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CANOPY OPENNESS AS A PREDICTOR OF GROWTH FOR *CASTANEA DENTATA* SEEDLINGS IN THE CUMBERLAND UPLANDS OF TENNESSEE

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A Thesis Submitted to the Faculty of the University of Tennessee at Chattanooga in Fulfillment of the Requirements of a Departmental Honors Thesis

The University of Tennessee at Chattanooga Chattanooga, TN

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ABSTRACT

Castanea dentata growth and reproduction in the forest ecosystem is limited by light. Canopy gaps could be used for restoration efforts; however, the lack of blight resistant planting material has limited what is known about the silvicultural requirements of *C. dentata*. I studied the survival and growth of chestnut seedlings in various sized light gaps in the Cumberland Uplands in the 2019 season. The Tennessee Chapter of the American Chestnut Foundation previously established Eagle Point Railroad (Cumberland Plateau) and the Starr Farm (Eastern Highland Rim), and I established a site near Barker Pounds trailhead (Cumberland Plateau). Results indicate that canopy openness, as well as seedling age and site selection, is a significant predictor of vertical growth for seedlings at Eagle Point Railroad and the Starr Farm. At Barker Pounds, first season mortality was 75.8%, and subsequent soil samples tested positive for *Phytophthora cinnamomi* which causes a root rot in *C. dentata*.

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TABLE OF CONTENTS

CHAPTER

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

INTRODUCTION

American chestnut, *Castanea dentata* (Marsh.) Borkh.*,* is a rapidly growing tree valued historically for timber and ecologically for mast (Ashe 1911). Chestnut blight, caused by *Cryphonectria parasitica* (Murr.) Barr*,* and root rot, caused by *Phytophthora cinnamomi,* have decimated the species across its entire range, including the Cumberland Uplands in Tennessee (Frienkel 2007). Breeding programs for blight resistance by crossing *C. dentata* with Asian chestnuts are ongoing (Hebard 2012). Advanced breeding material is now ready for reintroduction trials, but further study is needed on the ecological factors for seedling establishment in the forest (Clark et al. 2011).

Light limits, at least partly, *Castanea dentata* growth and reproduction in forest ecosystems (Paillet 2002). Pre-blight chestnut took advantage of the light made available through canopy gaps, created by windthrow or fire (Ashe 1911). Closed canopy reintroductions have not been successful; however, artificial and existing canopy gaps can be used for *C. dentata* seedling establishment for restoration efforts (Dalgleish et al. 2015). The silvicultural requirements of *C. dentata* is little understood because of the lack of blight resistant planting material to study. This includes its establishment in light gaps (Clark et al. 2011, Rhoades et al. 2009). During the 2019 season, I studied the survival and growth of 723 seedlings from the American Chestnut Foundation (TACF) in 35 various sized light gaps in the Cumberland Uplands. The Cumberland Upland locations include two sites previously established by Tennessee TACF volunteers at the private conservation easement at Eagle Point Railroad (Cumberland Plateau), and at the privately-owned Starr Farm (Eastern Highland Rim). I established a new location near the Barker Pounds trailhead of the Cumberland Trail in the North Chickamauga Creek Gorge State Natural Area (Cumberland Plateau) with 9 light gaps: 3 small, 3 medium, and 3 large (open field) plantings. I compared canopy openness to the growth rate and survival of the saplings. I measured height, root collar diameter (RCD), and survivorship in April/May 2019 and late September and October 2019. Canopy openness was measured by hemispherical photography in September. A hemispherical photograph taken at each seedling allowed calculation of percent canopy openness in Gap Light Analyzer 2.0 (Frazer et al. 1999). Results indicate that canopy openness is a significant predictor of vertical growth for seedlings at Eagle Point Railroad and the Starr Farm. Vertical growth increased with the age of the seedlings but is also site dependent. There was no significant difference in vertical growth between the B3F3 hybrid and the American chestnut seedlings. At Barker Pounds, first season mortality was 75.8%, and subsequent soil samples tested positive for *Phytophthora cinnamomi.* These results contribute to the silvicultural light requirements for *C. dentata* reintroductions into Cumberland Upland forests in Tennessee.

CHAPTER II

LITERATURE REVIEW

Canopy Gaps in the Forest Cycle

Light gaps are breaks in the forest canopy assemblage (Norman and Campbell 1998). The canopy is described as the composition of above ground plant material, including the distribution and structure of individual trees (Schleppi and Paquette 2017). Gaps in the canopy are created by disturbance as part of the forest cycle. All stages of succession (gaps, maturing stands, and mature stands) are intermittent in a forest (Whitmore 1989). There is variation in understory light levels based on the structure and geometry of the trees surrounding a gap (Canham 1988). Therefore, the size of the gap impacts the conditions influencing which species can flourish beneath (Poulson and Platt 1989, Norman and Campbell 1998). Increased insolation can alter soil moisture and temperature, air temperature, photosynthetically active radiation (PAR), transpiration, and evaporation. The canopy gap can also modify the intercepted wind and precipitation (Canham and Loucks 1984, Norman and Campbell 1998, Fu and Rich 2002).

Canopy gaps increase light availability for seedling establishment and growth and allow young trees to reach the forest canopy (Canham 1989). Even small openings, perhaps caused by the death of a single tree, can significantly increase light available to understory plants (Canham 1984). In fact, many tree species delay reproduction until they reach the canopy (Spurr and Barnes 1980). Light, or solar radiation from the sun, is necessary for growth, photosynthesis, evapotranspiration, and other functions. However, different tree species very in their tolerance to sun and shade (Schleppi and Paquette 2017). Shade-intolerant species, known as pioneer species, only germinate in full sun, such as in a canopy gap. It is difficult for them to germinate and establish in shade (Whitmore 1989). Some pioneer species depend on large canopy gaps for establishment (Canham 1988). Shade-tolerant species, known as climax species, can germinate in a closed canopy and persist in shade for years. When a canopy gap is formed above, an established climax species can increase its growth rate. However, some climax species only require a small canopy opening and others require a large canopy opening for this release (Whitmore 1989). Their growth response to introduced light is variable, ranging from a small to large reaction (Canham 1989). Climax seedlings that await sufficient light to grow are susceptible to drought, loss of leaves, and disease, considering that their root systems are not developed enough for environmental stressors (Waring 1987). An extended time under the closed canopy might "stunt" their response to introduced light (Poulson and Platt 1989).

In addition to light/shade-tolerance, light influences tree growth and shape. Growth rate is influenced by photosynthesis, to which radiation is a limiting factor. Shedding branches is due to a lack of light. Tree growth and development is further controlled by light in a process known as photomorphogenesis. This controls germination and flowering. as well as etiolation, which is the growth of a shaded tree towards light. Etiolation directs the growth of broadleaf trees for their whole life, as opposed to conifers. Hence, a large old broadleaf tree will recruit its canopy to fill a newly opened adjacent small canopy gap (Schleppi and Paquette 2017).

American Chestnut

Historically, American chestnut (*Castanea dentata* (Marshall) Borkhausen) took advantage of canopy gaps caused by natural disturbances such as wind or fire (Ashe 1911). After a disturbance or the creation of a canopy gap, *C. dentata* has a robust ability to sprout from its base or establish in the opening and grow rapidly into the canopy (Paillet and Rutter 1989). Light availability is probably the most limiting factor to the growth and reproductive success of *C. dentata* in a forest ecosystem. Chestnut trees will only bloom in full sunlight, so they need to reach the forest canopy to reproduce (Paillet 2002).

An introduced ascomycete fungus from Asia, *Cryphonectria parasitica* (Murr.) Barr, devastated American chestnut populations in the early 1900s. *C. dentata* populations in North America have been reduced to non-flowering shrubs in response; they may be functionally extinct (Hepting 1974, Anagnostakis 1987, Roane et al. 1986). *Phytophthora cinnamomi* Rands which causes a root rot in *C. dentata*, is also threatening the species (Crandall et al. 1945).

The American Chestnut Foundation (TACF) has developed chestnut blight resistant hybrids, primarily through a program of a backcross breeding begun in 1983 (Hebard 2012). The backcross breeding program was proposed to breed blight resistance from the Chinese chestnut (*Castanea mollissima* Blume) to *C. dentata.* It was proposed that the third backcross of an F1 hybrid between *C. mollissima* and *C. dentata* to the American tree would produce a timber-like tree, called a B3F1. Blight resistant progeny would be bred for a B3F2 generation and then a B3F3 generation (Burnham 1988). The backcross breeding program is now testing B3F3s for blight resistance; however, cankers sizes of selected B3F3 progeny are closer to that of the F1 generation than the Chinese chestnut. Blight susceptibility is likely polygenic. TACF plans to

improve the breeding program by increasing the accuracy of selection (Steiner et al. 2017, Westbrook et al. 2020).

American Chestnut Response to Light in the Forest

The lack of blight resistant planting material has limited what is known about the silvicultural requirements of *C. dentata*, including its establishment in light gaps (Clark et al. 2011). As with other plants under pressure by a pathogen, such as the butternut, *Juglans cinerea*, focus has been on developing resistance. Little has been carried out to restore the species ex situ (Thompson et al. 2006). Large scale progeny tests of advanced TACF hybrid chestnut trees under forest conditions were begun only relatively recently (Clark et al. 2011). TACF now has B3F3 hybrid seedlings planted in 5 to 10-year-old field trials but requires more time to test natural blight resistance (Westbrook et al. 2020). In the forest, there are external biotic factors such as animal and insect browse and disease. The abiotic factors, such as those influenced by the canopy gap, determine success. Therefore, field tests of improved genotypes are necessary because of the many challenges of *C. dentata* restoration and the large range of environment to which it will be introduced (Clark et al. 2014).

Literature is not conclusive on the light requirements of *C. dentata* (Ashe 1911, Joesting et al. 2009, Wang et al. 2006). Seedlings and sprouts can grow slowly in the deep shade of the canopy and then assume rapid growth in light. However, seedling growth might be stunted in prolonged low light levels. American chestnut has characteristics of a shade tolerant and intolerant species and can be classified to have intermediate shade tolerance (Ashe 1911, Joesting et al. 2009). However, Wang and his colleagues (2006) found that chestnut has a

relatively low light saturation and compensation point compared to other eastern trees, which suggests chestnuts are shade tolerant.

American Chestnut Reintroductions

American chestnut restoration needs to be strategic. Forest reintroductions and site maintenance are costly, and the chestnut hybrid founder stock is limited. An established site also has the risk to fail. This is reason to plant relatively few individuals, without sacrificing genetic diversity, at many locations (Pierson et al. 2007). There must be sufficient canopy openness to provide enough light for seedlings to grow. However, large plots or clearcuts destroy forest resources. Partial canopy retention is a viable treatment for survival and growth of seedlings (DeLong et al. 2005). Successfully established pioneer trees can reach the canopy and disperse seed to other light gaps (Paillet and Rutter 1989). I suggest that artificial and existing canopy gaps could be used for establishing *C. dentata* pioneer trees and may encourage flowering in existing trees for restoration efforts.

Measuring Light with Hemispherical Photography

Canopy gaps can be difficult to characterize. Canopy gaps even of the same size do not allow the same amount of light to reach the floor because of the variation in trees surrounding the gap (personal observation). However, canopy openness, which is the measure of diffuse light (Norman and Campbell 1989), can be measured in a canopy gap by photography. Canopy photos taken by an upward-facing hemispherical camera with a 180-degree field-of-view is an indirect

measurement of canopy structure (Norman and Campbell 1989). Programs such as Gap Light Analyzer 2.0 (Fraser et al. 1999) use geometric principals to describe the light conditions (Hall et al. 2017). Light reaches the forest floor through canopy gaps, as well as through and between tree crowns. Since hemispherical photography considers all angles of incident sun, the spatial variability of the canopy is represented in the photo (Schleppi and Paquatte 2017). It is more precise and less subjective than visual assessments (Chan et al. 1986) and is a useful method to measure the relationship between seedling growth and canopy structure (Mailly 2017).

The Cumberland Uplands

The Cumberland Uplands in Tennessee are one of the historical habitats of *C. dentata* (Schibig et al. 2006). The Cumberland Uplands contain the Cumberland Plateau and Eastern Highland Rim physiographic regions (Francis and Loftus 1977). The Cumberland Plateau is part of the Appalachian Plateaus Province (Fenneman 1938). Its southern section is divided by the Sequatchie Valley anticline. The eastern dissection is called Walden's Ridge; however, it is geologically alike. The eastern boundary rising 288 meters above the Tennessee Ridge and Valleys is called the Cumberland Escarpment. The western boundary ends in gorges and coves (Hinkle 1978). The tableland top is flat to rolling and greatly defined by the underlying bedrock of Pennsylvania sandstone (Fenneman 1938). The Eastern Highland Rim, descending some 800 meters, is a limestone bench that borders to the west in the Low Interior Plateaus Province (Fenneman 1938). The erosion of sandstone and limestone created its rolling plain (Francis and Loftus 1977).

The forests of the Cumberland Uplands were developed both naturally and culturally. The Cumberland Plateau is characterized by mixed mesophytic forest. This is a shared dominance association of species such as beech, tuliptree, basswood, sugar maple, sweet buckeye, chestnut, red and white oak, and hemlock. However, the tableland is mostly dominated by oak. The Eastern Highland Rim marks the beginning of the western mesophytic forest being an oak-hickory forest. However, it is an ecotone from the mixed mesophytic forest on the plateau to the stereotypical western mesophytic forest near the Tennessee River on the western border of the state. The Eastern Rim is characterized by oak forest and oak-hickory forest thriving on the rolling and isolated hills (Braun 1950). Native Americans encouraged the oak-chestnut forests on ridges, upper slopes, and cliff slopes by fire. Pre-European human populations, as an intermediate disturbance, enriched biodiversity through the creation of canopy gaps for garden plots. These forests have continued to change with modern deforestation and fire suppression. The introduction of chestnut blight was also the result of both human and biological disturbance (Delcourt and Delcourt 1998). Loblolly pine monoculture has been increasing in the region (Schultz 1997).

Castanea dentata composed 15% of forest trees on the Cumberland Plateau and 20% of forest trees in the Highland Rim (Ashe 1911, Braun 1950, Schibig et al. 2006). The tree clung to coves and north facing hills with deep and sandy soils (Ashe 1911). The American chestnut was effectively extirpated from the Cumberland Uplands by blight (Braun 1950) and was replaced by chestnut oak, northern red oak, red maple, sourwood, and scarlet oak (Woods and Shanks 1958). Even though the Cumberlands did not host the most abundant chestnut stands, chestnut survival is greater in high elevations, making the Cumberland Highlands an ideal location for reintroductions (Griffin 1991).

The Present Study

The present study sought to monitor *Castanea dentata* hybrids planted in various sized canopy gaps over the 2019 growing season at three sites in the Cumberland Uplands. I used hemispherical photography and Gap Light Analyzer 2.0 to measure percent canopy openness for each individual seedling. The specific objectives were to (1) determine the relationship between canopy openness experienced by an individual seedling in a gap to its vertical and root collar diameter growth in one season and (2) determine differences in growth by hybrid seedling type, seedling age, and site. I expected that greater canopy openness would increase growth and that the hybrid seedling type would grow similarly in height and root collar diameter to the American chestnut.

CHAPTER III

METHODS

Study Sites

Light gaps studies were previously begun with help of the Tennessee Chapter of the American Chestnut Foundation at two locations: Eagle Point Railroad (EPRR) and the Starr Farm.

EPRR (35°20'10.5"N 85°26'54.6"W, elevation 544 m) is a private conservation easement in Sequatchie County near Dunlap, Tennessee, USA on the rim of the Cumberland Plateau. Hardwood forest covers the site's plateau rim and steep slopes. The soil has a pH of 4.58. The phosphorus, potassium, calcium, and magnesium content are respectively 8 lb/acre, 32 lb/acre, 125 lb/acre, and 10 lb/acre (UT Extension). A chestnut genotype x environment study was started in 2013 and 2014 (Tom Saielli, personal communication). Additional seedlings were planted by the landowner beginning in 2011 and alongside naturally occurring sprouts. I studied 436 of the seedlings in 24 canopy gaps, including some native sprouts.

The Starr Farm (35°34'28.3"N 86°12'26.5"W, elevation 333 m) is in Coffee County in Noah, Tennessee, USA in the eastern Highland Rim. The site is dominated by hardwood forest on ridge tops and steep slopes. The soil has a pH of 5.07. The phosphorus, potassium, calcium, and magnesium content are respectively 15 lb/acre, 67 lb/acre, 654 lb/acre, and 78 lb/acre (UT Extension). The landowner culled trees to widen naturally occurring canopy gaps. Chestnut

seedlings have been planted in the gaps beginning 2014 to 2019. There were 8 canopy gaps consisting of 62 seedlings.

I established an additional site for a light gap study on the Cumberland Plateau near Barker Pounds trailhead at North Chickamauga Creek Gorge State Natural Area in Hamilton County near Soddy Daisy, Tennessee, USA (35°16'02.0"N 85°16'51.0"W, elevation 544 m). It is managed by Justin P. Wilson Cumberland Trail State Park. The area, known as Barker Pounds, was managed as a Loblolly pine plantation before state ownership and consists of the plateau rim with open field and Loblolly pine stands. The soil has a pH of 5.25. The phosphorus, potassium, calcium, and magnesium content are respectively 3 lb/acre, 37 lb/acre, 208 lb/acre, and 32 lb/acre (UT Extension). I created 3 relatively small, 3 medium, and 3 large (open field) canopy gap plots for a total of 9 plots and planted 219 seedlings.

Summer 2019 was a particularly hot and dry summer with periods of drought. According to the Standardized Precipitation Index (NOAA), east Tennessee ranged from near normal to very moist from April to August 2019. However, September 2019 was exceptionally dry. According to the Divisional Average Temperature Ranks (NOAA), the average temperature was above average beginning in April 2019, much above average in May 2019 and near average in June 2019. July 2019 began above average temperatures until August 2019. September 2019 had much above average temperatures.

Experimental Materials

The study monitored a total of 723 chestnut seedlings over the 2019 growing season. I planted at Barker Pounds one full sibling and three half sibling families of advanced backcross hybrids derived from the Clapper sources of resistance (Hebard 2012) descended from Tennessee parent trees (Hill Craddock, personal communication). It is expected that these families will segregate for blight resistance from susceptible to resistant (Craddock and Perkins 2019, Westbrook et al. 2020). The three-half sibling B3F2 generation hybrid families used were from seeds of open pollinated third backcross trees at the TN-TTU orchard at Tennessee Technological University in Cookeville, Tennessee. The full sibling TN-TTU-L13 (B3) x SA408 (B2F2) hybrid seedlings were planted as well. All seedlings were propagated in the UTC Chestnut Research Greenhouse, Chattanooga, TN. The pedigrees of the Barker Pounds trees are listed in Table 1.

The landowner at Starr farm began planting chestnut seedlings in 2014. Open pollinated B3F3 seedlings were derived from the Wagner and Duncan seed orchards at TACF's Meadowview Research Farms, near Meadowview, Virginia. The B3F2 seedlings are from the Tennessee Tech orchard. American seedlings served as controls. All are listed in Table 2. Other notes and observations from Starr Farm are compiled in Appendix 1 in a document from the landowner, Rogers Starr.

The landowner at EPRR began planting chestnut seedlings between 2011 and 2019 (Table 3). He planted B3F3 chestnut hybrid families from Duncan Farm and Wagner Farm at Meadowview Research Farms, Chinese chestnuts, and American chestnuts. A genotype x environment (G x E) experiment (Tom Saielli, personal communication) planted material starting in 2013. The pilot study for the G x E experiment planted B3F3 seedlings from Wanger Farm at TACF's Meadowview Research Farms. The source of blight resistance for these B3F3 seedlings was the Graves tree. American chestnuts from the seeds of open pollinated American chestnuts

were planted for controls as well as Chinese chestnuts. For the 2014 silvic study, the G x E experiment planted B3F3 seedlings from Duncan Farm at Meadowview Research Farm, American seedlings, an F1 hybrid family, and a Chinese chestnut family.

Table 1. Description of seedlings at Barker Pounds.

Table 2. Description of seedlings at the Starr Farm.

Table 3. Description of seedlings at EPRR. The two seedlings with unknown crosses were used for canopy openness analysis.

Establishing Barker Pounds

Justin P. Wilson Cumberland Trail State Park generously offered the site near Barker Pounds trailhead for this canopy gap chestnut reintroduction study. With the help of state park rangers, I selected naturally occurring canopy gaps in the Loblolly stands: 3 small and 3 medium canopy gaps (Figure 2). In an open field, I selected 3 plots to serve as "large gaps," having no canopy. A dozer with a fire line plow prepared all nine plots by removing understory vegetation and turning the soil (Figure 1).

Figure 1. TN State Forestry department plowed the sites at Barker Pounds using a dozer with a fire line plow.

Figure 2. American chestnut plots near Barker Pounds Trailhead near Soddy Daisy, Tennessee in Hamilton County.

The B3F2 seedlings were dormant, in D40 containers or bareroot, overwintered at 2-3 C in the cooler at the UTC Chestnut Research Greenhouse. In each plot, I planted the seedlings 1.2 m apart in 4.9 m x 4.9 m plots of 25 trees each, oriented north to south. The three families were divided equally between the plots in a randomized complete block design. There were 3 blocks, each including a small, medium, and large gap. Each tree's position within the plot was determined by a random number generator in Excel. One large gap received 19 trees instead of 25 because of a shortage of material. In total, 219 seedlings were planted at Barker Pounds for the 2019 spring planting. I planted the seedlings on May $7th$, 2019 with the help from Cumberland Trail State Park's rangers and students from Ivy Academy, Soddy Daisy, TN.

Seedlings received a unique numbered tag and labeled flag for identification (Figure 3) and were fertilized with a tablespoon of Osmocote.

Figure 3. All plots shared the same grid north-to-south layout with unique number tags for each seedling.

Seedling Measurements

Preseason growth measurements were taken at the Starr Farm on April 24, 2019, Barker Pounds on May 8th, 2019, and EPRR on April 23rd, 26th, and 27th, and May 2nd, 3rd, and 8th, 2019. Height was measured as the vertical distance in centimeters from the seedling base to the base of the new season growth, or the terminal bud scale scar set. A telescopic measuring rod measured trees taller than a meter. Root collar diameter (RCD) was measured in millimeters using a caliber (Rhoades et al. 2009). At EPRR, individual chestnut seedling locations were verified using maps created by the landowner and given a unique number tag for easy identification.

Figure 4. A seedling at EPRR measured by the telescopic measuring rod on September 24th, 2019.

End-of-season growth measurements were taken at the Starr Farm on October 3rd, 2019, at Barker Pounds on September 27th, 2019, and at EPRR on September 22nd and 24th and October

8th, 2019. I returned to EPRR on January 29, 2020 to measure 20 seedlings that had been missed when measuring in the fall. Height was measured as the vertical distance in centimeters from the base of the seedling to the terminal bud. RCD was again recorded in millimeters. Death and deer browse were recorded as well as death of the stem maximum, chestnut blight, and fallen tree shelters.

Hemispherical Photography and Gap Light Analyzer 2.0

Canopy photos were taken using a Nikon D750 SLR camera and a Sigma 4.5 f/2.8 EX DC HSM Circular Fisheye lens. This camera has a 180 field-of-view and a large aperture for understory conditions (Jonckheere et al. 2017). A hemispherical photo was taken for every tree to capture the gradient of light received by the understory based on position in the canopy gap. The camera was leveled one meter above the ground. The top of the photo was oriented north with a compass to simplify processing (Jonckheere et al. 2017). The best conditions for canopy photography are when the sky is uniform in irradiance. This is usually an overcast sky or when the sun in low in the sky in the morning or evening. Photos were taken generally during these conditions, although not always if it was determined that the sun did not obscure the canopy. If sun flecks were rendered in the photo, they were corrected in processing (Fournier et al. 2017). If a tree was taller than the camera apparatus, then the tree was gently pushed to the side to be out of the photo. If the tree was entirely too tall for this method, a north and a south photo was taken. In processing, these two photos were split and combined for a photo without the chestnut tree.

Summer is the stable period for the canopy in broadleaf forests before fall senescence (Fournier et al. 2017). Canopy photos were taken before senescence at Barker Pounds on

September 21^{st} and 27^{th} , 2019 , at EPRR on September 9^{th} , 22^{nd} , and 25^{th} , 2019 , and at the Starr Farm on October 1st, 2019.

Figure 5. Hemispherical photography in a small canopy gap at Barker Pounds.

Gap Light Analyzer 2.0 software (Simon Fraser University, Burnaby, BC, Canada, and the Cary Institute of Ecosystem Studies, Millbrook, NY) calculated canopy openness, which is the percentage of open sky this is visible from the understory (Hall et al. 2017). Since leaves absorb blue light and reduce blue scattering, the blue channel was used to contrast the sky and foliage (Jonckheere et al. 2017). The threshold was held constant 160, except for several overexposed photos in which 180 was used. Each seedling received a value for canopy openness for growth analysis.

Soil Samples

Soil samples were mailed to University of Tennessee Extension office for a soil nutrient test. A composite sample was created to represent each site. Samples were taken about three feet from each seedling to avoid capturing any fertilizer. At Barker Pounds, a sample was taken in each of the 9 plots beside a tree selected by a random number generator in Excel. At the Starr Farm, a sample was taken from each of the 9 canopy gaps in the same manner. 8 canopy gaps were selected randomly in Excel at EPRR. A soil sample was taken beside a tree randomly selected within that canopy gap. Results were reported to me by email.

Root rot was observed on seedlings in the fall at Barker Pounds. 5 samples composed a composite sample, four from the corners and one from the center of the plot, for each one small, medium, and large canopy gap. The soil samples were mailed to Clemson University for testing. *Phytophthora cinnamomi*, a root rot causing fungus, was recovered in each of the three composite samples. This is typical of pine plantation soils (Steven Jeffers, personal communication).

Barker Pounds Replant

Trees at Barker Pounds that did not survive the 2019 season were replaced on December 7th, 2019. The new seedlings were overwintered in D40 containers at 2-3 C in the cooler at the UTC Chestnut Research Greenhouse. Five hybrid families were randomly assigned to the open positions using a random number generator in Excel (Table 4). Seedlings were planted with a tablespoon of Osmocote and received the numbered tag of the deceased seedling.

Table 4. Descriptions of the hybrid families used to replant at Barker Pounds in Fall 2019.

Barker Pounds Fall Replant					
Cross Name	Pedigree	Seed Type	Resistance Source	Year	n
TVA SE 4-12	$(Myco4-6(American) \times VAS9) \times OpB3$	B3F2	Clapper	2019	42
TVA SE 4-5	$(Myco4-6(American) \times VAS9) \times OpB3$	B3F2	Clapper	2019	72
TVA NE 4-29	$(VA89 \times T2(American)) \times OpB3$	B3F2	Clapper	2019	39
TN-TTU-F32	(TNSUM1 x VA89) x OpB3	B3F2	Clapper	2019	5
TN-TTU-B7	(TNSUM1 x VA89) x OpB3	B3F2	Clapper	2019	

Statistical Analysis

Seedlings that experienced deer browse were not included in statistical analysis. When there was no observable deer browse, a seedling that decreased greater than 5 cm in vertical height was considered browsed and not included in analysis. However, a seedling that decreased less than 5 cm with no observable deer browse was considered to have no observable growth (0 cm growth) and was considered for statistical analysis.

I used R and R Studio (R Core Team 2017) to process all analyses for this study. Mean vertical growth and RCD growth was tested with a one-way ANOVA. Seedling growth in height and RCD was evaluated using step-wise multiple regression analysis. The linearity condition for each term (canopy openness and seedling age) was evaluated in a linear regression to growth. A partial F-test was used to test each term's significance in improving the model. The partial F-test was also used to assess a polynomial regression with canopy openness squared and interactions.

CHAPTER IV

RESULTS

Barker Pounds

First season mortality was extremely high at for the newly established seedlings at Barker Pounds. 5.02% of seedlings had died when checked on May 28th, 2019, 43.38% had died when checked on July $5th$, 2019, and 75.80% of the seedlings had died by the end of the growing season. Small, medium, and large canopy gap plots had 68.00%, 80.00%, and 79.71% mortality respectively. Deer browsed the area heavily. Signs of deer browse was present on 7.30%, 38.36%, and 48.40% respectively on May $28th$, July $5th$, and by the end of the growing season. Trees that lived through the growing season grew between 0.0 to 29.9 centimeters in vertical height and between 0 to 14 millimeters in RCD. High mortality prevented further statistical analysis.

Each of the three composite soil samples sent to Clemson University tested positive for *Phytophthora cinnamomi*. As a former pine plantation, it is likely the site had *P. cinnamomi* before the seedlings were planted (Steve Jeffers, personal communication). It appears that *P. cinnamomi* is present throughout the site.

Canopy Openness

Percent canopy openness at EPRR ranged from 15.31% to 84.43% for individual seedlings. At Barker Pounds canopy openness ranged from 21.24% to 88.75% for individual seedlings. At the Starr Farm, canopy openness ranged from 22.78% to 62.98% (Figure 6).
Figure 6. The frequency of the percent canopy openness that seedlings experienced. At Barker Pounds, the open field plots experienced high percentage canopy openness. At EPRR, seedlings in the middle of a large plot experienced similar light as an open field.

Canopy Openness for Seedlings at Barker Pounds

Seedlings within the same canopy gap experienced a range of light conditions (Figure 7 and Figure 8). Seedlings were planted in a grid at Barker Pounds. The seedlings in the small gaps received an average of 29.33%, 28.04%, and 33.83% canopy openness, seedlings in medium gaps received an average of 52.26%, 40.45%, and 47.51% canopy openness, and seedlings in the large (open field) gaps received 80.72%, 87.32%, and 82.71% canopy openness (Table 5). Percent canopy openness ranged for individuals in the small gaps on average 13.89%, in the medium gaps 8.79%, and the large gaps 9.67%. According to a one-way ANOVA, ranges of canopy openness, that is the range in light available to the individual that received the least

amount of light to the individual that received the most amount of light within that canopy size,

are not significantly different among gap sizes $(P = 0.501)$.

Table 5. Distribution of percent canopy openness at Baker Pounds.

Figure 8. Seedling in different positions in the plot in each gap received different levels of light.

Canopy Openness in Each Plot At Barker Pounds

Deer Browse

The percent of seedlings that had observable deer browse was 9.52% at EPRR. 0% of seedlings at Starr Farm had observable deer browse This is probably because each seedling had its own deer cage. Seedlings affected by deer browse were not included in the analysis of vertical and RCD growth.

Vertical Growth

After the 2019 growing season, seedlings from EPRR had a mean growth of 8.32 cm and grew between 0.0 cm (or no observable growth) to 82.0 cm. The effect of seedling type on

vertical growth was significant ($F_{3,309} = 2.742$, $P = 0.0434$). Post-hoc analysis with Tukey's test revealed that Chinese seedlings grew significantly less than American seedlings (difference = 7.5 cm, $P = 0.0244$). Chinese seedlings grew slightly significantly less than B3F3 seedlings with $p <$ 0.1 (difference $= 6.3$ cm, $P = 0.0693$). There was no significant difference in growth between the B3F3 and American seedlings (difference $= 1.3$ cm, $P = 0.876$).

Figure 9. Vertical growth over the 2019 growing season at Starr Farm and EPRR.

Seedlings at the Starr Farm had a mean growth of 62.7 cm and grew between 0.0 cm (or no observable growth) to 178.0 cm. The effect of seedling type on vertical growth was not significant ($F_{5,55} = 1.04$, $P = 0.362$).

Table 6. Vertical growth by seedling type.

Vertical Growth ~ Canopy Openness Model for EPRR

A multiple linear regression was tested to predict vertical growth based on percent canopy openness, age of seedling, and seedling type for the seedlings at EPRR. For testing the linearity assumption, a simple linear regression was calculated to predict vertical growth based on canopy openness. A significant regression equation was found $(F_{1,311} = 13.1, P = 0.000343)$, with an R^2 of 0.0405 (Figure 12). Vertical growth is equal to $-2.66 + 0.328$ (% canopy openness) cm when canopy openness is measured in percentages. Vertical growth increased 0.328 cm for each percent of canopy openness. I also tested the linearity of vertical growth based on the seedling age with a simple linear regression. A significant regression equation was found $(F_{1,311})$ $= 22.9$, P = 2.69e⁻⁶), with an R² of 0.0685. Vertical growth is equal to -17.1 + 4.87 (seedling age) cm when seedling age is measured in years since planting. Vertical growth increased 4.87 cm for each year since planting.

I used a step-wise multiple regression of nested models to improve the simple linear model that predicted vertical growth based on percent canopy openness. A partial F-test showed

that seedling age improved the model $(F_{1,310} = 20.4, P = 8.82e^{-6})$. However, using seedling type as a predictor did not significantly improve the model ($F_{3,307} = 2.09$, $P = 0.102$). An interaction term between canopy openness and seedling age improved the model according to the partial Ftest ($F_{1,309} = 6.10$, $p = 0.0141$). However, adding the polynomial term, canopy openness², to the model based on canopy openness and age of seedling also improved the model according to the partial F-test $(F_{1,309} = 9.11, P = 0.00275)$.

For EPRR, the model that predicted vertical growth based on the seedling age, canopy openness, and canopy openness² was selected over the model that predicted vertical growth based on canopy openness, the seedling age, and their interactions because of the improved \mathbb{R}^2 $(0.126 > 0.117)$. The polynomial model had a significant regression (F_{3,309} = 14.8, P = 5.06e⁻⁹). The predicted vertical growth is equal to $-45.0 + 4.30$ (age) $+ 1.54$ (% canopy openness) – 0.0175 (% canopy openness²) cm, where age is years since planting and canopy openness is in percentages (Figure 10). All predictors in this model were significant.

Predicted Growth for 2019 Season at EPRR by Year Since Planting

Vertical Growth ~ Canopy Openness Model for Starr Farm

A multiple linear regression was also tested to predict vertical growth based on percent canopy openness, age of seedling, and seedling type for the seedlings for the seedlings at the Starr Farm. Linearity of vertical growth based on canopy openness was calculated to test assumptions for the multiple regression model. A significant regression equation was found $(F_{1,56})$ $= 11.0$, P = 0.00162), with an R² of 0.164. Vertical growth is equal to -1.77 + 1.77 (% canopy openness) cm, when canopy openness is measured in percentages (Figure 12). Vertical growth increased 1.77 cm for each percent canopy openness. I also tested the linearity of vertical growth based on the seedling age. A significant regression equation was found ($F_{1,56} = 7.80$, $P =$

0.00714), with an \mathbb{R}^2 of 0.122. Vertical growth is equal to 33.6 + 10.0 (seedling age) cm (Figure 11). Vertical growth increased 10.0 cm for each year since planting.

I used a step-wise multiple regression of nested models to improve the simple linear model that predicted vertical growth based on percent canopy openness. A partial F-test showed that seedling age did not significantly improve the model ($F_{1,55} = 1.13$, $P = 0.293$). Adding seedling type as a predictor also did not significantly improve the model ($F_{2,54} = 0.565$, P = 0.572). When canopy openness² was added as a polynomial predictor to the model, the term was not significant ($P = 0.334$). Therefore, a simple linear regression for vertical growth based on canopy openness was selected for the Starr Farm (Figure 11).

Figure 11. Predicted vertical growth for the 2019 season at Starr Farm. Seedling age did not significantly improve the model at Starr Farm.

Predicted Vertical Growth for 2019 Season at Starr Farm

Figure 12. Growth based on canopy openness by site; EPRR and Starr Farm.

Root Collar Diameter Growth

After the 2019 growing season, seedlings from EPRR had a mean RCD increase of 3.25 mm and grew between 0.0 mm (or no observable growth) to 22.0 mm. The effect of seedling type on RCD growth was not significant $(F_{3,309} = 0.811, P = 0.488)$.

Seedlings at the Starr Farm had a mean RCD growth of 20.02 mm and grew between 1.0 mm to 92.0 mm. The effect of seedling type on RCD was significant ($F_{2,55} = 9.65$, $P =$ 0.000255). Post-hoc analysis with Tukey's test revealed that American seedlings grew in RCD significantly more than B3F2 and B3F3 seedlings (difference $=$ 32.6 mm and 23.2 mm, P $=$ 0.000204 and 0.00152, respectively). However, there was no significant difference in RCD growth of the B3F2 and B3F3 seedlings (difference $= 9.5$ mm, $P = 0.199$).

Root Collar Diameter Growth ~ Canopy Openness Model for EPRR

A multiple linear regression was tested to predict RCD growth based on percent canopy openness, seedling age, and seedling type for the seedlings at EPRR. A simple linear regression was calculated to predict RCD growth based on canopy openness. A significant regression equation was found ($F_{1,311} = 20.5$, $P = 8.33e^{-6}$), with an R^2 of 0.0620. RCD growth is equal to -0.643 + 0.116 (% canopy openness) mm. RCD growth increased 0.116 mm for each percent canopy openness. A linear regression of RCD growth based on seedling age was significant $(F_{1,311} = 12.8, P = 0.000407)$, with an R² of 0.0395. RCD growth is predicted by seedling age by the equation $-2.27 + 1.06$ (seedling age) mm. RCD growth increased 1.77 mm for each year since planting.

I used step-wise regression to improve the simple linear model of RCD growth based on canopy openness. A partial F-test showed that adding the seedling age as a predictor significantly improved the model (F_{1,310} = 10.5, P = 0.00129) and that adding the seedling type as a predictor did not significantly improve the model ($F_{3,307} = 0.429$, $P = 0.733$). Adding canopy openness and seedling age as an interaction term significantly improved the model based on canopy openness and seedling age, according to the partial F-test ($F_{1,309} = 4.91$, $P = 0.0274$). Adding a polynomial term, canopy openness², also significantly improved the model based on canopy openness and seedling age, according to the partial F-test $(F_{1,309} = 8.15, P = 0.00378)$. The polynomial model was selected over the interactions model because of the R^2 (0.117 > 0.107). In the polynomial model, the predicted RCD growth is equal to $-10.8 + 0.870$ (seedling age) $+ 0.456$ (% canopy openness) – 0.00485 (% canopy openness²), where age is years since planting and canopy openness is in percentages. All predictors in the polynomial model were significant (Figure 13).

Figure 13. Predicted RCD growth for the 2019 season at EPRR by seedling age, beginning at $age = 0.$

Predicted Diameter Growth for the 2019 Season at EPRR

Root Collar Diameter Growth ~ Canopy Openness Model for Starr Farm

A multiple linear regression was tested to predict RCD growth based on percent canopy openness, age of seedling, and seedling type for the seedlings at the Starr Farm. A simple linear regression of RCD growth based on canopy openness was significant ($F_{1,56} = 48.3$, $P = 4.17e^{-9}$), with a \mathbb{R}^2 of 0.463. RCD growth is predicted by canopy openness by -21.3 + 1.13 (% canopy openness) mm. RCD growth increased 1.13 mm for each percent canopy openness (Figure 14). The linearity of RCD growth based on seedling age was also significant ($F_{1,56} = 22.5$, $P = 1.51e^{-}$

⁵), with an R² of 0.286. RCD growth is predicted by seedling age by $3.09 + 5.84$ (seedling age) mm. RCD growth increased 5.84 mm for each year since planting.

The simple linear regression of RCD growth based on canopy openness was analyzed using step-wise regression. Adding seedling age and seedling type as a predictor did not significantly improve the model, according to the partial F-test ($F_{1,55} = 2.45$, $P = 0.123$ and $F_{2,54}$ $= 0.256$, P = 0.775, respectively). Adding a polynomial term, canopy openness², also did not improve the model according to the partial F-test $(F_{1,55} = 0.698, P = 0.407)$.

Figure 14. Predicted RCD growth for 2019 season at Starr Farm. Seedling age did not significantly improve the model.

Predicted Diameter Growth for 2019 Season at Starr Farm

Combining and Comparing Vertical Growth of EPRR to Starr Farm Seedlings

For this test, data from EPRR and the Starr Farm was combined for analysis and comparison. A simple linear regression of vertical growth based on canopy openness was significant (F_{1,369} = 29.6, P = 9.89e⁻⁸), with an R² of 0.0742. Vertical growth is equal to -14.0 + 0.908 (% canopy openness) cm. Adding the site and seedling age as predictors significantly improved the model according to the partial F-test ($F_{1,368} = 288$, $P = 2.20e^{-16}$ and $F_{1,367} = 25.6$, P $= 6.62e^{-7}$, respectively). The canopy openness² term was not significant when added to the model $(P = 0.139)$.

Therefore, the multiple regression model that predicted vertical growth based on the canopy openness, site (EPRR or the Starr farm), and age of seedling was selected. It was significant (F_{3,367} = 130, P = 2.20e⁻¹⁶), with an R² of 0.515. Vertical growth is equal to -39.5 + 0.482 (% canopy openness) + 67.0 (1 if Starr Farm, 0 if EPRR) + 6.07 (seedling age) cm (Figure 15).

Figure 15. Predicted vertical growth at EPRR and Starr Farm. Beginning at year since planting = 0, vertical growth in a season increases with seedling age. Growth varies with the site and has a positive relationship with canopy openness.

Predicted Vertical Growth at EPRR and Starr Farm by Year Since Planting

% Canopy Openness

Table 7. RCD Growth, and (5) Combined Data Vertical Growth. RCD Growth, and (5) Combined Data Vertical Growth.Regression model results (1) EPRR Vertical Growth, (2) EPRR RCD Growth, (3) Starr Farm Vertical Growth, (4) Starr Farm

 $+2<0.11$; **p<0.05; ***p<0.01

CHAPTER V

DISCUSSION AND CONCLUSION

Barker Pounds

High mortality rate in the first growing season was experienced by the B3F2 hybrid seedlings at Barker Pounds. Other studies have noted high mortality in the first few growing seasons after planting (Pinchot et al. 2017, Rhoades et al. 2009, McNab et al. 2003). In a multiyear study, Pinchot et al. (2017) found that mortality was greater in the first two seasons for seedlings established on the Cumberland Plateau in Kentucky. After four years, only 21% of one hybrid family survived. Rhoades et al. (2009) recorded 57% survival over two growing seasons at locations in the northern Cumberland Plateau. The canopy treatment had no effect on survival. McNab et al. (2003) recorded 66% survival after the first growing season on xeric sites in the southern Appalachian region of North Carolina. For Barker Pounds, I suggest that *Phytophthora* rot root (PRR), the especially hot and dry summer season, transplant shock, and heavy deer browse were all contributing factors.

Phytophthora cinnamomi has been recovered at other chestnut reintroduction sites; high seedling mortality in the sites was linked to PRR (Clark et al. 2009, Rhoades et al. 2009, Pinchot et al. 2017). The root rot kills the once vigorous root system, whereas blight kills only the above ground portion (Anagnostakis 2001). PRR likely contributed to the mortality of many of the seedlings at Barker Pounds. Resistance to PRR in chestnut is likely controlled by relatively few genes compared to chestnut blight. It will be important for TACF to breed chestnut trees for PRR tolerance as well as blight tolerance since the use of fungicides in silviculture reintroductions is

impractical and sometimes not allowed (Clark et al. 2009). Barker Pounds experienced significant drought in the late summer of the 2019 season, which contributed to the mortality and marginal growth of seedlings (personal observation). American chestnuts in a greenhouse study decreased growth after 20 days of water stress and had no growth after 24 days (Bauerle et al. 2006). Below average precipitation ex situ was noted to be a factor to seedling mortality in the first season even without *P. cinnamomi* (McNab 2003). However, American chestnut's water use efficiency increases in response to water stress (Bauerle et al. 2006). Transplant shock is the observation that hardwood nursery stock suffers slow growth when transplanted. This occurs in the establishment period before robust growth starts again (Struve 1990). Clark et al. (2009) notice transplanted chestnuts had marginal growth in the first and second year. Therefore, this study is limited by one season's study of the newly transplanted seedlings at Barker Pounds. 48.8% of the seedlings at Barker Pounds had observable signs of deer browse. Clark et al. (2009) also suggested that seedlings in large canopy openings are more exposed to animal browse. Some plots at EPRR had deer fences and seedlings at the Starr farm had a deer cage for each individual. Deer protection might be needed to best study the growth of chestnut seedlings.

Figure 16. A deer-browsed seedling at Barker Pounds.

Growth

Together, site, canopy openness and seedling age, accounted for 51.5% of variation in vertical growth:

As expected, canopy openness was a significant predictor of vertical growth and RCD growth for chestnut seedlings at the Starr Farm and EPRR. Seedling vertical and RCD growth had a significant correlation to percent canopy openness. 4.0% and 6.2% at EPRR and 16.4% and 46.3% at the Starr Farm, respectively, of the variation in seedling growth was explained by canopy openness. Ecology deals with countless biotic and abiotic effects; the amount of variance explained by canopy openness is expected to be small. This effect is still important because small effects over generations are exaggerated (Moller and Jennions 2002). According to Cohen (1992), canopy openness has a small effect on vertical and RCD growth at EPRR. Canopy openness at the Starr Farm had a medium effect size on vertical growth and a large effect on RCD growth.

These results are consistent with other silvicultural studies that suggest that reintroduced American chestnut grows more in increased light (Pinchot et al. 2017, Rhoades et al. 2009, McCament and McCarthy 2005, Belair et al. 2014, Saielli et al. 2014). Pinchot et al. (2017) found that in shelterwood cuts with 52% canopy openness, compared to thinning and mid-story removal treatments with 13% and 5% canopy openness, respectively, seedlings were 1.4 to 2 times taller and 1.4 to 1.9 times greater in RCD. It should be noted that Pinchot at al. (2017) measured canopy openness by a PAR ceptometer, making light levels difficult to compare to the present study. Rhoades et al. (2009) found that American seedling grew 3.4 times taller and 5.3 times greater in RCD in shelterwood treatments that received 47% of PAR than mid-story removal treatments that received 27% of PAR. McCament and McCarthy (2005) found that chestnut seedlings were significantly larger in thinned stands compared to the control. However, seedlings increased specific leaf area in low light conditions. A positive linear relationship best explained vertical and RCD growth at Starr Farm and for the data overall.

However, a parabolic function of canopy openness best fit the model of vertical and RCD growth for EPRR. This suggests that for the 2019 growing season there was an optimal canopy openness for growth at EPRR. Since many studies have shown that chestnut growth increases with light (Pinchot et al. 2017, Rhoades et al. 2009, McCament and McCarthy 2005, Belair et al.

2014, Saielli et al. 2014), it is possible that there are ecological conditions in the forest associated with increased light that decrease growth. Plots at EPRR were maintained by occasionally trimming of competition, whereas at Starr Farm, the plots were mowed. I observed at EPRR increased competition for chestnut seedlings in a large gap. Competition might reduce nutrient availability and result in decreased growth (Belair et al. 2014) even for seedlings still receiving a large amount of light. Seedlings shaded by competing plants were accounted for by an individual canopy openness measurement. Soil moisture has been found to be higher in canopy gaps, regardless of size, rather than under the closed canopy, though it decreases in years after gap formation and depends on microvariations (Ritter et al. 2005, Galhidy et al. 2006). Chestnut growth responds negatively to decreased soil moisture due to woody competition (Belair et al. 2014, Brown et al, 2014). The center of gaps, or positions with the greatest canopy openness, have a higher air temperature (Galhidy et al. 2006). It is also possible that the hot, dry 2019 summer likely furthered the effect of decreased soil moisture on chestnut seedlings. Optimal canopy openness for seedlings EPRR in the 2019 season appeared to be between 40% and 50% canopy openness due to ecological factors making high light environments detrimental after a threshold (Figure 10).

There was no difference between the American and the B3F3 and B3F2 hybrids in vertical growth. B3 hybrid seedlings theoretically have 15/16 of the American chestnut genes in order to resemble the American tree (Burnham 1987), and the B3 generation has morphology that recovers the American chestnut tree type (Diskin et al. 2006). Rapid growth is important for the recovery of its historical timber-form (Paillet 2002). However, there are genetic difference within hybrid families that could affect vertical growth as well (Diskin et al. 2006). Pinchot et al. (2017) found that a B2F3 hybrid grew slightly more in height than American chestnut, but

vertical growth varied among B2F3 hybrid families as well. The present study did not analyze differences within hybrid generations. Chinese chestnut grew significantly less than the American seedlings. This supports conclusions from Knapp et al. (2014) that explain that the maximum rate of photosynthesis of American chestnut and hybrid B3F3s is twice that of the Chinese chestnut.

RCD growth differed between the American trees and the hybrid seedlings at the Starr Farm. However, there was no significant difference in RCD growth at EPRR. Perhaps, this difference is because all American chestnuts planted at the Starr Farm shard the same canopy gap.

I found site to be a significant predictor of growth. In the predictive model, seedlings at the Starr Farm grew significantly more in the 2019 season than at EPRR. Natural species' distributions in the mesophytic forest, in which the study sites are situated, are influenced by a site's soil characteristics. The landscape aspect will impact the weathering of soils and vegetation structure (Muller 1982). American chestnut can persist on poor soils; however, it increases growth in fertile soils (Wang et al. 2013, Rhoades et al. 2009). The soils at EPRR were slightly more acidic (pH 4.58 compared to pH 5.07 at Starr Farm). However, these values fall in the soil pH of chestnut's natural distributions, about a pH of 4 to 5 (Burke 2011). Starr Farm's soils also had more phosphorus, potassium, calcium, magnesium than the other sites. EPRR and Barker Pounds had deficient magnesium (UT Extension). American chestnut growth has been linked to magnesium and potassium (McCament and McCarthy 2005). However, fertilizer was applied to seedlings at all sites. A favorable site elevation likely varies north to south (Burke 2011). Forest site index is the predicted capability of a forest landscape to grow trees based on site quality. The

index is calculated based on combined height of dominant tree species years at 50 years of age (Carmean et al.1989). This has not been developed for American chestnut since they were mostly devastated before the creation of the index. Therefore, site selections for chestnut reintroduction should be done thoughtfully.

Older seedlings grew more. This was true for EPRR and the combined data of EPRR and Starr Farm. McCament and McCarthy (2005) noted that silvicultural treatments had an increased in effect on seedling growth with age. This trend is not expected for the lifespan of the tree. Chestnut growth is more rapid in the first decade and thereafter begins to decline (Ashe 1911). The seedlings in the present study were all under 10 years old. However, seedling age did not have a significant effect on growth at Starr Farm perhaps because of sample size.

Canopy Openness and Competition

Large canopy gaps at EPRR where plots had minimal maintenance had more understory competition than the smaller canopy gaps (personal observation). An analysis of competition was not an objective of this study. However, it is apparent through the measure of canopy openness for each individual tree that not all seedlings receive the same amount of light in a canopy gap (Figure 17). In a large canopy gap at EPRR nicknamed "Tracy City", the difference in canopy openness ranged 43.8%. In another large canopy gap nicknamed "Rocky Top", the least canopy openness experienced by an individual seedling was 19.86% and the most was 54.11% while the average was 39.37%. This range exists because competing vegetation advantaged by the high light levels shadowed some seedlings. Compared to a small gap, nicknamed "Allen" with less

competing vegetation, the minimum canopy openness was 17.0% and the maximum was 26.72% with a range of only 9.72%.

Figure 17. Canopy openness ranged 43.8% in a single large canopy gap at EPRR because of the presence of competing vegetation.

Planted chestnuts are less likely to outcompete vegetation (Griffin et al. 1991, McNab 2003). Pinchot et al. (2017) noted that the silvicultural treatment with the most available light also had the most understory woody competition. In high light shelterwood cuts, 41% of chestnut seedlings were dominant in the understory while 53% were dominant in a lower light thinning treatment. The results reported by Pinchot et al. (2017) suggest that elevated vertical growth in the first few growing season is not the best indicator of success because of competition. Chestnut seedlings must maintain their dominance to reach the canopy. Even though chestnut has the

potential to grow more in high light conditions, fast-growing shade intolerant species and stump sprouts challenge introduced chestnut seedlings in high light (Loftis 1985, Belair et al. 2014). Reduced competition in the first years after planting may be critical for successful restorations (Belair et al. 2014). I found that moderate light levels still encouraged chestnut growth and observed reduced competition in moderate light levels. Chestnut compared to other hardwood species has a very plastic response to light (Wang et al. 2006, Joesting et al. 2009, Belair et al. 2014). Therefore, moderate light conditions, or smaller canopy gaps, for initial planting might be favorable for competition, and then, more light could be introduced (Rhoades et al. 2009, Belair et al. 2014, Wang et al. 2006). The canopy gaps could be culled after the seedlings are established to release the seedlings (Wang et al. 2006, Griscom and Griscom 2012).

Canopy Openness (Individual measurements versus whole gap measurements)

Available light has been measured in different ways in forest reintroductions for chestnut hybrids. McCament and McCarthy (2005) took a hemispherical photo in the center of each plot to show the difference in light among treatments. Some chestnut silvicultural studies have taken individual seedling measurements for an average canopy openness of each treatment (Saielli et al. 2014, Pinchot et al. 2017). Knapp et al. (2014) measured PAR and percent of full sunlight for each individual seedling, and the unique measurement was preserved in analysis. It is not sufficient for a canopy gap study to assume the amount of available light is consistent throughout the gap (Gray and Spies 1996). Microclimate variations can be studied by analyzing measurements at each seedling. Small scale reintroductions with limited resistant chestnut stock

should note the amount of light that each seedling could potential receive and select optimal positions for the seedling within the canopy gap.

Canopy Gaps for Chestnut Hybrid Reintroductions

Chestnuts can be reintroduced into a forest with minimal input and maintenance (McNab et al. 2003). The present study shows the early success of canopy gaps for reintroductions. To lessen establishment costs, canopy gaps are a possible alternative to high impact introductions. Chestnut hybrid founder stock is already limited and costly, and TACF is still working to improve blight resistant selections (Westbrook et al. 2020). Site quality will be important for successful reintroductions. Gaps should be selected based on canopy openness. Seedlings at the Starr Farm were predicted to grow well in any canopy openness, though they grew more with increased light. Starr Farm represents site where canopy gaps had regular maintenance. At EPRR, the overall model suggested that 80% canopy openness would encourage growth for seedlings planted in the same year, but a 10% canopy openness would only allow 6-year-old seedlings to marginally grow. However, EPRR represented a site with low maintenance input. Therefore, the specific site model suggests 40% to 50% canopy openness for all aged seedlings to grow optimally. Therefore, moderate canopy openness may be favorable for low maintenance sites. This should be considered for expansive plantings, where regular maintenance is not possible or too costly. Low maintenance sites might be culled once seedlings are better established (Wang et al. 2006, Griscom and Griscom 2012).

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APPENDIX 1

CHESTNUT RESTORATION TO MATURE, NATIVE FOREST RANGES

Chestnut Restoration to Mature, Native Forest Ranges

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Premise: Restoration to native forest ranges involves more than breeding orchards, seed orchards, or ceremonial/individual plantings. Breeding and seed orchard sites typically involve 3+ acres, well cleared and rogued, and planting of several hundred seedlings *of multiple, repeated lineage with controls. The addition of smaller, "semi-prepared" plats involving preparation of 0.1 to 0.2 acres will permit the establishment of restoration locations more broadly dispersed throughout the native ranges on private, state and federal lands.*

Selection **of "Semi-prepared" Sites for Chestnut Restoration**

Considerations for selection are:

- Sites at relatively high elevation with good soil drainage to minimize phytophthora issues are preferred. [My hilly sites are at 1100-1200 ft. elevation with surrounding valleys at 800-900 ft.]
- Southern or southwestern exposure is preferred.
- Sites should be suitable for 5 to 10 trees due to survival issues, reducing the prospect of survival of less than 2 trees and loss of pollination potential.
- Plat sizes evaluated in this study are $60x75$ ft. (approx. 0.1 acre) for four trees and $60x125$ ft. (approx. 0.2 acre) for 8 trees, all on 10-15 ft. centers, with optimal orientation, as will be discussed below. The sizes are selected to achieve 3 ½-5+ hrs. of direct sunlight exposure per day from early April to the end of September depending on surrounding canopy height.
- Site access for twice yearly maintenance (grass control, weed eating, bush hogging, brush/limb removal), watering up to 3 or 4 times if excessively dry, and overall stewardship for 4-5 years is almost a necessity for success.
- Planting of healthy seedlings, 2 years old and 30 to 40 inches in height with well-developed root systems, should improve the prospects of success. After all, if you are going to all this trouble, you might as well take the time to plant "good stock" considering that the absolute number of trees being planted is relatively small.

NOTE – The smaller plat size above can be utilized in difficult to access locations where limited clearing with little or no mechanized equipment is practical, as well as, in areas with zones of small (<4 in) to medium (~10 in) native trees requiring removal. In other words, exploit the zones between larger trees. Even at this size, 4-6 hours of work by 2-3 people will be required in mature forested areas. These smaller plat sizes are usually not suitable for canopy heights above 40 ft. as will be discussed below.

Where larger trees can be removed, usually involving heavier equipment, the plat size can be increased to the larger size cited above to accommodate 8 trees and/or provide more direct sun exposure.

Plat Size and Orientation

The minimum plat size to provide a favorable growth environment is determined by the hours of direct sunlight available to the planted seedlings. Three factors should be considered.

Factor (1) is the length of the east-west opening in the tree canopy. With the sun moving across the sky at 15 deg. per hour, an opening of 75 deg. in arc, accounting for height of the native canopy on the eastern and western boundaries of the plat, is necessary to achieve 5 hours of direct sun, for example. A fuller depiction of plat east-west dimension for various canopy heights and hours of direct sunlight is given in Figure 1. As an example, for a canopy height of 70 ft., a 70 ft. east-west opening gives 3 ½ hours of direct sunlight and a 120 ft. opening gives 5 ½ hrs. As will be discussed later, less than 5 hours will not be sufficient for reasonable growth and survival.

Factor (2) is the width of the plat to minimize the curtailment of the growing season as the north-south sun angle is diminished early in the season (e.g., March-April) and late in the season (e.g., September-October). Planted tree off-sets from the southern plat boundary of less than 40 ft. curtail direct sunlight in early April and September for a 70 ft. canopy height, for example, see Figure 2 for a more complete depiction. The south boundary off-set values in the chart should be considered as MINIMUMS due to the curvature of the sun path and impacts of southeast and southwest corner canopy trees.

A case can be made for accepting the reduction of direct sun exposure in the first half of April as the canopy density is substantially reduced during the earlier stages of leaf-out (except for evergreen canopies). A case might also be made for tolerating impact during the last half of September through mid-October as the Chestnut trees will be beginning to "shut down". In

either case a reduction of the south off-set to 30 ft. for a 70 ft. canopy will have a combined 6+ week impact on the direct sunlight exposure at the two ends of the 24 week growing season. This is a potential 20+% impact and somewhat equivalent to a one hour reduction in direct sunlight exposure on the south side of the "planting zone" for a plat that would otherwise have 5 hours of exposure.

Factor (3) is plat

orientation. The ideal orientation is a rectangle

with the long axis east-west and the shorter axis north-south. In this case the "planting zone" is equidistant between the east and west plat boundaries, extending no closer to either end than 40 ft. for a 70 ft. canopy height. The "planting zone" also starts at the north edge of the canopy and extends southward to no closer than 50 ft. to the south plat boundary for a 70 ft. canopy height. Without attention to plat orientation, a significantly larger site will have to be prepared – about 0.5 acre for the same planting zone as a 0.2 acre site optimally orientated as described above.

In a published study, roughly circular canopy openings of varying area, which should be equivalent to randomly orientated rectangular openings, were created. Planted oak tree growth, growth rates and tree health were assessed for 20 years. Such circular openings in area below 0.5 acre (or 170 ft. in diameter) experienced a significant reduction in both growth rate and health of the planted trees, even more-so in the "canopy shaded zones" (Reference 1). So,
randomly oriented rectangular plats should exceed 0.5 ac for good growth. Properly orientated rectangular plats achieve the same sunlit canopy openings at 0.2 ac and imply that 5-6 hrs. of direct sunlight should be the minimum goal. No information on the average surrounding canopy heights were noted in this reference, though the notation of a "site index of 23M for black oaks of 50 years in age" might imply a surrounding canopy of 70-80 ft.

See Figure 3 for small semi-prepared plat layouts utilized as a starting point for 8 of the dispersed sites of this study within a 70 ft. canopy. The smaller of the two sites is acceptable for a 40 ft. canopy but too small for a 70 ft. canopy as will be discussed further below- 3 to 31/2 hour direct sun exposure is insufficient. Even the larger plat, suitable for 8 trees, needs a 70 ft. width rather than 60 ft.

Combining Figures 1 and 2, with the goal of establishing practical sites for four trees in mature forests, the east-west and north-south dimensions are summarized in Figure 4. As discussed above, you should strive for more than 4 hrs. of direct sunlight—preferably 5+. The notes in Figure 4 describe additions to the site for more than 4 trees while retaining the requisite direct

sunlight exposure (for up to 9 trees). The dimensions given account for east-west off-sets, north and south boundary off-sets, and 10-15 ft planted tree spacing.

All of the above is based on geometry—angles, heights and lengths. Sometimes it is practical to use angles alone to layout a site. East-west openings in the native canopy of various sky arcs yield the following hours of direct sunlight at the east-west center of the plat:

- 60 deg. -4 hrs.
- 75 deg. -5 hrs.
- $90 \text{ deg.} 6 \text{ hr.}$
- 105 deg. -7 hrs.

The south boundary canopy edge off-set should be at least 35 deg. in sky arc from the vertical, based on 30-40 deg. N Latitude.

140 exposure N-S-Dimnesion, ft. E -W Dimension E - W Plat 120 **Dimension** 100 all hrs. of exposure 80 **N-S Plat Dimension** (30-40° N. Latitude) 60 40 40 80 100 120 60 Canopy Height, ft. Note: (1) add 15' to either E-W or N-S dimension for 2 additional trees (2) add 30' to either E-W or N-S dimension for 4 additional trees

(3) add 15' to both E-W and N-S dimension for 5 additional trees

Latitudes above 40 deg. will require larger sky angles by 1 deg. per degree above 40 deg. N Latitude. Sky angles within a plat increase as seedlings grow, increasing exposure by 0.5 hours at 10 ft. in height and reducing impact from the south by 4 weeks, for example. Yet the sunlight to promote reasonable growth over the first 4 or 5 years must remain the first priority.

Practical Observations

Canopy Density: It should be noted here that native forest canopies are rarely uniform – in height, in canopy density, in tree type—nor are the boundaries regular or without discrete openings or gaps – which provide some (limited?) increase in direct light exposure above that shown in Figures 1 and 2.

A sample of deciduous tree types and relative canopy density is given in Table 1. Varying degrees of "filtered sunlight" impinge on the plat even during periods when direct sunlight is obstructed, depending on surrounding canopy density.

Figure 4 Plat Size for 4 Trees vs. Canopy Height for Differing Lengths of Direct Sunlight

Exposure

Exploit Natural Openings: An "open end", either east or west, will have a significant positive impact on direct sun exposure, doubling 4 hours of exposure to 7-8 hours for any given east west length and canopy height combination on the 4 hour exposure curve, for example (see Figure 1), Also, refer back to arc angles discussion above. Such a case would not be normal in mature forests unless extensive dead fall, fire burn, wind damage, woodland meadows, or human intervention (such as logging, mining, roadways, powerlines) were associated with the site. So

exploit these types of features to full advantage. To reduce the site clearing required, creative rectangular or triangular "notches" on the east or west side of any generally northerly/southerly open feature or the north side of any generally easterly/westerly open feature such as clearings or roadway/powerline right of ways, can be utilized. Such features also permit the consideration of the smaller plat size of Fig 3 in canopies exceeding 40 ft.

The Nine Semi-Prepared Sites of this Study: These nine sites involve 70 American and B3F3 Chestnut seedlings/trees. Two of the nine native forest sites of this study definitely exhibit the detrimental impact of 4 or less hours of direct sunlight (sites similar to the 0.1 ac plat of Figure 3). Seven of the nine sites are similar to the 0.2 ac plat of Figure 3 with 5-7 hrs. of direct sunlight and good chestnut seedling growth over the first 4-5 years (approximately 3 ft. per year, average). All plats, even the larger size, exhibit the detrimental impact of a south canopy boundary off-set of less than 50 ft. (35 deg. sky arc) for seedlings on the south side of the planted zone.

The experience of this study indicates that a 4 tree site should not be smaller than 110 ft. E-W and 70 ft N-S for acceptable seedling growth in a 70 ft canopy. Further, every reasonable effort to achieve at least 5 hrs sunlight should be made, even if selective culling of native canopy trees on the east/west ends of the plat is required.

After two or three years of observation, the practice of this study has been to selectively cull native canopy trees at the E-W plat boundary to increase direct sunlight exposure, especially for the two 0.1 ac plats of Fig 3, and to open the south canopy to a 35 deg sky angle where possible on both the 0.1 and 0.2 ac plats. In fact, neither of the two 0.1 ac plats exist today, as both have been selectively "opened up" over the past three years on east, west, and south sides where possible.

Work Required: Finding sites meeting the considerations outlined above, in mature forests, is not as easy as it might seem and basic clearing of a 60x75 ft. (0.1 ac) site, even in the vicinity of a deadfall or wind damage, requires work – all for space to plant 4 trees with a high prospect of diminished growth rates. For these smaller sites, greater attention must be given to tree lean or canopy spread into the basil zone (canopy opening is what counts, not basil zone cleared).

Opting for a larger site, say 0.2 ac, giving more direct sunlight for a few trees and/or more trees (8), is even more demanding and will likely involve larger equipment to handle removal of several native trees exceeding 10 inches in diameter.

Deer Protection and Watering: In such "semi-prepared" and dispersed sites, deer fences are less practical than welded wire tree baskets, 20 inches in diameter and 4-5 ft. tall. I also put a 1 ½ inch PVC water pipe into the root zone of each tree planted for easy watering when required.

Site Access: Access to the site for preparation, planting, maintenance and stewardship for 5 or more years depending on growth rates must be considered as grasses, fast growing native trees, briars and other competition are all enabled and accelerated by the opening in the native canopy.

Reference

1. Landscape Forestry; Boyce, Stephen G.; USDA Forest Service data