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Deer browse susceptibility limits chestnut restoration success in northern hardwood forests

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ABSTRACT

Efforts to develop American chestnuts [*Castanea dentata*, (Marsh.) Borkh], with improved resistance to the chestnut blight fungus, *Cryphonectria parasitica* (Murr.) Barr, and Phytophthora root rot, caused by *Phythophthora cinnamomi* Rands, are ongoing. Establishing founder populations of improved chestnut will require understanding the ecological and silvicultural requirements of the species. In areas where white tailed deer (*Odocoileus virginianus* Zimmerman) hinder tree regeneration success, understanding how browsing will affect the establishment of planted chestnut is critical. We evaluated the impact of browsing by deer on survival, growth and competitive status of hybrid chestnuts planted in 15 northern hardwood sites in Pennsylvania. We found that after six years, chestnuts planted in fences were 65 percent taller and 35 larger in basal diameter than chestnuts in unfenced areas. Browsing by deer shifted the competitive dynamics faced by the chestnuts by favoring slower growing, browse tolerant species and reducing the heights of competing woody stems. Nevertheless, the competitive status of chestnuts in unfenced plots remained stagnant over time due to repeated browsing, while it increased in fenced plots over time. Our results suggest that fencing or other means of reducing herbivory will be necessary to protect planted chestnuts in areas with moderate or high deer densities.

1. Introduction

American chestnut [*Castanea dentata*, (Marsh.) Borkh], once an abundant species throughout much of eastern deciduous forests (Russell, 1987), was decimated by two non-native pathogens by the early 20th century (Anagnostakis, 2012). *Phytophthora cinnamomi* Rands, the causal agent of ink disease, increased chestnut tree mortality in the southern Appalachians beginning in the early- to mid-19th century (Anagnostakis, 2012) and the introduction of chestnut blight fungus [*Cryphonectria parasitica* (Murr.) Barr] in the late 19th century devastated chestnut populations throughout the species' range. By the 1950s, American chestnut was functionally extinct from the eastern U.S. Currently, only 10 percent of the pre-blight chestnut population remains, with most survivors found in small size classes (<2.5 cm DBH, Dalgleish et al., 2016), likely sprouts originating from blight-killed trees (Paillet, 1984).

Breeding to produce blight-resistant American chestnut has an over 100 year history (Anagnostakis, 2012; Hebard, 2005, Steiner et al., 2017; Van Fleet, 1914; Westbrook et al., 2020). Currently The American Chestnut Foundation (TACF) is the predominant entity leading this work, in collaboration with the American Chestnut Research and Restoration Project at the State University of New York School of Environmental Science and Forestry (Newhouse and Powell, 2021). The Connecticut Agricultural Experiment Station (CAES), which oversees the longest running chestnut breeding program in the U.S., has also produced backcross hybrid chestnut with increased resistance (Anagnostakis, 2012). Establishing founder populations of trees with improved resistance, once available, requires understanding the ecological and silvicultural requirements of the species. For species whose populations have been impacted for many years, planting and management strategies may be limited and incongruous with current ecological conditions and silvicultural approaches. Indeed, a recent

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survey of National Forest System managers underscored the general lack of knowledge on appropriate silvicultural strategies to reintroduce chestnut, including the relative risk of herbivory by rabbits and deer (Clark et al., 2020).

Excessive herbivory from increased ungulate densities poses a serious challenge to woody regeneration in many forests globally (e.g. Petersson et al. 2019; Simončič et al. 2019; Rooney and Waller, 2003). Chronic browsing reduces regeneration of species preferred by deer and can facilitate the dominance of unpreferred species, thereby drastically altering species competitive dynamics (Horsley et al. 2003; Perea et al. 2020). Excessive browsing by white tailed deer (*Odocoileus virginianus* Zimmerman) has been a major hindrance to hardwood regeneration in eastern forests for over four decades (reviewed by Rooney, 2001; Rooney and Waller, 2003). In parts of the Northeast, excessive browsing has caused regeneration failure on as much as 50 percent of recently harvested sites (Royo and Stout, 2019). Deer herbivory has similarly posed a challenge to artificial hardwood regeneration in areas with high deer densities (Frank et al., 2018; Gottschalk and Marquis, 1981; Long et al., 2012).

While it is anecdotally understood that American chestnut is highly susceptible to browsing by deer (Clark et al., 2020; Clark et al., 2014), we generally lack experiential evidence of browse impacts on planted backcross American chestnut establishment, survival and growth. Clark et al. (2014) found that browsing by deer reduced height growth for American, Chinese and backcross chestnuts planted in three southern National Forests. Owings et al. (2017) demonstrated a significant improvement in survival and growth of two-year old planted American chestnut seedlings grown in fences compared to unprotected chestnuts. Similarly, Burke (2011) found that fencing increased survival and abundance of naturally occurring American chestnut sprouts compared to unfenced control sites in Virginia. Dalgleish et al. (2015), however, found that browsing indirectly benefitted planted backcross chestnuts by controlling competing vegetation, with higher mortality and lower growth for fenced chestnuts. Many factors may interact to determine the impact of deer browsing on planted chestnuts, such as ambient deer density, forage availability, chestnut seedling quality (Clark et al., 2014) and composition of naturally occurring vegetation.

Deer exclusion fencing is an effective and commonly used tool to reduce herbivory on woody regeneration following silvicultural treatments in some regions with high deer densities (Redick and Jacobs 2020, Royo et al., 2017; Stout and Brose, 2014). As fencing can influence seedling and sapling growth, survival, and species composition (Augustine and McNaughton, 1998; Royo et al., 2017 Dalgleish et al., 2015), it is critical to understand how this tool will affect the competitive dynamics impacting American chestnut in reintroduction plantings.

In this study, our main objective was to evaluate the influence of browsing by white tailed deer on the survival, growth, and competitive status of backcross generations of hybrid chestnuts. We did this by planting hybrid chestnut seedlings within and outside of deer exclusion fences in 15 sites on the Allegheny Plateau and measuring response of the chestnuts and their tallest competitor over six years. We hypothesized that chestnuts in fences would exhibit better survival and growth (height and diameter), in line with one of the few studies evaluating effect of fencing on planted chestnut establishment (Owings et al., 2017), and that the improved growth in fences would translate to a higher probability of attaining a favorable competitive status.

2. Methods

2.1. Study area

We planted hybrid chestnut seedlings at 15 northern hardwood forest sites distributed throughout a 6500-km^2 area of the Allegheny Plateau region in northern Pennsylvania, USA, spanning from Warren County to Potter County. Common tree species found at the sites include red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), black cherry (*Prunus serotina Ehrh.*), and American beech (*Fagus americana* Ehrh.), with northern red oak (*Quercus rubra* L.), eastern hemlock [*Tsuga canadensis* (L.) Carrière]), sweet birch (*Betula lenta* L.), yellow birch (*B. alleghaniensis* Britt.), and white ash (*Fraxinus americana* L.) found in lesser abundance. Historical records indicate American chestnut was present in low abundance in the pre-settlement forests of the Allegheny Plateau (Black et al., 2006), with greatest numbers in hemlock-beech forests (Braun, 1950). The median deer density at the study sites in 2015 was 7.3 deer/km^2, ranging from 4.0 − 12.8 deer/km^2 (Royo et al., 2017), estimated using fecal pellet surveys (Royo et al. 2017). Pre-settlement deer densities for the region are estimated at three to eight deer/km^2 (McCabe and McCabe, 1997; Rooney, 2001).

Northern hardwood stands are commonly managed using a shelterwood sequence, which involves one or more initial shelterwood seed cuts followed by an overstory removal once desired woody vegetation is established (Nyland 2002). At 14 of the 15 sites used in this experiment, managers conducted the initial cut of a shelterwood sequence to reduce stand relative density (i.e., <75 % relative density) between 2008 and 2013; two to seven years prior to planting the chestnut seedlings. Broadcast herbicides (tank mix of glyphosate and sulfometuron methyl) were applied within four years of the initial harvest to control interfering plants (before the initial cut at nine sites and after at five sites, all occurring before 2013). This broadcast herbicide treatment is a common practice in the Allegheny Plateau to treat interfering regeneration due to the current and legacy effects of overbrowsing (Marquis et al., 1992). Typical interfering plants that often require control include rhizomatous ferns, including *Dennstaedtia punctilobula* (Michx.) Moore and *Thelypteris noveboracensis* (L.) Nieuwl and various graminoids (Horsley 1990).

Within each site, we established paired 4200 m^2 (60 × 70 m) plots, and randomly assigned one plot a deer exclosure (fence) treatment while the other served as an unfenced control. Fences (2.43 m tall) were installed in 2013, two years prior to planting the chestnuts. Over the course of the study, six of the sites, including the site that did not receive the initial shelterwood cut, received overstory removal harvests; the final harvest in the shelterwood sequence (Appendix 1). The removal harvest impacted fenced and unfenced treatment plots equally, and preliminary analyses assessed visually via boxplots found no substantial impact on height or basal diameter (BD) associated with overstory removal (Appendix 1). Consequently, sites with removal harvests were included in the subsequent analyses. Two control plots, one that was fenced as part of the operational management of the surrounding forest stand in 2017, and one that received an accidental herbicide treatment in 2018, were excluded from the analysis. Deer fences were occasionally damaged, allowing deer to enter and browse on seedlings. Fences were assessed for damage annually and repaired as necessary.

2.2. Experimental material

Three hundred and sixty chestnut seedlings from two CAES backcross hybrid families, W4-75 and W4-85, (Anagnostakis, 2012) were used in this study. The backcross hybrid chestnuts resulted from crosses between BC_3F_1 and BC_2F_1 parents. The mother trees were full-sibs (Windsor family 4, with resistance from *C. mollissima* Blume) and were male sterile. They were open pollinated by full-sib males from one family (Windsor family 1, with resistance from *C. crenata* Siebold and Zucc.); the only known pollen-producing chestnuts in the area. The resulting chestnuts were collected from the two mother trees at the Windsor Locks orchard of the CAES in the fall of 2014 and were stored in damp peat moss in a refrigerator until they were planted in early February 2015. Seeds were planted in 1:1:1 vermiculite, sphagnum peat, Perlite mix in rectangular containers 6.9 cm wide by 25.4 cm deep. The chestnuts were grown under grow lights and watered as needed in a greenhouse at the Delaware Forestry Sciences Laboratory (Delaware, OH) until they were planted in the study sites, May 26–29, 2015.

At each of the 15 sites, chestnut seedlings were planted inside (n = 8) and outside (n = 16) of deer exclosures. A greater number of seedlings

Table 1
Treatment and interaction effects for height, BD (years 1–4 and 6) and number of leaves (years 1–3) of planted chestnut seedlings, and height of the tallest woody competitor in microplots (years 2–4 and 6). Bold values denote statistical significance at the p < 0.05 level.

	Height		BD		No. leaves		Height of tallest woody competitor	
Source of variation	F-value	P-value	F-value	P-value	F-value	P-value	F-value	P-value
Fence	30.09	**<0.001**	14.89	**<0.001**	7.04	**0.02**	28.79	**<0.001**
Family	0.02	0.88	1.89	0.18	0.17	0.68	0.01	0.92
Fence*family	1.06	0.31	1.93	0.17	0.28	0.60	0.92	0.34
Year	77.09	**<0.001**	162.48	**<0.001**	433.37	**<0.001**	68.08	**<0.001**
Fence*year	8.08	**<0.001**	5.57	**<0.001**	13.31	**<0.001**	1.38	0.25
Year*family	0.09	0.99	0.43	0.79	0.14	0.87	0.17	0.92
Fence*year*family	0.36	0.84	1.05	0.39	0.84	0.43	0.22	0.88
Initial height	106.28	**<0.001**						
Initial BD			12.32	**<0.001**				
Initial leaf count					13.90	**<0.001**		

Table 2
Treatment and interaction effects for binary variables; probability that seedlings were browsed by white-tailed deer (years 2, 3 and 6), probability that seedling grew taller than the deer browse line (180 cm; years 4 and 6), probability of survival (years 1–4 and 6) and the probability of attaining a competitive status (years 2–4 and 6) of planted chestnut seedlings. Chestnuts that were ≥ 80 percent as tall as their largest competitor were categorized as competitive, and those that were shorter were categorized as not competitive (Spetich et al., 2002). Bold values denote statistical significance at the p < 0.05 level.

	Browse		Exceeding browse line (180 cm)		Survival		Competitive status	
Source of variation	F-value	P-value	F-value	P-value	F-value	P-value	F-value	P-value
Fence	77.52	**<0.001**	16.56	**<0.001**	0.08	0.78	2.31	0.14
Family	0.09	0.77	0.00	0.95	0.51	0.48	1.69	0.21
Fence*family	0.10	0.76	0.23	0.63	2.26	0.14	1.98	0.18
Year	2.28	0.10	37.57	**<0.001**	16.2	**<0.001**	3.75	**0.01**
Fence*year	3.46	**0.03**	1.35	0.25	2.29	0.06	5.52	**<0.001**
Year*family	2.70	0.07	0.10	0.75	1.12	0.35	0.90	0.44
Fence*year*family	0.87	0.42	1.28	0.26	0.81	0.52	0.73	0.54

were planted outside fences to ensure sufficient survival, as higher mortality of chestnuts was expected in this treatment. Seedlings were planted in grids, 3.7 m spacing within and 6 m spacing between rows.

2.3. Seedling measurements

We measured seedling height and basal diameter at the time of planting and toward the end of each growing season from 2015 to 2018 and 2020 (years one through four and six). Total height was measured from the ground line to the tallest terminal bud to the nearest centimeter. Basal diameter was averaged from two perpendicular measurements using digital calipers and recorded to the nearest 0.1 mm. We categorized seedlings that were at least 180 cm tall as having attained a height above the deer browse line, indicating they had escaped the most deleterious effects of browsing (Frerker et al., 2013). We evaluated evidence of deer browsing (clipping by deer on leaves or branches on all or part of a tree; present/absent). As browsing can lead to decreases in leaf biomass (Van Hees et al., 1996), we also counted the number of leaves on each chestnut seedling in years one through three.

We collected data on the tallest understory woody competitor using a 1.3 m radius microplot centered on each chestnut seedling during the second, third, fourth and sixth growing seasons. Data collected consisted of species identity and height of the tallest understory woody competitor (>0.3 m in height and < 3.8 cm DBH). Sweet birch and yellow birch, which are common across the Allegheny Plateau, are difficult to distinguish as seedlings, therefore these species were pooled together as "birch". Height of the tallest understory woody competitor was used to assess competitive status using an index of competitive asymmetry. Chestnuts that were ≥ 80 percent as tall as their largest competitor were categorized as competitive, and those that were shorter were categorized as not competitive (Spetich et al., 2002, Morrissey et al. 2010, Pinchot et al. 2017).

2.4. Statistical analysis

Response variables were analyzed using a repeated measures analysis of covariance split-plot design via a residual pseudo-likelihood estimation technique using generalized linear mixed models (PROC GLIMMIX). For binary variables the same experimental design was used without the analysis of covariance. All analyses were run using SAS software (SAS Institute Inc., 2011). Fencing was the whole-plot effect in the model and family was the subplot effect. Fixed effects in each analysis included fencing, chestnut family, year, and the associated interactions. Site and the site times fence interaction were the random effects in the model. Responses of seedlings from the same family were averaged within a subplot. Binary variables were probability of survival and competitive status in years one through four and six, probability of browse incidence in years two, three and six, and the probability that a chestnut seedling had grown above the 180 cm deer browse line in years four and six. The binary distribution and the logit link function were used in these analyses. Continuous variables analyzed were total height and BD for years one through four and six, and height of tallest woody competitor (years two through four and six). Chestnut and competing seedling heights were modeled with a normal distribution, while BD was modeled with a lognormal distribution and all three analyses used the identity link function. The discrete variable number of leaves collected for years one through three was modeled with a negative binomial distribution using a log link function. To control for initial variation in size among individuals, values of response variables at the time of planting (height, BD, number of leaves at planting) were covariates in the models. For each response variable the steps for analysis of covariance were run and an equal slopes model was found to be the best fit (Table 1). Finally, logistic regression (PROC LOGISTIC) outside of the experimental design was used to determine if the species identity of the tallest competitor near each chestnut could predict the probability of a chestnut achieving a competitive status (≥80 percent height of competitor). As birch was frequently the tallest competing species (in 32

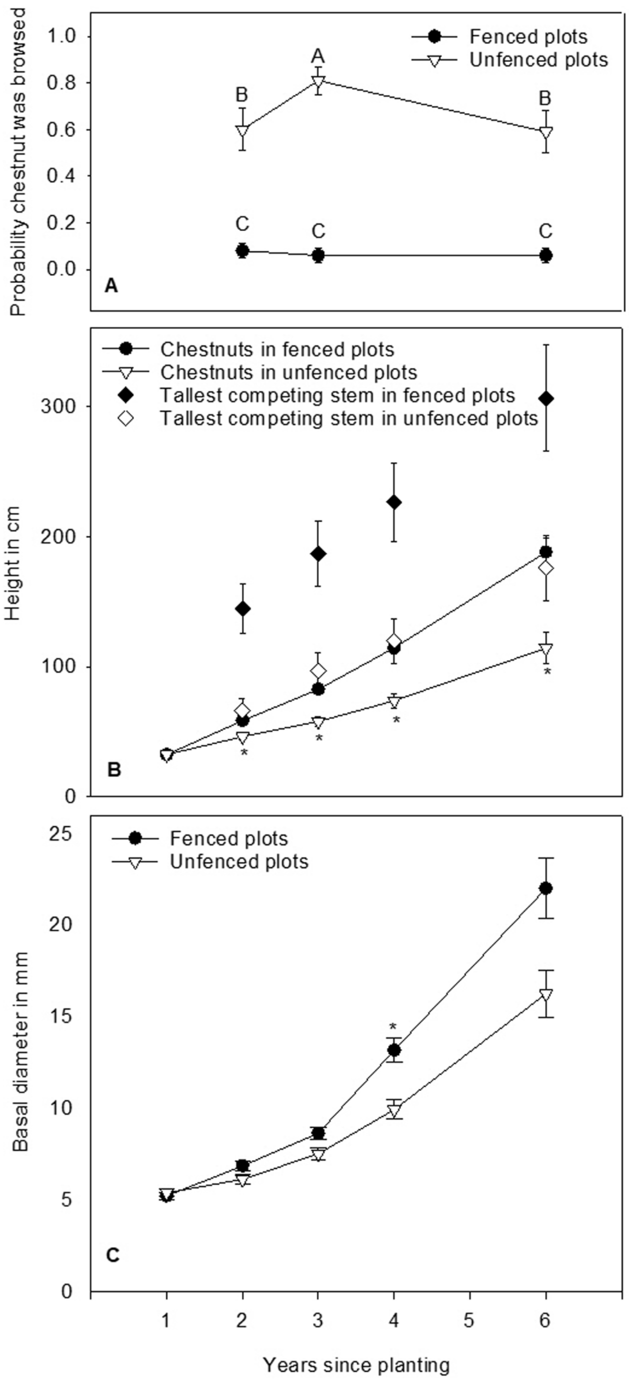

Fig. 1. **A.** Probability that chestnuts were browsed by white-tailed deer (years 2, 3 and 6) and standard error for hybrid chestnuts in fenced and control plots over time. Damage to fence lines permitted occasional browsing inside fences. Letters indicate differences in the probability of chestnuts being browsed between fence treatments and years (α = 0.05). **B.** Mean height and standard error of backcross chestnuts and tallest competing woody stem in fenced and unfenced plots over time. Asterisks indicates differences in mean height of chestnuts between fence treatments within year. Mean height of tallest competitor differed between fence treatments each year. **C.** Mean BD and standard error of backcross chestnuts in fenced and control plots over time. Asterisk indicates differences in mean height of chestnuts between fence treatments within year.

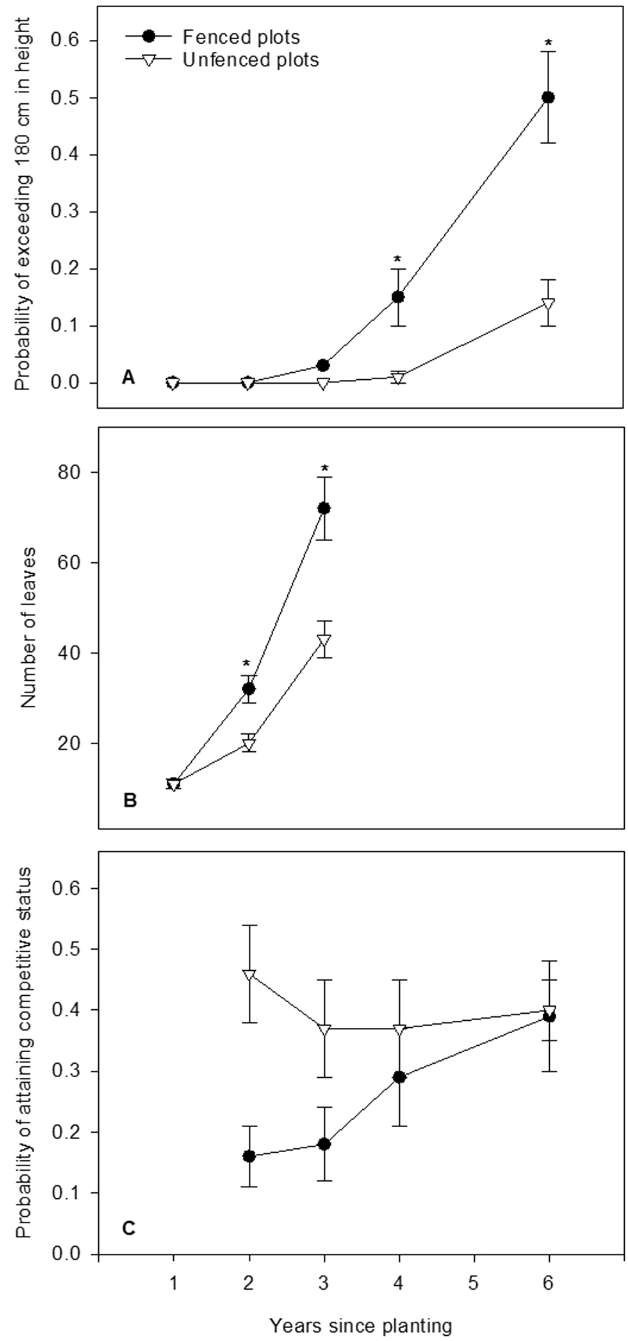

Fig. 2. **A.** Probability of hybrid chestnuts exceeding the deer browse line (180 cm). Bars indicate standard error. Asterisk indicates differences between treatments within year. **B.** Mean number of leaves and standard error on chestnuts in fenced and control plots over time. Asterisks indicates differences in number of leaves between fence treatments within year. **C.** Probability chestnut seedlings attained a competitive status (≥80 percent as tall as tallest woody competitor, Spetich et al. 2002) over time. Bars are standard errors. Chestnuts in fenced plots increased their probability of attaining a competitive status over time (year 6 was greater than years 2 and 3), while there was no statistically significant difference between fenced and unfenced plots any year.

percent of unfenced and 36 percent of fenced plots), we used this as the reference to compare against other competing species. The analysis therefore compared the probability that a chestnut seedling would achieve a competitive status when birch vs. each other species category was the tallest competitor. We included species that were the tallest competitor in at least five percent of the competition microplots (McCune and Mefford, 1999): striped maple (*Acer pensylvanicum* L.), red

Table 3
Frequency (percent of competition microplots/treatment) and mean height of tallest competitors in unfenced and fenced treatments in 2020.

	Unfenced		Fenced	
	Percent	Height (cm)	Percent	Height (cm)
Betula spp.	32	233 ± 21	36	399 ± 28
Acer rubrum	14	152 ± 29	5	170 ± 77
Amelanchier spp.	11	178 ± 41		
Acer pensylvanicum	10	271 ± 33		
Prunus serotina	8	129 ± 26	7	119 ± 44
Fagus americana	7	169 ± 27		
Liriodendron tulipifera			9	340 ± 45
Magnolia acuminata			5	239 ± 42

maple, serviceberry (*Amelanchier* spp. Medik.), American beech, pin cherry (*P. pensylvanica* L.) and black cherry. All species with fewer occurrences were binned into an “other” category.

To account for the correlation between years we used the autoregressive heterogeneous order 1 [ARH(1)] covariance structure for most analyses. For models with unequal spacing between years and which did not violate the homogeneity of variance assumption, we used the spatial power covariance structure. The Kenward Rogers denominator degrees of freedom adjustment method was used. Residuals were checked for normality via the Shapiro-Wilks test and homogeneity of variance visually via boxplots and statistically via the Levene’s test and models were adjusted by using a different distribution or adjusting for heterogeneity of variance when needed. LSMEANS were adjusted with the Tukey-Kramer option to get an experiment-wise error rate. All analyses were conducted at the alpha level of 0.05.

3. Results

3.1. Browse incidence

The probability of browse incidence was substantially greater for chestnuts in unfenced compared with fenced plots, as expected (Table 2, Fig. 1). The probability that unfenced chestnuts were browsed increased from 0.60 ± 0.09 in year two to 0.81 ± 0.06 in year three, then dropped to 0.59 ± 0.09 in year six. Chestnuts in fenced plots had a low probability of being browsed (<0.09) throughout the study.

3.2. Chestnut survival

Fencing treatment did not affect the probability that the chestnut seedlings would survive (Table 2). The probability of survival declined significantly over time (Table 2, 0.97 ± 0.01 in year one, 0.93 ± 0.02 in year two, 0.90 ± 0.02 in year three, 0.87 ± 0.03 in year four, and 0.77 ± 0.04 in year six). No treatment interactions were significant.

3.3. Chestnut growth

At the time of planting, the chestnuts averaged 33 ± 1 cm in height and 4 ± 0.1 mm in BD. By the end of their sixth growing season, surviving chestnuts averaged 142 ± 6 cm in height; with the tallest chestnut reaching 403 cm; and 20 ± 0.8 mm in BD across the treatments. Browsing limited chestnut height over time (significant fence*year interaction; Table 1.). By 2020, six years after planting, the mean height of chestnuts in unfenced plots (114 ± 12 cm) was 39 percent less than those within fenced plots (188 ± 11 cm), which was greater than the deer browse line (180 cm, Fig. 1). Mean BD of chestnuts in unfenced plots was 26 percent less than those in fenced plots in year three (significant treatment*year interaction, Table 1, Fig. 1). Despite a relatively large difference in BD between chestnuts in fenced (22.0 ± 1.6 mm) and in unfenced plots (16.3 ± 1.3 mm) in year six, means differences were no longer significant. There were no significant differences in either height or BD between families over the six-year study.

For the years tested (four and six), the probability that the chestnut seedlings would surpass the browse line (180 cm) was greater in fenced relative to unfenced plots (Table 2, Fig. 2). By year six, the probability that chestnuts in fences exceeded 180 cm in height was 0.49 ± 0.08 compared to 0.14 ± 0.04 for chestnuts in the unfenced plots (Fig. 2). Over time, as planted chestnuts grew, stems became leafier, with chestnuts in fences having on average 72 ± 7 leaves compared to 43 ± 2 in unfenced plots by 2020 (Table 1, Fig. 2). Browsing limited leaf number by 40 percent.

3.4. Height of tallest woody competitor

Browsing reduced the height of the tallest competitor substantially; by year six the tallest woody competitor in unfenced plots averaged 176 ± 25 cm, compared to 306 ± 41 cm in fenced plots (Fig. 1). Birch was most frequently the tallest woody competitor in both unfenced and fenced treatments (Table 3.), with an average height of 233 ± 21 cm and 399 ± 28 cm, respectively. In unfenced plots, red maple was the next most frequent tallest competitor, followed by serviceberry, striped maple, black cherry, and white ash. In the fenced plots, after birch, pin cherry was the most frequent tallest competitor, followed by yellow poplar (*Liriodendron tulipifera* L.), black cherry, red maple, and cucumber magnolia [*Magnolia acuminata* (L.) L., Table 3].

3.5. Chestnut competitive status

The competitive status of fenced chestnuts increased over time, while the status remained unchanged for chestnuts in unfenced plots throughout the study (Table 2., Fig. 2). In the first-year competitive status was evaluated (year two), the probability that surviving chestnuts achieved a favorable competitive status was 0.47 in unfenced plots compared with 0.16 in fenced plots. By year six, the probability that chestnuts were competitive was 0.40 for those in unfenced and 0.39 for

Table 4
A-C: Odds ratio estimates and Wald confidence interval for logistic regression model predicting probability of chestnut seedlings attaining a competitive status as a function of the species of tallest woody competitor. Asterisk denotes species against which chestnuts have a statistically greater chance of achieving competitive status relative to birch based on a Wald test. **D.** Sample number (N) for each competing species. **E.** Percent of chestnuts in a competitive status for each species of tallest woody competitor.

A. Competing species	B. Odds ratio estimate	C. 95 % Wald confidence interval		D. N	E. Percent of chestnuts in competitive status
Other species*	6.956	2.325	20.811	27	68 %
***Acer rubrum* ***	6.421	2.38	17.327	24	67 %
***Prunus serotina* ***	3.612	1.223	10.664	17	53 %
Amelanchier spp. *	3.567	1.264	10.066	19	53 %
Magnolia acuminata	2.14	0.546	8.389	10	40 %
Fagus grandifolia	1.605	0.435	5.926	12	33 %
Acer pensylvanicum	1.482	0.495	4.433	19	32 %
Prunus pensylvanica	1.482	0.495	4.433	19	31 %
***Betula* spp.**				80	24 %

Table A1
Timing of removal harvest (when applicable), mean (±standard error) year 6 survival, height, BD, and percent of chestnuts in a favorable competitive status for each site (averaging fenced and unfenced plots).

Site name	Season and year of removal harvest	Survival (percent)	Height (cm)	BD (mm)	Competitive status (percent)
Mean for sites without removal harvest		**81 ± 3**	**148 ± 7**	**19.1 ± 0.8**	**42 ± 4**
Bunts Run 21		78 ± 9	133 ± 25	25.7 ± 3.4	78 ± 10
C9 Herbicide Block		79 ± 8	117 ± 13	20 ± 2.1	58 ± 12
Close Call		100 ± 0	111 ± 27	13.3 ± 2.5	13 ± 13
First Hunt		88 ± 7	132 ± 17	14.7 ± 1.3	14 ± 8
Potter 11/ Kickoff		96 ± 4	146 ± 22	17.2 ± 2.3	22 ± 8
Potter6		71 ± 9	210 ± 21	23.9 ± 2.9	88 ± 8
Shakespeare		92 ± 7	164 ± 15	19.3 ± 1.9	59 ± 11
Sorry About That		83 ± 8	140 ± 17	18.7 ± 2.2	15 ± 8
Treed Bear		54 ± 10	166 ± 27	16.5 ± 2.1	15 ± 10
Mean for sites with removal harvest		**67 ± 4**	**128 ± 9**	**21.1 ± 1.5**	**48 ± 5**
Blanton Timber Sale	Winter 2017/ 2018	79 ± 8	147 ± 20	32.7 ± 3.8	74 ± 11
Cash Crop	Fall, 2017	63 ± 10	152 ± 19	21.1 ± 2.6	40 ± 13
Irvine Run	Winter 2018/ 2019	63 ± 10	124 ± 25	15.2 ± 2.6	40 ± 13
Mount Jewett	Winter 2017/ 2018	71 ± 9	122 ± 16	22.9 ± 3.1	65 ± 12
Shake-N-Bake	Winter 2016/ 2017	75 ± 16	221 ± 48	20.5 ± 3.4	0 ± 0
Spring Creek 56	Winter 2019/ 2020	60 ± 10	52 ± 10	10.7 ± 1.8	29 ± 13

those in fenced plots. Relative to birch, chestnut had a 542 percent, 261 percent, 257 percent, and 596 percent higher likelihood of achieving a competitive status when competing against red maple, black cherry, serviceberry, or other arborescent species, respectively. In contrast, chestnut's likelihood of reaching a competitive status against striped maple or pin cherry were poor and statistically similar to birch, the dominant competitor, although several of these species had very large confidence intervals (Table 4).

4. Discussion

Our study demonstrates the value of using deer exclusion fencing to protect planted backcross chestnut seedlings from herbivory in forests with moderate deer densities. Fencing facilitated increases in height and radial growth of chestnuts, as we hypothesized, whereas chestnuts outside fences had limited height gains and most remained well within reach of the deer six years after planting. The overwhelming majority (80 percent) of seedlings in unfenced plots will face continued browsing and associated depletion of stored carbohydrates (Sloan and Jacobs, 2008), which we expect will exacerbate the growth disparity of chestnuts between treatments. Our hypothesis that fencing would increase the probability of chestnut survival was not supported, though continued browsing may eventually reduce survival of the chestnuts (Owings et al., 2017), as has also been demonstrated for planted oak seedlings (Frank et al., 2018; Long et al., 2012). Moreover, browsing will probably prevent many of the unprotected seedlings from reaching reproductive maturity (Stewart et al., 2008), limiting future reproduction and recruitment, a major goal of chestnut restoration (Jacobs et al., 2013).

These results are consistent with the reports of Clark et al. (2014), which found high rates of browsing by deer were associated with lower growth of planted backcross chestnuts, Owings et al. (2017), which found substantially greater two-year survival and height and diameter growth of 1–0 bareroot chestnuts planted in fences compared with chestnuts exposed to deer browse, and Burke (2011), which demonstrated increased survival and abundance of naturally occurring American chestnut sprouts protected from browsing by fencing. Our results, however, contrast with the report by Dalgleish et al. (2015), which found that fencing enabled co-occurring woody vegetation to outcompete planted chestnuts, reducing their survival and growth compared with unfenced chestnuts. The chestnut seedlings planted in that study were substantially smaller (14 ± 5 cm tall) than the seedlings in this study (33 ± 5 cm tall). Initial height of chestnut seedlings at the time of planting is critically important to growth, with larger seedlings adding more growth and having a higher likelihood of attaining competitive canopy positions (Clark et al., 2016; Pinchot et al., 2017). Dalgleish et al. (2015) found a positive correlation between both height and root collar diameter and survival in the fenced plots, suggesting the small size of the seedlings contributed to the negative relationship between fencing and seedling growth and demonstrates the importance of using large seedlings when out-planting chestnut in forested settings.

It has long been understood that selective browsing can suppress the regeneration of palatable species while facilitating an increase in relative abundance of less palatable species (Horsley et al., 2003; Marquis, 1981; Royo et al., 2017). These dynamics are evident in our study. More palatable pin cherry and yellow poplar were common tallest competitors in fenced plots while relatively less palatable red maple, striped maple and serviceberry were more frequent in unfenced plots. Birch, the most common tallest competitor in both treatments, is browsed by deer but is somewhat browse tolerant (Horsley et al., 2003) and has proliferated across northern hardwood forests in recent decades (Royo et al., 2019). At our sites, deer browsing shifted the competitive dynamics faced by the planted chestnuts by favoring slower growing, browse tolerant species and by reducing the heights of all woody regeneration. Nevertheless, the competitive status of chestnuts remained stagnant over time in unfenced plots, while it increased in fenced plots. Thus, although browsing created conditions more amenable to chestnut establishment, preferential and extensive browsing on chestnuts nullified this potential benefit. Similarly, other studies have demonstrated that browsing pressure can nullify or even reverse expected growth and survival advantages to seedlings provided by increases in light (Krueger et al., 2009; Royo and Stanovick, 2019).

An important caveat to our study is that the overstory harvest occurred two to seven years before, and herbicide was used at least three years before chestnuts were planted, which enabled woody vegetation to establish before chestnuts were planted. Moreover, fences were installed two years before chestnuts were planted, facilitating different competitive environments inside and outside the fences. The initially very low probability of achieving competitive status, particularly in fenced areas, can be explained in part by this priority effect; the competitive advantage of species established earlier (e.g., Fukami, 2015), in this case several years before the chestnuts were planted. Yet, in the fenced treatment with relatively stronger priority effects, the chestnuts grew faster and improved their competitive status relative to unprotected chestnuts. Thus, our results are a conservative reflection of the potential growth responses of chestnuts protected from browsing in free-to-grow conditions.

This improved competitive status of the fenced chestnuts over time is particularly notable given that the height of the tallest competitor also increased substantially faster within fenced plots. The three most frequent tallest competitors in fences; birch, pin cherry, and yellow poplar; are particularly fast growing (Ristau and Horsley, 1999). Sweet birch seedlings can rapidly outcompete other hardwood species in shelterwood treatments (Royo et al., 2019), pin cherry can grow over a meter a year in high light treatments (Bicknell, 1982), and yellow poplar can outcompete intermediate shade tolerant species in full sun conditions (Loftis, 1990). Chestnuts are also fast growing (Ashe, 1911; Jacobs and Severeid, 2004; Latham, 1992; Reynolds and Burke, 2011; Zon, 1904), particularly when competitors are controlled (Belair et al., 2014; Clark et al., 2012). Jacobs and Severeid (2004) documented mean annual height growth of 84 cm by chestnuts that were planted in a field setting with annual vegetation control. Clark et al. (2012) found that chestnuts in a shelterwood harvest that received competition control at age three grew an average 50 cm per year in height and 4.3 mm per year in BD over their first five years. In that same study, competing woody stems outside of the vegetation control treatment areas averaged 76 cm taller than the planted chestnuts after five years, suggesting chestnut restoration risks failure in the absence of vegetation control. Chestnut is particularly adept at responding to increases in light following canopy disturbance (Ashe, 1911; Belair et al., 2014; Frothingham, 1924; Paillet, 1984) suggesting that competition control such as crop tree release, will likely favor chestnut over competing species.

4.1. Management implications

Increases in ungulate densities present a major obstacle to the regeneration of woody species in temperate forests globally (Côté et al., 2004). Excessive browsing can reduce species diversity, shift species composition away from preferred species, and can lead to alternate stable states that continue to resist establishment of formerly abundant tree species even when the herbivore densities decline (e.g. De La Cretaz and Kelty, 2002). Deer browsing reduced the growth of the planted chestnuts as well as naturally occurring woody vegetation in our study, underscoring the need for forest managers to consider how ungulate herbivory may impact management objectives and in particular tree species restoration plantings.

When planting chestnuts in forests with moderate or high deer densities, protecting the seedlings from browsing will be critical to ensure the long-term growth and likely reproductive potential of founder populations. Protecting seedlings using fencing is expensive (upwards of $20/meter, Vercauteren et al., 2006) and requires regular monitoring and maintenance. In some cases, it may be worth considering the longer-term investment of producing American chestnuts with increased tolerance, and the impacts of losing the valuable trees in areas without fencing as a protective measure. Ungulate browsing is not just a problem for planted chestnuts; federal and state landowners in some areas with high deer browsing pressure install deer exclusion to meet tree stocking goals after a regeneration harvest. For example, The Pennsylvania Department of Conservation and Natural Resources maintained deer exclusion fences across over 16,187 ha of forestland between 1995 and 2013 (Pennsylvania DCNR, 2013). In Pennsylvania, exclusion fences are often installed in tandem with overstory harvests to encourage the regeneration of hardwood forest stands. Incorporating American chestnut reintroduction into such sites, when the site and harvest intensity are appropriate, may offer a cost-effective approach to chestnut reintroduction on public lands.

While this study focused on sites in the Northeast, other studies have found deer to hinder planted chestnut establishment in the South (TN, VA; Clark et al., 2014) and the Midwest (IN; Owings et al., 2017), suggesting that deer herbivory could pose a challenge to American chestnut reintroduction efforts across the species range. Fencing is among the most effective means of reducing deer herbivory (Redick and Jacobs, 2020), however other methods to moderate the effect of browsing, including using tree shelters and culling efforts (Stout et al., 2013), may be preferred, depending on logistical and financial constraints.

Our results suggest that many planted chestnuts will fail to attain a favorable competitive status during the critical phase of seedling establishment, even with deer exclusion. The seedlings we used were relatively small at planting; 33 cm in height. Had we planted larger seedlings, a greater percentage would probably have become competitive over time (Clark et al., 2014; Davis and Jacobs, 2005; Pinchot et al., 2017). Nonetheless fast-growing competing vegetation can outgrow large chestnut seedlings, especially in high light environments (Pinchot et al., 2017), and we suggest that chestnuts planted in regeneration harvests will require some type of competition control to ensure a larger proportion of the surviving chestnuts may eventually attain a co-dominant or dominant canopy status. The manner, timing, and frequency of cost-effective competition control requires additional study.

CRediT authorship contribution statement

Cornelia C. Pinchot: Conceptualization, Methodology, Formal analysis, Writing – original draft. **Alejandro A. Royo:** Conceptualization, Methodology, Writing – original draft. **John S. Stanovick:** Formal analysis, Writing – original draft. **Scott E. Schlarbaum:** Methodology, Writing – review & editing. **Ami M. Sharp:** Methodology, Writing – review & editing. **Sandra L. Anagnostakis:** Methodology, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A

See Table A1.

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