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Evaluating the ecological niche of American chestnut for optimal hybrid seedling reintroduction sites in the Appalachian ridge and valley province

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Abstract This study examines the ecological niche of American chestnut (*Castanea dentata* (Marsh.) Borkh) and the latest blight resistant American chestnut × Chinese chestnut (*Castanea mollissima* Blume) hybrids. Planted seedlings of chestnut, tulip poplar (*Liriodendron tulipifera* L.) and chestnut oak (*Quercus prinus* L.) were subjected to two levels of light and two soil types in parallel field and greenhouse studies. The field study took place in the Appalachian ridge and valley province of Virginia. Growth and survival were quantified after three growing seasons. The interaction between light levels and topographic position (soil type) was significant for growth rates in the field and greenhouse. Species were significantly different from each other although hybrid varieties were not significantly different from each other or from pure American chestnut. Tulip poplar showed the greatest growth rates under all treatments in the field. Both tulip poplar and chestnut had the greatest growth rates in large gaps within mesic, mid and lower slope (MML) sites in the field. In contrast to growth, optimal conditions for survival differed among species. Tulip poplar had the greatest survival (71%) within large gaps in MML sites while chestnuts and oaks had the greatest overall survival (64%) in small gaps within xeric, upper slope and ridge (XUR) sites. In the greenhouse, tulip poplar did not outperform chestnut. Discrepancies in field and greenhouse studies were accounted for by uncontrolled factors, such as rodent predation. We conclude that optimal sites for planting American chestnut hybrids are in small gaps located within XUR sites.

Keywords Restoration · Seedling performance · Experimental gaps · Competition · Greenhouse

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Introduction

American chestnut [*Castanea dentata* (Marsh.) Borkh] was once a dominant canopy species in many eastern deciduous forests (Keever 1953; Russell 1987; Vandermast et al. 2002; Paillet 2002). Unfortunately, this ecologically and economically important species has been missing from the forest canopy for over 60 years due to an introduced fungal pathogen, *Cryphonectria parasitica* (Murrill) Barr. which killed or reduced American chestnut to stump sprouts throughout its native range (Merkle 1906; Keever 1953; Anagnostakis 1987; Ellison et al. 2005). American chestnut sprouts can be found in the understory, scattered through portions of its original range. In Virginia, where this study takes place, chestnuts are most likely to be found at higher elevations (857 m) and in acidic soils with a pH of 4–5 (Burke 2011). However, they rarely grow into the mid-story of the forest because the fungal pathogen invades the trees as soon as the bark begins to fissure.

We are almost at the point of introducing blight-resistant chestnut hybrids into eastern forests (Jacobs 2007). However, little is known about American chestnut's ecological niche and spatial distribution across the landscape because the blight occurred before the advent of modern ecological methods (Paillet 2002). In addition, few analyses have been done on the extent to which hybrids have retained American chestnut ecophysiological characteristics and growth. The two studies that have compared hybrids to American chestnuts have analyzed cold tolerance and response to nitrogen levels; both studies found differences (Gurney et al. 2011; Rieske et al. 2003).

We can use theoretical ecological models to frame our analysis of ecological niche towards informed decisions about effective species reintroduction. Two competing models explain spatial patterns of species performance relative to resource gradients: the fundamental niche differentiation model and the shifting competitive hierarchy model (Latham 1992; Huston 1994; Shipley and Keddy 1994; Howard and Goldberg 2001; Bigelow and Canham 2002). Both models predict that species performance hierarchy will change depending on resource availability. However, the fundamental niche differentiation model predicts that species have optimal growth at different points along an environmental gradient in the absence of competition while the shifting competitive hierarchy model predicts that in the absence of competition all species perform best at the resource-rich end of the gradient but differ in terms of relative performance across the resource gradient (Whittaker 1975; Keddy 1989; Latham 1992; Pacala et al. 1994; Bigelow and Canham 2002).

If the fundamental niche model is more applicable, reintroduction would be fairly straight-forward: we would test growth and survival parameters of only chestnut in the greenhouse and re-introduce chestnut seedlings in environments matching their optimal performance. However, if species distribution follows the shifting competitive hierarchy model, it is critical to determine performance relative to competition since performance in isolation would not inform optimal sites for restoration treatments. In this case, the ability of American chestnut to outcompete canopy dominants would depend upon careful observation of relative performance across the resource gradient.

In a previous greenhouse study, American chestnut seedlings had the greatest growth rates of all species tested regardless of varying light and nutrient levels, suggesting that it is a strong competitor across the resource gradient and does not fit either model (Latham 1992). Field studies (observational and within plantations) have also reported superior growth of American chestnut relative to other temperate forest tree species (Paillet and Rutter 1989; Jacobs and Severeid 2004; McEwan et al. 2006; Jacobs et al. 2009). However, other observations in the field, while not conclusive, have suggested that American chestnut is out-performed by tulip poplar (*Liriodendron tulipifera* L.) in high light, mesic conditions (Russell 1987; McNab 2003; Loftis 2005; McCament and McCarthy 2005), indicating that the shifting competitive hierarchy model is at play.

These past studies suggest a need to integrate field and greenhouse experiments to test American chestnut performance under different resource conditions relative to other tree species. We were also curious about the extent to which field and greenhouse experiments provide consistent conclusions about ecological niche. We experimented with two different resource levels of light and soil rather than a gradient, given the constraints of running parallel field and greenhouse studies. We selected tulip poplar and chestnut oak (*Quercus prinus* L.) as representative canopy competitors because they are dominant canopy species at opposite extremes of the resource gradient in Virginia: tulip poplar on mesic, mid and lower slope (MML) sites and chestnut oak on xeric, upper slope, ridge (XUR) sites.

Our null hypothesis was that seedling performance of American chestnut and hybrids, chestnut oak, and tulip poplar would not differ as a function of high and low levels of light and topographic position (field) or soil (greenhouse). Our prediction was that species would conform to the shifting competitive hierarchy model whereby all species would perform best under the highest light conditions and in MML soil but relative performance would shift (Fig. 1). The more resource demanding tulip poplar with high growth rates was predicted to compete best in resource rich environments and to perform poorly under resource limiting conditions while a species with slower growth rates, chestnut oak, was predicted to be a poorer competitor in nutrient rich conditions but survive better in resource poor conditions (Grime and Jeffrey 1977; Chapin 1980; Spurr and Barnes 1980; Loehle 1988; Walters and Reich 2000; Tripler et al. 2005). Optimal conditions for American chestnut reintroduction would be identified as sites where seedlings had greater growth and survival than tulip poplar or chestnut oak.

Methods

Species

American chestnut seeds were purchased from Itasca greenhouse in Minnesota, USA. The seeds were produced from a protected grove in Michigan and were not from blight resistant trees. Hybrid seeds were from the American Chestnut Foundation. Hybrids were initially created by crossing blight-resistant Chinese chestnuts (*Castanea mollissima* Blume) with American chestnut found in Virginia (F_1) (Diskin et al. 2006). This hybrid was then backcrossed three times with American chestnut. The first, second, and third backcrosses (BC_1F_3, BC_2F_3, BC_3F_2) were in sufficient supply for experimentation at the time of this study, which are 3/4th, 7/8th, and 15/16th American, respectively. Tulip poplar (small, wind-dispersed seeds) and chestnut oak (large, animal-dispersed seeds) were collected from adult trees on private forest land in Rockingham County, Virginia in the fall of 2006.

Field study

The field study took place in the foothills of the Massanutten range (in the ridge and valley province of Virginia), on private property abutting George Washington National Forest (38°30′30.69″N, 78°42′53.41″W). Elevation ranges from 300 to 550 m. The foothills are sandstone with overlying shale (USDA 1982). Ridges are narrow and rounded. Slopes are approximately 250 m in length, with a maximum slope of 50% on XUR sites and a

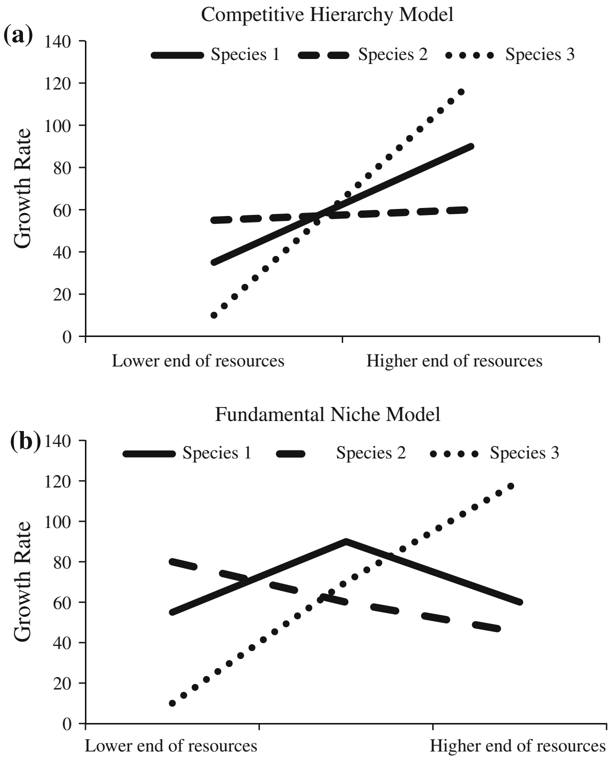

Fig. 1 Two models of predicted seedling performance. **a** The shifting competitive hierarchy hypothesis predicts that all species perform optimally at the high end of the resource gradient in the absence of competition. **b** The fundamental niche hypothesis predicts that the optimal performance of different species changes along a resource gradient in the absence of competition

minimum slope of 5% on MML sites. The average annual rainfall is 917 mm, with precipitation falling evenly throughout the year (65–90 mm every month) (National Climatic Data Center, http://www.ncdc.noaa.gov). The average temperature during the growing seasons of this study was 22.2°C (National Climate Data Center, http://www.ncdc.noaa.gov).

The forests in this region were heavily exploited for the charcoal industry in the 1800's and burned repeatedly (Bolgiano 1998). By the early 1900's no mature timber was left in this region and ridges were often bare (Bolgiano 1998). For the past 100 years, this tract of private forest has been selectively logged for timber and firewood. Forest stand age is 95–105 years old (determined by counting tree rings in gaps) and trees are on average 10 m in height on XUR sites and 12 m in height on MML sites. The study area is an oak-hickory-tulip poplar forest. American chestnut sprouts occur in the understory, tulip poplar is common in the canopy in MML sites while chestnut oak is more common in the canopy in XUR sites. Common tree species include *Q. alba* L., *Q. coccinea* Münchh, *Q. rubra* L., *Q. velutina* Lam., *Carya alba* (L.) Nutt, *C. glabra* (Mill.) Sweet, and *Acer rubrum* L.

Light was manipulated by creating medium and large sized gaps of 200 m^2 (30–45% of full sunlight) and 800 m^2 (60–75% of full sunlight) in MML and XUR sites (south/south–west aspect for all sites). The range of light conditions resulted from the replication of six sites within medium and large sized gaps. Immediately after gaps were created, light conditions were measured within the center of the gaps with hemispherical photography, which is not specific to a particular day. Photographs were taken with a NIKON FC-E8 fish-eye converter lens fitted to a Nikon Coolpix 950 digital camera. Hemiview software

(Delta T Devices Ltd.) was used to calculate the global site factor (GSF), which is the proportion of diffuse and direct light striking a point as a fraction of the amount of light that would strike the same point given no overhead obstructions over the course of a year. The resulting values range from 0 (no light) to 1 (complete light).

Twelve gaps were created to provide three replicates for each gap size in MML and XUR sites. Gaps were spaced at least 50 m apart to avoid spatial autocorrelation. Gap locations were randomly selected within the study area by creating a grid, blocking by topographic position (MML vs. XUR), and then selecting random quadrants. All ground vegetation (including all shrubs and saplings) was cut to ~10 cm height or less within the gaps at the time of the study with a weed-wacker.

Seeds were germinated in an outside nursery in D16 (5 × 18 cm) Deepots^{TM}. They were planted in the field as 1-year old seedlings in the spring of 2008. Seedling location within the gaps was random within a 10 × 10 m grid. Seedlings were planted 1 m apart and were protected from deer browse with a 2 m tall nylon mesh fence (100 × 100 m). There were initially 54 seedlings per species per treatment and thus a total of 216 seedlings per species for all four treatments combined.

Microclimate conditions were measured with SMA soil moisture smart sensor and and photosynthetically active radiation (PAR) smart sensors within the center of each gap attached to a HOBO® Micro Station Data Logger. Average values per treatment throughout the growing season are given in Fig. 2.

Greenhouse study

To test seedlings' response to different light intensities, 12 frames were constructed in the greenhouse out of PVC piping and covered with black greenhouse shade cloth of 60, 50, 30, and 20% of full sunlight. High light was classified as 50 or 60% full sunlight and low light was 20 or 30% full sunlight to partially mimic the range found within experimental gaps in the forest. Three frames (2.4 × 0.82 × 1.13 m) were used for each type of cloth. Seeds were planted in April 2007 in one gallon pots containing soil collected from XUR or

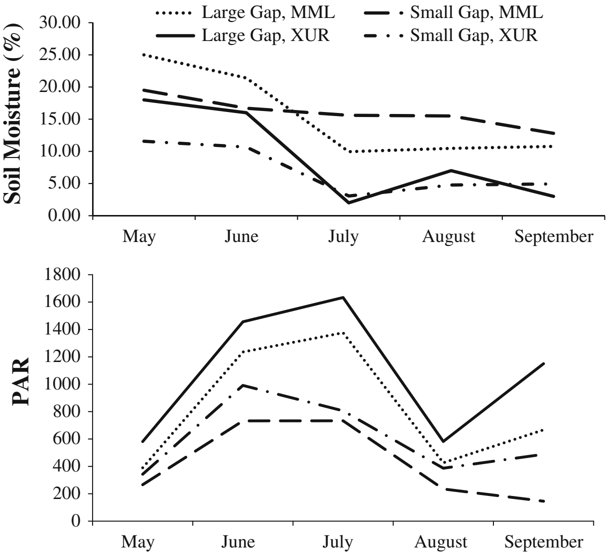

Fig. 2 Light (PAR) and soil moisture (%) monthly averages by treatment. SMA soil moisture and PAR smart sensors were attached to a microstation datalogger and placed in the center of experimental gaps (small and large) under two site conditions (MML or XUR)

Table 1 Analysis of soil collected from the field on upper slope, ridge and mid-lower slope locations at 20 cm depth in Virginia

	Collected from upper slope, ridge sites	Collected from mid, lower slope sites
Sand (%)	6	43
Silt (%)	50	37
Clay (%)	44	20
CEC (meq/100 g)	7.42	7.3
Base sat. (%)	43.7	59.24
pH $CaCO_3$	4.04	4.64
pH water	4.71	5.31
N (%)	0.31	0.35
P (ppm)	4.87	8.4
K (ppm)	42.9	65.7
Al (ppm)	330.3	602
Ca (ppm)	533	715
Cd (ppm)	0.09	0.12
Cr (ppm)	0.05	0.07
Cu (ppm)	2.89	0.44
Fe (ppm)	78.6	17.63
Mg (ppm)	56.4	65
Mn (ppm)	89.8	128.1
Mo (ppm)	0.02	0.02
Na (ppm)	11.76	9.07
Ni (ppm)	1.04	0.79
Pb (ppm)	1.31	1.87
Zn (ppm)	4.17	5.17

Nutrient levels, except for nitrogen, are given in ppm (parts per million)

MML sites. Soil was uniformly collected from the top 20 cm. Soil samples from the 12 sites (6 replicates per site type) were analyzed by the Soil, Plant and Water Laboratory at University of Georgia. Soil from XUR sites was very strongly acidic whereas soil from MML sites was strongly acidic with unusually high base saturation (Table 1). XUR sites were classified as clay loam to silty clay (Incepticol, Weikert-Berks soil series, low site index) and MML sites were classified as loam to sandy loam (Alfisol, Buchanan soil series, moderately high site index) (Table 1) (USDA 1982). A total of four treatments resulted, with one possible combination of the two levels of light and the two types of soil (topographic position)—(1) 20 or 30% light-MML soil, (2) 20 or 30% light-XUR soil, (3) 50 or 60% light-MML soil, and (4) 50 or 60% light-XUR soil. Fifteen seeds were used for each of the four treatments. One seed was planted in each pot, except for tulip poplar, where 5 seeds were planted and then randomly weeded to ensure sufficient germination.

Data collection and statistical analysis

Seedling height and diameter were measured in the fall of 2007 and 2008 in the greenhouse and fall of 2008–2010 in the field. Height was measured to the apical meristem. Diameter was measured 5 cm above the soil level. Dry biomass of greenhouse specimens was measured to determine root to shoot ratios. Specimens were extracted from the soil, roots were washed, fresh weights were obtained, and all samples were oven dried at 80°C for

2 weeks. Subsamples were weighed each day to create a drying curve. Dry measurements were recorded once samples reached stable weights.

SPSS 17.0 was used to analyze height and diameter (field and greenhouse) and root to shoot ratio (greenhouse only) by species (3 levels), soil type (2 levels) and light (2 levels). Relative growth rates were used for the field and greenhouse experiment, which had normal distributions $\left(\ln \text{height or} \ln \text{diameter}_{\text{time}_2} - \ln \text{height or} \ln \text{diameter}_{\text{time}_1}\right)/(\text{time}_1 - \text{time}_2)$. In the field, initial heights were recorded when they were out-planted in May and final heights were recorded after three growing seasons (4 year old seedlings). In the greenhouse, initial heights were from seed (starting from zero) and final heights were after two growing seasons (2 year old seedlings). A 3-way ANOVA using a univariate GLM (general linear model) was performed and significant differences among species were analyzed using Tukey's comparison of means test. Differences in survivorship between treatments in both greenhouse and field experiments were determined with the χ^2 test.

Results

Species effect

Pure chestnuts and hybrids were not significantly different from each other for any recorded metrics, and were thus combined for statistical comparisons with other species ($P > 0.05$). Species relative growth rates (RGR) for height and diameter were significantly different from each other in the field after 3 years ($P < 0.001$, Table 2). Tulip poplar growth (height and diameter) was significantly greater ($P < 0.05$) than American chestnut and chestnut oak (hereafter referred to as "oak") for all treatments while chestnut was significantly greater than oak ($P < 0.05$) within one of the treatments (low light, XUR sites) (Fig. 3). After 3 years in the field, tulip poplar had the greatest change in height (172 cm) and diameter (20 mm), followed by chestnut (pure and hybrids) (90 cm, 9 mm) and chestnut oak (16 cm, 3 mm) across all treatments. No significant difference in survival between species was detected when all treatments were combined ($P > 0.05$).

In the greenhouse, chestnut either matched or outperformed tulip poplar and always significantly outperformed oak (Figs. 4, 5). Chestnut seedlings showed significantly greater height (but not diameter) and biomass than tulip poplar in XUR soil (Figs. 4a, 5c) ($P < 0.05$). After 2 years in the greenhouse, chestnut had the greatest average height (59 cm) and diameter (6 mm) change, followed by tulip poplar (pure and hybrids) (46 cm, 6 mm) and chestnut oak (28 cm, 4 mm) across all treatments.

Soil and light treatment effect

Field

The interaction of soil and light had a highly significant effect on diameter ($F = 31.5$, $P < 0.001$) and height ($F = 23.5$, $P < 0.0001$) RGR of seedlings in the field (Table 2). Tulip poplar and chestnut seedlings had significantly higher growth rates in large gaps within MML sites (the highest resource end) than in the other three treatments (Fig. 3). Chestnuts also had significantly greater growth rates in small gaps within XUR sites (the lowest resource end) compared to large gaps within XUR sites (only for diameter) and

Table 2 Tree seedling performance in the greenhouse and field after 2 years as measured by diameter and height RGR

	df	RGR diameter			RGR height		
		MS	*F*	*P*	MS	*F*	*P*
Field							
Species	2	0.039	63.3	***	0.078	105.1	***
Gap size (light)	1	0.006	9.4	**	0.006	7.7	**
Soil type	1	0.006	9.9	**	0.011	15.2	**
Species × gap (light)	2	0.000	0.3	ns	0.000	0.6	ns
Species × soil	2	0.001	0.3	ns	0.004	4.8	**
Gap (light) × Soil	2	0.015	31.5	***	0.017	23.5	***
Greenhouse							
Species	2	0.017	3.95	*	0.048	78.3	****
Light	1	0.001	0.2	ns	0.000	0.3	ns
Soil type	1	0.001	0.2	ns	0.000	0.2	ns
Species × light	2	0.005	1.2	ns	0.001	1.3	ns
Species × soil	2	0.003	0.7	ns	0.008	13.6	****
Light × soil	2	0.002	0.4	ns	0.004	6.2	*

A three-way ANOVA was performed with independent factors of species (3 levels), soil (2 levels), and light (2 levels). Significance denoted is by *** <0.001; ** <0.01; * <0.05. *ns* not significant

small gaps within MML sites (Fig. 3). Oak growth rates were unaffected by resource conditions.

Although, growth rates were the greatest for tulip poplar and chestnut in large gaps within MML sites, overall survival rates were not the highest in this treatment (Table 3). Highest survival for chestnut and oak was found in small gaps within XUR sites (64%). The effect of soil and light on survival was significant for chestnut and oak while tulip poplar survival was unaffected (Table 3). Poorest chestnut and oak survival (11–13%) was found in small and large gaps within MML sites due to rodent predation (Table 3). Under these conditions rodent herbivory was responsible for 90% of all deaths, exhibited by gnawed-off main stems or tap roots.

Greenhouse

The interaction of soil and light was less pronounced in the greenhouse and only significant for height relative growth rate ($F = 6.2$, $P < 0.05$) (Table 2). The most obvious difference between field and greenhouse environments was soil water availability. In the field, XUR soil was lower in soil moisture, especially during the dry summer months (2.5% in XUR soil compared to 13% in MML soil in July) (Fig. 2). In the greenhouse, all seedlings were watered consistently every other day and soil moisture never dropped below 10%. Seedlings were also different ages but results after 2 years in the field showed the same trends as after 3 years.

Performance across treatments varied for seedlings in the greenhouse. Chestnut had significantly greater height growth under high light in XUR soil and MML soil compared to low light treatments in the same soil types (Fig. 4a). Tulip poplar was significantly taller under high light in MML soil compared to both high and low light levels of XUR soil

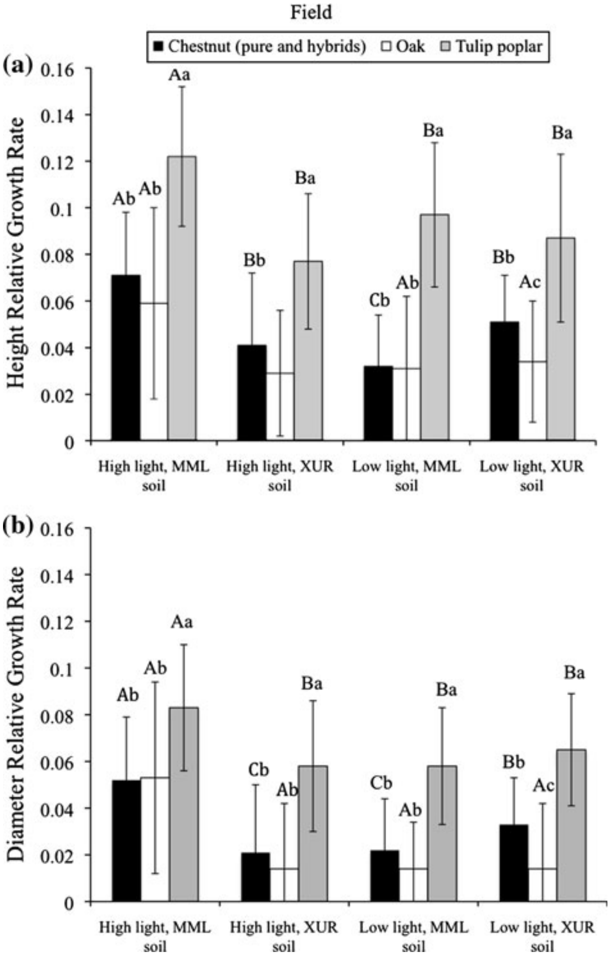

Fig. 3 Height relative growth rate (**a**) and diameter relative growth rate (**b**) of three tree species after three growing seasons under two sizes of gaps and two topographic position sites (MML or XUR) in Virginia. Seedlings were planted in experimental gaps in an oak-hickory forest. Significant differences between species within individual treatments were determined with the post-hoc Tukey's test ($P < 0.05$). *Lowercase letters* denote significance between species within a treatment ($a > b > c$). *Uppercase letters* denote the effect of treatments on each species ($A > B > C$). If they have the same *letter* they are not significantly different from each other

treatments (Fig. 4a). Similar to field results, oak growth was unaffected by soil and light treatments. Change in diameter of seedlings showed similar patterns (Fig. 4b). Total dry biomass data did not follow height and diameter growth data. Both tulip poplar and chestnut had significantly greater biomass in MML soil treatments (high and low light) rather than XUR soil treatments (high and low light) while chestnut oak had significantly greater biomass in low light, MML soil (Fig. 5a). All seedlings allocated more resources to below ground biomass (Fig. 5b). Chestnuts allocated significantly more resources to root systems in high light, XUR soil compared to MML soil treatments (Fig. 5b). Tulip poplar and chestnut oak allocated the least amount of resources to root systems in low light, slope soils.

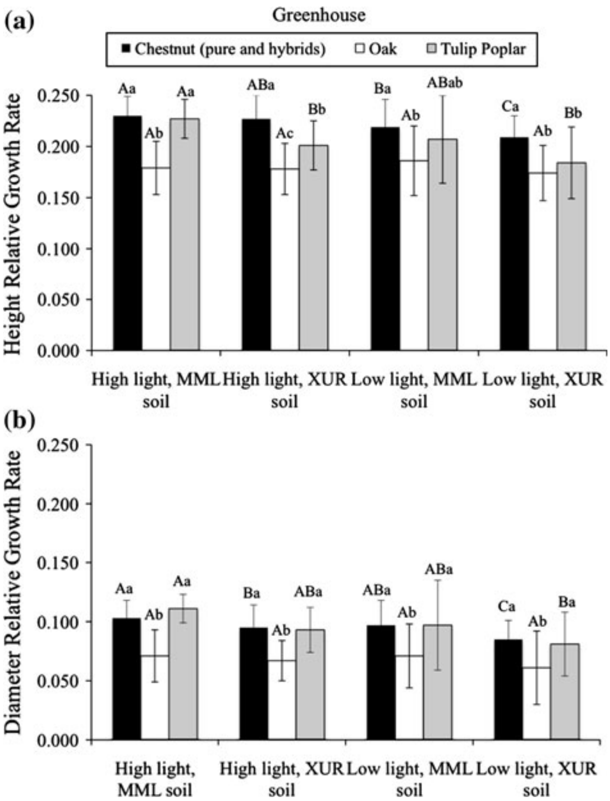

Fig. 4 Height relative growth rate (**a**) and diameter relative growth rate (**b**). Treatments were a combination of soil type (MML or XUR) and light levels after 2 years in the greenhouse. Significant differences between species within individual treatments were determined with the post-hoc Tukey's test ($P < 0.05$). *Lowercase letters* denote significance between species ($a > b > c$). *Uppercase letters* denote significance between treatments for each species ($A > B > C$). If they have the same *letter* they are not significantly different from each other

Survival was high overall in the greenhouse (>67%) but highest survival was found in high light, XUR soil (89%), a combination that resulted in high mortality in the field associated with water limitations. However, soil and light did not have a significant effect ($P > 0.05$) on the survival of any species in the greenhouse (Table 3).

Discussion

The most striking outcome of our study was a relatively static performance hierarchy found in the field experiment as well as in the parallel greenhouse experiment, yet results from the field offer different conclusions than those from the greenhouse. We interpret this as a cautionary note about using greenhouse results for application to reintroduction efforts, given the complex suite of factors determining successful survival and competition for resources in the field.

Tulip poplar demonstrated higher performance in the field, and American chestnut demonstrated higher performance in the greenhouse. In the field, tulip poplar had the

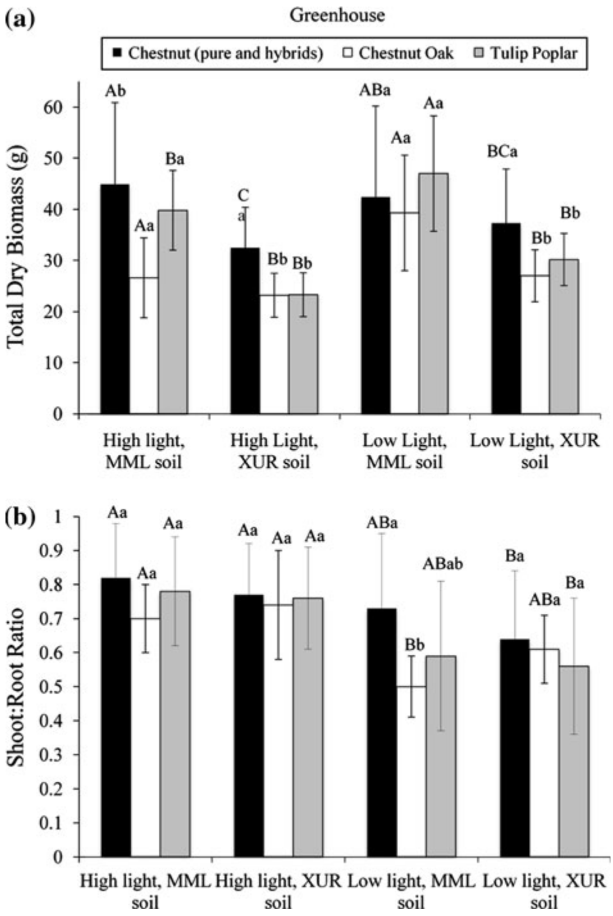

Fig. 5 Total dry mass (**a**) and root to shoot ratio (**b**) of species by treatment. Treatments were a combination of soil type (MML or XUR and light levels) after 2 years in the greenhouse. Significant differences between species within individual treatments were determined with the post-hoc Tukey's test ($P < 0.05$). *Lowercase letters* denote significance between species ($a > b > c$). *Uppercase letters* denote significance between treatments for each species ($A > B > C$). If they have the same *letter* they are not significantly different from each other

highest growth rates in all treatments, while American chestnut had consistently intermediate growth rates. This is contradictory to studies that have found that chestnut has superior growth relative to other temperate tree species in observational and plantation studies (Paillet and Rutter 1989; Jacobs and Severeid 2004; McEwan et al. 2006; Jacobs et al. 2009). Other studies have suggested (but not experimentally investigated) that light-demanding, fast-growing species, like tulip poplar will be strong competitors of chestnut and oak in productive soils in large gaps (Russell 1987; McNab 2003; Loftis 2005; McCament and McCarthy 2005; Rhoades et al. 2009; Morrissey et al. 2010). We found that this was the case, but in addition to MML sites, tulip poplar also significantly outperformed chestnuts (as well as chestnut oak) within XUR sites, although the difference was less pronounced.

Table 3 Percent seedling survivorship in the greenhouse and field by treatment

	High-light MML soil (%)	High-light, XUR soil (%)	Low-light, MML soil (%)	Low-light, XUR soil (%)	χ^2 value	Significance across treatments
Field						
Chestnut (pure and hybrids)	11	34	13	64	23.25	*
Chestnut oak	5	42	16	68	38.20	***
Tulip poplar	47	34	39	48	3.63	ns
Significance between species	***	ns	ns	ns		
Greenhouse						
Chestnut (pure and hybrids)	90	73	87	68	4.40	ns
Chestnut oak	98	97	67	84	2.52	ns
Tulip poplar	77	94	84	88	8.07	ns
Significance between species	ns	ns	ns	ns		

Treatment was a combination of light level and soil type, which was either MML or XUR. Significant differences in survival for each species in the four treatments were determined with χ^2 analysis. Significance denoted is by *** <0.001; ** <0.01; * <0.05. *ns* not significant

In the greenhouse, American chestnut growth was either significantly greater or was not significantly different from tulip poplar. Oak had the lowest growth performance, including all XUR soil treatments where it currently dominates the forest canopy. Our results from the greenhouse were similar to those from the one other experimental greenhouse study where both light and soil conditions were manipulated (Latham 1992); however, while Latham found that chestnut outperforms tulip poplar under all conditions tested, our results were only statistically significant for height growth within XUR soil and high light treatments. We believe the discrepancy in the field and greenhouse studies is due to the influence of uncontrolled factors. In the field, seedlings are subjected to drought, water inundation, and predation and chestnut appears to be more susceptible than tulip poplar. However, these results are from a short-term study and longer term monitoring may show tulip poplar more susceptible to extreme droughts (Morrissey et al. 2008).

Despite strikingly different outcomes from the field and greenhouse experiment, both experiments indicated that chestnut growth performance is most competitive in low light in XUR soil. These are the conditions where chestnut height growth was significantly greater than tulip poplar and oak in the greenhouse, where we found the smallest difference in growth between chestnut and tulip poplar in the field, and where chestnut had the greatest survival rates.

Neither the fundamental niche differentiation model nor the shifting competitive hierarchy model appear to clearly apply to the relative performance of these three species, since we did not see a difference in hierarchy with changing resource conditions in either the greenhouse or the field. However, we interpret our results as more indicative of the shifting competitive hierarchy model, since chestnut and tulip poplar both shared highest growth rates with the highest combination of resources (high light, MML soil).

In contrast, our results on survival suggest evidence of the fundamental niche model. In the field, tulip poplar had significantly higher survival than other species at the highest end of the resource gradient (high light, MML sites) while chestnut and oak had higher (but not significantly different) survival than tulip poplar at the lowest end of the resource gradient (low light, XUR sites).

We detected a dramatic shift in the form of response (growth vs. survival) to resource levels among the three species. We detected no response by oak to resource levels in terms of growth; however, chestnut oak was the most sensitive species to resource levels in terms of survival. Oak had significantly higher survival under the lowest resource conditions (low light, XUR sites) while we did not detect a strong response by tulip poplar to resource levels in terms of survival. However, tulip poplar was the most sensitive species by growth, showing strong preference for high light, MML sites. Finally, both survival and growth of chestnut were affected by treatments but these two variables were not correlated. In the field, chestnut growth was greatest in high light, MML sites (similar to tulip poplar) while survival was highest in low light, XUR sites (similar to chestnut oak).

The poor correlation between seedling survival and growth rates for chestnut appears to be due to habitat-mediated predation. Ground vegetation (mostly *Rubus* spp.) providing cover for rodents was dense in MML sites where we noticed that heavy mortality of chestnut and oak was due to rodents. Ground vegetation was sparse on the drier ridge sites where there was no evidence of mortality due to rodents. Habitat-mediated predation was found in another experimental study where the exclusion of deer increased rodent herbivory on tree seedlings in West Virginia because vegetation cover increased (Royo and Carson 2008). By excluding deer, we appear to have inadvertently increased rodent predation in mesic sites due to ground vegetation cover. This could not have been detected in the greenhouse where external factors like herbivory and herbaceous vegetation were completely controlled.

Finally, a secondary component of this study and an important finding in terms of reintroduction was assessment of the extent to which hybrids have retained American chestnut ecological performance. We did not detect a significant difference among American chestnut and the two hybrid strains for any performance parameters measured in the field or in the greenhouse under different levels of light and soil resources after 3 years of growth.

In summary, treatments that showed greatest chestnut growth (MML sites, large gaps) also had greatest chestnut mortality and highest growth rates of tulip poplar (suggesting intense competition). Chestnut seedlings had the greatest survival rates in small gaps, XUR site treatments but were outperformed by tulip poplar seedlings in terms of growth (not in terms of survival). We predict that with summer drought events, chestnut will eventually outperform tulip poplar on these sites.

Given these complex results, we suggest planting chestnut hybrids within small gaps located on XUR sites. Seedlings performed relatively well, had good survival rates, and were the most competitive with tulip poplar under these conditions. These trends may be accentuated during severe drought years when tulip poplar die-off is expected (Morrissey et al. 2008). Unless protection from rodents is provided, MML sites (within either large or small gaps) should be avoided even if deer density is low, as resulting heavy ground vegetation may foster heavy rodent-driven mortality. Further, competition with tulip poplar will likely be more intense under mesic conditions.

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