broadly, the experimental treatments represented various intensities of UAM. Two treatments represented active UAM, with a two-harvest treatment relating to harvests on a 15 year cutting cycle, and a one-harvest treatment that represented an approximately 30-year cutting cycle. There was also a control treatment, where no UAM was applied.

Using these methods, the study examined the separate ages of white oak stems and roots, as well as their relationships. The objective here was to determine if experimental treatment affected stem, root, or root-to-stem mean ages. This study also analyzed the relative densities of white oak advance reproduction (wOAR), which are the white oak seedlings and saplings that exist in the forest under- and mid-story in advance of harvesting. This study analyzed wOAR seedlings that had established through two observed stem establishment origins (true seedlings vs. resprouts) as well as the probability that a given wOAR was of either origin. The first stem origin consisted of seedlings established from an initial germination event (true seedlings), where seedlings had matching stem and root age. The second stem origin was by resprouting, where seedlings had root ages older than the corresponding stem. Here, the objective was to determine if experimental treatments had an effect on stem establishment. Finally, the study assessed growth rates in both seedling height and diameter for stems and roots. The objective here was to evaluate whether experimental treatments influenced stem (height and diameter) or root (diameter) growth.

Research questions and hypotheses

The first question this study investigated was: do either wOAR stem or root demographics differ as a result of variation in the cutting cycle associated with UAM? The hypothesis formed for this question was that more frequent cutting cycles will promote both wOAR stems and roots of younger ages than those under absent or less frequent cuttings cycles. The basis for this hypothesis was the idea that more frequent cutting cycles should promote a more continuously open canopy, resulting in seedlings of younger ages due to more regular seed input and faster recruitment rates. In contrast, prolonged canopy closure may trigger a lack of seed input and recruitment, resulting in greater ages due to lacking photosynthesis and extended suppression.

A second question this study investigated was: how does variation in a cutting cycle length affect wOAR stem establishment dynamics through either true seedling input or resprouting of existing wOAR? This was examined from two different standpoints: the estimated densities of each establishment source and the probability that a given wOAR had established as a resprouted seedling. The hypothesis was that the more frequent cutting cycle (15 years) would result in greater densities of both true and resprouted seedlings compared to absent, or longer (30 years) cutting cycles. It was also hypothesized that a more frequent cutting cycle would reduce the probability that a wOAR was of resprout origin. These hypotheses are based on the idea that more frequent harvesting and sustained canopy openness promotes understory conditions favorable to regeneration. In contrast, less frequent harvesting and reduced canopy openness may reduce true seedling establishment, prolong understory residency, and increase resprouting probability due to suppression.

The final question this study addressed was: how do wOAR respond to UAM in terms of growth? This question is approached from three different perspectives: stem height, stem diameter, and root diameter. The hypothesis for all three growth rates was the same; treatments that provided a more continuous and intense source of understory light would result in the greatest growth rates. These hypotheses were formed due to oaks intermediate shade tolerance. In settings where greater levels of shade are cast with more continuity, wOAR may be outcompeted by species that possess greater shade tolerance.

This study was guided by the preceding research questions and corresponding hypotheses, which were developed based on the objectives and knowledge gaps identified in the following chapters. By clearly stating questions and hypotheses, this research investigates the factors affecting wOAR regeneration and recruitment dynamics in UAM. Together, they establish a foundation for addressing the explored issues. In summary, this study addressed how UAM influences wOAR demography, establishment, and growth.

Figure 1: A resprouted wOAR featuring a large belowground root and a smaller aboveground stem. Although the number of resprouting events is unknown, microsectioning, imaging, and tree-ring dating permits the separate aging of root and stem to determine their ages, growth rates, and stem establishment origins (true seedling vs. resprout). *Photo credit: Abby Huffman*.

CHAPTER 2: LITERATURE REVIEW

Introduction

The oak genus (*Quercus*) has comprised a substantial proportion of eastern North American forests for much of the Holocene epoch, or roughly the last 10,000 years (Abrams, 1996). Today, oaks are widely distributed across North America, except for the northernmost latitudes, the western Great Plains, and the northern portion of the Rocky Mountain range (McWilliams et al., 2002). In the eastern U.S., *Quercus* dominates hardwood forests with roughly 40 unique species occurring across the northern hardwood, central hardwood, southern pine-hardwood, and forest-prairie transition regions (Little, 1979). In the eastern U.S., white oak is the most widely distributed and abundant oak species (Peters et al., 2020). Here, *Quercus* is considered a foundation genus. In times before European colonialization, oak abundance in the eastern U.S. consisted of 40% to 70% of total tree composition at the ecological province scale (Hanberry & Nowacki, 2016).

As a genus, oaks tolerate a wide range of climate and environmental conditions, allowing them to be widely distributed. Many individual oak species, such as Georgia oak (*Quercus georgiana* M.A. Curtis), are restricted to relatively small geographical areas (Peters et al., 2020). Others, such as white oak, maintain competitiveness across an expansive habitat range (Rogers, 1990; Peters et al., 2020). White oak's habitat range is generally limited to areas with mean annual temperatures of 7°C to 21°C, yearly precipitation from 760 to 2030 mm, and mean July relative humidity of approximately 45% to 70% (Rogers, 1990).

Due to its expansive range, white oak co-occurs with several tree species. The most important of these are upland oaks (*Quercus* spp.), such as black oak (*Quercus velutina* Lam.), chestnut oak (*Quercus montana* Willd.), and northern red oak (*Quercus rubra* L.), as well as hickories (*Carya* spp.), such as shagbark hickory (*Carya ovata* (Mill.) K. Koch) and pignut hickory (*Carya glabra* (Mill.) Sweet) (Rogers, 1990). Other hardwoods, such as yellow-poplar (*Liriodendron tulipifera* L.), American beech (*Fagus grandifolia* Ehrh.), sugar maple (*Acer saccharum* Marshall), red maple (*Acer rubrum* L.) and pine species including shortleaf (*Pinus echinata* Mill.), loblolly (*Pinus taeda* L.), and eastern white pine (*Pinus strobus* L.) also co-occur with white oak (Rogers, 1990).

When species co-exist, they are often grouped into forest cover types, or groupings of the most abundant tree species co-occurring at stand-level scales (Eyre, 1980). Of 145 defined forest cover types in the United States and Canada, 33 have an oak component; 23 of which occur in the eastern U.S. (Eyre, 1980). The most abundant cover type group in the eastern U.S. is the oak/hickory group (67 million ha), followed by the loblolly/shortleaf group (31 million ha) (Ruefenacht et al., 2008). The most abundant individual forest cover types in the eastern U.S. are loblolly pine (34 million ha) followed by the white oak/red oak/hickory type (29 million ha), the latter of which occurs prominently throughout the Central Hardwood Region (CHR) (Ruefenacht et al., 2008).

White oak forest values

Functionally, white oak contributes to the distribution and abundance of over 150 bird and mammal species by providing acorns as a year-long food source that is consumable during periods of vegetative dormancy (Rogers, 1990; McShea & Healy, 2002). The structural diversity in oak forests contributes to differences in the preferred habitat types among songbirds (Reidy et al., 2014). White oak also supports the habitat of hundreds of insect species including moths and butterflies (*Lepidoptera*), grasshoppers (*Orthoptera*), wood-boring beetles (*Coleoptera*), and true bugs (*Hymenoptera*) (Jeffries et al., 2006). In the Missouri Ozarks, the larvae of more than 100 unique moth and butterfly species are known to utilize *Quercus* species (Marquis et al., 2019).

Due to its expansive habitat range and abundance relative to many hardwood species, white oak plays a critical role in eastern U.S. forests' ability to sequester carbon (Haight et al., 2020; Peters et al., 2020). Models projecting the total carbon sequestration by forests in the conterminous U.S. from 2015 to 2050 suggest that eastern forests will account for as much as 80% of future total carbon sequestration (Haight et al., 2020). Including all U.S. forest land, the projected value of total carbon dioxide sequestered by forests from 2015 to 2050 is estimated at $115 to $1,550 billion. This range in estimated value differs based on potential policy changes, including reduced land development, afforestation and reforestation efforts, and fire mitigation strategies (Haight et al., 2020).

Economically, the forestry industry supports employment for potentially hundreds of thousands of U.S. citizens, contributing to local economies through labor income and product-driven sales (Young et al., 2007; Honey, 2019). In Missouri, it is estimated that the forestry and forest products industries account for nearly $10 billion of the state economy (Missouri Department of Agriculture, 2019). In other eastern states, such as Tennessee, it is estimated that these industries contribute roughly $25 billion to the state economy, while employing over 110,000 people (Honey, 2019). As a species, white oak provides our societies with several forest products including sawtimber for lumber, flooring, and cabinetry, as well as specialty products such as staves, which are the individual pieces of wood used to manufacture wine and whiskey barrels. In Missouri, white oak consistently ranks among the highest-value timber species (Missouri Department of Conservation, 2023). Recently, however, there have been sustainability concerns regarding the supply of high-grade white oak across the CHR due to problems associated with oak regeneration processes, harvesting practices, and the growing product demand from the wine and whiskey industries (Thomas et al., 2021). Failures associated with regenerating white oak, among other oak species, are believed to have evolved from a multitude of anthropogenic factors (Abrams, 2003).

Oaks and human disturbance

For thousands of years before Europeans colonized the Americas, Indigenous American populations used fire to manage surrounding forest, woodland, and prairie ecosystems for hunting, crop cultivation, and foraging (Anderson & Moratto, 1996). It is argued that before European colonialization, these human practices influenced the distribution and composition of oaks in forests, woodlands, and prairies due to variability in the frequency and duration of fire-free periods (Delcourt & Delcourt, 1997; Nowacki & Abrams, 2008). Before European colonization, on topographically rough sites with natural firebreaks in the Ozark Highlands of Missouri, mean fire intervals were as low as 2 to 5 years. However, some longer fire-free periods of up to 50 years or more did occur (Guyette et al., 2002). The widespread variability in fire-free periods throughout the eastern U.S. would have resulted in a mixture of forest ages and structures, exemplifying a “shifting-mosaic steady state,” of oak forest ecosystems (Bormann & Likens, 1979).

The westward movement of European colonizers from the mid-1700s to mid-1800s into the Appalachians and areas farther west, such as the Ozark Highlands, resulted in abrupt changes to the disturbance regimes of eastern North American forests (Guyette et al., 2002). Intensive land use and exploitation associated with homesteading, burning, agriculture, livestock grazing, coal production, and timber harvesting quickly altered the composition and structures of these forests (Abrams, 2003; Dey, 2014). Areas that experienced increased fire frequency, such as the Ozark Highlands, would have accumulated oak resprouts in the forest understory due to lacking fire-free time intervals needed for overstory recruitment (Guyette et al., 2002; Arthur et al., 2012).

By the mid-1900s, fire suppression efforts implemented during the 1920s had effectively halted the disturbance regimes across the eastern U.S. that had been active for centuries. During this time, large numbers of oak resprouts in woodland, savanna, and prairie ecosystems recruited into the overstory and densified into closed-canopy, oak-dominated forests (Anderson, 1998; Hanberry et al., 2014). These undisturbed forests with high tree densities would have created low-light environments that were not conducive to sustained oak recruitment (Larsen et al., 1997). Today, the oak component in these forests is quickly declining due to the lack of light, resulting in increased densities of later-successional, shade-tolerant species in the forest understory (Aldrich et al., 2005; Chapman et al., 2006). Changes to ecosystem structure and function due to human influence have resulted in ecosystem shifts throughout the eastern U.S. However, it is the changes in tree growth responses occurring at the cellular scale that have allowed these issues to become observable across the landscape.

White oak anatomy

White oak physiology cannot be fully understood without considering its anatomical basis. White oak anatomy includes its xylem and phloem vascular tissues, the vascular cambium and cork cambium growth tissues, and pith tissues, among others. The pith, located in the center of the tree stem, consists mostly of parenchyma cells that function in storing and transporting water and nutrients throughout the tree (Everett et al., 2025). Surrounding the pith is the xylem. The xylem is involved in critical plant processes like photosynthesis, internal water and nutrient transport, and structural support (Everett et al., 2025). The xylem boundary extends outward until it reaches the vascular cambium, which is the location of new cell formation (Everett et al., 2025). The vascular cambium is located at the outer boundary of the xylem and separates the xylem from the phloem. The phloem, which supports a bidirectional flow of photosynthates and nutrients from the leaves to the rest of the tree, is located between the vascular cambium to the inside and the cork cambium to the outside (Everett et al., 2025). Although the xylem and phloem have individual roles, they are physically connected, working symbiotically to maintain overall tree health and function.

The xylem of the *Quercus* genus consists of several cell types, each with its own traits and functions. The xylem in white oak consists mainly of vessel elements, vasicentric tracheids, libriform fibers, and ray and axial parenchyma cells, among others. Vessel elements are relatively large cells that are stacked end to end forming long, continuous pathways for water from the roots to the leaves (Everett et al., 2025). Vessel elements across several *Quercus* species including European oaks are reported to have an average diameter of 100 to 200 µm (Schweingruber et al., 2011), although some studies have reported vessel diameters up to 400 µm (Woodcock, 1989; Pérez-de-Lis et al., 2018). Vasicentric tracheids surround vessel elements, aiding in water transport. Higher densities of vasicentric tracheids have been linked to drought resistance in oak species

(Fontes et al., 2022). Libriform fibers function in mechanical support due to their thick cell walls. Axial and ray parenchyma are two cell structures that support the radial transport and storage of water, carbohydrates, and nutrients (Słupianek et al., 2021). Axial and ray parenchyma are oriented parallel and perpendicular to the stem, respectively. Both parenchyma cell types bridge the connection between the xylem and the phloem.

Xylem development is often of great interest within oak studies as it relates to tree responses to climate and environmental factors. The relationships between xylem characteristics and drought tolerance for white oak and other oak species have been of particular interest (Bahari et al., 1985; Abrams, 1990; Robert et al., 2017). Research involving temporal dynamics of xylem growth is made possible through the study of trees growing in temperate ecosystems, whose vascular cambiums enter a state of dormancy during the winter season (Speer, 2010). This annual dormancy of cambial activity results in annual growth bands, or tree rings that can be precisely dated in time. What appears as bands of tree rings to the naked eye can be observed at the cellular scale to view intra-annual changes in cell development, such as cell size and shape throughout a growing season. For angiosperms and gymnosperms, earlywood (EW) and latewood (LW) are two ways to categorize cells by size and shape (Speer, 2010). The transition between EW and LW cell development is often described as a density fluctuation, which can be sudden or continuous, and may be caused by genetic or climatic cues (Schweingruber, 2007). Density fluctuations can be used to describe tracheids, fibers, and vessels. In many oak species, the EW fiber cells, which are formed during the beginning of the growing season, have a greater cell-lumen-area-to-cell-wall-thickness (CLA:CWT) ratio compared to LW fiber cells. The EW fiber cells also appear tangentially flattened the nearer they form to the outermost boundary of the annual ring (Schweingruber, 2007).

Vessel structure may also be described based on its occurrence in the earlywood (EWV) or latewood (LWV). Many deciduous oaks like white oak that grow in temperate regions are classified as ring porous. Ring-porous species exhibit a growth strategy characterized by the production of large vessels at the start of the growing season, followed by a rapid reduction in vessel size and density as the season progresses (Schweingruber, 2007; Speer, 2010). The rapid transition in the size of vessels results in visibly distinct EW and LW segments. The EWVs typically align around the entire circumference of the tree ring, enhancing their visibility, which makes oaks a preferred species for many dendrochronological, or tree-ring, studies.

Physiologically, ring-porous species' large EWV structure permits an elevated level of hydraulic conductivity early in the growing season at the expense of greater risk of embolism to the water column (Robert et al., 2017). This results in a shorter growing season relative to species with a diffuse-porous structure (Wang et al., 1992), where the range in vessel size and density throughout a ring are less extreme. High rates of embolism due to freezing winter temperatures necessitate ring-porous species, such as oaks, to rely on new vessel production at the beginning of each growing season to re-establish hydraulic conductivity (Sperry & Sullivan, 1992).

Changes to xylem cell structure and arrangement may also occur due to external stresses that result in reaction wood formation. Reaction wood formation is a growth response to internal gravitational stress that produces specialized fiber cells (Timell, 1986; Du & Yamamoto, 2007). Reaction wood formation is a "mechanical self-optimization," that helps a tree adapt to physical stresses and resource availabilities (Mattheck, 1995). Although not unique to oaks or angiosperms, reaction wood is critical for plant survival (Gardiner et al., 2014). Conifers differ from most deciduous species in that conifers respond to internal stress by forming compression wood, whereas deciduous trees form tension wood (Schweingruber, 2007). Compression wood forms on the lower side of a leaning stem, while tension wood fibers, also called gelatinous fibers, are stretched on the upper side of the leaning stem (Jutte, 1956; Felten & Sundberg, 2013).

The location and orientation of tension wood are indicative of the directions and durations of internal force applied to the stem (Schweingruber, 2007). Where tension wood formation results from eccentric growth, tree-ring boundaries may become discontinuous, or locally absent. Discontinuous rings, where the annual increment is absent around some portion of the stem, can be caused by ecological factors such as limited resources or suppression from competition (Larson, 2012). Where tension wood is localized, vessel formation is often reduced in size and number, reducing the overall hydraulic conductivity (Fengel & Wegener, 2011; Gartner et al., 2003). Although reaction wood is conducive to the survival and vigor of the tree, it is often considered a defect in the forest products sector (Timell, 1986). Knowledge of cell characteristics, functions, and their responses to environmental and climatic changes permit a greater understanding of white oak ecology when considered from larger spatial scales.

White oak ecology

The anatomy of white oak lays out a framework for the species to utilize available resources such as light and water, and to compete and co-exist with other plant and animal species. Hardwood tree species display trade-offs between maximizing growth under high light availability and maintaining a minimum light compensation point, which is directly related to their shade tolerance (Walters & Reich, 1996). Oak species display a range of shade tolerance, although most including white oak are classified as intermediate (Johnson et al., 2019). Individual white oak trees can persist in the midstory and understory under a closed canopy for several decades (Merz & Boyce, 1956).

Closed-canopy oak forests lacking disturbance regimes may experience a shift in their regeneration layer toward greater dominance of shade-tolerant species. This transitional process, known as mesophication, is often initiated by fire suppression, which alters site conditions by increasing moisture and shade. As more moisture-demanding, shade-tolerant species establish, they further reduce site flammability and create a positive feedback loop that favors their own persistence over that of fire-adapted oaks (Nowacki & Abrams, 2008). A transition in dominance from oaks to more mesophytic species, such as maple and yellow poplar, is evident across the eastern U.S. (Aldrich et al., 2005; Chapman et al., 2006; Knapp & Pallardy, 2018).

As a genus, *Quercus* has been described as drought-tolerant (Abrams, 1990). Adaptations to fire and drought are believed to have contributed to the sustained regeneration of *Quercus* in precolonial times (Abrams, 1996). A morphological trait of *Quercus* contributing to drought tolerance is its deeper rooting compared to many co-occurring species (Hinckley et al., 1981). Physiologically, due to greater water availability at increasing soil depths, the deeper roots of white oak saplings in Missouri are related to higher pre-dawn water potentials than those of mesophytic species such as sugar maple and flowering dogwood (*Cornus florida* L.) (Bahari et al., 1985). In the same study, white oak saplings showed greater rates of photosynthesis during drought and maintained stomatal aperture at lower osmotic potentials than did sugar maple and flowering dogwood (Bahari et al., 1985). Other morphological traits of *Quercus* that contribute to drought tolerance are high stomatal density and leaf thickness relative to other hardwoods (Abrams & Kubiske, 1990).

Quercus is also considered a disturbance-adapted genus, especially concerning fire (Abrams, 1990; Abrams 1992; Arthur et al., 2012). In a comparison of red maple and sugar maple with three upland oak species in central Pennsylvania, white oak leaves exhibited the lowest water absorption, fastest drying rate, and highest flammability (Kane et al., 2021). In the southern Appalachians, white oak and chestnut oak leaves exhibited slower decomposition rates than did red maple and flowering dogwood, potentially contributing to the fuel loads necessary for fire continuity (Knoepp et al., 2005; Arthur et al., 2012). The use of prescribed fire to control litter depth has been linked to oak germination success (Wang et al., 2005; Nation et al., 2021). White oak and Shumard oak (*Quercus shumardii* Buckley) acorns had greater survival post-fire in shallower fuel beds (Nation et al., 2021), indicative of a relationship with frequent low-intensity fires. A separate study examining the effects of prescribed fire on 1-year-old white oak seedlings indicated that lower leaf litter depths and greater light availability resulted in higher seedling density and biomass (Wang et al., 2005). However, in a long-term (40-year) experiment in an oak-hickory forest in the Ozark Highlands, high-frequency burning regimes without sufficiently long fire-free periods did not permit adequate seedling establishment or canopy recruitment (Knapp et al., 2017).

Other oak adaptations to fire include generally having thicker bark than other tree species (Spalt & Reifsnyder, 1962). Oak bark is also coarser than many smooth-barked species, such as red maple. Compared to two upland oak species, the smoothness of red maple stems has been observed to introduce up to 2 to 3 times more water into the surrounding soil surface through stemflow, potentially changing site conditions over time (Alexander & Arthur, 2010). Additionally, many oak species produce tyloses, which are specialized cell contents that enhance resistance to water and fungal hyphae penetration into xylem vessels (Ruppitsch et al., 2021). Tyloses help compartmentalize wounds and scars from bole damage, with the white oak section (Leucobalanus) believed to be particularly effective at this (Abrams, 2003). Compartmentalizing injuries of woody tissue is a physiological trade-off necessary for maintaining tree health and function (Smith, 2015). In this process, trees may synthesize, reallocate, and block resource movement to seal damaged tissue, which often reduces hydraulic conductivity (Smith, 2015). Oak species' adaptations to disturbance contribute not only to their survival but also to their ability to regenerate and sustain recruitment over time (Arthur et al., 2012).

White oak regeneration ecology

The white oak regeneration process begins at the start of flowering, which typically coincides with the timing of leaf out (Rogers, 1990). Oak species are monoecious, producing male and female flowers on the same tree (Rogers, 1990). Oak trees that have reached flowering age and size typically produce numerous flowers of both sexes (Johnson et al., 2019). Male flowers in oaks produce catkins, where pollen storage occurs until the catkin reaches maturity (Johnson et al., 2019). With favorable weather conditions, pollen shedding typically completes within 48 to 72 hours (Rogers, 1990, Johnson et al., 2019). However, a comparison between white and red oak pollination at the same location revealed that pollen shedding in white oaks occurred 2 weeks after that of red oaks (Stairs, 1964).

White oak trees can begin producing acorns around age 20 but typically become good producers once reaching the ages of 50 to 80 years old (Rogers, 1990; Johnson et al., 2019). White oak acorns take only a single growing season to mature, whereas red oak acorns take two (Johnson et al., 2019). Many eastern U.S. oak species, including white oak, can have highly variable acorn crops, producing larger crops every 2 to 4 years (Sork et al., 1993). Consistent variability in annual acorn production, or periodicity, may be influenced by a combination of current or previous years' climates, environmental factors, and reproductive events (Sork et al., 1993; Smith et al., 2021). Even when conditions are favorable and there is abundant acorn production, data suggest that insects can damage up to half of all acorns yearly (Bellocq et al., 2005). Due to high rates of insect damage and predation by birds and mammals, years of high acorn production, or mast years, permit the greatest chance for oak establishment (Kellner et al., 2013; Johnson et al., 2019). Animal dispersal of acorns is critical for oak regeneration as it reduces intraspecies competition by increasing growing space for seedlings, while contributing to genetic mixing across the landscape (Johnson et al., 2019).

For white oak acorns to survive harsh winter conditions and maintain germination viability, moisture content must remain above 40% (Korstian, 1927). Because acorns typically drop before leaves fall, leaf litter cover is critical for protecting acorns from desiccation and freezing through winter months (Korstian, 1927). Acorn germination in all oak species is hypogeal, meaning that the cotyledons of the seed remain below ground during initial growth (Johnson et al., 2019). The germination and taproot development between red and white oaks differ in that red oaks do not begin until the spring (Johnson et al., 2019). In contrast, white oak acorns germinate in the fall, during which the radicle rapidly develops into a taproot up to 15 cm long (Rogers, 1990; Johnson et al., 2019). The immature stem, or epicotyl, then enters dormancy, ceasing growth once exposed to prolonged winter temperatures (Farmer, 1977).

At the beginning of spring, soil temperature is an important control of the timing and rate of root growth for oaks (Larson, 1970). When soil temperatures have triggered growth, seedlings delay shoot growth and allocate photosynthates toward root development (Reich et al., 1980). By the time the seedling has depleted its acorn nutrients, it has formed a lateral root system branching from the taproot and developed three or four fully expanded leaves which allow the seedling to survive by itself (Johnson et al., 2019). Shoot development occurs successively in three linear stages for oak seedlings at least 1 year old; rapid shoot elongation, rapid leaf expansion, and a resting (lag) phase (Hanson et al., 1986; Dickson, 1991). For first-year seedlings, the first stage of the shoot growth cycle typically lasts a week, followed by the resting phase, during which a terminal bud develops (Johnson et al., 2019). For first-year seedlings in a forest setting, the resting phase typically occurs for the rest of the growing season, resulting in no further shoot growth (Johnson et al., 2019).

Significant root growth of oak seedlings occurs primarily during the resting phase, when shoots and leaves are not growing (Reich et al., 1980). Multiple leaf and stem growth cycles, or flushes, may occur within a single growing season if climate and environmental factors are conducive to oak seedling growth (Reich et al., 1980). Each flush increases the total leaf area resulting in increased photosynthetic capacity. Multiple flush events promote increased root growth and larger root-to-shoot carbon allocation ratios (Reich et al., 1980). Dickson (1991) found that up to 90% of photosynthates from first-flush leaves in northern red oaks support second-flush leaf development, while 95% of photosynthates from second-flush leaves are translocated to the lower stem and roots.

A seedling whose above-ground stem has died back and resprouted at least once is a seedling resprout. The ability to re-initiate growth following stem dieback, or top kill, is characteristic of all oak species, but more prevalent in the upland species physiologically adapted to more frequent burning and droughty conditions (Johnson et al., 2019; Abrams 1990). Repeated, or recurrent shoot dieback is a characteristic of oaks that grow in a closed-canopy forest setting (Merz & Boyce, 1956; Crow, 1992). In conditions of intense water and light stress, oak reproduction struggles to maintain photosynthetic rates that match respiration rates, resulting in low survivability (Hanson et al., 1986). Promoting the causes of recurrent shoot dieback at appropriate times is believed to facilitate effective oak forest management (Rogers et al., 1993).

While seedling resprouts are seedlings whose above-ground stem has died back and resprouted at least once, the term stump sprout typically refers to stems that have resprouted from a top-killed tree at least 5 cm in diameter (Roach & Gingrich, 1967). Ten years after overstory removal in a Missouri clearcut on sites with a site index of 13 to 19 m at base age 50, stump sprouts showed the greatest 10-year average in height growth (6.4 m) as compared to seedling resprouts (4.6 m) and seedlings (0.6 m) (McQuilkin, 1975). The probability of stump sprouting is known to decrease with increased tree age and diameter (Johnson, 1977). The various forms of oak regeneration and their differences in growth rates influence the wide range of success observed across different sites, and even on the same site over time.

Oak advance reproduction: population dynamics

Oak advance reproduction (OAR) is the total oak seedlings and saplings established in a forest understory before disturbance or regeneration events occur. OAR consists of all growth forms of oaks (seedlings, seedling resprouts, and stump sprouts) present in a stand (Johnson et al., 2019). Considering these growth forms, oaks regenerate by utilizing two reproductive processes, seeding and resprouting (Clarke et al., 2013; Johnson et al., 2019). All forms of OAR contribute to the reproductive potential of a forest (Rogers et al., 1993). However, oaks have a greater likelihood of regenerating by resprouted advance reproduction, than by seedling establishment occurring after canopy disturbance (Johnson et al., 2019). Yet, the relative importance of each reproduction source varies by species and depends on physical site factors and disturbance regimes (Rogers et al., 1993). For instance, droughty regions, like the Missouri Ozark Highlands, are more dependent on resprouted seedlings than new seedling establishments (Liming & Johnston, 1944). Here, small populations of seedling resprouts (500 to 1,000/ha) are believed to support continued oak dominance (Sander, 1984).

Many forests across the eastern U.S. exhibit how managing for oak regeneration success becomes increasingly difficult as sites become more productive, promoting non-oak species' increased competitiveness over oaks (Trimble, 1973; Loftis 1990). Changes in overstory density through time and physical site factors also influence the total seedling population that can exist at any time (Larsen et al., 1997; Kabrick et al., 2008; Kabrick et al., 2014). In the Ozark Highlands, oak accumulation is strongly affected by slope position and aspect, which influences soil moisture, solar insolation, and light availability (Kabrick et al., 2014). The total OAR potential can change at any time through periodic additions from stem establishment by seeding or resprouting, losses from mortality, or growth of trees resulting in canopy recruitment (Johnson et al., 2019). However, the reproductive potential of the stand is more accurately represented by the combined factors of the numbers, sizes, and spatial distributions of each class of OAR reproduction (Sander, 1984; Kabrick et al., 2014).

Ecosystems are often labeled as intrinsic or recalcitrant accumulators to distinguish their ability to accumulate oak reproduction (Johnson et al., 2019). Ecosystems labeled as intrinsic accumulators possess characteristics allowing for oak accumulation to occur over time, such as in dry upland sites (Trimble, 1973). This is readily apparent in upland oak ecosystems where OAR (< 11.43 cm diameter at breast height (dbh)) root systems have been found up to 37 years old (Merz & Boyce, 1956). Here, dbh refers to the standard measurement of tree diameter taken at 1.37 meters (m) (~ 4.5 ft) above ground level. In contrast, recalcitrant site accumulators, such as productive bottomland forests, do not promote continued accumulation over time (Johnson, 1975). However, ecosystems labeled as recalcitrant accumulators may not necessarily struggle to establish seedlings. For example, bottomland oak forests have been found to establish up to approximately 250,000 seedlings/ha in a single mast year (Johnson, 1975). Likewise, ecosystems that intrinsically accumulate oak may not necessarily rely on high numbers of input from seed, as evidenced in the Ozark Highlands where 350 to 650 seedlings/ha are considered high for a single year (McQuilkin, 1983).

Site productivity, aspect, overstory canopy density, and oak competitor presence strongly influence the ability of sites to accumulate OAR (Matney 1974; Kabrick et al., 2008; Kabrick et al., 2014). Oak regeneration potential has been conceptualized through a "regeneration window," where gradients of light and moisture levels interact to allow for narrow or broad ranges of success (Johnson et al., 2019). The window for regeneration success widens as sites become drier, allowing oaks to be more competitive across a wider range of light levels (Hodges & Gardiner, 1993). This effect is exhibited in eastern U.S. forests due to oak species' greater drought tolerance but lower competitiveness in low-light environments (Abrams, 1990; Vickers, et al., 2014). Acorn predation, irregular acorn production, and the effects of disturbance, such as fire, are also factors that may influence fluctuations in the capacity of a site to accumulate oak reproduction (Sork et al., 1993; Bellocq, et al., 2005; Hutchinson et al., 2012).

The total regeneration potential of a stand changes over time as OAR density (size and number) fluctuates and disturbances occur at various frequencies and spatial extents (Larsen et al., 1997; Izbicki et al., 2020). Forest tree species display a range in their ability to exploit canopy gaps formed by disturbance due to differences in physiological and morphological traits (Kaelke et al., 2001). Three regeneration modes describe the scale of disturbance that best matches a species regeneration strategy: gap-phase, catastrophic, and continuous regeneration (Veblen, 1992). White oak's regeneration mode aligns with the gap-phase strategy, described as regeneration occurring in canopy gaps due to the sudden or gradual loss of a single or few trees in a small patch (approximately 0.5 ha) (Watt, 1947). Disturbances that initiate gap-phase regeneration typically occur endogenously due to maturity and senescence, yet exogenous factors like fire, wind, lightning, and insect outbreaks also initiate regeneration events (Watt, 1947).

Forest stand dynamics

A forest stand is a group of trees sharing common traits growing in an area of relatively homogeneous physical site qualities. Stand development of an even-aged forest follows four developmental stages: stand initiation, stem exclusion, understory reinitiation, and the old-growth stage (Oliver & Larson, 1996). Stand initiation follows stand-resetting disturbance where new trees and plants begin to occupy a site (Oliver & Larson, 1996). During the stem exclusion stage, tree regeneration is reduced, and many stems die off due to intense competition (Oliver & Larson, 1996). Understory reinitiation occurs as growing space opens in the understory and regeneration begins accumulating beneath the overstory (Oliver & Larson, 1996). Lastly, the old-growth phase starts when canopy gaps form from disturbance, allowing sub-canopy trees from younger cohorts to recruit into the overstory (Oliver & Larson, 1996).

Forest change results from disturbance, defined as discrete events that disrupt ecosystem structure, alter resource availability, or change the physical environment (White & Pickett, 1985). Disturbances fall into three categories based on size and effects on stand development: gap-scale, incomplete stand-scale, and stand-initiating (Johnson et al., 2019). Gap-scale disturbances remove single trees or small groups from the canopy. Many silvicultural regeneration practices, such as single-tree and group selection harvesting, aim to mimic gap-scale effects (Law & Lorimer, 1989; Larsen et al., 1999).

Disturbances result in opportunities for new trees to regenerate and recruit in the presence of newly formed canopy gaps. Successful regeneration and recruitment are considered the two pillars of oak sustainability (Dey, 2014). Dey (2014) suggests that successful regeneration alone will not sustain oak as an overstory component because competition dynamics during the recruitment phase can reverse successful regeneration. By examining the effects of crop tree release practices, Ward (2009) found that few intermediate and suppressed oaks reach the canopy without a release from competition.

Upland oaks, such as white oak, are disturbance adapted. Thus, the absence of a disturbance regime that promotes their regenerative competitiveness often leads to their successional displacement by more shade-tolerant species (Dey & Guyette, 2000; Aldrich et al., 2005). Yet, disturbances such as frequent fire can increase oaks' competitiveness by reducing the abundance of more shade-tolerant species. An experiment in western Kentucky comparing single-, multiple-, and no-burn treatments over 10 years showed that the multiple-burn treatment reduced the density of red maples and increased the density of white oak, regardless of their location within canopy gaps (Izbicki et al., 2020).

To reach the goals of a targeted stand structure and composition, stand densities are commonly used to assess the appropriate types and timings of silviculture treatments (Law & Lorimer, 1989; Larsen et al., 1999). Percent stocking (STK), a measure of relative tree density that can be viewed graphically, is often used to evaluate stand development relative to silvicultural goals (Gingrich, 1967). The Gingrich stocking chart for upland hardwoods is based on species-specific equations for minimum and maximum tree crown area that reflect the total growing space occupied by all trees within a stand (Gingrich, 1967). Tree-area estimates are species specific, yet oaks co-occur with many species displaying similar tree-area relationships. Thus, one equation is usually sufficient to calculate STK for upland hardwood ecosystems (Gingrich, 1967). However, species-specific STK calculations may provide greater accuracy when tree species of different tree-area relationships co-exist (Zhang et al., 1995).

Stand-level STK can be controlled through silvicultural practices. Thinning operations have been shown to promote the radial growth of residual oak trees between harvests, especially when done periodically and when oaks targeted for release are less than 30 years old (Shifley, 2004). However, upland oak stands of ages 80 to 125 years have exhibited individual tree release that maintains stand volume growth when thinned to 60% to 62% stocking (Ward & Wikle, 2019). By thinning overstory oaks, managers can promote residual tree crown expansion, live branch density, and acorn production capacity until diameter or age thresholds are met (Dey, 1995). In the southern Appalachians, regeneration harvests that reduced stand basal area to 4.3 to 5.9 m^2/ha resulted in a roughly 70% greater average number of acorns/m^2 of crown and dbh growth than in that of closed-canopy mature forests (Greenburg, 2021). The same study found that retaining 20 to 40 mature oaks/ha during regeneration harvests would likely result in 50% to 100% of the total acorn production of a mature, closed-canopy stand as residual trees increased in growth and acorn capacity.

Oak Silviculture – Uneven-Aged Management

Silviculture has been defined in many ways. One way to define silviculture is as the art and science of tending to forests for social or economic purposes by applying knowledge of forest ecology and individual species' silvics (Ashton & Kelty, 2018). Silviculture systems are broadly separated by the canopy and age structures that are created through management with even-aged and uneven-aged being the two most commonly recognized forest age structures (Ashton & Kelty, 2018). In even-aged management (EAM) forests contain trees of the same age class, or cohort. Tree ages in an even-aged stand should range by less than 20% of the intended harvest rotation (Nyland, 2016). In contrast, in UAM, forests consists of at least three cohorts intermingled or in small groups, with either balanced or unbalanced diameter distributions (Helms, 1998; Ashton & Kelty, 2018). Both EAM and UAM broadly classify some of the most common silvicultural systems.

Generally, one of three regeneration harvesting methods is utilized for what is classified as EAM: clearcutting, shelterwood, or seed tree methods (Ashton & Kelty, 2018). In clearcutting, the overstory trees are completely removed from the stand (Nyland, 2016). When clearcutting is not a viable regeneration option, partial-retention methods like the seed-tree and shelterwood systems may help favor the growth of desirable species, serve as a seed source for the future stand, and retain a more desirable aesthetic (Nyland, 2016). The seed tree method involves a near-complete overstory removal where only a few widely spaced residual trees are left as a seed source for the newly developing stand (Nyland, 2016). Whereas shelterwood harvests involve multiple cuts, each focused on controlling stand density to levels that favor the development of desired species' advance reproduction by providing an adequate shade shelter before a final removal of the remaining overstory (Ashton & Kelty, 2018).

Concerning regeneration with EAM methods, the objective is to recruit a new cohort of desired tree species throughout the stand with a final harvest of a mature overstory (Ashton & Kelty, 2018). The clearcutting, shelterwood, and seed tree methods are regarded as successful oak regeneration practices in upland ecosystems (Roach & Gingrich, 1968; Johnson et al., 2019). Despite the success of EAM in regenerating oak, these management forms are generally not as well perceived by the public as are UAM practices due to the latter's continuous canopy coverage, both through time and space. Surveys have noted the public's preference for stands with large, variably spaced trees in multiple canopy layers, further progressed in stand development (Giergiczny et al., 2015).

In UAM, the goal is to promote regeneration densities and canopy recruitment rates that maintain a desired uneven-aged structure while sustaining consistent harvest yields, among other objectives (Ashton & Kelty, 2018). Therefore, regeneration, tending, and harvesting are occurring simultaneously (Nyland, 2016). The uneven-aged structure is retained with a cutting cycle, or harvest frequency. The cutting cycles maintain a desired STK through periodic reductions in stand density across size classes (Law & Lorimer, 1989; Larsen et al., 1999). In contrast to the area-based harvesting treatments of EAM, UAM utilizes selection-based harvesting (Ashton & Kelty, 2018). As with EAM, harvesting using UAM methods promotes new tree regeneration but occurs on much smaller spatial scales and much more frequently (Ashton & Kelty, 2018). The single-tree and group selection systems are two commonly used UAM methods (Nyland, 2016). In the Missouri Ozarks, the single-tree selection method for oak forest management has been commercially applied at Pioneer Forest since the early 1950s (Guldin, 2008). The single-tree and group selection methods have been experimentally applied and monitored at MOFEP since the 1990s (Kabrick et al., 2002; Sheriff, 2002).

Single-tree selection results in newly formed canopy gaps of approximately one tree crown area, typically between approximately 40 to 135 m^2 (Johnson et al., 2019).

The practice of single-tree selection is based, in part, on the concepts of self-thinning and balanced forest structure (Johnson et al., 2019). As forests mature, self-thinning occurs as the number of stems decreases due to competition-induced mortality, while the crown and bole area of surviving stems increases (Reineke, 1933). One indicator of uneven-aged forest structure is a balanced, or reverse-J-shaped diameter distribution, which shows an exponential decrease in the number of trees in successively larger size classes (Law & Lorimer, 1989; Shifley et al., 1995). The idea that a balanced stand structure can be sustained over time is based in part on the structure of balanced virgin forests, where in the absence of exogenous disturbance, regeneration and growth are offset by individual tree mortality, resulting in relatively stable volume yields and structure (Meyer, 1952).

Target diameter distributions, or guiding curves, can be calculated to guide timber harvests or thinning operations that promote sustainable harvest yields and a continued uneven-aged structure (Law & Lorimer, 1989). A popular UAM harvest guide is the BDq system. In this system, a stand-specific guiding curve is calculated including metrics for the diameter distribution and largest diameter tree to be retained (LDT), a q-value, and a targeted residual basal area (RBA) (Law & Lorimer, 1989). The slope of the diameter distribution, or q-value, is defined as the average ratio of the number of trees between successive size classes (Law & Lorimer, 1989). The LDT is used to sustain stand structure and volume yield. As the slope increases, more trees in smaller diameter classes are required to sustain yield and structure (Law & Lorimer, 1989). The appropriate, and thus sustainable diameter distribution of a stand depends on the silvicultural objectives, site qualities, and the stand dynamics of the forest ecosystem (Larsen et al, 1999). A q-value of 1.2 to 1.3 (for one-inch size classes) has been recommended for the UAM of oak ecosystems in the Missouri Ozarks (Larsen et al., 1999).

Concern has been raised about the single-tree selection method's applicability for regenerating oaks due to the difficulties sustaining a balanced diameter distribution (Gingrich, 1967; Keyser & Loftis, 2013). Sustaining oak regeneration with single-tree selection is especially challenging on dry-mesic to mesic sites, where oaks are more readily displaced by shade-tolerant species such as maples and yellow-poplar. (Nowacki et al., 1990). In these ecosystems, over time, the less shade-tolerant oaks typically form a bell-shaped, normal diameter distribution (Nowacki et al., 1990; Aldrich et al., 2005). In contrast, the shade-tolerant, later-successional species generally develop a subcanopy regeneration layer with a reverse-J distribution (Nowacki et al., 1990; Aldrich et al., 2005). However, there is evidence that the single-tree selection system can produce balanced diameter distributions on more xeric sites that accumulate oak regeneration intrinsically, such as at Pioneer Forest in the Missouri Ozarks (Loewenstein et al., 2000).

In contrast to single-tree selection, the group selection method differs in the size of canopy gaps created during harvests. With group selection, the diameter of canopy gaps should be 1 to 2 tree heights depending on aspect (Law & Lorimer, 1989). The minimum size openings for group selection are based on the observed minimum sunlight intensity of 30% required to sustain maximum photosynthetic rates in planted northern red oak seedlings (Phares, 1971; Fischer, 1981). At MOFEP where the site index for white oak is approximately 19 to 22 m depending on site factors, group selection harvests have diameters of roughly 21 m on south-facing slopes, 32 m on level areas, and 43 m on north-facing slopes (Sheriff, 2002; Kabrick et al., 2004).

As with single-tree selection, the applicability of group selection to maintain a balanced diameter distribution has also been doubted for oak management (Roach, 1974). In comparisons of clearcutting, single-tree, and group regeneration methods 6 years after harvest in the Ozark Highlands, white oak reproduction (trees < 11.43 cm dbh) densities in clearcut patches were more than 2 to 4 times greater than those in group and single-tree selection patches. (Jensen & Kabrick, 2008). In the same study, the clearcut inventory taken 10 years post-harvest showed a 79% reduction in white oak stems, displaying competition-induced mortality indicative of the stem exclusion stage of stand development (Oliver & Larson, 1996; Jensen & Kabrick, 2008). In contrast, stem density within the group opening patches had increased by roughly 7%, displaying more limited growth potentially associated with reduced photosynthesis in this lower light environment (Hanson et al., 1986; Jensen & Kabrick, 2008).

Several considerations are important when determining if uneven-aged silvicultural is suitable for a site and management goals. Economically, at the stand scale, group selection harvesting in hardwood stands can reduce production rates by 17% to 52% compared to clearcutting (Shaffer et al., 1993). Additionally, tree selection in Appalachian hardwood systems resulted in residual tree damage amounting to 6% of the RBA, with 85% of this damage occurring to saplings (<12.7 cm dbh) (Lamson et al., 1985). Furthermore, the likelihood of epicormic sprouts forming along the lower boles of trees increases along group opening edges, which can reduce log grade and timber value (Miller, 1996). These are just a few of many considerations that can help determine if UAM is applicable for a given site and management goals.

Future research needs

For the effective management of oak using UAM silviculture, additional understanding of the oak regeneration process, OAR population dynamics, as well as canopy ascension rates must be gained. Much research has provided foundational knowledge on topics such as the variability between oak stem and root ages, OAR vs. competitor densities under varying overstory conditions and management practices, and OAR seedling height growth and survival in relation to sunlight (Merz & Boyce, 1956; Crow, 1992; Clark & Hallgren, 2003; Clark et al, 2007). Despite a need for added understanding, this research has highlighted the complex nature of oak regeneration. This research has also emphasized the importance of advance reproduction and the ability of oaks to persist in the understory through recurrent dieback and resprouting.

Merz and Boyce (1956) were two of the first to document their observations of OAR stem and root age demography through annual ring counts of oak seedlings in a southeastern Ohio oak-hickory stand. Here, out of 100 oak seedlings examined, only 26 had matching stem and root ages; yet in some cases, stem and root ages differed by up to 31 years. The two largest OAR were approximately 3 cm in diameter, aged 30 and 32 years old with corresponding stem ages of 20 (2.25 cm) and 7 years old (0.5 cm), respectively (Merz & Boyce, 1956).

In an old-growth cross timbers forest in Oklahoma, similar results were seen in blackjack oak (*Quercus marilandica* Münchh.) and post oak *(Quercus stellata* Wangenh). Here, Clark and Hallgren (2003) found stems averaging 6 years old and roots averaging 20 years old. Although, the oldest tree sampled was a post oak with a 67-year-old root and an 8-year-old stem, demonstrating a persistence often associated with oak resprouting adaptations. Additionally, 99% of the population was assessed as a resprout, either from stump resprouting, seedling resprouting, or root sprouting (Clark & Hallgren, 2003). While the adaptation of resprouting is believed to favor oak growth, less is known about the relationship between root-to-stem age and growth relationships.

In old-growth *Quercus* forests in Tennessee that experienced a mortality event in the 1980s but no further disturbances, the density of sugar maple and yellow-poplar increased over 22 years in both the smallest (0 to 27.43 cm) and largest (> 137 cm in height, 6.35 to 13.72 cm dbh) size classes (Clark et al., 2007). During the same time, white oak had increased in the smallest size class but had become absent in larger size classes. The reduced presence of oaks in increasingly densified midstories due to diminished or absent disturbance regimes has been observed throughout the eastern U.S. (Abrams, 1992; Abrams & Nowacki, 1992; Aldrich et al., 2005; Hanberry et al., 2014). Widespread reduction in oak recruitment highlights the need for added knowledge of OAR densities and diameter distributions that will sustain oak overstory dominance. Furthermore, disturbance regimes that sufficiently control oak competition while promoting oak establishment and growth must be identified.

Aside from OAR demography and densities, studies on OAR height and diameter growth have also contributed to the current understanding of oak regeneration. Crow (1992) observed a cohort of northern red oak seedlings over 6 years and found seedling mortality was strongly related to overstory density. Seedling survival rates were 92% when grown in full sunlight but down to 36% when shaded under a complete overstory. Microsite differences also contributed to differences in survival rates with 67% of mortality occurring on shoulder landform positions, despite these microsites making up only 27% of total microsites (Crow, 1992). In the same study, seedling height growth was inversely related to canopy density. Seedlings grown in full sunlight reached up to twice the height of seedlings grown under the complete understory by the end of the first year, and 3 times the height (roughly 40 cm) by the end of the sixth year (Crow, 1992).

In Pennsylvania, diameter growth and root:shoot dry weight ratios were analyzed over 2 years between red oak, black oak, red maple, and black cherry (*Prunus serotina* Ehrh.) growing in screen tents transmitting varying levels of sunlight (8% to 94% full sunlight). Here, all species responded with a significant reduction in diameter growth in the lowest level of sunlight (8%) during the first and second years (Gottschalk, 1985). However, comparisons of diameter growth between pairs of the six other treatments ranging from 20% to 94% sunlight resulted in no significant differences in either year. Root:shoot dry mass ratios were also affected with reductions of percent sunlight decreasing the root:shoot ratio. Root:shoot ratios decreased in all species from the first to the second year, but the oak species still allocated a greater dry weight to root systems than did black cherry and red maple (Gottschalk, 1985). A similar study examining stem growth under canopy shading over longer time intervals may provide greater insight into energy allocation and transfer from roots to shoots within a range of light environments.

Several studies mentioned here and previously have made great contributions to our understanding of the oak regeneration process, including advance regeneration population dynamics and growth. Yet, few attempts have been made to re-observe these processes at finer resolutions using more modern advances in technology and methods, such as those utilized in QWA (von Arx et al., 2016). Using QWA methods, thin microsections (approximately 10 to 20 μm) of xylem tissue can be microscopically imaged and digitized for pixel-based analyses of the xylem’s anatomical structure and growth (von Arx et al., 2016).

Research utilizing these advancing tools and methods would allow the ongoing oak regeneration problem across the eastern U.S. to be studied from spatial scales rarely observed. By utilizing tree-ring dating methods applied in dendrochronology studies, such as annual ring-width normalization and cross correlation, examining young oaks from the cellular perspective permits a more resolute assessment of growth (Fritts, 2014). Incorporating QWA and dendrochronology methods into studies involving wOAR would enhance our understanding of its regeneration and recruitment dynamics. These methods would also help assess the effectiveness of current silvicultural practices and identify those that better support sustainable management.

CHAPTER 3: MATERIALS AND METHODS

3.1 Site description

This study took place at MOFEP, located in southeastern Missouri, USA, within Carter, Reynolds, and Shannon counties. MOFEP was established in 1989 as a long-term research forest to study the effects of forest management on forest structure, composition, and wildlife communities (Brookshire et al., 1997b). Situated in the interior of the Ozark Highlands, MOFEP lies within the Current River Hills Subsection. The bedrock geology of MOFEP includes Ordovician sandstones, chert, and dolomites (Kabrick et al., 2000). The parent materials associated with the upland portions of MOFEP include hillslope sediment, loess, and residuum. From these parent materials, soils are comprised mostly of weathered Ultisols and Alfisols (Meinert et al., 1997).

At MOFEP, from 1984 to 2024, the mean annual temperature was 13.7°C, with mean monthly temperatures of 0.6°C in January and 25.7°C in July. During the same timeframe, the mean yearly precipitation was 1120 mm (National Centers for Environmental Information, 2025a). Within Missouri climate division five, no annual cases of Palmer Drought Severity Index (PDSI) extreme (< -4.0) or severe (-3.0 to -3.99) values were recorded from 1984 to 2024; however, moderate drought (-2.0 to -2.99) occurred in 2000 and 2012. For individual months within the growing season (April through October), severe drought was recorded in April and May of 2000, and from June through September in 2012 (National Centers for Environmental Information, 2025b).

The climate of the interior Missouri Ozark Highlands supports temperate deciduous forest ecosystems characterized by upland oak-hickory and oak-pine forest communities. Here, the dominant overstory tree species are white oak, black oak, scarlet oak (*Q. coccinea* Muench.), post oak, shortleaf pine, and hickories. Common understory tree species include flowering dogwood, blackgum (*Nyssa sylvatica* Marsh.), and red maple (Brookshire et al., 1997b). The 20 most abundant tree species occurring at MOFEP are provided (Table 1).

MOFEP has a long and intensive land-use history. Historically, the area had been occupied by several Indigenous tribes, namely the Quapaw, Osage, Cherokee, and Shawnee before Euro-American westward expansion reached the area in the early 1800s (Guyette & Larsen 2000). During this time, fire intervals were variably frequent, ranging from 2 to 12 years or longer (Guyette & Larsen, 2000). However, these fire frequencies would have also included some fire-free periods of up to 50 years or more, permitting periods of overstory recruitment (Guyette et al., 2002). Beginning around the 1930s, fire suppression efforts became widely initiated in U.S. and continued for several decades. Within much of the Ozark Highlands, including MOFEP, extensive cutovers occurred from the late 1800s into the early 1900s. These widespread land clearings resulted in the reforestation of even-aged forests with little variation in stand age and structure across the landscape. Intensive livestock grazing practiced from the mid-1800s to the late 1900s is cited as a primary factor in the declines of fire frequency (Guyette & Larsen, 2000).

Table 1: A list of the top 20 tree species at MOFEP in order of decreasing basal area. (Adapted to metric units from Kabrick et al. (2008))

Latin	**Common name**	**Basal Area (m2 /ha)**	**TPH**
Quercus velutina Lam.	black oak	5.33	143
Quercus coccinea Muenchh.	scarlet oak	4.66	121
Quercus alba L.	white oak	4.50	321
Pinus echinata Mill.	shortleaf pine	1.84	52
Quercus stellata Wangenh.	post oak	1.33	54
Carya glabra (Mill.) Sweet	pignut hickory	0.87	121
Carya texana Buckl.	black hickory	0.83	109
Carya tomentosa Poir. Nutt.	mockernut hickory	0.78	138
Cornus florida L.	flowering dogwood	0.73	862
Nyssa sylvatica Marsh.	blackgum	0.53	213
Quercus muehlenbergii Engelm.	chinkapin oak	0.14	12
Quercus marilandica Muenchh.	blackjack oak	0.11	7
Acer rubrum L.	red maple	0.09	133
Sassafras albidum (Nutt.) Nees	sassafras	0.09	257
Juglans nigra L.	black walnut	0.07	2
Ulmus rubra Muhl.	slippery elm	0.07	49
Ulmus alata Michx.	winged elm	0.07	47
Fraxinus americana L.	white ash	0.05	44
Juniperus virginiana L.	eastern red cedar	0.02	7
Acer saccharum Marsh.	sugar maple	0.02	7

3.2 MOFEP design

The experimental units of MOFEP are the nine different sites, defined as unique administrative units (Figure 2). During MOFEP's establishment in 1989, sites must have met several criteria including: (1) occupying a minimum size of 240 hectares (ha), (2) having minimal edge presence, and (3) having been free from management for at least 40 years (Brookshire et al., 1997b). Within each site, forest stands that are approximately 5 ha in size delineate the boundaries of experimental treatment (Brookshire et al., 1997b). The nine study sites were equally split between three forest management treatments: EAM, UAM, and no-harvest management, which serves as experimental control. The EAM and UAM methods were structured according to the Missouri Department of Conservation Forest Land Management Guidelines (1986). Since MOFEP's establishment, prescribed fire has not been utilized on any site. Within the no-harvest sites, there is no management except in the case of extreme natural catastrophes, such as wildfires or insect outbreaks, which are suppressed (Brookshire et al., 1997b). For the purpose of this study, the sites associated with EAM are disregarded. Readers interested in the complete description of MOFEP's experimental design should refer to the original and updated *Proceedings of the Missouri Ozark Forest Ecosystem Project* (Brookshire & Shifley, 1997a; Shifley & Kabrick, 2002).

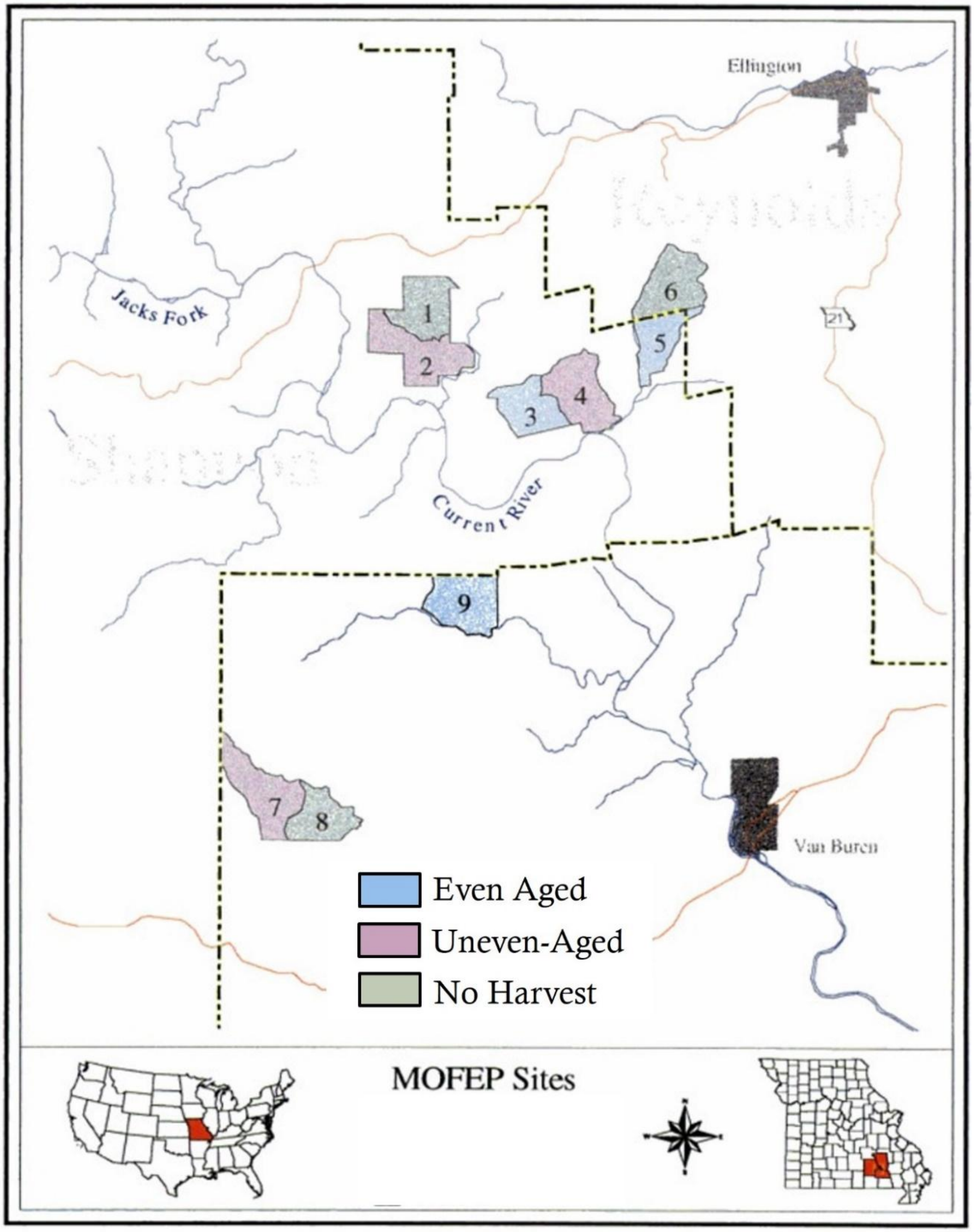


Figure 2: A map of MOFEP depicting its geographical location within the United States and Missouri (bottom). MOFEP has nine unique study sites that are split evenly among three forms of forest management. Forest stands from sites 1, 2, 4, 6, and 7 were utilized for this study.

Within UAM sites, harvesting practices include single-tree and group selection. To date, harvest entries in the UAM sites at MOFEP occurred in 1996 and 2011. Group selection created canopy gap sizes that followed the Central Hardwoods UAM guideline suggestions of 1 to 2 tree heights (Law & Lorimer, 1989). With a white oak site index of approximately 19 to 22 m depending on site factors, canopy gaps created through group selection had diameters of up to 32 m on level areas and 43 m on north-facing slopes (Sheriff, 2002; Kabrick et al., 2004). During the first harvest, the total area of group openings was approximately 5% of the total area harvested (Sheriff, 2002).

Within the UAM sites, a diameter distribution curve (guiding curve) was established to guide harvesting decisions. Guiding curves were calculated using stand-specific management objectives for the LDT to be retained, an RBA, and a q-value. The LDT was equal to the desired sawtimber size for similar EAM stands (51 to 61 cm for white oaks) (Sheriff, 2002). The RBA was equivalent to B-level Gingrich stocking (~ 58%) (Roach & Gingrich, 1968; Sheriff, 2002). The q-value, which ranged from 1.3 to 1.7 (Law & Lorimer, 1989), is a quotient that influences the proportion of tree counts between successive size classes and is graphically represented as a reverse-J distribution.

Concerning UAM protocols, forest managers at MOFEP are allowed to adjust prescriptions within UAM areas so long as harvesting operations fall within the same year and timeframe as the other UAM sites (Sheriff, 2002). As such, slight differences in UAM practices have occurred between harvest entries as newer harvesting guidelines specific to the Ozark Highland's more xeric upland ecosystems had become available (Larsen et al., 1999). These guidelines recommended a slightly lower RBA target of approximately 11.5 m^2/ha and a lower q-value of 1.2 to 1.3 (for one-inch size classes).

The lower RBA and q-value are recommended to effectively sustain competitive OAR and promote their continued recruitment (Larsen et al., 1999). Furthermore, according to J. Kabrick (personal communication, May 2025), large, circular group openings were implemented during the first (1996) stand entries. In contrast, the second stand entry in 2011 more greatly emphasized single-tree selection. Another key difference between the first and second entries at MOFEP is that several stands in 1996 were harvested to a much lower residual STK compared to others. These differences are evident between the one- and two-harvest treatments, as described and seen below (Figure 3).

3.3 Experimental design

This study evaluated the effects of repeated stand entries utilizing UAM harvesting on white oak regeneration and recruitment at MOFEP. Three experimental treatment levels representing varying UAM intensities and cutting cycles lengths were used to assess the effects of periodic reductions in overstory density on wOAR demography, establishment trends, and growth rates. There were three experimental treatments used for this study. Three stands made up the one-harvest treatment (1H) using UAM (1996), representing a roughly 30-year cutting cycle across just one stand entry, although wOAR were assessed at year 26 post-harvest. A second treatment included three stands harvested twice (2H) using UAM (1996 and 2011), representing a 15 year cutting cycle across two stand entries. Lastly, three unharvested stands (0H) from the no-harvest management sites were used for a control, which represented prolonged canopy closure in the absence of large-scale canopy disturbance.

Each stand used in this study was selected based on requirements for site classifications (Table 2), white oak densities, as well as pre- and post-harvest stand structure (Figure 3). The MOFEP inventory data identified potential stands for experimental treatments (Shifley et al., 2000). Stands were chosen based on repeat inventories of MOFEP's permanent plots from 1995 to 2017, ensuring similar developmental patterns. On MOFEP, site classifications for each stand are centered around ecological land type (ELT) and ecological site description (ESD) designations for natural community types. Roughly 90% of MOFEP fits into ELT classification 17 (south- and west-facing slopes), 18 (north- and east-facing side slopes), and 11 (ridgetop). (Miller, 1985; Shifley & Brookshire, 2000).

As ELTs were typically more coarsely scaled, these were used first . Stands with an ELT 18 classification, which were located on protected aspects (337.6° to 112.5°), were included in this study. These protected aspects at MOFEP typically have a greater proportion of white oak than stands on exposed aspects (112.6 to 337.5°), where red oak species (scarlet and black) and shortleaf pine are more abundant (Kabrick et al. 2004). ELT 18 sites were also selected for their more mesic conditions, which present greater challenges for oak regeneration. The ESDs for selected sites generally followed the description of a low-base Chert protected backslope woodland.

Considering all MOFEP sites classified as ELT 18, white oak had a high relative abundance, which influenced its importance value of 22.98%. After white oak, scarlet oak (15.87%) and black oak (15.43%) had the next highest importance values (Shifley et al., 2000). Regardless of experimental treatment, all nine stands must have been fully stocked (70% to 90%) in 1995, the year before the first harvest entry (Figure 3). For each stand in the control treatment, STK must have increased between each sampling year. For each stand in the 1H and 2H treatments, STK must have been reduced to approximately Gingrich B-level (~ 58%) or below during years of stand entry (1996, 2011).

Stand-level densities (TPH, BA, and STK) were calculated from individual tree lists collected during inventories from 1995 to 2017 on MOFEP's permanent ~ 0.20 ha (1/2 acre) fixed-area plots. Trees under 11.43 cm (4.5 in) dbh were excluded from MOFEP inventories. Stand-level STK was calculated for each inventory year using species-specific equations: for upland hardwoods, (-0.00507 + (0.01698 * diameter) + (0.00317 * (diameter ^{2}))); and shortleaf pine, (0.008798 + (0.009435 * diameter (in)) + (0.00253 * (diameter ^{2}))) (Gingrich, 1967; Rogers, 1983).

Table 2: Forest stands within MOFEP included in this study. Site and stand numbers were used as stand identifiers. ELT designation 18 was used to ensure uniformity among physical site factors.

Site	Stand	MOFEP Treatment	Experimental Treatment	ELT
1	**26**	**No harvest**	**Control**	18
1	**36**	**No harvest**	**Control**	18
6	**6**	**No harvest**	**Control**	18
2	**32**	**UAM**	**One-harvest**	18
4	**9**	**UAM**	**One-harvest**	18
4	**12**	**UAM**	**One-harvest**	18
2	**27**	**UAM**	**Two-harvest**	18
7	**132**	**UAM**	**Two-harvest**	18
7	**142**	**UAM**	**Two-harvest**	18

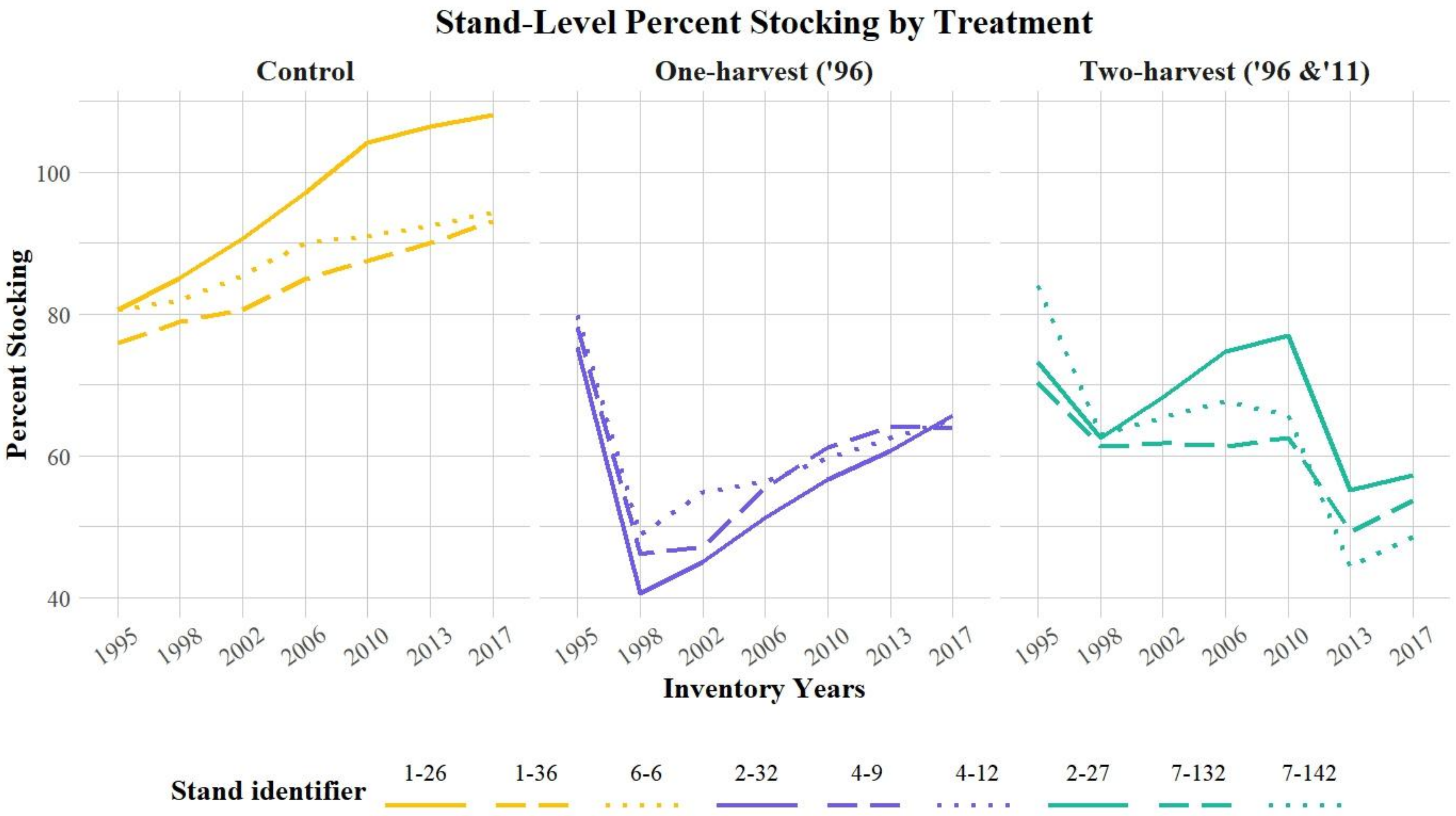


Figure 3: Gingrich stocking through time for each stand selected for each of the three treatments. Reductions in STK within the treated stands between inventory years 1995 and 1998 (1H and 2H) and between 2010 and 2013 (2H) represent changes in stand density from UAM harvesting that occurred during harvest years (1996, 2011).

3.4 Field sample collection and inventory data

Field data and wOAR collection occurred in the dormant season of 2022. Within each stand, 20 research plots were established. For this, a square grid of points was generated over a map of each stand using ArcGIS (Esri, 2020). Grid intersections were sequentially numbered and spaced 20 m apart. The numbered grid intersections that fell at least 20 m from stand boundaries were randomly selected as potential research plots. Potential research plots that fell within the boundaries of MOFEPs permanent inventory plots were excluded (Figure 4). Potential research plots were then located in the field. Research plots were established at the nearest sub-canopy white oak to represent the plot center if it met the following criteria: (1) the sub-canopy white oak was free from defects, (2) dbh was between 10.2 and 17.8 cm, and (3) at least three wOAR (between 15 and 137 cm in vertical height above ground level) were present within an 8.02 m radius of the sub-canopy white oak. The third criterion was the most common reason for rejecting potential plots. Hereafter, vertical stem height above ground level is referred to as stem height.

For plots that met research criteria, GPS coordinates were recorded at the plot center. The plot was divided into three sections by placing pins 4.01 m away from the target tree at the 0°, 120°, and 240° azimuths (Figure 5). The wOAR nearest each pin was then selected for sampling. Each wOAR selected for sampling was measured in stem height (cm), checked for signs of browse or stem resprouting, and the number of living and dead stems was recorded. The wOAR was then excavated, given a sample ID, and packaged for further lab preparation. At the end of field sample collection, a total of 540 individual white oak seedlings had been obtained.

Inventories of overstory trees and saplings in a 1/20th ac plot (~ 1/50th ha) and seedlings in a 1/100th ac plot (~ 1/250th ha) were conducted using fixed-area sampling (Figure 5). Tree species, dbh, and crown classification of overstory trees (> 11.43 cm dbh) were recorded. Trees at least 137 cm tall and less than 11.43 cm dbh were classified as saplings. Saplings were tallied by species and diameter class (0 to < 0.5 in [0 to < 1.27 cm], 0.5 to < 1.5 in [1.3 to < 3.8 cm], 1.5 to < 2.5 in [3.9 to < 6.3 cm], 2.5 to < 3.5 in [6.4 to < 8.9 cm], and 3.5 to < 4.5 in [9.0 to < 11.4 cm]). Trees less than 137 cm tall were classified as seedlings. Seedlings were tallied by species and height class (0 to 25, 26 to 50, 51 to 100, and 100 to 137 cm).

Stand- and treatment-level densities for inventory year 2022 were calculated from individual tree lists using the same species-specific STK equations used to calculate MOFEP inventory metrics from 1995 to 2017. For the 2022 inventory, stand- and treatment-level density metrics were calculated with the exclusion of saplings (dbh < 11.43 cm), as was done for MOFEP inventories. The STK associated with each research plot was calculated from the 2022 inventories (Figures 6 - 8). Stand- and treatment-level mean, minimum, and maximum densities were calculated from the 2022 inventories (Tables 3 and 4). Inventories from the 2022 field collection did not occur within the permanent inventory plots used for MOFEP inventory data.

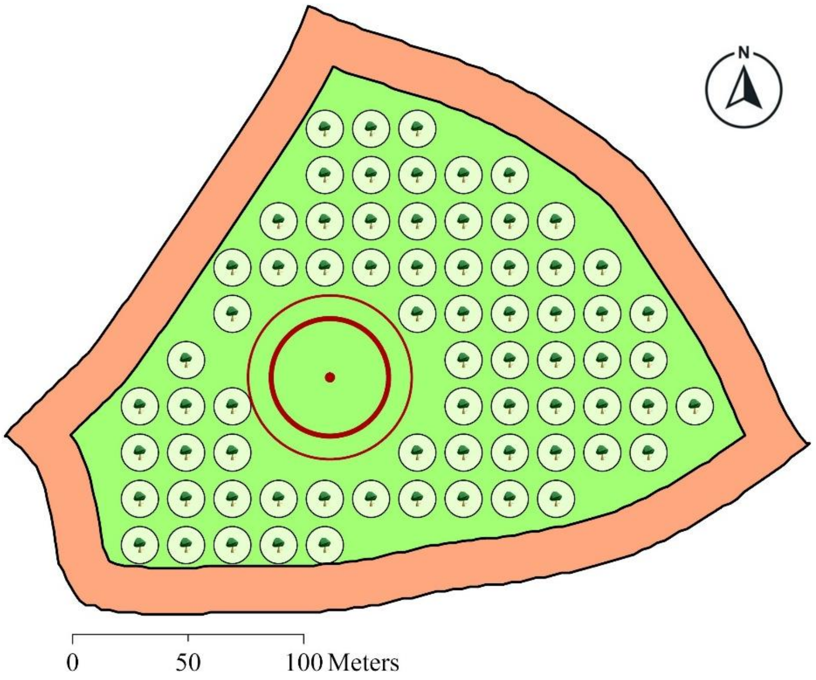


Figure 4: A representation of the research plot selection process. The salmon-colored area represents a 20 m buffer around the stand boundary. The maroon-colored point, thick circle, and thin circle represent the MOFEP permanent inventory plot center, area of the plot (1/2 acre), and 10 m buffer around the plot, respectively. Trees and their boundaries represent potential research plots (~ 1/50th ha).

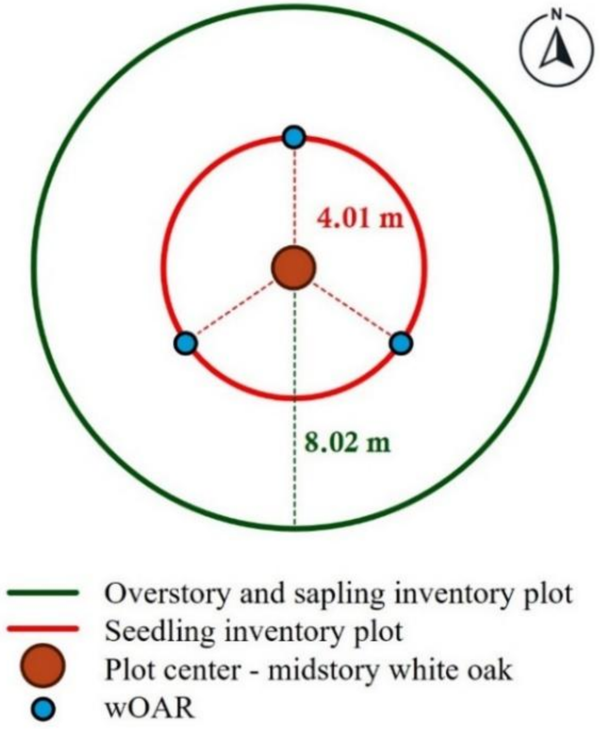


Figure 5: A schematic representation of research plots. A sub-canopy white oak was randomly selected to represent the plot center. Overstory, sapling, and seedling layer inventories were collected within each research plot. Three wOAR located along three different azimuths were measured and inspected before being excavated for further lab preparation.

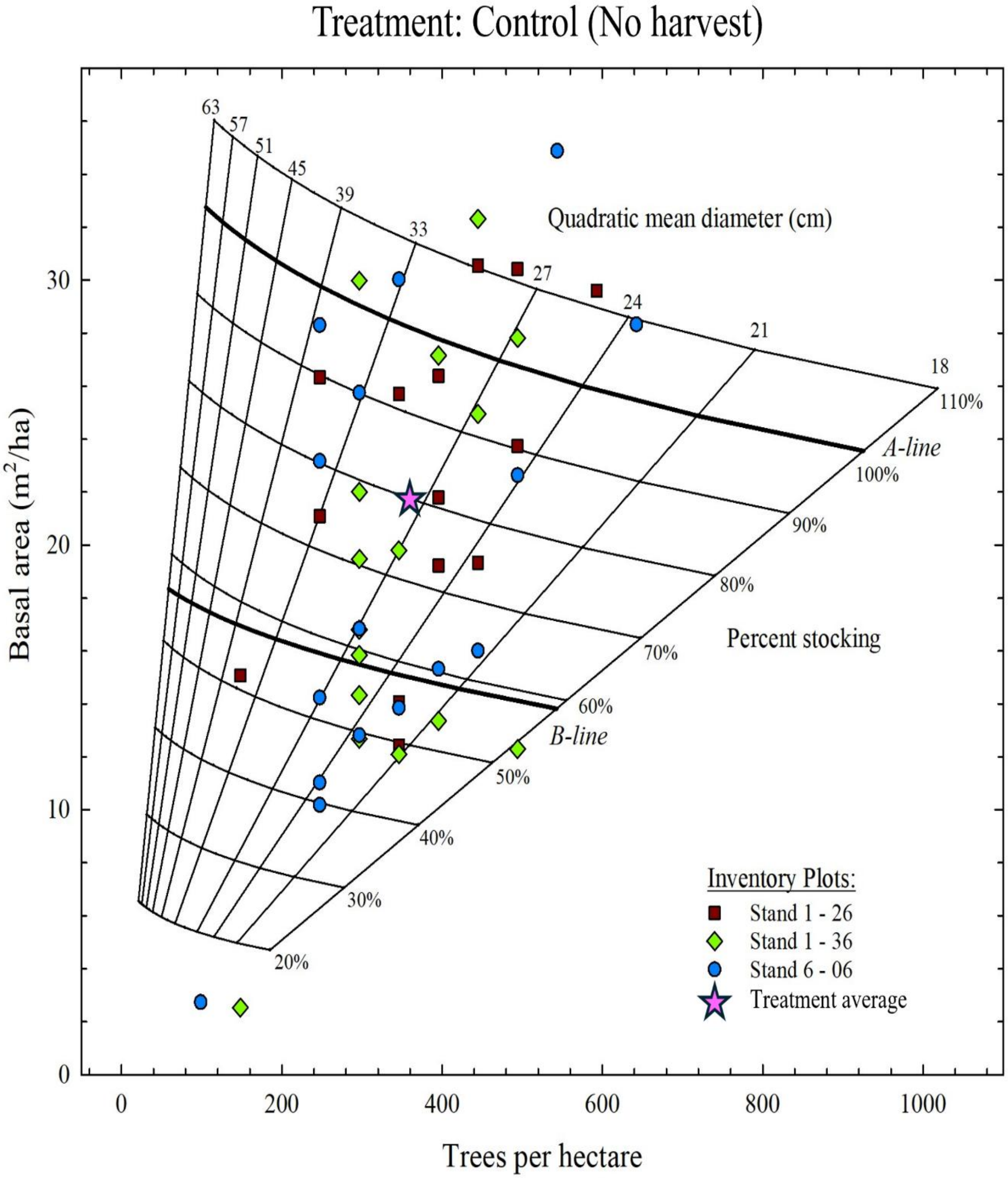


Figure 6: A Gingrich stocking diagram for upland hardwoods that depicts the 2022 STK for each research plot within the 0H treatment. Individual plots are color and shape coded by stand. The pink star represents the treatment-level mean. Plots with a shortleaf pine component contributing to more than 15% of total plot STK are excluded from the graph.

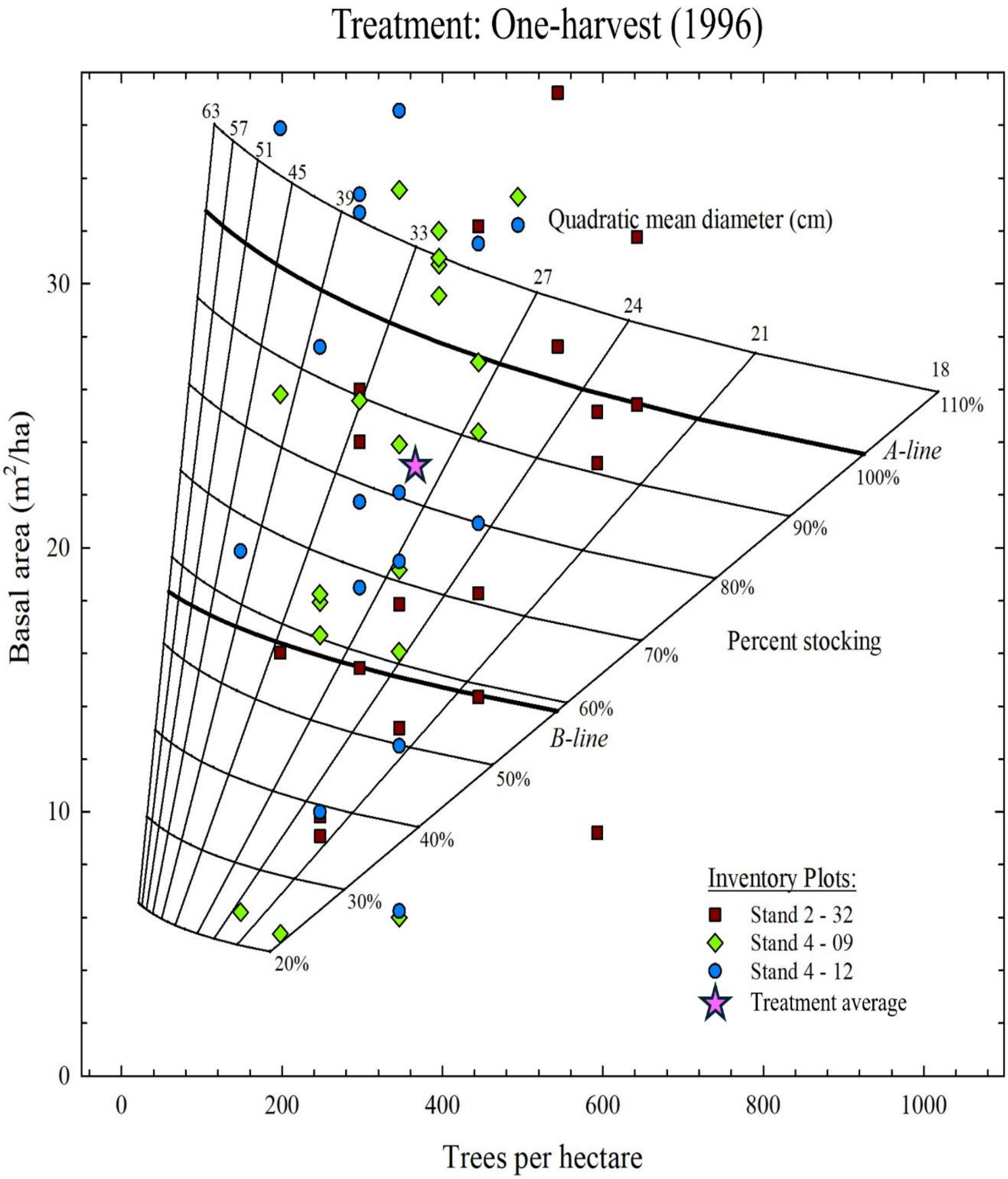


Figure 7: A Gingrich stocking diagram for upland hardwoods that depicts the 2022 STK for each research plot within the 1H treatment. Individual plots are color and shape coded by stand. The pink star represents the treatment-level mean. Plots with a shortleaf pine component contributing to more than 15% of total plot STK are excluded from the graph.

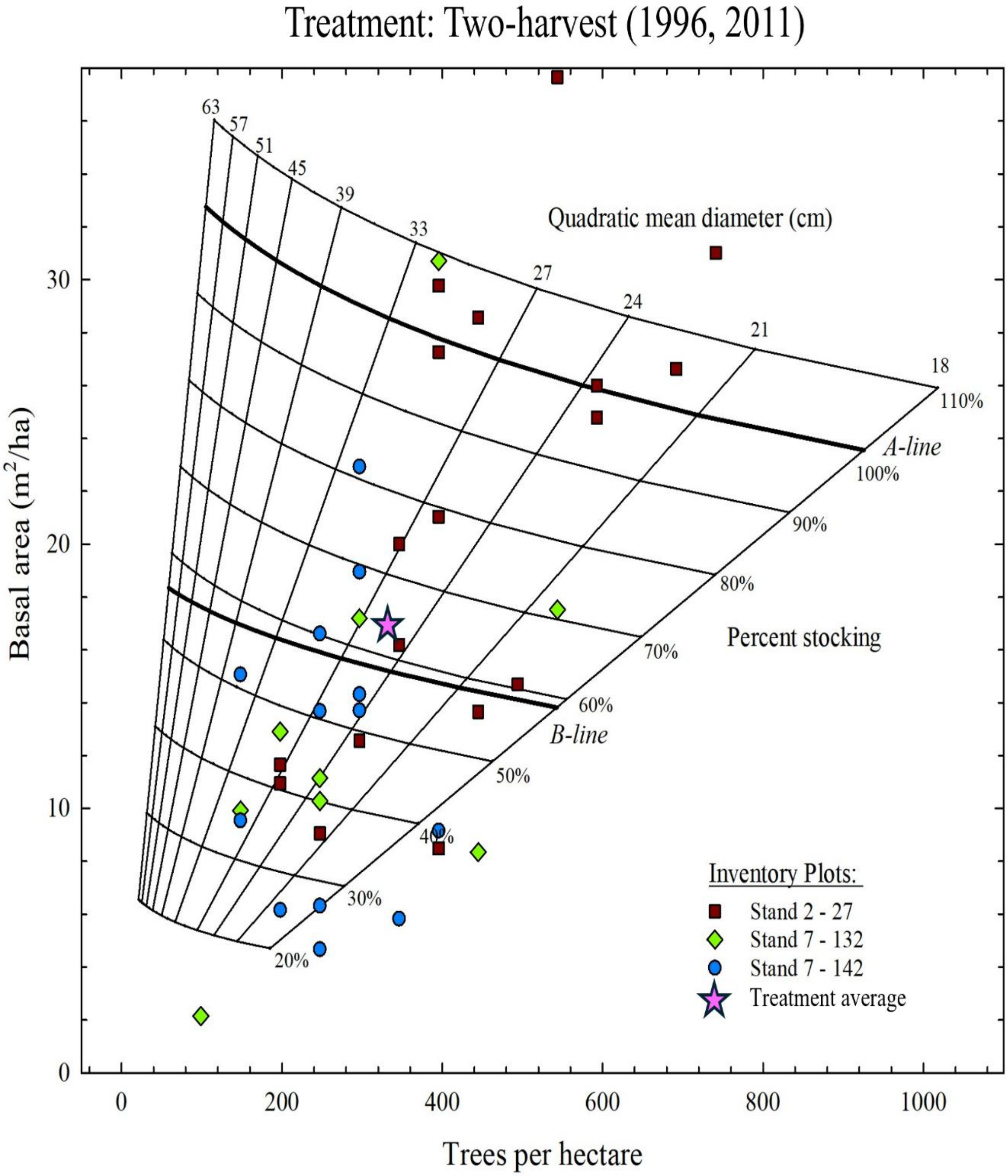


Figure 8: A Gingrich stocking diagram for upland hardwoods that depicts the 2022 STK for each research plot within the 2H treatment. Individual plots are color and shape coded by stand. The pink star represents the treatment-level mean. Plots with a shortleaf pine component contributing to more than 15% of total plot STK are excluded from the graph.

Table 3: 2022 stand-level density calculations of data gathered within research plots.

Site	**Stand**	**Treatment**	**Mean BA (m2/ha)**	**Min BA**	**Max BA**	**Mean TPH**	**Min TPH**	**Max TPH**	**Mean QMD**	**Min QMD**	**Max QMD**	**Plot-lvl Mean STK**	**Plot-lvl Min STK**	**Plot-lvl Max STK**
1	**26**	**Control**	24.1	12.4	45.8	405	148	642	27.5	19.8	36.8	84.2	49.6	142.6
1	**36**	**Control**	19.8	2.5	32.3	361	148	494	26.5	14.7	35.9	72.5	12.0	115.2
6	**6**	**Control**	23.0	2.7	46.3	356	99	642	28.7	18.8	38.9	81.1	11.7	150.1
2	**32**	**One-harvest**	22.3	9.1	38.4	440	198	642	25.4	14.1	33.4	81.8	36.1	134.1
4	**9**	**One-harvest**	21.6	5.4	33.6	334	148	494	28.7	14.9	40.8	76.0	22.9	118.0
4	**12**	**One-harvest**	27.2	6.2	53.3	353	148	593	31.3	15.2	48.1	93.2	29.2	177.6
2	**27**	**Two-harvest**	20.4	8.5	37.7	430	198	741	24.6	16.5	31.0	75.7	36.1	134.2
7	**132**	**Two-harvest**	17.1	2.2	31.8	292	99	544	27.3	15.5	34.1	56.3	9.6	108.5
7	**142**	**Two-harvest**	15.5	4.7	26.7	297	148	445	25.8	14.6	36.0	53.7	21.6	83.1

Table 4: 2022 treatment-level density calculations of data gathered within research plots.

Treatment	**Mean BA (m2/ha)**	**Min BA**	**Max BA**	**Mean TPH**	**Min TPH**	**Max TPH**	**Mean QMD**	**Min QMD**	**Max QMD**	**Stand-lvl Mean STK**	**Stand-lvl Min STK**	**Stand-lvl Max STK**
Control	22.3	2.5	46.3	374	99	642	27.6	14.7	38.9	79.2	72.5	84.2
One-harvest	23.7	5.4	53.3	376	148	642	28.5	14.1	48.1	83.7	76.0	93.2
Two-harvest	17.7	2.2	37.7	339	99	741	25.9	14.6	36.0	61.9	53.7	75.7

3.5 Sample preparation, microsectioning, and slide digitization

To gather separate ages for wOAR stems and roots, each seedling was split into two separate segments. Following the methods of Dee et al. (2022), each wOAR was cut just above and below the root collar to obtain separate stem and root segments. Once split, the separate stem and root segments were tagged at their cut ends and placed into separate bags filled with water. The cut ends of each sample were tagged so that their orientation was maintained, ensuring the microsectioning process began with the end closest to the root collar. This ensured the preservation of each annual growth ring formed by the tree (Figure 9). From here on, the word sample refers to either the separated stem or root segment, while wOAR refers to the entire tree.

Stem and root diameters were recorded by averaging the length in millimeters (mm) of two perpendicular radii. Diameter measurements were taken in the lab on samples that had been stored in water, likely inflating the measurement relative to those taken in situ or as they had air-dried post-excavation. However, this method provided uniformity in diameter measurements as all samples were measured with similar moisture contents. Separate stem and root samples were then individually microsectioned.

A strict protocol was developed from a review of QWA guidelines for microsection preparation methods and analysis techniques (von Arx et al., 2016). A reproducible protocol was necessary to ensure all microsections retained a quality that accurately represented their anatomical form. From here on, the use of the word microsection refers to a single microsection of either the stem or root sample, while sample is still used to refer to an un-sectioned stem or root segment. Each sample was microsectioned with the use of a sledge microtome. Samples were first oriented in the sledge microtome so that its cross-sectional plane was perpendicular to the axial direction of the xylem. Sharp blades fixed at appropriate angles and steepness were required to obtain cohesive microsections that retained true anatomical structure. Dull or imperfect blade edges often resulted in ruptured cell walls and uneven cutting thickness. All microsections were cut to the same thickness; approximately 15 micrometers (µm).

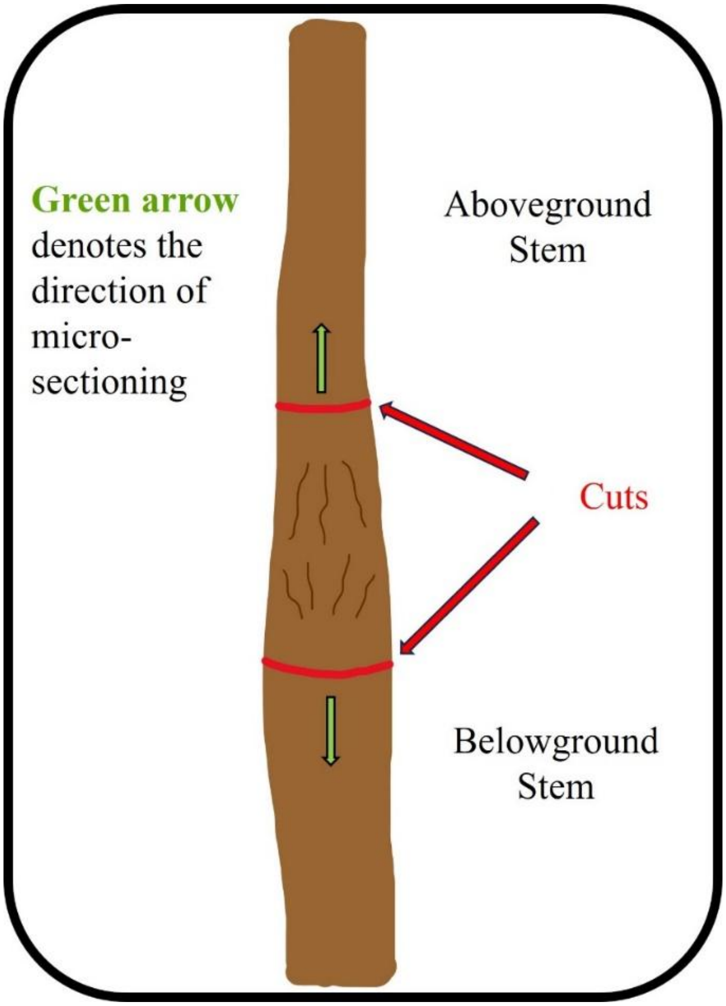


Figure 9: A representation of how wOAR were partitioned into separate stem and root samples. Microsectioning began with the end nearest the root collar to ensure preservation of all tree rings.

Upon obtaining a cohesive and comprehendible microsection, it was first bleached to remove tannins and to enhance the brightness and contrast of the microsection once stained. Microsections were stained with a double-stain mixture consisting of equal parts Astra Blue and Safranin O. The double-staining method enhanced the contrast between cellulose and lignin, as each had a stronger affinity to Astra Blue and Safranin O, respectively. The stained microsections were then rinsed with increasing ethanol concentrations (70% to 90% to 99%) to remove any excess stain from the microsections. The ethanol-rinsed microsections were then permanently mounted to glass microscope slides.

Before imaging, excess mounting medium, dust, and fingerprints were removed from each microsection slide to ensure consistent image quality for each section. A high-resolution camera attached to a compound light microscope was used to manually capture overlapping, highly magnified (40x) images of the individual microsections (Figure 10). Configuring the microscope using the Köhler illumination method enhanced image contrast, resolution, and white balance (Saxena et al., 2015; von Arx et al., 2016). Re-focusing the field of vision using the zoom function (every 3 to 5 images), ensured consistent focus throughout the imaging process. The PTGui image-stitching software (New House Internet Services B.V., Rotterdam, NL) was used to stitch separate images from the same microsection into a single composite image based on matching control points across the overlapping images (Figure 11). Once digitized, microsection images could be observed on a computer monitor without active microscope use.

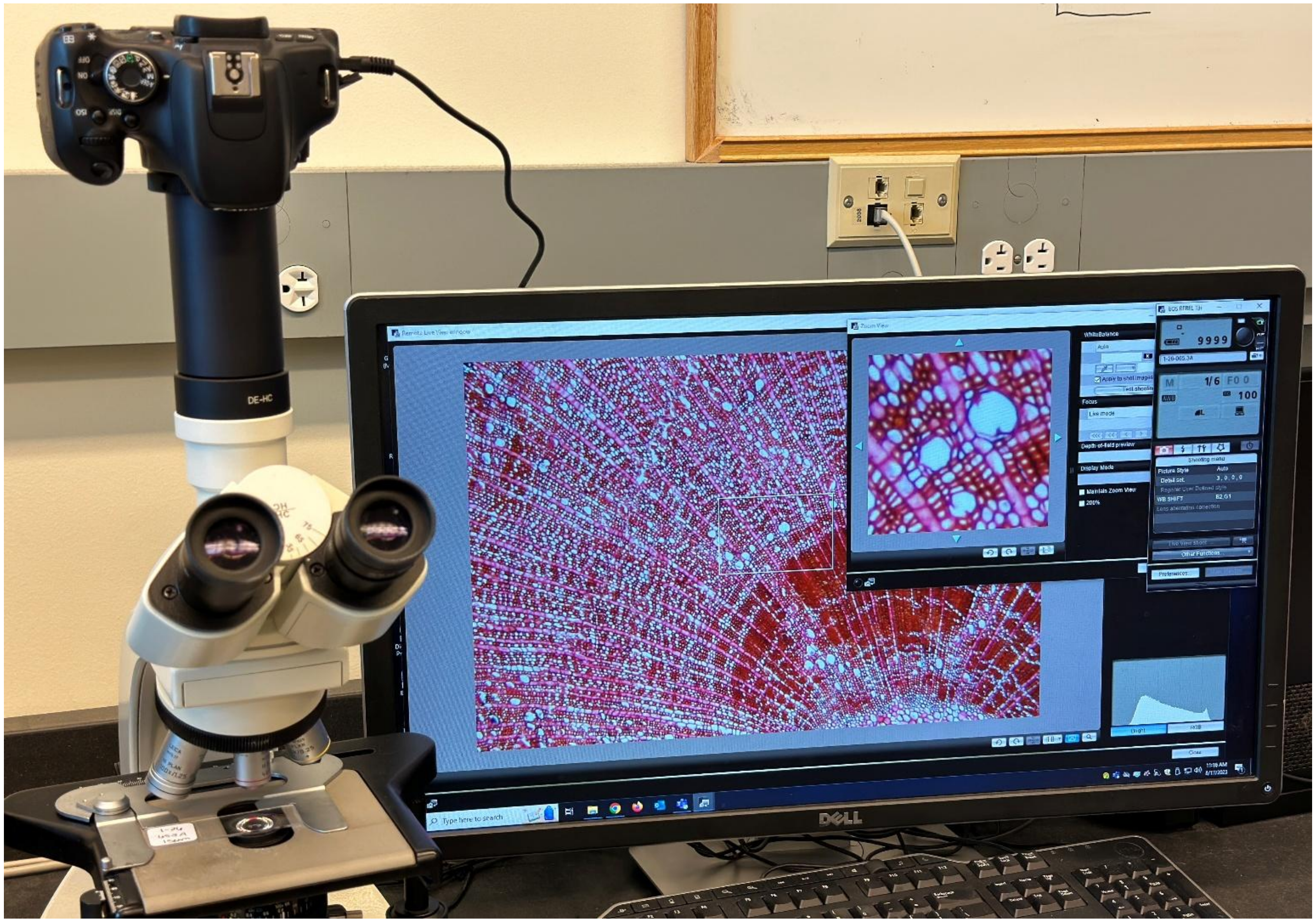


Figure 10: The image-capturing process. A high-resolution camera is attached to the top of a light microscope. The monitor displays use of the zoom function, which ensures consistent focus.

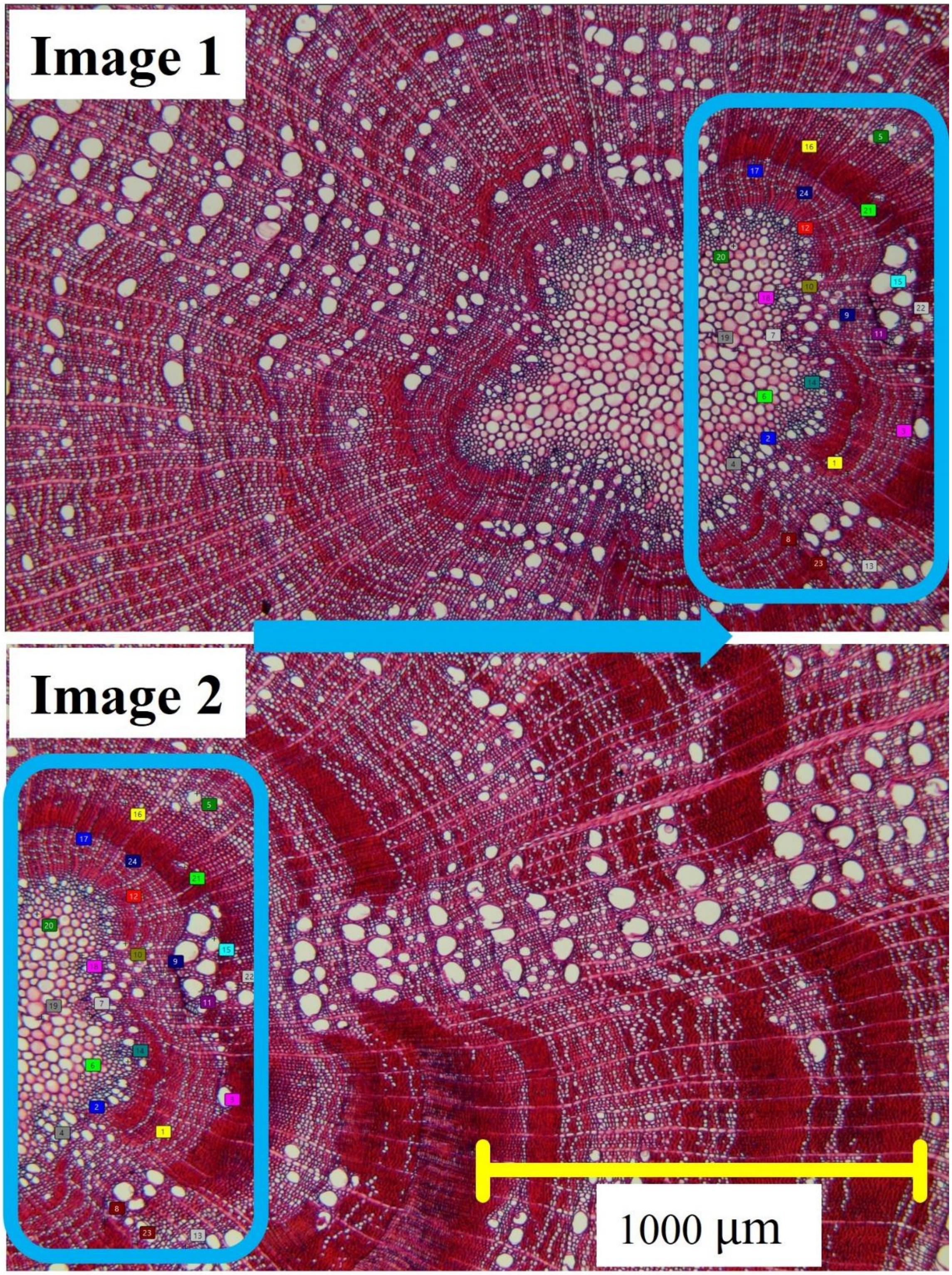


Figure 11: The microsection digitization process. Individual images are stitched together based on matching control points. The precise alignment of individual images based on matching control points is repeated for all overlapping images of an individual microsection.

3.6 White oak anatomy: visual inspection and the influence of tension wood

An understanding of wood xylem anatomical traits was necessary to make informed decisions regarding tree-ring delineation. For this study, xylem visual inspection is defined as the assessment of tree-ring boundaries based on the visual characteristics of xylem anatomical traits. Xylem tissue was visually inspected for variability in the size and shape of cells, most notably xylem vessels and libriform fiber cells. The most apparent anatomical feature aiding the tree-ring delineation process was an abrupt increase in the diameter of the water-conducting xylem vessels, which signal the beginning of the growing season. Large xylem vessels, or EWVs, often formed along the entire boundary of the new tree ring (Figure 12). This type of EWV formation was common across all samples as white oak displays a ring-porous vessel structure.

Visual inspection was also based on the variability in fiber tracheid cell formation. As fiber tracheids divide and grow outward, they form with gradual decreases in the CLA:CWT ratio. Fiber tracheids formed at the end of a growing season in the latewood's outer cell rows also undergo a tangential flattening of the cell wall (Figure 12). Abrupt increases in the CLA:CWT ratio due to the onset of a new growing season typically coincided with EWV formation. Other xylem anatomy traits that aided visual inspection included abnormal cell formations in response to scars and injuries, ring boundaries extending through aggregate ray parenchyma, radially projected strings of xylem cells, alternating bands of parenchyma cells and fiber tracheids, and tension wood formation.

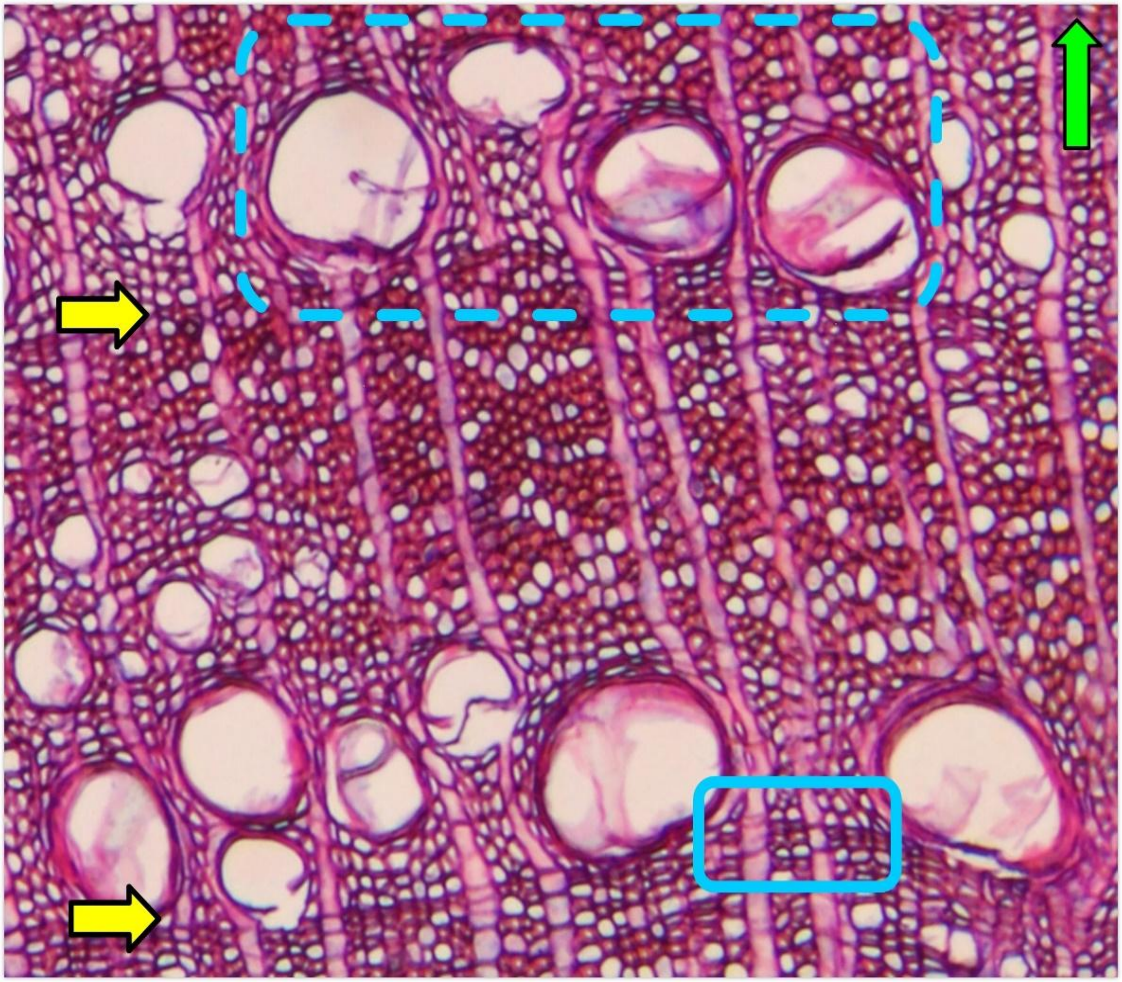


Figure 12: An image depicting a few of the xylem anatomical characteristics that aided the tree-ring delineation process. The green upward arrow denotes the direction of cell growth. The yellow rightward arrows show the boundaries between successive tree rings. The solid blue box is enclosed around fiber tracheids displaying decreasing CLA:CWT ratios and tangential cell wall flattening. The dashed blue box surrounds earlywood xylem vessel (EWV) formation that occurred at the onset of the new growing season.

Tension wood was a prevalent anatomical feature observed in a large proportion of the samples. Tension wood is characterized by the formation of a gelatinous layer (G-layer), either attached or detached to the cell wall of libriform fibers (Schweingruber, 2007; Bowling & Vaughn, 2008). Once double-stained, libriform fibers with a G-layer appeared in a different color than fiber tracheids lacking a G-layer due to their greater cellulose content. Tension wood formation can be extensive, making visual inspection easier in instances where rings were widely spaced, or more difficult in instances where its formation reduced xylem density, both in number and size.

Tension wood formation often results in eccentric tree-ring formation where tree-ring widths are variable around the circumference of the stem. Highly eccentric tree-ring formation had the potential to result in wedging, or discontinuous tree rings, where the ring boundary was evident around only a small portion of its circumference. This anatomical adaptation prevented the ability to measure multiple radii of the same cross section as different radii often resulted in unequal ring counts. The widest radii from the pith to the xylem boundary was preferentially measured to avoid wedging rings and because it provided greater precision and accuracy in tree-ring boundary placement. Tension wood was a common anatomical formation within the sampled population, and its presence often prohibited the acquisition of matching ring-counts along separate radii. Therefore, individual ring-width measurements could not be analyzed without biasedly applying the measured ring-width to the entire circumference of individual tree-rings.

3.7 Tree-ring data collection

CooRecorder and CDendro software (Cybis Electronics, Sweden) were used for tree-ring data collection. CooRecorder had a maximum image size limit for image uploads. However, this restriction was due to the computer's graphics card rather than the software itself. For the system used, the limit was approximately 530 megabytes (MB). Due to this limitation, many images were cropped to fit within the 530 MB limit. Cropped images were typically shaped into rectangles with boundaries parallel to the longest cross-sectional radius from pith to xylem. The maximum pith-to-xylem radius was chosen to ensure that all rings formed by the tree were retained during the ring-counting process, as discontinuous rings influenced by tension wood were often evident only along this radius. Also, many samples had periods of intense suppression that made ring boundaries difficult to distinguish. Intense suppression was often more easily distinguishable along the longest radii, as even just one to two additional rows of cells occurring here often provided the clearest pathway (pith-to-phloem) for ring counting.

Due to the size of the largest root microsections in this study, several images could not be reduced to under 530 MB while retaining the full pathway from the pith to the xylem boundary. For these microsections, the image was split into two: one image for the inner xylem boundary and one for the outer boundary. To ensure continuity, at least 5 tree rings in the middle of the microsection overlapped between the two images. This overlap was essential for accurately combining tree-ring counts from the separate images. Without it, there would be no way to statistically assess the accuracy of tree-ring boundary placement at the start and end points within each image. By cross correlating the same 5 or more tree rings between the two images, statistically identifying the exact points in the xylem where tree-ring counts needed to start and stop between the two images was made possible, ensuring that no tree rings were double-counted.

A critical step in the tree-ring data-collection process is determining whether there was a presence of the pith-to-xylem and xylem-to-phloem boundaries. However, retaining the cellular integrity of a microsection was often difficult due to injuries and scarring, or when samples were at either end of the diameter range physically supported by the microtome. Furthermore, pith cells (inner) and phloem cells (outer) were more difficult to preserve within microsections. When cells were missing from the inner and outer boundaries, visual inspection of the xylem boundaries helped determine if a microsection contained evidence of the inner- and outer-most years.

Often, however, enough pith cells were retained during the microsectioning process to make the pith-to-xylem boundaries visible. In many microsections, pith pinching was observed at the pith-to-xylem tissue interface where localized areas of xylem cells projected outward in a convex fashion along the pith borders. Pith pinching often occurred at multiple points along the pith-to-xylem interface. When little or no phloem tissue was attached to the outer boundary of the xylem, other visual cues often made the xylem boundary apparent. For instance, in the absence of retained phloem, many microsections displayed an uninterrupted, cohesive boundary along a wide portion of the xylem perimeter. In other cases, a small portion of attached phloem was sufficient for determining xylem boundaries (Figure 13).

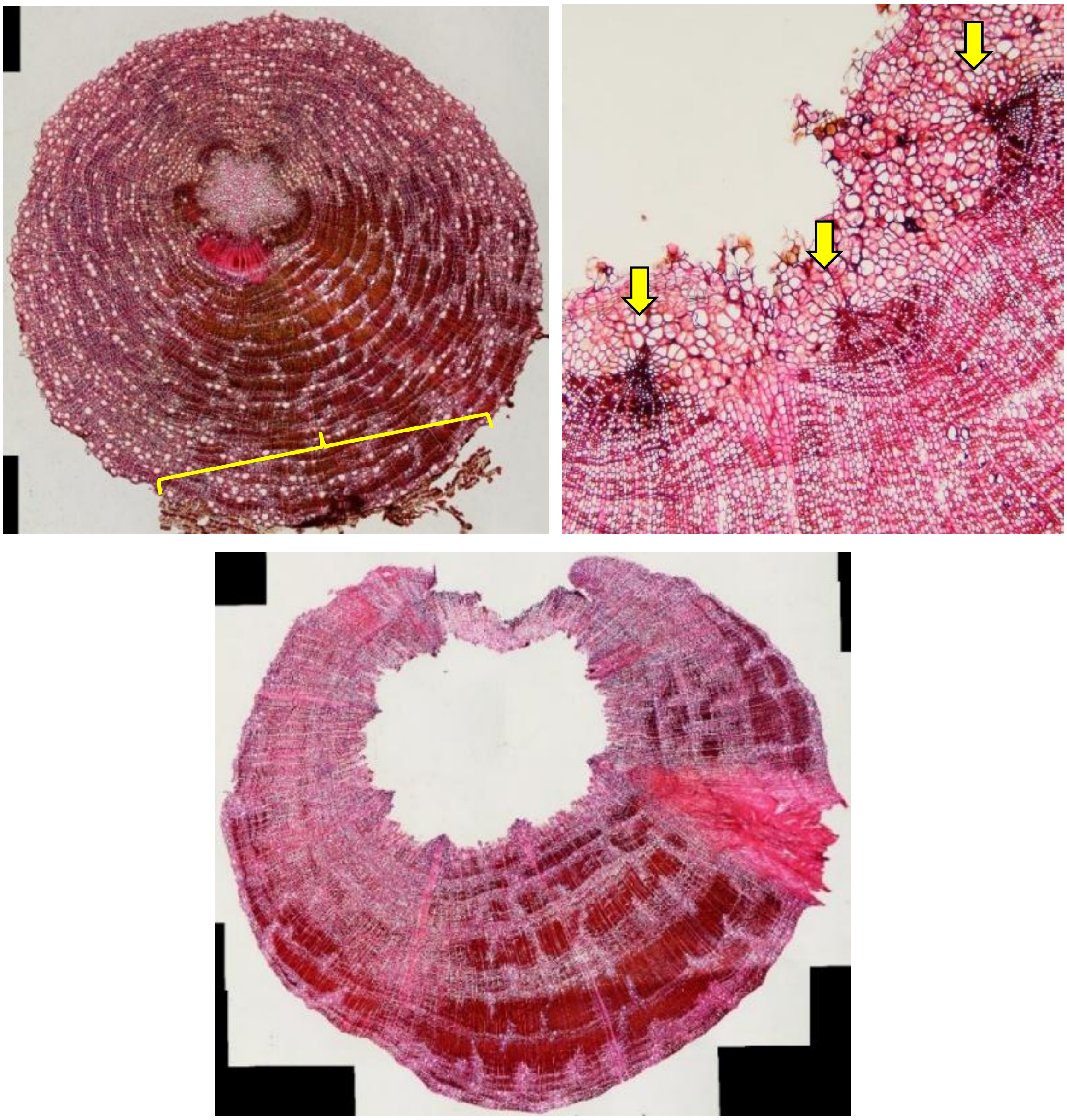


Figure 13: Three xylem boundary characteristics aided in boundary determination. The top left microsection retained a portion of the phloem at the xylem-to-phloem interface (yellow bracket). The top right microsection exhibited pith pinching at three locations along the pith-to-xylem interface (yellow arrows). The bottom microsection had no phloem attached but displayed a smooth, continuous, and cohesive xylem boundary.

CooRecorder was used to individually count rings on separate stem and root microsections for each wOAR sample. CDendro software assigned calendar years to each tree ring by statistically cross dating ring-width series from stem and root sections. This process involved calculating correlation coefficients (CCs) between the ring-width patterns of the stem and root sections, allowing for precise alignment of growth years. Tree-ring widths were measured by converting pixel lengths to micrometers, using calibration images of a stage micrometer taken with the same microscope configuration as was used for imaging microsections. Dendrochronological techniques, including normalization and correlation of annual ring widths (Fritts, 2014), were applied to both stem and root microsections to compare and assess tree-ring dating accuracy (Figure 14).

Correlation analyses were performed only between the stem and root of individual trees, not across the population. As a result, years of root growth in resprouted seedlings that occurred before the corresponding stem's establishment could not be cross correlated. This resulted in a greater reliance on visual inspection for resprouted wOAR, especially as age differences between root and stem increased. Cross correlations could not be calculated using CDendro if either the stem or root microsection of a wOAR contained fewer than 5 rings. For wOAR with either a stem or root ring count of 5 or less, cross dating relied solely on visual inspection, including ring-width plot comparisons using CDendro. Additionally, marker years often helped ensure accurate tree-ring counts, particularly for rings that could not be cross correlated. In this study, marker years are defined as annual rings that displayed similar ring widths, or that exhibited injuries or scar formations visible in both microsections at the same numbered tree ring.

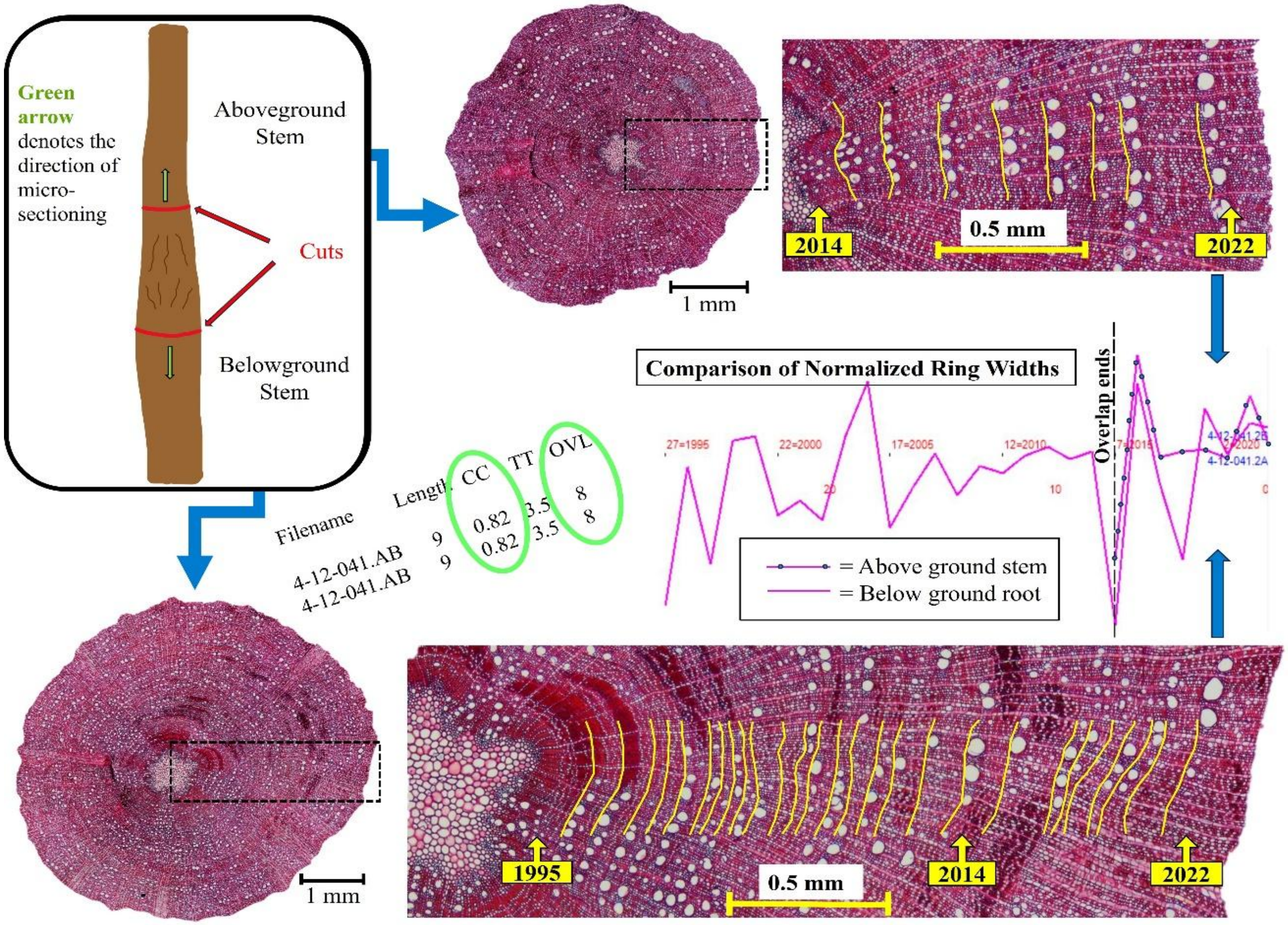


Figure 14: A flow chart depicting the tree-ring data collection process. Starting at the top left, a wOAR was split into separate stem and root samples, then individually microsectioned. A zoomed portion of each microsection represented a clear xylem pathway, where annual growth boundaries were placed between successive tree rings. Separate ring-width chronologies were statistically and visually cross dated using CDendro. Root-to-stem CCs were calculated to compare ring-width chronologies and validate the accuracy of tree-ring delineation. The CCs aided in accuracy assessments for periods of overlap between root and stem samples but could not be used for root growth that preceded stem growth.

When one or both xylem boundaries were missing, full ring counts could not be obtained, making the microsection unusable for age and growth analyses. No microsections lacked the outermost portion of the xylem (the most recent years of growth). However, in such cases, cross dating may have determined the number of missing rings. In contrast, when the entire pith was absent and its xylem border (earliest years of growth) was unidentifiable, a full ring count could not be confidently recorded, and these samples were removed from age and growth analyses. In these instances, cross correlation would not have helped determine the number of missing rings.

Conventional dendrochronological methods require that only cross-correlated samples be included in analyses. Initially, only wOAR samples with cross-correlated stem and root ring widths were to be included, as these provide the most accurate ring counts and calendar year assignments. However, excluding non-cross-correlated samples would have resulted in an insufficient data set for analysis. In other words, including only the wOAR with the highest correlations would have biased the data against suppressed or resprouted individuals, making the dataset unrepresentative of the larger wOAR population. Specifically, wOAR with larger stem and root age differences or those exhibiting prolonged suppression would have been disproportionately excluded.

Instead, only samples with unattainable ring counts or low confidence in ring identification were excluded. This included samples missing pith-to-xylem or xylem-to-phloem boundaries, or those with multiple sections where ring placement was unclear due to extended suppression. Although this approach increased some potential for user error in ring counts, it was necessary to maintain a representative dataset.

Using these methods, of the 540 total stem and root segments, ring counts were obtained for 525 and 450 wOAR, respectively. The lesser number of roots than stems for which ring counts were obtained was due to: (1) roots inherently having a greater mean ring count than stems, (2) the lacking ability to correlate ring widths for years of root growth that preceded stem growth, and (3) greater difficulty in identifying EWV formation in roots, which introduced a higher probability for uncertainties regarding tree-ring placement. Other factors contributing to the higher number of stems compared to roots with usable data included: (1) greater reliance on visual inspection for root samples in xylem regions where stem tree ring overlap was absent due to age differences, (2) a higher likelihood of roots experiencing periods of suppressed or less-distinct growth, and (3) increased difficulty in identifying EWV formation in roots, as roots typically had smaller and less dense xylem vessels than stems.

Stem origin (i.e., establishment as true seedling vs. resprout) was determined by comparing root and stem ring counts. Equal stem and root ages indicated that the wOAR had established from seed and survived from its initial germination event (true seedling). In contrast, when the root ring count exceeded the stem ring count, the wOAR was classified as originating from a top-kill event (resprout). If confidence in tree-ring counts was low and the difference between stem and root ring counts was 3 or fewer, the stem origin was labeled as unidentified. However, when dating was dependable, either statistically, visually, or both, a root age difference as small as 1 year was often sufficient to classify a wOAR as a resprout. Conversely, if dating confidence was low, stem origin was classified as a resprout only when the root age difference was 4 years or more. If a microsection was unobtainable for either the stem or root, stem origin was determined using diameters measured during sample preparation. Stems with a diameter less than 50% of the root diameter were classified as resprouts, while those with a diameter greater than 50% of the root diameter were left unidentified. Using these criteria, stem origins were determined for most wOAR samples (n = 505).

The innermost rings in many microsections, particularly in roots, were often less discernible than those from later years of growth. This led to many wOAR having higher stem ring counts than those obtained from its corresponding root. Since stems being older than roots is biologically improbable, for all wOAR (n = 51) with stem ring counts greater than root ring counts, stem age was used to represent the root age. This ensured that the root age difference was not negative and allowed these wOAR to be categorized as true seedlings. This limitation is discussed in greater detail in the discussion section.

3.8 Statistical analyses

Here forward, the term age is used synonymously with ring count. The demographic analyses for this study were centered on identifying differences in the mean stem age, mean root age, and the mean root-stem age ratio of wOAR between the applied experimental treatments. Separate establishment analyses were conducted to determine if there were statistical differences in the probability that a given wOAR was of resprout origin between treatments, as well as estimated densities (per ha) of wOAR of true seedling or resprout origin. Growth analyses were centered on determining treatment differences in the mean stem height, mean stem diameter, and mean root diameter. For all analyses, a significance threshold of $\alpha = 0.05$ was used. Each statistical analysis was conducted using the R programming language version 4.5.0 (R Core Team, 2025). The glmmTMB function from the glmmTMB package (v1.1.11; Brooks et al., 2017) was used to build generalized linear mixed models (GLMM) for all but one analysis.

3.9 Statistical analyses: demography

The mean stem and root age analyses followed the same model-building process. First, any wOAR ring count that was obtained with a lack of dating confidence (i.e., multiple or prolonged periods of suppression that resulted in uncertainties of ring counts) was removed from the dataset. As stem and root ages were recorded in discrete whole number counts beginning with one, GLMMs with zero-truncated Poisson (ZTP) distributions (log link) were fit. A nested random effects term was included in both models (1 | Stand/Plot), which accounted for the dependence of observations and the hierarchical structure of the data. The balance of the data was confirmed across treatments (stem age: n = 173 to 176; root age: n = 141 to 155). Dispersion and uniformity were assessed using the plot function from the DHARMa package (0.4.7; Hartig, 2024). The residuals of stem and root age using ZTP distributions violated the models' assumption of having no overdispersion. Due to these violations, GLMMs with zero-truncated negative binomials (ZTNB) with a log link were fit. The GLMMs with ZTNB then passed dispersion and uniformity assumptions.

The final model form was represented by:

$$\textit{Mean Stem or Root Age} \leftarrow \textit{Treatment} + (1 \mid \textit{Stand/Plot})$$

Analysis of variance (ANOVA) was used to evaluate the significance of fixed effects; the Anova function from the car package was used (3.1.3; Fox & Weisburg, 2019). A Type II Wald chi-square test was used as the models included no interaction terms. If significant differences were found between treatments, post hoc pairwise comparisons using estimated marginal means (EMMs) were conducted using the emmeans function of the emmeans package (1.11.0; Lenth, 2025). Because a log link was specified, the emmeans function also back-transformed the estimated model means to their original scale.

The analysis of root-to-stem age ratios began by filtering the data to include only wOAR identified as resprouted seedlings (i.e., stem age < root age). The root-to-stem age ratio was fit to several candidate distributions (normal, log-normal, gamma, and exponential), with the log-normal distribution providing the best fit based on Akaike information criterion (AIC) comparisons. The data were fit to several GLMM forms using log-normal and gamma distributions, with full (1 | Stand/Plot) and simplified (1 | Stand) nested random effects terms. However, each model form violated the assumptions of dispersion and uniformity. Due to the violated assumptions for several model forms, a simple linear model was built. The model included Treatment as a fixed effect and the natural logarithm of the root-to-stem age ratio as the response variable. Diagnostic plots were then visually assessed to confirm that the model assumptions of normality and homoscedasticity of residuals were met. The data associated with this variable was marginally balanced across treatments (n = 96 to 132).

The final model form was:

$$\mathit{Log(Mean\ Root\text{-}to\text{-}Stem\ Ratio)} \leftarrow \mathit{Treatment}$$

An ANOVA was conducted using the Anova function from the car package, as was done for the stem and root age analyses. A Type II Wald chi-square test was used as the models included no interaction terms. Because the model included a log link, the emmeans function was used to back-transform estimated model means to the original scale.

Although not statistically analyzed, root establishment rates were visually compared with vector plots of the lifespans of sampled wOAR (Figure 15). To further investigate the rates of accumulation, cumulative distributions of sampled wOAR for the years of root establishment were calculated for each treatment (Figure 16). Accumulation rates were calculated using only the wOAR that were confidently ring counted.

3.10 Statistical analyses: establishment

As a reminder, a wOAR with a stem origin that had established from seed may also be referred to as a true seedling, while a wOAR whose stem origin established from resprouting may be referred to as a resprout. Any wOAR whose stem origin could not be confidently assessed (n = 20) was removed from establishment analyses. Seedlings with unidentified stem origins, due to either dating difficulties or incomplete xylem-to-pith pathways in the microsection, were excluded from all establishment analyses, unless stem and root diameter measurements could be used to categorize stem origin, as described above. The response variable for the probability model was a binomial variable (Yes or No). For the estimated densities of wOAR of either true seedling or resprout origin, the response variable was a discrete, whole number count.

The modeling process for establishment variables closely followed that of the demographic variables. A GLMM with a binomial distribution (logit link) was used to test for treatment differences in the probability for a wOAR stem to be of resprout origin.

The model included the binary response variable (Resprouted), a fixed effect (Treatment), and a random effect term (Plot nested within Stand).

The model form was represented by:

Probability of resprout origin ← *Treatment + (1 | Stand/Plot)*

Model assumptions of uniformity and dispersion were assessed by simulating model residuals and visually inspecting diagnostic plots using the plot function from the DHARMa package. The data were balanced across treatments (n = 167 to 170). The significance of the treatment effect was evaluated using ANOVA via the Anova function from the car package. A Type II Wald chi-square test was used as the models included no interaction terms. Post hoc analyses were conducted using the emmeans function for pairwise comparisons which also provided back-transformed model estimates (probabilities) of a wOAR to be a resprouted seedling.

The response variables for the estimated densities included estimated seedlings/ha and estimated resprouts/ha, respectively. The estimated densities of true seedlings and resprouted seedlings were stand-level estimates calculated from the 1/100th ac plot (~ 1/250th ha) seedling inventories conducted at each of the 20 research plots within a stand. Stem origin densities were assessed from the stem and root age comparisons of the ~ 60 wOAR sampled within each stand.

Plot-level estimates were not calculated because only 3 wOAR were sampled per research plot. In many cases, all 3 sampled wOAR had the same stem origin, resulting in ratios such as 3:0 or 0:3 (or 2:0 or 1:0 if one or more wOAR could not be classified). Applying these all-or-none ratios to the entire plot would have greatly exaggerated the number of wOAR from either origin. For example, at the plot level, if there were 400 wOAR seedlings inventoried, and all three sampled wOAR were found to be of resprout origin, all 400 seedlings within the plot would have been categorized as resprouts. Although this method resulted in only nine observations across treatments (one per stand), it prevented unreliable extrapolation of plot-level densities. Additionally, several plots had zero wOAR seedling counts, which may have introduced zero inflation into the model-building process.

For the separate analysis of estimated true seedlings per hectare and resprouts per hectare, GLMMs with Poisson distributions and a log link were used to test for treatment differences. The variables resproutHa (estimated resprouts per hectare) and seedHa (estimated true seedlings per hectare) were calculated at the stand level. These estimates were derived by applying the ratio of resprouts to true seedlings, based on stem and root age comparisons, to the wOAR densities obtained from seedling inventories.
The model form was represented by:

Resprout or True Seedling Density (/ha) ← *Treatment + (1 | Stand)*

Model assumptions of uniformity and dispersion were assessed by simulating model residuals and visually inspecting diagnostic plots using the plot function in the DHARMa, package. The data was balanced between treatments (n = 3), but not of sufficient size due to the need to conduct stand-level estimates. The significance of the treatment effect was evaluated using ANOVA via the Anova function from the car package. A Type II Wald chi-square test was used as the models included no interaction terms. Post hoc analyses were conducted using the emmeans function for pairwise comparisons between treatments and converting the log-scaled models back to their original scales. Due to the small sample size, estimates of random effects are likely unreliable and may not adequately detect differences between treatments.

Although not statistically analyzed, descriptive statistics were calculated for the proportions of seedlings and saplings by species groups. All species inventoried were first split into four different species groupings: white oak species, red oak species, shortleaf pine, and oak competitors. The oak competitor grouping included all species that did not fall into the white oak, red oak, or shortleaf pine groups. The top 5 species included in the oak competitor group with the greatest densities in the seedling size class were *Vaccinium* species (i.e., blueberry), flowering dogwood, red maple, hickory species, and sassafras. The top 5 species included in the oak competitor group with the greatest densities in the sapling class were red maple, flowering dogwood, blackgum, spicebush (*Lindera benzoin (*L.) Blume), and ash species (*Fraxinus* spp.). The proportional contributions for each species group were calculated at the stand and treatment levels. As noted previously, the distinguishments between seedling and sapling size classes were made with a height threshold (saplings ≥ 137 cm in height).

3.11 Statistical analyses: growth

To ensure that wOAR growth was compared under similar environmental and climatic conditions, all seedlings established before the first growing season after the initial harvest interval (1997) were excluded from analysis. All 1-year-old stems and roots were also removed from growth analyses. The wOAR included in stem and root growth analyses then reflected the years 1997 to 2021, a duration of 25 years. This process also ensured that all wOAR from treated stands were compared from the point of the initial disturbance event (1996) for each treatment. In addition to age restrictions for samples included in the growth analyses, any samples recorded as having two piths (n = 2 for stems, n = 3 for roots) were excluded, as merged stems or roots within these samples likely influenced growth differently than cases with multiple unmerged stems or roots. Considering these data restrictions, 141 of 525 total wOAR stems were removed for stem height growth analysis (n = 384), 143 of 525 total wOAR stems removed from stem diameter growth analysis (n = 382), and 91 of 450 total wOAR roots were removed from the root diameter growth analysis (n = 359).

The growth response variable (GRV) for the separate GLMMs representing each growth model included stem height, stem diameter, and root diameter. Stem age, root age, root to stem age ratio, and the 2022 plot level basal area were considered as fixed effect variables. However, root to stem age ratio and 2022 plot level basal area did not improve model fit and were excluded from all growth models. Fixed effects retained were treatment and stem age for the stem height growth and diameter growth models, and treatment and root age for the root diameter growth model. For each model, a nested random effects term (1 | Stand/Plot) was included to account for the hierarchical structure and dependence of the data.

Each GRV followed the same model building and analysis process. As each variable was continuous and strictly positive, candidate distributions (normal, log-normal, gamma, and exponential) were first fit to the data. The AIC values for these distributions were compared, with gamma and log-normal distributions fitting each GRV well. For each GRV, two GLMMs were built using a Gaussian (normal) distribution with a log link (one with an interaction term between treatment and the age variable used, and one without), and two using a gamma distribution with a log link (again one with and one without an interaction term). Model selection was based on AIC comparison among these four models. The GLMMs with gamma distributions and no interaction terms provided the best fit (lowest AIC) for each GRV. However, these models violated the assumptions of dispersion and uniformity of residuals, as assessed by DHARMa diagnostic plots. The GLMMs with Gaussian distributions and log links met the dispersion assumption but showed some deviation from uniformity in Kolmogorov-Smirnov (KS) tests. Because the KS test is sensitive to large sample sizes across treatments (stem height: n = 122 to 134; stem diameter: n = 121 to 134; root diameter: n = 107 to 126), greater emphasis was placed on a visual inspection of the diagnostic plots. The diagnostic plots showed only minor deviations, with no major patterns or issues in the residuals.

The final model form for each GRV was represented by:

$$\textit{Mean GRV} \leftarrow \textit{Treatment} + \textit{Stem or Root Age} + \textit{(1 | Stand/Plot)}$$

For each GRV, the significance of treatment effects was assessed using ANOVA with the Anova function from the car package. A Type II Wald chi-square test was used as the models included no interaction terms. Post hoc analyses were conducted using the emmeans function for pairwise comparisons between treatments. The emmeans function was also used to back-transform the log-scaled model means to their original scales.

CHAPTER 4: RESULTS

4.1 White oak advance reproduction stem ages

There was no statistically significant difference in mean stem ages among treatment groups (Type II Wald $X^2(2) = 1.33$, $p = 0.523$). Interpretations should be made cautiously due to the model's non-significant result, yet the EMMs for stem age back-transformed from the log scale were 8.6 years (0H), 8.7 years (1H), and 9.4 years (2H).

Despite the lack of significant differences among treatments, a wide range of stem ages were observed at the stand and treatment levels (Tables 5 and 6). Across stands, stems ranged from 1 to 41 years old. The widest range in stem ages was observed in Stand 2-27 (1 to 41 years old), which was within the 2H treatment. The narrowest range in stem ages was observed in stand 2-32 (3 to 16 years old), which was within the 1H treatment. Notably, while individual stem ages spanned 40 years across stands, the treatment-level arithmetic means for stem ages remained relatively consistent, ranging from just 8.8 to 9.5 years old, a difference of less than a full year. Considering all wOAR included in the analysis (n = 525), only 23 stems were aged 20 or older (17 of which were in the 1H and 2H treatments); with two of those being over age 30 (31 and 41, both within the 2H treatment). In contrast, 134 wOAR had stem ages of 5 or younger (0H treatment n = 55; 1H treatment n = 46; 2H treatment n = 33).

Table 5: Stand-level arithmetic mean, minimum, maximum, and standard deviation of the stem ring counts (ages).

Site	Stand	Treatment	Mean Stem Ring Count	Min	Max	SD
1	26	Control	9.5	3	22	4.9
1	36	Control	7.9	1	29	5.5
6	6	Control	9.0	1	22	4.6
2	32	One-harvest	9.1	3	16	3.4
4	9	One-harvest	7.2	1	27	4.3
4	12	One-harvest	10.5	3	27	6.5
2	27	Two-harvest	9.6	1	41	6.0
7	132	Two-harvest	9.1	1	24	5.1
7	142	Two-harvest	9.8	1	31	5.9

Table 6: Treatment-level arithmetic mean, minimum, maximum, and standard deviation of the stem ring counts (ages).

Treatment	Mean Stem Ring Count	Min	Max	SD
Control	8.8	1	29	5.0
One-harvest	8.9	1	27	5.1
Two-harvest	9.5	1	41	5.7

4.2 White oak advance reproduction root ages

This analysis revealed a marginally non-significant effect of treatment on mean root age (Type II Wald $X^2(2) = 5.99$, $p = 0.055$). The EMMs for root age, back-transformed from the log scale to the original scale, were 16.0 years for the 0H treatment, 19.5 years for the 1H treatment, and 16.8 years for the 2H treatment. Post hoc pairwise comparisons showed that the 1H treatment had a marginally non-significant greater mean root age than the 0H treatment ($p = 0.055$), whereas differences between other treatment pairs were not statistically significant (0H–2H: $p = 0.851$; 1H–2H: $p = 0.179$).

Across stands, root ages ranged from 2 to 91 years old (Tables 7 and 8). Stand 6-6 exhibited the most extensive age range, with roots varying from 3 to 91 years old, a span of 88 years. In contrast, stand 7-132 showed the least variation, with root ages between 5 and 32 years, a span of 27 years. It is worth noting that although the 91-year-old root represents an extreme outlier, it is a valid observation within the study's methodological framework. Despite the wide spread of individual root ages across nine decades, the treatment-level arithmetic mean root ages showed modest variation, ranging from 17.0 to 20.5 years. Considering the roots aged 40 years old or greater, there were 26 observations that were relatively evenly split among treatments (9, 8, and 9 observations for the 0H, 1H, and 2H, respectively). In contrast, considering roots aged 10 or younger, there were 102 observations that were also relatively evenly split among treatments (119, 128, and 119 observations for the 0H, 1H, and 2H, respectively).

Table 7: Stand-level arithmetic mean, minimum, maximum, and standard deviation of the root ring counts (ages).

Site	Stand	Treatment	Mean Root Ring Count	Min	Max	SD
1	**26**	**Control**	18.9	3	46	10.5
1	**36**	**Control**	16.5	2	42	11.0
6	**6**	**Control**	15.6	3	91	12.8
2	**32**	**One-harvest**	21.4	9	77	11.9
4	**9**	**One-harvest**	17.4	2	47	8.2
4	**12**	**One-harvest**	22.7	3	45	10.7
2	**27**	**Two-harvest**	20.3	4	48	12.5
7	**132**	**Two-harvest**	16.2	5	32	6.7
7	**142**	**Two-harvest**	16.1	3	52	9.6

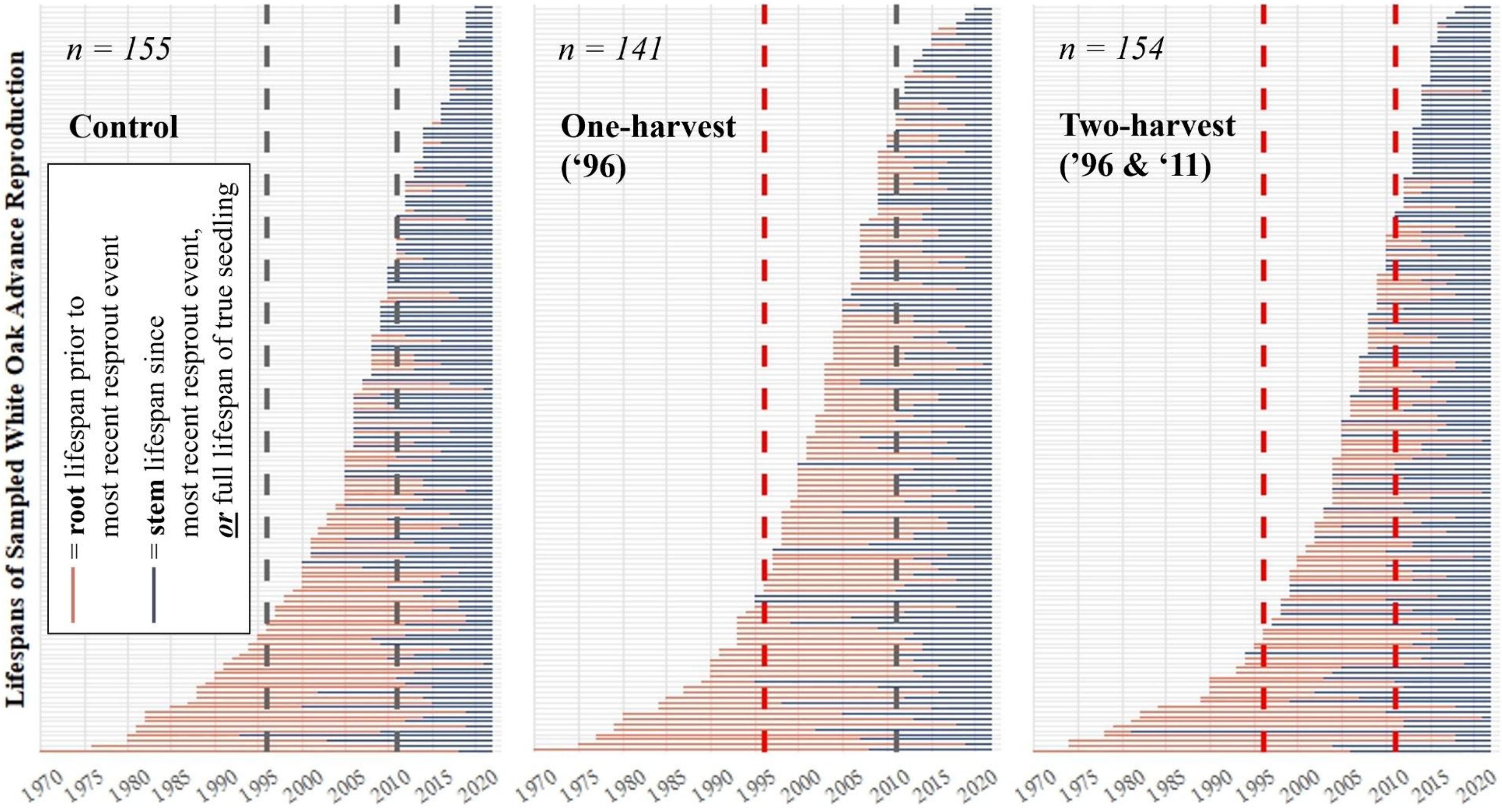
Table 8: Treatment-level arithmetic mean, minimum, maximum, and standard deviation of the root ring counts (ages).

Treatment	Mean Root Ring Count	Min	Max	SD
Control	17.0	2	91	11.5
One-harvest	20.5	2	77	10.5
Two-harvest	17.4	3	52	9.8

4.3 Cumulative distribution of white oak advance reproduction by root establishment

Although not statistically analyzed, the lifespans associated with individual wOAR were plotted by combining the data related to the sampled wOAR populations' separate stem and root ages (Figure 15). Also shown are the timings of the most recent resprouting event (if occurred) with respect to treatment timings (1996 and 2011). Of the possible 180 sampled wOAR per treatment, at least 141 were used to create treatment level distributions of establishment years. Cumulative distributions associated with each treatment were also plotted to identify differences in the rates of wOAR accumulation concerning the frequency and intensity of uneven-aged harvesting practices (Figure 16).

Within the 0H treatment, the cumulative percentage was 18.1% for establishment year 1996 and 72.3% for establishment year 2011, a difference of 54.2%. For comparison, within the 1H treatment, the cumulative percentage was 24.1% and 87.9% in the years 1996 and 2011, respectively; a difference of 63.8%. The 2H treatment had cumulative percentages similar to the 0H treatment, with cumulative percentages of 16.9 and 72.7% for the years 1996 and 2011, respectively; a difference of 55.8%. A major difference in the cumulative percentages between treatments is that at year 2011, the difference between the 1H and 2H treatments was 15.2% but the 2H treatment surpasses this difference by year 2016, just 5 years after the timing of the second harvest entry that occurred within the 2H treatment.



Lifespans of Sampled White Oak Advance Reproduction by Treatment

Figure 15: Vector plots display the lifespans of all wOAR up to 2022 across the three treatments. Dashed lines indicate harvest years: red for entries within the treatment (1996 and 2011), gray for those that did not occur in that treatment. Lifespans beginning before 1970 are not shown; one wOAR in the control (1931) and one in the one-harvest treatment (1945) were established prior to 1970.

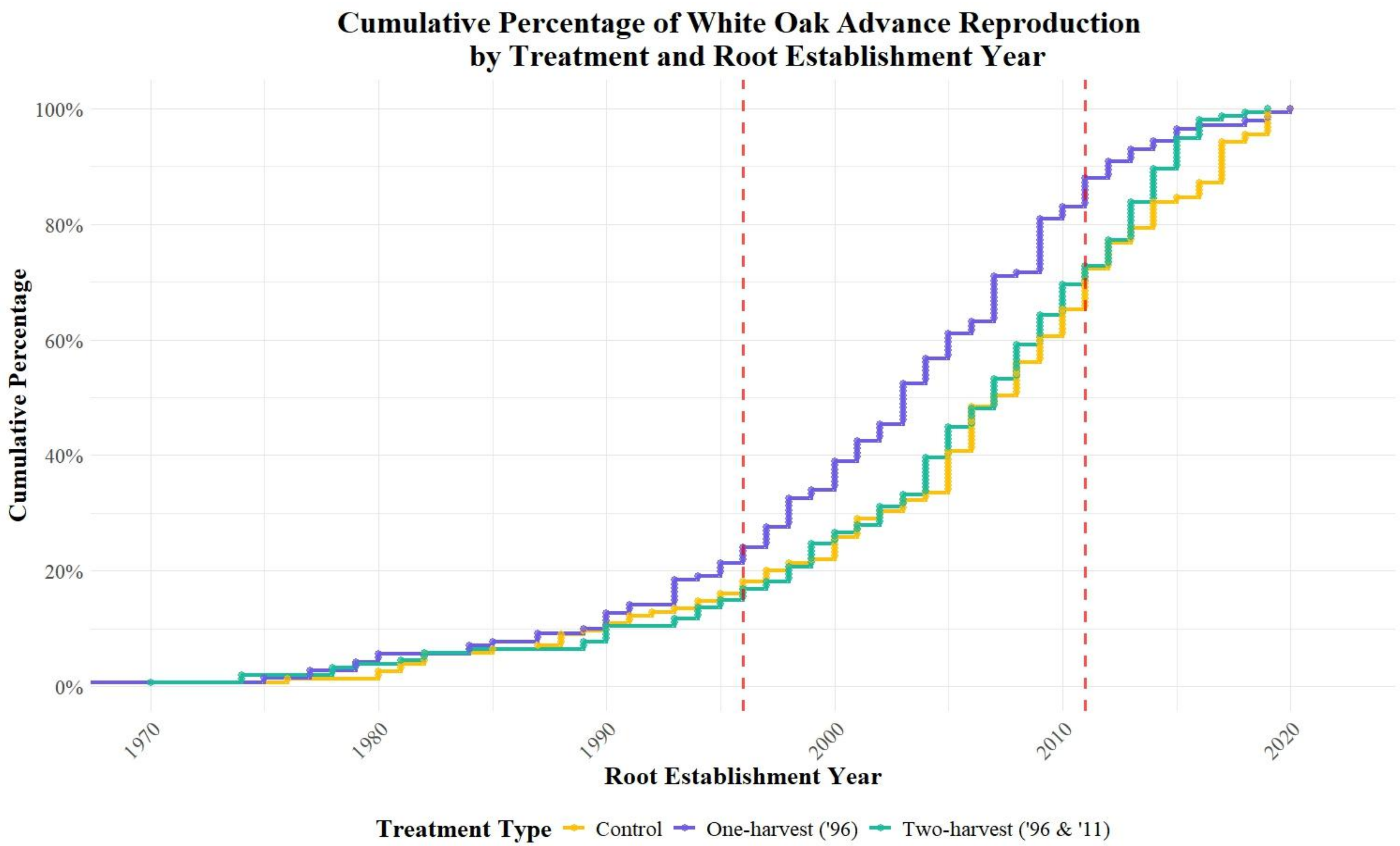


Figure 16: Cumulative percentage of wOAR by root establishment year. Red dashed lines mark harvest years: 1996 (1H and 2H) and 2011 (2H). Roots established before 1970 are excluded; one wOAR in 0H (1931) and two in 1H (1945, 1958) occurred prior to 1970.

4.4 White oak advance reproduction root-to-stem age ratios

The ANOVA indicated no statistically significant difference in the log-transformed mean root-to-stem age ratio among the treatment groups (F(2, 335) = 1.10, *p* = 0.333). Although these results were not statistically significant, the EMMs for the root-to-stem age ratio, back-transformed from the log scale, were 3.2 for the 0H treatment, 3.0 for the 1H treatment, and 2.8 for the 2H treatment. Each pairwise treatment comparison showed no statistical significance (all: $p > 0.342$)

Across stands and within treatments there was substantial variability in the root-to-stem age ratios of resprouted wOAR (Tables 9 and 10; Figure 17). The maximum observed ratio reached a value of 40.0 in stand 2-27, with the next highest value being 31.0 in Stand 6-06. Because the true seedlings were excluded from this analysis, values of 1.0 (equal stem and root age) were not recorded. Notably, all stands had minimum ratios close to the allowable minimum (1.1), ranging from 1.1 to 1.4. However, the maximum ratios varied substantially, ranging from as low as 8.0 in stand 7-142 to as high as 40.0 in stand 2-27. Considering the entire sample size (n = 338), only 18 wOAR had root-to-stem age ratios larger than 10.0 (a root age that was 10 times the stem age or greater). In contrast, 108 wOAR had ratio values of 2.0 or less, where the root age was no more than 2 times the stem age).

Table 9: Stand-level arithmetic mean, minimum, maximum, and standard deviation of the root-to-stem age ratios.

Site	Stand	Treatment	Mean Root-to-stem age ratio	Min	Max	SD
1	**26**	**Control**	3.8	1.4	13.7	3.0
1	**36**	**Control**	3.9	1.3	15.0	3.1
6	**6**	**Control**	5.5	1.2	31.0	7.4
2	**32**	**One-harvest**	3.4	1.3	9.1	1.7
4	**9**	**One-harvest**	4.0	1.3	19.0	3.6
4	**12**	**One-harvest**	3.4	1.1	10.8	2.0
2	**27**	**Two-harvest**	4.4	1.2	40.0	6.5
7	**132**	**Two-harvest**	3.5	1.3	18.0	3.8
7	**142**	**Two-harvest**	3.1	1.2	8.0	1.7

Table 10: Treatment-level arithmetic mean, minimum, maximum, and standard deviation of root-to-stem age ratios.

Treatment	Mean Root-to-stem age ratio	Min	Max	SD
Control	4.3	1.2	31.0	4.7
One-harvest	3.6	1.1	19.0	2.6
Two-harvest	3.7	1.2	40.0	4.5

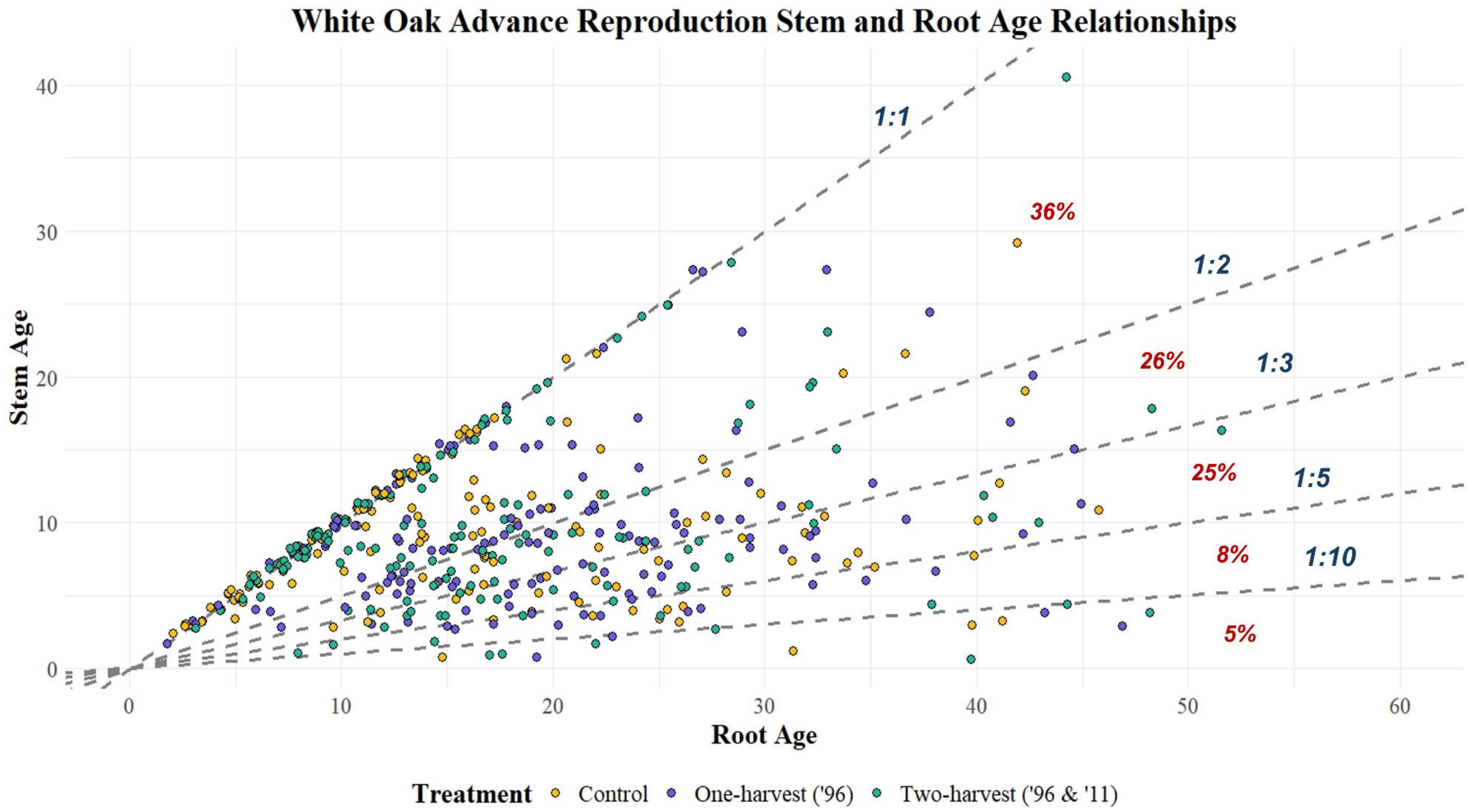


Figure 17: A scatterplot of individual wOAR by their root-to-stem age ratio. True seedlings appear on the 1:1 line (jittered for visibility), while resprouted wOAR (also jittered) fall below this line, illustrating the variability between root and stem ages. Dashed gray lines indicate various root-to-stem age ratios (blue), with the percentage of resprouted wOAR between each ratio shown in red. Two wOAR with root ages of 77 and 91 years and stem ages of 14 and 4 years, respectively, are not plotted for clarity.

4.5 Probability for a white oak advance reproduction to be of resprout origin

There was a statistically significant differences in the probability of wOAR to be of resprout origin among treatments (Type II Wald $X^2(2) = 12.483$, $p = 0.002$). This indicated that experimental treatments significantly affected resprouting likelihood, or potentially the persistence of true seedlings (although not statistically analyzed), which would have indirectly influenced this result. The EMMs, back-transformed from the log-scale to the probability scale, indicated that the probability for a wOAR to be of resprout origin was 61.0% (SE = 4.9%) for the 0H treatment, 82.1% (SE = 3.6%) for the 1H treatment, and 66.5% (SE = 4.7%) for the 2H treatment (Table 12; Figure 18).

Post hoc Tukey pairwise comparisons showed that wOAR within the 1H treatment had a 21.1% higher estimated probability of being a resprout than the 0H treatment ($p = 0.002$) and a 15.6% higher probability than the 2H treatment ($p = 0.020$). The 2H treatment had a 5.5% higher estimated resprouted probability than the 0H treatment, but this difference was not statistically significant ($p = 0.688$). Seedling origin assessments were made from ~ 60 wOAR sampled within each stand (Table 11).

Table 11: Stand-level seedling origin assessments of wOAR (n = ~ 60) destructively sampled per stand. Of 540 total wOAR sampled, 35 could not be assessed. These stand-level assessments were used for model estimations of the probability that a given wOAR stem was of resprout origin.

Site	Stand	Treatment	Total Seedling Origins Identified	Resprouted Seedlings (n)	True Seedlings (n)	Unidentified Seedlings (n)
1	26	**Control**	55	34	21	2
1	36	**Control**	52	39	13	5
6	6	**Control**	60	27	33	0
2	32	**One-harvest**	51	41	10	3
4	9	**One-harvest**	58	45	13	0
4	12	**One-harvest**	59	48	11	1
2	27	**Two-harvest**	58	39	19	2
7	132	**Two-harvest**	53	36	17	3
7	142	**Two-harvest**	59	35	24	1

Table 12: Probability that the stem of a wOAR was of resprout origin (± SE) for each treatment group was calculated using EMMs from a binomial GLMM. Probabilities were obtained by back-transforming EMMs from the logit scale to the probability scale.

Treatment	Resprout Probability (%)	SE (%)
Control	61.0	4.9
One-harvest	82.1	3.6
Two-harvest	66.5	4.7

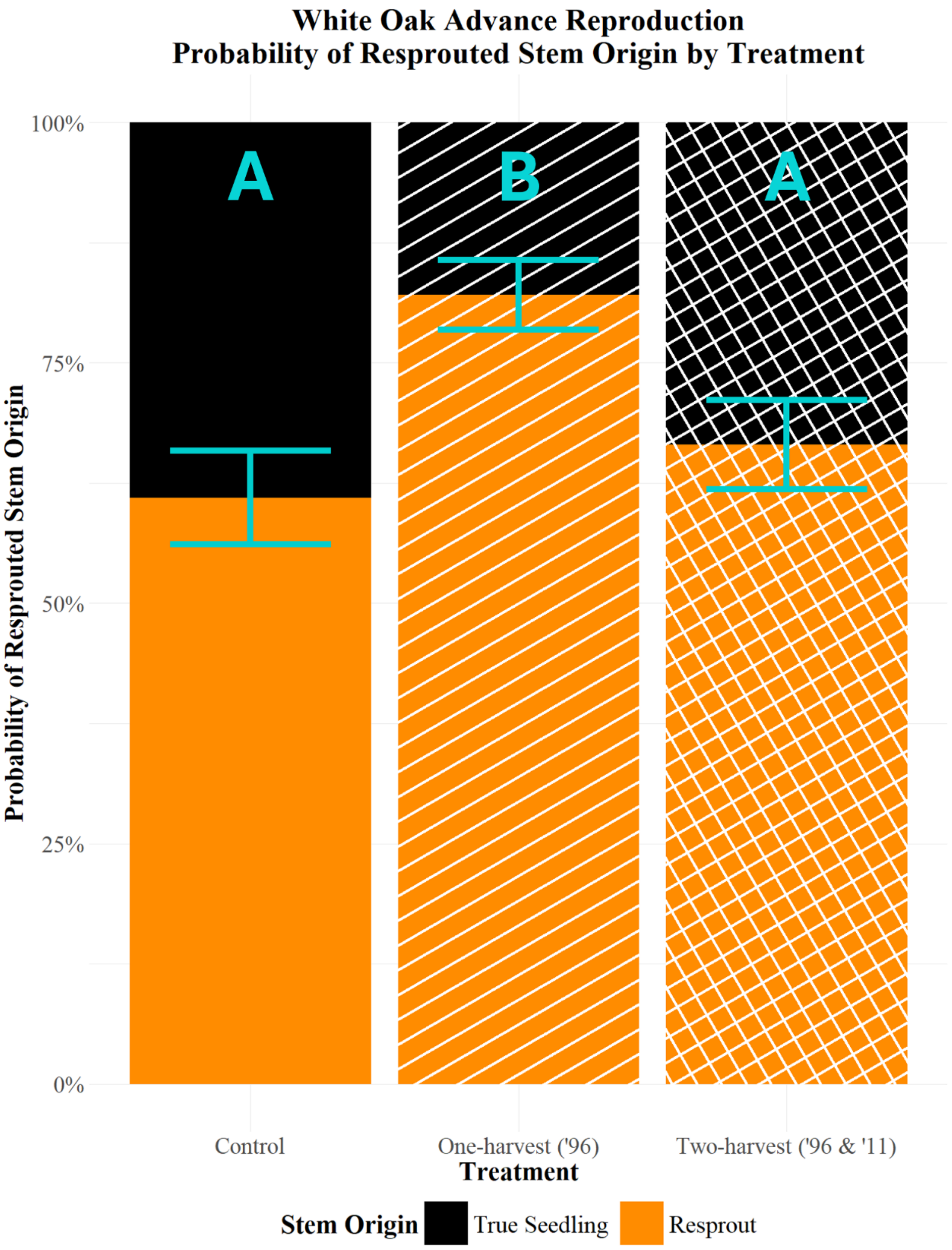


Figure 18: Estimated probabilities that a wOAR stem was of resprout origin for each treatment. Probabilities were obtained by back-transforming the logit scale results to the probability scale. Letters (A, B) above bars indicate statistically significant differences between treatments ($p < 0.05$) based on pairwise comparisons. Treatments not sharing a letter had a statistically significant difference.

4.6 Estimated white oak advance reproduction densities of resprout origin

No statistically significant differences in estimated wOAR densities of resprout origin among treatment groups was found (Type II Wald $X^2(2) = 3.36$, $p = 0.186$). The EMMs from the model, back-transformed from the log scale to the count scale (sprouts/ha), were 569 (SE = 165) for the 0H treatment, 405 (SE = 118) for the 1H treatment, and 859 (SE = 249) for the 2H treatment. While these differences were not statistically significant and should be interpreted with caution, they provide insight into possible treatment effects.

Stand- and treatment-level variability in the number of estimated resprouts was substantial (Tables 13 and 14). Stand-level estimates of resprouts/ha ranged from 256 to 1483 (Figure 19). Within the 0H treatment, stand 1-36 held the maximum estimated density of 1483 resprouts/ha, while stand 6-6 showed the minimum estimated density of 256 resprouts/ha, the widest range in estimated resprout density within a single treatment. The 1H treatment displayed the lowest density overall, with stand 2-32 having a treatment-level minimum density of 269 resprouts/ha, while stand 4-9 held the maximum treatment-level density of 546 resprouts/ha. The 2H treatment also showed considerable variability, ranging from 540 resprouts/ha in stand 2-27 to 1356 resprouts/ha in stand 7-142. Several research plots in stand 1-36 had wOAR at high densities, making it an extreme outlier within the control treatment (Figure 19).

Table 13: Stand-level estimated densities of the wOAR population that is of resprout origin.

Site	Stand	Treatment	Estimated Resprout Density (stems /ha)
1	**26**	**Control**	481
1	**36**	**Control**	1483
6	**6**	**Control**	256
2	**32**	**One-harvest**	269
4	**9**	**One-harvest**	546
4	**12**	**One-harvest**	452
2	**27**	**Two-harvest**	540
7	**132**	**Two-harvest**	865
7	**142**	**Two-harvest**	1356

Table 14: Treatment-level arithmetic mean, minimum, maximum, and standard deviation for the estimated densities of the wOAR population that are of resprout origin.

Treatment	Mean Estimated Resprout Density (stems /ha)	Min	Max	SD
Control	740	256	1483	653
One-harvest	422	269	546	141
Two-harvest	920	540	1356	411

4.7 Estimated white oak advance reproduction densities of true seedling origin

The analysis of estimated densities of wOAR of true seedling origin revealed statistically significant differences among treatment groups (Type II Wald $X^2(2) = 24.96$, $p < 0.001$). The EMMs from the model, back-transformed from the log scale to the count scale (true seedlings/ha), were 358 (SE = 80.5) for the 0H treatment, 103 (SE = 23.7) for the 1H treatment, and 465 (SE = 105.0) for the 2H treatment. These results indicate that treatment had a significant effect on wOAR true seedling densities.

Post hoc pairwise comparisons revealed that the 0H and 2H treatments both had significantly more wOAR of true seedling origin than the 1H treatment ($p < 0.001$ for each pairwise comparison). The difference between the 0H and 2H treatments was not statistically significant ($p = 0.687$). Based on the model, the 0H treatment had an approximately 3.5 times greater seed-origin density than the 1H treatment. The 2H treatment had an approximately 4.5 times greater density than the 1H treatment.

As was seen in the resprout-origin estimated densities, stand- and treatment-level true seedling estimates showed high variability (Tables 15 and 16; Figure 19). Examining arithmetic means at the stand level, within the 2H treatment, stand 7-142 had the highest estimated density of 930 true seedlings/ha, whereas stand 2-27 had the lowest at 263 seeds/ha. This was the widest range in estimated true seedling wOAR densities within a treatment. The 1H treatment displayed the lowest minimum and lowest maximum treatment-level densities; stand 2-32 had the minimum: 65 seeds/ha, while stand 4-9 had the maximum: 158 seeds/ha.

Table 15: Stand-level estimated densities of the wOAR population that is of true seedling origin.

Site	**Stand**	**Treatment**	**Estimated True Seedling Density (stems /ha)**
1	**26**	**Control**	297
1	**36**	**Control**	494
6	**6**	**Control**	312
2	**32**	**One-harvest**	65
4	**9**	**One-harvest**	158
4	**12**	**One-harvest**	104
2	**27**	**Two-harvest**	263
7	**132**	**Two-harvest**	408
7	**142**	**Two-harvest**	930

Table 16: Treatment-level arithmetic mean, minimum, maximum, and standard deviation for the estimated densities of the wOAR population that are of true seedling origin.

Treatment	**Mean Estimated True Seedling Density (stems /ha)**	**Min**	**Max**	**SD**
Control	368	297	494	110
One-harvest	109	65	158	47
Two-harvest	534	263	930	351

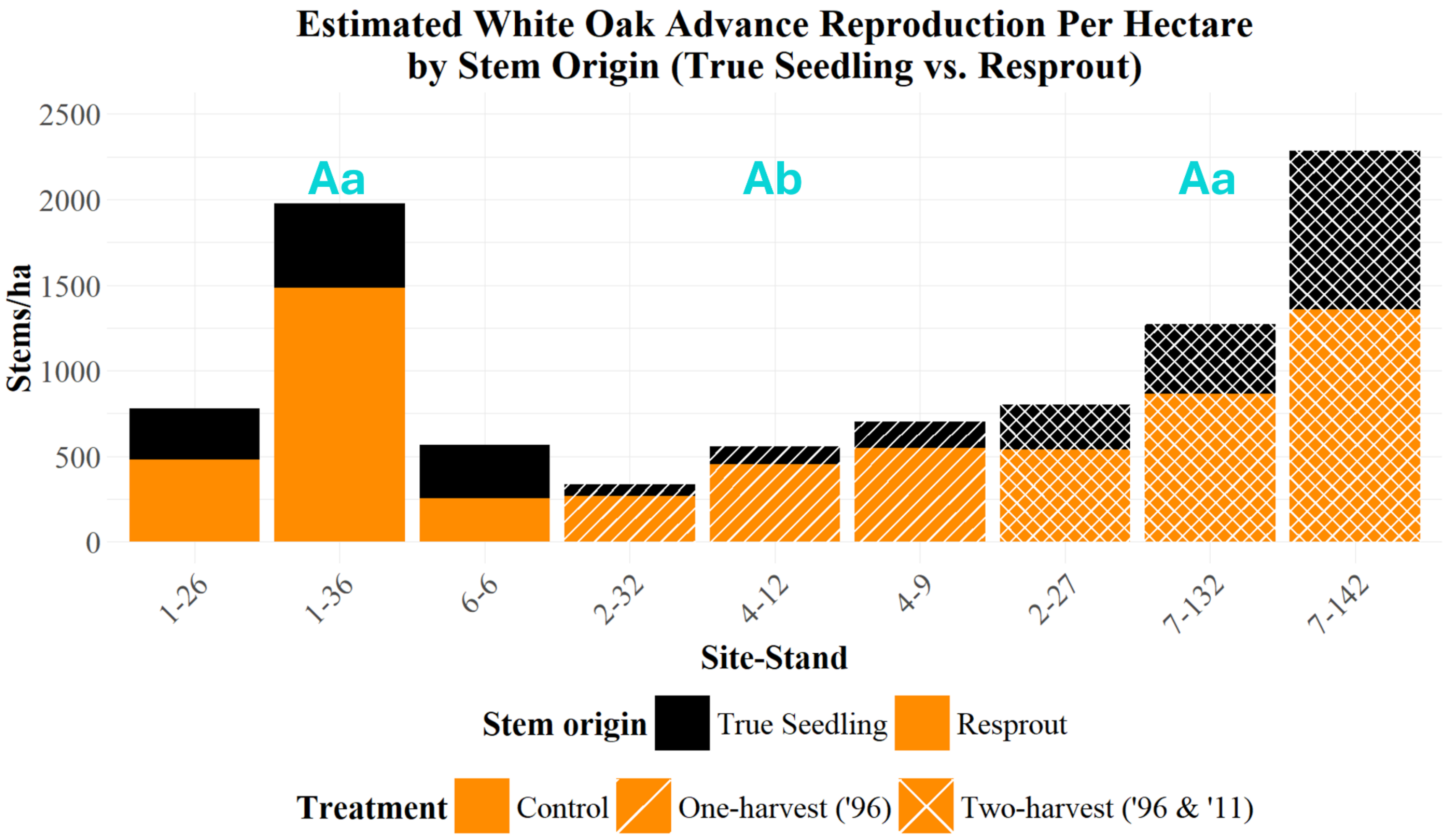


Figure 19: Estimated stand-level wOAR densities (stems/ha) by stem origin. Uppercase (A, B) and lowercase (a, b) letters above bars indicate statistically significant differences ($p < 0.05$) in estimated resprout and true seedling densities between treatments, respectively. Treatments not sharing a letter differ significantly.

4.8 Species group densities for seedling and sapling size classes

Although not statistically analyzed, the species group proportional differences between seedling and sapling size classes showed variation at the stand and treatment levels (Figure 20). Within the seedling size class, species groupings reveal that the white oak proportions ranged from 3.4% (1H) to 9.4% (2H), a difference of almost threefold (Tables 17 and 18). In the sapling size class (Tables 19 and 20), white oak showed similar proportional contributions across treatments, ranging from 4.6% (1H) to 9.9% (2H) .

The most apparent difference between the seedling and sapling size classes was the proportional differences for the other species group. Within the seedling size class, the other species group density proportions between treatments ranged from 73.4% (2H) to 82.9% (0H). In contrast, within the sapling size class, the other species group ranged from a total treatment-level share of 87.1 (2H) to 94.6% (1H). The 2H treatment showed the lowest other species group proportions within both size classes.

Shortleaf pine had small contributions to stand- and treatment- level densities as shortleaf pine seedlings were present on only five of the nine observed stands. Shortleaf pine contributed to more than 10% of total stem density proportions in just two of those stands; 7-132 and 7-142, which were 10.8% and 30.5%, respectively. Within the sapling size class, shortleaf pine (n = 13) was present within only stand 7-132. The red oak group was largely absent in the sapling size class, ranging from just 0.5% (0H) to 2.7% (2H).

Table 17: Stand-level seedling counts by species group and each species group’s proportional contributions to seedling density.

Site	Stand	Treatment	Total Seedlings	White Oak Seedlings	White Oak Proportion	Red Oak Seedlings	Red Oak Proportion	Shortleaf Pine Seedlings	Shortleaf Pine Proportion	Other Spp. Seedlings	Other Spp. Proportion
1	**26**	**Control**	1340	63	0.047	32	0.024	10	0.007	1235	0.922
1	**36**	**Control**	1193	161	0.135	161	0.135	0	0.000	871	0.730
6	**6**	**Control**	785	46	0.059	93	0.118	0	0.000	646	0.823
2	**32**	**One-harvest**	1423	30	0.021	17	0.012	1	0.001	1375	0.966
4	**9**	**One-harvest**	1020	58	0.057	255	0.250	0	0.000	707	0.693
4	**12**	**One-harvest**	1500	46	0.031	517	0.345	2	0.001	935	0.623
2	**27**	**Two-harvest**	1493	68	0.046	40	0.027	0	0.000	1385	0.928
7	**132**	**Two-harvest**	1409	105	0.075	37	0.026	430	0.305	837	0.594
7	**142**	**Two-harvest**	956	188	0.197	55	0.058	103	0.108	610	0.638

Table 18: Treatment-level seedling counts by species group and each species group’s proportional contribution to seedling density.

Treatment	Total Seedlings	White Oak Seedlings	White Oak Proportion	Red Oak Seedlings	Red Oak Proportion	Shortleaf Pine Seedlings	Shortleaf Pine Proportion	Other Spp. Seedlings	Other Spp. Proportion
Control	3318	270	0.081	286	0.086	10	0.003	2752	0.829
One-harvest	3943	134	0.034	789	0.200	3	0.001	3017	0.765
Two-harvest	3858	361	0.094	132	0.034	533	0.138	2832	0.734

Table 19: Stand-level sapling counts by species group and each species group’s proportional contributions to sapling density.

Site	Stand	Treatment	Total Saplings	White Oak Saplings	White Oak Proportion	Red Oak Saplings	Red Oak Proportion	Shortleaf Pine Saplings	Shortleaf Pine Proportion	Other Spp. Saplings	Other Spp. Proportion
1	**26**	**Control**	579	50	0.086	3	0.005	0	0.000	526	0.908
1	**36**	**Control**	598	56	0.094	1	0.002	0	0.000	541	0.905
6	**6**	**Control**	500	15	0.030	4	0.008	0	0.000	481	0.962
2	**32**	**One-harvest**	1880	71	0.038	5	0.003	0	0.000	1804	0.960
4	**9**	**One-harvest**	576	38	0.066	18	0.031	0	0.000	520	0.903
4	**12**	**One-harvest**	763	38	0.050	3	0.004	0	0.000	722	0.946
2	**27**	**Two-harvest**	2370	51	0.022	16	0.007	0	0.000	2303	0.972
7	**132**	**Two-harvest**	1403	179	0.128	43	0.031	13	0.009	1168	0.833
7	**142**	**Two-harvest**	1737	318	0.183	89	0.051	0	0.000	1330	0.766

Table 20:Treatment-level sapling counts by species group and each species group’s proportional contribution to sapling density.

Treatment	Total Saplings	White Oak Saplings	White Oak Proportion	Red Oak Saplings	Red Oak Proportion	Shortleaf Pine Saplings	Shortleaf Pine Proportion	Other Spp. Saplings	Other Spp. Proportion
Control	1677	121	0.072	8	0.005	0	0.000	1548	0.923
One-harvest	3219	147	0.046	26	0.008	0	0.000	3046	0.946
Two-harvest	5510	548	0.099	148	0.027	13	0.002	4801	0.871

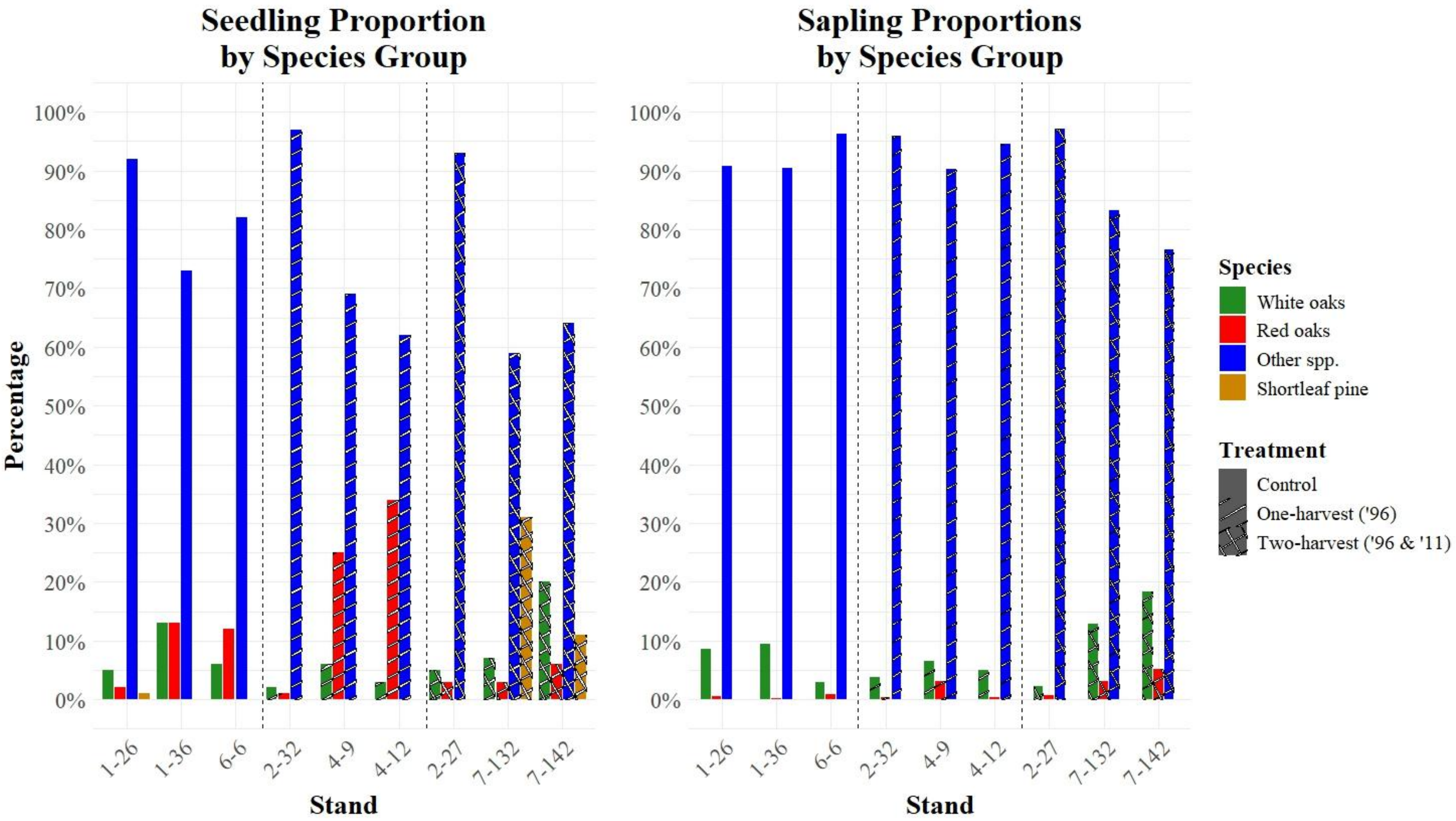


Figure 20: The seedling (left) and sapling (right) stand-level density proportions of various species groups. Species groupings include white oak spp. (green), red oak spp. (red), shortleaf pine (burnt orange), and other spp (blue). Shortleaf pine was excluded from the sapling plot as only one stand (7-132) had shortleaf pine inventoried (13 saplings).

4.9 White oak advance reproduction stem height growth

The ANOVA revealed significant differences in mean stem heights among treatment groups (Type II Wald $X^2(2)=31.21$, $p < 0.001$). Within the model, stem age also had a significant effect on stem height growth ($X^2(1)=84.42$, $p < 0.001$). Back-transforming the data from the log scale to the original scale showed that the mean stem height for the 0H treatment was 23.8 cm, while the 1H and 2H treatments resulted in mean heights of 28.9 cm and 32.5 cm, respectively. Tukey post hoc pairwise comparisons showed that the 0H–1H ($p = 0.002$) and 0H–2H ($p < 0.001$) differences were statistically significant, while the 1H–2H difference was only marginally non-significant ($p = 0.088$).

Across all measured wOAR, stem heights ranged from 15 to 133 cm (Tables 21 and 22). The wOAR with the 15 tallest stem heights observed (68 to 133 cm) had stem ages ranging from 3 to 25 years old; 11 of which were from the 2H treatment. Just 4 of the tallest 15 wOAR were identified as true seedlings. In contrast, of the 15 shortest wOAR (15 to 16 cm); 12 of which were from the 0H treatment, while 11 of those same 15 were identified as true seedlings.

Logarithmic models show similar growth patterns across treatments (Figure 21). The 0H treatment exhibited the relationship $y =9.74 + 7.24 \log(x)$ ($R^2 = 0.119$), indicating a positive logarithmic association between height growth and stem age. The 1H treatment showed a similar pattern ($y = 9.72 + 9.89 \log(x)$; $R^2 = 0.124$), though it had a slightly increased slope. The 2H treatment showed the steepest slope ($y = 4.54 + 14.24 \log(x)$); ($R^2 = 0.126$) with a roughly 2 times greater slope that the 0H treatment.

Table 21: Stand-level arithmetic mean, minimum, maximum, and standard deviation of stem height values.

Site	Stand	Treatment	Stem Height (cm)	Min	Max	SD
1	**26**	**Control**	22.4	15.0	49.0	7.9
1	**36**	**Control**	23.7	16.0	81.0	11.8
6	**6**	**Control**	26.8	15.0	74.0	12.2
2	**32**	**One-harvest**	32.2	16.0	68.0	13.8
4	**9**	**One-harvest**	28.8	15.0	81.0	14.3
4	**12**	**One-harvest**	27.3	16.0	103.0	17.5
2	**27**	**Two-harvest**	31.6	16.0	68.0	11.1
7	**132**	**Two-harvest**	37.0	16.0	133.0	23.1
7	**142**	**Two-harvest**	33.7	16.0	97.0	20.4

Table 22: Treatment-level arithmetic mean, minimum, maximum, and standard deviation of stem height values.

Treatment	Stem Height (cm)	Min	Max	SD
Control	24.6	15.0	81.0	11.0
One-harvest	29.4	15.0	103.0	15.1
Two-harvest	34.2	16.0	133.0	19.2

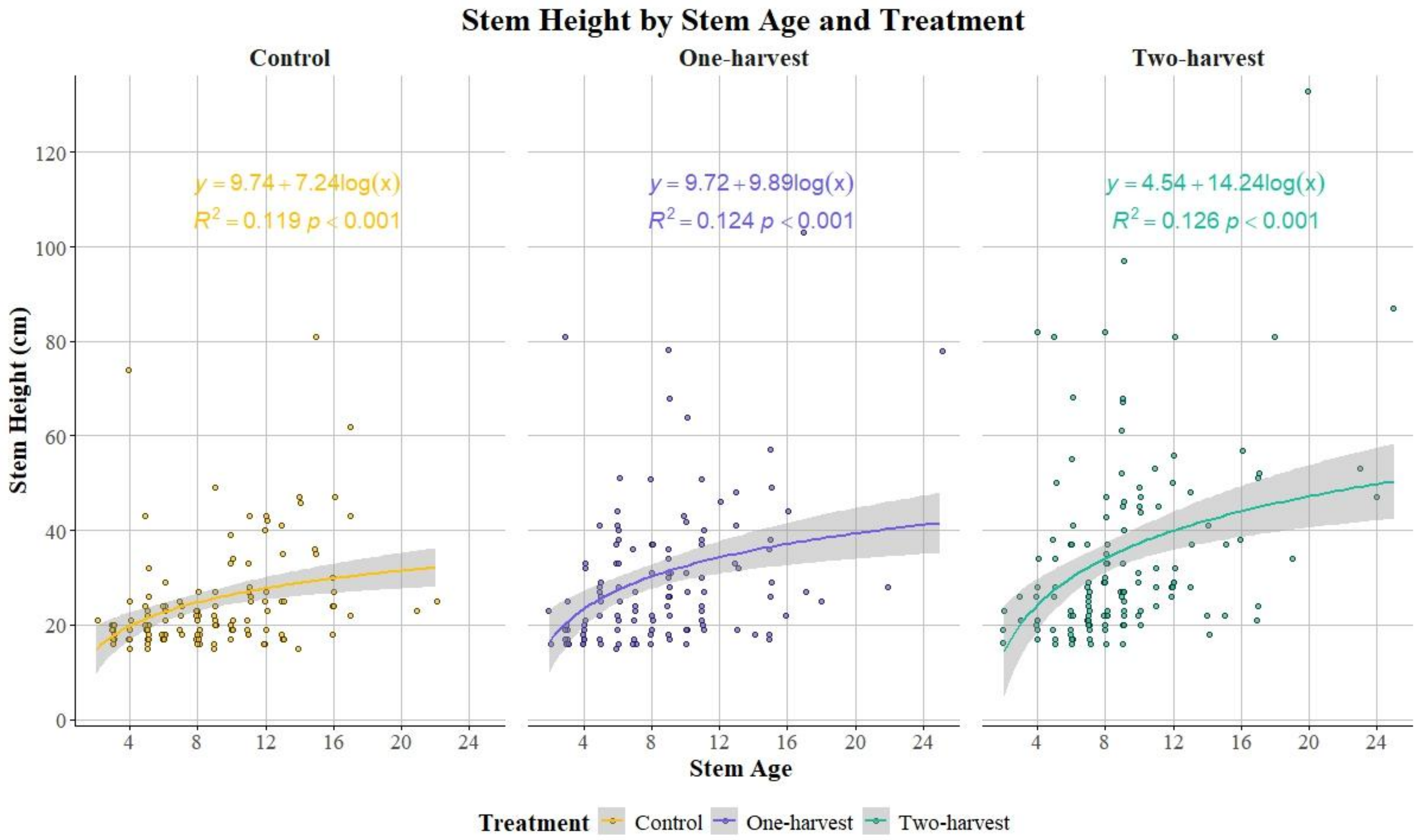


Figure 21: Relationship between stem height growth and stem age across treatments. Points represent individual measurements (jittered for visibility). Solid lines show treatment-specific linear regressions with 95% confidence intervals (gray).

4.10 White oak advance reproduction stem diameter growth

Mean stem diameters resulted in significant differences among the treatments (Type II Wald $X^2(2) = 12.45$, $p = 0.002$). Stem age was also a significant predictor ($X^2(1) = 205.14$, $p < 0.001$). When model estimates were back-transformed to the original scale, the mean stem diameter was 3.8 mm for the 0H treatment, 4.5 mm for 1H, and 5.1 mm for 2H. Tukey-adjusted pairwise comparisons revealed a significant difference for the 0H–2H treatments ($p = 0.001$), while differences between 0H–1H ($p = 0.125$) and 1H–2H ($p = 0.265$) were statistically non-significant.

Stem diameters across all measured wOAR ranged from 1.6 to 19.0 mm (Tables 23 and 24). Among the 20 largest stem diameters (10.2 to 19.0 mm), stem ages ranged from 4 to 25 years (the maximum analyzed age). However, excluding the 4-year-old stem, the next youngest stem was 9 years old. Of these 20 fastest stem diameter growth rates, 18 of them were in either the 1H or 2H treatments, with 15 of those 20 being from the 2H treatment. In contrast, of the smallest 20 stem diameters (1.6 to 2.4 mm), stem ages ranged from 2 to 8 years old, with 6 of those 20 being from the 0H treatment.

The logarithmic models between treatments indicate varying growth responses (Figure 22). For the 0H treatment, the relationship was described by $y = 0.54 + 1.68 \log(x)$ ($R^2 = 0.336$), reflecting a modest positive logarithmic correlation between stem age and stem diameter growth. The 1H treatment displayed a slightly steeper slope ($y = 1.01 + 1.79 \log(x)$; $R^2 = 0.152$), although its overall fit was not as strong. The 2H treatment showed the steepest slope: ($y = -1.94 + 3.60 \log(x)$) with only slightly less explanatory power ($R^2 = 0.296$) than the 0H treatment. These results suggest that treatments influenced the response of stem diameter growth with increasing stem age.

Table 23: Stand-level arithmetic mean, minimum, maximum, and standard deviation of stem diameter values.

Site	Stand	Treatment	Stem Diameter (mm)	Min	Max	SD
1	26	Control	3.7	2.0	6.5	1.0
1	36	Control	3.8	2.0	13.2	1.9
6	6	Control	4.3	2.0	10.2	1.5
2	32	One-harvest	5.4	2.4	19.0	3.5
4	9	One-harvest	4.0	1.8	7.4	1.4
4	12	One-harvest	4.6	2.0	14.1	2.3
2	27	Two-harvest	4.2	1.6	7.9	1.4
7	132	Two-harvest	6.2	2.2	18.0	3.4
7	142	Two-harvest	6.1	2.2	17.6	3.7

Table 24: Treatment-level arithmetic mean, minimum, maximum, and standard deviation of stem diameter values.

Treatment	Stem Diameter (mm)	Min	Max	SD
Control	4.0	2.0	13.2	1.5
One-harvest	4.6	1.8	19.0	2.5
Two-harvest	5.6	1.6	18.0	3.2

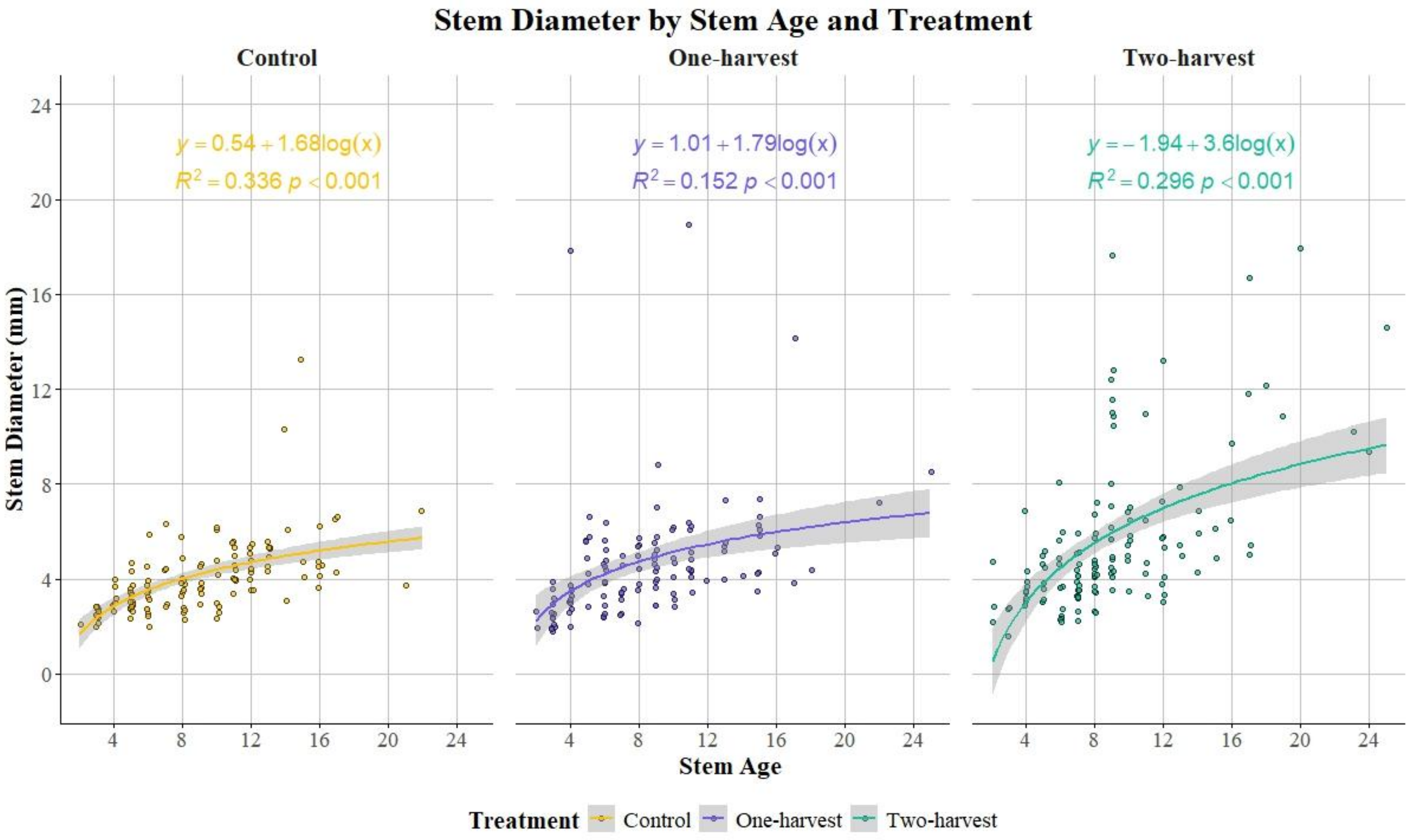


Figure 22: Relationship between stem diameter growth and stem age across treatments. Points represent individual measurements (jittered for visibility). Solid lines show treatment-specific linear regressions with 95% confidence intervals (gray).

4.11 White oak advance reproduction root diameter growth

The mean root diameter growth ANOVA resulted in significant variation among treatment groups (Type II Wald $X^2(2) = 13.40$, $p = 0.001$). Stem age was a significant predictor for root diameter ($X^2(1) = 426.74$, $p < 0.001$). Back-transforming the model estimates to the original scale, showed the mean root diameter was 7.9 mm for the 0H treatment, 9.0 mm for the 1H, and 10.2 mm for the 2H. Tukey-adjusted pairwise comparisons showed the 0H–2H treatment as statistically significant ($p < 0.001$), whereas the 0H–1H ($p = 0.136$) and 1H–2H ($p = 0.206$) comparisons showed non-significance.

Across all measured wOAR, root diameters ranged from 3.0 to 49.5 mm (Tables 25 and 26). The largest 20 root diameters ranged from 19.2 to 49.5 mm; 19 of which were from either the 1H or 2H treatments. Of the largest 20, there were 16 attached to a resprouted stem. The smallest 20 root diameters (3.0 to 4.4 mm) had just 7 belonging to the 1H or 2H treatments, only 1 of which was identified as a resprout. The 20 largest root diameters ranged in age from 13 to 25 years old (the max age included in analysis) while the smallest 20 root diameters ranged in age between 3 and 16 years old.

The treatment-specific logarithmic equations related to root diameter growth revealed various responses to increasing root ages (Figure 23). The 0H treatment wOAR showed the greatest explanatory power across all three growth analyses: $y = -1.30 + 3.71 \log(x)$ ($R^2 = 0.496$), indicating a slightly positive relationship between root diameter growth and root age. The wOAR within the 1H treatment showed a similar trend ($y = -3.46 + 5.25\log(x)$; $R^2 = 0.259$), though with greater variability. Notably, the 2H treatment showed the greatest age-related increase in root diameter ($y = -12.94 + 9.51 \log(x)$; $R^2 = 0.369$); with a slope approximately 2.6 times greater than that of the 0H treatment.

Table 25: Stand-level arithmetic mean, minimum, maximum, and standard deviation of root diameter values.

Site	Stand	Treatment	Root Diameter (mm)	Min	Max	SD
1	26	Control	7.6	3.0	14.1	2.7
1	36	Control	7.3	3.4	13.7	2.8
6	6	Control	8.0	4.0	23.7	3.2
2	32	One-harvest	11.1	5.1	29.0	5.7
4	9	One-harvest	10.6	3.3	21.8	4.4
4	12	One-harvest	10.3	3.9	19.6	4.4
2	27	Two-harvest	7.9	3.9	11.9	2.4
7	132	Two-harvest	12.9	3.2	49.5	8.5
7	142	Two-harvest	11.7	4.8	31.4	5.9

Table 26: Treatment-level arithmetic mean, minimum, maximum, and standard deviation of root diameter values.

Treatment	Root Diameter (mm)	Min	Max	SD
Control	7.7	3.0	23.7	3.0
One-harvest	10.6	3.3	29.0	4.8
Two-harvest	11.2	3.2	49.5	6.5

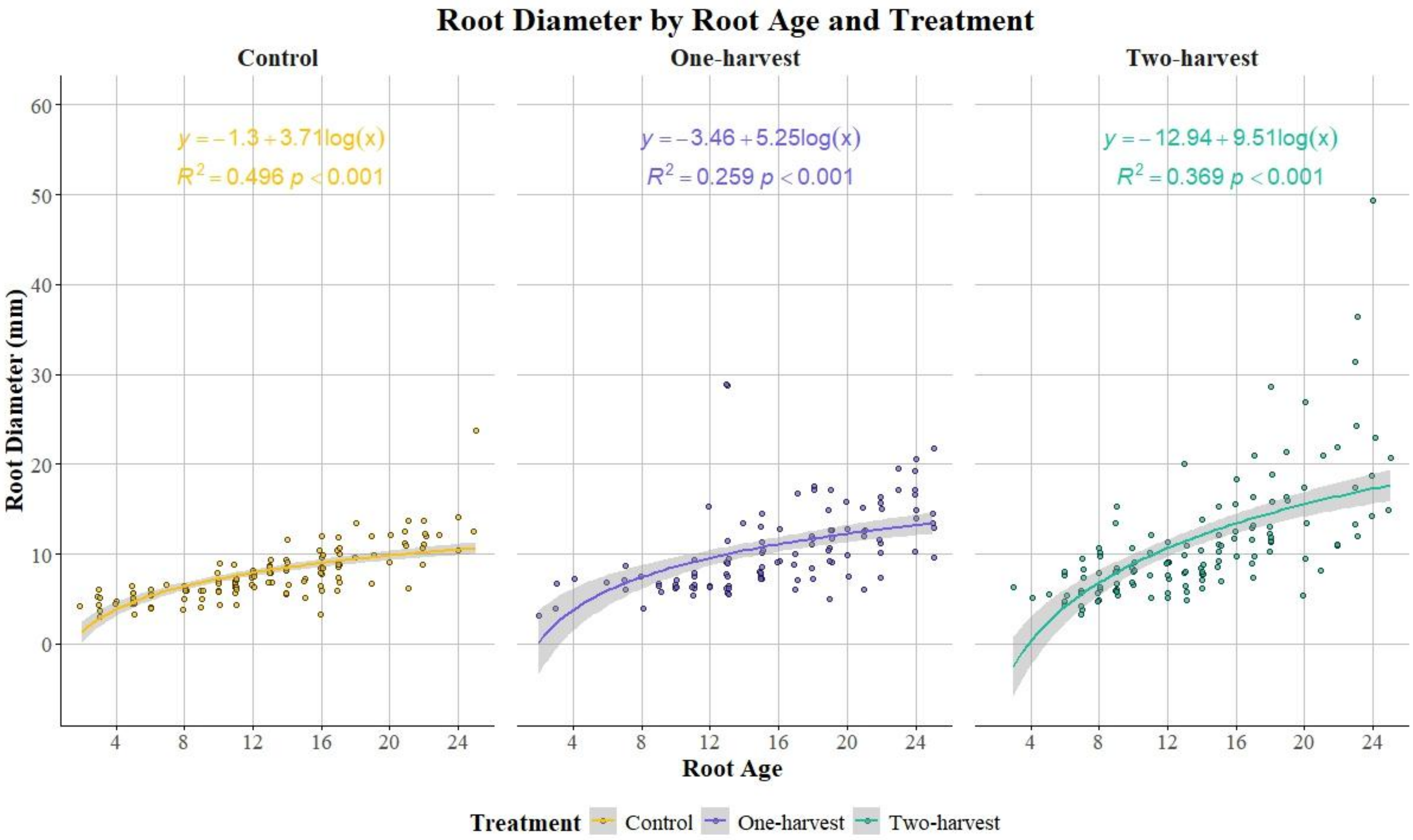


Figure 23: Relationship between root diameter growth and root age across treatments. Points represent individual measurements (jittered for visibility). Solid lines show treatment-specific linear regressions with 95% confidence intervals (gray).

CHAPTER 5: DISCUSSION

5.1 White oak advance reproduction demography

The demography of stems and roots varied widely, both within and between true seedlings and resprouts. However, the analyses showed little variation among stand- and treatment-level means for both stem and root ages when considered individually (Tables 5 and 6). This may be expected due to the recurrent resprouting typical of upland oak species. However, it was hypothesized that the 0H stands would consist of slightly older wOAR than the treated stands. This hypothesis was formed because overstory disturbance in old-growth forests can promote OARs' ascent to the overstory (Rentch et al., 2003a). In contrast, persistent low light in closed-canopy conditions can suppress growth when oak seedlings cannot sustain photosynthetic rates sufficient for growth (Hanson et al., 1986). When suppression limits growth, wOAR likely persist in the seedling layer longer than those growing under more open understories that provide sufficient light for continued growth. However, whether that understory persistence is more likely as a suppressed true seedling, or by resprouting (perhaps recurrently) would require future analysis.

In addition to individual stem and root ages, a wide variability was observed in the stem-to-root age relationships (Figure 17). This suggests that wOAR can experience stem dieback and resprouting at many different times in their life. Previous studies have also documented relatively old oak roots with substantial differences between their corresponding stem. Merz and Boyce (1956) found root ages in Ohio oak-hickory stands as old as 37 years, with stem age differences as large as 31 years. In Oklahoma old-growth forests, oak seedling roots under closed canopies averaged about 20 years old, with a maximum of 67 years (Clark & Hallgren, 2003). Notably, that 67-year-old root supported a stem of just 8 years old. Similarly, Tryon and Powell (1984) found white oak roots as old as 36 years in 70- to 90-year-old even-aged hardwood stands in northern West Virginia, and up to 50 years old for other upland oaks. Despite the mentioned studies utilizing different methods, the results from this study closely aligns with their findings, as treatment-level mean root ages ranged from 17 to 21 years (Tables 7 and 8).

Within this study, the two wOAR with the oldest roots observed were 77 and 91 years old, each supporting much younger stems (14 and 4 years, respectively). In the absence of intermediate disturbance, it is likely that these wOAR had succumb to top kill by prolonged suppression. These two wOAR were in the 0H and 1H treatments, which generally maintained longer periods of canopy closure than did the 2H treatment, although during their lone entry, the 1H stands were cut substantially harder than the 2H stands (Figure 3). While such large root-stem age differences were rarely observed, they highlight the persistence of wOAR to maintain resprouting capability with relatively old root age. Yet, with so few observations, it is unclear whether white oak seedlings with large root-to-stem age disparities maintain competitive stem growth. Furthermore, while stem resprouting typically favors root carbon allocation over time, it is also possible that oak seedlings are forced to use most of their limited carbon accumulation to simply maintain survival (Hanson et al., 1986).

Similar stem and root ages between treated and untreated stands suggest that density management alone may not be sufficient to promote white oak recruitment into larger size classes. In treated stands, if sapling recruitment or true seedling establishment had increased, either temporarily or continuously, it might be predicted that treated stands would have resulted in different mean stem or root ages compared to the 0H treatment. For instance, greater rates of true seedling establishment would theoretically lower mean ages if young seedlings showed persistence, either as true seedling or recent resprouts. On the other hand, successful recruitment into larger size classes might also reduce mean ages if a significant portion of the maturing population was successfully recruited. Conversely, successful recruitment could potentially increase mean ages if sapling recruitment was so great that it created a bottleneck that limited further recruitment, causing many individuals to remain in the seedling class. Supporting this possibility, white oak sapling density was much higher in the 2H treatment than in other treatments, yet seedling density remained similar across treatments (Tables 18 and 20). While demographic data help clarify seedling population dynamics, comparisons against larger size classes, and consideration of establishment and growth rates in tandem with demographics further explain these patterns.

Similar studies comparing stem and root ages of oaks in the central U.S. have found that 90% to 99% of individuals exhibit unequal stem and root age, often in areas where fire was prevalent (Clark & Hallgren, 2003; Dee et al., 2022). At MOFEP, in fire's absence, a large portion of the wOAR population also showed differences between stem and root ages. While wOAR exhibited large root-to-stem age discrepancies, 62% of the observed resprouted wOAR population had a root-to-stem age ratio of 3:1 or less, meaning their root was 3 times the age of the stem or younger (Figure 17). Whereas, only 13% of the resprouted wOAR population had a root-to-stem age ratio greater than 5:1.

These differences in root-to-stem age ratios imply that as roots mature to ages increasingly disproportionate to stems, this either promotes successful recruitment or reduces the ability of seedlings to continue resprouting. Root-to-stem age ratios were chosen as a variable over age differences because it was originally thought that ratios might relate to root-stem carbon allocation strategies. However, a simpler analysis of age differences may have revealed other patterns. Nevertheless, these results further highlight wOARs' persistent and recurrent resprouting adaptation despite the absence of periodic fire, which some might consider necessary for promoting resprouting.

Furthermore, with fire disturbance, a significant portion of the advance reproduction population would result in fairly synchronous resprouting events, as seen by Dee et al (2022). This was not observed within this population, which can be seen in the root-to-stem age scatterplot, which shows no systematic pattern of root establishment (Figure 15). The vector plots showing stem and root age establishment years also show wide variation in the stem establishment years of resprouted individuals (Figures 17). However, it is important to note that uncertainty in determining the absolute ages of seedlings limits the ability to pinpoint specific disturbance events and attribute widespread resprouting to them, unless the timing of the disturbance is known. In this study, aside from harvesting, such events were either nonexistent or not observed.

Notably, several (n = 34) wOAR seedlings in this study reached relatively old stem ages (15 to 30 years) without having older roots (Figure 17). These cases accounted for only 7.7% of the observed seedling population. Despite the persistence displayed by true seedlings greater than age 15, the experimental treatments did not seem to have an effect on their occurrence, as seedling counts were 11, 12, and 12, for the 0H, 1H, and 2H treatments, respectively. Yet of the top 30 wOAR by stem height, 6 had equal stem and root ages, all of which were in treated stands. Their existence raises the question of whether multiple resprouting events is always necessary for canopy recruitment.

Considering both true seedlings and resprouted seedlings, wOAR rarely persisted beyond a stem age of 20 years. Of the 444 total wOAR seedlings for which both stem and root ages were assessed, only 17 individuals (3.8% of the observed population) reached a stem age greater than 20 years (Figure 17). Among these, 9 persisted as true seedlings and 8 as resprouted seedlings. Such few wOAR reaching these ages makes it difficult to assess whether true seedlings or resprouted seedlings are more likely to achieve this length of persistence.

Several growth dynamics could contribute to this apparent 20-year threshold: seedlings may succumb to mortality without resprouting and be permanently removed from the population, or they may recruit to a larger size class by this age and thus no longer be counted among seedlings. Alternatively, seedlings that stagnate in the seedling class due to suppression may resprout, perhaps repeatedly, as might be suggested by the wide variability in root ages observed (Figure 17). It would be interesting to determine whether this 20-year threshold represents a general biological limit for seedling stem persistence, or if it is an artifact of the study's methods, such as the imposed height threshold or the focus on currently existing seedlings.

In intensively managed uneven-aged systems it is possible that wOAR may reach larger size classes on drought-prone sites without such heavy reliance on recurrent resprouting. However, intermediate disturbances that target non-oaks may be necessary to promote oak's existence relative to faster-growing competing species (Vickers et al., 2019). This idea could significantly alter current assumptions about the timeframes necessary for white oak canopy recruitment in today's uneven-aged forests within the Ozark Highlands. Here the process is often described as a gradual, long-term, and often multi-decadal process, especially when considering the perceived needs of restored fire regimes to promote competitive oak establishment among fast-growing, shade-tolerant species (Dey, 2014; Johnson et al., 2019). With more targeted disturbances, such as midstory thinning or herbicide application, species composition and stand structure may be more readily restored to align with historic forest conditions. Such restoration could potentially shorten the timeframes associated with white oak recruitment.

5.2 White oak advance reproduction establishment trends

In this study, the probability for a wOAR to be a resprout ranged from roughly 60% to 80%, depending on treatment (Figure 18). The probability that a wOAR seedling was a resprout was much higher in the 1H treatment compared to both the 0H and 2H treatments (Figure 19). This was contrary to the initial hypothesis that both the 1H and 2H treatments would result in a lower probability of stems established as a resprout. This hypothesis was made due to an expected greater rate of true seedling establishment triggered by periodic canopy disturbance.

The explanation for the 0H treatment having roughly equal probability for a wOAR to be of resprout origin as the 2H treatment is not clear. One possibility is that persistent canopy closure led to intense understory suppression. This may have caused existing seedlings to lose their resprouting ability and eventually succumb to mortality, creating space for greater true seedling input over time. Additionally, the greater success of shade-tolerant species' regeneration under prolonged canopy closure could have resulted in white oak true seedlings existing only ephemerally. Alternatively, the research plot locations in this study may have coincidentally fallen in more open areas within the 0H stands, resulting in observed higher probabilities of true seedlings than were actually present. Uneven-aged forests have inherently heterogeneous structure and density, which can influence variation in species' regeneration success (Hanewinkel, 2004; Fan et al., 2015). As such, plot placement in the more open microsites could have influenced results, despite establishing an adequate number of research plots.

One potential explanation for the 1H treatment having the greatest probability that a wOAR was a resprout is that the 1H stands had not been re-entered since the initial harvest in 1996. The 26-year period without further canopy disturbance may have prevented continued true seedling establishment. Within this study, the probability that a wOAR was a resprouted seedling was lower than the observed proportions reported in other studies, but was still quite high (Clark & Hallgren, 2003; Dee et al., 2022). This suggests that factors other than fire may influence white oak resprouting processes.

The lower STK in the 1H stands (approximately 40% to 50%) following the first harvest likely promoted higher initial rates of true seedling establishment compared to the 2H stands, which was cut to a greater residual STK (~60%, just above the Gingrich B-level). It is known that regeneration is more likely at STK values below the Gingrich B-level, as lower STK increases understory light and growing space. This may be reflected in the cumulative distributions of wOAR, where the 1H treatment initially showed a higher percentage of wOAR established after the first harvest (Figure 16).

In contrast, the 2H treatment maintained its trajectory and eventually surpassed the 1H in cumulative establishment, though the cumulative distributions do not account for the removal of established regeneration from the seedling size class, either through recruitment into larger size classes or loss by mortality. The first harvest in 2H stands did not reduce residual density as much as in 1H stands, so 2H stands remained above the B-level even immediately after harvest.

It was only after the second harvest in 2011, when STK was brought below the B-level (Figure 3), that conditions may have become more favorable for seedling establishment and canopy ascension by existing regeneration. This would have created similar growing conditions to those achieved in the 1H stands after their 1996 harvest. Therefore, a major distinction between these treatments in creating similar growing conditions is that comparable residual STK post-harvest was achieved 15 years apart. The 1H treatment achieved this in 1996 while 2H achieved it 15 years later in 2011. Although these residual STK values were similar, seedlings were observed under much different growing conditions at the time of sampling. The 1H treatment might have initially provided favorable conditions but included an approximately 10-year period of residual STK greater than B-level during later observation years. Conversely, 2H seedlings were likely observed more exclusively during a period of more favorable growing conditions.

These patterns are further supported by greater stand-level stem origin densities in 2H stands compared to all three 1H stands and two of the three 0H stands (Figure 19). It is possible that, due to the timing of similar growing conditions being 15 years apart that seedlings in the 1H stands had enough time to undergo resprouting, whereas this process may not have yet occurred as prominently in the 2H stands. The elevated density observed in 0H stand 1-36 appears to be influenced by outlier plots, as it contained three of the five densest plot-level white oak seedling inventories. Without these outliers, the 0H treatment may have shown significantly lesser true seedling establishment.

One potential explanation for the 2H treatment having sustained trajectory of its cumulative distribution is that the 2H treatment may have maintained conditions conducive to seedling establishment for a much longer period of time. Despite this treatment not achieving STK below B-level during the first entry, it was likely reduced enough to promote some seedling establishment, even if only for a short duration of time, especially compared to the 0H treatment which maintained even greater STK through the full observation period. However, as these are cumulative proportions and not absolute densities, the trajectories of these lines could have been influenced by much different population numbers, which might be inferred from the white oak seedling densities at the treatment level (Table 18). So, although the 2H treatment did not catch up to the 1H treatment until approximately year 2014 on the cumulative distribution figure, seedling density measures revealed that the 2H treatment resulted in almost 3 times as many seedlings as the 1H treatment (Figure 16).

Another possible explanation for the separation observed in the cumulative distributions is that despite much different STK in the 1H and 2H stands, they may have initially achieved similar numbers of seedling establishment. Afterwards, it is possible that greater seedling mortality occurred in the 2H treatment, as STK more quickly grew to rates less favorable to maintaining seedling growth. While residual STK rates near 60% may be conducive for initial seedling establishment dynamics, greater densities may not be favorable for maintaining growth and recruitment as fully stocked conditions were more quickly reached between stand entries. This potential explanation and those prior highlight how growth dynamics not captured by this study, such as mortality, can obscure the interpretation of these establishment results, descriptive statistics, and figures.

The differences in cumulative distribution between the 1H and 2H treatments involve another growth dynamic not captured in the experimental framework: recruitment. Recruitment of seedlings into sapling size classes may have reduced the cumulative percentage of seedling establishment. In the 1H stands, where an initial flush of regeneration was followed by a prolonged absence of further canopy disturbance, lower recruitment rates may have persisted for several years, creating a bottleneck that could have restricted true seedling establishment in more recent years leading up to the 2022 field sampling.

Another important consideration between the 1H and 2H stands concerns their conditions after the first harvest in 1996. The stands selected for the 2011 harvest may have been chosen based on stand inventory metrics reflecting pre-harvest conditions. For example, if all stands were considered for the second entry (2011), those ultimately selected for harvesting may have been chosen because their rates of STK, as measured during the 2010 inventory, were greater than those of stands not selected (now classified as 1H stands). In other words, although the original goal may have been to achieve similar residual STK across all stands after the first harvest, stands not cut as heavily may have grown more quickly and thus became candidates for the 2011 harvest, while those cut more heavily continued to develop without further intervention.

For instance, while 2H stands were reduced to approximately 60% residual STK in 1996, it was not until 2011 that stands now considered 1H reached that same STK level. This suggests that the decision to harvest a stand in 2011 may have been driven more so by variation in residual STK and stand structure established after the first harvest, rather than by predetermined designations as a one- or two-harvest stand. Therefore, it is important to recognize that the post-1996 stand conditions, specifically residual STK and stand development, may have played a large role in harvest scheduling.

Moving on to considerations of absolute densities, the 1H stands, which experienced the single harvest followed by 26 years with no further disturbance, had the lowest total estimated wOAR density, although this was not statistically analyzed (Figure 19). These results are consistent with Clark et al. (2007), who found that *Quercus* and *Carya* regeneration was almost entirely absent in larger seedling size classes (30 to 134 cm tall) in Tennessee old growth *Quercus* forests after a mortality event followed by a 22 year period without further disturbance. Shade mid-tolerant species such as *Quercus* and *Carya* struggle to regenerate without periodic canopy disturbances (Larsen & Johnson, 1998). This often results in a shift toward greater dominance of shade tolerant mesophytic species in smaller size classes (Larsen & Johnson, 1998; Nowacki & Abrams, 2008). This trend may be especially pronounced in closed-canopy forests where an initial disturbance releases the accumulation of shade-tolerant species, but no further disturbance follows.

The seedling and sapling species group proportions further support these claims. In the 1H stands, saplings of the other species group made up 90% or more of saplings, while their seedling proportion was much lower (65% to 75%) in two of the three stands (Figure 20). These results were nearly identical to those in the 0H stands. In the 2H stands, which experienced overstory canopy disturbance on a 15-year cutting cycle, two of the three stands had slightly lower other species group sapling proportions (about 75% to 85%) compared to the 0H and 1H stands. However, this difference was not statistically tested. These descriptive statistics suggest that oak seedling establishment did not translate to successful recruitment into the sapling size classes.

Furthermore, although the 1H stands were cut more heavily than the 2H stands during the first entry, these density measures alone do not account for environmental conditions. Notably, two of the 2H stands came from Peck Ranch (Site 7), which exhibited distinct stand structure and species composition (Figure 20). It is possible that despite higher residual STK in the 2H stands, micro-environmental conditions strongly favored white oak recruitment compared to those in the 1H stands. While site conditions were controlled by selecting only stands designated as ELT 18 (Table 2), this classification is broad and likely insufficient to account for the variability in micro-environmental factors that may greatly influence seedling establishment and growth.

Both of the 2H stands located at Peck Ranch also exhibited lower sapling proportions for the other species group (Figure 20). These stands exhibited more shortleaf pine among larger overstory trees (30 to 50 cm dbh) and in the seedling layer, where they made up about 10% to 30% of species group proportions. These compositions suggests that physical site factors, such as light availability and microtopography, may partially explain the observed differences in regeneration composition. Microtopographic variation is known to influence resources like soil moisture and sunlight, which impact species distributions and survival during regeneration (Kabrick et al., 2014; Zhang et al., 2024).

Only stands that were classified as ELT 18 and that possessed comparable ESDs were included in this study to account for broad spatial similarities among site qualities. Yet, unmeasured local factors such as subtle variations in topography, soil properties, tree-neighbor interactions, and timber-marking decisions may contribute to the differences in composition and regeneration dynamics observed among stands. These compositional and structural patterns highlight the significance of the physical environment not only with seedling establishment, but also the subsequent growth and development of wOAR.

5.3 White oak advance reproduction height and diameter growth

Growth of wOAR was assessed using stem height, stem diameter, and root diameter, with each metric providing insight into different aspects of white oaks' competitive ability. Stem height and diameter reflect their capacity to capture understory light and resist overtopping by non-oak competitors. Stem and root diameters are related to resistance to top kill from disturbances and the potential for resprouting, although this study did not include intermediate disturbance treatments (Brose & Van Lear, 2004). Root diameter may also indicate whether photosynthesis rates are sufficient to support the root carbon allocation strategy observed in many upland oak species (Lockhart et al., 2008).

Analysis of stem height revealed a linear increase in modeled logarithmic slopes among treatments, with the 0H treatment having the shallowest slope and the 2H treatment the steepest (Figure 21). This pattern supports the hypothesis that wOAR stems achieve greater heights in treated stands compared to those in the 0H treatment at a given stem age. However, stem heights were similar among treatments until stem ages of approximately 6 years. This threshold may reflect early resource allocation to bud development for adequate leaf area, preferential root growth strategies at early ages, or the need to ensure sufficient stem and root stability for height growth. However, it is important to note that this stem age threshold included both resprouted and true seedlings.

Beyond stem ages of 8 years, more stems in the 1H (n = 7) and 2H (n = 9) treatments exceeded 40 cm in height than in the 0H (n = 2), indicating that wOAR may respond to canopy openings at relatively young ages given adequate light. Again however, this analysis included both true seedlings and resprouted seedlings, which may show differences in the ages at which they can respond to canopy openness with increased growth. Notably, stems in the 2H treatment maintained a steeper growth trajectory, reaching a mean height of 40 cm by 12 years of age. This height was not reached in the 1H treatment until 21 years of age and was not achieved in the 0H treatment during the study period. This sustained growth in 2H is likely due to the additional harvest entry and more frequent cutting cycle, which prolonged canopy openness, increasing and sustaining light availability.

Stem and root diameter growth followed similar trends, with significant differences observed only between the 2H and 0H treatments. At the treatment level, mean stem diameter (by stem age) and mean root diameter (by root age) showed little variation before ages of 8 years (Figures 22 & 23). By stem ages of 16, stem diameter in the 2H treatment reached 8 mm, a size not reached in models for the 0H or 1H treatments. Root diameter differences were less pronounced, with mean values similar (~ 8 to 12 mm) across treatments up to 14 years of root age. Root diameter surpassed 15 mm only in the 2H treatment, at a root age of 20 years. As with stem height, sustained diameter growth might be attributed to greater and more consistent light availability in the 2H treatment, which likely promoted higher rates of photosynthesis and biomass accumulation. In contrast, lower light availability due to continued canopy closure in the 0H and 1H treatments likely limited diameter growth.

In UAM, canopy gap closure typically occurs rapidly following harvest, with closure increasing exponentially and being more detectable at gap edges than centers (Valverde & Silvertown, 1997). In response to canopy gap formation, sugar maple and American beech can exhibit height growth, lateral branch growth, and shoot development that resulted in canopy closure much more rapidly than had occurred by sapling ingrowth (Canham, 1988). Canopy closure also tends to occur more quickly on protected aspects, which support greater tree height, biomass, and canopy cover (Yang et al., 2020). As such, harvesting strategies that rely more on single-tree selection, especially on more productive sites or aspects, may experience more rapid gap closure, discouraging the recruitment of slow-growing species like white oak. This is particularly relevant for wOAR populations lacking a disturbance regime to promote root carbon allocation strategies that favor competitive aboveground growth, and especially so for populations growing on more productive, protected aspects.

A potential cause of the observed slow growth trajectories is that only the seedling layer was assessed. Including or separately analyzing saplings may have yielded different results. By focusing only on seedlings, successful recruitment into larger size classes may have been overlooked, potentially influencing the observation of slow growth rates. Additionally, the results reflect only those seedlings that survived, while mortality, which would have occurred in both the 0H and treated stands, was not accounted for. This survival dynamic could inflate inferred growth rates, as the surviving seedlings may have grown faster than those removed from the population due to mortality. Therefore, failing to capture the full range of seedling growth dynamics, including mortality and successful recruitment, limits the accuracy of estimating seedling growth rates over time.

However, these results do capture seedlings that have successfully persisted, either through resprouting or as true seedlings. Additionally, the analyses included young seedlings that were likely too immature to be recruited. While many older seedlings had failed to recruit to larger size classes by the time of sampling, the analyses also included seedlings with relatively young stems that likely had not yet lived long enough to recruit. Therefore, these young seedlings cannot be considered as contributing growth that prevented their recruitment to the sapling layer.

Similarly to how these growth analyses captured only certain growth strategies described above, they also included true seedlings and resprouted seedlings in the same analyses. In example, a 5-year-old true seedling was potentially grouped with 5-year-old stems of resprouted seedlings with varying levels of stem-to-root age differences. It would be interesting to see how growth of true seedlings compared to resprouted seedlings in a separate analysis, as well as to resprouted seedlings of varying age differences. This is something that could potentially be achieved with the existing dataset.

The absence of frequent understory disturbance may have contributed to the relatively slow growth trajectories observed. If intermediate disturbances that controlled competitor abundance and competition dynamics had occurred, the results may have differed significantly from those observed. Statistically significant differences did occur within the 2H treatment. However, even those growth rates may be insufficient for wOAR to maintain competitive standing against faster-growing, shade-tolerant species dominating the sapling layer. Studies have shown that thinning, especially when combined with fire, can increase light to levels that promote oak growth but also stimulate competing species (Iverson et al., 2008; Schweitzer et al., 2019). This would be especially true if additional treatments had incorporated management practices that directly controlled competition. Such treatments could then be compared against existing treatments that did not directly attempt to control competing species.

However, while fire may help control competitor density, excessive fire frequencies can reduce oak growth, sprouting, and survival, ultimately limiting their recruitment to larger size classes (Alexander et al., 2008; Arthur et al., 2015). Repeated intermediate treatments can promote enhanced wOAR growth, either by resprouting or enhancing light availability. Yet, oak's competitive success is likely dependent on sustaining adequate light availability while simultaneously reducing the presence of competing species. Even on harsher sites, without adequate disturbance or competition control, enhanced oak growth may not ensure long-term oak dominance in the presence of mesophytic competitors.

5.4 Influence of tension wood and eccentric growth

Xylem development is linked to a tree's photosynthetic capacity and total hydraulic conductivity (Brodribb, 2009). Tension wood formation has been associated with reductions in xylem vessel size and density in various hardwood species (Jourez et al., 2001; Ruelle, 2013). However, in *Quercus ilex* seedlings, tension wood formation did not significantly affect total seedling hydraulic conductivity or vulnerability to embolism, despite changes in vessel frequency and size along the stem (Gartner et al., 2003). This finding suggests that tension wood can alter mechanical properties without limiting hydraulic function. Tension wood may also form in response to site-specific physical stresses, such as slope and aspect, or from competition dynamics, including stems leaning to access light in canopy gaps or preventing themselves from being overtopped by neighboring trees (Richter & Richter, 2015). Consequently, during years with extensive tension wood formation, xylem growth may be driven by a need to counteract gravitropic stress or competition more so than by the influence of resource availability.

The results from this study do not clarify whether tension wood xylem formation in wOAR limits seedlings' ability to respond to canopy release. Larger seedlings respond with faster growth to changes in climate and physical site factors, such as increased precipitation and decreasing slope percentage, highlighting the significance of initial tree size to increased ability for growth responses (Charles et al., 2018). While increased radial growth was observed in many stem microsections following harvests, the magnitude and duration of these releases were highly variable. Heterogeneous stand structures resulting from UAM harvesting and the lack of spatial data on canopy gaps often made it difficult to determine the drivers of wOAR growth responses. Additionally, challenges in precisely dating highly suppressed wOAR further masked whether radial growth was triggered through management activity or from tension wood formation.

It is likely that tension wood formation leads to eccentric tree-ring patterns and non-symmetrical radial growth, though the precise drivers of eccentric growth remain unclear. Eccentric growth may be an inherent part of seedling establishment, as seedlings require stable stem bases to support vertical growth and increasing biomass. This could represent an additional benefit of resprouting adaptations, helping seedlings maintain structural integrity during early development. Micro-environmental factors such as slope and substrate may further influence tension wood formation and eccentric growth. On steep slopes, seedlings must accumulate greater structural support to resist downhill gravitational forces compared to those growing on summits or gentler slopes. Also, in the

Ozark Highlands, rocky soil substrates may further constrain root expansion in certain directions, contributing to asymmetric stem growth. Light availability from canopy gaps may further shape growth dynamics, as seedlings redirect stem growth to reach available light in uneven-aged forest settings that possess patchy, and highly heterogenous canopy gap formations. It is likely that a combination of these factors, and others not discussed, interact to control or at least influence tension wood formation and eccentric growth.

Eccentricity appears to be a key growth factor determining a seedling's ability to respond to canopy releases resulting from management. This formation extends beyond direct reductions in xylem vessel density but is also potentially influencing variation in seedling size classes, differences between stem and root ages, and growth responses on a variety of topographical position. Although eccentricity was not initially considered a major factor in this study's data collection or interpretations of growth dynamics, it is clear that greater focus on eccentricity may help uncover regeneration dynamics not previously considered. In other words, greater attention to eccentricity and tension wood formation could reveal new insights into regeneration processes. Incorporating explicit focus on these factors in future research may uncover cell formation strategies, growth patterns, and environmental mechanisms currently overlooked in white oak regeneration.

5.5 Future research directions

Previous studies assessing stem and root ages of oak seedlings in central and eastern U.S. forests have mainly relied on traditional surface preparation methods, such as air drying and sanding, to count annual rings (Merz & Boyce, 1956; Clark & Hallgren, 2003; Heggenstaller et al., 2012). Some studies even mention only measuring roots with clearly visible rings, despite referencing more advanced techniques like thin tissue sectioning and staining, or x-ray analysis for roots that are difficult to assess (Tryon & Powell, 1984). However, traditional approaches of sanding can limit accuracy, especially for suppressed or resprouting individuals where ring boundaries are often indistinct.

In contrast, this study and Dee et al. (2022) applied QWA methods, including tissue microsectioning, staining, microscopic imaging, and image analysis, to achieve greater precision in age determinations; even for the most suppressed individuals. These advanced techniques outlined by von Arx et al. (2016), enable detailed and accurate assessment of oak seedling demography and establishment. The use of QWA methods clearly display anatomical features that surface preparation alone might miss. The improved resolution and accuracy of QWA methods are valuable for studies aiming to capture absolute precision of time and fine-scale temporal dynamics in oak regeneration. Their inclusion should be considered in future research where precise ageing is critical.

While this study made observations at only a single point in time, tree-ring dating methods enabled retrospective assessment of tree growth across the full range of observed wOAR ages. The post-management timeframe captured in this study (26 years) is equal to or longer than several other long-term investigations of white oak regeneration dynamics (Clark et al., 2007; Spetich, 2020; Swaim et al., 2016). This is particularly important in studies of regeneration, as wOAR may require several decades to reach the canopy due to recurrent resprouting. This prolonged duration necessary for oak canopy recruitment is supported by studies documenting OAR roots as old as 30 to 60 years (Merz & Boyce, 1956; Clark et al., 2004; Dee et al., 2022).

Additional evidence for prolonged understory persistence comes from a tree-ring study using a radial growth averaging technique, which estimated understory residence times for white oak of up to approximately 90 years, depending on gap-phase recruitment dynamics (Rentch et al., 2003a). Consequently, a clear research direction is to implement more treatments with additional UAM harvest entries over longer periods. A major advantage of adding more treatments at this study site would be that much data from existing treatments has already been collected.

In addition to incorporating treatments with additional cutting cycles, as well as with greater variation and precision in residual STK from entry to entry, future research should examine combinations of various management practices. This approach may help identify interactive effects between harvesting strategies and other practices. For instance, several studies have compared the effects of individual and combined management practices (such as thinning, fire, and herbicide application) on oak regeneration and recruitment (Albrecht & McCarthy, 2006; Holzmueller et al., 2014; Schweitzer et al., 2019). Similarly, treatments with equal cutting cycles could be compared by including additional practices. For example, two treatments may share similar cutting cycles and management durations, but one incorporates prescribed fire and another uses herbicide application. Two treatments could also share similar combined practices (such as fire and midstory thinning practices) but differ in lengths of the cutting cycle or residual STK.

To examine factors beyond harvest frequency and stem or root age, future studies should incorporate physical site variables such as slope, aspect, elevation, and slope position. Previous research has highlighted the influence of topography on oak regeneration success (Shostak et al., 2004; Kabrick et al., 2008; Kabrick et al., 2014; Frey & Ashton, 2018). These physical site factors can be extracted from digital elevation models (DEMs) using ArcGIS, combined with the GPS coordinates of observed plots.

However, field measurements would provide more precise resolution. Site variables can then be used individually in model-building or combined into a landform index, such as the Topographical Relative Moisture Index (TRMI). The TRMI integrates topographic position, slope aspect, steepness, and slope configuration into a single value that reflects soil moisture availability in mountainous terrain (Parker, 1982). Simultaneously assessing site factors and UAM harvest frequency may help identify the sites that are most conducive to successful regeneration.

In addition to physical site factors, future studies could also incorporate understory light availability. Light availability is closely related to stand dynamics (Oliver & Larson, 1996). In closed-canopy Quercus forests, photosynthetically active radiation (PAR) has been observed as low as 1% to 13% of available sunlight, depending on site quality (McCarthy & Robinson, 2003; Blizzard et al., 2013; Brose & Rebbeck, 2017). These studies quantifying light availability help explain how resource availability influences wOAR growth. Light availability can be measured using hemispherical photography, spectrophotometers, or, for more intensive studies, continuous seasonal measurements with quantum sensors and dataloggers (Lieffers et al., 1999). Assessing the light availability occurring within canopy gaps formed from various combinations of harvest intensities and cutting cycles may further aid in the identification of specific management practices favorable to oak regeneration and sustained recruitment.

An area of research that would further advance our understanding of stem and root relationships is the investigation of growth occurring within the first year of OAR establishment. As mentioned previously, the xylem near the pith was often the most difficult area to interpret ring boundaries. Within this region, a lacking confidence in tree-ring boundary placement frequently prevented precise calendar year assessments of seedling establishment. This difficulty may be due to insufficient image resolution, slow initial seedling growth, or a limited understanding of root development and its seasonal senescence. Enhanced ability in determining absolute ages would enable additional analyses that require precise ages or exact timings of specific disturbance events.

Additionally, distinguishing anatomical differences between true seedlings and resprouted stems in the first year of xylem formation further complicated interpretations. For instance, root and stem ring counts were often just a year apart, yet highly correlated and with no lacking confidence of ring placement near the outward xylem boundary extent. Whether observations were true age differences or a product of limited knowledge concerning stem and root ecology of first-year seedlings was uncertain.

Challenges in delineating tree-ring boundaries within stems and roots during the first year of xylem development might be addressed through a greenhouse study. In such a setting, stems and roots could be grown with precise knowledge of their establishment timing. Seedlings could then be exposed to temperature and light fluctuations that mimic the ecosystem seasonality that influences changes in cell development. Assessing xylem development under controlled climatic and environmental conditions would allow for temporally precise observations of cell formation. This resolution could be further enhanced using the pinning technique; a wood anatomy method that assists observation of xylem cell development by intentionally damaging the cambium at known times (Kuroda & Shimaji, 1984; Seo et al., 2007). In this method, the cambium is acutely (spatially and temporally) damaged, after which growth continues, producing a visible scar through malformations of the surrounding xylem cells. The resulting scar effectively serves as a timestamp within the xylem.

Additionally, by repeatedly pinning the xylem at known times and locations around the stem and root circumference, intra-annual changes in cell development can be observed. Such a study would enhance our knowledge of stem and root development over time. Furthermore, it would allow for distinctions in cell development and growth processes between stems and roots, as well as between the establishment processes of true seedlings and resprouts. This approach would refine our ability to precisely date tree rings in seedlings and improve our understanding of early growth dynamics.

Concerning tension wood, incorporating the spatial locations of canopy openings relative to wOAR sampling sites would help clarify the effects of tension wood formation on seedling responses to canopy release. While retaining the cardinal orientation of seedlings during microsectioning and slide preparation is challenging, it is possible, and it would provide valuable context for interpreting growth responses. Physical site factors, such as slope, aspect, and microtopography, are known to induce mechanical stresses that drive tension wood formation (Charles et al., 2018). This may influence how seedlings respond to environmental changes like canopy harvests. To fully understand the implications of tension wood formation on seedling release, future studies should keep track of seedling orientation, their position relative to canopy gaps, and relevant topographical characteristics. This integrated approach would allow for a more precise assessment of how demography, environmental factors, and management interact to shape seedling growth and wood anatomy following canopy disturbance.

5.6: Experimental design and methods limitations and considerations

Several components of this study's experimental design allowed for a direct comparison of various UAM silvicultural intensities within the interior Ozark Highlands of Missouri. Forest stands were selected for their similar development histories and physical site characteristics, ensuring that differences in site or initial stand conditions did not confound the results. This design allowed the evaluation of the effects of different cutting cycle intervals across broad spatial (landscape) and temporal (26-year) scales. Additionally, the requirement that study areas remained unmanaged for at least 40 years before MOFEP's establishment provided a consistent baseline for assessing management effects over time even though the first UAM harvest did not occur until 1996. This selection process ensured the sites had similar forest structure, composition, age, and density, which strengthened the analyses' reliability.

Even with a diligent stand selection process, slight differences in stand attributes could have influenced the treatment differences observed in the results of several analyses. For instance, stands were selected based on STK from inventories conducted in MOFEP's permanent plots in 1995, prior to the first harvest. Yet, despite applying similar harvesting strategies (single-tree and group selection) in both the 1H and 2H treatments, in 1996 the 1H stands were cut to a lower STK than the 2H stands (Figure 3). After the first harvest, the 1H stands ranged from STK values of roughly 40% to 50%, while STK within the 2H stands were approximately 60%. The lower STK in 1H stands could have led to greater differences in wOAR growth, as well as modes of seedling establishment and their respective densities, which may have persisted for several years. The lower STK after the first entry in 1H stands may explain the differences seen in the wOAR cumulative percentage rates over time (Figure 16). While greater similarities in residual STK were desired in the stand selection process, these differences helped assess harvests of different intensities. However, greater consistency being achieved in residual STK, either across treatments or from entry to entry, would allow for more confident assessment of the growth dynamics influenced by residual STK.

Randomly selecting wOAR only at the time of destructive sampling in 2022 introduced some interpretive limitations. Although QWA sample preparation and dendrochronological dating provided age data spanning over nine decades from a single sampling year, this approach also had drawbacks. By eliminating the need for labor-intensive annual tagging and tracking, the methods used increased efficiency. However, in these UAM forests, suppression under partially or fully closed canopies made it difficult to obtain accurate ring counts and precise calendar years for many samples. Some wOAR lacked clear tree-ring boundaries, and in highly suppressed individuals, consecutive years of growth sometimes produced tree rings that were only a single xylem cell wide, complicating age assessments. As such, several highly suppressed samples were excluded from age and growth analyses, but their exclusion may have been avoided with methods that tracked wOAR from the point of their initial establishment.

Despite challenges in obtaining precise tree-ring calendar year determinations and absolute seedling ages, the analyses selected for this study did not require such high resolution. If analyses had focused on the timing of seedling establishment relative to specific harvest events, the available data might not have provided sufficient resolution. However, because this study broadly addressed existing ages, stem origin establishment modes, and growth over a 25-year period, a margin of error of 1 to 2 rings had little influence on the results. Nevertheless, the limited precision in age determination clearly shaped which types of analyses could be meaningfully included in this study. Despite the inclusion of seedlings that possessed such a small margin of error, seedlings were excluded as their margin of error came became greater and confidence became lacking in tree-ring determination.

Another limitation of these methods is that only the most recent resprouting event could be recorded. Repeated monitoring would have provided an ability to identify whether multiple resprouting events had occurred, not just the most recent one. With the employed methods, only the latest resprouting event could be inferred from root and stem age comparisons, limiting insights into the frequency of top kill, resprouting cycles, and carbon allocation strategies. Carbon allocation strategies in oak seedlings are known to transition between roots and stems intra-annually as leaf flushing occurs, and whether allocations are stored in roots or stems differs under various overstory light intensities (Reich et al., 1980; Dickson, 1991; Dickson & Tomlinson, 1996; Lockhart et al., 2008). Despite current knowledge, less is understood about how root-to-stem carbon allocation strategies change with repeated resprouting, or varying root-to-stem age relationships.

The analyses of estimated wOAR seedling densities (seedlings/ha) of true seedling or resprout origin presented some limitation in detecting treatment-level differences. As described in the methods, sampling only three wOAR per plot resulted in all-or-none ratios of true seedling to resprouts, or vis versa. These ratios were then used to extrapolate estimated densities of each stem origin from plot-level white oak seedling inventories. Because many plots had all-or-none stem origin ratios, and some plots were extreme outliers in seedling density, the resulting extrapolations were often highly inflated or underestimated. By sampling a greater number of wOAR at the plot level, this may have been avoidable.

Of the 180 plots in this study, only 19 had estimated white oak seedling densities of 100 or more per hectare. Among these 19 plots, which accounted for 52.6% of the total estimated white oak seedlings/ha across all plots, eight had all-or-none ratios. Notably, of the plots with the top five estimated seedling densities, four had all-or-none ratios, representing 37.9% of the total estimated white oak seedlings/ha across all 180 plots. These statistics provide evidence for how a few influential plots disproportionately affected these results and limited the ability to detect true plot-level variability. To reduce the influence of these outliers, stand-level densities were analyzed instead, but this approach yielded only nine total observations. Due to the low number of observations, results from the stem origin density analyses should be considered exploratory, and interpretations made thoughtfully.

Because sampled wOAR were limited to a maximum height of 137 cm, only seedling-sized individuals were included. However, sapling-sized trees, which have a much higher probability of reaching overstory status, are typically considered OAR and are often included in OAR assessments (Larsen et al., 1997; Kabrick et al., 2014; Vickers et al., 2014). Therefore, the sampling process used here may have resulted in an overrepresentation of individual wOAR that had lost the race to overstory status, while potentially excluding many of the winners. While this height threshold enabled assessment of the seedling layer, it prevented evaluation of seedling recruitment success to the sapling size class across the wOAR population.

This maximum height sampling threshold provided some limitations in the growth analyses. Because GRVs were calculated only for wOAR under 137 cm, the observed range of GRV values may not fully represent the growth potential of the entire wOAR population. Although a maximum sampling height was necessary, including sapling-sized wOAR could have increased the variability observed in treatment-level GRV means. This effect may have been especially pronounced in treated (1H and 2H) stands, as seedling survival and recruitment success is more likely in the presence of canopy disturbances (Crow, 1992; Keasberry et al., 2016; Spetich, 2020). In summary, including sapling-sized wOAR in the analyses may have led to additional and significantly larger differences in pairwise treatment comparisons of GRVs.

A final limitation of this study relates more to the biological architecture of stem and root development during initial establishment. As described in the methods, several wOAR roots had fewer rings than their corresponding stems. Biologically, this is improbable, given that microsections were taken just above and below the root collar, following the methods of Dee et al. (2022). Interestingly, many wOAR showed high ring-width correlations (CCs > 0.80) despite unequal ring counts. For relatively young trees, such high correlations with unequal ring counts suggest that missing rings were likely at the beginning or end of the tree-ring chronology. In most cases, ring boundary placement was accurate for the most recent years of growth. This indicates that most age comparison discrepancies, where stems appeared to have more rings than roots, were due to rings near the pith of the root sections being either unobservable or absent. Indistinct or missing rings, especially near the pith of roots, can make accurate ring counting difficult, leading to an underestimation of root age compared to stems.

CHAPTER 6: MANAGEMENT RECOMMENDATIONS

6.1 Uneven-aged white oak management: ecological considerations and economic implications

The applicability of white oak UAM is limited to a narrow portion of the species' range, largely due to its slow growth relative to many competitors (Vickers et al., 2019). In areas farther east, on more productive sites such as the Appalachians or southern Indiana, canopy gaps created by the mortality or harvesting of single trees or small groups rarely permit successful recruitment of white oak. On these sites, such disturbances favor the regeneration and rapid growth of both shade-tolerant and intolerant oak competitors such as American beech, red maple, and yellow poplar (Jenkins & Parker, 1998). In contrast, on the less productive, drier sites of the Missouri Ozarks, shade-tolerant species generally lack the drought tolerance required to reach overstory status through gap-phase recruitment, despite physical site changes permitting their increased presence in recent decades (i.e., edaphic compensation and mesophication) (Iverson et al., 2008; Nowacki & Abrams, 2008; Warman & Moles, 2009).

Even so, although shade-tolerant species may not persist long enough to become canopy dominants, the species composition in smaller size classes on MOFEP indicates they are maintaining adequate presence in the seedling and sapling size classes to significantly impact oak regeneration and recruitment success. On MOFEP, the non-oak species group made up 90% or more of sapling species group proportions in seven of the nine stands within this study (Figure 20). White oak has historically achieved and maintained current canopy dominance in the Ozark Highlands, however inadequate disturbance regimes likely contribute to the species' decline in smaller size classes over the past century, especially on sites associated with ELT 18 where promoting oak regeneration is more challenging.

Findings from this study suggest that true seedling establishment declined in the 1H stands, which maintained STK above the Gingrich B-level for approximately 10 years prior to sampling (Figure 2). A similar pattern is observed in the 2H stands, where rates of new seedling establishment were statistically comparable to those in the 0H stands. This indicates that harvesting strategies alone may not sufficiently enhance establishment of new true seedlings. This may be especially so in the absence of understory disturbances, which can increase regeneration success by modifying seedbed conditions or reducing competitor abundance. This is illustrated by site photographs, which show dense leaf litter layers barring regeneration, and heavily shaded conditions promoting dense layers of shade-tolerant regeneration (Figure 24).

Sustaining white oak as a canopy-dominant species in uneven-aged systems will require continuous attention to regeneration and recruitment processes. Managers should prioritize harvesting practices that maintain adequate light levels for oak seedlings and saplings throughout the entire cutting cycle. The results of this study underscore the importance of relatively frequent, large-scale canopy disturbances in promoting ongoing white oak regeneration and recruitment in uneven-aged stands. This is evident in the growth data, where the 2H treatment, on a 15-year cutting cycle, produced the highest growth rates in stem height, stem diameter, and root diameter. Yet, even on this cycle, growth remained slow. This is reflected in the non-linear logarithmic relationships between stem height and stem age, which showed that average stem height reached only about 50 cm at stem ages of approximately 25 years (Figure 21). Given such slow growth rates, it is likely critical that white oak seedlings are consistently maintained over time.

Suitably sized canopy gaps created on site-specific cutting cycles that maintain relatively low STK will likely promote continued recruitment. However, achieving and maintaining these conditions in practice can be challenging due to variability with regeneration input, extreme weather events that cause unplanned mortality on variable spatial scales, or forest health implications. Additionally, harvesting alone on prescribed intervals, without intermediate disturbances that control competing species, such as fire, herbicide, or midstory thinning are unlikely to maintain desired species composition or oak recruitment rates necessary for sustainable management (Brose et al, 1999; Clark et al., 2007; Schweitzer et al., 2016). This may be especially so for ecosystems that are far detached from historic structures and compositions.

This study's results cannot confidently identify the most productive canopy gap sizes to incorporate, due to differences in gap structure between the 1996 and 2011 stand entries and among treatments within the 1996 entry. These differences likely influenced regeneration dynamics, and because observations were made at only a single point in time, meaningful comparisons are difficult. However, implementing small group selections, rather than strictly adhering to either end of the single-tree to group selection spectrum, may yield interesting results. The use of small group selections should be considered in practical management and included in future experimental comparisons with single-tree and group selection methods.

When managing white oak in the Ozarks using uneven-aged silviculture, a cutting cycle of 15 to 20 years is likely optimal for maintaining low residual STK, supporting continuous growth of advance reproduction, and promoting adequate growth among overstory trees (Loewenstein, 2005; Fan et al., 2015). Harvests on more frequent cycles may not allow enough time for merchantable volume to accumulate, reducing economic incentives for stand entry, even when high-value white oak stave logs are present. Furthermore, more frequent harvest cycles may not be necessary to support sustainable regeneration layers if they are cut to appropriate residual STK. In contrast, longer cutting cycles are likely to result in repeated canopy closure, which can suppress regeneration input and slow the growth of advance regeneration, both of which were observed in this study. Cutting cycles may also need to be adjusted based on site aspect, with shorter cycles being more appropriate for protected sites and longer cycles for exposed sites. Further research, including treatments on exposed aspects, would help clarify the extent that cutting cycles should be determined by site conditions.

A recommended cutting cycle of 15 to 20 years may help sustain oak regeneration within a time frame that promotes persistence. Results showed that only about 4% of seedlings survived beyond a stem age of 20 years without being forced to resprout, recruit (which was not observed), or die off. Yet, because white oak typically has mast years every 4 to 6 years, maintaining or increasing oak reproduction should be readily achievable, as individual seedlings often persist well beyond this interval (Johnson et al., 2019). Longer cutting cycles could increase seedling mortality, reduce recruitment, or both. Conversely, shorter cycles may not yield economically justified gains in growth or establishment if seedlings need many years to establish and respond to release events.

The appropriate cutting cycle within the recommended range will largely depend on site productivity and harvest intensity. Harvests that reduce STK below the Gingrich

B-level (~58%) will likely be necessary to maintain regeneration and recruitment. Thus, residual STK should be cut to below 50% to ensure it remains under the B-level throughout the cutting cycle. In the 0H treatment, where STK was maintained above the Gingrich B-level throughout the study, both stem and root growth were heavily suppressed. Significant differences in stem height were also observed between the 1H and 2H treatments. It would be interesting to see how much greater the differences in growth, establishment densities, and inventory densities for both the seedling and sapling layers would have been in the 2H treatment if residual STK in the first entry had been reduced to levels as low as those achieved in the second entry.

Maintaining STK below the Gingrich B-level should promote prolonged canopy openness, as crown closure occurs at the B-level. Understory disturbances may help keep STK below fully stocked conditions between cutting cycles, which is especially relevant for stands that do not reach the desired post-harvest STK. In these cases, understory disturbances may reduce STK more cost-effectively than additional harvesting.

Stands managed with UAM for longer periods may allow for higher residual STK if trees of greater quality and vigor are preferentially retained at each harvest. Adopting a "cut the worst and leave the best" approach increases the proportion of larger-diameter trees, so fewer trees account for a greater share of total STK while promoting wider spacing over time. This structure, with more widely spaced canopy-dominant trees, would permit greater light penetration, supporting the growth of advance regeneration at greater STK levels. While maintaining low STK values may be economically less desirable, it is likely critical for sustaining a healthy and vigorous regeneration pool. Including stands managed under UAM for longer periods, such as those at Pioneer

Forest, could help determine the extent to which older stands have developed structures with larger trees and thus differences in stand structure.

Regarding the demography of white oak seedlings on MOFEP, a substantial portion of the seedling population was established before the implementation of treatments. Despite their age, these older seedlings generally exhibited small aboveground stem sizes, both in height and diameter. However, their belowground root systems were often much older and significantly larger. This suggests that rather than progressing with a root carbon allocation strategy, these seedlings may be capable of responding with enhanced stem growth upon canopy release. It is important to recognize that MOFEP sites tend to accumulate these older seedlings in the understory, and that the seedling layer often consists of relatively old individuals despite their small size. This understanding is critical for informing appropriate management strategies on these sites.

The persistence strategy and long understory residence times of wOAR seedlings on these sites suggest that white oak is quite tolerant of management that does not perfectly support optimal growing conditions. In other words, there may be flexibility in harvest timing and intensity, allowing for a margin of error. Because of this persistence, stands that are not as rigorously or regularly managed can likely still have their structure or composition altered to promote more suitable growing conditions in the future. However, this may not hold true on more productive sites farther east, where understory residence times may be shorter and the growth of competing species is less constrained by site quality. This is an important economic consideration, given how intensive and costly UAM can be. In forests farther east, there may be less room for error in sustaining oak regeneration, increasing economic risks from with imperfect management.

Figure 24: Top: a research plot in stand 7-142 (2H) with a high density of non-oak saplings casting a dense shade that greatly restricted regeneration on the forest floor. Bottom: a research plot in stand 4-9 (1H) that has a heavily shaded understory with a high density of non-oak seedlings that dominated the seedling layer. *Photo credit: Abby Huffman.*

Yet even on xeric sites with harsh growing conditions, maintaining light levels favorable to oak growth between cutting cycles is likely essential for stimulating white oak recruitment. Incorporating selective, non-fire disturbances, such as midstory thinning or targeted herbicide applications to control competing species, may further enhance recruitment by reducing reliance on resprouting from prescribed fire or top-kill by suppression. Top-kill by suppression, likely the primary driver of resprouting on these sites, may not necessarily promote a root carbon allocation strategy if seedlings are photosynthesizing at rates barely sufficient for survival.

This targeted disturbance approach aligns with recommendations for managing competition and light to support oak regeneration (Miller et al., 2017; Dugger & Clatterbuck, 2024). This may be particularly relevant where fire is not feasible or where environmental and climatic conditions could result in fires of greater severity. While fire can promote oak regeneration by reducing competitor abundance and encouraging resprouting, supplementing it more targeted understory disturbances, like thinning or herbicide application, allows for a more selective control of undesirable species, while supporting the slow recruitment processes of seedlings that have already attained the competitive status needed for recruitment.

The slow growth measures observed in seedlings in this study, with stem heights of just 50 cm even at stem ages of 25 years or older, further highlight the benefit of targeted disturbances. Targeted disturbances may promote the observed slow recruitment processes without completely resetting stem growth in seedlings that otherwise may have been repeatedly top-killed by fire or prolonged suppression events. Notably, a significant portion of the population persisted as true seedlings. Although their growth was not compared to that of resprouted seedlings, managing competition dynamics around these stems might still accelerate canopy recruitment more effectively than relying solely on recurrent resprouting. Furthermore, non-oak-targeted disturbances may help extend cutting cycles by helping to maintain lower stand-level STK, potentially reducing the need for more frequent and costly harvests to control stand density.

Complete and continuous control of competitors through harvesting and intermediate disturbance can be challenging. Strict adherence to low intensity disturbance frequencies may disrupt recruitment processes or negatively impact desirable oak regeneration. Similarly, scheduled harvests at set intervals may not always be appropriate. Flexibility in skipping or extending a harvest cycle may be necessary, and in such cases, thinning or targeted herbicide practices aimed at rebalancing species composition and diameter distribution in smaller size classes may be needed. Therefore, monitoring regeneration and incorporating adaptive management is essential for successful white oak UAM. Fire and other disturbances should be applied flexibly and responsively, guided by ongoing monitoring of stand conditions and regeneration dynamics.

6.2 Conclusion

By applying QWA techniques, this research achieved high precision in age determination and provided new insights into the anatomical and demographic processes inherent in oak regeneration. This methodological framework is particularly valuable for future studies aiming to resolve fine-scale temporal dynamics in seedling establishment and growth. This approach further enhanced the ability to understand long-term oak regeneration processes and helps to incorporate more informed decision-making in sustaining oak-dominated ecosystems. Additionally, these methods can be utilized for a wide range of tree species, experimental frameworks, and ecological concepts.

This study's results advances our understanding of wOAR stem and root demography, establishment, and growth dynamics in uneven-aged white oak forests by comparing various UAM cutting cycles and intensities. Results showed that individual stem and root ages varied widely, and individuals displayed persistence to relatively old ages. However, treatment-level means were consistent, perhaps influenced by the recurrent resprouting typical of upland oaks. This longevity and persistence of white oak necessitate managers to adopt a long-term perspective. Despite relatively old ages achieved by seedling stems and roots at MOFEP, they often possessed small aboveground stems. However, because the sites at MOFEP are considered intrinsic accumulators of wOAR, as they persist through recurrent resprouting, it should not be assumed that such small seedlings do not possess the ability respond to canopy release.

Notably, 60% to 80% of wOAR had unequal stem and root ages even in fire's absence, indicating that factors beyond fire, such as overstory density through time and site heterogeneity, also influence resprouting dynamics. Despite these relatively high rates of resprouting, it should not be assumed that the controls of this resprouting dynamic are beneficial to the wOAR layer. If seedlings are resprouting due to top-kill from extended periods of prolonged suppression, sustainable advance reproduction populations may be more easily achieved if these resprouting rates were lower. In other words, promoting true seedlings for continued persistence may result in faster recruitment rates than by recurrent resprouting prompted by stem dieback due to suppression.

Concerning wOAR establishment, although not statistically analyzed, the 2H treatment supported the highest combined densities of true seedlings and resprouted seedlings. The 1H stands had the highest probability for wOAR to be of resprout origin, perhaps due to a lack of true seedling establishment from prolonged canopy closure after an initial release event from harvesting. The 0H and 2H sprouting probabilities were nearly identical, despite large differences in canopy disturbance and overstory density. However, even with similar sprouting probabilities, the 2H treatment showed larger estimated densities for the separate stem origins. Lastly, the 1H and 0H treatment resulted in a greater dominance of shade-tolerant, non-oak saplings, likely due to lacking canopy disturbances. These patterns underscore the importance of canopy disturbances of appropriate intensities and frequencies, as well as local site factors that promote advance regeneration capable of sustained canopy recruitment.

Growth responses of wOAR were most pronounced in the 2H treatment, where repeated harvesting sustained higher light levels and led to significantly greater stem height, stem diameter, and root diameter compared to the 0H and 1H treatments. However, these growth rates were quite slow, even at relatively old seedling stem and root ages (25 years). Even within the 2H treatment, wOAR was most likely outperformed by shade-tolerant, non-oak competitors that maintained dominance from the seedling to sapling layer. These results indicate that while increased canopy disturbance frequency can enhance oak growth, it alone may not be sufficient to ensure white oaks' competitive success without additional management to control competing species. Therefore, integrated management strategies combining appropriate harvesting practices with competitor control measures such as midstory thinning, prescribed fire, and targeted herbicide applications, may be necessary to sustain white oak dominance.

Intensive management of uneven-aged white oak stands in the Ozark Highlands presents significant operational and economic challenges, yet these investments are likely necessary for long-term sustainability. Growth analyses indicate that frequent harvest entries and lower STK are required to promote oak regeneration, even if they are occurring at rates that many may view as not conducive to long-term sustainability. Despite added costs and complexities, and the relatively long time frames that these regeneration dynamics occur on, the ecological and silvicultural benefits of sustaining uneven-aged white oak forests are substantial. Furthermore, the persistence shown by wOAR across treatments suggests that white oak is forgiving to imperfect management, reducing the risk of management failures due to problems associated with successional processes occurring in the understory.

Ultimately, intensive, adaptive management will be critical for successful white oak regeneration and recruitment. Management that incorporates site-specific cutting cycles, appropriate harvest intensities, adequate canopy gap sizing and spacing, and competitor control by fire and non-oak targeted disturbances are likely essential for maintaining uneven-aged stand structure. Even still, such intensive efforts are justified by the long-term productivity and ecological resilience of white oak dominated forest systems in the Ozark Highlands.

However, for UAM to be truly sustainable in these settings, greater attention must be given to the seedling and sapling layers. This includes promoting continuous growth of seedlings and saplings without resprouting from top-kill due to suppression, as well as improving establishment conditions to support ongoing regeneration. It may be necessary to temporarily pause harvesting and instead focus on restructuring and enhancing the seedling and sapling layers, as their condition will largely determine the long-term success of UAM for future cohorts. Given the slow growth of white oak, time and effort spent restructuring and recomposing the seedling layer are unlikely to cause long-term setbacks and instead will likely promote increased yields and growth rates. Undoubtedly, promoting appropriate canopy structure and light availability is critical, yet focusing solely on these factors without considering the dynamics of smaller size classes may undermine the sustainability of white oak UAM. Therefore, it is essential to closely monitor and manage growth and establishment processes on the forest floor, rather than concentrating exclusively on the canopy above.

Lastly, research forests like MOFEP provide unique opportunities to study the long-term effects of management on forest structure and composition. At MOFEP, detailed stand inventories, site descriptions, and harvest records help unravel the complexities of advance reproduction and the influence of various management practices. This study's findings contribute to a growing body of knowledge informing adaptive management strategies for white oak forests, while stressing the need for continued, long-term collaborative research. Ongoing monitoring and adaptive management are critical to balance ecological goals with long-term economic incentives. As white oak forest ecosystems face growing pressures from climate change and economic shifts, management strategies that encourage ongoing regeneration input and continuous recruitment will be critical for promoting white oaks' benefits of ecological integrity, economic incentives, social values, and the preservation of white oak's cultural legacy.

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