

The Pennsylvania State University

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**RECONSTRUCTION OF THE COMPETITIVE DYNAMICS OF MIXED OAK
FORESTS**

A Thesis in

Forest Resources

by

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Abstract

Oaks are some of the most ecologically and economically important tree species in the eastern United States. Regeneration of oak-dominated stands has been problematic in this region, where young stands are often dominated by competitors such as red maple, sweet birch and black cherry. In some cases, young oaks may be eliminated early in stand development by these faster growing competitors, resulting in new stands where oak is only a minor component. Other evidence suggests oaks are able to persist, and eventually emerge as canopy dominants over these competitors. The goal of this study was to determine how the height growth dynamics of oaks and non-oak competitors differed during early stand development. Six oak-mixed hardwood stands in the Appalachian Plateau and Ridge and Valley regions of Pennsylvania were selected for this study. Each stand was systematically sampled to locate dominant and subordinate oaks with at least two adjacent non-oaks (red maple, sweet birch, and black cherry) of equal crown class. In each stand, 20 such neighborhoods were randomly selected for the study. Each tree cluster was mapped, and stem cross-sections were collected and aged every meter from below the root collar to the top of each tree to determine height growth patterns. Most oaks were found to have root systems older than their above ground stems, suggesting that these trees were seedling or sapling sprouts. Dominant chestnut oaks in the Ridge and Valley were never more than 1 meter shorter than neighboring red maple and 0.5 meters shorter than neighboring sweet birch. Chestnut oaks in the Ridge and Valley that fell further behind became subordinate and are not likely to survive much longer. On the Appalachian Plateau, dominant northern red oaks were never more than 2 meters shorter than black cherry and red maple, and 1.5 meters shorter than sweet birch. No northern red oaks that were more than 1 meter shorter than sweet birch or red maple at age 20 became dominant by age 30. In general, oaks that were significantly behind at age 15 were likely to become subordinate by age 30, implying release treatments must occur early (age 10-15), before oaks become overtopped.

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Chapter 1

A review of the developmental dynamics of mixed oak forests in Pennsylvania

Oak (*Quercus* spp. L.) forests occupy approximately 2.4 million hectares in Pennsylvania and another 8 million hectares in the mid-Atlantic region (Moser et al. 2006). Oaks are long lived, economically valuable, and extremely important sources of mast and habitat for native fauna (Rodewald 2003, McShea et al. 2007). As a result, many silvicultural prescriptions in Pennsylvania are intended to regenerate oak dominated stands. Unfortunately, successful oak regeneration has proven difficult across central hardwoods region (Lorimer 1983, 1984, Gould et al 2006, Fei and Steiner 2007). Trends indicate that other species, such as red maple (*Acer rubrum* L.) and sweet birch (*Betula lenta* L.) are becoming more frequent components of ecosystems previously dominated by oaks (Lorimer 1984, Moser et al. 2006, Fei and Steiner 2007).

Oak species exhibit a characteristic growth pattern different from their tree competitors (Loftis 1990, Brose 2008). Young oaks focus more energy on root growth than height growth, and are often overtopped by competitors in the absence of disturbance (Larsen and Johnson 1998). This strategy is likely an adaptation to periodic fires, which may have perpetuated oak forests prior to effective fire suppression (Abrams and Nowacki 1992, Ruffner and Abrams 1998, Brose et al. 2001). Now, however, most mature oak stands in Pennsylvania are regenerated without the low intensity surface fires that may have once given oaks a competitive advantage by reducing the density of competitors. Instead, oaks must directly compete with faster growing competitors in the new stand. It is unclear if oaks are able to compete effectively in the absence of the

disturbance regime that may have favored their unique growth strategy. The following will review the historic distribution and ecology of oak forests in Pennsylvania and the uncertainty in predicting the development of regenerating stands.

Oak silvics

Oak species regenerate chiefly through sprouting or seeding (Larsen and Johnson 1998). The relative importance of each regeneration type varies with species, and more importantly, the local disturbance regime. Continuous seedling growth from an acorn to a successful tree has likely never played a large role in oak reproduction (Abrams 1992, Abrams and Nowaki 1992, Larsen and Johnson 1998). Because most oak species are at least moderately intolerant of shade, seedlings are unable to survive in the low light levels found in the understory of a densely stocked deciduous forest for more than a few years (Loftis 1990). However, because oak seedlings develop an extensive root system at the expense of early height growth, they are able to die back and sprout repeatedly in this shaded understory condition, provided light levels are greater than about 5% full sunlight (Larsen and Johnson 1998, Dey et al. 2007, Brose et al. 2008). Merz and Boyce (1956) found that of 100 oak seedlings collected in southern Ohio, only 26 could be reliably aged by counting the growth rings of above ground tissue. The remainder had root collar ages that were between 3 and 31 years older than the above ground seedling tissue, indicating that many of these seedlings had died-back and sprouted repeatedly from extensive root systems.

Thus the goal of many oak silvicultural systems is to accumulate an abundance of advanced oak seedlings over time (potentially a few decades) and then release them by

removing the overstory and providing adequate light for sustained height growth (Loftis 1990, 1992, Lorimer 1983, Brose et al. 2008). Although oak growth is often rapid after release, competing species, many of which also originate from sprouts (often stump sprouts, following a commercial harvest), commonly out-compete oaks, at least early in stand development (Lorimer 1983, Loftis 1992, Abrams 1998). In Pennsylvania and throughout the east, this phenomenon is most common on moist productive sites where competing species make more efficient use of higher water and nutrient levels (Gould et al. 2004, 2005).

The role of fire and Native Americans

It has been suggested that the oak growth strategy outlined above is linked to the periodic occurrence of understory fires in pre-settlement oak forests (Abrams 1992, Brose et al. 2001). Work from southern Ohio stands indicates fire return intervals between 9 and 11 years for the period between 1870 and 1935 (Hutchinson et al. 2008). Similarly, Shumway et al. (2001) examined fire scars on oak cross-sections in an old growth oak stand in western Maryland. The authors found a 7.6 year fire return interval between 1616 and 1959. Continuous oak recruitment was also evident during this period. After the cessation of periodic fires, red maple and birch recruitment showed a marked increase, leading to the supposition that perhaps their thin-barked seedlings with smaller root systems were selectively killed by frequent surface fires prior to fire suppression.

Although Shumway et al. (2001) did not attempt to elucidate the cause of these fires, additional studies have proposed that Native American activity resulted in frequent forest fires. Black et al. (2006) examined witness tree distribution in the Allegheny

National Forest region of northwestern Pennsylvania. A correlation was found between proximity to Native American villages and tree species. Oaks, hickories (*Carya* spp. Nutt.), and American chestnuts (*Castanea dentata* (Marsh.) Borkh.) composed more than 34% of the witness trees within areas of high Native American influence (mainly along the Allegheny River), while these species comprised only 1.4% of the witness trees in the Allegheny Mountains east of the river; an area with much lower Native American influence. Whether Native Americans perpetuated oaks or Native Americans chose to live where oaks were already present remains unclear.

Whitney and Decant (2003), in a study of witness tree distribution west of the Allegheny River in northwestern Pennsylvania, also proposed that periodic Native American burning maintained white oak (*Quercus alba* L.) as the dominant species on the glaciated sections of their study area. Interestingly, these authors suggest that fires were more common on level ridge tops than moist river valleys, partially explaining the distribution of white oak on ridges, and beech–maple (*Fagus*–*Acer*) forests in river valleys in their study area. This is in contrast to the findings of Black et al. (2006) and Black and Abrams (2001) who proposed that oaks were most common along river valleys, where Native American populations were higher.

Although many studies have claimed that Native American burning occurred, and subsequently encouraged the development of oak forests, little or no evidence has been shown to support this beyond historical accounts of fire coupled with what is known about the seedling ecology of oaks (Abrams 1992, Abrams and Nowaki 1992, Abrams et al. 1995, Abrams 1998, Abrams 2003). Though compelling due to the frequency of such accounts in early writings, most evidence that Native Americans used fire to manage

forests is anecdotal, sometimes substantiated by fire scar and soil charcoal findings (Day 1953, Delcourt 1987). Further, a considerable number of historical accounts indicate that very open, park-like oak forests were the result of these fires (see Tome 1854, Day 1953). The relative importance of lightning fires is unclear, but they also probably contributed to some areas burned.

Some evidence suggests that Native Americans may have numbered in the tens of millions at the time of first contact in the 16th century (Denevan 1992). Historical records indicate that much of the eastern United States was heavily populated and, as a result, may have been highly managed. But, as Native Americans met the first explorers, diseases were exchanged that would result in as much as a 95% reduction in the Native American population within a few decades (Delcourt 1987). In some cases, 150-200 years would have passed before European settlers entered the de-populated interior and, by the time land the survey data were collected, 300-350 years may have passed (Denevan 1992). Thus the evidence upon which some of these hypotheses are based is questionable for areas that may have at one time been heavily impacted by native populations. It is possible that the forest composition and structure encountered by early settlers and surveyors was that of a recovering forest that had been managed, and possibly cleared for a thousand years prior to the 16th century.

Though the depopulation hypothesis is intriguing and thought to be especially applicable to the southeastern United States, it may be less valid for northern Pennsylvania. Records of Native American villages and trails have shown large areas of the Appalachian Plateau as largely uninhabited because of poor soil and difficult terrain (Wallace 1981). These factors did not change with the arrival of Europeans, so it is

reasonable to assume that many areas in Pennsylvania did not change drastically between the 15th and 18th centuries.

Abiotic controls and small scale spatial heterogeneity

In addition to supporting the fire hypothesis, Whitney and DeCant (2003) suggest that soil and climatic controls were also important in determining the distribution of pre-settlement oak forests. They discovered that white oak, the most common witness tree in the entire study area, was far more common in the southern, un-glaciated section (35.5% of witness trees), than in the glaciated northern section (15.8%). Also, the combined frequency of beech (*Fagus grandifolia* Ehrh.) and sugar maple (*Acer saccharum* Marsh.) in the un-glaciated section was 2.1%, whereas it was 26.4% in the glaciated section. Other oak species and American chestnut also were moderately more common in the un-glaciated southern section. In addition, both oak and hickory species were significantly more abundant on southern aspects throughout the study area. It is unclear whether that trend was equally as evident in both un-glaciated and glaciated sections. Soil factors were also shown to be correlated to tree species distribution. Fine glacial till, often high in calcium, was highly associated with sugar maple and basswood (*Tilia americana* L.), both of which are known to require rich calcium soils. Oaks, on the other hand, were more commonly associated with nutrient-poor residuum, formed in sandstone and shale parent material.

These data are consistent with Jennings (1927) and Lutz (1930a), who proposed that in Pennsylvania the northern boundary of the oak range runs roughly along the southern extent of the last glacial maximum. In a study of the pre-settlement vegetation

distribution of Indiana (Lindsay et al. 1965), also found that beech-maple forests were largely confined to areas that had been glaciated by the Illinois ice sheet, whereas oak-hickory forests were dominant south of the glacial maximum. Also, the authors found significant correlations between soil series and dominant forest type. Beech-maple forests were chiefly found on fine-textured silt loams, and silty clay loams. Oak-hickory forests were similarly present (though not dominant) on silt loams, but they also occupied a wide range of coarse textured soils, such as sandy loams, gravelly loams and fine sand. Beech-maple forests did not occur on these soil types. The authors suggest that in areas where drainage class and soils were conducive to both species, small scale aspect differences likely played a large role in determining the vegetation type.

Hough and Forbes (1943), in an extensive study of the historic vegetation of the Appalachian High Plateau of northwestern Pennsylvania, also propose that small scale aspect differences in addition to climatic and soil factors play a large role in defining the boundaries between forest types. They suggest that shallow-rooted northern hardwoods and associated species (eastern hemlock (*Tsuga canadensis* L.) , birch, beech) are limited in their southern range by warmer temperatures that exacerbate the effects of severe droughts. In addition, they contend that the northward expansion of oaks on the Plateau is limited by severe cold and growing season frosts. Interestingly, they note that oaks do occur on the Plateau, but are limited largely to south facing slopes and river valleys. In a survey of several of the remaining old-growth areas on the Appalachian Plateau, they also found oaks were a common associate of white pine (*Pinus strobus* L.). They observed (by counting stumps of pre-settlement origin pines) that white pine occurred mostly in groves several hectares in size, and always on south or west facing slopes. They suggested

that these groves of pine (and subsequently oak) originated almost exclusively following severe fire or windthrow. Of all the oaks present in the 120 acre Heart's Content old growth area (one of their study areas), 40% regenerated around 1644, which was a severe drought and fire year across northern Pennsylvania (Lutz 1930b).

The preceding studies have indicated that, at least according to witness tree records, historical accounts, and surveys of virgin stands, oak was never a large component of Appalachian Plateau forests in northern Pennsylvania outside of areas inhabited by Native Americans. Many studies allude to an area south of the Plateau that was historically oak dominated. Somewhat clearer evidence exists supporting oak dominance in western Pennsylvania as well as the Ridge and Valley Province of central and southern Pennsylvania.

Oak dominance in southern and western Pennsylvania

In his extensive study of the vegetation of central and western Pennsylvania, Jennings (1927) refers to large regions of southwestern Pennsylvania as being an area of "white oak hills." The proposition that white oak was a dominant species seems odd to modern foresters and ecologists because white oak is rarely a dominant species in contemporary oak forests (Abrams 2003). However, witness tree evidence suggests that white oak accounted for more than 35% of witness trees in unglaciated portions of Venango and Mercer Counties in western Pennsylvania, as well as the majority of witness trees in southwestern Pennsylvania, eastern Ohio and northern West Virginia (Whitney and DeCant 2003, Rentch and Hicks 2005). The importance value of white oak in this region was nearly twice as high as the next most common species, which was commonly

black oak (*Quercus velutina* Lam.) or hickories (Rentch and Hicks 2005).

Dendroecological studies in old growth mixed oak forest in southwestern Pennsylvania also found that white oak was historically dominant, followed by black oak (Abrams and Downs 1990). Abrams (2003) points to physiologic traits that allowed white oak to prosper in pre-settlement forests. First, it is somewhat more shade tolerant than other oak species, such as northern red oak (*Quercus rubra* L.) or chestnut oak (*Quercus prinus* L.). Also, white oak is more resistant to fire and drought and is able to persist over a wider range of soil and moisture conditions. Also, other oak species were more likely associated with catastrophic fires or windthrow events that cause large light gaps whereas white oak was able to regenerate in the understory, assuming the canopy was sufficiently thinned as a result of periodic low intensity fires. And finally, white oak can live much longer than other oak species (more than 400 years), allowing it to persist in stands after other oaks have died.

Interestingly, Ellsworth and McComb (2003) suggest that massive flocks of passenger pigeons may have contributed to white oak dominance by selectively consuming acorns of other species. Passenger pigeons fed most heavily in the spring, by which time fall germinating white oak acorns would not provide a useful food source. Other oak species do not germinate until the spring, which would have made them a more favorable meal for passenger pigeons that numbered in the hundreds of millions.

Evidence points to dominance by several oak species in the Ridge and Valley of central Pennsylvania. Studies of witness tree data and a remnant old growth stand in southern Pennsylvania found that chestnut oak, white oak and black oak were the most common witness trees, with chestnut oak dominating the most xeric ridge tops, and white

and black oak being most common in valley floors (Mikan et al. 1994). Additional work on witness tree distribution and remnant old growth stands also suggest white oak dominance of valley floors in the Ridge and Valley Province of central Pennsylvania (Jennings 1927, Abrams and Nowaki 1992, Abrams et al. 1995, Abrams 2003).

Southern Pennsylvania oak stands likely persisted most commonly through periodic low intensity fire. Native American habitation and influence were much higher in the fertile river valleys of central and western Pennsylvania than on the rugged Allegheny Plateau (Wallace 1981, Black and Abrams 2001). Therefore it is reasonable to assume that the warmer, drier climate coupled with more Native American activity resulted in more frequent fires. These stands were probably dominated by white oaks and regenerated in an uneven-aged fashion. Today, oak stands on similar (though drier) sites in the Ozark highlands are maintained by partial cutting and low stocking densities ($<14 \text{ m}^2 \text{ ha}^{-1}$) such that there is enough light to allow regeneration of oak saplings and recruitment into the overstory (Larsen et al. 1997, Loewenstein et al. 2000). Frequent low intensity fires, though usually not fatal to overstory trees, do result in some mortality, and could have perpetuated a similar condition of low stocking coupled with more available light. Advanced oak reproduction was probably abundant and competitive and could have entered the canopy via windthrow gaps.

White oak, though certainly common, was not ubiquitous throughout this region. Like the northern Appalachian Plateau, vegetation distribution was related to topographic and edaphic factors. Moist water gaps were probably inhabited by hemlocks and pines. Extremely xeric sites probably grew chestnut oaks and chestnuts. Frost pockets and areas where fires were uncommon may have harbored isolated patches of northern hardwoods.

According to all the previously mentioned studies, northern red oaks were found very rarely (Ruffner and Abrams 1998).

Contemporary Oak Forests

The vast forests that covered Pennsylvania at the time of European arrival were nearly gone by 1930 (Whitney 1990). The first and lightest wave of timber harvesting began in the late eighteenth century with the extraction of large white pines along waterways for the purpose of producing British and American ship masts (Whitney 1990). Low levels of harvesting continued until the introduction of the logging locomotive in the 1880s. Locomotives, in conjunction with new band saw mills and heightening demand for tannic acid from eastern hemlocks led to “the highest degree of forest utilization the world has ever seen in any commercial lumbering area” (Marquis 1975). Between 1880 and 1930, towns in northern Pennsylvania boomed and busted with timber harvesting rates and for a time, Williamsport, PA was the wealthiest city in the nation. When the timber supply finally ran out, the bare land covering much of Pennsylvania was severely eroded and burned by repeated fires (Dana 1918). The result of these repeated disturbances was the development of oak forests in areas of northern Pennsylvania that previously were dominated by pine, hemlock, or northern hardwoods. Oak’s previously mentioned adaptations to fire, along with the open light conditions allowed the genus to become dominant during the early twentieth century. The century-old oak forests that currently cover the state are the result of this era (Marquis 1975, Abrams and Nowacki 1992). Recent FIA data indicate that although oaks continue to be dominant in older classes, oak forests are inadequately stocked with oak regeneration, especially in the larger sapling size classes. Seedlings and saplings of competing species

such as ash (*Fraxinus* spp. L.), maple, birch and black cherry (*Prunus serotina* Ehrh.) far outnumber oaks (Woodall et al. 2008). Though the reasons for this shift in understory composition are not completely clear, a few key environmental changes have occurred that may be the cause. First, the deer herd in Pennsylvania and across the oak range has been too large for decades and has resulted in over-browsing of certain species, including oak (Waller and Alverson 1997). Also, the absence of fire has favored the reproduction of thin-barked, shade tolerant species and resulted in dense mid- and understory shade, which precludes successful oak seedling growth (Abrams 1992). There is even some evidence that northern red oak regeneration may be hindered by soil acidification and nitrogen saturation; the combined effects of acid deposition (Decker and Boerner 1997).

Because much of Pennsylvania's forest land today is 80-120 years old, many forest stands will be harvested in the coming decades. Many recent harvests on productive sites appear to have subsequently become dominated by mesic site species instead of oak (Gould et al 2006). Although the likelihood of failure is greatest on rich sites, where species such as red maple, tulip poplar (*Liriodendron tulipifera* L.), black cherry and birch regularly out-compete oak in the first several years of stand development, competition from sweet birch and red maple are also problematic on nutrient poor, dry sites (Della-Bianca 1983, Lofits 1990, Gould et al. 2004). Even-aged harvests of second-growth stands were uncommon more than 30 years ago, and therefore it is unclear how these third-growth stands will develop, and which species will be dominant by crown closure. Many regenerated stands lack an oak component altogether (Gould et al. 2005), so these will certainly develop into stands dominated by other species. But in stands where oaks are present but currently overtopped, there is some

evidence that the growth of competing species may slow, allowing oaks to overtop them (Oliver 1977, 1980). This hypothesis, suggesting that oaks will eventually emerge above their competitors to form a dominant layer, has not been tested in Pennsylvania. If true, however, many stands in which oak regeneration is in a subordinate position may yet develop a strong oak component without management intervention.

Even-aged mixed species stratification

The phenomenon of mixed species stratification has been well documented in early ecological literature (see Smith 1973) and subsequently quantified in a variety of forest types. During the first few years of development, height differences among individuals in mixed species stands are the result of microsite differences, stochastic environmental conditions and growth rate variations among species (Oliver and Larsen 1996). However, as stands age, differences in height among species groups become apparent, and are increasingly the result of differential growth characteristics. Several outcomes are possible. First, the fast growing species can maintain its rapid growth rate for an extended period, such that other slower species are relegated to lower strata. These suppressed species may persist in the shade and await overstory senescence or perish, depending on their shade tolerance. Second, it is also possible for the initially fast-growing species to slow, due to a short life span or intraspecific competition. In some cases, the once-overtopped species may emerge and maintain dominance (Oliver and Larson 1996).

Studies of the development of a variety of species mixtures have supported the general hypotheses offered above (Palik and Pregitzer, Norland and Hix 1996, Liptizin and Ashton 1999, Lockhart et al. 2006). It is also clear, however, that these patterns are

variable and the same mixtures of species behave differently in different regions and even on different sites. Further, mixed stands, in which the competing species' growth rates and shade tolerances are similar, may not stratify as readily. This was shown to be the case in a northern hardwood stand consisting primarily of sugar maple and beech (Guldin and Lorimer 1985). Both species exhibit similar shade tolerance and relative growth rates following release, allowing both species to occupy dominant canopy positions several decades after harvest. Researchers in the Lower Mississippi Alluvial Valley advise against afforestation with oak monocultures for a similar reason (Lockhart et al. 2006). They found that when only oaks are present, intraspecific competition is fierce and few trees emerge as dominants. Instead, it is suggested to plant a mixture of oaks and other species, such as sweetgum (*Liquidambar styraciflua* L.). Although sweetgum grows much faster than oak initially, cherrybark oak can emerge above sweetgum by age 21 (Lockhart et al. 2006). As long as the oaks receive some overhead sunlight (i.e., not overtopped) they are able, possibly through crown abrasion, to maintain growing space long enough for the sweetgum growth to slow. Once the oaks are taller, their large, spreading crowns easily emerge above the narrower sweetgum crowns. Similarly, in Kentucky it was found that 11 years after clearcutting, initially overtopped oaks and hickory saplings were beginning to catch up to taller red maple saplings, as the growth of red maple slowed (Arthur et al. 1997).

The most applicable stand development and stratification studies for Pennsylvania have been conducted in New England and the southern Appalachians. In a hemlock-hardwood stand in central New England, Oliver (1977, 1980) found that northern red oaks typically overtopped sweet birches and red maples after several years of stand

development, even though the initial growth rates of the latter two species appeared to be faster than that of northern red oak. Other work done in the Harvard forest points to early dominance by pioneers such as grey birch (*Betula populifolia* Marsh.) and pin cherry (*Prunus pensylvanica* L.f.), which slow in growth or die, allowing red oak to form a dominant upper canopy by age 30 to 40 (Hibbs 1983). Further work from New England has shown similar stand trajectories of early maple and birch dominance followed by red oak ascension to the upper canopy, especially on dry, nutrient poor soils (Liptzin and Ashton 1999). Ward and Stephens (1999) tagged and tracked tree seedlings in Connecticut for 12 years following a clearcut. On average, 40% of oaks that were dominant at age 12 were less than a foot tall immediately post harvest, and were likely overtopped by their neighbors, indicating some ability to upgrade dominance class.

There is also evidence that supports an alternative hypothesis in which oaks remain overtopped and are out-competed, especially on moist, productive sites in the absence of fire. A review of the regeneration problem in the southern Appalachians similarly concluded that on many mesic sites there may be ample advanced oak regeneration, but it is simply out-grown by other species (Cook et al. 1998). In southern Appalachian coves, it is clear that yellow-poplar and black locust (*Robinia pseudoacacia* L.) can permanently overtop northern red oak (Della-Bianca 1983). Work in Michigan found that northern red oak was easily overtopped by aspen (*Populus* spp.L.) and some red maples (Palik and Pregitzer 1993). These results were largely attributed to the rapid growth of aspens and maples compared to seedling and slower vegetative growth of oaks. Other researchers suggest that even if sufficient stocking of advanced oak regeneration is accumulated before harvest, competing tree species will likely need to be controlled for

successful oak establishment (Loftis 1992). Work from Wisconsin has shown that oaks are typically poorly represented in stands developing after clearcuts, especially on mesic sites (Hix and Lorimer 1991). Suppressed oaks are less likely to respond to release than suppressed red maples or birches, indicating that advanced maple and birch regeneration is at an advantage immediately after overstory removal (Kobe et al. 1995, Casperson and Kobe 2001). Furthermore, studies have indicated that once oaks fall behind into lower strata, they are less likely to ever advance into a higher crown class (Ward and Stephens 1994, Dey et al. 2007, Drobyshch et al. 2007, Ward 2008).

Clearly, there are gaps in our understanding of oak stand dynamics. There is some uncertainty about how well oaks compete with other species early in stand development. It is especially unclear how this varies by region or site. A variety of methods have been employed to address these uncertainties, from long-term monitoring of permanent plots to retrospective stem analysis. Permanent plot studies are especially valuable since they have the potential to capture very early dynamics and mortality, evidence of which is usually unavailable to the retrospective investigator. Unfortunately, the establishment and continued monitoring of stand development plots is difficult and expensive, and therefore rare (Bakker et al. 1996). Retrospective stem analysis studies are slightly more common, but often attempt only to tell the ecological tale of a single stand instead of determining a pattern of development for a larger region.

The development of mixed oak forests in Pennsylvania and the mid-Atlantic region has received little attention. Due to differences in climate, soils and competing species, applying conclusions drawn in New England or the southern Appalachians may be unwise. Understanding these developmental dynamics is especially critical

considering many hectares of oak forests in this region are reaching maturity and are slated for regeneration harvests in the near future. Data are needed that can provide managers with region-specific information regarding the competitiveness of young oaks. If it is found that overtopped oaks rarely emerge as dominants, foresters must act quickly following overstory removal to ensure that young oaks survive the fierce post-harvest competition phase.

Chapter 2

Reconstruction of the competitive dynamics of mixed oak stands

Introduction

Understanding early stand development is crucial for the successful application of any silvicultural system. The presence of abundant desirable regeneration does not guarantee that a mature stand will be fully stocked with desirable species after a harvest, especially where competing tree species are present (Loftis 1990). Particularly unclear is the development of even-aged mixed-species stands. Immediately following an overstory removal, dozens of potential overstory tree species can be present as seedlings, stump sprouts or seedling sprouts. To further complicate the prediction of developmental trajectories, similar species mixtures can develop into very different mature stands depending on region or site type (Hix and Lorimer 1991).

Throughout the central Appalachian region, millions of hectares of mature forests are dominated by oaks (*Quercus* spp. L.), which are notoriously difficult to successfully regenerate (Lorimer 1983, 1984, Abrams 2003, Cook et al. 1998, Gould et al 2006, Fei and Steiner 2007). In Pennsylvania, there are ten recognized plant community types in which oaks play a dominant role, covering roughly 2.4 million hectares throughout the state (Fike 1999, Moser et al. 2006). These communities represent a diverse range of site types from dry oak-heath to bottomland oak palustrine forests, and are vital ecological and economic resources (Fike 1999, Rodewald 2003, McShea et al. 2007). Trends indicate that other species, such as red maple (*Acer rubrum* L.) and sweet birch (*Betula*

lenta L.) are becoming more frequent components of forests previously dominated by oaks, potentially resulting in the replacement of oaks in future stands (Lorimer 1984, Moser et al. 2006, Fei and Steiner 2007, 2009).

The establishment of advanced regeneration prior to harvest has been shown to be a crucial step toward successful oak regeneration (Larsen and Johnson 1998). However, how successfully young oaks compete after overstory removal is quite uncertain. Oaks exhibit a characteristic growth pattern different from their tree competitors (Lofits 1990, Brose et al. 2001). Young oaks focus more energy on root growth than height growth, and are often overtopped by competitors in the absence of a top-killing disturbance (Larsen and Johnson 1998). Following disturbance, oaks are able to sprout from their extensive root system more readily than their competitors. This strategy could be an adaptation to periodic surface fires, which may have perpetuated oak forests prior to effective fire suppression (Abrams and Nowacki 1992, Ruffner and Abrams 1998, Brose et al. 2001). Now, however, most mature oak stands in Pennsylvania are regenerated without the low intensity ground fires that may have once given established oak seedlings a competitive advantage. Instead, oaks must directly compete with faster growing competitors in the new stand. Abundant competitive regeneration may be of little value if necessary disturbances never occur to ensure that oak seedling have a competitive advantage in recruitment. Although it is well known that oak seedlings typically have root systems older than their above-ground tissue (Merz and Boyce 1956), few studies have examined how large this age difference is in successful oaks later in stand development.

Thousands of hectares of previously oak-dominated forests have been harvested in Pennsylvania over the last 15 years (PA Department of Conservation and Natural Resources). Many of these stands have not regenerated with a strong oak component (Gould et al. 2005). As these stands begin to transition into the stem exclusion stage, the few oaks that are present are often overtopped by fast growing species such as red maple, sweet birch and black cherry (*Prunus serotina* Ehrh.) (Gould et al. 2004, Fei et al. 2005). Because few stands in Pennsylvania were harvested (and monitored) more than 30 years ago, it is still unclear how oaks will fare as the canopy closes and interspecific competition begins.

A number of studies completed in the eastern United States have found that oaks fail to successfully compete in the absence of disturbances, particularly on mesic, productive sites (Beck and Hooper 1986, Elliot et al. 1997, Stanturf et al. 1997, Brashears et al. 2004). As long as prescribed fire remains politically and operationally problematic in the Northeast, mechanical and chemical intervention may be necessary to ensure oak survival in young stands. Even these treatments, though, are fraught with problems. Thinning young hardwood stands, whether mechanically or chemically, is time consuming, expensive, and provides no immediate financial return (Miller 1984). Furthermore, the efficacy of very early crop tree release treatments (less than 10 years old) is questionable (Trimble 1974).

Interestingly, other studies have revealed a different developmental pattern; one that implies that early release treatments may not be necessary for oak survival. In a hemlock-hardwood stand in central New England, Oliver (1975) found that northern red oaks (*Quercus rubra* L.) typically overtopped sweet birches and red maples after the first

10 years of stand development, even though the initial growth rates of the latter two species appeared to be faster than that of northern red oak. Other stand development studies from New England have found a similar pattern of oak stratification over red maple and birch by the second or third decade of stand development (Hibbs 1983, Liptzin and Ashton 1999).

Though the previously mentioned studies have addressed these very issues in other parts of the Appalachians, the competitive environment in Pennsylvania can be quite different. Many of the studies finding that oaks are permanently overtopped have been conducted on fairly productive cove sites in the southern Appalachians where fast-growing tulip poplar (*Liriodendron tulipifera* L.) is often the dominant competitor (Della-Bianca 1983, Beck and Hooper 1986). On the other hand, many of the studies finding that oaks can be successful long-term competitors were completed in New England, and often involved oaks of both seed and stump-sprout origin (Oliver 1977, Ward and Stephens 1999). Although the common competitors in New England are more similar to Pennsylvania than those of the southern Appalachians due to differences in climate, soils and competing species, applying conclusions drawn in New England or the southern Appalachians may be unwise.

Furthermore, many studies have attempted to elucidate stand development patterns by measuring changes in species abundance, dominance, height, or importance values across sites using either chrono-sequences of stands, or by repeatedly measuring permanent plots (Della-Bianca 1983, Beck and Hooper 1986, Liptzin and Ashton 1999). These studies provide excellent evidence of overall trends in species dominance, but often do not provide sufficient information about the performance of individual trees.

Other studies, using stem analysis techniques that were also employed in the present study, have been able to further clarify the results found in the stand-based studies by providing the height growth trajectories of individual trees in a developing stand (Oliver 1977, Palik and Pregitzer 1993, Tift and Fajvan 1999). In most cases the mean heights at given ages were averaged across sites or regions for a certain species and compared to the mean heights of other species at the same age. Although this method can detect very distinct differences in species height growth trajectories, height variation within a given species across a stand may dampen the detected height differences between species. Furthermore, it is possible that very few of the individuals of one species included in a study were never spatially near any individuals of the other species, potentially confounding height comparisons with species microsites. For example, a species may only occur on certain microsites in a stand, and therefore comparing the average height of one species to the average height of another species that may commonly occur on another microsite may be misleading. Thus, true species-related height growth pattern differences may be masked by microsite differences.

Filling these knowledge gaps is especially critical considering many hectares of oak forests in this region are or will soon be a century old and may be harvested in the near future. Data are needed that can provide managers with regionally specific information regarding the competitiveness of young oaks. If it is found that overtopped oaks rarely emerge as dominants, foresters must intervene at an early age.

The goal of this study was to determine if and how the difference in height between oaks and their nearby competitors changed over time in two heavily forested regions of Pennsylvania. More specifically, our objectives were to determine (1) What

proportion of oaks were true seedlings versus seedling or sapling sprouts, (2) how height growth trajectories differed between oaks and common oak competitors following even-aged harvests, (3) whether the height differences between oaks and their neighbors varied by the species of the neighbor, (4) whether dominant oaks were ever shorter than their neighbors, and if so, at which age they equaled or surpassed their neighbors, (5) at what age subordinate oaks began to fall behind, and (6) whether regional mean height differences through time based on neighborhoods were different from those based on stand-level estimate..

Methods

Study Area

Six stands were selected from two physiographic provinces in central and northern Pennsylvania, in which two distinctly different oak forest types are present (Figure 1). Three stands were located in the Ridge and Valley physiographic province of central Pennsylvania. In these stands, chestnut oaks competing with red maple and sweet birch were sampled. Three stands are located on the Appalachian Plateau physiographic province of northern Pennsylvania. In these stands, northern red oaks competing with sweet birch, red maple and black cherry were sampled. Botanical nomenclature follows the USDA Plants Database (www.plants.usda.gov).

Contemporary oak communities in Pennsylvania are diverse; ranging from dry, acid ridges, dominated by chestnut oak (*Quercus prinus* L.) and ericaceous shrubs to rich northern red oak, basswood (*Tilia americana* L.), sugar maple (*Acer saccharum* Marsh.) types, (Abrams et al. 1998a, Fike 1999). This gradient of site occupation by oaks in

Pennsylvania is best exemplified by the two oak species mentioned above; chestnut oak and northern red oak.

Chestnut oak ranges throughout the Appalachians, and within Pennsylvania it is found most abundantly south of the Appalachian Plateau, dominating the ridges in the Ridge and Valley province. Chestnut oak is typically found on dry, nutrient-poor ridge tops and south or southwest facing slopes, growing in abundance on shallow, rocky, sandy and droughty soil (McQuilken 1990). The range of northern red oak extends across Pennsylvania, north into southern Canada and south into the southern Appalachians (Sander 1990). Northern red oak is found most commonly on northeastern aspects or well drained valleys on moist soil. Though common on moist sites across the state, northern red oak is particularly abundant on the Appalachian Plateau of northern Pennsylvania.

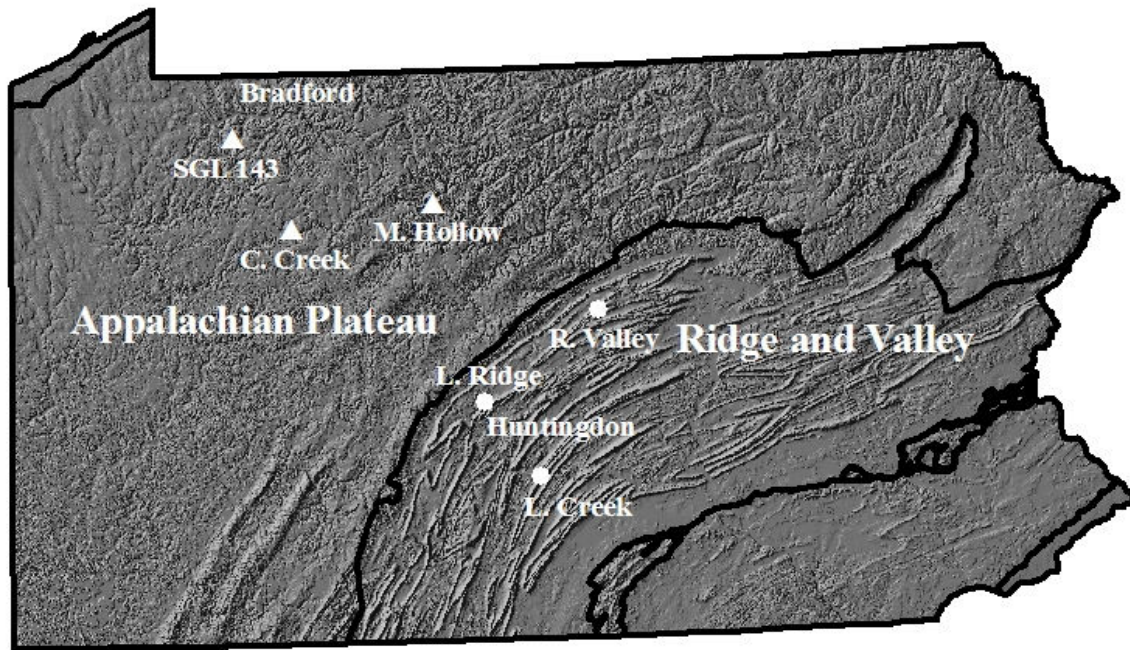


Figure 1. Map of Stand Locations. Three stands were located in the Ridge and Valley Province (●) and three on the Appalachian Plateau (▲).

The three Ridge and Valley stands are located approximately 2 km south of Mackeyville, PA (Rag Valley, in Bald Eagle State Forest), 12 km north of Huntingdon, PA (Leading Ridge, in Rothrock State Forest), and 9.4 km east of Mount Union, PA (Licking Creek, Tuscarora State Forest). The topography in this region is typified by long, narrow ridges and valleys that run northeast to southwest. The ridges are very steep, rocky, infertile and usually forested. The valleys have largely been converted to agriculture or development. The study stands are located on nearly level to slightly south-facing ridges underlain by sandstone and shale on gentle slopes (Merkel 1978, Shultz 1999). Soils are typically stony to very stony, well drained and weathered from

sandstone and shale (Merkel 1978) (Table 1). Mean annual temperature for Huntingdon, PA is 17°C, and mean annual precipitation is 96.5 cm (Merkel 1978) (Table 1).

Table 1. Stand Descriptions

Site Name	Region	Elevation (m)	Lat. Long.	Soil Series	Aspect	Northern Red Oak Site Index	Year Harvested	Number of Complete Plots Used
Licking Creek	Ridge and Valley	410	40° 24' 14" N 77° 44' 17" W	Laidig extremely stony loam	level-NW	69	1969	18
Leading Ridge	Ridge and Valley	350	40° 38' 36" N 78° 00' 20" W	Hazleton-Dekalb	level-SE	74	1976	19
Rag Valley	Ridge and Valley	470	41° 02' 24" N 77° 26' 13" W	Hazleton channery sandy loam	SE	74	1972	16
Clear Creek	Plateau	550	41° 20' 43" N 79° 01' 57" W	Cookport very stony loam	level	75	1972	17
May Hollow	Plateau	490	41° 26' 37" N 78° 11' 55" W	Harleton channery silt loam	level-S	75	1974	20
State Gamelands 143	Plateau	550	41° 50' 13" N 79° 24' 27" W	Hanover silt loam	level	81	1984	20

The current tree species composition includes northern red, black (*Quercus velutina* Lam.), white (*Quercus alba* L.), chestnut and scarlet oak (*Quercus coccinea* Münchh.), sweet birch, red maple, black gum (*Nyssa sylvatica* Marsh.), white pine (*Pinus strobus* L.) and striped maple (*Acer pensylvanicum* L.).

The three Appalachian Plateau stands are located in Clear Creek State Forest, Elk State Forest and State Game Lands Number 143, 19 km north of Brookville, PA (Clear

Creek), 7.7 km south of Emporium, PA (May Hollow), and just west of Pittsfield, PA (SGL 143), respectively. The Appalachian Plateau is an area of elevated topography north and west of the Ridge and Valley Province that has been deeply dissected by stream action, forming a landscape of flat-topped ridges and steep, V-shaped stream valleys, fertile hollows and rolling hills (Shultz 1999). Since most of the area has never been cultivated, soil mapping is often limited in specificity to an association. Soils are formed in sandstone, siltstone and shale residuum or colluvium (Kopas 1993) (Table 1). Mean annual temperature for Bradford, PA is 6.2° C, and mean annual precipitation is 108 cm (Kopas 1993).

Historically, the Appalachian Plateau was dominated by American beech (*Fagus grandifolia* L.), sugar maple, white pine and eastern hemlock (*Tsuga canadensis* L.) (Whitney 1990). Beginning in the mid 1800s and ending in 1915, northern Pennsylvania was repeatedly logged, first for hemlock and pine lumber and later for chemical wood (Marquis 1975, Taber 1975). Currently, these stands are comprised of northern red oak, red maple, sweet birch, black cherry, white ash (*Fraxinus americana* L.), and yellow-poplar.

During the late 1960s and early 1970s the Pennsylvania Bureau of Forestry and Game Commission clear-cut these stands for various reasons. Available details for each stand differ, but some useful stand history information is as follows: Licking Creek was harvested around 1969 and was previously dominated by low quality chestnut oak, with some red maple and sweet birch present. The reason for the clearcut is unknown, though at that time there was some interest in creating even-aged openings for wildlife. Leading Ridge was lightly harvested through a “select cut” in 1958. The extent of this harvest is

unknown, but most likely very light, since the stand appeared to have regenerated in an even-aged fashion following the harvest around 1976. Clear Creek was damaged by a tornado in 1968 and was salvage clear-cut around 1972, again indicating four years of reduced stocking prior to harvest. May Hollow may have suffered oak leaf roller (*Archips semiferanus* (Walker)) damage prior to overstory removal. No stand history information exists for Rag Valley Road or State Gamelands 143. All stands selected for this study were between 24 and 39 years old at the time of sampling. None of the stands had received any silvicultural treatments since the overstory removal.

Selection and Sampling Procedures

Each stand was systematically surveyed to locate suitable chestnut oaks (CO) or northern red oaks (NRO), depending on region, for sampling. Sampling criteria were oaks judged to be of seed origin (straight, single stemmed, no scars or knots near the base) and directly competing (crown touching) with two non-oaks (sweet birch, red maple or black cherry) of equal crown class. Oaks were tagged, numbered, and their location was recorded. From this list, ten neighborhoods centered on dominant and ten neighborhoods centered on subordinate oaks were randomly selected for sampling in each stand (i.e. 20, neighborhoods per stand). The term “dominant” hereafter refers to both dominant and co-dominant trees and “subordinate” refers to both intermediate and suppressed trees. In the Ridge and Valley, dominant chestnut oaks competing with two dominant competitors (either two sweet birches, two red maples or one competitor of each species) were sampled. On the Appalachian Plateau, dominant northern red oaks competing with two dominant competitors (either two sweet birches, two red maples, or

one red maple and one sweet birch, one red maple and one black cherry, or one sweet birch and one black cherry; no neighborhoods contained two black cherries).

Subordinate plots consisted of the same potential species combination in each region, but the oak and one competitor were subordinate.

Table 2. The number of oak-neighbor comparisons by region, oak crown class and neighboring species.

Region	Neighborhood Type	Red Maple	Sweet Birch	Black Cherry
Appalachian Plateau	Dom. Oak	14	25	13
	Sub. Oak	21	17	14
Ridge and Valley	Dom. Oak	33	27	0
	Sub. Oak	24	18	0

The stems of the oak and its two neighboring non-oak competitors were marked at 0 cm (as close to soil surface as possible, typically 3-5 cm above groundline), 30 cm, 60 cm, 1.4 m (breast height), and 2 m with a marking crayon. The three trees were then felled with a notch cut between the 60 cm and 1.4 m marks. Once on the ground, the stems of each tree were marked every meter (starting at 2 m) to the top of the tree. Cross-sections (approx 2-4 cm thick) were cut at each of the marked points (0 cm, 30 cm, 60 cm, 1.4 m, 2 m, 3 m etc.), starting at the base and cutting toward the top. As one worker cut discs, the second worker followed and labeled the discs with the forest district ID, the neighborhood ID number, the species of each tree, and the height value of the sample was taken. For example: 08-73-RM-9 is district 8, NRO neighborhood 73, competitor is a red maple, sample taken at a height of 9 meters. Discs were cut along the primary stem until the diameter was less than 3 cm, at which point the top was cut, limbed, and

transported to the lab for complete dissection to avoid losing small discs in the field. Each top was labeled with the same set of information, including height of the base of the top section in meters. Each tree was cut and processed individually before the next tree was felled, to facilitate safe cutting conditions. Cross-sectional discs and tops were collected, carried in backpacks to a vehicle, and transported to the lab for sanding and processing.

During the preliminary analysis it was noted that some oaks grew more than a meter during the first post-harvest year while having basal ages that were equivalent to or one year younger than the harvest year. Because one-year-old oak seedlings typically focus energy on root growth, rather than height growth we suspected that some of these oaks were seedling sprouts or sprouts from small diameter trees (Merz and Boyce 1956, Clark and Watt 1971). It is well known that advanced oak seedlings have the ability to frequently die back and sprout in the understory of closed canopy forest, resulting in root systems that can be much older than the above-ground stem (Merz and Boyce 1956). It is also known that oak sprouts (both from seedlings and larger stumps) grow more rapidly than true seedlings (Brose 2007, Del Tredici 2001).

We hypothesized that many of the oaks in our study were seedling sprouts. To determine what proportion of the trees in the study were seedling sprouts, we attempted to relocate all oak stumps to ascertain their root system age. Because some stumps could not be relocated, were rotten, or could not be accurately aged, a subset (22 chestnut oaks and 33 northern red oaks) of the oak stumps were excavated and cut off just below the root collar (typically 5-10 cm below ground level). Many of the stumps had already begun sprouting since our first cut, so the stump-cut was made below the level of the

lowest sprouts. Ages of these cross sections were compared to the age of the basal cross-section cut from the same tree, which was cut as close the soil surface as possible.

Sample Processing

Cross sections were temporarily stored in burlap sacks to facilitate drying. As soon as possible, cross sections were arranged on wire racks to finish air drying. Samples were sanded with progressively finer sandpaper to #400 grit to prepare a surface suitable for ring detection. A 6 X 48- inch belt sander was used for all samples. Some samples required additional hand sanding with finishing film down to 9 microns. A stereo dissecting microscope was used to count the number of true rings on all samples. Rings were tallied from the bark inward on two transects at 90 degree angles. If irregularities occurred such as false or missing rings, additional transects were counted and averaged (Stokes and Smiley 1968). Some samples were stained with water or oil to facilitate ring counting.

Data Analysis

The approximate harvest age was subtracted from the age of the root system to determine whether each oak was present prior to the harvest, and if so, how old they were at the time of the harvest. To ascertain whether the oaks in this study were undamaged seedlings or seedling sprouts, their mean growth rate (cm/yr) was calculated for the first five years of stand development. Because undamaged advanced seedlings in open light

conditions typically grow between 17-27 cm/yr (Brose and Van Lear 1998), growth rates drastically higher will be taken to indicate sprout origin (Objective 1).

Heights of oaks and competing species were averaged across stands and plotted to provide a visual indication of the average height growth trajectories for each species by crown class (Objective 2). Two example neighborhoods (one with a dominant oak and one with a subordinate oak) from each stand were plotted and are included in Appendix A. Because the number and crown class of each competing species was not controlled in the sampling of individual oaks, the number of competitors varied by site. Species-crown class combinations that occurred fewer than five times in a given site were not plotted.

Because each stand was potentially harvested in a different season, examining tree heights becomes problematic. In addition, the precise harvest year for most sites could not be determined. Typically the Pennsylvania Bureau of Forestry and the Pennsylvania Game Commission (the managers of all the sites) have logging contracts that last 1 to 3 years. Each stand could have been cut all in one year or over the course of the contract. For these reasons, neighborhood-level height differences between oaks and their nearest non-oak competitors were normalized as follows: the height of the non-oak neighbor at ages 0, 5, 10, 15, 20, 25, and 30 was subtracted from the height of the central oak in each neighborhood at each respective age. These neighborhood-level height differences were then averaged across the three stands in each region for a grand average of the height differences between each oak (by crown class) and each competing species at the 5 year age intervals listed above. Comparing these height difference values is more useful than comparing straight height values, as it permits combining the three sites in each region for regional means. These height differences were tested for significance using a mixed

model repeated measures analysis (Littell et al. 2006) in SAS Version 9.1 to determine whether or not (1) the differences were greater or less than zero and (2) the differences were different between species and crown classes.

To determine whether height differences varied among competing species, separate models were evaluated for each competing species (Objective 3). To determine whether dominant oaks were ever shorter than their dominant neighbors and, if so, when the oaks surpassed their neighbors, the height difference between dominant oaks and dominant neighbors was tested at 5-year intervals from age 0 to age 30 (Objective 4). Height difference values significantly greater than zero indicated that oaks were taller on average, whereas values significantly less than zero indicated that oaks were shorter on average at that age. To determine at which age subordinate oaks began to fall behind their neighbors, the height differences between subordinate oaks and their dominant neighbors were tested at 5-year intervals from age 0 to age 30 (Objective 5).

By treating each neighborhood as an individual experimental unit we normalized height differences in each neighborhood by subtracting the height of each crown-touching competitor from the oak height at equivalent ages in a neighborhood. This way we controlled for differences in microsite and were able to compute stand-level and regional mean height differences for different species that were in close spatial proximity and therefore were actually competing with one another. To determine whether or not and to what extent this more intensive neighborhood method provides a clearer picture of height differences through time than the more common method of averaging tree heights first and then taking the height difference between species, we also calculated region-

based parameters by simply subtracting the mean height of all individuals of a given competing species from the mean height of all oaks at the same age (Objective 6).

The number of rings on the root collar cross-section was subtracted from the number of rings on the basal cross-section to determine age differences between the below ground and above ground tissue. A paired t-test was performed to determine whether the average age difference was equal to zero, and whether the average age difference was the same for dominant oaks and subordinate oaks.

Results

Root system ages and early growth rates

Oaks in both regions were commonly found to have root systems older than their above ground stems. Of the 65 stumps sampled, 88% were older than their above ground tissue. In the Ridge and Valley, chestnut oak root systems were found to be 0-60 years older than their above ground tissue. The mean difference of 4 years ($SE = 3$) was significantly different from 0 ($P = 0.003$). Two stumps with root systems 45 and 60 years older than their above ground stems were considered outliers and were not used to calculate average values. The root systems of northern red oaks on the Appalachian Plateau were also found to be significantly older than their above ground tissue by an average of 3 years ($SE = 0.5$, $P < 0.001$). Age differences ranged from 0 to 14 years.

The difference in age between above and below ground tissue was not different for different oak crown classes. The average difference for dominant oaks in the Ridge and Valley was 4 years, whereas the average difference for subordinate oaks was 2 years (difference of 2 years, $SE = 2$, $P = 0.46$). On the Appalachian Plateau the average age

difference for dominant oaks was 2 years, whereas the average difference for subordinate oaks was 3 years (difference of 1 year, $SE = 1$, $P = 0.42$).

Although precise harvest dates are unavailable, these data suggest that most oaks were not more than 5 years old at the time of harvest (FigureX). Oaks in May Hollow that appear to have germinated 4 to 6 years post harvest are an obvious anomaly. It is likely that the harvest date for that stand provided by the Bureau of Forestry was several years older than the actual harvest date. Bureau of Forestry contracts typically extend 2 to 3 years, but must have extended longer in the case of May Hollow, as it is highly unlikely that oak germinants had 5-year growth rate averages greater than 10 cm/yr. In fact, as Figure Y shows, only one chestnut oak had a 5 year growth rate low enough (<10cm/yr) to be a new germinant (Phares 1971, Crow 1992). Only 10% of the oaks had 5-year growths between 10 and 30 cm/yr, a growth rate common for undamaged advanced regeneration (Brose and Van Lear 1998). Finally, 89% had five year growth rates in excess of 30 cm/yr, with some as high as 94 cm/yr, indicating that these oaks were advanced regeneration that was probably damaged during the harvest and sprouted (Sander 1971, Brose and Van Lear 1998)

Figure 2. Root system ages of a sub-sample of oaks aged below the soil surface in relation to harvest year.

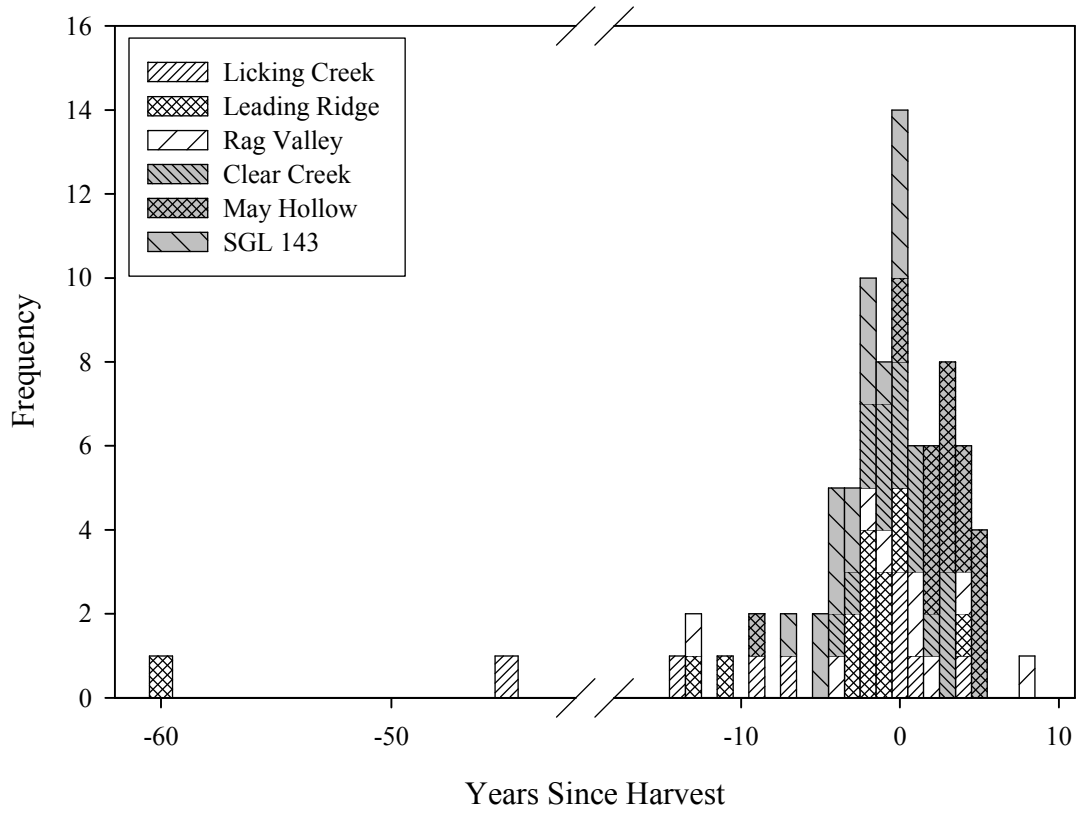
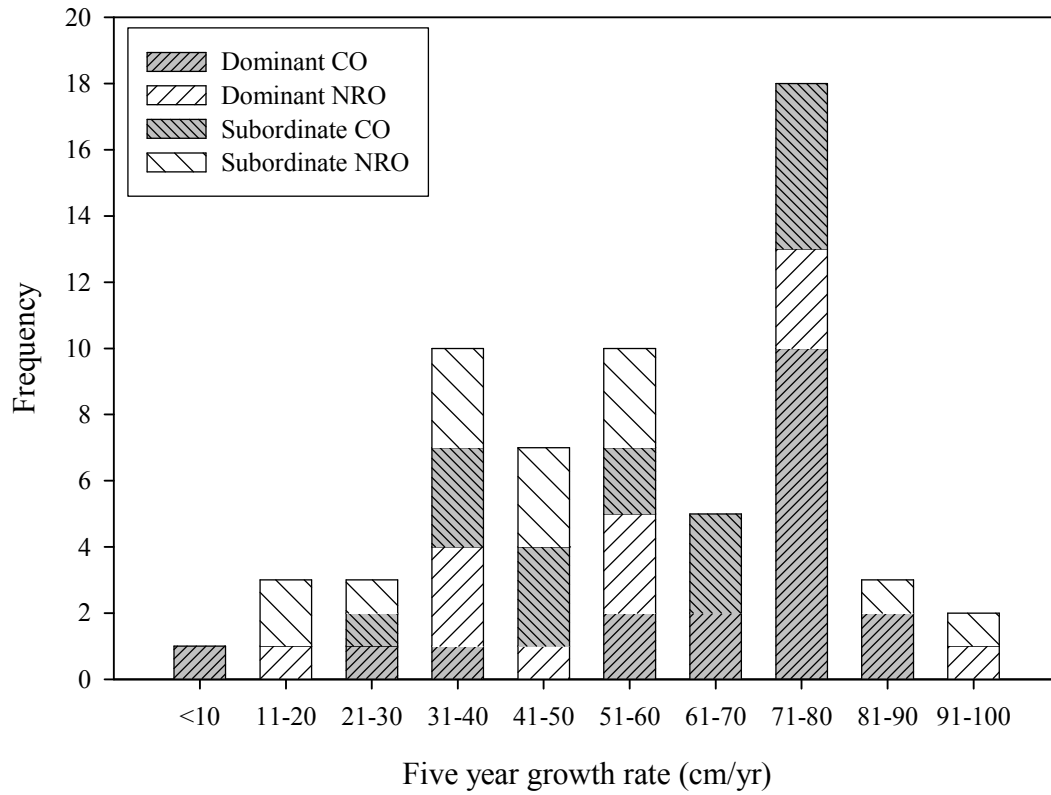


Figure 3. Average growth rates (cm/yr) for the first 5 years for oaks in both regions. New germinants typically grow less than 10 cm/yr (Phares 1971, Crow 1992).



Height Growth

At approximately thirty-years post-harvest, dominant chestnut oaks in the Ridge and Valley ranged from 14 to 21 m tall, while northern red oaks on the Plateau were between 15 and 19 m tall (Table 2). Subordinate chestnut oaks in the Ridge and Valley ranged from 8 to 19 m tall, while subordinate northern red oaks on the Plateau were between 10 and 18 m tall.(Table 2).

Early in the study it was noted that oaks classed as subordinate by the standard basis of not receiving light from any side, were not always shorter than nearby dominant oaks. Although dominant oaks were taller than subordinate oaks in all stands at age 30 (age 23 in SGL 143), the difference was statistically significant only in two stands (based on t-test, Table 2). In contrast, diameter at breast height (dbh) was significantly different between subordinate and dominant oaks in five of the six stands.

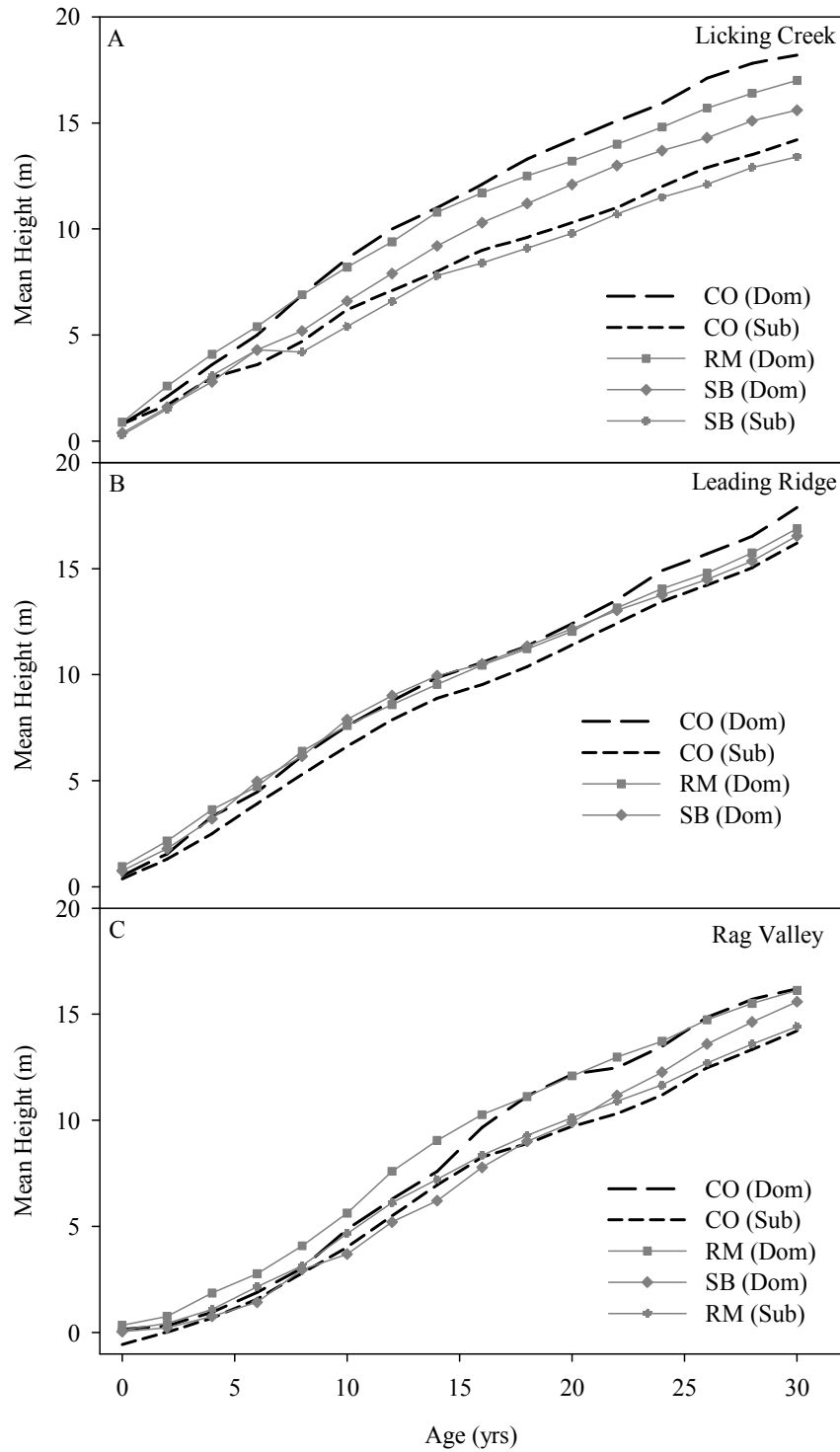
Table 2. Mean diameter and height of dominant and subordinate oaks in both provinces at approximately 30-years post-harvest (23-years for SGL 143). An asterisk indicates a statistically significant difference ($P < 0.05$) between dominant and subordinate oaks (based on t-test). Dbh = diameter at breast height; SE = standard error.

Site Name	Region	Mean dbh (cm) of dominant oaks (SE)	Mean dbh (cm) of subordinate oaks (SE)	Difference in mean dbh (cm) between dominant and subordinate oaks	Mean height (m) of dominant oaks (SE)	Mean height (m) of subordinate oaks (SE)	Difference in mean height (m) between dominant and subordinate oaks
Licking Creek	Ridge and Valley	28.14 (1.87)	18.25 (1.43)	9.89*	18.75 (0.18)	14.19 (1.07)	4.56*
Leading Ridge	Ridge and Valley	13.58 (.54)	11.44 (0.97)	2.14	17.33 (0.88)	16.37 (.60)	0.96
Rag Valley	Ridge and Valley	18.83 (0.38)	11.33 (1.50)	7.5*	16.19 (0.51)	14.21 (1.34)	1.98
Clear Creek	Plateau	19.83 (2.22)	10.86 (1.30)	8.98*	17.81 (0.54)	13.98 (.91)	3.82*
May Hollow	Plateau	18.43 (1.56)	11.07 (1.43)	7.36*	15.76 (0.20)	13.97 (1.18)	1.79
SGL 143	Plateau	12.2 (0.76)	9.8 (0.98)	2.4*	16.5 (0.50)	15.43 (0.95)	1.07

Height growth trajectories – Ridge and Valley

Mean heights of chestnut oaks and their competitors were plotted at two-year intervals to assess overall height growth patterns in each stand. The growth patterns of chestnut oak, red maple and sweet birch were similar in the three Ridge and Valley stands (Figure 2). In all three stands, dominant chestnut oaks had stratified over dominant red maples and dominant sweet birches by age 30. The magnitude and timing of stratification varied slightly by species. In all three stands, the average height of dominant chestnut oaks was

Figure 3. Mean heights of chestnut oaks and competing species by stand in the Ridge and Valley Province.



less than the average height of at least one of the competing species during the first several years of stand development.

The average height growth pattern of dominant chestnut oaks in the Ridge and Valley was most similar to that of red maple (Figure 2). Dominant chestnut oaks were shorter than dominant red maples until age 10 at Licking Creek, age 15 at Leading Ridge, and age 20 at Rag Valley. From age 20 to age 30, dominant chestnut oaks were taller than dominant red maple at Licking Creek and Leading Ridge and similar in height to dominant red maples at Rag Valley. Dominant chestnut oaks were taller than dominant sweet birches in all years (0-30) at Licking Creek and Rag Valley, whereas at Leading Ridge, dominant sweet birches were nearly equal in height to dominant chestnut oaks until age 15-20, when dominant chestnut oaks became taller.

Dominant red maples were taller than dominant sweet birches at Licking Creek and Rag Valley from age 0 to age 30, but similar in height to dominant sweet birches at Leading Ridge throughout the study period. At Leading Ridge, dominant sweet birches were slightly taller than dominant red maples between age 10 and 15, but were slightly shorter between age 25 and 30.

At all ages and in all stands in the Ridge and Valley, the average height of subordinate chestnut oaks was shorter than the average height of dominant chestnut oaks (Figure 2). At Licking Creek and Rag Valley the height difference between subordinate chestnut oaks and dominant chestnut oaks was more than 2 meters by age 20, whereas the difference was just over one meter at Leading Ridge. Subordinate chestnut oaks were also never taller than dominant red maples. However, subordinate chestnut oaks were similar in height to dominant sweet birches at Licking Creek until age 5, and Rag Valley

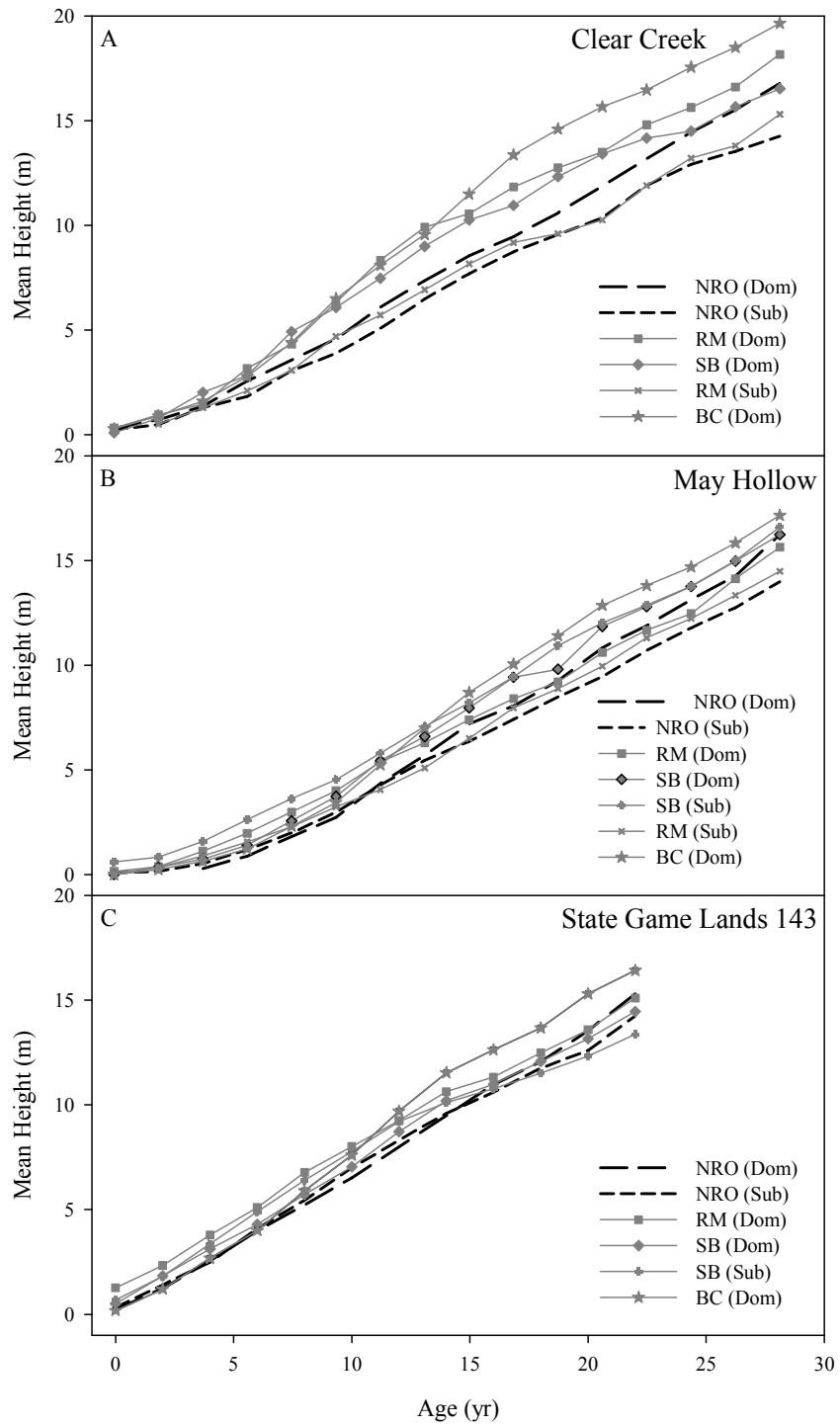
until age 10. At Leading Ridge, subordinate chestnut oaks were shorter than all three dominant species throughout the study period.

Although subordinate competing species were not specifically examined in this study, some interesting results were noted. At Licking Creek, the average height of subordinate sweet birches was slightly greater than or equal to the average height of dominant sweet birches until age 5. Just after age 5, the average height of future subordinate sweet birches fell behind future dominants and remained so until age 30. At Rag Valley, subordinate red maples were taller than future dominant oaks and sweet birches at age 5, fell behind oaks by age 10, but remained taller than dominant sweet birches until age 20.

Height growth trajectories – Appalachian Plateau

Height growth patterns of northern red oak, black cherry, red maple, and sweet birch were more variable on the Appalachian Plateau (Figure 3). Black cherry had the tallest average height in all the Appalachian Plateau stands by age 30. In all three stands, future dominant black cherries were shorter than future dominant red maples and sweet birches until age 15, after which black cherry remained the tallest species. Dominant black cherries were not shorter than dominant northern red oaks in any of the stands at any time during the study period. Interestingly, dominant black cherries were shorter than subordinate sweet birches for the first decade of stand development at both May Hollow and SGL 143.

Figure 4. Mean heights of northern red oaks and competing species by stand on the Appalachian Plateau.



Dominant northern red oaks in all three Appalachian Plateau stands were shorter than the other dominant species during most of the study period. At Clear Creek, dominant northern red oaks were shorter than dominant black cherries, red maples and sweet birches from age 0 to 25, at which point the oaks had become equal in height to dominant birches, but were still shorter than dominant maples and cherries. Dominant northern red oaks at May Hollow were shorter than all other species and crown classes, including subordinate northern red oaks, between ages 5 and 10. By age 20 to 30, dominant northern red oaks had become taller than subordinate northern red oaks and red maples, equaled the height of dominant sweet birches, but remained shorter than subordinate sweet birches and dominant black cherries and red maples. Similarly, at SGL 143, dominant northern red oaks were shorter than all other species and crown classes at age 10, but had become taller than subordinate oaks by age 15. Between age 15 and 20, dominant northern red oaks had become taller than dominant and subordinate sweet birches, and were equal in height to dominant red maples.

Although black cherry was the tallest species in all three Appalachian Plateau stands at age 30, the second tallest species varied between sites as the relative height growth of sweet birch and red maple differed in each stand. By age 30, dominant red maples were clearly taller than dominant sweet birches at Clear Creek and SGL 143, but shorter than both dominant and subordinate sweet birches at May Hollow.

Unlike the Ridge and Valley stands, in which subordinate chestnut oaks often fell behind early and remained overtopped, subordinate northern red oaks on the Appalachian Plateau were often similar in height to their dominant counterparts for the first several years of stand development. At May Hollow and SGL 143, subordinate northern red

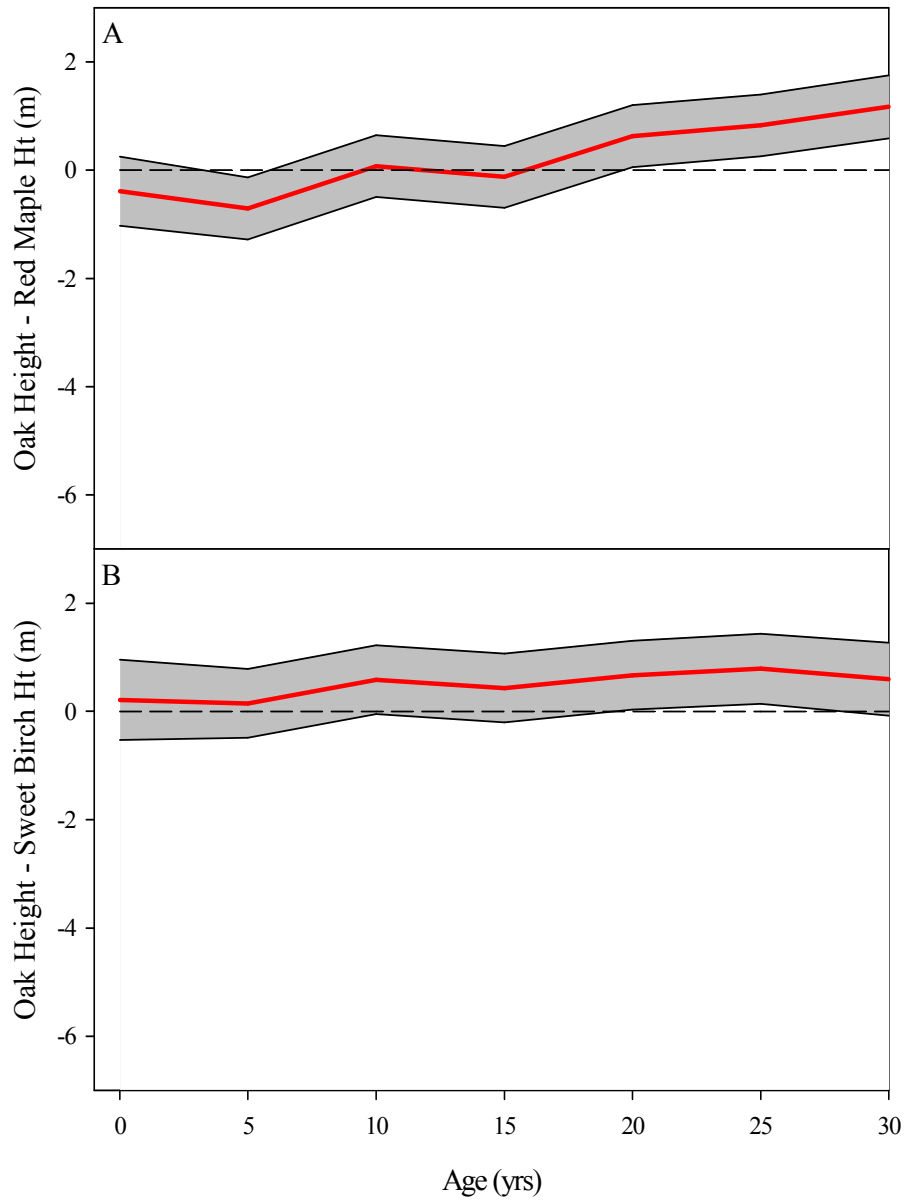
oaks were equal in height or taller than dominant northern red oaks until ages 10 and 15, respectively. However, at Clear Creek by age 5, subordinate northern red oaks were shorter than dominant northern red oaks. Because both the dominant and subordinate northern red oaks were usually the shortest species/crown classes in all three Appalachian Plateau stands, subordinate northern red oaks were typically shorter than all dominant competitors throughout the study period.

At both May Hollow and SGL 143, sufficient numbers of subordinate sweet birches was sampled to detect an interesting growth pattern in each stand. At May Hollow, subordinate sweet birches were the tallest trees on average until nearly age 15 (even taller than dominant black cherry). By age 30 they were shorter than dominant black cherries and approximately equal in height to dominant sweet birches. Similarly at SGL 143, subordinate sweet birches were second only to dominant red maples from age 0 to 10, after which they also fell behind dominant black cherries. Subordinate sweet birches remained taller than both northern red oak crown classes until after age 15. By age thirty subordinate sweet birches were shorter than all other species/crown class combinations.

Height differences through time – dominant chestnut oaks in the Ridge and Valley

Neighborhood-level height differences between oaks and their competitors were not significantly different among stands (ANOVA, $P > 0.05$), so stands were grouped for regional means (Figure 4). Dominant chestnut oaks were not significantly shorter than their sweet birch neighbors at any time during the first thirty years of stand development. Dominant chestnut oaks were slightly shorter than their red maple

Figure 5. Height differences between dominant chestnut oaks and dominant red maples (A) and sweet birches (B) in the Ridge and Valley Province. Dark bands above and below the mean line indicate 95% confidence intervals. Dashed lines indicate a height difference of 0 m.



neighbors initially, but were taller by age 10. Subordinate chestnut oaks fell behind both competitors early and were significantly behind sweet birch by age 10 and red maple by age 20.

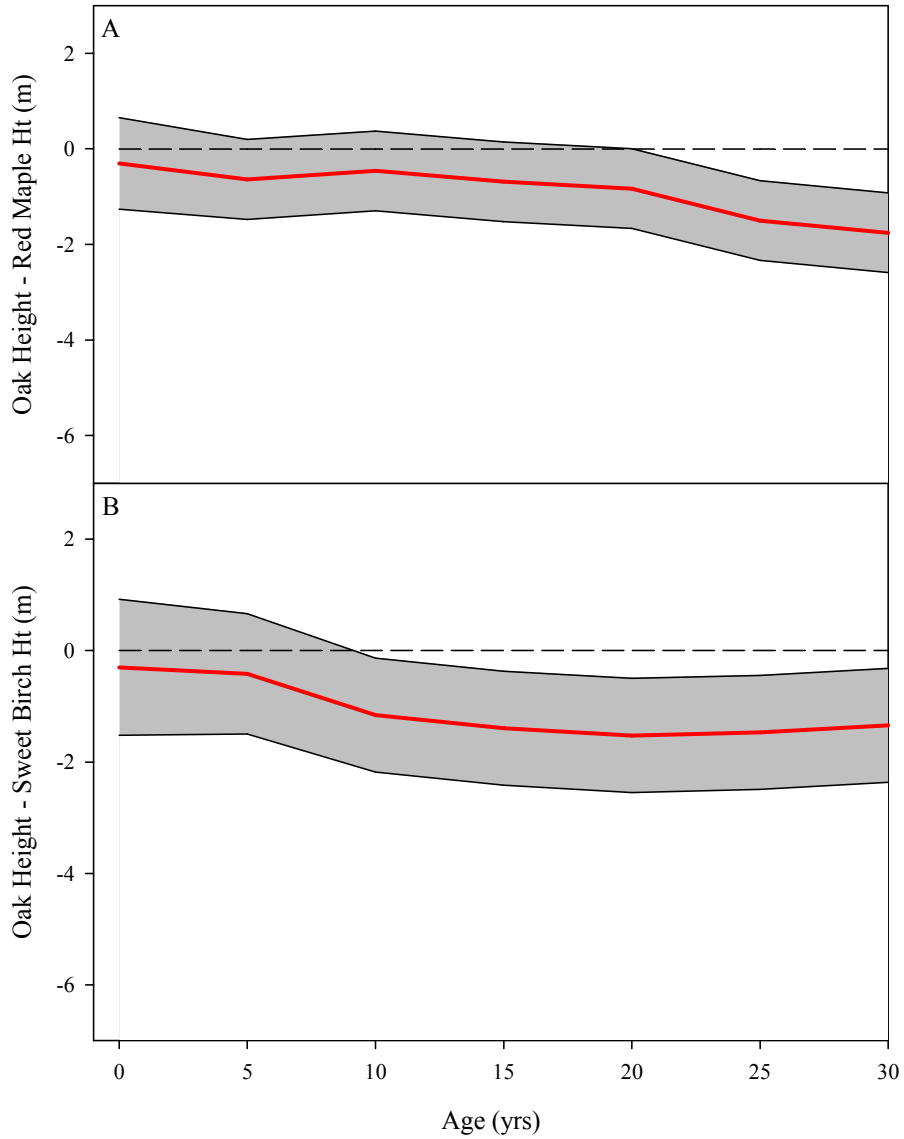
Dominant chestnut oaks were significantly shorter than their red maple neighbors at age 5 (by -0.71 m, $SE = 0.29$, $P = 0.015$), not different in height at ages 10 and 15, and significantly taller beginning at age 20 (by 0.63 m, $SE = 0.29$, $P = 0.032$). By age 30, dominant chestnut oaks in the Ridge and Valley were 1.2 m ($SE = 0.30$) taller than their red maple neighbors ($P < 0.001$) (Figure 4A).

Dominant chestnut oaks competing with sweet birches displayed a slightly different competitive pattern. Between ages 0 and 15, there were no significant differences in height. Chestnut oaks overtopped sweet birches and were significantly taller at ages 20 and 25 (by 0.67 m, $SE = 0.32$, $P = 0.039$, and by 0.79 m, $SE = 0.33$, $P = 0.017$). By age 30, dominant chestnut oaks were 0.6 m ($SE = 0.34$) taller than their sweet birch neighbors, but the difference was not statistically significant ($P = 0.08$). It is important to note that, on average, 30-year dominant chestnut oaks were never shorter than their sweet birch neighbors (Figure 4B).

Height differences through time – subordinate chestnut oaks in the Ridge and Valley

The height differences between 30-year-old subordinate chestnut oaks and their dominant competitors were calculated to determine at what age future subordinate oaks began to fall behind in height growth. Subordinate chestnut oaks were shorter than their red maple neighbors every year, beginning at age 0. The difference was not statistically significant until age 25, however, at which time subordinate chestnut oaks were 1.50 m

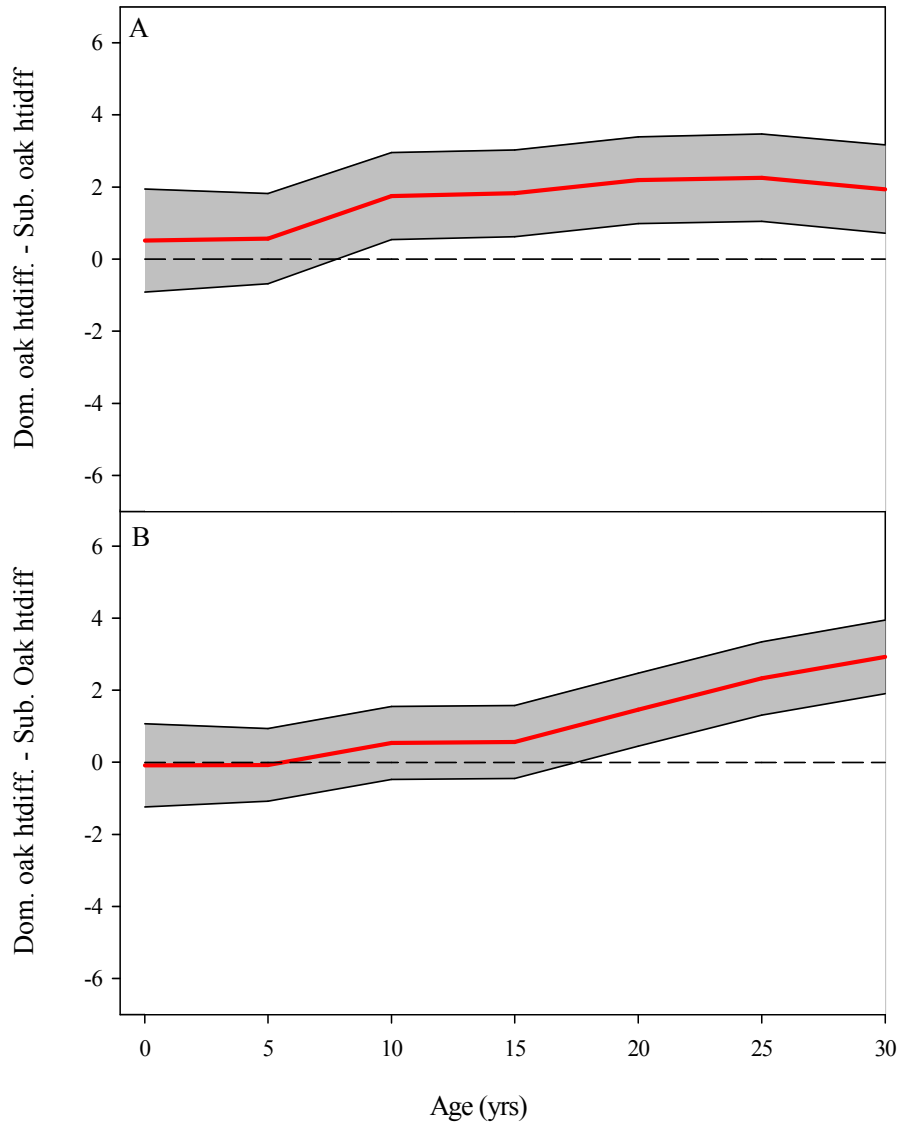
Figure 6. Height differences between subordinate chestnut oaks and dominant red maples (A) and sweet birches (B) in the Ridge and Valley Province. Dark bands above and below the mean line indicate 95% confidence intervals. Dashed lines indicate a height difference of 0 m.



($SE = 0.42$) shorter than the dominant red maples ($P < 0.001$). By age 30, the difference had increased to 1.75 meters ($SE = 0.42$, $P < 0.001$) (Figure 5A). Thirty-year-old subordinate chestnut oaks competing with dominant sweet birches displayed a similar developmental pattern, but they fell behind sooner. These subordinate chestnut oaks were significantly shorter (by -1.16 m, $SE = 0.52$, $P = 0.026$) by age 10. The largest height deficit was achieved (-1.52 m, $SE = 0.52$, $P = 0.004$) at age 20, after which the difference decreased somewhat to -1.34 m ($SE = 0.51$) at age 30 ($P = 0.010$) (Figure 5B).

The developmental differences between future dominants and future subordinates were clear by age 20 for chestnut oaks competing with red maples. By age 20, the height difference between dominant chestnut oaks and their red maple neighbors had already begun to significantly diverge from the height difference between subordinate chestnut oaks and their red maple neighbors ($P = 0.005$) (Figure 6A). Similarly, by age 10, the height difference between dominant chestnut oaks and their sweet birch neighbors was significantly different from the height difference between subordinate chestnut oaks and their sweet birch neighbors ($P = 0.005$) (Figure 6B).

Figure 7. The difference in height difference through time for dominant and subordinate chestnut oaks competing with dominant sweet birches (A) and dominant red maples (B) in the Ridge and Valley Province. Dark bands above and below the mean line indicate 95% confidence intervals. Dashed lines indicate a height difference of 0 m.



Height differences through time – dominant northern red oaks on the Appalachian Plateau

Dominant northern red oaks displayed a similar developmental pattern with all three competitors on the Appalachian Plateau. Dominant northern red oaks were shorter than their black cherry neighbors throughout the study period, although the height deficit lessened by age 30 (Figure 7A). Dominant northern red oaks were shorter than their red maples neighbors until age 20, but were taller by age 30. Dominant northern red oaks were shorter than dominant sweet birches throughout stand development, but the difference in height became statistically insignificant by age 30. Subordinate northern red oaks fell behind their black cherry neighbors by age 10 and remained shorter for the duration of the study period. Subordinate northern oaks were shorter than their red maple neighbors throughout the study period, but the difference was never statistically significant. Subordinate northern oaks fell behind their sweet birch neighbors by age 10, and continued to be overtopped for the remainder of the study period.

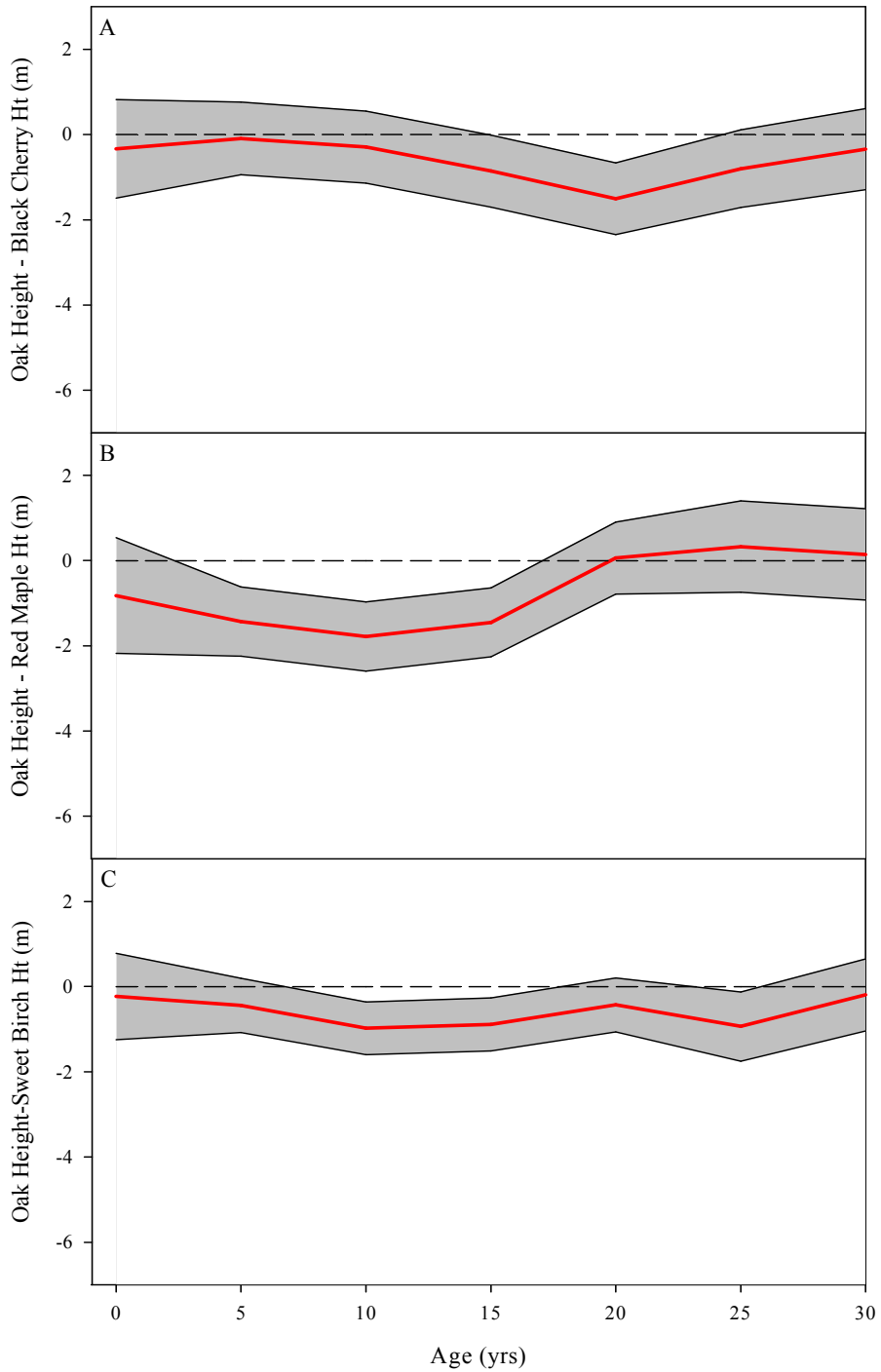
Thirty-year-old dominant northern red oaks were not significantly different in height from black cherry until age 15, at which time they fell statistically significantly behind for a ten year period (1.50 m shorter by age 20, $SE = 0.42$, $P = 0.046$). By age thirty, northern red oak was still behind by 0.34 meters ($SE = 0.48$), but the height difference was no longer statistically significant ($P = 0.47$) (Figure 7A).

Thirty-year-old dominant northern red oaks competing with dominant red maples exhibited a pattern of height growth dynamics similar to dominant chestnut oaks and red maples in the Ridge and Valley, albeit delayed (Figure 7B). These dominant northern red oaks were significantly shorter than their dominant red maple neighbors from age 5 to

age 15. At age 10, future dominant northern red oaks were, on average, 1.8 m ($SE = 0.41$) shorter than their red maple neighbors ($P < 0.001$). From age 20 to 30, the height difference was not significant, and by age 30, the northern red oaks were slightly taller (by 0.15 m, $SE = 0.54$, $P = 0.79$).

The development of 30-year-old dominant northern red oaks and their dominant sweet birch neighbors was somewhat erratic. Sweet birch was statistically significantly taller at ages 10, 15 and 25, but not at age 20. The height difference at age 10 (-0.98 m, $SE = 0.31$, $P = 0.002$) is similar to the height difference at age 25 (-0.94 m, $SE = 0.40$, $P = 0.025$), but much greater than the height difference at age 20 (-0.43 m, $SE = 0.32$, $P = 0.18$). By age 30, the height difference had diminished to -0.19 m ($SE = 0.42$), which was not statistically significant ($P = 0.65$) (Figure 7C). Although the reasons for the anomalous decreases in height difference at age 20 are unclear, the trend is similar to that observed for dominant northern red oaks competing with red maples on the Appalachian Plateau.

Figure 8. Height differences between dominant northern red oaks and dominant black cherries (A), red maples (B), and sweet birches (C) on the Appalachian Plateau. Dark bands above and below the mean line indicate 95% confidence intervals. Dashed line indicates a height difference of 0 m.



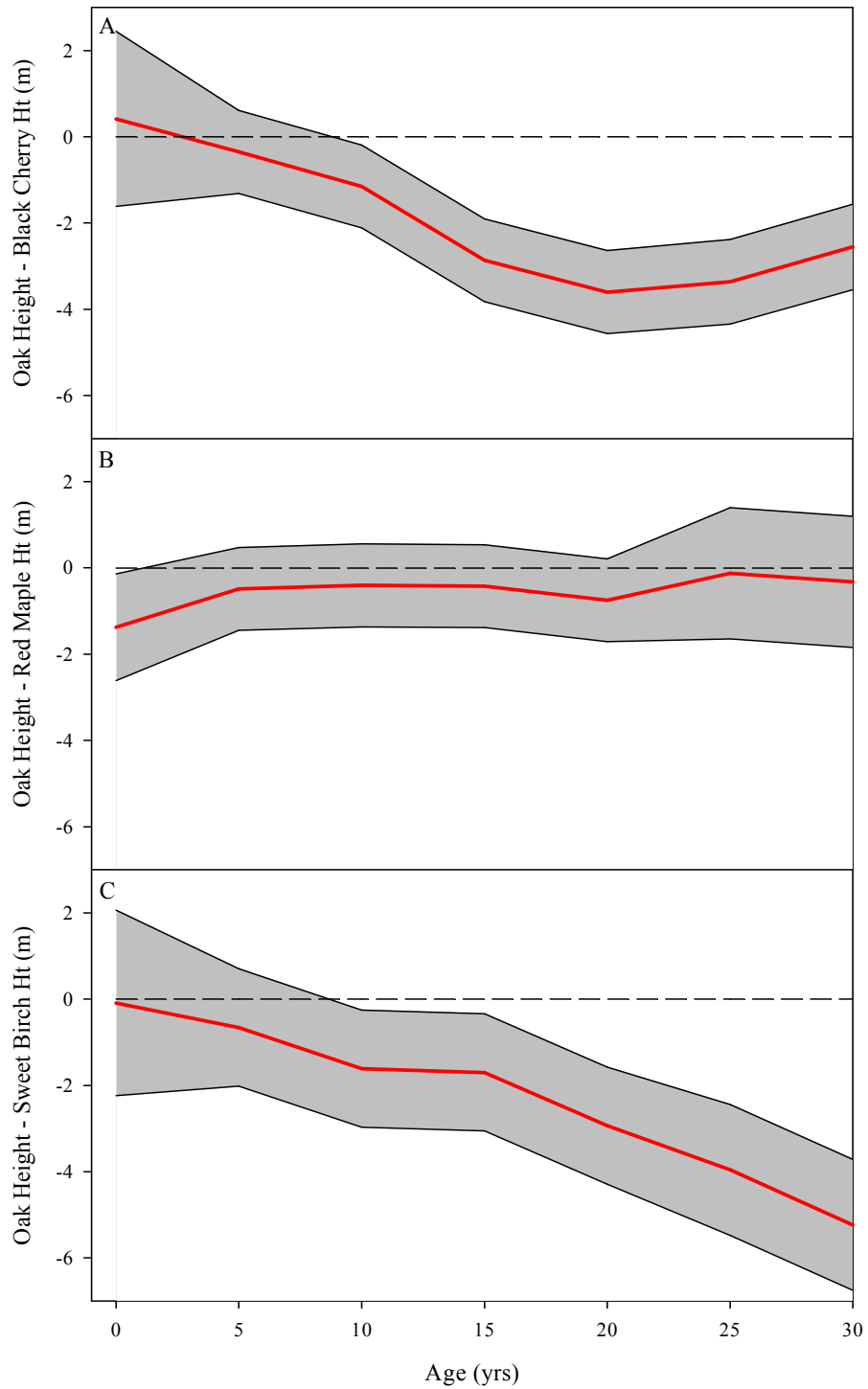
Height differences through time – subordinate northern red oaks on the Appalachian Plateau

Thirty-year subordinate northern red oaks on the Appalachian Plateau displayed similar height growth dynamics as subordinate chestnut oaks in the Ridge and Valley (Figure 8A). Subordinate oaks on the Appalachian Plateau growing next to dominant black cherries began to fall behind early and were statistically significantly shorter than their black cherry neighbors by age 10 (by -1.5 m, $SE = 0.48$, $P = 0.019$). These oaks continued to be overtopped and were, on average, 2.6 m ($SE = 0.50$) shorter than their black cherry neighbors by age 30 ($P < 0.001$).

The development of subordinate northern red oaks and dominant red maple neighbors is complicated (Figure 8B). Only at age 0 were these oaks significantly shorter than their red maple neighbors (by -1.3 m, $SE = 0.62$, $P = 0.03$). From age 5 through 30, subordinate northern red oaks were slightly shorter than their red maple neighbors, but the difference was not statistically significant. At age 20 the average height deficit was -0.75 meters ($SE = 0.48$, $P = 0.12$), which was reduced to -0.3 m ($SE = 0.76$) by age 30 ($P = 0.67$).

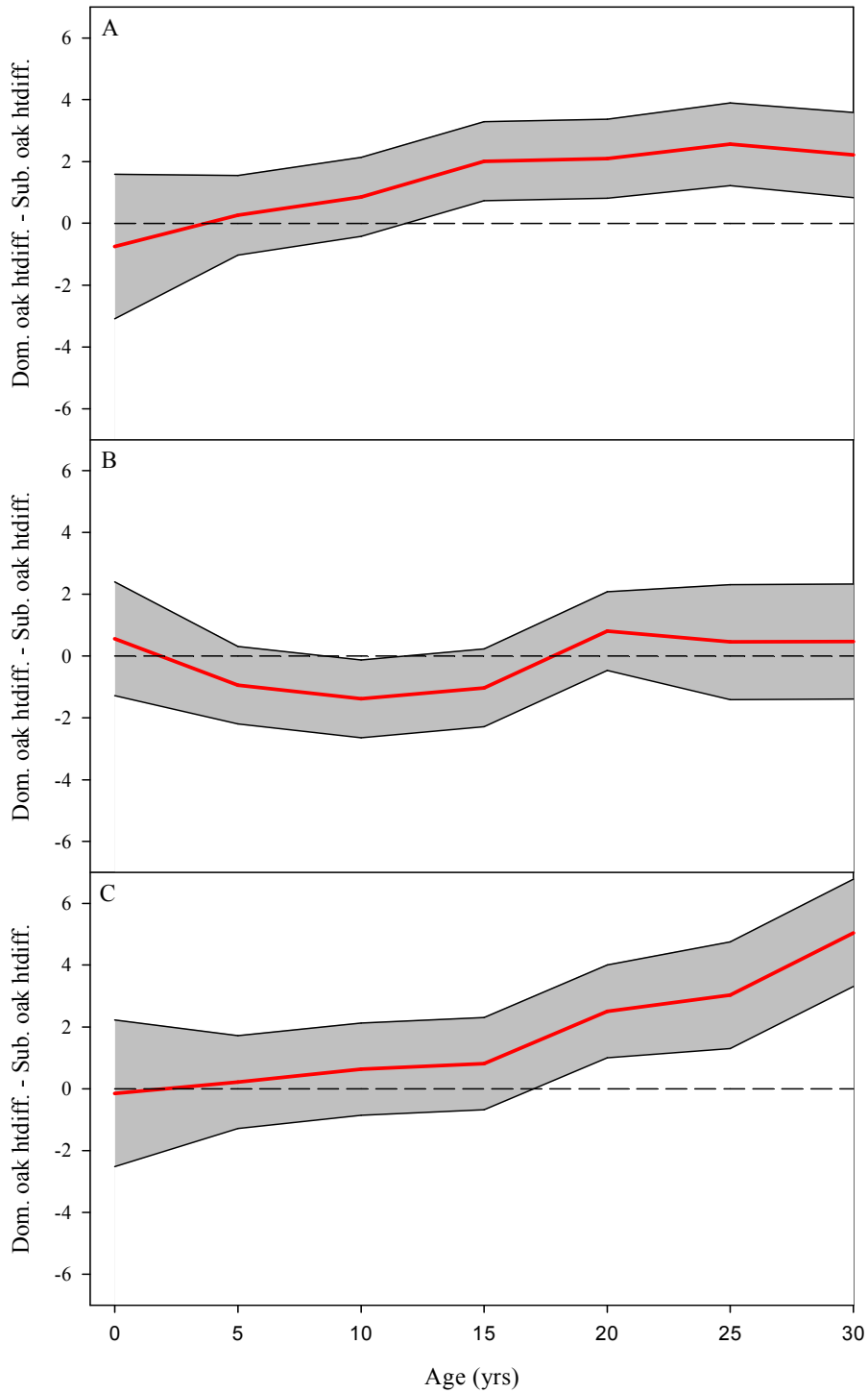
Subordinate oaks followed a similar developmental pattern with dominant sweet birch as with black cherry (Figure 8C). By age 10, subordinate northern red oaks were 1.6 m ($SE = 0.68$) shorter than their sweet birch neighbors ($P = 0.021$). This difference increased to over 5 m ($SE = 0.76$) by age 30 ($P < 0.001$).

Figure 9. Height differences between subordinate northern red oaks and dominant black cherries (A), red maples (B), and sweet birches (C) on the Appalachian Plateau. Dark bands above and below the mean line indicate 95% confidence intervals. Dashed lines indicate a height difference of 0 m.



The developmental differences between future dominants and future subordinates were clear by age 15 for northern red oaks competing with black cherry. By age 15, the height difference between dominant northern red oaks competing with black cherries and subordinate northern red oaks competing with black cherries had diverged significantly ($P = 0.003$) (Figure 9A). Because subordinate northern red oaks and their red maple neighbors were not significantly different in height for most of the first thirty years of stand development, the height differences between subordinate northern red oaks and red maples and dominant northern red oaks and red maples were also not different (Figure 9B). The height difference between dominant northern red oaks competing with sweet birches was significantly different from the height difference of subordinate northern red oaks competing with sweet birches beginning at age 20 ($P = 0.011$). By age thirty, this divergence had increased to 5 meters ($SE = 0.87$, $P < 0.001$) (Figure 9C).

Figure 10. The difference in height difference through time for dominant and subordinate northern red oaks competing with dominant black cherries (A), red maples (B), and sweet birches (C) on the Appalachian Plateau. Dark bands above and below the mean line indicate 95% confidence intervals. Dashed lines indicate a height difference of 0 m.



Neighborhood-level versus stand-level investigation

Although both neighborhood- and stand-level methods of evaluating height differences revealed similar patterns, important differences were identified between the two methods. Mean height differences calculated across stands had slightly larger confidence intervals than mean height differences calculated at the neighborhood level (Figures 10 to 13). Figures 10, 12 and 13 show that the stand-level evaluation resulted in fewer instances of significant height differences, and masked short term trends that were observed with the neighborhood-level method. Also, the stand-level evaluation of the height difference between chestnut oaks and sweet birches in the Ridge and Valley shown in Figure 11 gives the falsely optimistic impression that chestnut oaks had fully overtopped their sweet birch neighbors by age 30. Similarly the stand-level height differences for northern red oaks competing with red maples in Figure 12 suggest that northern red oaks may be on a trajectory to quickly overtop the red maples, whereas the neighborhood-level differences show that the mean height difference was again nearing 0 at age 30. Similarly,

Figure 11. Comparison of stand-based (A) and neighborhood-based (B) height difference methods for the difference between dominant chestnut oaks and dominant red maples in the Ridge and Valley Province. Dark bands above and below the mean line indicate 95% confidence intervals. Dashed lines indicate a height difference of 0 m.

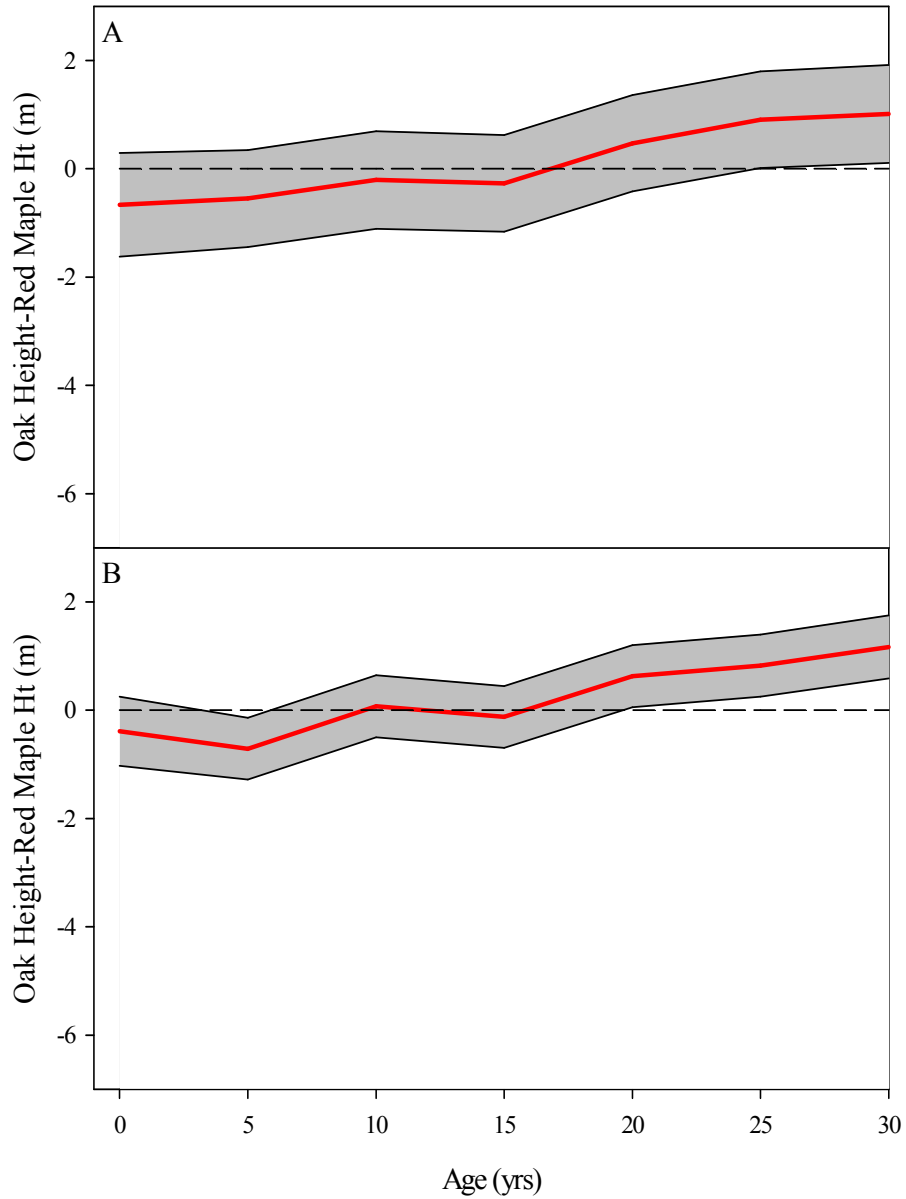


Figure 12. Comparison of stand-based (A) and neighborhood-based (B) height difference methods for the difference between dominant chestnut oak and dominant sweet birches in the Ridge and Valley Province. Dark bands above and below the mean line indicate 95% confidence intervals. Dashed lines indicate a height difference of 0 m.

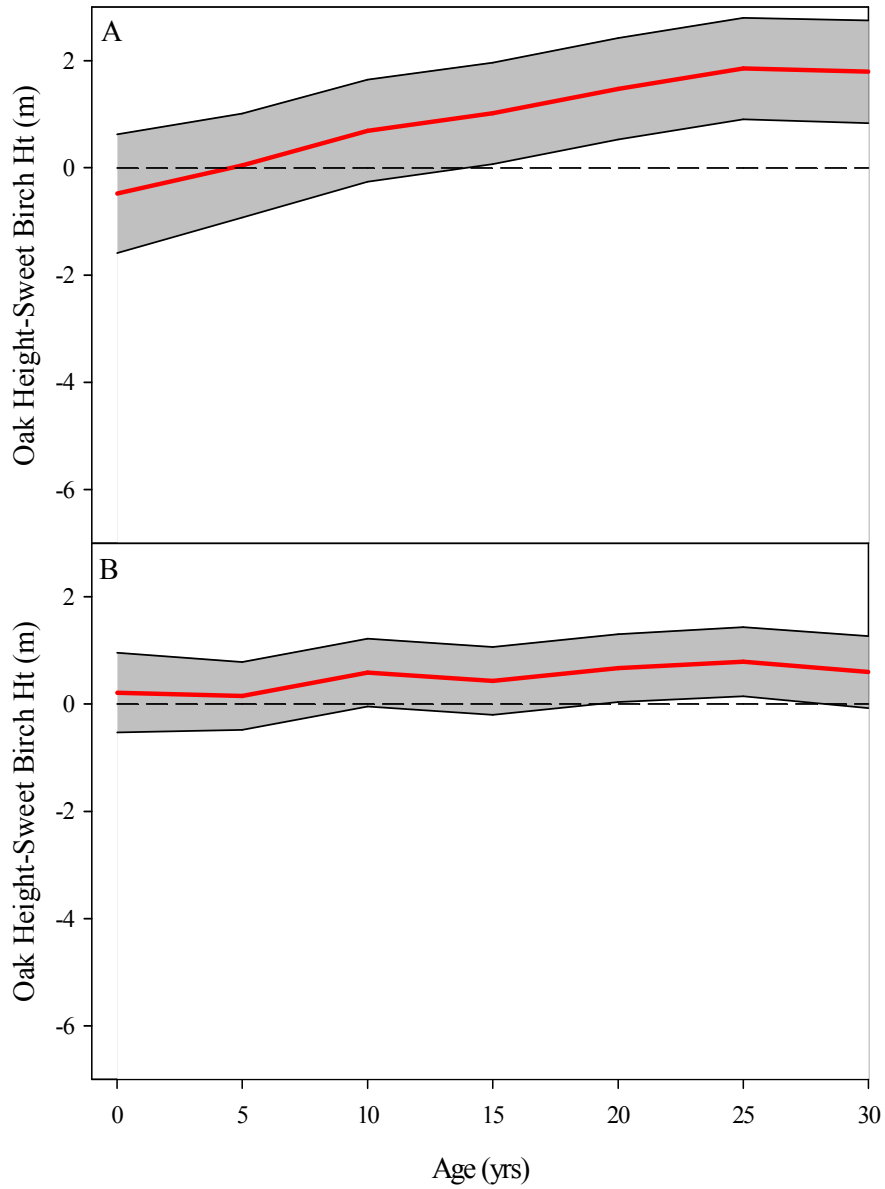


Figure 13. Comparison of stand-based (A) and neighborhood-based (B) height difference methods for the difference between dominant northern red oak and dominant red maples on the Appalachian Plateau. Dark bands above and below the mean line indicate 95% confidence intervals. Dashed lines indicate a height difference of 0 m.

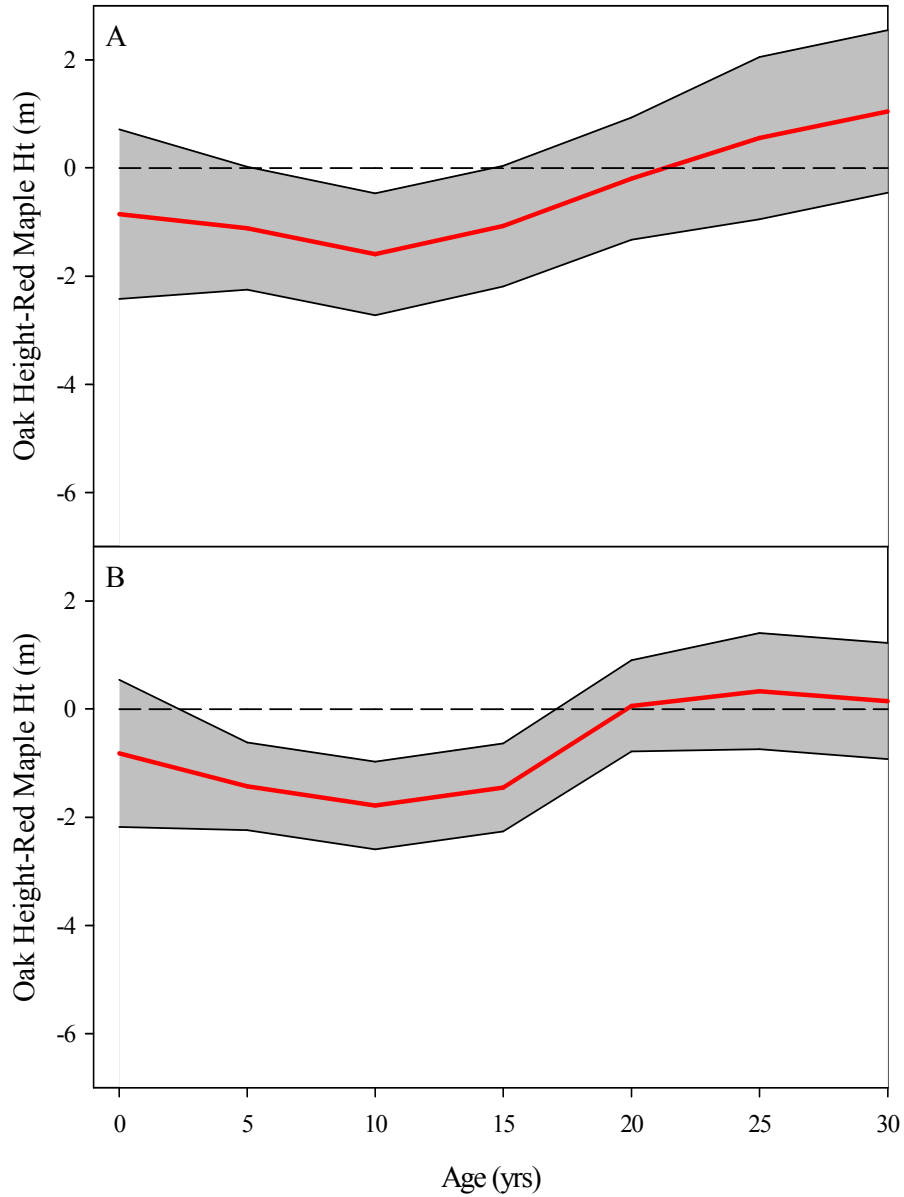
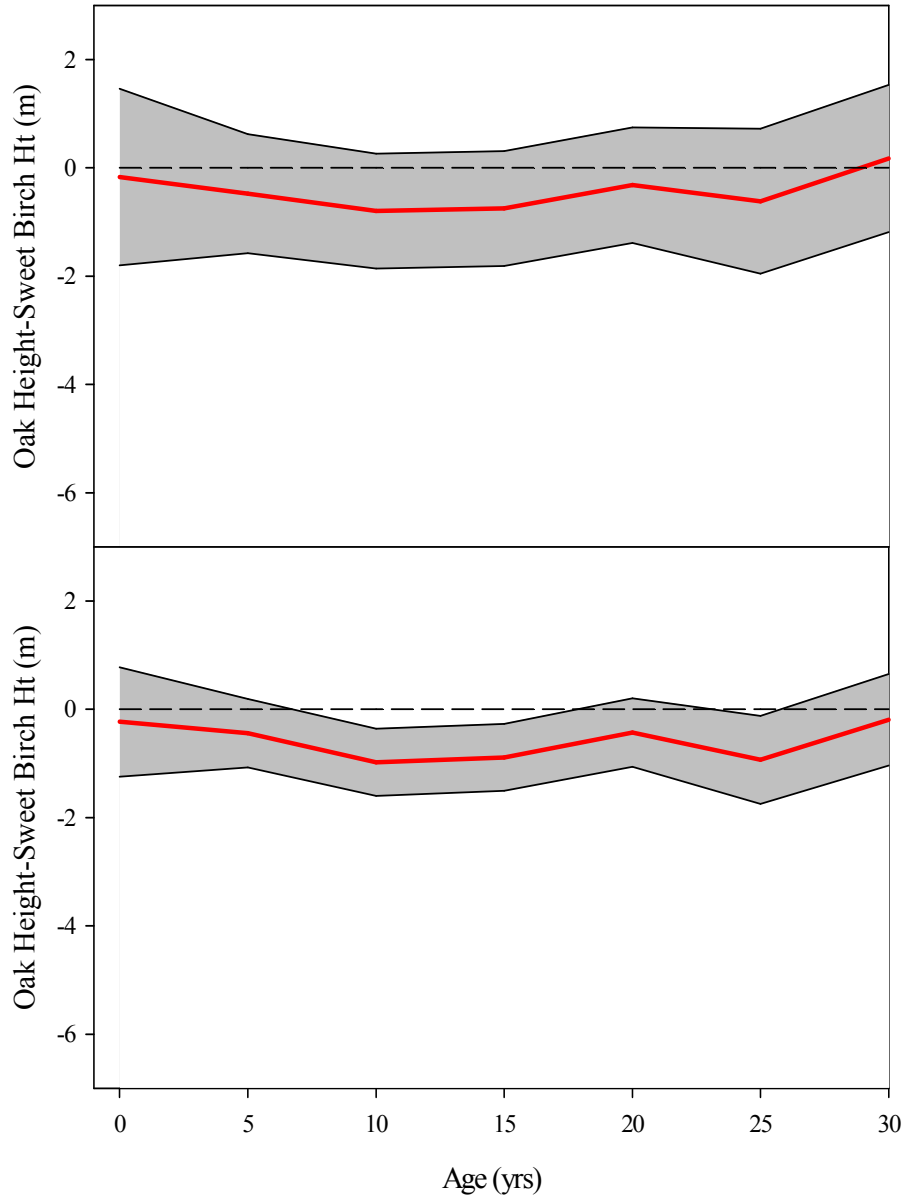


Figure 14. Comparison of stand-based (A) and neighborhood-based (B) height difference methods for the difference between dominant northern red oaks and dominant sweet birches on the Appalachian Plateau. Dark bands above and below the mean line indicate 95% confidence intervals. Dashed lines indicate a height difference of 0 m.



Discussion

Sprouting and advance regeneration

Because height growth rates of most oaks in the first 5 years of stand development exceeded 10 cm/yr and 89% exceeded 30 cm/yr, we hypothesize that these oaks were present prior to the harvest as advanced regeneration (Phares 1971), and sprouts of advanced seedlings that may have been damaged during the harvest. The histogram of root ages in Figure X is in keeping with results from Virginia and Ohio that show oak sprouts originating from advanced root systems have the potential to grow nearly a meter per year during the first few years of stand development (Sander 1971, Brose and Van Lear 1998). Because Bureau of Forestry logging contracts can be at least 3 years long, one must consider that the harvest dates could be three years sooner than those listed to calculate the values on Figure X. If the harvest dates are moved ahead by 1 to 3 years, our data suggest that most oaks were advanced seedlings approximately 3 to 5 years old at the time of harvest. Even with a harvest year shift of three years, some oaks appear to have germinated a year or two after the harvest. If our lowest cut was not low enough to capture the true root collar on a particular seedling, it would appear younger than it really was.

Although it is widely known that oak seedlings are capable of repeatedly dying back and re-sprouting from older root systems, few studies have investigated the age difference between the above ground stems and the root systems of oaks past the regeneration age. It is likely that many of the oaks in the present study were seedling sprouts that originated after harvest damage or exposure-induced dieback following clearcutting. We found that on average root systems were 4 years older than above-

ground stems for chestnut oaks and 3 years older for northern red oak. Many of these oaks had above-ground ages that were very similar to the age of the harvest, suggesting that many re-sprouted following harvest. The root systems of two chestnut oaks were 45 and 60 years older than their above-ground tissues. Both of these trees clearly originated from small saplings (< 5 cm basal diameter) that must have been top-killed during the harvest. The presence of 45-60 year old saplings in the 90-100 year-old pre-harvest stands points to either an open (or irregular) canopy or a gap opening that had occurred when the previous stand was 30-40 years old. Nonetheless, seedling sprouts clipped following a harvest grow quite rapidly, many of which can average nearly a meter of annual height growth (Sander 1971). In contrast, un-damaged advanced seedlings are known to grow quite slowly following release, especially compared to seedling and stump sprouts (Clark and Watt 1971, Brose and Van Lear 1998). It is possible that undamaged oak seedlings are able to survive and compete effectively only if they are quite large (Liming and Johnston 1944). Of 65 stumps sampled in this study, only 8 had root collar ages equal to their ages at 0 meters, suggesting that these trees were undamaged advanced seedlings that recruited into the overstory. These 8 trees were evenly split between dominant and subordinate oaks. It is not surprising that no difference in root age was found between subordinate and dominant oaks because future dominants and subordinates did not stratify into different crown classes until after the first decade of stand development (i.e. they had very similar heights in the first decade), so it is also reasonable to assume that few differences existed in their origins. Most small seedlings that were not damaged and therefore did not re-sprout after the harvest may not have survived to crown closure (Liming and Johnston 1944).

Although it is clear that sprouts grow faster than seedlings initially, little evidence exists that supports clipping or top killing seedlings as means of increasing the competitiveness of young oaks (Lockhart et al. 2000). When oaks are top killed by fire, they typically re-sprout and grow rapidly, often enabling them to compete with otherwise fast-growing species, but this is partially because many of the competing stems have been eliminated (Abrams 1992, Brose et al. 2001). In the present study, it is unknown whether only seedling sprouts were successful or if only seedling sprouts were present to compete in the first place. Given that almost 88% of the oak stumps sampled in the study point to seedling sprouts as the predominant form of a successful oak recruit, we conclude that silvicultural systems that attempt to accumulate advance regeneration in the understory of mature mixed-oak forests might more reliably regenerate oaks than those that do not. In either case, these results might spur future work regarding the competitiveness of various types of oak regeneration following even-aged harvests.

Height growth dynamics by region

Oaks in both regions were able to overcome slight height deficits early in stand development to become dominant by age 30. These findings are generally consistent with work from New England, which found that overtopped oaks were eventually able to out-compete their neighbors. A successional model proposed for the Harvard Forest in western Massachusetts suggests three stages of stand development. The first stage is dominated by pioneer species such as pin cherry and grey birch. In the second stage (age 15-40), red maple, birch and cherry are partially dominant over northern red oak. The

third stage, beginning around age 40, is marked by the emergence of a dominant layer of northern red oak with continued co-dominance by red maple and birch (Hibbs 1983).

Our findings seem to indicate a similar developmental pattern to that described by Hibbs (1983), although the competitiveness of oak and the behavior of individual competing species clearly differed by region. On the Appalachian Plateau, red maple and sweet birch were dominant for the first few years of stand development, even outgrowing black cherry. Beginning at about age 10, black cherry ascended to a dominant position over sweet birch and red maple. The delay in cherry dominance may result from early height advantages enjoyed by red maple and sweet birch advance regeneration or sprouts competing with new cherry germinants. This study period was not long enough, however, to observe northern red oak form a dominant layer over these other species, but the height difference between oaks and the other species had become negligible by age 30. In slight contrast to the stand development pattern hypothesized by Oliver (1975), the northern red oaks observed in this study did not achieve absolute dominance by age 20 (or even age 30).

No even-aged stand development studies exist for the Ridge and Valley province in Pennsylvania. However, studies of old growth forests have found chestnut oak dominance on sandstone ridges in the region and it is reasonable to expect that chestnut oak would also be fairly competitive (Mikan et al. 1994, Ruffner and Abrams 1998). The accepted theory has been that chestnut oak dominates these sites due its ability to withstand severe drought and tolerate infertile soils, although there is some debate regarding these points (see Keever 1973, Blackman and Ware 1982, Casperson and Kobe 2001). In addition, the pre-settlement vegetation community on ridges was likely

maintained by occasional fires and gap scale recruitment of oaks into an un-even aged overstory (Abrams 1992). Although the stands used in the present study regenerated in the absence of fire through clearcutting, chestnut oak is likely a competitive species on these sites, but its dominance following even-aged timber harvests is not always ensured (Gould et al. 2004). Our results indicate that 30-year old dominant chestnut oaks in the Ridge and Valley did not undergo any significant suppression by red maple or sweet birch. Similarly, chestnut oak with red maple and yellow poplar maintained a dominant canopy position 26 years following clearcutting on south-facing dry-mesic sites in southeastern Ohio (Norland and Hix 1996). Further, on low-quality sites in Ohio, Kentucky, and Indiana, chestnut oak was abundant and dominant at age 15, even when competing with yellow- poplar (Hilt 1985). Consequently, chestnut oak can be expected to be quite competitive on dry sites similar to the Ridge and Valley sites in our study.

Height growth dynamics by competing species

Sweet birch is likely more competitive on the Appalachian Plateau than in any other part of Pennsylvania, and possibly more competitive than on many sites in southern New England. A review of the silvical characteristics of sweet birch indicates that its growth rates in northwestern Pennsylvania exceed those of most other competing species in the region and are equaled only by black cherry (Leak 1958). In New England, however, sweet birch success seems to be highly variable and is primarily a function of small scale changes in soil type. Surveys of the Harvard Forest in Petersham, Massachusetts, have shown two distinct site types in which northern red oak and sweet birch interact differently. On loams underlain by fine textured glacial till, the increased

soil moisture favors species such as white ash, birch and sugar maple, whereas on loams underlain by coarse textured till, the drier soil conditions favor oaks (Stout 1952). The cool, moist climate and productive soils of northwestern Pennsylvania seem to favor prolonged sweet birch dominance.

In northwestern Connecticut, a stand development study was conducted on two adjacent site types: a thin glacial till (xeric) and a swale-till (mesic). On the more productive swale-till site, northern red oak nearly disappeared from the stand by age 30, being overtopped by sweet birch and black cherry. On the less productive thin-till site, northern red oaks were overtopped early by pin cherry and sweet birch, but by age 30 had achieved a strong co-dominant position as sweet birch had begun to rapidly self-thin (Liptzin and Ashton 1999). The developmental pattern observed in our study seems to generally mirror the results on the thin-till sites in Connecticut, though sweet birch on the Appalachian Plateau in Pennsylvania seems to be able to maintain a dominant canopy position. Therefore, it is likely that sweet birch competition in northern Pennsylvania is a serious long-term barrier to the ascension of northern red oak into the dominant layer of young forests.

The role of sweet birch on the sandstone ridges of Central Pennsylvania is less clear. Although sweet birch is typically considered a mesic site, or “cove,” species, its distribution is clearly more wide-spread (Cain 1931). Sweet birch is often present as seedlings and saplings across a wide range of site types in the Ridge and Valley, occupying lower slope eastern hemlock stands and rocky ridge tops (Leak, 1958). FIA data have shown that the number of sweet birch stems in Pennsylvania nearly doubled between 1989 and 2004, being second only to red maple in abundance (McWilliams et al.

2004). The majority of these stems are scattered throughout the Ridge and Valley province and most are less than 10 cm dbh in size. Sweet birch is known for its prolific seeding, and consequently its ability to colonize recent clearcuts and other disturbances; however its ability to maintain long-term site dominance across a range of site types is unclear. Dense stands of regenerating sweet birch have been documented across a wide range of site types, but in most cases, particularly on dry sites, the importance or density of sweet birch rapidly declines as crown closure occurs (Beck and Hooper 1986, Brashears et al. 2004). In the Ridge and Valley stands in this study, high sweet birch mortality was evident, as sweet birch snags in various stages of decay were common (personal observation).

Leupold and Parker (1985) suggest that sweet birch may be able to colonize sites on which it will not be able to sustain dominance. The authors propose that saplings are successful initially as a result of increased soil moisture and nutrients following disturbance, but are unable to compete as abundant regeneration results in lower resource availability. This may have occurred in the sites in this study, allowing chestnut oaks within dense clusters of sweet birch to maintain a co-dominant crown position as the sweet birch self-thinned.

Although red maple was probably not common across the Appalachian Plateau prior to the establishment of the second growth forest, the species is now ubiquitous and is likely to become even more common (Abrams 1998). Our results indicate that at least in some cases, northern red oaks can successfully compete with red maple neighbors. Work from Michigan has shown northern red oak and red maple to have similar growth rates following even-aged harvests, but with oak maintaining a slight height advantage

throughout stand development (Palik and Pregitzer 1993). Our results from the Appalachian Plateau seem to indicate that red maple in this region of Pennsylvania may be somewhat more competitive than in Michigan because dominant northern red oaks on the Appalachian Plateau did not achieve absolute dominance over red maple even by age 30.

Red maple's short-lived height advantage in the Ridge and Valley could be a result of a combination of factors. First, many red maples in the Ridge and Valley sites were of stump sprout origin. Sprouts often exhibit more rapid early height growth rates than seedlings, but sprout clusters that fail to develop an adequate root system by age 10 often slow in height growth as the connection to the old root system deteriorates (Wilson 1968, Del Tredici 2001). Second, although red maple is considered a generalist and somewhat tolerant of droughty soil conditions, evidence suggests that chestnut oak is probably more tolerant of such conditions (Hilt 1985, Abrams et al. 1998b, Casperson and Kobe 2001). In a study of radial growth reductions following droughts in the Ridge and Valley province, red maple growing on ridges suffered a more severe and prolonged growth decline than chestnut oak (Abrams et al. 1998b). These results are in contrast to work from West Virginia where red maple was found to maintain rapid growth for more than 40 years, allowing it to overtop both northern red and chestnut oaks, even on "dry" sites (Tift and Fajvan 1999). Although these authors characterized their site as "dry," mean annual precipitation for their region is nearly 40 cm greater than for Pennsylvania. In addition, the presence of yellow-poplar, even on their dry site, suggests the results may not be applicable to the Ridge and Valley stands in our study, as none of our stands contained any yellow-poplar, which is an indicator of more productive sites. Work from

Indiana has shown that red maple importance values typically decline through time in clearcut stands, whereas importance values of oaks increase (Arthur et al. 1997). This decline of red maple was in relative basal area, not stem density, suggesting that perhaps red maple's shade tolerance prevents stem mortality and encourages suppression and height growth stagnation of individuals in monospecific groups. It is possible that oaks growing in the midst of such a group are at a competitive advantage as red maple height growth slows. Many of the oaks in our study were isolated from other oak individuals and surrounded by red maple, sweet birch and other competitors, which may have actually provided the oaks with a competitive advantage.

For example, cherrybark oaks (*Quercus pagoda* Raf.) in the Lower Mississippi Alluvial Valley are typically out-competed by sycamores (*Platanus occidentalis* L.) in young stands, but if the oaks are far enough away from a sycamore stem to avoid direct overhead suppression, the oaks may eventually assume dominance as sycamore growth slows (Oliver et al. 1990). Further, cherrybark oak are typically out-competed by sweetgum (*Liquidambar styraciflua* L.) during the first 10 to 20 years of stand development (Johnson and Krinard 1988, Lockhart et al. 2006). However, cherrybark oaks that are able to maintain some level of overhead sunlight are able to stratify over the slowing sweetgum to achieve dominance by age 21 in a trajectory very similar to oaks in the present study competing with red maple. The authors propose several reasons for why this phenomenon may occur. First, sweetgum crowns are relatively narrow and therefore do not directly overtop nearby oaks, whereas oak crowns tend to be more spreading. Second, the stronger oak branches likely batter the weaker sweetgum branches, resulting in disproportionate crown damage of sweet gum following wind

storms. Third, high initial sweetgum densities can result in sluggish sweetgum height growth due to heavy intraspecific competition. Lastly, the authors propose that because bud break in cherrybark oak begins at the terminal bud, and sweetgum bud break begins at the crown base, cherrybark oaks have the potential to grow slightly more in height than their sweetgum neighbors.

Although our study did not attempt to investigate the causal mechanism of oak canopy ascension, it is conceivable that some of these factors (with perhaps the exception of the bud break differences) may also apply to oaks and their competitors in Pennsylvania. Black cherry, red maple and sweet birch all have much finer branches, making them potentially susceptible to crown abrasion by oak neighbors. Also, all three species (particularly black cherry and sweet birch) typically have much narrower crowns than similar aged oak species (Lamson 1987). Further studies are needed to better understand the mechanisms that allow oaks to overcome initial height disadvantages to achieve dominance in Pennsylvania.

The divergence of dominant and subordinate oaks

Across all stands in both regions, oaks that were subordinate at age 30 had begun to fall behind in height by age 10 to 15. Although 30 year-old stands have already undergone heavy mortality, it is probably reasonable to expect that oaks in a subordinate crown class at age 30 have little chance of surviving until the end of the rotation (Ward and Stephens 1994, Ward 2008). Studies of radial growth rates of subordinate trees indicate that oaks rarely increase their radial growth after crown class decline had begun (Drobyshev et al. 2007). Height growth trajectories of subordinate oaks in West Virginia

support the notion that oaks in subordinate crown status at age 25 rarely emerge as dominants (Tift and Fajvan 1999). In this study, many of these oaks were still in a competitive position at age 10. Across all stands, 38% of all oaks that became subordinate by age 30 were less than 0.44 meters shorter than their red maple neighbors at age 10, which was the same average height difference for future dominant oaks and their red maple neighbors at the same age, and 20% of future subordinate oaks that were competing with sweet birch neighbors had height differences equal to, or less negative, than their future dominant oak counterparts at age 10. By this conservative estimate, one in five subordinate oaks was just as competitive as dominant oaks at age 10.

Not surprisingly, subordinate chestnut oaks in the Ridge and Valley had not fallen nearly as far behind their neighbors as subordinate northern red oaks on the Appalachian Plateau. The Ridge and Valley sites are probably more conducive to oaks in general due to their dry, infertile soils, and subordinate oaks may be able to compete longer there than on the more mesic Appalachian Plateau.

Subordinate northern red oaks on the Appalachian Plateau fell much further behind sweet birch than red maple or even black cherry, again suggesting that sweet birch may be an important long-term competitor on the Appalachian Plateau. In the Ridge and Valley province, the pattern was reversed, in that subordinate chestnut oaks fell further behind red maple than birch, again suggesting that the long-term competitiveness of sweet birch is weaker in the Ridge and Valley.

It is also important to note that in addition to subordinate oaks, many of the 30-year old dominant and co-dominant oaks examined in this study may not survive until the end of the rotation. Work from New England has shown that during the second thirty

years of stand development over 30% of dominant and 40% of co-dominant oaks did not survive (Ward and Stephens 1994).

The utility of neighborhood scale investigation

In nearly all cases, the neighborhood-level method generated values with smaller confidence intervals than the stand level method (Figures 10-13), thereby making height difference patterns more easily evident. Interestingly, one stand-based height difference graph (Figure 11) actually displays a trend that is somewhat different from the corresponding neighborhood-based height difference graph. The stand-based graph for dominant chestnut oaks competing with dominant sweet birches in the Ridge and Valley Province implies that oaks significantly stratified over sweet birches by about age 15 and continued to become significantly taller until age 30. This is in contrast to the data from the neighborhood-based method, which suggests that chestnut oaks remained similar in height to sweet birches throughout stand development and never fully overtopped their sweet birch neighbors. The stand-based graph shows essentially an inflated level of competitiveness on the part of dominant chestnut oaks, which could be errantly interpreted as evidence that sweet birch competitors were not out-competed by age 15. However variation in each species' preferred microsite is probably the cause for the difference in outcomes between these two methods. Randomly selected plots that included sweet birch competitors were commonly found on rockier portions of the study stands (personal observation). The fact that the small-seeded sweet birch is able to colonize very stony mountainsides in central Pennsylvania has been well documented (see Leak 1958). It is likely that the shallower soil and rock-strewn surface of these areas

resulted in depressed growth rates of the chestnut oaks growing on them as well. The shorter average height of chestnut oaks on these surface types compared to an overall higher stand average of chestnut oaks could explain the difference between the stand-level height differences and the neighborhood-based height differences. We therefore conclude that neighborhood-based height differences may better express the competitive relations among the tree species in this study than stand-level differences, which may mask the true competitive level experienced by the oaks.

Caveats of Retrospective Research

Because the monitoring of long-term research plots is expensive and operationally difficult, retrospective stem analysis of stand development is a useful method for researchers to investigate long periods of historic stand development and species growth rates (Henry and Swan 1974, Oliver 1978, Tift and Fajvan 1999). However, all retrospective studies have inherent limitations to the potential conclusions to be drawn from their results. The most important caveat to consider in the present retrospective study is that the number of oak trees that were present following the clearcut harvest is unknown, and consequently the number of individuals (oaks and competitors) that died until age 30 is unknown. It is reasonable to assume that the oaks that survived until age 30, whether they were subordinate or dominant, were probably the most competitive seedlings immediately following harvest, as high mortality of seedlings has been well documented during early stand development (Peet and Christensen 1987). Work from Connecticut has shown that mortality of suppressed and intermediate oaks in young stands (age 7-22) is quite high, with 18 year survival rates of less than 20% for

suppressed tree and less than 40% for intermediate trees (Ward 2009). Although we have no way of knowing how many oaks (and other species) were lost during this early period on our study sites, it is likely that the seed origin oaks constituted but a small fraction of the seedling oaks that were present following the harvest. If so, the trees we examined in this study would have been exceptional. It is also possible that these oaks represent a fairly high proportion of the seedlings oaks that were present following harvest, because individual oaks have a higher likelihood of survival and crown-class improvement in stands with lower oak densities (Ward and Stephens 1994, Ward 2009).

Due to these uncertainties, inferences of the present study are restricted to conclusions about oak's competitiveness in mixed-species neighborhoods, even though it is tempting to draw more general conclusions about the success or failure of oak regeneration in these study stands. We can say with confidence only how the oaks that were still competing at age 30 interacted with their nearby neighbors, not how oaks as a species group succeeded or failed in these stands.

Conclusions and Management Implications

This work supports the widely held notion that to compete successfully in young stands oaks must be present before the harvest as advanced reproduction (Sander 1971, Loftis 1990). Furthermore, these results suggest that oak sprouts from relatively small seedlings damaged during the harvest were successful competitors in the new stand. Though it is not possible to determine whether only seedling-sprouts were successful, these data are highly suggestive that top killing of advanced seedlings during the harvest does not negatively impact their ability to compete.

Dominant chestnut oaks in the Ridge and Valley were never more than 1 meter shorter than their red maple neighbors and 0.5 meters shorter than their sweet birch neighbors. Chestnut oaks in the Ridge and Valley that fell further behind became subordinate and are not likely to survive much longer. On the Appalachian Plateau, dominant northern red oaks were never more than 2 meters shorter than black cherry and red maple, and 1.5 meters shorter than sweet birch. No northern red oaks that were more than 1 meter shorter than sweet birch or red maple at age 20 became dominant by age 30.

These results suggest that although oaks are able to compete effectively against sweet birch, red maple, and black cherry, there is a point from which oaks do not recover. If a manager enters a ten year old stand in the Ridge and Valley and finds sweet birch and red maple overtopping chestnut oaks by more than 1 meter, our results imply that those chestnut oaks likely become permanently suppressed. Likewise, on the Appalachian Plateau, northern red oak seedlings that are more than 2 meters shorter than their neighbors at age 10, or more than a meter shorter at age 20, are likely relegated to a subordinate crown class. If a high proportion of oaks fall into these categories, managers might consider interventions to ensure sufficient future oak stocking.

The efficacy of pre-commercial crop tree release as a means of increasing oak survival has been shown by researchers throughout the oak region, though the proper timing of such treatments remains unclear (Trimble 1974, Miller 2000, Ward 2009). Early work from West Virginia suggests that full release of northern red oaks at age 7 was not an effective method of preventing crown class retrogression and mortality, particularly for trees that were already intermediate (Trimble 1974). The authors suggest that release in this case (a five foot radius around the stem) was either carried out too

early or not heavy enough, as rapidly growing sprout clusters outside the 5 foot radius quickly filled in the openings created by release. Heavier release at such an early age would likely trigger increased branching and reduced clear stem length; other results show that heavier releases (full release + five more feet) can actually retard height growth in some species, particularly of those that are less shade-tolerant (Miller 2000).

Work from Maryland and West Virginia supports the notion that later releases (age 12-16) are more effective (Miller 2000). Nearly all co-dominant trees that received full releases survived and maintained co-dominant canopy positions. Many oaks in our study that had regressed to a subordinate crown class by age 30 were likely co-dominant between age 12 and 15, suggesting that a full release might have prevented their regression.

For oaks that have already fallen into an intermediate crown class by age 10-15, the efficacy of crop tree release is questionable. In some cases, released intermediates display very high 10-year survival rates, with some individuals even upgrading dominance class (Miller 2000). Other work has shown that nearly half of the intermediates will either die or regress to the suppressed crown class following full release (Ward 2009). The decision to release oaks in subordinate crown classes should be viewed as a last resort, and reserved only for cases where insufficient numbers of more competitive oaks are available. Some released intermediates will likely survive and some may require additional releases, significantly increasing the cost to the manager.

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Appendix

Example neighborhood height growth trajectories

Figure 15. Stand 3, Neighborhood 14. Dominant chestnut oak competing with a dominant sweet birch and a dominant red maple.

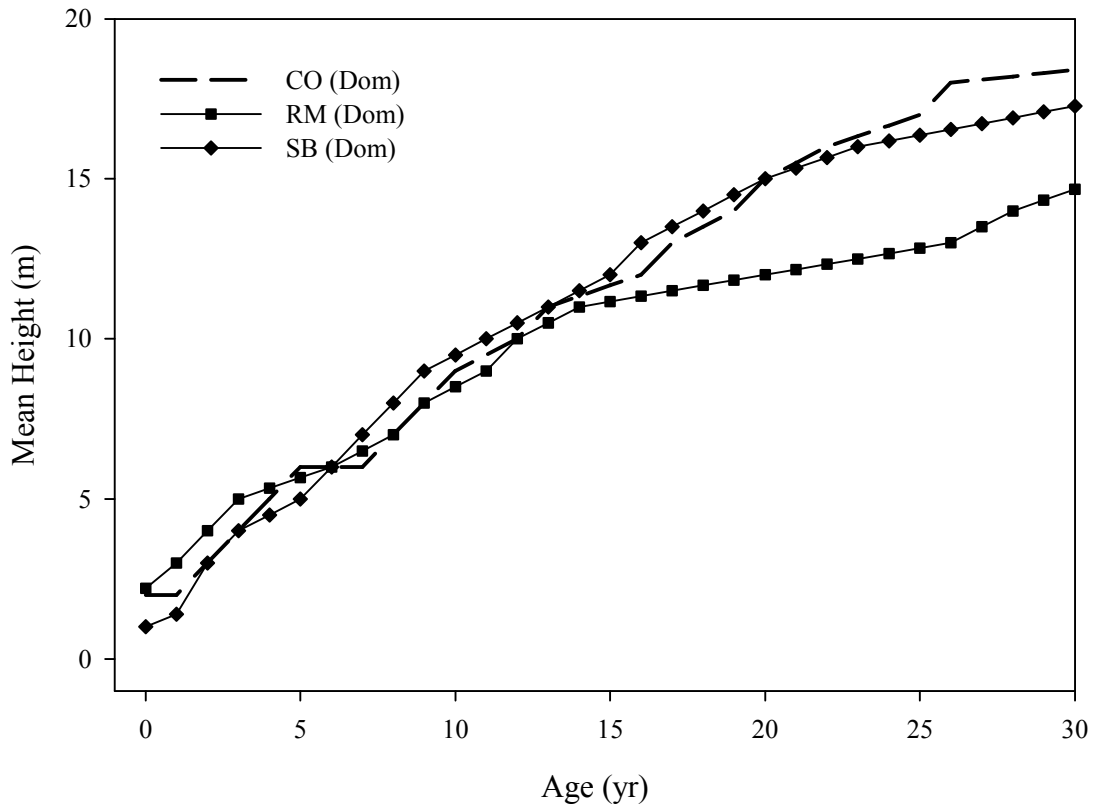


Figure 16. Stand 3, Neighborhood 1. Subordinate chestnut oak competing with a dominant sweet birch and subordinate red maple.

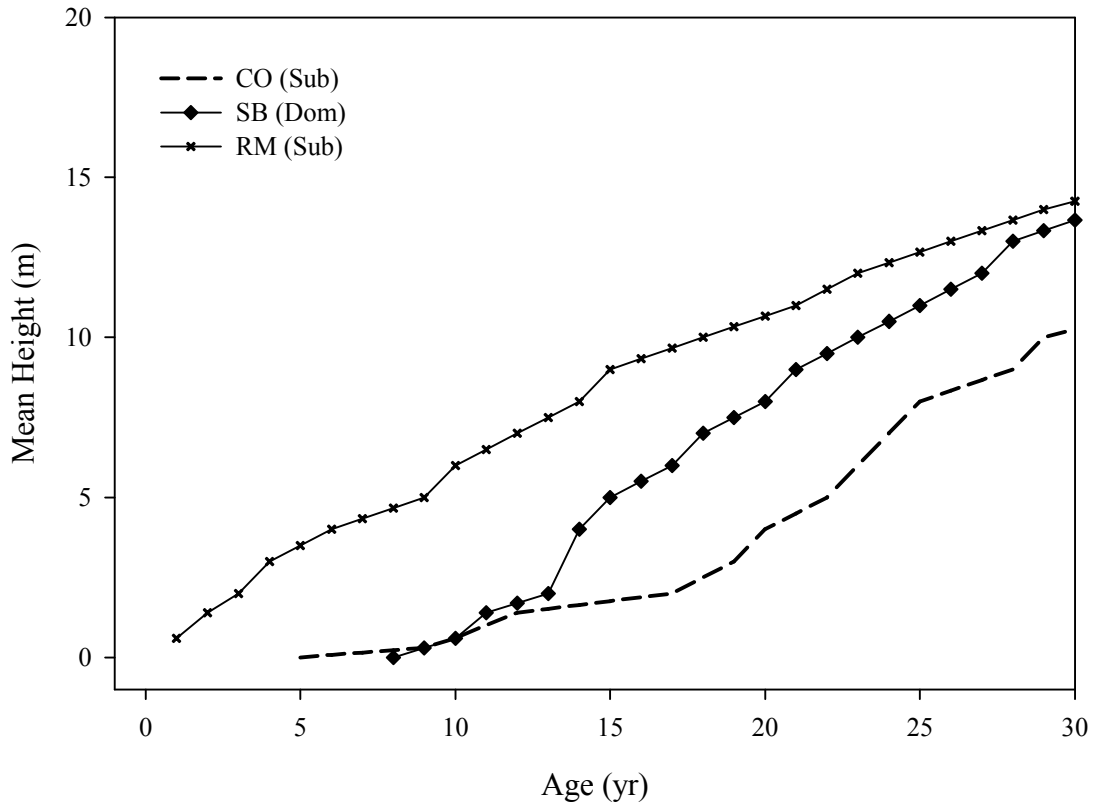


Figure 17. Stand 5, Neighborhood 14. Dominant chestnut oak competing with a dominant sweet birch and dominant red maple.

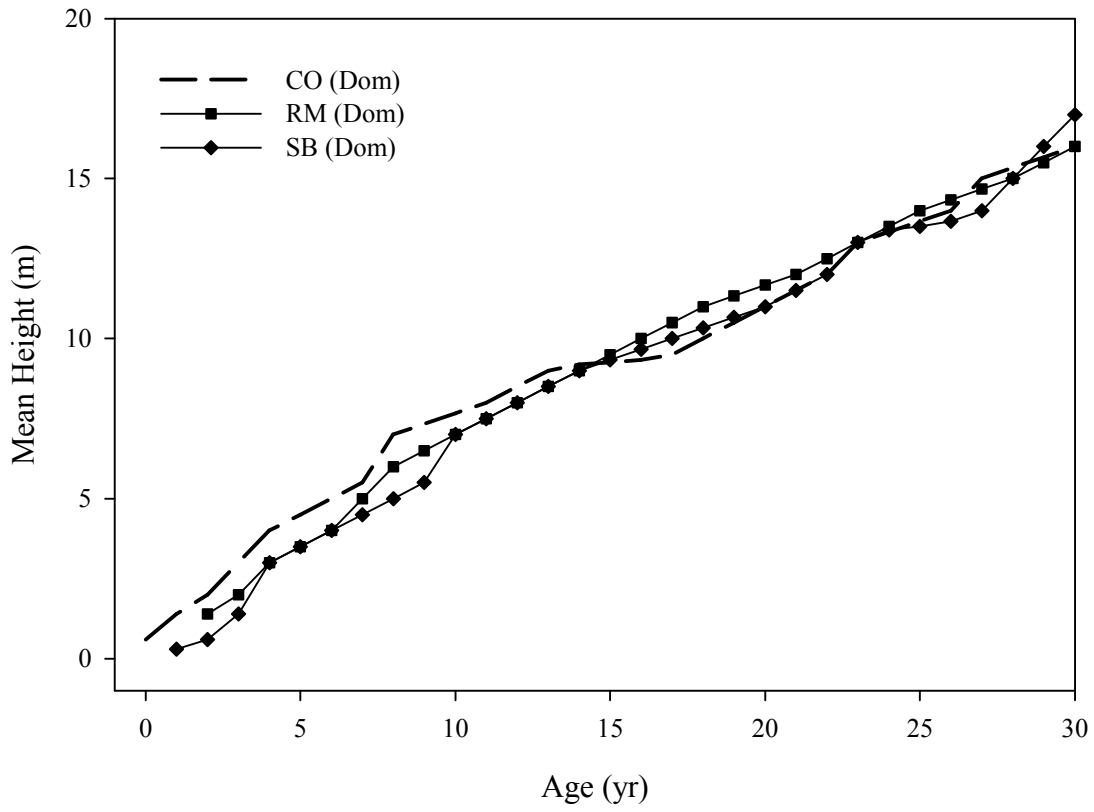


Figure 18. Stand 5, Neighborhood 26. Subordinate chestnut oak competing with a dominant red maple and a subordinate red maple.

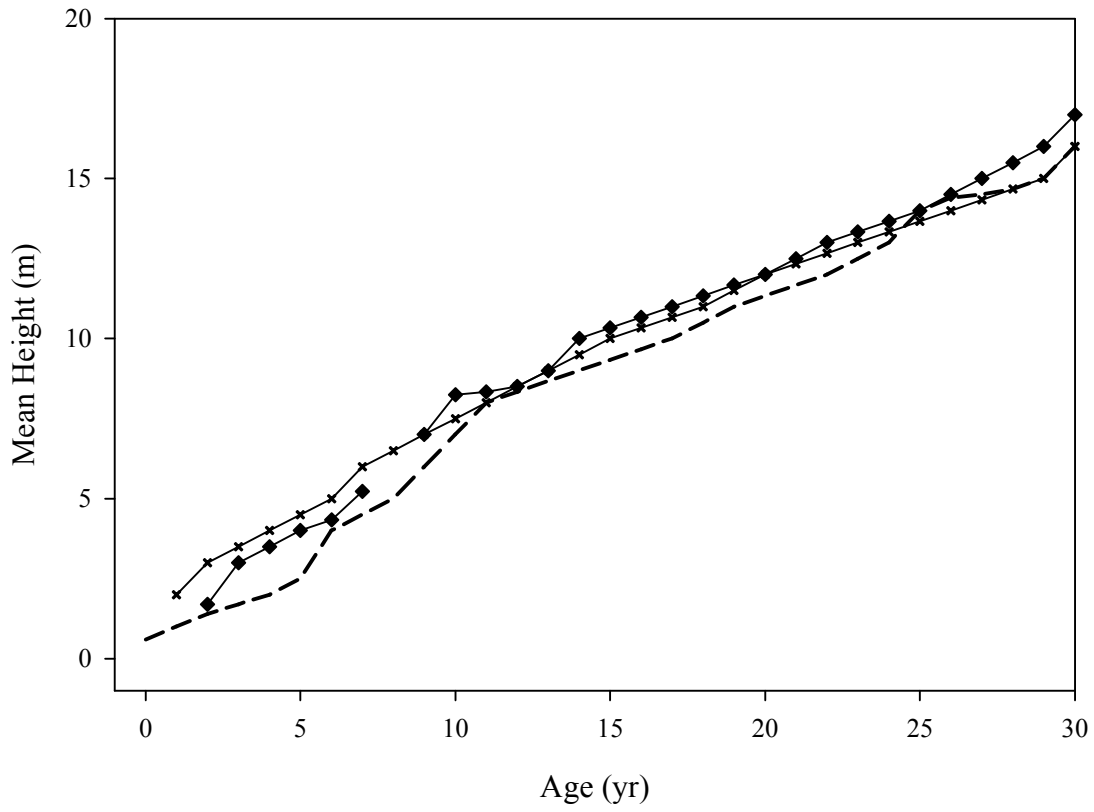


Figure 19. Stand 7. Neighborhood 2. Dominant chestnut oak competing with a dominant sweet birch and dominant red maple.

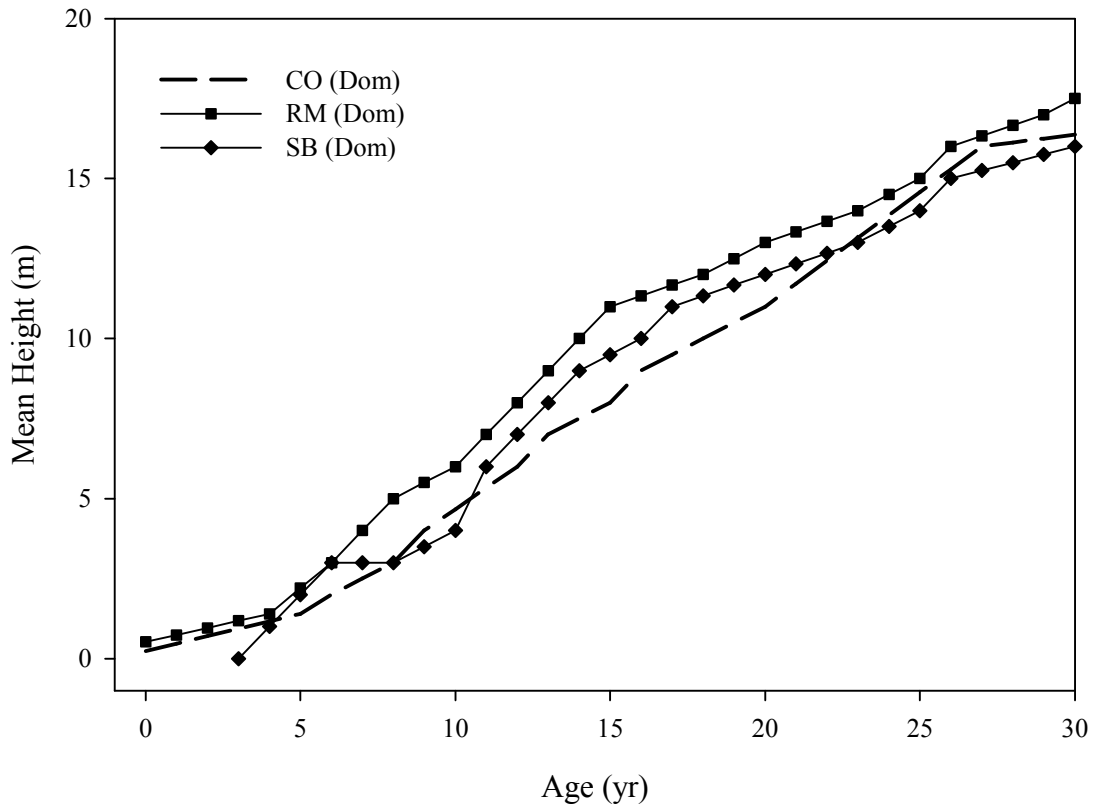


Figure 20. Stand 7, Neighborhood 26. Subordinate chestnut oak competing with a dominant red maple and subordinate red maple.

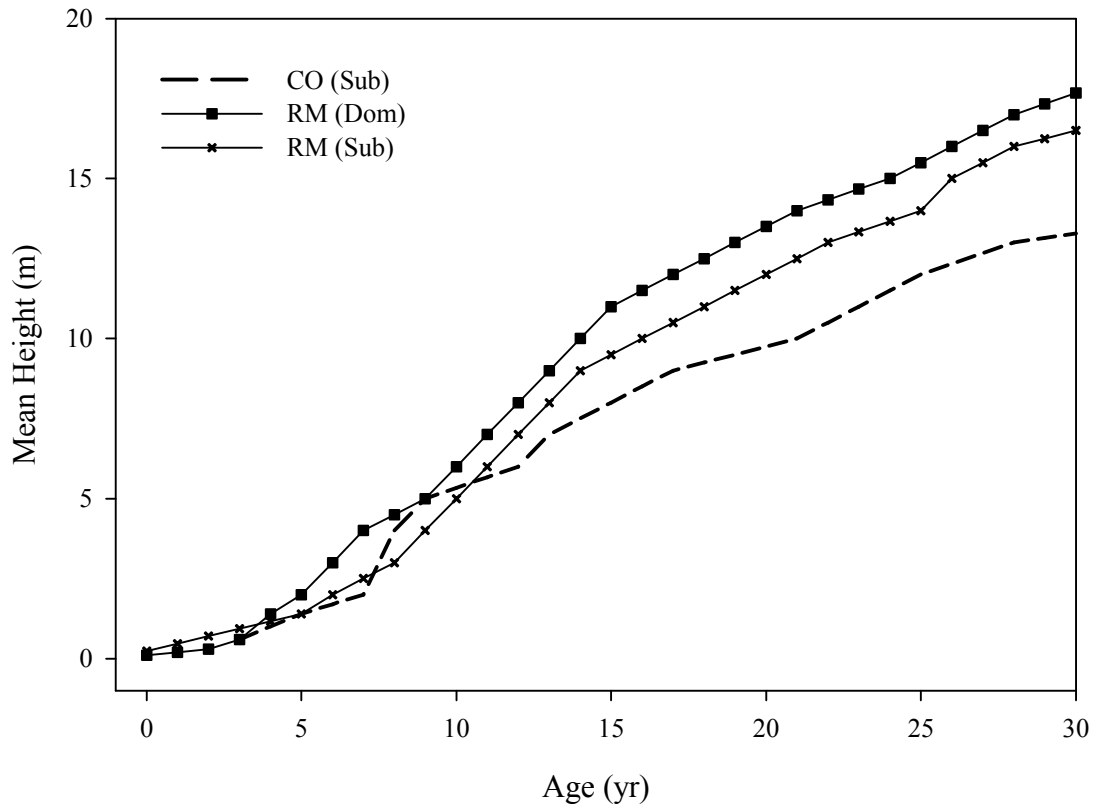


Figure 21. Stand 8, Neighborhood 16. Dominant northern red oak competing with a dominant sweet birch and dominant red maple.

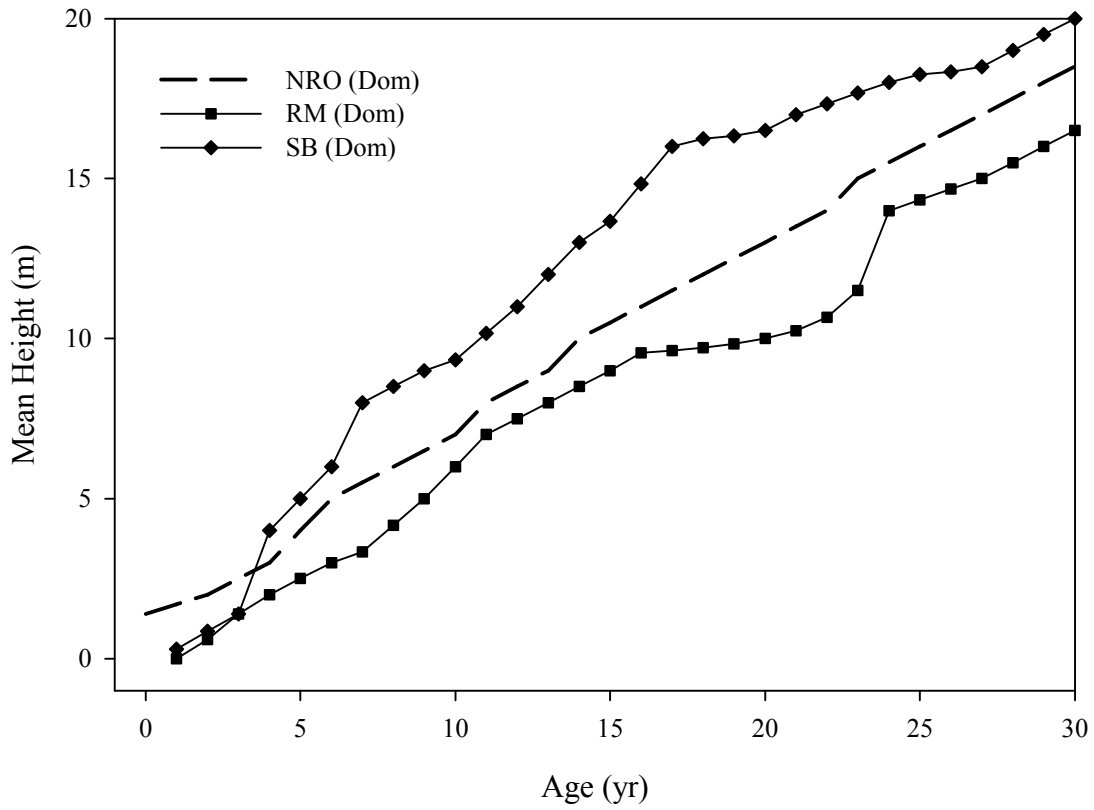


Figure 22. Stand 8, Neighborhood 8. Subordinate northern red oak competing with a subordinate sweet birch and dominant black cherry.

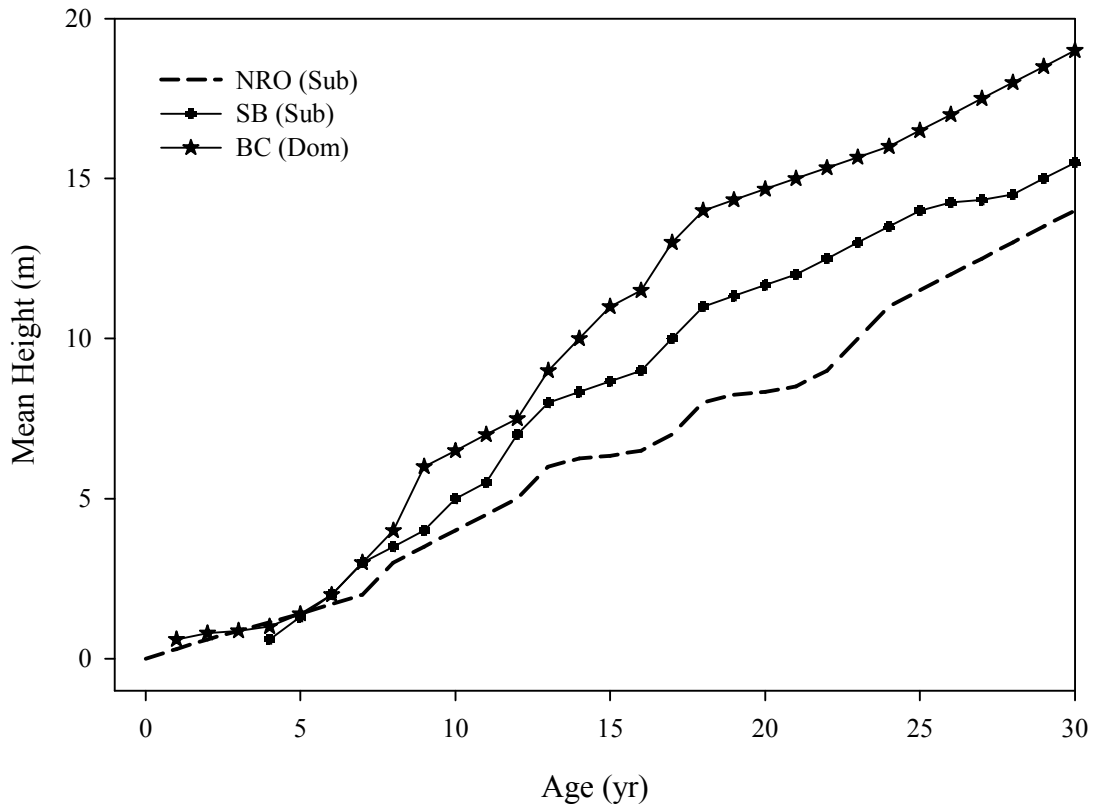


Figure 23. Stand 13, Neighborhood 21. Dominant northern red oak competing with a dominant red maple and dominant black cherry.

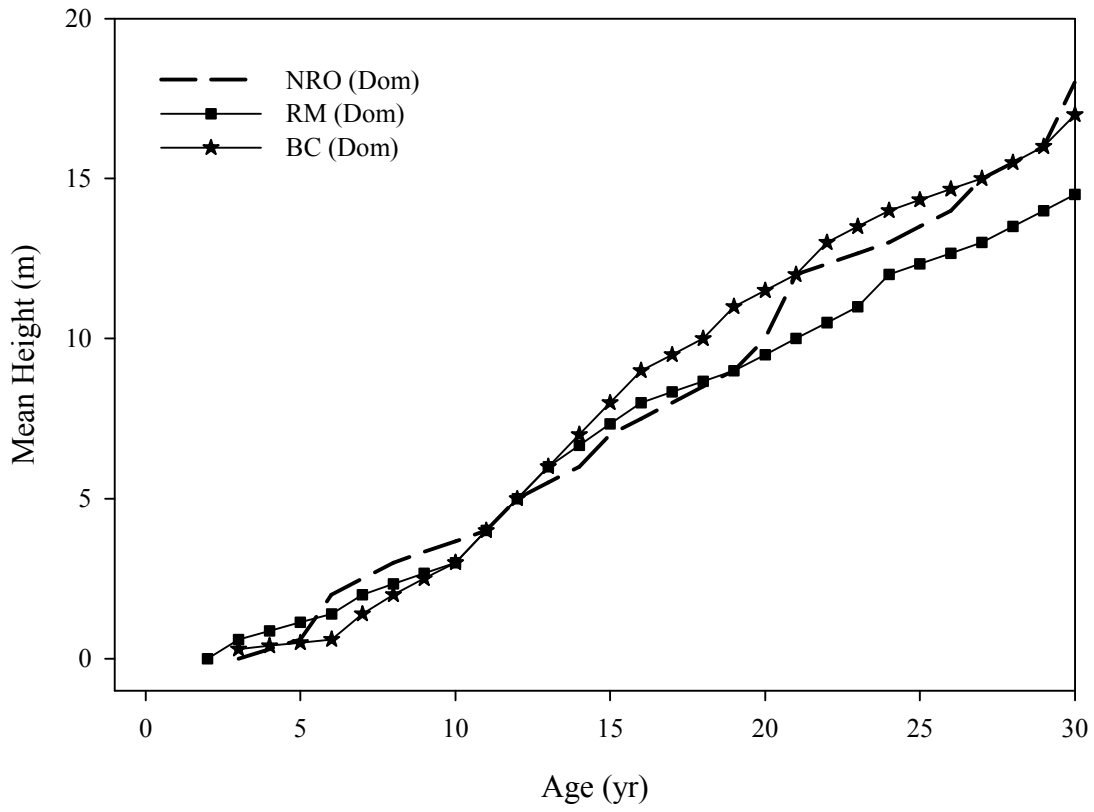


Figure 24. Stand 13, Neighborhood 45. Subordinate northern red oak competing with a subordinate red maple and dominant black cherry.

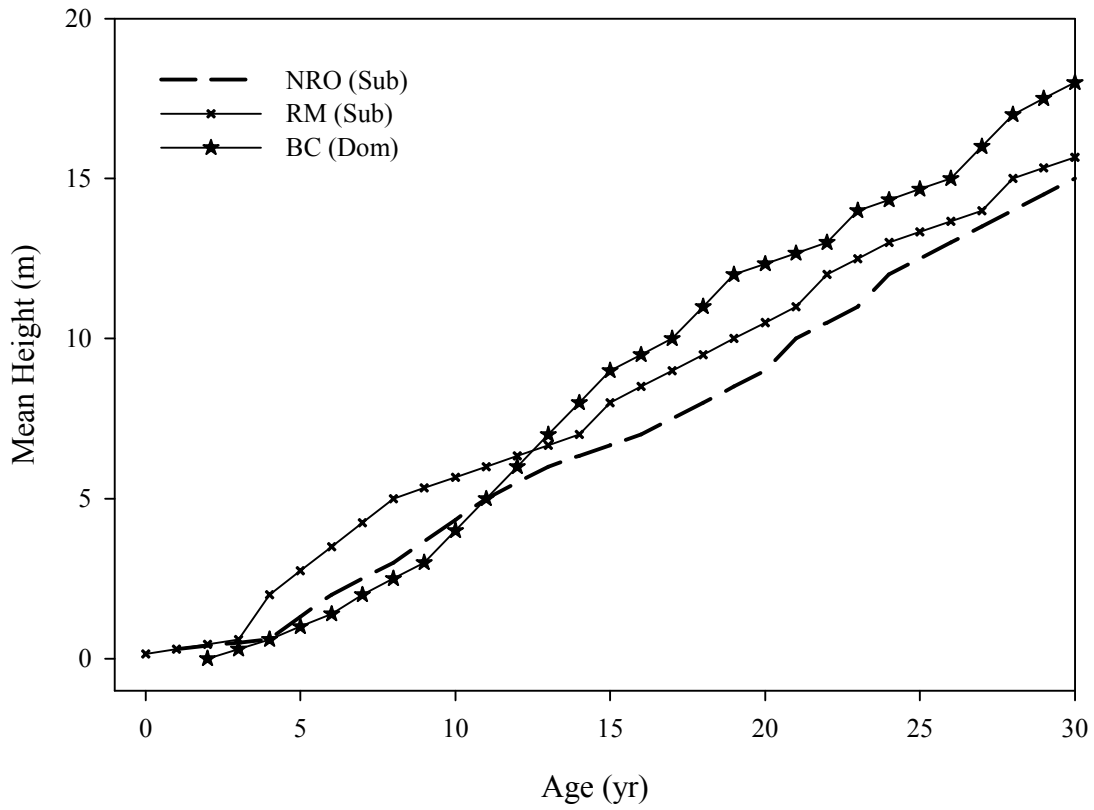


Figure 25. Stand 143, Neighborhood 14. Dominant northern red oak competing with a dominant red maple and dominant black cherry.

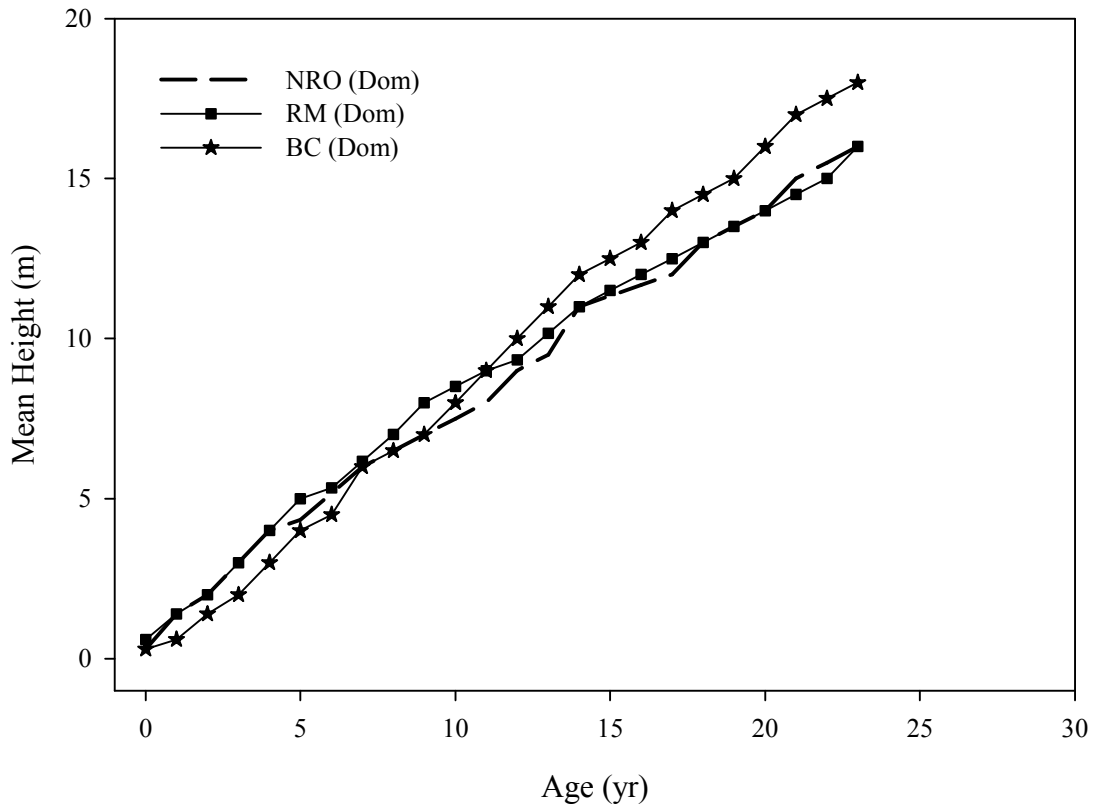


Figure 26. Stand 143, Neighborhood 100. Dominant northern red oak competing with a dominant red maple and subordinate sweet birch.

