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Growth, survival, and competitive ability of chestnut (*Castanea* Mill.) seedlings planted across a gradient of light levels

Cornelia C. Pinchot[1] · Scott E. Schlarbaum[2] · Stacy L. Clark[3] · Arnold M. Saxton[4] · Ami M. Sharp[2] · Callie J. Schweitzer[5] · Frederick V. Hebard[6]

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Abstract There has been an increased interest in tree breeding for resistance to exotic pests and pathogens, however relatively little research has focused on the reintroduction of these tree species. Understanding the durability of resistance in field settings and the field performance of improved trees is critical for successful species reintroduction. To evaluate methods for reintroducing American chestnut [*Castanea dentata* (Marsh.) Borkh] to managed forests on the Cumberland Plateau, we quantified four-year survival and growth and three-year competitive ability of chestnut seedlings planted on the Daniel Boone National Forest in southeastern Kentucky, USA. We used a split-plot design to compare chestnut response among three silvicultural treatments spanning a gradient of light levels; midstory removal, thinning, and shelterwood with reserves (2, 24, and 65% available photosynthetically active radiation, respectively) and three chestnut breeding types; American, Chinese (*C. mollissima* Blume.), and BC_2F_3 hybrid. One of two hybrid families planted had similar survival to American chestnuts, 21 and 27% survival, respectively,

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✉ Cornelia C. Pinchot
corneliapinchot@fs.fed.us

1 US Department of Agriculture Forest Service, Northern Research Station, 359 Main Rd, Delaware, OH 43015, USA

2 Department of Forestry, Wildlife and Fisheries, The University of Tennessee, Rm 274 Ellington Plant Science Building, Knoxville, TN 37996, USA

3 US Department of Agriculture Forest Service, Southern Research Station, Rm 274 Ellington Plant Science Building, Knoxville, TN 37996, USA

4 Department of Animal Science, The University of Tennessee, 232 Brehm Animal Science Building, Knoxville, TN 37996, USA

5 US Department of Agriculture Forest Service, Southern Research Station, 730-D Cook Ave, Huntsville, AL 35801, USA

6 The American Chestnut Foundation, 30056 Smyth Chapel Rd., Meadowview, VA 24361, USA

while the other had better survival, 57%. Chinese chestnut survival was better than the other breeding generations (90%). High mortality among American and hybrid chestnut seedlings was likely caused by infection from *Phytophthora cinnamomi* Rands. Incidence of blight infection was low. While chestnut seedling growth was greatest in the high-light treatment, competitive ability of chestnut, evaluated by comparing planted seedling height to height of understory competitors, was maximized in the intermediate light treatment. These results demonstrate the importance of evaluating competition pressure from co-occurring vegetation and field performance of resistant genotypes when assessing methods for reintroducing tree species to forested settings.

Keywords *Castanea* · Species restoration · Silvicultural treatment · Competitive ability

Introduction

Non-native pest and pathogen invasions have had catastrophic impacts on an increasing number of tree species worldwide (Boyd et al. 2013; Santini et al. 2013; Campbell and Schlarbaum 1994, 2002, 2014). In response, there has been a growing effort to identify or breed populations of tree species resistant to their respective pests and pathogens, for example the development of disease resistant white pine species (*Pinus* spp. L.) in the Western United States (Sniezko 2006), American butternut (*Juglans cinerea* L.) in the Eastern U.S. (Ostry and Moore 2008), and elm (*Ulmus* spp. L.) in the U.S. and Europe (Santini et al. 2008; Townsend and Douglass 2001; Townsend et al. 2005). Sparse research, however, has focused on the reintroduction of resistant tree populations (Thompson et al. 2006). Understanding the durability of resistance in field settings (Sniezko 2006), and the field performance of improved genotypes (Clark et al. 2014; Jacobs 2007; Jacobs et al. 2013; Oldfield 2009; Seddon 2010) is critical for successful species reintroduction. This is of particular importance when reintroducing tree species to ecosystems that have undergone significant change since the loss of that species (Maunder 1992). In these cases forest dynamics and management goals may have changed substantially, requiring a new approach to manage the reintroduced species (Maunder 1992).

One of the most well-known tree species restoration efforts is that of American chestnut [*Castanea dentata* (Marsh.) Borkh]. American chestnut was a dominant forest tree throughout much of the Eastern U.S. until the early 20th century. The tree was ecologically important as a source of mast for wildlife (Diamond et al. 2000; Schlarbaum 1990), and economically valuable for its rot-resistant lumber, high-tannin content, and edible nuts (Ashe 1911; Emerson 1846; Frothingham 1924). Two non-native pathogens contributed to the near decimation of American chestnut. *Phytophthora cinnamomi* Rands (Crandall et al. 1945), which incites *Phytophthora* root rot, is an exotic soil-borne oomycete that attacks and kills the root systems of American chestnut. Because its spores spread with the flow of water, it is more abundant in poorly drained and compacted soils (Anagnostakis 2001; Rhoades et al. 2003) and by the late 19th century, *Phytophthora* root rot had killed most American chestnuts in mesic sites in southeastern states (Anagnostakis 2001; Crandall et al. 1945). Mortality attributed to the chestnut blight fungus, *Cryphonectria parasitica* Murrill, was first described in 1904 in New York city (Murrill 1906), although the pathogen was probably imported into the U.S. on Japanese chestnut (*C. crenata* Sieb. and Zucc.) nursery stock in the late 1800s (Anagnostakis 2006; Burnham 1988). Most large chestnut trees throughout the species' range were dead or dying by 1950 (Burnham 1988). Occasional large survivors and sprouts are located throughout the range of American chestnut (Griffin et al. 1983).

Currently, the American Chestnut Foundation (TACF) and the Connecticut Agricultural Experiment Station (CAES) both utilize a backcross breeding approach in attempt to develop a highly blight-resistant American chestnut hybrid (Anagnostakis 2012; Hebard 2001). Their shared approach incorporates an initial cross between an Asian chestnut species, usually Chinese (*C. mollissima* Blume.) or Japanese chestnut, and an American chestnut. This cross is followed by a series of backcrosses to American chestnuts and finally two intercrossing generations. The goal of the breeding programs is to develop a hybrid similar to American chestnut in morphological and ecological traits, and to Asian chestnuts in blight resistance (Anagnostakis 2012; Burnham 1988; Hebard 2001). TACF has recently incorporated genomic selection to more quickly and accurately select progeny with high levels of blight-resistance (Steiner et al. 2017). Both TACF and CAES now also incorporate resistance to *P. cinnamomi* into their breeding programs (Anagnostakis 2001, 2012; Jeffers et al. 2009).

The second component of American chestnut restoration is establishing founder populations throughout the species' range. This will require a tremendous and expensive effort, thus understanding how to maximize success is essential. Historic literature and modern research offer insights into potential management strategies for chestnut reintroduction. The rapid growth of planted American chestnut (Clark et al. 2012; Jacobs and Severeid 2004; Latham 1992; Rhoades et al. 2009) suggests that it would flourish in silvicultural treatments designed for shade-intolerant species, such as clearcuts or shelterwood cuts. Unlike many species capable of rapid growth, however, American chestnut has been categorized as intermediate in tolerance to shade (Schenck 1912) or shade tolerant (Clark et al. 2012; Joesting et al. 2009; Wang et al. 2013), though growth and survival of planted chestnut seedlings in various light environments has received limited testing (Clark et al. 2012; Rhoades et al. 2009). Field biologists and foresters have long noted the unique ability of American chestnut seedlings to survive for decades in deep shade, and then to produce rapid stem growth when a disturbance causes increased light availability (Emerson 1846; Frothingham 1924; Paillet 1984). This growth plasticity can be explained in part by chestnut's high photosynthetic rates when grown both in high light and in shade, and its low light compensation point when grown in shade (Joesting et al. 2009; Wang et al. 2006). The unique combination of rapid growth and shade tolerance may enable American chestnut to become established under a variety of treatments.

Several recent studies have evaluated planted chestnut establishment among various silvicultural treatments. Clark et al. (2012) and Rhoades et al. (2009) found that chestnut seedling growth was substantially greater in shelterwood areas than in lower-light treatments. The removal of shade-intolerant, undesirable species in the midstory preceding an overstory harvest, designed to create adequate light conditions for oak seedling establishment (Loftis 1990a), has been found to promote American chestnut establishment (Brown et al. 2014; Clark et al. 2012; Rhoades et al. 2009). These studies found that early chestnut survival was not negatively impacted by midstory removal treatments compared to shelterwood or thinning harvests (Clark et al. 2012; McCament and McCarthy 2005; Rhoades et al. 2009); though Belair et al. (2014) found that four year survival was negatively related to canopy cover. American chestnut growth within the first several years in midstory removal treatments, however, is consistently greater in treatments that create higher light levels (Belair et al. 2014; Clark et al. 2012; McCament and McCarthy 2005; Rhoades et al. 2009).

Many studies evaluating success of planted seedlings evaluate growth and survival of the planted seedlings alone (e.g. Paquette et al. 2006). The long-term success of planted seedlings depends, however, on their growth and survival *relative* to that of competing vegetation (Spetich et al. 2002). Seedlings demonstrating good early growth and survival will not perform well in the long-term if they cannot compete with natural regeneration (Loftis 1990b). It is necessary, then, to understand what biotic factors, such as genotype and seedling quality, as well as abiotic factors, such as light and soil moisture, influence the planted seedling's "ability to survive and grow at a rate sufficient to attain and maintain dominance among its competitors" (*vide* Spetich et al. 2002). While the growth of planted chestnut has been compared with that of planted seedlings of other species in plantation and field settings (Belair et al. 2014; Jacobs and Severeid 2004; Gauthier et al. 2013), planted chestnut's growth relative to *natural* regeneration, which tends to grow more vigorously than planted seedlings of the same species, has not been tested.

Our specific objectives for this study were (1) to compare survival, growth, and competitive ability of chestnuts (a) among three silvicultural treatments representing a gradient of light levels, and (b) among breeding types: two advanced generation hybrid chestnut (BC_2F_3, sensu Hebard 2001) families, American and Chinese chestnut seedlings and (2) to evaluate the effects of abiotic and biotic factors on seedling survival, growth, and competitive ability.

Methods

Study sites

Chestnut seedlings were planted in fifteen stands located in the London Ranger District of the Daniel Boone National Forest on the Cumberland Plateau in southeastern Kentucky, USA (37°03′N, 84°11′W, elevation 370 m). The landscape, underlain by sandstone and shale, consists of a series of plateaus and rolling plains dissected by steep slopes. Thirty-year average annual precipitation and temperature for the weather station closest to the study sites was 140.0 cm and 12.2 °C (NOAA). Braun (1950) described this area of Kentucky as part of the mixed-mesophytic forest region, abundant with beech (*Fagus grandifolia* Ehrh.), white oak (*Quercus alba* L.), black oak (*Quercus velutina* Lam.), and hickory (*Carya* spp Nutt.). Other common hardwoods include chestnut oak (*Quercus prinus* L.), particularly on ridges, maple (*Acer* spp. L.), black gum (*Nyssa sylvatica* Marsh), yellow-poplar (*Liriodendron tulipifera* L.), sourwood (*Oxydendrum arboreum* DC), sassafras [*Sassafras albidum* (Nutt.) Nees.], and pine (*Pinus spp.* L.) (Schweitzer et al. 2014). Before the chestnut blight epidemic, American chestnut was a dominant canopy tree on the Cumberland Plateau, particularly at higher elevations (Braun 1950). The historical widespread distribution of chestnut in the area is further evidenced by its continued presence in the understory as small sprouts (personal observation).

Silvicultural treatments

This study was nested within a larger USDA Forest Service study established with the goal of improving oak resilience prior to the anticipated arrival of gypsy moth (*Lymantria dispar* L.) to the area (Schweitzer et al. 2014). Study sites were located on broad ridges, in stands ranging from 70 to 150 years old with a mean pre-harvest basal area of 21.6 m^2/ha

Table 1 Pre-treatment (time = 0 years) and three years post-treatment basal area (m^2/ha) and stems per hectare for each silvicultural treatment (Schweitzer et al. 2014), all located in the Daniel Boone National Forest on the Cumberland Plateau in southeastern Kentucky

Silvicultural treatment	Pre-treatment basal area (m^2/ha)	Pre-treatment stems per hectare	Post-treatment basal area (m^2/ha)	Post-treatment stems per hectare
Midstory removal	21.0	301	21.5	240
Thinning	24.0	311	16.8	128
Shelterwood w/reserves	19.9	316	4.0	40

(Schweitzer et al. 2014; Table 1). Our study utilized three of the silvicultural treatments implemented in Schweitzer et al.'s (2014) study: shelterwood with reserves (SW), thinning (TH), and oak shelterwood, hereafter called midstory removal (MR). The SW treatment was a commercial tree harvest that left an average residual basal area of 4 m^2/ha of overstory. Residual trees were selected to promote forest health conditions and to improve wildlife habitat (Schweitzer et al. 2014). The TH treatment left stands thinned to the B-level of Gingrich stocking (Gingrich 1967), with an average basal area of 16.8 m^2/ha of overstory (Schweitzer et al. 2014). Although not a regeneration treatment, thinnings may provide adequate light for seedling establishment or recruitment of species that are moderate in shade tolerance, while discouraging the least shade-tolerant species. In the MR treatment, all stems greater than 7.6 cm diameter at breast height of undesirable species in suppressed and intermediate (i.e. midstory) canopy positions were killed using triclopyr amine stem injection (*c.f.* Loftis 1990a), leaving an average basal area of 21.5 m^2/ha of intact overstory in the MR treatment sites (Schweitzer et al. 2014). The goal of midstory removal treatments is to increase light on the forest floor to favor oak regeneration, while retaining enough overstory to inhibit shade-intolerant species (Loftis 1990a). The overstory will be removed once adequate oak seedling stocking has been achieved. All harvest treatments were completed between August, 2007 and February, 2009. Detailed changes in the overstory, midstory and reproduction can be found in Schweitzer et al. (2014).

Experimental materials

Three-hundred American chestnut seedlings and one hundred-fifty seedlings each of Chinese chestnut and BC_2F_3 generation hybrid families SA330 and SA417 (Hebard 2001, 2012) were used in this study. These families were chosen because of their high blight resistance and availability (Fred Hebard, personal communication). The open-pollinated hybrid chestnut nuts were harvested at TACF's Meadowview Research Farms, Meadowview, VA, in the fall of 2007, and the open-pollinated American chestnuts were harvested in 2007 from sprouts in the Jefferson National Forest near Meadowview. The American and Chinese chestnut seedlings were bulked from multiple parents. Nuts from each family were manually sown at the Georgia Forestry Commission's Flint River Nursery near Byromville, GA in January, 2008 at a density of 65 nuts per square meter. Fertilization and irrigation of the seedlings followed guidelines developed by Kormanik et al. (1994). The 1-0 seedlings were lifted in February 2009, and stored in a cold room (~1 °C) until they were planted. The bare-root 1-0 Chinese chestnut seedlings were purchased from Forrest Keeling Nursery (PO Box 135, Elsberry, MO) in February, 2009. Hereafter, the term 'breeding type' will refer to seedlings of a chestnut species (American or Chinese) or the hybrid generation [BC_2F_3 generation hybrid (Hebard 2001)] which were used in this study. The seedlings were processed for planting in February, with roots trimmed to 15 cm from the main tap root to facilitate planting. Chestnut seedlings with signs of disease were discarded. Seedlings were individually tagged to maintain pedigree and associated seedling size data. Seedlings were planted with a Jim Gem KBC© bar, modified by adding 5 cm to each side of the blade, creating a blade 20 cm at the top, tapering to the tip. Seedlings were planted between March 2nd and 9th, 2009.

Experimental design

Silvicultural treatments were arranged in a completely randomized design. Treatments were implemented at the stand level, and stands were randomly chosen from a pool of potential stands located across the landscape (Schweitzer et al. 2014). Within each silvicultural treatment, the chestnut seedlings were arranged using a randomized complete block design in blocks of five seedlings, each with two American seedlings, one Chinese seedling, and one seedling of each of the two hybrid families. Thus the experimental design incorporates a split-plot, with silvicultural treatment in the main-plot and chestnut breeding type in the subplot. Due to timing of harvesting treatment, silvicultural treatments were not replicated evenly; the study consisted of five SW, four TH, and six MR replicates. Blocks were evenly distributed among the three silvicultural treatments, thus between fifty to sixty-five seedlings (ten to thirteen blocks) were planted within each of the main effect replicates. Seedlings were planted in linear transects using a 2.5 m spacing with one transect per replicate. Specific placement of transects within a treatment was guided by microsite uniformity. For example, transects were placed along rather than across ridges to reduce environmental variation among planting spots. Transects were located at least 30 m from the treatment boundary.

Assessment of solar radiation and canopy openness

Instantaneous photosynthetically active radiation (PAR, 400–700 nm wavelengths) measurements were taken for each chestnut seedling in the first and the second growing seasons (June 2009, July 2010), on either completely cloudless or overcast days when possible (Klinka et al. 1992; Parent and Messier 1996; Smith 1991). Light intensity was quantified with an AccuPar linear PAR/LAI ceptometer (Decagon Devices, Inc., Pullman, WA). A total of three readings was taken above each seedling: one measurement above the midcanopy of the seedling on the south side of each tree taken in the morning (9:30 am–11:30 am), midday (12:30 pm–2:30 pm), and in the afternoon (3:30 pm–5:30 pm), and were averaged to produce mean PAR for each seedling. Percent full sunlight was calculated from mean PAR and adjacent full-sun openings.

A convex spherical densitometer (Lemmon 1956) was used to estimate percent canopy openness on all seedlings within ten randomly selected treatment sites, representing three to four replications of each silvicultural treatment. Readings were taken at breast height on the south side of each chestnut seedling in each of the four directions (Buckley et al. 1999; Lhotka and Loewenstein 2006). Readings were taken during the first and fourth growing seasons (July, 2009 and June, 2010) and an average closure for each seedling per year was used in the analysis.

Seedling measurements

Seedling height, root collar diameter and root volume (by water displacement, Novoselov 1960) were measured in February, 2009 prior to planting. Height and ground level diameter (GLD) were measured and mortality assessed in September or October of the first four growing seasons after bud set was complete.

Competition characterization

A 2.6-meter-diameter competition plot was centered on each chestnut seedling and competition data on understory woody plants collected at the end of the first, second, and third growing seasons. Competition data were collected on living and dead seedlings in year one and only on living seedlings in years two and three. Data collected included species and height of the tallest understory woody competitor [>0.3 m in height and <3.8 cm diameter at breast height (DBH)], and the number of understory woody competitors, growing within each competition plot. In year one, woody plants and vines in the understory were recorded as an understory competitor, including green briar (*Smilax* spp. L.) and blackberry (*Rubus* spp. L.). In years two and three, only arborescent species were recorded as understory competitors.

Presence of *Phytophthora cinnamomi*

To investigate the cause of high mortality during the first year after planting, roots and associated soil from two symptomatic American chestnut seedlings were evaluated for presence of *Phytophthora cinnamomi* in the spring of the second growing season (Dr. Steven N. Jeffers, Clemson University, Meadows et al. 2011). Additionally soil samples were taken at least three meters from the planting transect in two SW, two MR, and one TH site to determine whether *P. cinnamomi* was present on site prior to planting. The presence of *P. cinnamomi* was tested using baiting bioassay (Meadows et al. 2011).

Statistical analyses

All analyses for this study were processed using SAS 9.3 software (SAS Institute 2011). Seedling response was analyzed using a repeated-measures, mixed-model analysis of variance (ANOVA) using an autoregressive covariance structure [type = AR(1)] to determine significant differences among the fixed effects of silvicultural treatment, chestnut breeding type, year, and their interactions on total height and GLD from the first to the fourth growing season. The square root of GLD and the log of height were used in order to meet the assumption of normally distributed residuals. Data were checked for homogeneity of variance with Levene's test and normality using Shapiro–Wilks statistic or Kolmorgorov–Smirnov test, before analysis. Unequal variance was added to the model if the Akaike Information Criterion (AICc, corrected for small samples) was significantly improved. Least-significant-difference tests were performed to compare means where significant differences ($P \leq 0.05$) were found. PROC GLIMMIX was used to test the effect of silvicultural and chestnut-breeding-type treatments and their interactions on seedling survival by year, using a binary response distribution.

Logistic regression (Proc Logistic) was used to evaluate whether independent variables (Table S1) could predict: (1) the survival of the seedlings after the fourth growing season; (2) dominance probability (DP) of living seedlings during the third growing season; and (3)

DP of living seedlings from years one to three after planting. Surviving seedlings that had attained at least 80% of the height of the tallest competitor within 1.3 meters were defined as dominant (Spetich et al. 2002). Dummy variables were used for categorical variables for silvicultural treatment and breeding type. For univariate tests with dummy variables, we ran the logistic regression model using each treatment level as the baseline, separately, in order to determine significant differences between the other two treatment levels (Table S1). We used model building approaches described by Hosmer and Lemeshow (2004). The most parsimonious model with the lowest corrected AICc value was selected for each dependent variable. Hosmer–Lemeshow goodness-of-fit statistic was used to test that the model adequately explained the data.

The effects of silvicultural treatment on canopy openness (years one and four), available PAR (years one and two), and the height of the tallest competitor and density of competing seedlings in competition plots (years one, two and three) were each tested separately using mixed-model ANOVAs. Dependent variables were transformed in order to meet the assumption of normally distributed residuals: log of canopy openness in year one, cube of canopy openness in year four, and the square root transformation was used for PAR in year two. When Levene's test for equal variance indicated heterogeneity in variance among treatments, unequal variance was added to the ANOVA model.

We used multiple regression with indicator variables to develop a model using abiotic and biotic factors (Table S1) to predict GLD throughout the four-year study. Variables that were strongly related to GLD in univariate regression were then added to multiple regression models. Backwards selection as well as manual variable selection methods were used to select variables in the final model based on the lowest AICc value. Variables in the final model were tested for linearity, interactions, multicollinearity, autoregression and homogeneity of variance. The natural log of GLD and canopy cover in year one were used in the regression analyses to meet the assumption of normally distributed residuals. Proc Autoreg was used to obtain parameter estimates to correct for autocorrelation among the variables. Continuous variables were centered. Two-thirds of the data were randomly selected to use during model building and the remaining one-third of the data was used as a holdout sample to test the final model.

Results

Site characteristics and seedling quality

Three growing seasons after treatment, the silvicultural treatments differed considerably in their basal area and number of overstory stems per hectare, each decreasing with increasing canopy removal (Schweitzer et al. 2014; Table 1). The number of regeneration stems between 1.4 and 3.8 m in height was 173 stems/ha in MR and 478 stems/ha in SW sites (Schweitzer et al. 2014). Available PAR in the first two years differed considerably among the silvicultural treatments ($F = 105.5$, $P < 0.0001$ in year one, $F = 48.98$, $P < 0.0001$ in year two). In year one, seedlings in SW sites received 65% (± 2) of PAR, while seedlings in TH sites received 24% (± 3) and seedlings in the MR sites received only 2% (± 2) PAR. Forty-seven % (± 1) of PAR reached the seedlings in SW treatments in year two, compared to 22% (± 3) in TH and 9% (± 2) in the MR treatments.

Canopy openness was also greater in SW sites than either MR or TH for both measurement periods, though there was no significant difference between the two lower-light treatments. In year one, SW sites averaged 52% (±2) canopy openness compared with 13% (±1) in TH sites and 5% (±1) in MR sites (F = 17.79, $P = 0.0010$). Canopy openness followed a similar trend in year four—average canopy openness in SW sites was 39% (±3), 17% (±2) in TH sites, and 12% (±1) in MR sites (F = 39.92, $P = 0.0004$).

Height of tallest competing seedling did not differ among silvicultural treatment and averaged 223 cm ± 6 for year three ($P = 0.0809$). In years one and two, the number of competing seedlings was greatest in SW sites (16 ± 0.3, year two, F = 41.3, $P < 0.0001$, F = 127.6, $P < 0.0001$, years one and two, respectively), followed by TH (12 ± 0.4, year two) and then MR sites (9 ± 0.3, year two), but did not differ among silvicultural types in year three ($P = 0.1071$). In all three years that competition measurements were taken, red maple (*Acer rubrum* L.) was the most abundant competing woody species. In years two and three, when only arborescent species were tallied, yellow-poplar, sassafras and the red oak sub genus were the next most abundant competing woody species.

Phytophthora cinnamomi was recovered from one of the two chestnuts tested and all soil samples taken (Steve Jeffers, personal communication). These results suggest that *P. cinnamomi* was widespread within the sampled sites prior to the establishment of this study.

Survival

After four growing seasons, 47% of the seedlings were alive across all treatments and breeding types. Most of the mortality occurred in the first two years after planting (Table 2). The main effect of silvicultural treatment was not significant in any year, but breeding type and its interaction with silvicultural treatment did significantly affect survival in years one and four. American and SA330 chestnut seedlings had lower first and fourth year survival in the SW sites than in the MR sites (Table 2). Chinese and SA417 breeding types did not differ in survival among silvicultural treatments in any year.

The main effect of breeding type on survival was significant for all four years. Chinese chestnuts consistently had better survival rates than any other breeding type over the four years, with 90% surviving to the end of the four year study. After four years American and SA330 BC_2F_3 breeding types had the lowest survival rates (27 and 21% respectively), and SA417 exhibited an intermediate rate of survival (57%).

The most parsimonious logistic regression model (Model 1, Table 3) to predict probability of survival included only breeding type as a response variable. When compared with the American chestnut seedlings, Chinese and SA417 seedlings had 15- and 2.7-times greater odds of surviving, while SA330 and American seedlings had similar odds of survival. When comparing the seedlings to SA330 chestnuts, Chinese and SA417 seedlings had 17- and 3-times greater odds of surviving (Table 4). Initial height and root volume were also strongly related to survival (Table S1), but did not greatly improve the model's predictive power and were not included in the model.

Growth

After four growing seasons, seedlings averaged 155 cm in height and 18.9 mm in GLD; 57 cm taller, and 6.5 mm larger in diameter than they were at the beginning of the study (Table 5; Figs. 1, 2, 3, 4). Across all treatments, total GLD steadily increased over the four year study (F = 127.52, $P < 0.0001$; Figs. 1, 2, 3, 4), while total height increased significantly only in year three (F = 12.2, $P < 0.0001$). By the end of the study, seedlings in the SW study were 1.4- and 2-times taller (F = 31.19, $P < 0.0001$) and 1.4- and 1.9-times

Table 2 Treatment and interaction effects for percent survival ± standard error for each of the four years after planting

Silvicultural treatment	Breeding type	Year 1		Year 2		Year 3		Year 4	
Midstory removal (MR)	American	75 ± 7 deg		50 ± 8		47 ± 8		41 ± 8 de	
	BC_3F_2: SA330	59 ± 10 fh		44 ± 9		40 ± 10		37 ± 9 def	
	BC_3F_2: SA417	84 ± 6 bdce		67 ± 9		65 ± 9		61 ± 9 c	
	Chinese	94 ± 4 abc		87 ± 6		85 ± 6		81 ± 7 ab	
Thinning	American	58 ± 10 gh		43 ± 9		34 ± 9		26 ± 7 efg	
	BC_3F_2: SA330	64 ± 11 egh		39 ± 10		29 ± 9		23 ± 8 efg	
	BC_3F_2: SA417	82 ± 7 cdf		70 ± 9		69 ± 10		65 ± 10 bcd	
	Chinese	96 ± 2 ab		94 ± 4		93 ± 4		93 ± 4 a	
Shelterwood with reserves (SW)	American	47 ± 10 h		22 ± 6		19 ± 6		16 ± 6 fg	
	BC_3F_2: SA330	28 ± 8 i		17 ± 6		15 ± 9		10 ± 5 g	
	BC_3F_2: SA417	76 ± 8 cdefg		44 ± 10		45 ± 10		45 ± 10 cde	
	Chinese	98 ± 1 a		91 ± 5		96 ± 4		92 ± 4 a	
Fixed effects		*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Silvicultural treatment		0.31	0.736	2.49	0.1177	0.72	0.505	1.11	0.3566
Breeding type		27.9	<0.0001	31.59	<0.0001	35.69	<0.0001	42.87	<0.0001
Silvicultural treatment × breeding type		2.54	0.0241	1.07	0.3787	1.94	0.0792	2.53	0.02

Within columns, means with the same letter are not significantly different ($\alpha = 0.05$)

Table 3 Logistic regression models to predict (1) fourth year survival ($Surv_{Year4}$), (2) dominance probability in year three (DP_{Year3}), (3) dominance probability throughout years one through three ($DP_{Years1-3}$), and (4) a multiple regression model to predict ground level diameter over the course of the study ($GLD_{Years1-3}$)

Model number	Model	$Type_{AM}$	$Type_{CH}$	$Type_{SA417}$	$Type_{SA330}$
1	$Surv_{Year4} = 1/(1 + \exp(-(-0.72 + Type)))$	0	2.71	0.99	−0.14
2	$DP_{Year3} = 1/(1 + \exp(-(-6.69 + 0.009{*}Canopy_{Y1} - 0.004{*}Dens\,^{2}_{UnderY2} + 0.17{*}GLD_{Plant})))$				
3	$DP_{Years1-3} = 1/(1 + \exp(-(-1.11 + 16{*}GLD_{Plant} + 0.01{*}Canopy_{Y1} - 5.9{*}(1/Dens\ _{UnderY2}) + 110{*}(1/Dens\ _{UnderY2})^{2}$				
4	$GLD_{Years1-3} = 13.17 + 2.51(year) + 0.11(Canopy_{Y1}) + 0.90(GLD_{Plant}) + 2.09(Dom) + Type + 0.004(GLD_{Plant}{*}GLD_{Plant}) - 0.0004(Canopy_{Y1}{*}Canopy_{Y1}) + 0.08{*}(Year{*}Canopy_{Y1}) + 0.09(Dom{*}Canopy_{Y1})$	0	2.67	0.73	−0.53

Models with silvicultural treatment use thinning ($Silv_{TH}$) as the baseline treatment. Dominant (Dom) is an indicator variable (1 = dominant, 0 = non dominant). See Table S1 for explanation of the names of variables in the models. Values listed in the type columns in models 1 and 4 are parameter estimates for type using American chestnut as the baseline. All continuous variables in models are centered

Table 4 Logistic regression model and odds ratio estimates for probability of seedling survival as a function of breeding type

Parameter	Parameter estimate	Wald statistic	*P* value	Odds ratio estimate	95% confidence interval	
Am versus CH	2.71	93.83	<0.0001	15.04	8.70	26.03
Am versus SA330	−0.14	0.41	0.52	0.87	0.57	1.33
AM versus SA417	0.99	23.00	<0.0001	2.68	1.80	4.01
CH versus SA330	−2.84	85.64	<0.0001	0.06	0.03	0.11
CH versus SA417	−1.72	32.92	<0.0001	0.18	0.10	0.32
SA330 versus SA417	1.13	21.52	<0.0001	3.08	1.92	4.96

Table 5 Initial height, ground level diameter (GLD) and root volume of seedlings among breeding types and families

Breeding type	Family	N	Initial height (cm)	Initial GLD (mm)	Initial root volume (cm^3)
Chinese	Bulked	150	111 ± 2	12.2 ± 0.2	97 ± 4
American	Bulked	300	96 ± 1	11.3 ± 0.2	51 ± 2
BC_2F_3	SA330	150	85 ± 2	10.6 ± 0.2	53 ± 3
	SA417	150	103 ± 1	12.6 ± 0.2	81 ± 4

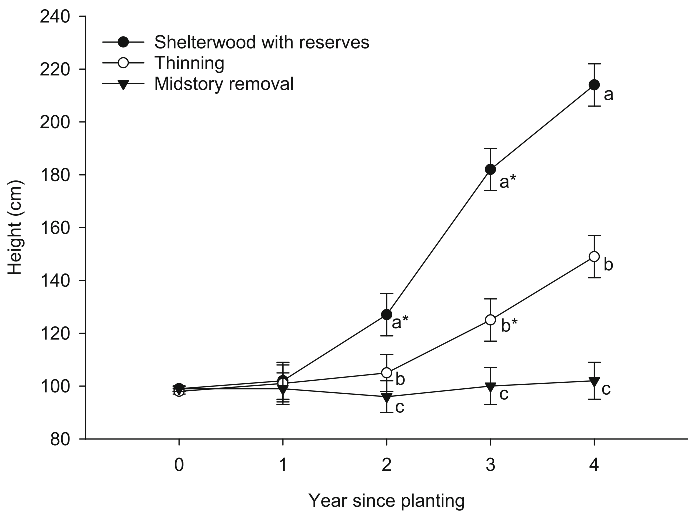

Fig. 1 Mean seedling height and standard error among silvicultural treatments over the first four years since planting. *Letters* indicate differences in height among silvicultural treatments within year (α = 0.05). *Asterisks* indicate a change in height from the previous year

larger in GLD (F = 24.25, $P < 0.0001$) than seedlings in the TH and MR treatments, respectively (Figs. 1, 2).

The interactions of silvicultural treatment by year were significant for both height (F = 14.19, $P < 0.0001$) and GLD (F = 38.82, $P < 0.0001$). Seedling height and GLD

Fig. 2 Mean seedling diameter and standard error among silvicultural treatments over the first four years since planting. Diameter in year 0 was measured at the root collar while diameter in subsequent years was measured at ground level (GLD). *Letters* indicate differences in GLD among silvicultural treatments within year ($\alpha = 0.05$). *Asterisks* indicate a change in GLD from the previous year

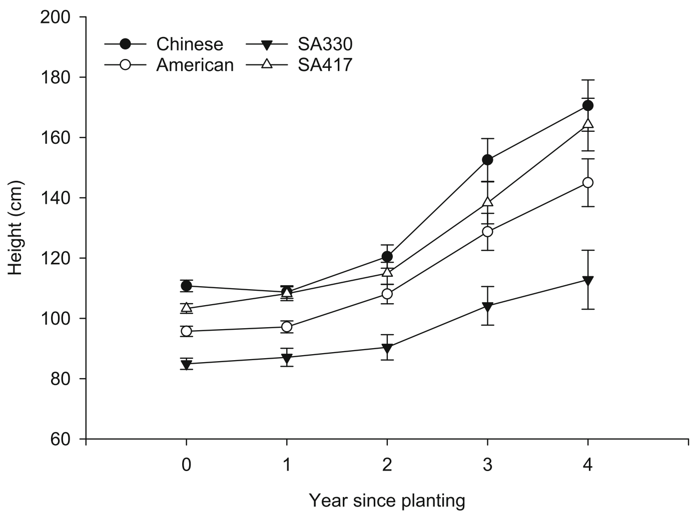

Fig. 3 Mean height and standard error of breeding types over the first four years since planting. *Letters* indicate differences in height among breeding type within year ($\alpha = 0.05$). Breeding type by year interaction was not significant

among the silvicultural treatments started to diverge in year two, when seedlings in the SW treatment were significantly taller and larger in GLD than seedlings in the other two treatments (Figs. 1, 2). Seedling height did not differ in the MR sites over four years, while diameter decreased in year one, likely because pre-planting root collar diameter was used for time 0 diameter and GLD, measured slightly above the root collar diameter, was used

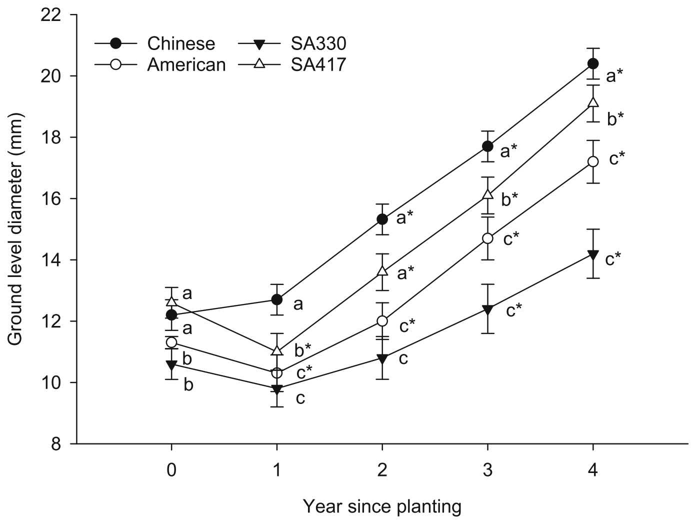

Fig. 4 Mean diameter and standard error of breeding types over the first four years since planting. Diameter in year 0 was measured at the root collar while diameter in subsequent years was measured at ground level (GLD). *Letters* indicate differences in breeding types within years (α = 0.05). *Asterisks* indicate a change in GLD from the previous year

thereafter. GLD was marginally greater in year three compared to years one and two. Seedling diameter in the TH treatments also decreased in year one, and then increased annually over the remainder of the study. Height was greater in year three than years one or two for seedlings in the TH treatment. Breeding type by silvicultural treatment interaction was significant for height ($F = 2.82$, $P = 0.0104$) but not GLD ($P = 0.1081$). Across years, Chinese and American chestnut seedlings has the best growth in SW, followed by TH and then MR sites, whereas there was no difference in height between SW and TH sites for SA330 and for TH and OS sites for SA417.

Across all treatments, Chinese chestnut seedlings grew larger in height than American and SA330 seedlings and larger in GLD than all other breeding types ($F = 34.25$, $P < 0.0001$, $F = 42.94$, $P < 0.0001$, respectively, Figs. 3, 4). Year by breeding type interaction was not significant for height ($P = 0.8704$). Chinese chestnut GLD increased significantly in years two through four ($F = 3.31$, $P < 0.0001$). SA417 grew larger in GLD than American and SA330 chestnut seedlings, and added significant GLD growth in years two through four Figs. 3, 4) across all silvicultural treatments. American chestnut seedlings grew larger in height and GLD than SA330 seedlings, and increased in GLD in years one through four for all treatments. SA330 seedlings increased in GLD in years two and three.

The multiple regression model that best explained GLD throughout the four year study included GLD at planting, DP (as an indicator variable), year (continuous variable), year one canopy openness, and breeding type ($R^2 = 0.49$, $P < 0.0001$, Model 4, Table 3). The model also included the interaction between year and year one canopy openness, and the interaction between dominance and year one canopy openness. This model fit the holdout data well ($R^2 = 0.53$, $P < 0.0001$). According to the model, seedlings with larger GLD at planting remained larger. GLD was greater in dominant than non-dominant chestnut seedlings. The positive relationship between dominance and GLD increased as canopy openness increased, and the positive relationship between canopy openness and GLD increased over time.

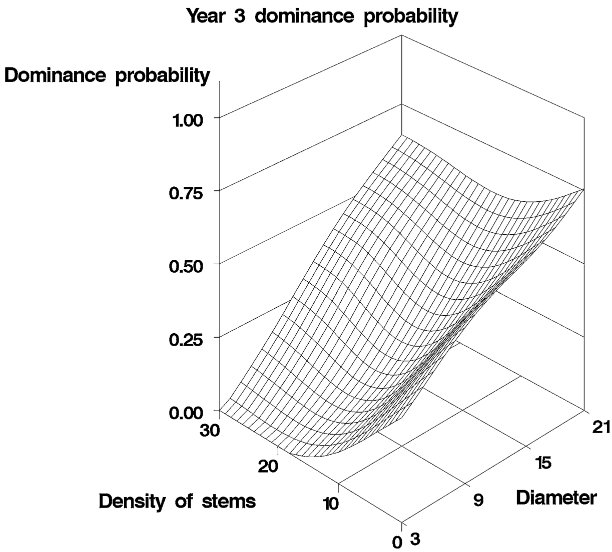

Fig. 5 Regression model using ground level diameter at planting and density of stems in competition plots to predict dominance probability in year three

Competitive ability

Third year DP of surviving seedlings was most strongly affected by initial GLD, density of competing stems and canopy openness in year two (Model 2, Table 3; Fig. 4). Ground level diameter and canopy opening were positively related, and density of competing stems was negatively related, to DP. The interaction between initial GLD and density of competing stems was significant; the negative effect of competing stem density became less important as GLD increased (Fig. 5).

The model that best explained dominance probability for the chestnuts throughout the first three years included GLD at planting (DP increased with GLD), canopy openness in year one (DP increased with canopy openness), and density of competing seedlings in year two (DP decreased with increasing number of seedlings) and its square (Model 3, Table 3).

Discussion

Survival

Seedling survival was lower than expected for the American and SA330 BC_2F_3 hybrid chestnut seedlings in this study (27 and 21%, respectively), and was inferior for each in the SW sites compared to TH and MR treatments in years one and four. While low survival in forest plantings of oak, a close relative of chestnut, has been a challenge, (Johnson 1971, 1976; Kormanik et al. 1997), early survival rates of 80% or greater for plantings using high-quality oak seedlings are not uncommon (Dey and Parker 1997; Johnson 1984; Teclaw and Isebrands 1993). Survival of chestnut forest plantings has varied. Rhoades et al. (2009) recorded 57% second-year survival of American chestnut seedlings planted under two silvicultural treatments in Kentucky; McNab (2003) recorded 66% second-year survival of American chestnut seedlings planted in clearcut and control sites; and Clark et al. (2016) reported four year survival rates of 71–82% among seedlings planted in highly productive sites in the southern Appalachians.

Based on observation, fewer than 10% of seedlings in our study exhibited symptoms of blight infection by year four, therefore blight was probably not the cause of high mortality among the American and SA330 chestnut breeding types. However, *P. cinnamomi* was found in every soil sample tested. This leads us to believe that the reduced survival among American and hybrid compared to Chinese chestnut seedlings was caused primarily by *P. cinnamomi,* because Chinese chestnut trees are much more resistant to this pathogen than American chestnut (Crandall et al. 1945). The two BC_2F_3 hybrid families used in this study have not been tested for resistance to *P. cinnamomi*, however other families in the same lineage have been tested and have not shown resistance to the pathogen (T. Saielli, TACF, personal communication). Testing for the presence of *P. cinnamomi* is recommended as a part of the site selection process for American chestnut reintroduction plantings.

Growth

By year four, chestnut seedlings growing in the SW treatments were 70–120 cm larger in height and 6–12 mm larger in GLD than those in the MR or TH sites. The competition parameters that differed most significantly among silvicultural treatments were canopy openness and available PAR, which were greatest in SW sites. GLD growth was positively influenced by canopy openness, suggesting that chestnut growth is strongly correlated with light. Previous studies using American chestnut also found this correlation (Boring et al. 1981; Griffin 1989; Latham 1992; Paillet 1984) and that American chestnut exhibits the best growth in silvicultural treatments that increase light availability to the understory (Belair et al. 2014; Clark et al. 2012; McCament and McCarthy 2005; Rhoades et al. 2009). Our results find that backcross hybrid chestnuts also share these traits.

While the SW treatment had the greatest amount of available light at the time of measurement, this treatment initially also had the greatest number of large (taller than 1.4 m and less than 3.8 cm DBH) understory hardwood stems (Schweitzer et al. 2014). American chestnut seedlings have been found to grow as fast as or faster than many hardwood competitor seedlings in some settings (Ashe 1911; Brown et al. 2014; Frothingham 1924; Hawley and Hawes 1912; Jacobs and Severeid 2004; Latham 1992; Mattoon 1909), though planted and naturally occurring chestnuts are less adept at competing with fast-growing sprouts, particularly in highly-productive sites (Griffin et al. 1991; McNab 2003). The large size of the seedlings in this study likely enabled them to compete more effectively with fast-growing sprouts, as Clark et al. (2016) found with chestnut hybrids grown in the southern Appalachians and others have found with high quality oak seedlings (Spetich et al. 2002; Teclaw and Isebrands 1993). By year three, 41% of chestnuts in the SW sites were dominant. It will be essential for these seedlings to maintain their dominant and codominant positions as competing sprouts continue to grow and the amount of light reaching lower strata declines. To ensure the long-term success of planted chestnut, competition control may be necessary in harvest treatments with low residual basal area.

Chestnut seedlings growing in the MR treatment sites were smallest in mean height and GLD over the course of this study, which is not surprising given the low light levels in those sites. These findings are consistent with other studies evaluating chestnut establishment in midstory removal treatments (Clark et al. 2012; Rhoades et al. 2009). Of interest was the increase in PAR and canopy openness from year one to two, presumably due to gradual degradation of dead standing stems in the midstory. The delayed increase in light may have encouraged shade tolerant species, including chestnut, while discouraging shade-intolerant species. Chestnut's ability to respond to increases in light (Paillet 1984) more rapidly than other shade tolerant species may enable them to compete successfully when overstory harvesting takes place in this treatment.

The TH sites presented intermediate light conditions (22% PAR in year two compared with 47% in SW and 19% in MR sites). While chestnut height growth of surviving seedlings was 1.5-times greater in the SW treatment sites than in the TH sites by the end of the study, 53% of the chestnuts in the TH sites were dominant compared with 41% in SW sites. Presumably the intermediate light conditions in the TH sites were low enough to hinder fast growth of shade-intolerant species, but high enough to support moderate growth of the shade-tolerant chestnut, while the high light conditions in the SW enabled more of the competing stems to surpass the planted chestnuts. For our study, greatest growth after four years is probably not a good indicator of longer-term success among treatments. Studies have found that planted oak seedlings reach their maximum photosynthetic capacity at 30–50% full sunlight, however they are out-competed on mesic sites by fast-growing species in silvicultural treatments with these light levels (McGee and Loftis 1986; Schuler and Robison 2010). Johnson (1984) found that planted northern red oak performed better in sites thinned to the B level of the Gingrich stocking guide than those planted in clearcuts. Similarly, we found superior chestnut DP in the TH treatments, at moderate levels of light. These treatments may yield the highest success rates for planted chestnuts and require less competition control than higher-light treatments.

Seedling quality

The competitive ability of the planted chestnut seedlings was strongly positively related to initial GLD both in the regression models predicting third year DP and DP throughout the first three years of the study. For the model predicting year three DP, density of competing stems in year two negatively affected dominance probability in year three, however the negative effect was buffered for seedlings with large GLD at planting. For example the average DP of a seedling with mean initial GLD of 5 mm and density of 25 seedlings was approximately 10%, whereas the DP for a seedling with a GLD of 17 mm with 25 nearby competing stems was close to 60%. Many studies have evaluated the importance of hardwood seedling quality on early growth and have also found that initial GLD is a strong predictor of future GLD (Clark et al. 2016; Teclaw and Isebrands 1993; Zaczek et al. 1997; Wendel 1980). No studies that the authors are aware of, however, have evaluated the importance of seedling quality on the competitive ability of planted chestnuts. Our results show that seedling quality is not only important for early growth, but also for early competitive ability of planted chestnut seedlings. Our study illustrates the significant advantage of using high-quality seedlings in chestnut reintroduction plantings.

Hybrid chestnut performance

After four years, 57% of SA417 chestnut seedlings were alive, compared with only 30% of the SA330 and 37% of American chestnut seedlings. SA417 seedlings had grown nearly 1.5 times greater in height and diameter than SA330 seedlings and were marginally greater in height and diameter than American seedlings. Clark et al. (2016), interestingly, found no differences in height and diameter growth between SA330 and SA417 hybrid American chestnuts planted in the southern Appalachians. Chinese chestnuts had better survival (88%), as well as height and diameter growth in our study than any of the other breeding generations. Few studies evaluating planted chestnut seedling performance have included pedigree as a treatment (exceptions include Clark et al. 2012, 2016). Our results suggest that some genotypes that exhibit high blight-resistance may not perform satisfactorily in some forested settings. Testing field performance among genotypes of improved trees species prior to establishing operational reintroduction plantings is critical.

Conclusions

This study illustrates BC_2F_3 hybrid chestnut's ability to successfully establish under a gradient of light availability; for one of two families tested, growth was maximized under highest light. Survival was similar across light levels. Competitive ability of both families was maximized in TH sites, most likely due to an intermediate level of light which allowed chestnut seedlings to respond without releasing fast-growing shade-intolerant species. Chestnuts in high-light treatments will likely require release from competing vegetation. Canopy harvest following chestnut establishment in midstory removal treatments may enable chestnut seedlings to outcompete shade-intolerant species, however this hypothesis remains untested. Based on these results, moderate light conditions may maximize the competitive ability of planted chestnut. These results underscore the importance of evaluating performance, particularly competitive ability, of improved tree seedlings in field settings prior to implementing reintroduction efforts. Both pathogen/pest resistance and the ability to compete in field settings are necessary for the successful establishment of founder populations of threatened tree species. Pedigree can affect performance, which suggests including seedlings from multiple source populations is wise to increase the probability of long-term success.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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