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Dominance of interplanted American chestnut (*Castanea dentata*) in southwestern Wisconsin, USA

Douglass F. Jacobs[a,*], Larry R. Severeid[b]

[a]*Department of Forestry and Natural Resources, Hardwood Tree Improvement and Regeneration Center, Purdue University, West Lafayette, IN 47907-2033, USA*
[b]*Walnut Council International Office, Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN 47907-2033, USA*

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Abstract

American chestnut (*Castanea dentata* (Marsh.) Borkh.) once dominated the eastern deciduous forests of the USA before nearly all trees throughout the range were annihilated by the introduced pathogen *Cryphonectria parasitica* (Murr.) Barr. It is anticipated that a blight-resistant hybrid form of American chestnut will be available for reintroduction in the near future, and many reintroduction programs will likely involve mixed interplantings with other hardwood species. Little is known, however, about plantation performance of American chestnut relative to other species. This study assessed early plantation development (seven or eight growing seasons following direct seeding) of American chestnut relative to black walnut (*Juglans nigra* L.) and northern red oak (*Quercus rubra* L.) on a site with no evidence of blight in southwestern Wisconsin (43°54′N, 90°53′W). American chestnut exhibited greater height (47 and 77% more) and diameter at breast height (DBH) (50 and 140% more) growth than black walnut and northern red oak, respectively. Mean total height of American chestnut was 6.4 m (0.84 m per year), while mean total DBH was 6.4 cm (0.83 cm per year). American chestnut also had better stem form, measured as deviation in stem straightness for the first 2 m, than the other two species. This data reaffirms historical observations of pre-blight growth rates for American chestnut. The reintroduced hybrid chestnut tree will be predominately American chestnut, and is expected to exhibit similar silvical characteristics to the tree tested here. Thus, on suitable sites, American chestnut reintroduction may provide a valuable new resource for plantation forestry.

Keywords: Forest restoration; Silvicultural management; Afforestation; Reforestation

1. Introduction

The range of American chestnut (*Castanea dentata* (Marsh.) Borkh.) was greater than 800,000 km^2 (Latham, 1992) (Fig. 1) and was thought to have represented 40–50% of trees in the forest canopy in portions of its range in Appalachia (Braun, 1950; Keever, 1953). American chestnut was extremely important economically to the Appalachian region (Youngs, 2000), providing a major source of timber, tannic acid, and nuts (Frothingham, 1912; Steer, 1948).

Introduction of the pathogen *Cryphonectria parasitica* (Murr.) Barr., an aggressive diffuse canker disease (Anagnostakis, 1987) caused widespread mortality throughout the natural range of American chestnut. The disease was first discovered in 1904 at the

* Corresponding author. Tel.: +1-765-494-3608; fax: +1-765-496-2422.
E-mail address: djacobs@fnr.purdue.edu (D.F. Jacobs).

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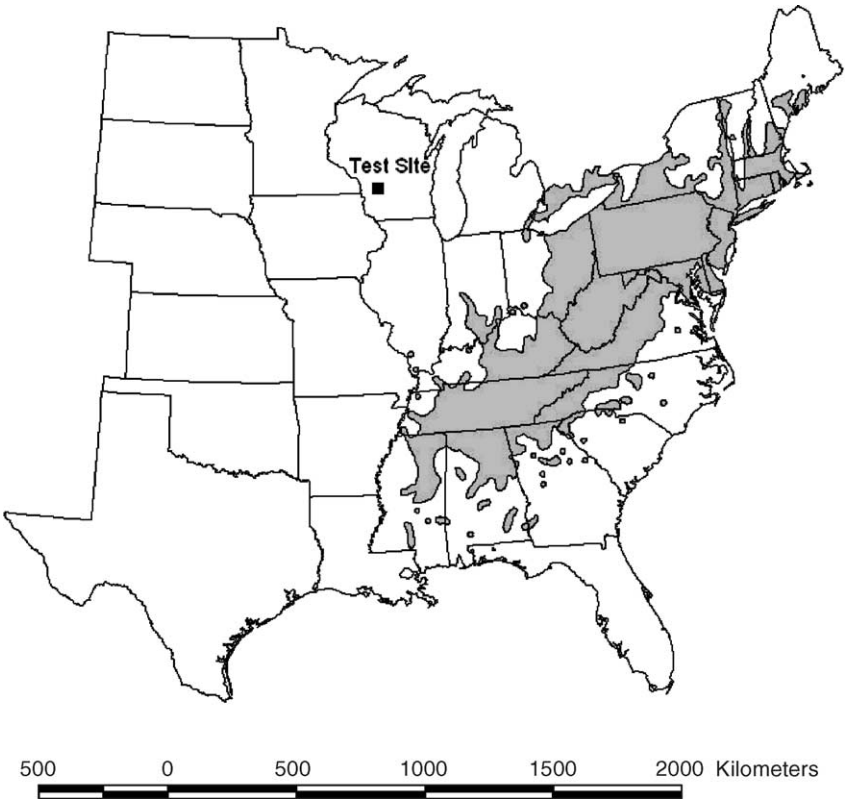

Fig. 1. The range of American chestnut (adapted from Little (1977)) and the location of the Rockland, WI tree plantation test site.

Bronx Zoological Park in New York City (Roane et al., 1986), and within 40 years it was found in all areas of the natural range (Griffin, 2000). Nearly every tree was killed in the natural range, destroying the economic value of the species (Hepting, 1974; McCormick and Platt, 1980; Anagnostakis, 1987; Youngs, 2000). The majority of trees currently present are sprouts that originated from mature trees that were killed (Russell, 1987; Stephenson et al., 1991). A cycle of sprouting, infection, dieback, and re-infection may persist for decades (Paillet, 1984), with sprouts infrequently growing to reproductive maturity (Paillet, 2002).

Significant progress toward reintroduction of American chestnut has been made through breeding programs (Burnham et al., 1986; Hebard, 2002) and it is expected that a blight-resistant hybrid form of the tree will be available in 10–15 years (Ronderos, 2000). Breeding programs involve backcrossing blight-resistant Asian chestnuts (primarily Chinese chestnut (*Castanea mollissima* Blume)) with American chestnut with the goal of producing a blight-resistant hybrid containing predominantly American chestnut characteristics (Burnham, 1981; Hebard, 2002). When reintroduced, American chestnut will likely be incorporated into reforestation and afforestation plantings both within and outside the native range.

Many afforestation plantings in the eastern USA involve interplantings of multiple hardwood species. American chestnut is rarely used in these plantings because it is assumed that trees will inevitably succumb to blight. Thus, little modern data is available concerning the early plantation growth of American chestnut relative to other species. Reports from early in the last century indicate that American chestnut is highly competitive and fast growing initially (Zon, 1904; Graves, 1905), reaching 50% of ultimate height growth by age 20 (Ashe, 1912). A more complete understanding of the plantation performance of American chestnut relative to other commonly-planted hardwood species is needed to better understand the ecology of the species and to aid

in developing silvicultural guidelines for reintroduction. The objective of this study was to assess the early plantation performance of American chestnut relative to two other commonly planted hardwood species, northern red oak (*Quercus rubra* L.) and black walnut (*Juglans nigra* L.).

2. Methods

2.1. Study site

The study site was located in the non-glaciated driftless area of southwestern Wisconsin near Rockland, WI (43°54′N, 90°53′W). This area is approximately 600 km away from the range of American chestnut (Fig. 1), but represents topographic and soil conditions similar to those found in its native range in the Appalachian region (Paillet and Rutter, 1989). Mean annual temperature in Sparta, WI (approximately 15 km from the study site) is 7.1 °C (ranging from −10.4 °C in January to 21.7 °C in July), and mean annual precipitation is 83.8 cm (NOAA, 2003). This site provided a unique opportunity to study early plantation development of American chestnut because the plantation is isolated from the range and currently shows no evidence of blight.

Historically, the study site was intensively cultivated and grazed, but these activities were abandoned on the property as of 1978. Subsequently, tree species from adjacent woodlots began to encroach upon the study site, including boxelder (*Acer negundo* L.), red maple (*Acer rubrum* L.), paper birch (*Betula papyrifera* Marsh.), quaking aspen (*Populus tremuloides* Michx.), black cherry (*Prunus serotina* Ehrh.), black oak (*Quercus velutina* Lam.), and American elm (*Ulmus americana* L.). Additional species present included staghorn sumac (*Rhus typhina* L.), Alleghany blackberry (*Rubus allengheniensis* Porter), black raspberry (*Rubus occidentalis* L.), and prickly ash (*Xanthoxylum americanum* Mill.).

2.2. Plantation establishment

During the winter months of 1995 and 1996, the project area was cleared of existing vegetation in

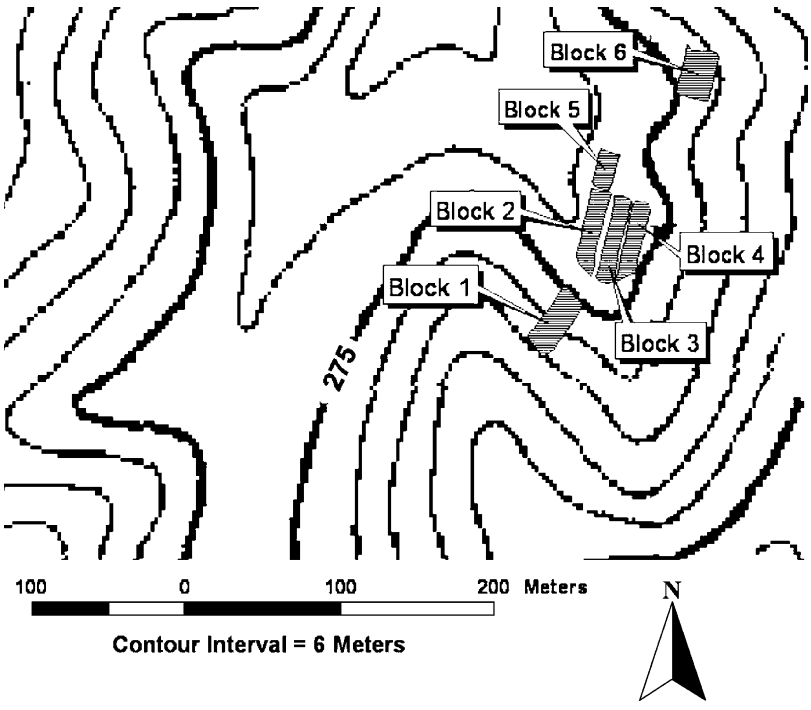

Fig. 2. Distribution of experimental blocks within study area.

Table 1
Environmental parameters for experimental blocks

Block	Aspect (°)	Slope (%)	Topographic position	Soil series	Site index (m)[a]
1	40	17	Mid-slope	Downs	19.8
2	335	4	Bottom	Council	20.1
3	310	5	Bottom	Council	20.1
4	270	14	Toe-slope	Council	20.1
5	250	7	Toe-slope	Council	20.1
6	255	12	Mid-slope	Urne	18.3

[a] Derived for *Q. rubra*, base age 50 (USDA, 1981).

preparation for planting. Only aboveground portions of existing vegetation were removed and the site was not tilled prior to planting. Six planting blocks were designated for the study (Fig. 2). The size and position of blocks were adjusted to provide access between blocks and to maintain uniformity within blocks, and blocks ranged in area from 0.03 to 0.07 ha. Blocks differed from each other in terms of aspect, slope, soil series, and site index (Table 1), but conditions were relatively homogeneous within each block. Among the blocks, three different soil series were represented including Council (coarse-loamy, mixed, mesic Fluvaquentic Hapludoll), Downs (fine-silty, mixed, mesic Mollic Hapludalf), and Urne (fine-silty, mixed, mesic Mollic Hapludalf) (USDA, 1981). Soil was collected on 1 October 2003 from two depths (0–15 and 15–30 cm) within each block and composite samples (from six to eight samples collected in each block) were processed (A&L Great Lakes Laboratories Inc., Fort Wayne, IN, USA) to quantify variation in soil chemical characteristics among the blocks (Table 2).

Three species were used to establish the study: American chestnut, northern red oak, and black walnut. American chestnut seeds were collected from a stand near West Salem, WI, believed to have been established from seed of Pennsylvania origin (Paillet and Rutter, 1989), and from a stand near Trempealeau, WI. Northern red oak and black walnut seeds were collected within 300 km of the study site from various sources in southeastern Minnesota, northeastern Iowa, and southwestern Wisconsin. Seedlings of all species were established on the site by direct seeding. Seeds were stratified over the winter months and only germinated seeds were sown. Seeds were sown at a 1.5 m × 1.5 m spacing into replicated plots in the spring of either 1995 (four blocks) or 1996 (two blocks). To protect seedlings from browsing and herbicide damage, conical tree shelters 0.6 m in height

Table 2
Soil parameters for experimental blocks

Block	Organic matter (%)	P (ppm)	K (ppm)	Ca (ppm)	Mg (ppm)	pH	CEC (meq per 100 g)
0–15 cm depth							
1	4.3	32	96	1000	165	5.9	9.0
2	4.7	44	134	1250	220	6.0	10.8
3	3.9	31	95	1100	200	6.0	9.8
4	2.8	23	87	800	180	5.8	8.1
5	3.3	23	94	900	160	6.2	7.3
6	3.7	33	118	1050	220	6.6	8.6
15–30 cm depth							
1	1.8	31	62	550	110	5.4	6.2
2	1.9	25	58	800	145	5.6	7.8
3	2.0	20	55	800	155	5.6	7.8
4	2.0	15	59	750	170	5.6	7.7
5	2.1	21	64	750	140	5.5	7.5
6	1.8	19	77	800	155	6.0	6.7

were installed immediately after sowing and removed the following spring.

Herbicide applications (1.7 kg/ha simazine and 3.4 kg/ha glyphosate) using a backpack sprayer were made in the spring of each year, prior to budbreak, for the first 3 years following sowing to control competing woody (i.e., stump sprouts from cleared tree species, Alleghany blackberry, and black raspberry) and herbaceous (e.g., reed canary grass (*Phalaris arundinacea* L.)) vegetation. Mechanical cutting to remove woody vegetation and stump sprouts was also performed once per year for the first 3 years following sowing. A chemical deer repellent (Bitrex®) was applied to terminal buds of all seedlings each fall for the first 3 years following sowing. No fertilizer was ever applied. Corrective pruning to promote a dominant leading shoot was performed as necessary during each winter on trees of all species until year 5. Some lateral branch pruning was conducted on American chestnut trees during the first 5 years to reduce suppression of surrounding trees by lower branches. Corrective pruning was performed as necessary on trees of all species after year 5 to promote quality timber form.

2.3. Measurements

The study was measured on 2 and 3 November 2002 after seven (two blocks) or eight (four blocks) growing seasons. A total of 721 trees were measured in the experiment (i.e., 186 American chestnut, 236 black walnut, and 299 northern red oak). Total height, basal diameter (10 cm above groundline), and diameter at breast height (1.37 m above groundline) (DBH) were measured for any surviving trees greater than 1 cm DBH. Stem form, defined as deviation in stem straightness (MacDonald et al., 2001) as measured in cm, was assessed for the first 2 m of the stem from groundline. At the time of measurement, no evidence of chestnut blight was observed on this plantation, although blight has infected a nearby mature stand of American chestnut since 1987 (Paillet and Rutter, 1989).

2.4. Experimental design and data analysis

The experiment was established as a randomized complete block design with six blocks. Seeds from the different species were interplanted randomly throughout rows in each block. Due to differences among species in initial planting densities within blocks, the number of trees measured for each species varied among and within blocks with a mean (±S.E.M.) per block of 31.0 (5.3) for American chestnut, 39.3 (7.6) for black walnut, and 49.8 (6.5) for northern red oak.

The experimental unit used for data analysis was the mean measurement (computed from the individual tree sampling units) for each species within a block. Data were subjected to analysis of variance (ANOVA). To ensure the validity of the assumptions of ANOVA, tests for normality and constant variance of the residuals were performed and no transformations were necessary. When $P \leq 0.05$ in the ANOVA, Fisher's protected least significant difference procedure was used to determine significant differences among species at the $\alpha = 0.05$ level. SAS software (SAS Institute Inc., Cary, NC, USA) was used for all data analysis.

3. Results

Survival 5 years following sowing for both American chestnut and black walnut was observed to be greater than 95% while survival for northern red oak was approximately 85%. Most of the mortality to northern red oak occurred within 2 years of sowing and was related to seed predation. Canopy closure occurred approximately 6 years following sowing.

Species differed significantly for all parameters of interest (Table 3) and plantation performance of American chestnut was exceptional (Fig. 3). Both basal diameter and DBH were significantly greater for American chestnut (Table 4) than for black walnut and northern red oak. Black walnut had a significantly greater basal diameter and DBH than northern red oak. Mean American chestnut basal diameter was 56% greater than black walnut and 138% greater than northern red oak. Likewise, mean American chestnut DBH was 50% greater than black walnut and 140% greater than northern red oak. American chestnut mean annual growth was 1.20 cm per year for basal diameter and 0.83 cm per year for DBH. Individual trees of American chestnut reached a maximum basal diameter of 13.7 cm and DBH of 10.2 cm. American chestnut also had the greatest total height, and black walnut had a significantly greater total height than northern red oak (Table 4). Mean American chestnut

Table 3
Analysis of variance (ANOVA) results for different response variables

Source of variation	Degrees of freedom	Mean square	*F*-statistic	Probability > *F*
Basal diameter				
Block	5	4226.19		
Species	2	159990.00	129.27	0.0001
Error	10	1237.68		
DBH				
Block	5	2975.72		
Species	2	79134.31	85.12	0.0001
Error	10	929.72		
Height				
Block	5	16.72		
Species	2	445.32	73.36	0.0001
Error	10	6.07		
Height:DBH				
Block	5	5572.41		
Species	2	110019.27	58.81	0.0001
Error	10	1870.68		
Stem deviation				
Block	5	19.95		
Species	2	97.65	6.08	0.0187
Error	10	16.05		

height was 47% greater than that of black walnut and 77% greater than that of northern red oak. Mean annual height growth for American chestnut was 0.84 m per year and maximum total height was 9.1 m.

The ratio of height to diameter (on equivalent metric scales) was significantly greater for northern red oak and did not differ between American chestnut and black walnut (Table 4). American chestnut had the lowest deviation in stem straightness relative to black walnut and northern red oak (Table 4). Stem straightness did not differ significantly between black walnut and northern red oak.

Evaluation of performance among species within individual blocks and planting years is shown in Table 5. Within each individual block or planting year, American chestnut always had the greatest basal diameter, DBH, and total height. American chestnut also always had the lowest deviation in stem straightness, and nearly always had the lowest height to DBH ratio (excepting block 5). Black walnut nearly always ranked higher than northern red oak for basal diameter, DBH, and total height. Black walnut always had a lower ratio of height to DBH than northern red oak, although ranking for stem straightness varied relatively evenly between the species.

4. Discussion

4.1. American chestnut performance

American chestnut was clearly the fastest growing species over the entire range of environmental conditions tested in this trial. American chestnut had dramatically greater height and diameter growth during early plantation establishment than the other two species. Differences were evident in spite of some early pruning of lower branches that was performed only on American chestnut. Rapid initial height growth and extensive lateral branching are characteristics that American chestnut has adapted to overtop and shade out competitors. This probably acted to suppress growth of the associated species in this study, contributing to the observed growth differences. This supports early observations of rapid initial height growth (Ashe, 1912) and high competitive ability (Zon, 1904; Graves, 1905) of American chestnut.

It should be noted that American chestnut height growth was not attained at the expense of diameter growth, as height to diameter ratios were actually significantly lower for American chestnut than for northern red oak. Additionally, American chestnut had superior stem form relative to the other two

Table 4
Mean values (±S.E.M.) for response variables of American chestnut, northern red oak, and black walnut plantation growth

Species	Basal diameter (cm)	DBH (cm)	Height (m)	Height:DBH	Stem deviation (cm)
C. dentata	9.1 a (0.3)	6.4 a (0.3)	6.4 a (0.2)	104.5 b (3.6)	3.5 b (0.2)
J. nigra	5.9 b (0.4)	4.3 b (0.4)	4.4 b (0.2)	109.3 b (5.5)	4.8 a (0.3)
Q. rubra	3.8 c (0.2)	2.7 c (0.1)	3.6 c (0.1)	142.6 a (2.0)	4.6 a (0.2)

For each parameter, species with the same letter did not differ significantly at $\alpha = 0.05$.

Fig. 3. Typical American chestnut 8 years following direct seeding.

species. This was probably partly a function of the dominance of American chestnut in this mixed planting, as much of the deviation in straightness of all trees appeared to be associated with growth toward canopy light patches. Maintenance of this relatively straighter form in mixed plantings, particularly when combined with exceptionally rapid growth, may make American chestnut a highly desirable species choice for timber production.

This is the first known study to report on the performance of American chestnut during early plantation growth (i.e., 5–10 years of age). Several studies, however, have described the growth and competitive ability of American chestnut at various other life stages. In a controlled experiment, Latham (1992) evaluated seedling competitiveness of American chestnut relative to six co-occurring species by altering resources experimentally. American chestnut ranked highest in traits associated with competitive ability over the broadest range of resource level combinations. Although the aforementioned study did not include black walnut, northern red oak was the species that most often tied in rank with American chestnut in growth and allocation responses. In a related study, Latham (1990) found that American chestnut yearlings were outranked in early field growth by other tree species only at very low light levels. American chestnut will sprout vigorously following cutting and it has been reported to grow as rapidly as any other hardwood species following clearcutting (Mattoon, 1909; Smith, 1977). There is also evidence that leachate from American chestnut litter may have allelopathic properties that suppress the development of competing vegetation (Vandermast et al., 2002).

Table 5
Mean species values for response variables within each block and for each planting year

	Species	Basal diameter (cm)	DBH (cm)	Height (m)	Height:DBH	Stem deviation (cm)
Block						
1	*C. dentata*	9.5 (1)	6.5 (1)	7.1 (1)	111.0 (3)	3.2 (3)
	J. nigra	5.1 (2)	3.5 (2)	4.2 (2)	126.1 (2)	5.3 (1)
	Q. rubra	3.6 (3)	2.6 (3)	3.7 (3)	146.4 (1)	4.3 (2)
2	*C. dentata*	10.0 (1)	7.0 (1)	6.6 (1)	95.5 (3)	2.9 (3)
	J. nigra	6.6 (2)	4.9 (2)	4.6 (2)	99.6 (2)	4.9 (2)
	Q. rubra	3.8 (3)	2.6 (3)	3.5 (3)	144.1 (1)	5.5 (1)
3	*C. dentata*	9.4 (1)	6.5 (1)	6.1 (1)	98.4 (3)	4.3 (3)
	J. nigra	5.6 (2)	3.9 (2)	4.0 (2)	106.5 (2)	5.5 (1)
	Q. rubra	4.0 (3)	2.8 (3)	4.0 (2)	146.6 (1)	5.0 (2)
4	*C. dentata*	7.6 (1)	5.2 (1)	5.7 (1)	117.9 (3)	3.9 (3)
	J. nigra	4.4 (2)	3.1 (2)	3.6 (2)	124.6 (2)	5.7 (1)
	Q. rubra	3.4 (3)	2.3 (3)	3.1 (3)	145.3 (1)	4.0 (2)
5	*C. dentata*	8.5 (1)	5.9 (1)	6.1 (1)	110.0 (2)	3.4 (2)
	J. nigra	6.7 (2)	4.9 (2)	4.5 (2)	94.0 (3)	4.5 (1)
	Q. rubra	3.6 (3)	2.6 (3)	3.5 (3)	137.8 (1)	4.5 (1)
6	*C. dentata*	9.5 (1)	6.9 (1)	6.8 (1)	100.2 (3)	3.2 (3)
	J. nigra	7.1 (2)	5.4 (2)	5.3 (2)	102.3 (2)	3.5 (2)
	Q. rubra	4.4 (3)	2.9 (3)	3.8 (3)	134.9 (1)	4.8 (1)
Planting Year						
1995	*C. dentata*	8.9 (1)	6.1 (1)	6.1 (1)	105.5 (3)	3.6 (3)
	J. nigra	5.8 (2)	4.2 (2)	4.2 (2)	106.2 (2)	5.2 (1)
	Q. rubra	3.7 (3)	2.6 (3)	3.5 (3)	143.5 (1)	4.7 (2)
1996	*C. dentata*	9.5 (1)	6.7 (1)	6.9 (1)	105.6 (3)	3.2 (3)
	J. nigra	6.1 (2)	4.5 (2)	4.8 (2)	114.2 (2)	4.4 (2)
	Q. rubra	4.0 (3)	2.8 (3)	3.8 (3)	140.7 (1)	4.5 (1)

For each response variable, species rank is shown in parentheses for each individual block or planting year (averaged over blocks means).

Prior to the detrimental influence of chestnut blight, productivity of mature American chestnut trees in Connecticut was measured to be at least 25% greater than that of oak species (Frothingham, 1912). Mean annual DBH growth of American chestnut trees has been measured at nearly 1 cm per year (Zeigler, 1920; Paillet and Rutter, 1989). A productivity of 2.9 m^3/ha per year was reported for American chestnut stands on 60-year rotations in the Blue Ridge Mountains (Buttrick et al., 1925). These reports, along with the current evidence for rapid initial growth, help to explain the former dominance of American chestnut throughout its natural range.

4.2. Implications for American chestnut reintroduction

In the near future, a blight-resistant hybrid form of American chestnut will be available for reintroduction and will likely be incorporated into mixed hardwood plantings both within and beyond its native range. The hybrid tree will be approximately 94% American chestnut and 6% Chinese chestnut (Hebard, 2002). Although the hybrid tree cannot be compared directly to the pure American chestnut tree tested here, the expectation is that the reintroduced tree will exhibit predominantly American chestnut characteristics (Burnham, 1981; Hebard, 2002). Therefore, under similar environmental conditions to those tested in this study, performance of the hybrid tree may be fairly well-correlated with that of American chestnut reported here.

These results are encouraging for the successful reestablishment of American chestnut within mixed species plantations. Careful attention to species selection may be necessary when designing planting prescriptions involving American chestnut. Black walnut and northern red oak, the other species used in this experiment, are fast growing and often used in mixed species plantings. The results presented here suggest

that, without intervention, these species may eventually be overtopped and their growth suppressed by the faster-growing American chestnut. To prevent the competitive exclusion of other species by American chestnut, it may be necessary to employ wider planting densities than those used in this study. Species that grow much slower than either black walnut or northern red oak may not be viable options for interplanting with American chestnut, unless species are separated into independent planting groups.

5. Conclusions

American chestnut appears to be an extremely fast growing species, as illustrated by the much more rapid growth rates on this study site compared to black walnut and northern red oak. This data helps to confirm pre-blight observations found in historical literature regarding exceptional American chestnut growth. With increasing optimism toward the release of a blight-resistant form of American chestnut in the near future, these results are encouraging for the successful reintroduction of American chestnut into mixed species plantations. American chestnut reintroduction will provide foresters with a new option when establishing plantations. Rapid growth, good timber quality, and excellent wildlife properties make American chestnut a highly desirable plantation species.

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