Forest Ecology and Management 329 (2014) 21–29

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Four-year response of underplanted American chestnut (*Castanea dentata*) and three competitors to midstory removal, root trenching, and weeding treatments in an oak-hickory forest

Ethan D. Belair[a], Mike R. Saunders[a,*], Brian G. Bailey[b]

[a] Department of Forestry and Natural Resources, Purdue University, 715 State Street, West Lafayette, IN 47906, United States
[b] Washington State Department of Natural Resources, 919 N Township Street, Sedro Woolley, WA 98284, United States

ARTICLE INFO

Article history:
Received 11 February 2014
Received in revised form 3 June 2014
Accepted 5 June 2014

Keywords:
American chestnut
Forest restoration
Underplanting
Midstory removal
Reintroduction
Oak

ABSTRACT

American chestnut (*Castanea dentata*) has been killed or reduced to recurrent stump sprouts throughout its range following the importation of multiple pathogens in the 19th and early 20th centuries. Understanding what drives chestnut growth and survival would aid the development of appropriate silvicultural guidelines for restoring the species once blight resistant stock is available. Here we compare the response of planted American and hybrid chestnut seedlings to that of important competitors, northern red oak (*Quercus rubra*), sugar maple (*Acer saccharum*) and red maple (*A. rubrum*), under treatments designed to evaluate the effects of various sources of competition on seedling growth and survival. After four years, American and hybrid chestnut was significantly taller in trenched plots (181.8 ± 12.4 cm; mean ± SE) compared to untrenched plots (127.5 ± 7.9 cm), weeded plots (174.5 ± 12.7 cm) compared to unweeded plots (130.1 ± 6.5 cm) and in midstory removal plots (156.6 ± 7.8) versus full canopy (88.8 ± 11.7 cm), and had outperformed the other species in most competitive environments. Chestnut was the only species to respond to every treatment with significant growth increases, displaying a notable ability to capture growing space when it became available. We suggest that American chestnut restoration may be more successful where early stand management provides chestnut a brief period of reduced competition. Specifically, midstory removal can increase survival and growth of underplanted American chestnut, and when combined with multi-stage shelterwood removals of the overstory and some amount of competition control, may constitute a viable restoration strategy for chestnut in many of the eastern oak-hickory forests where it was originally dominant.

1. Introduction

American chestnut (*Castanea dentata* (Marsh.) Borkh.) was a dominant hardwood species in eastern North America prior to the importation of two pathogens: cinnamon root rot (*Phytophthora cinnamon* Rands.) in the 1860s and chestnut blight (*Cryphonectria parasitica* (Murr.) Barr.) in the 1900s (Anagnostakis 2012; Foster et al., 2002). The two pathogens caused widespread and near complete mortality of the species, respectively leading to a range contraction in the southern US and to functionally extirpating the species elsewhere. On *Phytophthora*-free sites, American chestnut now only exists as recurrent stump sprouts which rarely reach sexual maturity (Paillet, 2002). Consequently, American chestnut been replaced on the landscape by a variety of other tree species, most prominently oaks (*Quercus* spp. L.; Paillet, 2002; Vandermast and Van Lear, 2002).

American chestnut has little to no natural resistance to either pathogen. Although tree breeding efforts to confer resistance to *Phytophthora* has only recently started, a long history of backcrossing by the U.S. Forest Service, the Connecticut Experiment Station and, most recently, The American Chestnut Foundation has produced putatively blight-resistant hybrids of American chestnut and Asian species; these are being field tested for eventual restoration in plantings across the former range (Anagnostakis, 2012; Jacobs et al., 2012; Worthen et al., 2010). The current scarcity and expense of this planting material necessitate a shift in research focus away from describing the ecophysiology of American chestnut (Bauerle et al., 2006; Joesting et al., 2009; Latham, 1992; Wang et al., 2006), and toward developing nursery, planting and silvicultural protocols that will lead to high survival (Clark et al., 2012a,b; Jacobs et al., 2012). Reintroduction strategies for planted American chestnut in intact forests and other natural settings is

---

* Corresponding author. Tel.: +1 765 430 1440; fax: +1 765 494 9461.
E-mail address: msaunder@purdue.edu (M.R. Saunders).

http://dx.doi.org/10.1016/j.foreco.2014.06.011
0378-1127/

strongly needed, yet this research remains uncommon (Gauthier et al., 2013; McCament and McCarthy, 2005; Rhoades et al., 2009).

While many studies have described American chestnut in afforestation plantings (e.g., Gauthier et al. 2013; Jacobs and Severeid, 2004), particularly on mine reclamation sites, relatively few have looked at reintroduction in existing forests (Clark et al., 2012a; McCament and McCarthy, 2005). The numerous benefits of reintroducing American chestnut in understory environments likely include lower competitive pressure, fewer environmental extremes, and lower browse pressure (Comeau et al., 2005; Motsinger et al., 2010; Paquette et al., 2006). Underplanting often requires minimal site preparation as canopy shade has suppressed shrub and herbaceous growth, expedites the development of mature forest characteristics, and maintains high levels of forest-based ecosystem services (Comeau et al., 2005; Paquette et al., 2006). Finally, underplanting systems are advantageous on sites following overexploitation, local extirpation, or any other causes of insufficient natural regeneration of the desired species (Dey and Parker, 1997; Lhotka and Loewenstein, 2013; Paquette et al., 2006). Plantings need not cover a large area nor be at high densities; given the goals of restoration, introducing a new species through dispersed, low density planting which mimic natural forest succession may be preferable to classic plantation establishment.

Though American chestnut's performance has rarely been compared to competitor species in the understory, historical writings and paleoecological pollen records indicate that chestnut was found across a wide range of environments (Foster et al., 2002; Wang et al., 2013). Underplanting chestnut in oak-dominated stands may be an effective means of capitalizing on American chestnut's competitive ability and intermediate shade tolerance to increase its dominance relative to competing species (Clark et al., 2012a; Griscom and Griscom, 2012; Joesting et al., 2009; Rhoades et al., 2009). Many oak stands require control of shade-tolerant midstory stems preceding an overstory harvest in order to increase light availability and promote establishment of oak advance regeneration (Bailey et al., 2011; Lhotka and Loewenstein, 2013; Lhotka and Zaczek, 2003; Motsinger et al., 2010). These midstory removal treatments are now commonly used as a first stage in shelterwood regeneration systems in eastern oak forests rather than a traditional establishment cut that would otherwise encourage the encroachment of less desirable, shade-intolerant species (Loftis, 1990; Lhotka and Loewenstein, 2013; Motsinger et al., 2010). Maintaining partial canopy cover and, thereby, excluding fast-growing, intolerant species should increase the growth and survival of planted American chestnut seedlings (Clark et al., 2012a; Latham, 1992; McCament and McCarthy, 2005; Rhoades et al., 2009; Wang et al., 2013).

In addition to directly altering light competition, silvicultural treatments indirectly alter belowground competition. Reduction of root competition can improve seedling performance as much as the increased light availability resulting from crown thinning (Barberis and Tanner, 2005; Coomes and Grubb, 2000). Even herbaceous vegetation can provide sufficient competitive pressure to negatively impact seedling growth (Davis et al., 1998). Unfortunately, the degree to which root competition limits aboveground growth still remains poorly understood (Barberis and Tanner, 2005; Coomes and Grubb, 2000). The rooting habits of American chestnut in particular have not been extensively studied, although the species is hypothesized to have tendencies similar to co-occurring oak species which invest heavily in belowground structures early in development (Clark et al., 2012b; McCament and McCarthy, 2005; Wang et al., 2006). This may be a tenuous assumption as American chestnut grows more quickly in height and stem diameter than oak across a variety of light levels and competitive environments (Jacobs and Severeid, 2004; Latham, 1992; Wang et al., 2006).

The objectives of this study were to compare the growth and survival of underplanted American and hybrid chestnut to three common competitors, northern red oak (*Quercus rubra* L.), red maple (*Acer rubrum* L.) and sugar maple (*A. saccharum* Marsh.), under a range of competitive conditions produced by combinations of midstory removal, trenching and weeding. Using a blocked, split-split plot design that juxtaposed midstory removal, trenching and weeding treatments with full canopy and untreated controls, we isolate sources of competition affecting seedling survival and growth and make inferences on restoration strategies for the species in intact, natural forests. We predicted that the shade-tolerant maple species would survive better and grow faster than chestnut or oak in the heavily shaded control treatments, but that all species' survival and growth would increase after midstory removal. We also predicted that due to the reduction of competition resulting from weeding and trenching treatments, all species would respond to those treatments with increased growth. Finally, due to its potentially high growth rates, our final hypothesis was that chestnut would more readily respond to increased growing space resulting from midstory removal, trenching and weeding treatments.

2. Materials and methods

2.1. Study sites

This study was conducted on two Purdue University properties in north-central Indiana: the Cox–Haggerty Property (40°25.7′N, 86°58.2′W) and Meigs Research Farm (40°17.3′N, 86°52.5′W). Both sites are in the Central Till Plain, Beech-Maple Section (McNab et al., 2005), and have a mean annual temperature of 10.9 °C and annual precipitation of 105.4 cm (NCDC, 2012). Monthly precipitation is slightly higher in the spring and summer months (maximum: May, 11.3 cm avg.), than in the fall and winter months (minimum: February, 5.8 cm avg.; NCDC, 2012). The region has relatively short, mild winters and long, hot summers. Average day of last freeze is April 22 and average day of first freeze is October 16 (NCDC, 2012).

The Cox–Haggerty canopy is dominated by white oak (*Q. alba* L.) and red oak (*Q. rubra* L.) as well as several hickory species (*Carya* spp. Nutt.), with a midstory of primarily sugar maple, sassafras (*Sassafras albidium* Nutt.), Ohio buckeye (*Aesculus glabra* Willd.) and the invasive exotic Amur honeysuckle (*Lonicera maackii* Rupr.). The understory at Cox–Haggerty is somewhat sparse and consists primarily of regenerating sugar maples, various grasses, and Amur honeysuckle. Average overstory basal area is 36 m^2 ha^{-1} with a site $index_{50}$ for upland oaks of 24–26 m (Bailey, 2011; NRCS, 2014). Soils are Miami silt loam grading into the clay loam Strawn-Rodman complex. Both are well-drained and derived from loamy glacial till (NRCS, 2014). Planting blocks were located in areas that minimized the effects of topography, usually in areas below 20% slope.

The Meigs canopy is dominated by hickory, elm (*Ulmus* spp. L.) and black cherry (*Prunus serotina* Ehrh.), with the midstory layer dominated by elms and hackberry (*Celtis occidentalis* L.). Meigs is a very productive site with a thick understory consisting of a variety of herbaceous species, including poison ivy (*Toxicodendron radicans* (L.) Kuntze), mayapple (*Podophyllum pelatumi* L.) and wood nettle (*Laportea canadensis* (L.) Weddell). Average overstory basal area is 26 m^2 ha^{-1} with a site $index_{50}$ for upland oaks of 24–28 m (Bailey, 2011; NRCS, 2014). Soils range from Crosby-Miami silt loam complex to Richardville silt loam; both soils are derived from loess over loamy glacial till (NRCS, 2014). The site lacks major topographical relief (i.e., slopes between 0% and 2%) and adjoins a restored wetland area, with soils at or above field capacity during much of the growing season in most years.

2.2. Experimental design and field measurements

This study was installed in March and April 2009 using a blocked split-split plot design with individual trees as experimental units (Bailey, 2011). Sites were treated as blocks with whole plot treatments consisting of five different techniques of midstory removal plot plus an untreated control. Whole plots ranged from 0.15 ha to 0.36 ha. Techniques differed only by equipment used and application of herbicide; all treatments removed subcanopy stems < 15 cm dbh. On average, midstory removal reduced basal area by 5.1 m^2 ha^{-1} (14%) at Cox–Haggarty and 4.4 m^2 ha^{-1} (17%) at Meigs.

Within each whole plot, 4 subplots measuring 4 m × 12 m were established. Two randomly selected subplots were trenched using a Vermeer® RT200 23HP walk-behind trencher, which severed overstory roots to a depth of 45–60 cm. The trenches were then lined with landscaping cloth to exclude ingrowth of overstory roots and backfilled. All 4 subplots within a whole plot were then divided in half (i.e., a sub-subplot), and each half randomly assigned to a weeded or unweeded condition. Weeding was conducted as needed throughout the initial two growing seasons, and biannually thereafter, through complete removal of the aboveground components of all herbaceous and woody materials, using either a Stihl X-series 345F clearing saw and/or by hand-pulling. After leaf-out of the second growing season, a 2% mixture of glyphosate in water was applied to herbaceous growth in the weeded treatment in order to decrease the frequency of manual weeding treatments. Finally, 1.5 m tall metal fencing was installed around each subplot to exclude browsing by white-tailed deer (*Odocoileus virginianus* Zimmerman).

In May 2009, subplots were planted at both sites on a 2 m × 2 m grid, for an average density of 2500 seedlings/ha. Northern red oak, sugar maple, and a mix of pure and hybrid (BC_3F_2) American chestnut seedlings were planted at the Cox–Haggerty property, while northern red oak, red maple, and a mix of pure and hybrid (BC_3F_2) American chestnut seedlings were planted at the Meigs property. Genetic differences between the two chestnut stock types were not tracked; previous studies have suggested that BC_3F_2 hybrids should function in an ecologically equivalent manner to American chestnut (Diskin et al., 2006; Worthen et al., 2010; Knapp et al., 2014). Red maple was planted at Meigs due to consistently saturated soils' negative effects on growth and survival of sugar maple (Burns and Honkala, 1990; Hutnik and Yawney, 1961); based on our knowledge of the site characteristics, we felt that sugar maple was unlikely to be a strong competitor at Meigs and, conversely, red maple to be a strong competitor at Cox–Haggarty. Four seedlings of each species were randomly planted in each subplot, two in unweeded and two in weeded conditions, for a site total of 96 seedlings per species and a total of 576 seedlings across the experiment. All putatively blight resistant stock (BC_3F_2) was obtained from the Hardwood Tree Improvement and Regeneration Center (HTIRC) at Purdue University. A mixed seed lot, with no family or genetic tracking, was collected from the seed orchard at the FNR Research Farm in West Lafayette, IN, and mixed with seeds from locally collected pure American chestnut. All chestnut, northern red oak and red maple was grown for a full growing season at the Indiana Department of Natural Resources State Tree Nursery in Vallonia, IN before being lifted in spring 2009 as 1 + 0 bareroot stock. Sugar maple seedlings were 2 + 0 bareroot stock acquired from the Wilson State Tree nursery in Boscobel, WI and were top pruned in accordance with that nursery's standard cultural procedures. All seedlings were planted with the aid of a planting auger. Initial height and ground line diameter (GLD) were recorded for each seedling soon after planting.

In July 2013, two hemispheric photographs were taken of the canopy in both the weeded and unweeded halves of each subplot using a Canon® EOS (SLR) 20D digital camera (Canon Inc., Tokyo, Japan) with a Sigma F3.5 EX DG 8 mm circular fisheye lens (Sigma Corp., Fukushima, Japan), held approximately one meter above the ground and leveled with a block level. Images were analyzed using Gap Light Analyzer 2.0 (Millbrook, NY) with standardized protocols to determine canopy openness, or the proportion of each photo comprised of open sky. Canopy openness as a proxy for the photosynthetically active radiation each seedling is receiving (Canham, 1988); it was estimated for each half of a subplot by averaging estimates from the two images in each weeded or unweeded section.

Survival, total height and GLD were recorded for each seedling annually, during each dormant season. Total height was measured to the nearest 0.01 m from ground line to the tallest terminal bud. GLD was averaged from two perpendicular measurements using precision dial calipers and recorded to the nearest 0.1 mm.

2.3. Statistical analyses

We used generalized linear and linear mixed models to assess the effects of covariates and treatments on survival and four-year seedling height and GLD growth. Midstory removal was pooled across the various midstory removal techniques to create a single, binary variable for midstory removal to compare treatment groups; Bailey (2011) found that canopy openness across all midstory removal plots ranged from 14% to 17%, and that there was no significant difference in growth or survival of underplanted trees between midstory removal techniques. However, we also chose to include canopy openness as a covariate in our growth and survival models due to its important effect on microsite conditions. Because canopy openness was highly collinear with midstory removal, we excluded the midstory removal main effect from our models. We also included initial seedling height and GLD as covariates to standardize growth response (Bevilacqua, 2002) since absolute growth is often positively correlated with the size of an individual. This method of standardization is preferable to the use of relative growth rate, which tends to decline as total tree size increases (Bevilacqua, 2002).

Main effects in the models, therefore, included trenching (two levels: trenched or untrenched), weeding (two levels: weeded or unweeded) and species (four levels: hybrid and American chestnut, red oak, red maple, and sugar maple). Site was used as a blocking variable and subplot as a random variable to capture unmeasured variation. A binomial response variable denoting survival of seedlings through the fourth growing season was tested with a generalized linear model in R 2.15.1 (R Core Team, 2012). Preliminary analysis demonstrated that the causes of mortality differed strongly among species, so species-specific survival models were created. Seedling height and GLD through the fourth growing season was testing using linear mixed models in lme4 1.0 (Bates et al., 2014). These response variables were log transformed when assumptions of normality and homoscedasticity were not met. In all models, individual predictors were kept or discarded based on their effect on the model's overall AIC. We chose this approach as it is more robust for unbalanced datasets than traditional ANOVA, and was employed in response to unexpectedly high mortality in full canopy controls. A model selection approach based on second-order AIC (AICc) and Akaike weights was employed to determine if a superior fit could be identified through model averaging (Symonds and Moussalli, 2011).

Due to the large impact of light heterogeneity in these types of selective harvests, the degree to which each species reacted to the gradient of light availability was assessed by regressing canopy openness with four-year growth of individuals. This simple regression was intended to show the strength of each species' reaction to increased light availability, as well as the variability in reaction of individuals of a species to those various light levels.

Significant differences between treatments and species means were determined using Games–Howell coefficients, a method similar to Tukey's HSD. This approach is intended for unbalanced study designs and was employed in our analysis due to unequal mortality between treatments and species (Games and Howell, 1976). *P*-values for species' mean height and GLD in each treatment were calculated using the Satterthwaite approximation for degrees of freedom and a Welch's *t*-test, an adaptation of Student's *t*-test intended for use with two samples with unequal variances (Ruxton, 2006). These comparisons are intended to illustrate the effect of individual treatments and utilize treatment and species means rather than results from mixed effects growth models.

3. Results

3.1. Survival

Seedling survival differed among species in terms of what factors contributed to mortality (Table 1). American and hybrid chestnut and sugar maple were affected similarly by the various factors. Modeled four-year survival of chestnut significantly declined from 89% in highest light environment (42% canopy openness) to 45% in the lowest light environment (6% canopy openness) ($p = 0.004$). For sugar maple, the decline was not nearly as steep, declining from 84% in the highest light environment it was planted in (27% canopy openness) to 27% in the lowest (6% canopy openness) ($p = 0.035$). Trenching and weeding did not affect survival of either chestnut or sugar maple (*p*'s > 0.10). Red oak was affected by both canopy openness ($p = 0.006$) and initial height ($p < 0.001$). In the lowest light environment (6% canopy openness), a red oak with the average initial height of 82 cm had modeled survival of 51% whereas its survival was 91% in the highest light environment (42% canopy openness). Additionally, at the average canopy openness (17%), red oak seedlings with the greatest initial height (135 cm) had four-year modeled survival of 90% as opposed to 33% for those with the lowest initial height (28.5 cm). Red maple responded weakly to initial height ($p = 0.057$), but not to canopy openness ($p > 0.10$). Modeled red maple survival actually declined with initial height as 81% of the shortest seedlings (10 cm) survived while 27% of the tallest survived (60 cm). Trenching increased modeled red maple survival but there was high variably in the response ($p = 0.134$).

Strictly in terms of canopy openness, annual mortality patterns differed among species as well. Numbers of American and hybrid chestnut and sugar maple declined rapidly in the first year, particularly in heavily shaded environments, and became relatively stable thereafter, while numbers of red oak and red maple declined consistently throughout the four years (Fig. 1).

Table 1
Predicting variables and their associated coefficients, standard errors and *P*-values, used in final, simplified models to predict survival and size of seedlings four years after planting. Survival models were species-specific. For main factors, the null level is given in parentheses. Coefficients and standard errors are presented in a log transformed scale.

Response	Effect	Mean ± SE	*P* value
Survival year 4 chestnut			
Chestnut	Canopy openness	0.065 ± 0.022	0.004
Red oak	Canopy openness	0.033 ± 0.011	0.006
	Initial height	0.064 ± 0.023	<0.001
Red maple	Initial height	−0.082 ± 0.036	0.057
Sugar maple	Canopy openness	0.065 ± 0.036	0.035
log Height year 4			
	Site (Cox–Haggerty = 0)		
	Meigs	0.051 ± 0.025	0.013
	Canopy openness	0.007 ± 0.003	<0.001
	Initial height	0.003 ± 0.001	<0.001
	Initial ground line diameter	0.005 ± 0.006	0.215
	Trenching (Untrenched = 0)	0.124 ± 0.029	0.004
	Weeding (Unweeded = 0)	-0.109 ± 0.049	0.003
	Canopy openness × weeding	0.008 ± 0.003	0.003
	Species (Chestnut = 0)		
	Red maple	0.082 ± 0.038	0.035
	Red oak	−0.043 ± 0.025	0.096
	Sugar maple	−0.040 ± 0.041	0.165
	Species × Trenching		
	Red maple in trenched plots	−0.101 ± 0.046	0.030
	Red oak in trenched plots	−0.115 ± 0.035	0.001
	Sugar maple in trenched plots	−0.131 ± 0.050	0.010
log GLD year 4			
	Site (Cox–Haggerty = 0)		
	Meigs	0.014 ± 0.019	0.370
	Canopy openness	0.007 ± 0.002	<0.001
	Initial height	0.001 ± 0.000	<0.001
	Initial ground line diameter	0.023 ± 0.005	<0.001
	Trenching (Untrenched = 0)	0.074 ± 0.016	<0.001
	Weeding (Unweeded = 0)	−0.038 ± 0.043	<0.001
	Canopy openness × weeding	0.007 ± 0.002	0.002
	Species (Chestnut = 0)		
	Red maple	−0.061 ± 0.029	0.040
	Red oak	−0.100 ± 0.021	<0.001
	Sugar maple	0.006 ± 0.034	0.864
	Species × weeding		
	Red maple in weeded plots	0.081 ± 0.035	0.024
	Red oak in weeded plots	−0.039 ± 0.028	0.167
	Sugar maple in weeded plots	−0.138 ± 0.039	0.001

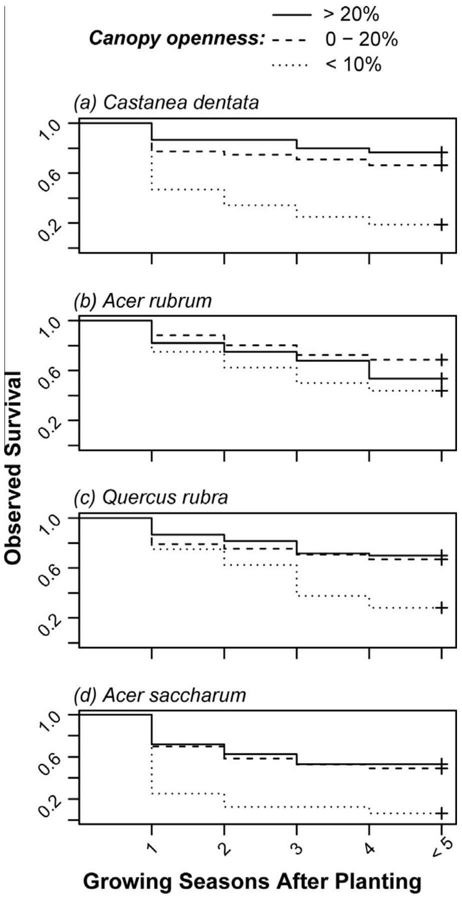

Fig. 1. Curves showing patterns of observed survival for (a) American chestnut, (b) red maple, (c) northern red oak and (d) sugar maple in three different canopy openness ranges. The lowest range (<10% open) contained 88% of the control blocks, while the middle (10–20% open) and high (>20% open) ranges contained roughly half of the midstory removal blocks each. Survival was recorded during the dormant season following each of the first 4 growing seasons and in the spring of the fifth growing season at the conclusion of the study. The final recording of survival is denoted by <5 on the *x* axis.

3.2. Growth

All main effects and covariates were significant predictors of seedling growth in our models, with the exception of initial GLD as a predictor of final height (Table 1). There were also significant interaction effects for canopy openness by weeding treatment in both models, species by weeding treatment in the GLD model, and species by trenching treatment in the height model. These models had Akaike weights of 0.99, meaning that model averaging would have little effect on the predictive capabilities.

Canopy openness had a positive effect on both seedling height and diameter across treatments (Fig. 2). Although all four species' height growth reacted positively to canopy openness (all $p < 0.001$), the effect of increasing canopy openness varied considerably between species. American and hybrid chestnut showed the strongest reaction to canopy openness, with four-year height growth increasing 7.8 ± 0.9 cm (mean ± SE) on average for every 1% increase in canopy openness through the range of measurements (6–42%), and 39.6% of the variation in height growth determined by canopy openness. Meanwhile, northern red oak showed the weakest relation, with four-year height growth increasing just 2.1 ± 0.4 cm on average for every 1% increase in canopy openness, and canopy openness accounting for a scant 18.1% of the variation in four-year height growth. Weeded seedlings generally showed a much stronger increase in growth with canopy openness than unweeded ($p = 0.003$, Table 1); this was particularly pronounced for chestnut and red maple.

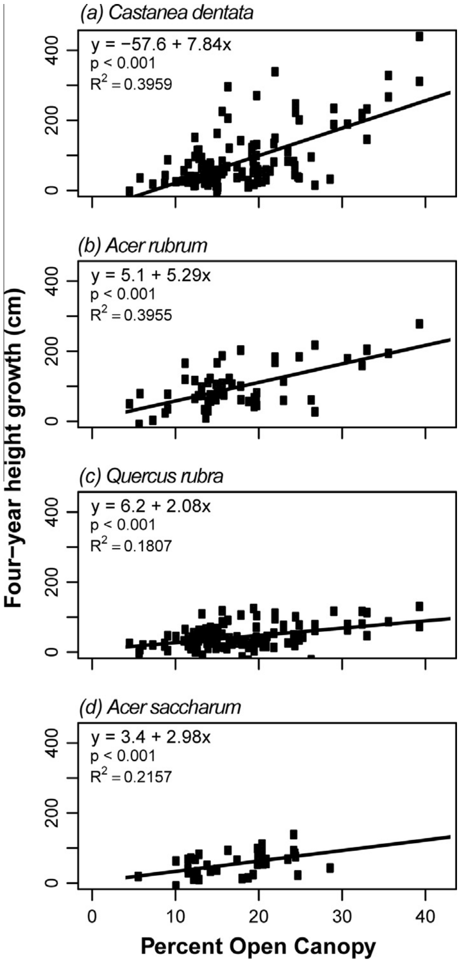

Fig. 2. Simple linear regression using percent open canopy as a predictor of total seedling height for (a) American and hybrid chestnut, (b) red maple, (c) northern red oak and (d) sugar maple.

Trenching generally increased height and GLD, although trenching effects differed by species (Table 1, Fig. 3). American and hybrid chestnut responded to trenching with significant increases in both total height (trenched: 181.8 ± 12.4 cm, untrenched: 127.5 ± 7.9 cm, $p < 0.001$) and GLD (trenched: 18.4 ± 1.1 mm, untrenched: 13.5 ± 0.7 mm, $p < 0.001$). Northern red oak had significantly greater GLD in trenched plots (trenched: 12.7 ± 0.6, untrenched: 10.7 ± 0.4, $p = 0.006$), although no significant differences were observed in height growth. Neither maple species responded to trenching for either height or GLD (Table 2).

Like for trenching, weeding differentially increased height and GLD across species (Table 1, Fig. 3). Weeding yielded significantly taller (weeded: 174.5 ± 12.7 cm, unweeded: 130.1 ± 6.5 cm, $p = 0.002$) and stouter (weeded: 18.2 ± 1.1 mm, unweeded: 13.2 ± 0.6 mm, $p < 0.001$) American and hybrid chestnut. Red maple responded to weeding with similar increases in both total height (weeded: 150.1 ± 12.5 cm, unweeded: 107.1 ± 8.7 cm) and GLD (weeded: 13.5 ± 0.9 mm, unweeded: 9.0 ± 0.9 mm) while northern red oak displayed a moderate increase in total height (weeded: 132.1 ± 5.4 mm, unweeded: 117.6 ± 4.6 mm), but not in GLD (Table 2). Surprisingly, sugar maple responded to periodic weeding treatments with decreases in both total height and GLD, although these responses were not statistically significant (Table 2).

American and hybrid chestnut were generally benefitted by midstory removal; when averaged across all plots receiving midstory removal, trees were significantly taller ($p < 0.001$) and stouter ($p = 0.003$) than in controls (Table 2). Red maple showed similar height growth increases with midstory removal, but with a more moderate increase in GLD. Red oak showed moderate increases in both height and GLD. Sugar maple, however, had such low survival under full canopy (6%, $n = 1$) that it prevented statistical testing of midstory removal effects on morphology.

4. Discussion

4.1. Seedling survival

The most reliable predictors of seedling survival were canopy openness and initial seedling height. Both factors can affect stand development by altering growth and survival of species with varying shade tolerance. Underplanted chestnut trees will need locations with light levels sufficient to ensure high rates of survival. Our results indicate locations with greater than 10% canopy openness would be ideal for high chestnut survival and rapid establishment. While a higher light environment, such as a clearcut, would increase growth rates (Clark et al., 2012a; Jacobs and Severeid, 2004; Rhoades et al., 2009), more moderate light levels will minimize the influx of fast growing intolerant species. Chestnut maintains a positive carbon balance in these environments (Wang et al., 2006), and can respond quickly to increased light resources following extended periods of suppression (Paillet, 2002). Therefore, we can assume that underplanted chestnut will persist until the formation of natural canopy gaps, or if accelerated recruitment is desired, the creation of small gaps through harvesting (Griscom and Griscom, 2012). This conservative planting strategy will be especially important on highly productive sites where less desirable, intolerant species can establish quickly, or where invasive species are common (Bailey et al., 2011; Dey and Fan, 2009; Johnson et al., 2009).

Initial height affected survival of all species except hybrid and American chestnut. Chestnut seedlings were taller at planting (68.2 ± 1.2 cm) than red (31.7 ± 0.8 cm) or sugar (21.5 ± 0.7 cm) maple (Fig. 3); this may have reduced the effect of size on survival rates for chestnut relative to those species. However, as it was significantly shorter than red oak (75.6 ± 1.8 cm) at the time of planting ($p < 0.001$), we suspect that chestnut's survival was largely controlled by autecological characteristics, such as shade

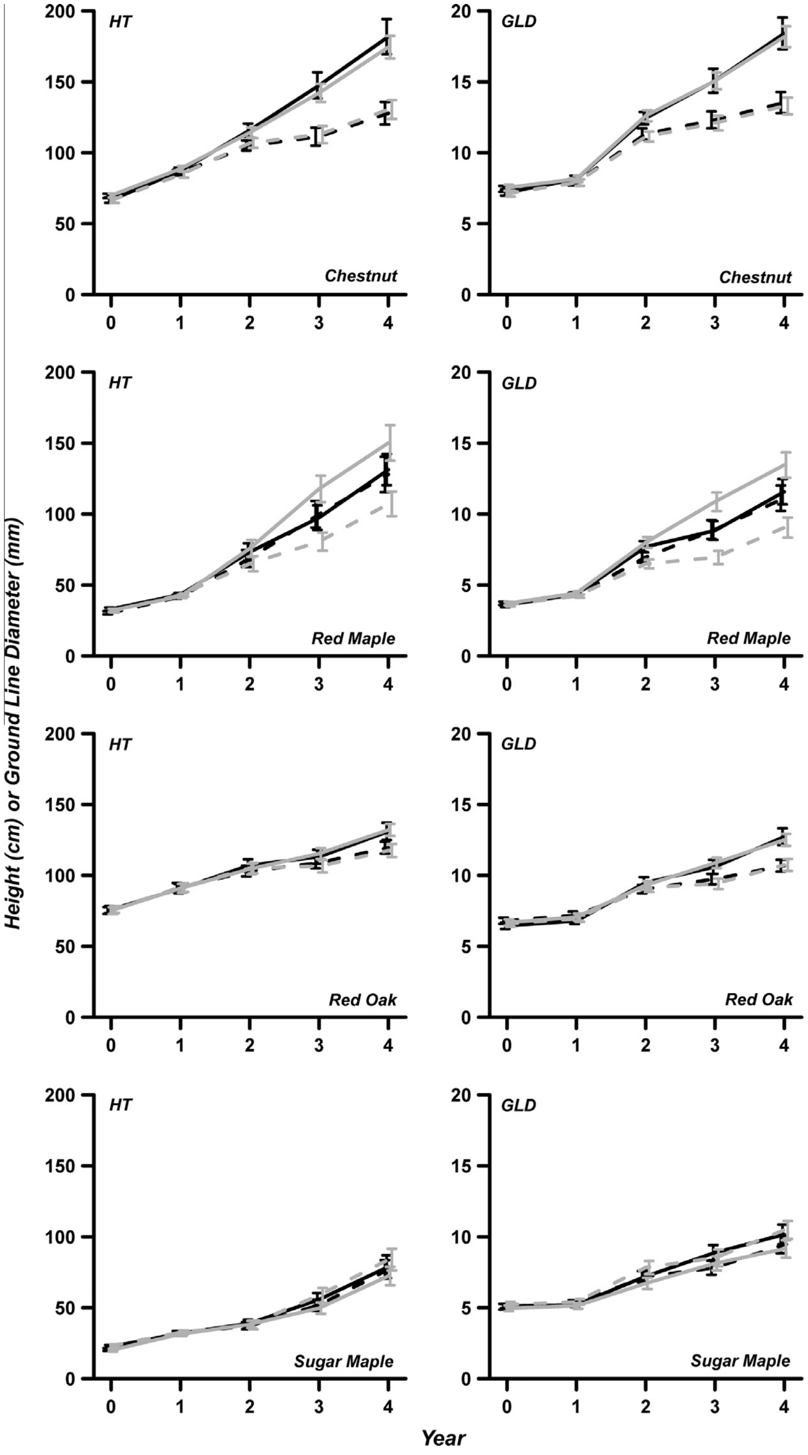

Fig. 3. Annual observed mean height (HT) and ground line diameter (GLD) for American and hybrid chestnut, red maple, northern red oak and sugar maple as affected by trenching (black solid = trenched, black dashed = untrenched) and weeding (gray solid = weeded, gray dashed = unweeded). Error bars are ±1 standard error.

tolerance (Joesting et al., 2009; Wang et al., 2006), rather than its height advantage over local competition. Smaller American and hybrid chestnut seedlings may have reacted to low light by continuing to fund maintenance respiration and the creation of fine roots and foliage, while effectively eliminating primary growth. This strategy would maximize short term survival, and is consistent with the strong effects of light on chestnut growth rates.

Notably, sugar maple survival rates were well below what we expected from a shade-tolerant, seedling bank species (Burns and Honkala, 1990; Marks and Gardescu, 1998). Sugar maple survival was negatively affected by percent open canopy, as greater than 93% of seedlings under full canopy died by the fourth growing season. Survival may have been impacted by the mismatch between climate at our Indiana site and the much cooler climate in Wisconsin where the seed was collected. Sugar maple seedlings have been reported sensitive to temperature, usually through increased soil evaporation and the resulting water stress (Von Althen, 1977; Webb, 1974). Low survival may also have been related to sugar maple's establishment strategy, as it tends to produce a large crop of seedlings annually, even when seed production is below average

Table 2
Effect of midstory removal, trenching and weeding on chestnut, red oak, red maple and sugar maple height and ground line diameter (GLD) after four growing seasons at two sites in northern Indiana. Different letters within columns indicate significant differences between species in that treatment and (*) indicates a significant difference between treated and untreated individuals within a species (e.g., midstory removal versus full canopy). Insufficient sample size for hypothesis testing is indicated by (^). All significant differences based on Games–Howell pairwise comparison tests at $\alpha = 0.05$. All measurements are recorded in cm.

	Midstory removal			Full canopy			Trenched			Untrenched			Weeded			Unweeded		
	n	Height	GLD	*n*	Height	GLD	*n*	Height	GLD	*n*	Height	GLD	*n*	Height	GLD	*n*	Height	GLD
Am. chestnut	117	156.6a*	1.62a*	6	88.8a	0.94a	59	181.8a*	1.84a*	64	127.5a	1.35a	65	174.5a*	1.82a*	58	130.1a	1.32a
Red oak	113	127.2b*	1.19b*	9	93.3a	0.80a	55	131.0b	1.27b*	67	119.6a	1.07b	60	132.1b	1.25b*	62	117.6ab	1.07b
Red maple	50	138.0ab*	1.20b*	7	71.0a	0.73a	31	131.3b	1.16bc	26	127.9a	1.11ab	30	150.1ab*	1.35b*	27	107.1bc	0.90b
Sugar maple	43	78.9c	0.99c	1	32.0^	0.36^	20	78.9c	1.01c	24	77.0b	0.95b	23	72.4c	0.91c	21	83.9c	1.05b

(Boerner and Brinkman, 1996; Marks and Gardescu, 1998). Sugar maple can thereby remain competitive in a stand despite individuals having low survival rates (Boerner and Brinkman, 1996), though the success of this strategy is not reflected in studies utilizing artificial regeneration. Therefore, chestnut regeneration from seed in natural stands with sugar maple may have lower survival than we observed because the chestnut must compete with exceedingly large crops of sugar maple regeneration.

4.2. Midstory removal and canopy openness

The shade tolerance of a given species is determined by its ability to persist in a particular light environment, maintaining positive carbon balance, while coping with the other stresses at that site (Valladares and Niinemets, 2008). However, when underplanting intermediate species following midstory removal, the goal is not for seedlings to persist indefinitely without release, but rather to establish and gain an early advantage over less desirable, intolerant species which cannot persist in a shaded understory (Bailey et al., 2011; Lhotka and Loewenstein, 2013). More tolerant but less plastic species, such as sugar maple, are often unable to utilize the increased light resulting from midstory removal, and are competitively disadvantaged where light exceeds their saturation level (Lhotka and Loewenstein, 2013; Lhotka and Zaczek, 2003; Valladares and Niinemets, 2008).

We used canopy openness to characterize light environment, and canopy openness was a significant, albeit weak, predictor of seedling morphology after four growing seasons for all species. American and hybrid chestnut showed the strongest connection between light level and height growth after 4 years (Fig. 2). Chestnut did not appear to become light saturated at observed light levels, generally agreeing with previous studies (Clark et al., 2012a; Griscom and Griscom, 2012; McCament and McCarthy, 2005; Rhoades et al., 2009). Wang et al. (2006) found chestnut became light saturated at levels slightly higher than red maple; these species were not significantly different in response to light in our study. A classic shade-tolerant species, sugar maple's height growth was little affected by canopy openness, likely because the majority of our plots had canopy openness values which exceeded the levels at which sugar maple generally becomes light saturated (Burns and Honkala, 1990; Canham, 1988). Logan and Krotkov (1968) found no difference in aboveground morphology of sugar maple grown at 13%, 25%, 45%, or 100% of full sunlight, indicating that the trees were light saturated at or below 13% full sunlight. Similarly, Canham (1988) found no correlation between height growth in sugar maple and canopy light transmittance, and that lateral growth increases leveled off at approximately 20% total PAR. This same asymptotic trend in growth rates has been noted in northern red oak, with seedling growth leveling off around 35% full sunlight (McGee, 1968; Phares, 1971). It is, therefore, surprising that we did not see a more positive relationship between canopy openness and the growth of red oak seedlings.

Despite poor performance as a single predictor of height growth, canopy openness had a substantial effect on seedling height and diameter after four growing seasons. We believe that canopy photographs captured much of the variation in post-harvest canopy structure including heterogeneous crown expansion of residual trees, crown dieback and windthrow, all of which can alter the amount and quality of light reaching the understory level of the stand (Canham, 1988). The effect of individual tree disturbances vary spatially and temporally (Canham, 1988), and in the context of this study, these disturbances likely influenced light availability within or among subplots, particularly at Meigs where we noted loss of small overstory trees in some areas in year two of the study.

4.3. Trenching

The trenching treatment had no effect on the growth of red oak, red maple or sugar maple, but resulted in a large increase in both the total height and GLD of hybrid and American chestnut. It is often assumed that chestnut, similar to oak species, invests preferentially in belowground structures early in development (McCament and McCarthy, 2005; Wang et al., 2006). If this is true, the reduction in root competition afforded by trenching may have sped chestnut's aboveground development by decreasing the period of time when resources were preferentially allocated to root growth. More efficient root expansion could result in increased height growth if the seedling was able to more quickly establish a large root mass capable of acquiring resources to fund shoot growth and subsequently divert the majority of its resources to aboveground structures (Latham, 1992). Under this hypothesis, we would expect red oak to respond similarly to trenching treatments. Our results show a small, but significant increase in GLD of oak seedlings in response to trenching treatments, but no response in height growth. Therefore, red oak may have just begun to express the benefits of decreased root competition, or may have been so limited by light that trees were unable to take advantage of the decreased belowground competition. Conversely, the effect of trenching on American and hybrid chestnut may be related to some other changes that did not affect red oak seedlings in the same manner. For example, chestnut may have disproportionately benefitted from the increased availability of soil nutrients and water resulting from the elimination of overstory roots (Barberis and Tanner, 2005; Coomes and Grubb, 2000); previous studies have found the species quite plastic in its growth response to increase resources (Latham, 1992; McCament and McCarthy, 2005). Most oak species, on the hand, are less plastic and will only outperform competitors on more water- and nutrient-limited sites (Dey and Parker, 1997; Johnson et al., 2009) than we used in this study.

4.4. Weeding

Response to weeding varied markedly by species. American and hybrid chestnut responded to weeding with increases in both height and diameter growth, as did red maple. Chestnut and red maple seedlings planted in weeded plots also displayed a greater reaction to increasing canopy openness than those planted in unweeded plots. When weeding treatments reduced local competition, chestnut and red maple were more able than their competitors to take advantage of the opportunity, perhaps as a result of their indeterminate growth habits (Burns and Honkala, 1990). Chestnut and red maple also tend to have the higher growth rates in the forest matrix and small gaps, often leading to an early height advantage and increased likelihood of achieving dominance over slower-growing species like red oak and sugar maple (Foster et al., 2002; Hutnik and Yawney, 1961; Jacobs and Severeid, 2004; Latham, 1992; Wang et al., 2013). The ability to rapidly respond to increased growing space and establish early dominance can be critical in stand development, as an early height advantage gives seedlings better access to sunlight, and increases its probability of canopy recruitment (Loftis, 1990).

Weeding treatments may also have affected microsite soil moisture, and if soil moisture was limiting growth, weeding treatments could have precipitated a release for American and hybrid chestnut and red maple. However, previous work with a subset of our seedlings suggested weeding treatments increased water use efficiency of chestnut, but did not affect soil volumetric water content (Brown et al., in press). Regardless, American chestnut displays notable drought resistance in both field and greenhouse studies (Bauerle et al., 2006; Gauthier et al., 2013), and was historically a dominant species in some riparian areas and cove forests, indicating it is competitive under various hydrologic regimes (Wang et al., 2013; Vandermast and Van Lear, 2002). Likewise, red maple is widely considered one of the most plastic forest trees in terms of soil moisture requirements, occurring on a diverse array of sites including xeric ridge tops and perpetually inundated swamps and bogs (Burns and Honkala, 1990; Hutnik and Yawney, 1961). Given their flexibility in response to moisture regimes, it seems unlikely that either chestnut or red maple was limited by soil moisture at our sites. Rather, we believe light competition from groundstory shrubs and herbaceous plants limited growth in unweeded plots, as reduced growth in response to light competition has been noted in both species previously (Hutnik and Yawney, 1961; McCament and McCarthy, 2005; Rhoades et al., 2009; Wang et al., 2006). Amur honeysuckle substantially decreased light levels in unweeded plots at Cox–Haggerty, especially in the later years of the study, and tall herbaceous plants at Meigs provided a considerable source of light competition to seedlings in unweeded conditions, particularly for those seedlings < 1 m in height. Weeding treatments likely increased ground level PAR, and ultimately the amount of available growing space (Canham, 1988; Davis et al., 1998; Rhoades et al., 2009).

Red oak responded to weeding with increased diameter growth, but showed no difference in total height between treatments. Increased GLD may indicate that red oak was preferentially allocating resources to belowground structures during this period of low aboveground competition. This pattern has been previously noted for oak species, and is an adaptation to frequent surface fires and droughts (Dey and Fan, 2009; Johnson et al., 2009). Interestingly, sugar maple responded negatively to weeding treatments in both height and diameter growth, although the weeding effect was not significant. Sugar maple is sensitive to soil moisture levels, preferring mesic soils (Burns and Honkala, 1990), and as previously noted, may have been maladapted to the local climatic conditions.

4.5. Effect of initial seedling size

Initial seedling size is consistently one of the most reliable predictors of growth following out-planting (Dey and Parker, 1997; Jacobs et al., 2005), and both initial height and GLD were important covariates in our growth models. Taller seedlings have an immediate advantage at outplanting, when height growth and a resultant increase in light availability can often form a positive feedback loop (Clark et al., 2011; Loftis 1990). Initial GLD was used as a proxy measure of total root mass, and thereby nonstructural carbohydrate storage capacity. Nonstructural carbohydrates affect a seedling's ability to produce the large network of fine roots necessary to access soil water reserves and dissolved nutrients (Clark et al., 2009; Dey and Parker, 1997; Jacobs et al., 2005), and seedlings with large carbohydrate reserves have a distinct advantage at planting (Clark et al., 2009; Dey and Parker, 1997; Jacobs et al., 2005). Additionally, larger seedlings invest more heavily root structures after planting, helping them to avoid transplant shock (Clark et al., 2009, 2011).

5. Conclusions

The results of this study provide a positive outlook for future attempts at landscape-scale restoration of American chestnut under intact forest canopies. American and hybrid chestnut was quite plastic in its growth responses and generally outperformed northern red oak, red maple and sugar maple in the various competitive environments created by midstory removal, trenching and weeding. Therefore, midstory removal as part of a multi-stage shelterwood silvicultural system, may be a viable restoration strategy for chestnut in many eastern oak-hickory forests. This partial harvesting approach would require great care to minimize damage to chestnut seedlings during later overstory removal stages, and could potentially increase harvest costs by slowing down operations. We observed that although growth of established chestnut seedlings increased in response to trenching and weeding, survival was high in all treatments; these observations indicate the added expense of competition control treatments may be an unnecessary luxury during landscape restoration. Nevertheless, a seedling's future success may be greater when early competition control can be used to provide chestnut a brief period of enhanced growth, and when the quality of underplanted chestnut seedlings can be maximized (Clark et al., 2012). Given the low availability and high expense of the current generation of blight-resistant chestnut hybrids, further research to identify optimal competitive environments for chestnut establishment is warranted.

Midstory removal treatments are an important piece in solving the oak recruitment problem in North America, especially when paired with competition control or site preparation treatments such as scarification (Lhotka and Zaczek, 2003). Midstory removal creates canopy structure similar to that found after repeated surface fires, while potentially being more pragmatic to apply in fragmented and suburbanized landscapes. Our results may increase the appeal of midstory removal to private landowners focused on the economic returns of forest management, while providing an opportunity to introduce blight-resistant chestnut seedlings on their lands, an avenue not fully explored to this point.

Acknowledgements

We acknowledge the financial support of the Hardwood Tree Improvement and Regeneration Center, as well as Purdue University's Department of Forestry and Natural Resources Wright Endowment and Purdue University's College of Agriculture Mission-oriented, Internal Grants Program. M. Jenkins and S. Clark provided invaluable advice for improving earlier versions of this manuscript. Lastly, we also wish to thank J. Arseneault, B. Beheler, C. Brown, J. Dyer, M. Loesch-Fries, D. Jacobs, M. Kraushar, J. McKenna, A. Meier, R. Morrissey, J. Schmal, B. Thompson and B. Uppencamp for their technical and field assistance.

References

Anagnostakis, S.L., 2012. Chestnut breeding in the United States for disease and insect resistance. Plant Dis. 96, 1392–1403.

Bailey, B.G., 2011. Above- and belowground strata isolation upon regenerating American chestnut and other hardwoods following midstory removal. M.S. thesis. Dept. of Forestry and Natural Resources, Purdue University, West Lafayette, IN. 96 p.

Bailey, B.G., Saunders, M.R., Lowe, Z.E., 2011. A cost comparison of five midstory removal methods. In: Fei, S., Lhotka, J.M., Stringer, J.W., Gottschalk, K.W., Miller, G.W, (Eds.), 2011. Proceedings, 17th Central Hardwood Forest Conference: 2010 April 5–7, Lexington, KY. Gen. Tech. Rep. NRS-P-78. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station, pp 535–543.

Barberis, I.M., Tanner, E.V., 2005. Gaps and root trenching increase tree seedling growth in Panamanian semi-evergreen forest. Ecology 86, 667–674.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-6. <http://CRAN.R-project.org/package=lme4>.

Bauerle, W.L., Wang, G.G., Bowden, J.D., Hong, C.M., 2006. An analysis of ecophysiological responses to drought in American chestnut. Ann. For. Sci. 63, 833–842.

Bevilacqua, E., 2002. Using specific volume increment (SVI) for quantifying growth responses in trees – theoretical and practical considerations. In: McRoberts, Ronald E., Reams, Gregory A., Van Deusen, Paul C., Moser, John W. (Eds.), Proceedings of the Thrid Annual Forest Inventory and Analysis Symposium: 2003 October 17–19; Traverse City, MI. Gen. Tech. Rep. NC-230. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Research Station, pp. 195–201.

Boerner, R.E.J., Brinkman, J.A., 1996. Ten years of tree seedling establishment and mortality in an Ohio deciduous forest complex. Bull. Torrey Bot. Club 123, 309–317.

Brown, C.E., Bailey, B.G., Saunders, M.R., Jacobs, D.F., in press. Effects of root competition on development of chestnut and oak regeneration following midstory removal. *Forestry* (in press). http://dx.doi.org/10.1093/forestry/cpu014.

Burns, R.M., Honkala, B.H., 1990. Silvics of North America. Agricultural Handbook 654. U.S. Department of Agriculture Forest Service, Washington, DC.

Canham, C.D., 1988. Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. Ecology 69, 786–795.

Clark, S.L., Schweitzer, C.J., Schlarbaum, S.E., Dimov, L.D., Hebard, F.V., 2009. Nursery quality and first-year response of American chestnut (*Castanea dentata*) seedlings planted in the southeastern United States. Tree Plant. Notes 53, 13–21.

Clark, S.L., Schlarbaum, S.E., Saxton, A.M., Hebard, F.V., 2011. Making history: field testing of blight-resistant American chestnut (Castanea dentata) in the southern region. In: Fei, S., Lhotka, J.M., Stringer, J.W., Gottschalk, K.W., Miller, G.W. (Eds.), 2011. Proceedings, 17th Central Hardwood Forest Conference: 2010 April 5–7; Lexington, KY. Gen. Tech. Rep. NRS-P-78. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station, pp. 656–657.

Clark, S., McNab, H., Loftis, D., Zarnoch, S., 2012a. American chestnut growth and survival after planting in two silvicultural treatments in the southern Appalachians, USA. Forests 3, 1017–1033.

Clark, S.L., Schlarbaum, S.E., Saxton, A.M., Hebard, F.V., 2012b. Nursery performance of American and Chinese chestnuts and backcross generations in commercial tree nurseries. Forestry 85, 589–600.

Comeau, P.G., Kabzems, R., McClarnon, J., Heineman, J.L., 2005. Implications of selected approaches for regenerating and managing western boreal mixedwoods. For. Chron. 81, 559–574.

Coomes, D.A., Grubb, P.J., 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. Ecol. Monogr. 70, 171–207.

Davis, M.A., Wrage, K.J., Reich, P.B., 1998. Competition between tree seedlings and herbaceous vegetation: support for a theory of resource supply and demand. J. Ecol. 86, 652–661.

Dey, D.C., Fan, Z., 2009. A review of fire and oak regeneration and overstory recruitment. In: Hutchinson, T.F., ed. Proceedings of the 3rd fire in eastern oak conference: 2008 May 20–22, Carbondale, IL. Gen. Tech. Rep. NRS-P-46. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station, pp. 2–20.

Dey, D.C., Parker, W.C., 1997. Morphological indicators of stock quality and field performance of red oak (*Quercus rubra* L.) seedlings underplanted in a central Ontario shelterwood. New For. 14, 145–156.

Diskin, M., Steiner, K.C., Hebard, F.V., 2006. Recovery of American chestnut characteristics following hybridization and backcross breeding to restore blight-ravaged *Castanea dentata*. For. Ecol. Manage. 223, 439–447.

Foster, D.R., Clayden, S., Orwig, D.A., Hall, B., Barry, S., 2002. Oak, chestnut and fire: Climatic and cultural controls of long-term forest dynamics in New England, USA. J. Biogeogr. 29, 1359–1379.

Games, P.A., Howell, J.F., 1976. Pairwise multiple comparison procedures with unequal n's and/or variances: a Monte Carlo Study. J. Educ. Stat. 1, 113–125.

Gauthier, M.M., Zellers, K.E., Löf, M., Jacobs, D.F., 2013. Inter-and intra-specific competitiveness of plantation-grown American chestnut (*Castanea dentata*). For. Ecol. Manage. 291, 289–299.

Griscom, H.P., Griscom, B.W., 2012. Evaluating the ecological niche of American chestnut for optimal hybrid seedling reintroduction sites in the Appalachian ridge and valley province. New For. 43, 441–455.

Hutnik, R.J., Yawney, H.W., 1961. Silvical characteristics of red maple (Acer rubrum). Station Paper NE-142. Upper Darby, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station, 18 p.

Jacobs, D.F., Severeid, L.R., 2004. Dominance of interplanted American chestnut (*Castanea dentata*) in southwestern Wisconsin, USA. For. Ecol. Manage. 191, 111–120.

Jacobs, D.F., Salifu, K.F., Seifert, J.R., 2005. Relative contribution of initial root and shoot morphology in predicting field performance of hardwood seedlings. New For. 30, 235–251.

Jacobs, D.F., Dalgleish, H.J., Nelson, C.D., 2012. A conceptual framework for restoration of threatened plants: the effective model of American chestnut (*Castanea dentata*) reintroduction. New Phyt. 197, 378–393.

Joesting, H.M., McCarthy, B.C., Brown, K.J., 2009. Determining the shade tolerance of American chestnut using morphological and physiological leaf parameters. For. Ecol. Manage. 257, 280–286.

Johnson, P.S., Shifley, S.R., Rogers, R., 2009. The Ecology and Silviculture of Oaks, second ed. CABI Publishing, Wallingford, UK.

Knapp, B.O., Wang, G.G., Clark, S.L., Pile, L.S., Schlarbaum, S.E., 2014. Leaf physiology and morphology of Castanea (Marsh.) Borkh., *Castanea mollisima* Blume, and three backcross breeding generations planted in the southern Appalachians, USA. New For. 45, 283–293.

Latham, R.E., 1992. Co-occurring tree species change rank in seedling performance with resources varied experimentally. Ecology 73, 2129–2144.

Lhotka, J.M., Loewenstein, E.F., 2013. Development of three underplanted hardwood species 7 years following midstory removal. South. J. Appl. For. 37, 81–90.

Lhotka, J.M., Zaczek, J.J., 2003. Effects of scarification disturbance on the seedling and midstory layer in a successional mixed-oak forest. North. J. Appl. For. 20, 85–91.

Loftis, D., 1990. Predicting post-harvest performance of advanced red oak reproduction in the southern Appalachians. For. Sci. 36, 908–915.

Logan, K.T., Krotkov, G., 1968. Adaptations of the photosynthetic mechanism of sugar maple (*Acer saccharum*) seedlings grown in various light intensities. Physiol. Plant 22, 104–116.

Marks, P.L., Gardescu, S., 1998. A case study of sugar maple (*Acer saccharum*) as a forest seedling bank species. J. Torrey Bot. Soc. 125, 287–296.

McCament, C.L., McCarthy, B.C., 2005. Two-year response of American chestnut (*Castanea dentata*) seedlings to shelterwood harvesting and fire in a mixed-oak forest ecosystem. Can. J. For. Res. 35, 740–749.

McGee, C.E., 1968. Northern red oak seedling growth varies by light intensity and seed source. Res. Note SE-90. Asheville, NC: U.S. Department of Agriculture Forest Service, Southeastern Forest Experiment Station, 4 p.

McNab, W.H., Cleland, D.T., Freeouf, J.A., Keys, J.E., Nowacki, G.J., Carpenter, C.A., comps. 2005. Description of the ecological subregions: sections of the conterminous United States [CD-ROM]. U.S. Department of Agriculture Forest Service, Washington, DC, 80 p.

Motsinger, J.R., Kabrick, J.M., Dey, D.C., Henderson, D.E., Zenner, E.K., 2010. Effect of midstory and understory removal on the establishment and development of natural and artificial pin oak advanced reproduction in bottomland forests. New For. 39, 195–213.

National Climatic Data Center [NCDC], 2012. United States Climate Normals 1981–2010. West Lafayette 6NW Station, Indiana. <http://gis.ncdc.noaa.gov/land-based-station-data/climate-normals/1981-2010-normals-data> (accessed 01.28.14).

Natural Resources Conservation Service [NRCS], 2014. Web soil survey. websoilsurvey.nrcs.usda.gov (accessed 01.20.14).

Paillet, F.L., 2002. Chestnut: history and ecology of a transformed species. J. Biogeogr. 29, 1517–1530.

Paquette, A., Bouchard, A., Cogliastro, A., 2006. Survival and growth of under-planted trees: a meta-analysis across four biomes. Ecol. Appl. 16, 1575–1589.

Phares, R.E., 1971. Growth of red oak (*Quercus rubra*) seedlings in relation to light and nutrients. Ecology 52, 669–672.

R Core Team, 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. <http://www.R-project.org/>.

Rhoades, C., Loftis, D., Lewis, J., Clark, S.L., 2009. The influence of silvicultural treatments and site conditions on American chestnut (*Castanea dentata*) seedling establishment in eastern Kentucky, USA. For. Ecol. Manage. 258, 1211–1218.

Ruxton, G.D., 2006. The unequal variance *t*-test is an underused alternative to Student's *t*-test and the Mann–Whitney U test. Behav. Ecol. 17, 688–690.

Symonds, M.R.E., Moussalli, A., 2011. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behav. Ecol. Sociobiol. 65, 13–21.

Valladares, F., Niinemets, U., 2008. Shade tolerance, a key plant feature of complex nature and consequences. Annu. Rev. Ecol. Evol. Syst. 39, 237–257.

Vandermast, D.B., Van Lear, D.H., 2002. Riparian vegetation in the southern Appalachian mountains (USA) following chestnut blight. For. Ecol. Manage. 155, 97–106.

Von Althen, F.W., 1977. Planting Sugar Maple: Fourth-year Results of an Experiment on Two Sites with Eight Soil Amendments and Three Weed Control Treatments. Great Lakes Forest Research Centre, Sault Ste. Marie, Ont.

Wang, G.G., Baurle, W.L., Mudder, B.T., 2006. Effects of light acclimation on the photosynthesis, growth, and biomass allocation in American chestnut (*Castanea dentata*) seedlings. For. Ecol. Manage. 226, 173–180.

Wang, G.G., Knapp, B.O., Clark, S.L., Mudder, B.T., 2013. The silvics of Castanea dentata (Marsh.) Borkh., American chestnut, Fagaceae (beech family). Gen. Tech. Rep. SRS-173. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station, 18 p.

Webb, D.P., 1974. Effects of competition on microclimate and survival of planted sugar maple (Acer saccharum, Marsh.) seedlings in southern Ontario. Can. For. Serv., Sault Ste. Marie, Ontario. Information Report O-X-209. 14p.

Worthen, L.M., Woeste, K.E., Michler, C.H., 2010. Breeding American chestnuts for blight resistance. Plant Breed. Rev. 33, 305–339.