Restoring a keystone tree species for the future: American chestnut assisted migration plantings in an adaptive silviculture experiment

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ABSTRACT

Species ranges are forecast to change in response to warming temperatures and altered precipitation patterns, yet tree migration rates fail to track the pace of climate change. In anticipation of these changes, various forest adaptation management strategies have been broadly proposed, including intentionally modifying species composition via assisted migration of future climate adapted species. Despite the potential utility of these adaptation measures, practical evaluations are limited, particularly those applied to meet other ecological objectives such as supporting vulnerable, underrepresented, or degraded populations of foundational species. In this study, we examined the 4-year seedling survival and morpho-physiological response of American chestnut (*Castanea dentata* (Marsh.) Borkh.; n = 959 seeds sown), a functionally extirpated species. American chestnuts were grown within sixteen replicated 0.1 and 0.4 ha harvest gaps as part of a 160 ha co-developed (manager-scientist designed), operational-scale silvicultural trial (conditions of sufficient scope to be representative of commercial forest operations) in a northern-hardwood forest in the northeastern US. Chestnut restoration and migration potential (e.g., survival, absolute and relative growth rates, photosynthetic capacity) was assessed against the biophysical controls exerted on seedlings (e.g., understory competition, injury associated with browse and extreme cold winter temperatures) and in comparison to seedlings planted from eight other tree species (n = 480 planted per species) identified for assisted migration. Our results show the performance of American chestnut seedlings is controlled by the strength of local competition (odds of survival increased 2.6 times between four understory competition classes, p < 0.001) and cumulative winter shoot injury (relative growth in aboveground biomass adjusted for injury R2 = -0.85, p < 0.001) associated with cold intolerance likely linked to northward movement of chestnut seedlings transferred outside of their parental range. Still, the combined survival-growth response for American chestnuts ranked among the highest (2nd out of 6 possible rankings) relative to the other species tested, and even outperformed other comparable assisted migration species introduced from outside of their parental range. The implications of these findings highlight the potential for American chestnut plantings to be incorporated within both restoration and broader climate adaptation frameworks. Despite these promising outcomes, important biophysical (e.g., vegetative competition, harvest treatment, and variability in insulative snowpack) and climatic barriers for the reestablishment of this species remain. Given the paucity of reproductively viable American chestnuts or disease resistant breeding programs along northern range limits, this may generate a reliance on plant material obtained from outside of historically recognized safe transfer distances; however, increasingly shifting climate and species ranges may lead to better climate matches in the long term. Nevertheless, the broader applicability of this work illustrates the potential for cultural and ecological keystone species restoration efforts to be incorporated within climate adaptation frameworks to assist in the establishment of compositionally diverse and future climate-adapted forests.

1. Introduction

Increasing global temperatures and threats to forests from the escalating severity and frequency of disturbances, such as pests, pathogens, and fire, have generated interest in the implementation of adaptive forest management practices to maintain forest function, structure, and composition (Millar, Stephens, and Stephenson 2007; Nagel et al. 2017). Of these adaptation strategies, planting seedlings potentially adapted to these changing dynamics has been identified as an option to maintain or adapt forested ecosystems to global change (D'Amato et al. 2018; Domke et al. 2020). Notably, tree dispersal and migration rates lag the pace of climate change leading to potential misalignments of current species assemblages with future climate conditions (Sittaro et al. 2017; Zhu, Woodall, and Clark 2012). Therefore, to facilitate migration and keep pace with the rate of changing climate, the use of assisted migration has been proposed to deliberately plant tree species and/or southerly genotypes forecasted to be better suited to future climatic conditions (Pedlar et al. 2012; Williams and Dumroese 2013; Aitken et al. 2008). Although this climate adaptation strategy has been demonstrated through model simulations (Duveneck and Scheller 2015) and widely debated (Aubin et al. 2011; Pedlar et al. 2012), the novelty of assisted migration has left nascent few experimental evaluations of the efficacy of the practice (Clark et al. 2021; Palik et al. 2021) — especially in the context of ecological restoration or non-commodity purposes (Palik et al. 2022). With respect to contemporary efforts to restore degraded culturally and ecologically important keystone tree species (e. g., American Chestnut (*Castanea dentata* (Marsh.) Borkh.)) that play a foundational role in maintaining ecological functioning or cultural traditions to forested landscapes (see Costanza et al. (2017)), rapidly shifting climate regimes may confound already challenging restoration targets beyond the bounds of historic conditions. Therefore, efforts are needed to assess the role of restoration strategies for keystone tree species within a climate adaptation framework, principally through assisted migration trials.

The challenges and particularities of assisted migration has been well described in the literature (Williams et al., 2015), particularly in forested settings (Pedlar et al. 2012; Palik et al. 2022). Various classifications of assisted migration terminology have been used to differentiate among assisted migration types (see Dumroese et al. 2015). For instance, *assisted population expansion* refers to the movement of species or genotypes relatively short distances, such that movements occur within the current distribution but often at the northern latitudinal (or elevational) limits (Williams and Dumroese 2013). *Assisted range expansion* refers to "modest" movement of species to environments outside of historic ranges, but to areas forecasted to be better suited to track the pace of climate change (Williams and Dumroese, 2013). While other classifications of assisted migration types exist, for the purposes of this study, we focus our evaluation on assisted population expansion and assisted range expansion within the context of adaptation and restoration plantings.

Since its functional extirpation from forests, advances have been made in recent decades towards developing blight-resistant American chestnut varieties (e.g., Chinese-American B3F3 backcrosses (Steiner et al. 2017) and transgenic chestnuts (Powell, Newhouse, and Coffey 2019)) for restoration within its former native range in the Eastern US. Given these positive advances, concurrent evaluations have framed the restoration of *Castanea* species within current and future conditions influenced by climate change (Freitas et al. 2021). Considering the potential implications for shifts in its historic range, recent efforts to map and forecast habitat suitability of American chestnut under different climate change scenarios reveal a general northward expansion, under both low and high emmission scenarios (Noah et al. 2021). Indeed, Barnes and Delborn, (2019) project that shifts in suitable habitat could be so great that American chestnut could become largely a Canadian species by 2080. However, an actual population shift is unlikley without assisted migration because of limited seed production from native trees

(Dalgleish et al., 2016). Despite the utility of model simulations, empirical evaluations of American chestnut plantings under northward assisted migration are needed, especially given that factors other than climate may influence the establishment of this species (e.g., canopy disturbance, seedbed and soil type, vegetative competition).

Efforts to develop blight-resistant American chestnut progeny derive plant material from the remaining viably reproductive sources—most often from specimens found central to its historic range. Matching regional bioclimate zones is a well-recognized process for reforestation plantings (Dumroese et al. 2016; Pike et al. 2020), and efforts to incorporate climate and provenance with American chestnut and associated backcrosses exist (Fei et al. 2012). Given that historic population densities of American chestnuts were lower along northern range margins, there is an inherently limited and declining amount of reproductively viable material found in northern latitudes (Van Drunen et al. 2017). Still, organizations like The American Chestnut Foundation (https://www.acf.org) have worked to conserve local germplasm to incorporate into disease breeding programs, including approximately six wild specimens along the northern margins of its range in Vermont and New Hampshire. Despite this effort, it will be years if not decades before disease resistant material that represent diverse, northerly seed zones is available for restoration outplanting at operational scales (of sufficient scope to be representative of routine or commercial forest operations (see Palik et al. 2022)). Therefore, obtaining regionally appropriate blight-resistant American chestnut planting material for assisted migration plantings may be a challenge for restoration efforts. In lieu of blight resistant planting material from northern range limits, testing the performance of assisted range expansion of American chestnuts outside of their parent ranges will be important to assess its restoration potential within an assisted migration framework. These evaluations will also be critical to examining this species in the context of achieving other ecological, wildlife, cultural, and climate change mitigation objectives (Gustafson et al. 2017), especially given its reliable, nutrient-rich mast and rapid aboveground growth rates relative to other eastern hardwoods (Jacobs and Severeid 2004; Jacobs, Selig, and Severeid 2009; Dalgleish and Swihart 2012).

Recent efforts have improved scientific understanding as to the silvical characteristics of American chestnut (Wang et al. 2013). Despite these advances, forest-based research on the species is still lacking, such that there are comparatively few silvicultural field trials compared to plantations, likely due to the added complexity and scale of silvicultural treatments relative to plantations (e.g., Clark et al. 2012; Saielli et al. 2014; Clark et al. 2021). Moreover, biophysical controls found in managed forested settings, such as vegetative competition, predation, and variability in site (e.g., soils and seedbed) or silvicultural treatment may also influence the success of American chestnut restoration efforts in forests. For instance, evidence from field trials in central hardwood forests suggests that American chestnut seedlings may outperform other hardwoods under competitive vegetative environments (Belair, Saunders, and Bailey 2014). Additionally, Dalgleish et al., (2015) report that in canopy gaps, the presence of herbivory may benefit American chestnut regeneration (directly and indirectly) by reducing local competition as well as by stimulating a growth response in chestnuts. Lastly, evidence from field trials show potential for the establishment of American chestnut at its northern range limits but reveal challenges due to climate maladaptation under extremely cold temperatures (Gurney et al. 2011; Saielli et al. 2014; Schaberg et al. 2022). Each of these biophysical factors may exert considerable control over the success of American chestnut reintroduction efforts, particularly along its northern range limits.

The purpose of this study was to examine the potential for blight-resistant American chestnut introductions—with parent seed sources from wild collections—through assisted migration trials in a northern hardwood forest outside of the species' historic range limits. This experiment capitalized on a portion of the northeastern US installation of the Adaptive Silviculture for Climate Change (ASCC) project, an

international, co-developed (manager-scientist designed; Enquist et al. 2017) study representing the examination of various silvicultural strategies aimed at climate change adaptation (Nagel et al. 2017; Clark et al. 2021). The specific objectives of our experiment were to 1) assess the four-year performance of assisted range expansion American chestnut seedling backcrosses relative to the inter-species response of seedlings from a functionally diverse suite of species representing assisted population expansion and assisted range expansion migration strategies, and 2) examine the biophysical factors that influence the performance of American chestnut plantings in managed northern hardwood forests. We hypothesize that a) American chestnuts will perform similarly to other species planted outside of their native range (e.g., assisted range expansion species), relative to more locally adapted species (e.g., assisted population expansion), and b) chestnut performance will be most mediated by factors such as vegetative competition and winter shoot injury associated with being planted outside of its range.

2. Materials and methods

2.1. Study site

American chestnut seedlings were evaluated as part of the New England installation of the ASCC project (NEASCC), located at Dartmouth College's Second College Grant (SCG) in northern New Hampshire (Fig. 1). The site is located at approximately 550 m.a.s.l. within the Northeastern Highlands biophysical region on soils predominately consisting of coarse-loamy, frigid spodosols (Griffith et al., 2009) and metapelite and quartzite bedrock (Lyons et al. 1997). The forests are dominated by northern hardwood, where pretreatment stand basal area was 26.6 ± 1.5 m^2 ha^{-1} and composed of sugar maple (*Acer saccharum* Marshall; 34%), American beech (*Fagus grandifolia* Ehrh; 24%), yellow birch (*Betula alleghaniensis* Britt.; 17%), red maple (*Acer rubrum* L; 9%), red spruce (*Picea rubens* Sarg; 6%), and other hardwoods (11%) and softwoods (1%). Regional climate is characterized by cold, long winters and warm, short growing seasons (110–120 days). Observed climate during the experimental period (2018–2021) obtained from the nearest available meteorological stations (Errol, NH, June 2018-May 2019) and later measured onsite with local meteorological station (June 2019 – October 2021) include mean annual temperature (6.7 °C), extreme minimum temperature (-34.1 °C), extreme maximum temperature (33.8 °C), January mean minimum temperature (-27.7 °C), July mean maximum temperature (30.7 °C), and mean annual precipitation (1239.1 mm).

2.2. Treatments and experimental design

Although the broader NEASCC experiment examines a suite of silvicultural strategies designed to test differing degrees of adaptation to future climatic conditions across a 160 ha experiment, this examination focused on 40 ha of this experiment devoted to the treatment type termed 'Transition', which aims to shift forest overstory composition to better reflect expected composition under future climate and disturbance conditions (see Appendix 1 and Nagel et al. (2017) for additional treatment details and theoretical context regarding the Resistance, Resilience, Transition climate change response framework). To achieve this, four 10 ha treatment blocks were randomly established across two study areas (Merrill and Alder Brook) and harvested in summer-fall 2017 to promote incidental scarification of seedbeds. Within each block, a continuous cover irregular shelterwood was employed where 20% of the area contained harvested gaps (including both 0.1 ha and 0.4 ha), 10–20% remained uncut, and approximately 60% thinned to 16–18 m^2 ha^{-1}. Although all trees within gaps were designated to be harvested, within each 0.4 ha gap, at least one reproductively mature retention tree was intentionally left as a seed source from species identified for restoration (e.g., red spruce), future climate adaptation (e.g., black cherry (*Prunus serotina* Ehrh.), or wildlife importance (e.g., American

beech). Based on vegetation inventories not otherwise examined here, approximately 144 ± 39 saplings greater than 5 cm in diameter per hectare were present within gaps post-harvest treatment.

Within each treatment block ($n = 4$), two 0.1 ha and two 0.4 ha harvest gaps were planted (2 harvest gaps per gap size per block, or $n = 8$ per gap size). These canopy gaps sizes were selected based on the historic range of variability in regional mesoscale disturbances (Seymour et al., 2002) and to reflect the shade tolerance of species forecasted to have increased future habitat in this region, including American chestnuts (shade tolerance = 3.1 on a 1–5 scale, where 1 = very intolerant and 5 = very shade tolerant; Joesting, McCarthy, and Brown 2009; Paquette and Messier 2011; Wang et al. 2013) relative to species presently occupying these forests (mean shade tolerance 4.5 ± 0.3; Hanson & Lorimer, 2007; Raymond et al., 2018).

To facilitate shifts in future overstory composition, Transition treatments include plantings of nine future climate-adapted species selected based on (1) future habitat suitability informed by species distribution models (Janowiak et al., 2018; Peters et al., 2020) and (2) localized recommendations by regional manager and scientist knowledge (Table 1). Although one of the primary aims of this experiment was to test the effect of assisted migration type (e.g., assisted population expansion or assisted range expansion, a proxy for source transfer distance), considerable emphasis was placed on the functional attributes of this mixed species adaptation planting as well as the restoration potential of historically and functionally important species (e.g., red spruce, American chestnuts). Although the emphasis of this work is on the assisted range expansion (and restoration) of American chestnut, eight additional species were tested. Of these, two were classified as assisted range expansion including black birch (*Betula lenta* L.) and bitternut hickory (*Carya cordiformis* (Wangenh.) K. Koch). Concurrently, several assisted population expansion species were tested including red spruce, black cherry, eastern white pine (*Pinus strobus* L.), bigtooth aspen (*Populus grandidentata* Michx.), northern red oak (*Quercus rubra* L), and eastern hemlock (*Tsuga canadensis* (L.) Carrière).

Seedling stock and source was sightly variable among species tested. With the exception of American chestnut (see explanation below), each of the eight additional species were planted as two–three year old bareroot seedlings obtained from various state and private tree nurseries. Due to the limited regional nursery capacity to differentiate among seed sources (Tepe and Meretsky 2011; Clark et al., in review), we were unable to test the role of provenance among specific seed zones within species (see Table 1 for seed source locations as reported by tree nurseries). Rather, we focus our evaluation on the within-species differences in performance linked to functional attributes (Aubin et al. 2016) and model projections for future adaptability in this region (Iverson et al. 2019). Additionally, given that the experimental design of NEASCC is co-developed and operational in scale, this work intentionally represents the conditions that a forester would encounter if they were to pursue similar treatments under current nursery capacity.

The American chestnuts used in this experiment were obtained as nuts from The American Chestnut Foundation and were hybrid B3F3 chestnuts which represents backcrossing efforts to breed for tolerance to chestnut blight (*Cryphonectria parasitica* (Murrill) Barr) through controlled pollination between surviving American chestnut trees and disease-tolerant Chinese chestnut (*C. mollissima* (Blume); Steiner et al. 2017). The breeding process resulted in progeny that retain 96% of the American chestnut phenotype. For clarity, we refer to the seedlings used in this experiment as "American chestnuts," unless otherwise noted. Four chestnut backcrosses were tested, with two sources each derived from both Clapper and Graves lines of disease resistance. Clapper trees were developed in a USDA breeding program in which Chinese chestnut were hybridized with American chestnut then backcrossed back with American chestnut (referred to as hybrid B-26); Graves trees were developed by the Connecticut Agricultural Experimental Station and also represent hybrid-backcrossed stock, but here a specific "Mahogany" variety of Chinese chestnut was used (Worthen, Woeste, and Michler
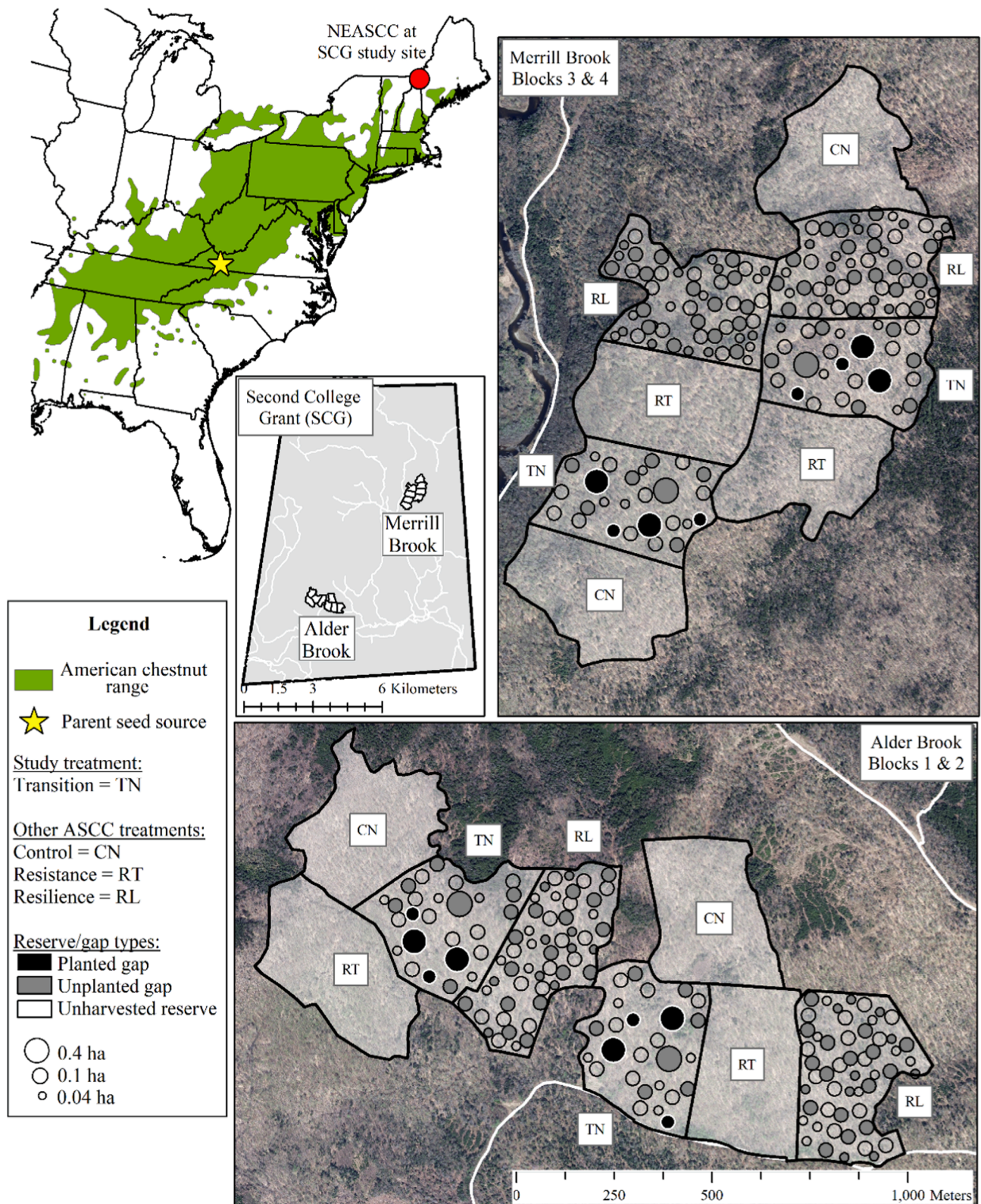
Fig. 1. Location and study design of the New England Adaptive Silviculture for Climate Change (NEASCC) project study sites relative to the historic range of American chestnut in the eastern United States (Little 1971). The parent seed source depicts the location of the last American chestnut parent for backcrossed B3F3 chestnut hybrids tested. NEASCC is located at the Second College Grant in New Hampshire, USA, with four 10 ha replicated treatments across Alder and Merrill Brook research areas. Adaptation plantings, including American chestnuts, were tested within a subset of 0.1 and 0.4 ha harvest gaps (black circles) in 'Transition' treatments (see Clark et al., (2021) for descriptions of treatment not examined in this study, including Control, Resistance, and Resilience).

Table 1

Species and seed source location information, assisted migration (AM) type (PE = assisted population expansion, RE = assisted range expansion), initial sizes when planted (mean and standard error (±)), and species silvical characteristics for seedlings tested. Each chestnut backcross originated from a unique American chestnut parent source. Since American chestnuts were sown as seed, initial size measurements (root collar diameter (RCD), height) are from one season of growth. Seed source locations are those reported directly from the vendor (American chestnuts obtained from The American Chestnut Foundation. All other seedlings obtained from state and private nurseries).

Species	Backcross and source of resistance	Seed source location	AM type	Initial Size		Species silvical characteristics			
				RCD mm	Height cm	Shade tolerance[a]	Drought tolerance[a]	Growth rate[b]	Leaf habit[b]
American chestnut B3F3	**Clapper A** - In the AG200 line. Female Am. chestnut parent	Smyth County, Virginia	RE	4.0 ± 0.1	35.9 ± 1.5	3.1	3	Rapid	Deciduous
Castanea dentata (Marshall) Borkh.	**Clapper B** - In the CH271 line. Male Am. chestnut parent			4.2 ± 0.1	42.0 ± 1.8				
	Graves A - In the BG531 line. Female Am. chestnut parent			3.6 ± 0.1	28.3 ± 1.2				
	Graves B - In the BG393 line. Female Am. chestnut parent			3.8 ± 0.1	32.2 ± 1.3				
Black birch	*Not applicable*	Pennsylvania	RE	6.0 ± 0.1	79.8 ± 1.0	3.2	3	Moderate	Deciduous
Betula lenta L.									
Bitternut hickory		Illinois	RE	4.9 ± 0.1	23.8 ± 0.2	2.1	4	Slow	Deciduous
Carya cordiformis (Wangenh.) K. Koch									
Red spruce		Nova Scotia	PE	6.5 ± 0.1	54.3 ± 0.4	4.4	2.5	Moderate	Evergreen
Picea rubens Sarg.									
Eastern white pine		New Hampshire	PE	3.8 ± 0.1	10.9 ± 0.3	3.1	2.3	Rapid	Evergreen
Pinus strobus L.									
Bigtooth aspen		Michigan	PE	2.9 ± 0.0	22.8 ± 0.3	1.2	2.5	Rapid	Deciduous
Populus grandidentata Michx.									
Black cherry		Pennsylvania	PE	2.6 ± 0.0	23.9 ± 0.3	3.5	3	Rapid	Deciduous
Prunus serotina Ehrh.									
Northern red oak		New Hampshire	PE	4.5 ± 0.1	24.7 ± 0.3	2.8	2.9	Moderate	Deciduous
Quercus rubra L.									
Eastern hemlock		Michigan	PE	3.7 ± 0.1	26.3 ± 0.2	4.8	1	Slow	Evergreen
Tsuga canadensis (L.) Carrière									

RCD = root collar diameter (mm); Height (cm); Silvical tolerances on a 1–5 scale, where 1 = very intolerant and 5 = very tolerant.

[a] (Niinemets and Valladares 2006; Wang et al. 2013).

[b] (USDA-NRCS 2021).

2010). Both Clapper and Graves sources show a moderate level of blight resistance and exhibit stem forms consistent with good timber production. For this experiment, the last wild-type American chestnut parent for all backcrosses tested was the same within source and varied among sources, but all originated in Smyth County, Virginia (source elevation ranges 600–1000 m), representing the predominant genotype within crosses. Given that American chestnuts were never historically part of the landscape where this experiment took place (northern New Hampshire), the movement of these chestnut specimens represents an assisted range expansion trial. All chestnuts were obtained and sown as seed, following cold stratification and sowing protocols outline by Bonner and Karrfalt, (2008).

Planting occurred in late May–June 2018 with 200 seedlings planted in 0.1 ha gaps (n = 20 per bare-root species) and 400 seedlings planted in 0.4 ha gaps (n = 40 per bare-root species); however, because American chestnuts were planted as seed, sowing numbers for American chestnuts were doubled to account for germination failure (n = 40 and 80, respectively). Plantings occurred on a 2 × 2 m spacing where species locations were randomized, and seedlings were planted at suitable microhabitats within 0.5 m of pre-determined locations. To minimize predation and herbivory, 45 cm protective hard plastic tubes were placed around half of the planted chestnuts, while 60 cm mesh tubes were places around other species planted. Hard plastic tubes placed firmly in contact with the ground were specifically used for American chestnuts to protect from predation of nuts by small mammals during the germination stage. Lastly, after the first year of growth, competing vegetative understory plants within 1 m radius of half of all seedlings was mowed annually using brush saws, yielding a split-split plot design.

2.3. Field data collected

All seedlings were measured and tracked for four growing seasons (2018–2021) including baseline measurements, collected within two weeks of planting, and biannual measurements, collected at the beginning and end of the growing season (approximately June 1 and October 1). Measurements included survivorship, collected every measurement period, and absolute growth in terms of root collar diameter (mm) and stem height to apical bud (cm) collected after each growing season. Local site conditions of seedlings were classified by assessing seedbed (scarified or undisturbed soils) and presence/absence of woody overstory vegetation that may influence light levels, in the form of trees forming gap edges, retention trees, or mature saplings greater than 6 cm diameter at breast height within 2 m from the seedling planting site. The amount of understory competition was assessed each year starting in the second growing season, due to the limited amount of naturally occurring vegetation present in year one. To accomplish this, vegetation within 1 m² of all planted seedlings was visually examined based on the relationship of planted seedling height and crown spread relative to local vegetation and was recorded using ordinal competition classes from highest to lowest levels of competition, termed *suppressed*, *intermediate*, *co-dominant*, and *free-to-grow*. Additionally, visual observations of seedling conditions were recorded (e.g., presence of browse, foliar frost damage, percent shoot winter injury) to account for potential impact of survivorship and growth constraints. Percent winter injury (shoot mortality evident as sunken portions of shoots that displayed dark coloration) was estimated to the nearest 10 percent class based on the proportion of stems and shoots with visible overwinter damage.

Although height measurements were always recorded in the fall, during one spring inventory (2020), chestnut heights were remeasured as a secondary metric of dieback associated with winter injury.

Lastly, light response curves were generated to better examine the impact of competition on American chestnut photosynthetic performance, utilizing a subset of American chestnuts (n = 12) within a single 0.4 ha treatment unit using a LI-6400 infrared gas-exchange analyzer (Li-Cor Inc., Lincoln, NE, USA). Varying photosynthetic photon flux density (PPFD) levels were generated using the LI-6400 light source to determine photosynthetic parameters. These measurements were taken in June 2021 between 10:00 AM and 15:00 PM on the first mature leaves from individuals growing under two understory vegetation treatment conditions a) competition control (mowing) and b) no competition control. Light-response curves were then constructed in the statistical program R version 3.6.1 (Marshall and Biscoe 1980; R Core Team, 2019), whereby three photosynthetic parameters were generated: (1) maximum rate of photosynthesis (A_{max}; μmol·m–2·s–1) where higher values indicate increased photosynthetic capacity, (2) Light Compensation Point (LCP) where higher LCP typically reflects shade intolerance, and (3) Light Saturation Point (LSP), where additional light does not positively affect photosynthetic capacity.

2.4. Statistical analysis

Generalized linear mixed models (binomial error distribution; Bolker et al., 2009) and linear mixed-effects models (Gaussian error distribution) were used to test the abiotic and biotic factors affecting American chestnut survival and growth, respectively. These models use the glmmTMB (Brooks et al. 2017) and lme4 packages (Bates et al. 2015) in R. All statistical analysis was conducted in R.

Given the elevated levels of mortality associated with seed germination failure, two survival models were produced. The first model tested all sown chestnuts seeds and limited survival to the first year to focus the examination on the factors influencing germination. The second model examined factors influencing four-year survival by restricting tests to only successfully germinated chestnuts (here forward referred to as *chestnut seedlings*) and served as the primary survival model. Fixed effects evaluated included American chestnut backcrosses type (categorical), harvest gap size (binary), predation protection (binary), planting seedbed conditions (binary), proximal woody overstory vegetation (binary), understory vegetative competition (ordinal)*, winter injury (continuous numeric)*, and their interactions. Effects denoted with an asterisk (*) are omitted in the first survival model (all sown chestnut seeds), as these data were not available for testing given the data type and restricted timeframe. Block was included as a random effect in each model.

Similar to the chestnut seedlings survival model, the same fixed and random effects were tested to assess factors influencing chestnut growth. Growth assessments were limited to those individuals alive after the four-year period. To control for between-species variation in initial sizes, seedling growth was assessed using relative growth rate in aboveground biomass. Given that species-specific seedling allometry models for volume are generally limited, green wood volume was assumed to be conical and calculated as:

$$V_{gw} = \frac{1}{3}\pi h r^2$$

where h is seedling height (mm) and r is radius of RCD (mm). Biomass was calculated using methods modified from Woodall et al., (2011):

$$Biomass = V_{gw} * SG_{gw} * W$$

where SG_{gw} is species' specific gravity in green wood (Miles and Smith 2009) and W is weight of water. Relative growth rate is calculated as the difference in seedling sizes between first and last measurements over the four-year monitoring period (Hunt and Cornelissen, 1997),

where D is individual seedling biomass:

$$Relative\,growth\,rate = \frac{lnD2 - lnD1}{t2 - t1}$$

We examined 32 germination models, 65 seedling survival models, and 65 growth models representing different *a priori* hypotheses regarding ecological factors affecting American chestnut response. To determine the best approximating model in a given candidate set, model selection was performed using Akaike Information Criterion (AIC; Burnham and Anderson, 2002) in the AICcmodavg package (Mazerolle 2020). A null model containing solely intercept and error terms were included for all three model types tested. Multiple competing models were compared and ranked according to change in AIC (ΔAIC), where top candidate models were considered to have strong support when ΔAIC values were < 6 (Burnham and Anderson 2002).

To further analyze relationships of covariates tested, predictors from best supported models were isolated for post hoc testing. Student's *t*-test and analysis of variance (ANOVA) were used for factors, and linear regressions were used for linear relationships (significance threshold α = 0.05). Each test was assessed to pass model assumptions of linearity and normality of residuals. Given that the other non-chestnut species were not included in models, we examined the performance of chestnut seedlings relative to these species and grouped by assisted migration type using ANOVAs. To relativize comparisons of species planted at different life stages (e.g., bare-root seedlings vs. sown seed chestnuts), these comparisons were restricted to a subset of data that omitted any chestnut that failed to germinate or bare-root seedlings that died within two weeks of planting. Although these evaluations between life stages are imperfect, this method most conservatively allows for assessment of differences between groups. Additionally, we used a ranking procedure to generate an ordinal measure of seedling performance that integrated survival and growth among chestnut seedlings and other species tested. Here, survival and growth performance were ranked from highest (9) to lowest (1) and then summed for each species. The resulting number allowed an ordinal comparison of overall performance among the nine species tested.

3. Results

3.1. Survival

Across the entire experiment, 959 B3F3 American chestnuts were sown, with 598 germinating during the first year, and 440 surviving through the fourth growing season (Table 2). Overall mean survivorship among backcrosses was 45.7% (±3.5), although these values are tempered by elevated levels of germination failure (mean 37.6 ± 3.7%).

Initial chestnut germination and survival (year one survival, all sown chestnut seeds) was best explained by backcross type (p < 0.001), predation protective tubes (p < 0.001), and initial planting site located under woody overstory vegetation and at gap edges (p = 0.029; model AIC weight = 0.59; Table 3). In the top candidate model, based on the predicated odds of survival, the likelihood of survival was over two times as high when protective predation tubes were used (odds ratio (OR) = 2.26, (confidence interval (CI) = 1.72 – 2.96) and 36% higher when sown under woody overstory vegetation and at gap edges (OR = 1.36 CI = 1.03 – 1.80). The ranked order for American chestnut backcrosses based on highest predicted odds of survival relative to the reference was Graves B (1.37 CI = 0.94 – 2.00), Graves A (1.15 CI = 0.79 – 1.68), Clapper A (reference), Clapper B (0.56 CI = 0.38 – 0.82).

Four-year survival for chestnut seedlings (germination failure excluded) was best explained by understory vegetation competition (p < 0.001) and cumulative winter injury (p = 0.036; model AIC weight = 0.30). Despite the relatively low model weight, nearly all candidate models included combinations of these parameters, particularly understory vegetation competition. For every increase in understory competition (four classes), the likelihood of survival increased by nearly 3

Table 2

Summary statistics for American chestnut tested in this experiment, presented by backcross type. Germination refers to those seeds that produced a living shoot during the first growing season (typically within two weeks of sowing). Germination failure is the proportion of seeds sown that did not germinate. Survival is presented in terms of a) the proportion of seedlings that survived after four years relative to the total number of seeds sown, as well as b) a truncated proportion of only those seeds that germinated and survived for this same time period. Shoot winter injury frequency refers to the proportion (%) of seedlings that germinated per plot that exhibited any winter injury during three winters. Letters within columns denote backcross groups that are significantly different (p < 0.05).

Chestnut Backcross	Total number sown / number germinated / number surviving	Germination failure (%)	Survival[a] - All seeds (%)	Survival[b] -Germinated seeds only (%)	Absolute Height (cm)	Aboveground Biomass (kg)	Winter injury (%)
Clapper A	237 / 154 / 110	36.2 ± 4.3 [a]	44.6 ± 5.1 [ab]	66.2 ± 6.6	91.0 ± 4.67	19.8 ± 2.5	74.0 ± 4.5
Clapper B	241 / 109 / 82	57.4 ± 4.2[b]	32.9 ± 3.3[b]	79.6 ± 4.2	81.2 ± 4.77	23.9 ± 8.0	67.0 ± 3.5
Graves A	238 / 165 / 117	28.6 ± 4.9 [a]	51.2 ± 4.9 [a]	71.4 ± 2.0	91.6 ± 4.2	21.8 ± 2.7	67.3 ± 3.7
Graves B	243 / 170 / 131	28.7 ± 5.3 [a]	54.3 ± 1.7[a]	74.5 ± 3.9	89.2 ± 2.8	19.7 ± 2.3	71.8 ± 3.5
All Chestnuts Combined	*959 / 598 / 440*	*37.6 ± 2.7*	*45.7 ± 3.5*	*72.9 ± 2.4*	*88.8 ± 2.2*	*1905.3 ± 91*	*70.2 ± 1.9*

times (OR = 2.63 CI = 1.54 – 4.49). Concurrently, the predicted odds of survival associated with damage from winter freezing injury decreased the likelihood of survival by 2% (OR = 0.98 CI = 0.96 – 1.00) for every unit of increase (in 10 percent classes).

Mean four-year survivorship among backcrosses for all sown chestnut seeds was significantly different between backcrosses ($F_{(3,60)}$ = 4.117, p = 0.010), although this difference was not apparent for chestnut seedlings once germination failure was accounted for ($F_{(3,60)}$ = 1.377, p = 0.259). Ostensibly, differences in early survivorship were strongly associated with elevated germination failure between backcross groups ($F_{(3,60)}$ = 8.547, p < 0.001), such that pairwise differences were greater among Clapper B backcrosses (57.4 ± 4.2%) compared to other backcross classes (pooled mean = 31.2 ± 2.5%).

Four-year survivorship was significantly different among species tested ($F_{(8,135)}$ = 24.84, p < 0.001). Rank order for all species tested in terms of four year survivorship (%) was red spruce (78.8 ± 3.05[a]) > northern red oak (76.9 ± 2.70[a]) > eastern white pine (70.1 ± 3.00[a]) > eastern hemlock (51.7 ± 3.92[b]) > bitternut hickory (51.5 ± 3.54[b]) > American chestnut (sown seed: 45.7 ± 3.54[b], > black cherry (37.9 ± 4.11[b]) > black birch (37.4 ± 4.01[b]) > bigtooth aspen (35.4 ± 3.4[b]) (letters denote pairwise differences in group means p < 0.05). When American chestnut germination failure is excluded from analysis, four-year survivorship of chestnut seedlings increases to the third ranked survivor (71.9 ± 2.86%) and group means do not differ from red spruce, northern red oak, and eastern white pine but is significantly different compared to eastern hemlock, bitternut hickory, black cherry, black birch, and bigtooth aspen (p ≤ 0.05). When American chestnut seedling backcrosses are compared to other species grouped by assisted migration type, groups are significantly different from one another ($F_{(2,45)}$ = 26.96, p < 0.001). Specifically, American chestnut seedling survivorship was 9.7% higher than assisted population expansion species and 25.6% greater than assisted range expansion species, however, this relationship was only significantly different when compared to the assisted range expansion species (Fig. 2a).

Suppressed seedlings survivorship was lower (64.7 ± 7.5%, p < 0.01) compared to other competition classes, which collectively did not significantly differ (pooled mean survivorship for intermediate, co-dominant, free-to-grow classes: 89.6 ± 0.7%; Fig. 3a). Compared to other species, American chestnut seedlings and assisted population expansion species performed similarly across all understory competition classes with no differences among these groups. Similarly, they outperformed assisted range expansion species across nearly all competition classes (p ≤ 0.02); however, under low light conditions associated with suppressed understory vegetation, American chestnut seedlings and assisted range expansion species did not differ.

Although predation protection significantly affected germination and first year survival ($F_{(1,30)}$ = 8.124, p = 0.007) such that protected

seeds germinated and survived at higher rates (68.1 ± 4.3%) compared to unprotected seeds (50.4 ± 4.4%), this difference deteriorated whereby four-year survival was not-statistically different ($F_{(1,30)}$ = 3.085, p = 0.08) between protected (76.7 ± 3.1%) and unprotected (65.8 ± 5.4%) chestnut seedlings. No differences in chestnut germination or seedling survival were observed among other covariates tested, including harvest gap sizes (0.1 and 0.4 ha) and seedbed (scarified and unmodified litter).

3.2. Growth

Among chestnut seedling backcrosses, average absolute growth in terms of height and aboveground biomass was 88.8 ± 2.2 cm and 21.1 ± 1.9 kg, respectively. No pairwise differences in absolute growth existed between backcrosses. Relative growth in terms of aboveground biomass was best explained by chestnut backcross (p < 0.001), understory vegetation competition (p < 0.001), and winter injury (p < 0.001; model AIC weight = 0.66). The ranked order for backcrosses based on effect size relative to the reference was Graves A (0.05 CI = 0.00 – 0.09), Clapper A (reference), Graves B (0.003 CI = -0.04 – 0.04), and Clapper B (-0.07 CI = -0.11 – −0.03). The model estimates for understory vegetation competition and winter injury were 0.05 (CI = 0.03 – 0.06) and −0.0015 (CI = -0.002 – −0.001) for every unit of increase in size.

Relative growth rates were significantly different among other species tested (F(8,135) = 67.77, p < 0.001). Rank order for all species in terms of relative growth rate in aboveground biomass (g g^{-1} year^{-1}) was bigtooth aspen (3.49 ± 0.10[a]) > eastern white pine (3.41 ± 0.07[a]) > black cherry (3.34 ± 0.10[a]) > American chestnut (2.15 ± 0.04[b]) > eastern hemlock (2.12 ± 0.04[b]) > black birch (1.99 ± 0.06[b]) > red spruce (1.90 ± 0.02[b]) > northern red oak (1.90 ± 0.04[b]) > bitternut hickory (1.24 ± 0.04[c]) (letters denote pairwise differences in group means p ≤ 0.05).

3.3. Ranked performance, assisted migration, and biophysical factors

Combined growth and survival ordinal scores, ranked from highest to lowest performance revealed the following order: (1) eastern white pine > (2) American chestnut > (3) red spruce > (4) northern red oak = eastern hemlock, = black cherry = bigtooth aspen > (5) black birch > (6) bitternut hickory. When compared to other planted seedlings grouped by assisted migration type, groups significantly differed from one another (F(2,45) = 58.9, p < 0.001). On average, American chestnut growth was 16.1% lower than assisted population expansion species and 39.0% greater than assisted range expansion species. Although these groups differed significantly, variability among growth rates in chestnut backcrosses modified these differences (Fig. 2b).

Winter injury negatively impacted most American chestnut

Table 3

Summary of confidence set models (including intercept-only null model) for survival and growth based on the Akaike information criterion (ΔAIC ≤ 6). One year survival includes all sown American chestnuts to examine parameters important for germination and initial one-year survival. In the four-year survival models, American chestnuts that did not germinate (mean failure = 37.6%) were not included to better assesses the parameters important for seedling survival. Parameter estimates accompany main effects and interaction terms, whereas values for logistic Generalized Linear Mixed Effect Models (GLMM) are odds ratios and values for Gaussian Linear Mixed Effects (LME) models are actual estimates. Parameter estimates for categorical variables with ≥ 3 factors are presented as mean and SE.

Response and Model	Model Form	K	AIC	ΔAIC	AICWt.
Survival (logistic GLMM):					
One-year survival (all sown chestnuts)	~ β_0*[0.50]* + **Bc** *[1.02 ± 0.17]* + **Pp** *[2.26]* + Wv[1.36] + ε_{Block}	7	1246.62	0	0.59
	~ β_0*[0.50]* + **Bc** *[1.02 ± 0.17]* + **Pp** *[2.26]* + Sb[1.27] + ε_{Block}	7	1249.11	2.49	0.17
	~ β_0*[0.59]* + **Bc** *[1.02 ± 0.17]* + **Pp** *[2.24]* + ε_{Block}	6	1249.4	2.78	0.15
	~ β_0*[0.59]* + **Bc** *[1.02 ± 0.17]* + **Pp** *[2.23]* + Ht[0.99] + ε_{Block}	7	1251.42	4.81	0.05
	~ β_0[0.64] + Bc × Pp[1.22 ± 0.17] + Bc[0.95 ± 0.17] + Pp[1.9] + ε_{Block}	9	1252.15	5.54	0.04
	~ β_0[0.84] + $\varepsilon_{p, cc, cg}$	2	1298.51	51.89	0
Four-year survival (only germinated chestnut seedlings)	~ β_0*[3.93]* + **Uc** *[2.63]* + Wi[0.98] + ε_{Block}	4	136.53	0	0.3
	~ β_0[6.00] + Uc × Wi[1.00] + Uc [2.20] + Wi[0.97] + ε_{Block}	5	138.4	1.88	0.12
	~ β_0[0.13] + Uc × Sb[0.16] + Uc [12.93] + Sb[24.93] + ε_{Block}	5	138.78	2.25	0.1
	~ β_0[2.00] + **Uc** *[2.55]* + ε_{Block}	3	138.88	2.35	0.09
	~ β_0[1.66] + **Uc** *[2.53]* + Ht[2.28] + ε_{Block}	4	139.06	2.54	0.08
	~ β_0[9.16] + Uc × Pp[2.41] + Uc[1.55] + Pp[0.07] + ε_{Block}	5	139.67	3.15	0.06
	~ β_0[2.53] + **Uc** *[2.60]* + Pp[0.63] + ε_{Block}	4	140.1	3.58	0.05
	~ β_0[2.87] + **Uc** *[2.53]* + Sb[0.64] + ε_{Block}	4	140.42	3.89	0.04
	~ β_0[1.66] + **Uc** *[2.56]* + Wv[1.42] + ε_{Block}	4	140.44	3.91	0.04
	~ β_0[1.87] + Uc × Ht[1.36] + **Uc**[2.41] + Ht[1.12] + ε_{Block}	5	140.93	4.4	0.03
	~ β_0[4.31] + **Uc** *[2.63]* + Wi[0.98] + Bc[1.01 ± 0.19] + ε_{Block}	7	141.41	4.88	0.03
	~ β_0[1.83] + Uc × Wv[1.09] + Uc	5	142.46	5.93	0.02

Table 3 (*continued*)

Response and Model	Model Form	K	AIC	ΔAIC	AICWt.
	[2.46] + Wv[1.16] + ε_{Block}				
	~ β_0*[2.77]* + ε_{Block}	2	691.29	554.77	0
Relative Growth Rate (Gaussian LME):					
Four-year growth in in aboveground biomass	~ β_0*[0.14]* + **Bc** *[1.02 ± 0.17]* + **Uc** *[0.05]* + **Wi** *[-0.001]* + ε_{Block}	8	−347.6	0	0.66
	~ β_0*[0.13]* + **Uc** *[0.05]* + **Wi** *[-0.002]* + ε_{Block}	5	−346.23	1.37	0.33
	~ β_0*[0.23]* + ε_{Block}	3	−315.3	32.3	0

Parameter codes and reference factors: Bc = chestnut backcross type (reference: Clapper A), Wv = woody overstory vegetation (reference: absence), Pp = Predation protection (reference: no protective tube), Sb = seedbed (reference: scarified), Ht = harvest treatment (reference: 0.4 ha gap), Uc = understory competition, Wi = winter injury.

Significance: italic = p ≤ 0.05, **bold** = p ≤ 0.01, ***bold-italic*** = p ≤ 0.001.

seedlings, such that out of 563 seedlings, 420 seedlings (74.6%) experienced some level of winter injury at least once. Mean winter injury to individual chestnut seedlings was 29.2 ± 1.9%, which did not differ among backcrosses ($F_{(3,60)}$ = 0.27, p = 0.844). For those measurement periods when data were available, the mean difference between fall-spring live seedling heights for chestnuts with winter injury was a −36.5 ± 2.2 cm (n = 170; $t_{(1,335)}$ = 7.3825, p < 0.001), with 28.2% (n = 48) experiencing a greater than 50% reduction and 11.1% (n = 19) experiencing greater than 80% reduction in total height. Despite this reduction in height, the one-year growth response in terms of absolute height of winter injured seedlings was not different relative to undamaged seedlings ($F_{(1,457)}$ = 0.209, p = 0.647). When examined against relative growth in aboveground ground biomass, the effect of cumulative winter injury was negatively correlated with growth (adjusted R^2 = 0.85, p < 0.001; Fig. 4).

Understory vegetation competition significantly affected American chestnut relative growth rates in terms of aboveground biomass ($F_{(3,57)}$ = 11.26, p < 0.001). Chestnut seedlings suppressed due to a competitive understory exhibited significantly lower growth compared to other competition classes (e.g., intermediate, co-dominant, free-to-grow), which collectively did not differ (Fig. 3b). Concurrently, compared to American chestnuts, growth rates from species classified as assisted population expansion were significantly higher under suppressed and free-to-grow conditions (p ≤ 0.05), while growth rates of species classified as assisted range expansion were significantly lower under intermediate and free-to-grow conditions. No differences were observed among other vegetation.

No differences in growth were observed among other covariates tested, including harvest gap sizes (0.1 and 0.4 ha), seedbed (scarified and unmodified litter), and predation protection.

3.4. Photosynthetic response to light availability

American chestnut seedlings treated with understory competition control (competing understory vegetation mowed) reached higher maximum rate of photosynthesis (A_{max} = 6.55 ± 0.31 µmol·m^{-2}·s^{-1}, p < 0.0401) compared to those growing with understory competition (3.45 ± 0.67 µmol·m^{-2}·s^{-1}). Collectively, those treated with competition control had a higher Light Compensation Point (LCP = 44.38 µmol·m^{-2}·s^{-1}) and Light Saturation Point (LSP = 313.22 µmol·m^{-2}·s^{-1}) compared to seedlings within competitive understory environments (LCP = 33.24; LSP = 281.25 µmol·m^{-2}·s^{-1}).
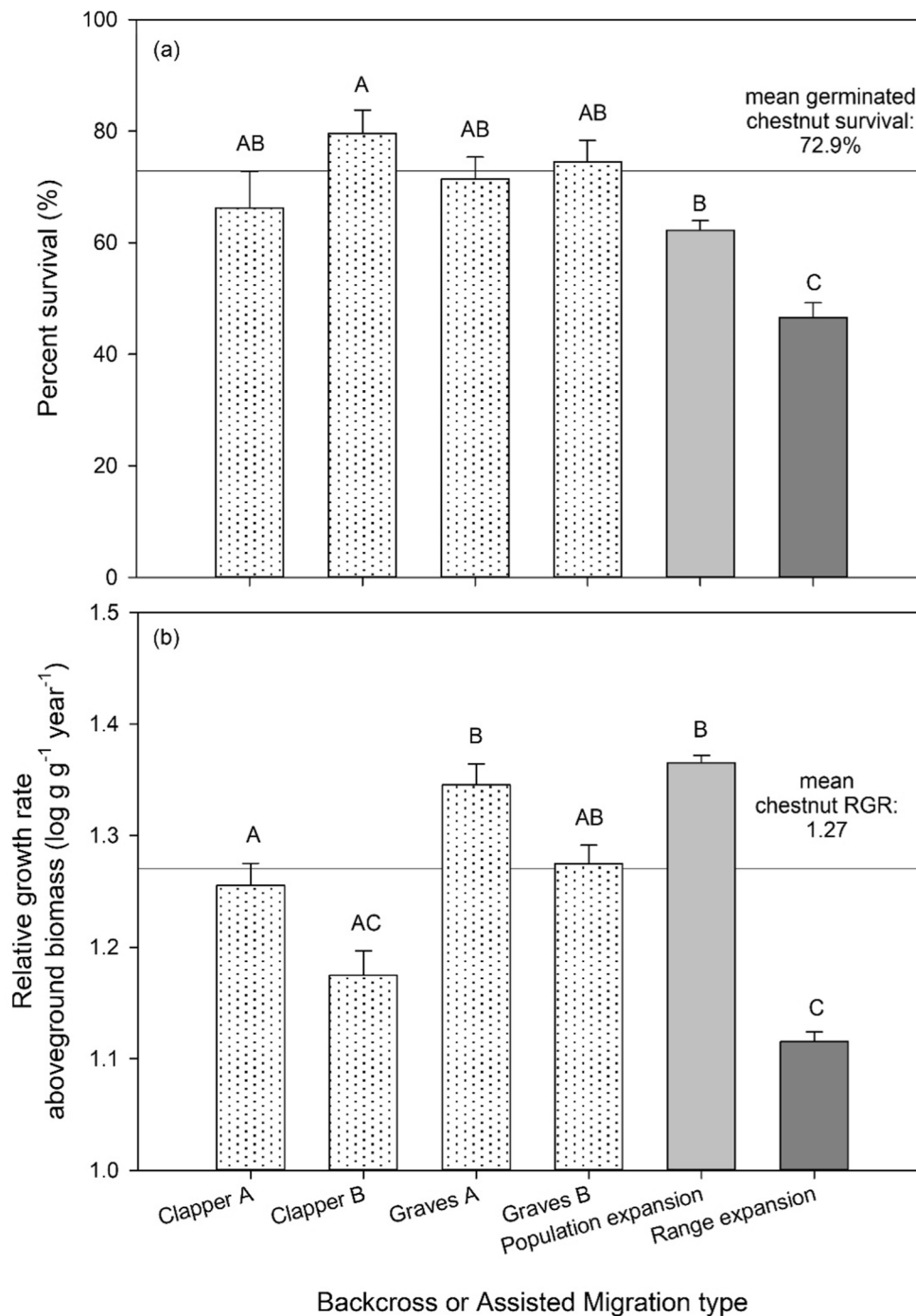
Fig. 2. (a) Four-year survival and (b) relative growth rate in terms of aboveground biomass of American chestnut seedling backcrosses (Clapper and Graves) relative to other species tested, grouped by assisted migration type (assisted population expansion, assisted range expansion). To better compare the performance between these groups planted at different life stages (e.g., sown seeds vs planted seedlings), American chestnut survival was relativized to only include seeds from individuals that successfully germinated. Letters denote groups that are significantly different (p < 0.05).

4. Discussion

The ability of forests to adapt to warming temperatures and changing conditions associated with climate change may be constrained by the capacity for tree species to adapt or migrate to new suitable habitats (Aitken et al. 2008). Historic tree migration rates dramatically lag the pace of climate change (Sittaro et al. 2017; Zhu, Woodall, and Clark 2012), this leads to potential misalignments of current species assemblages with future climate conditions. To accommodate anticipated changes in forest composition, many scientists and conservation biologists have called for novel approaches to deliberately shift species ranges to better match forecasted conditions, namely through assisted migration (Pedlar et al. 2012;Williams and Dumroese 2013; Dalgleish et al. 2016). To date, much of this work relies on computer simulation models (Duveneck and Scheller 2015) or provenance tests in plantation settings (McLane and Aitken 2012), with very few operational scale silvicultural trials that test a mix of species (Muller, Nagel, and Palik 2019; Etterson et al. 2020; Clark et al. 2021), particularly those with auxiliary ecological benefits other than assisted migration such as the restoration of keystone species (e.g., American chestnut or red spruce). Our findings regarding habitat suitability are consistent with the few model simulations that project northward shifts in historic (reconstructed) American chestnut ranges (Barnes and Delborne 2019; Noah et al. 2021), but add to the comparatively few silvicultural field trials. The outcomes of this work highlight the capacity of the species to establish, survive, and grow even under long distance transfers, at least in the near-term (see Palik et al. 2022). The flexibility in chestnut response is further amplified relative to other species tested and
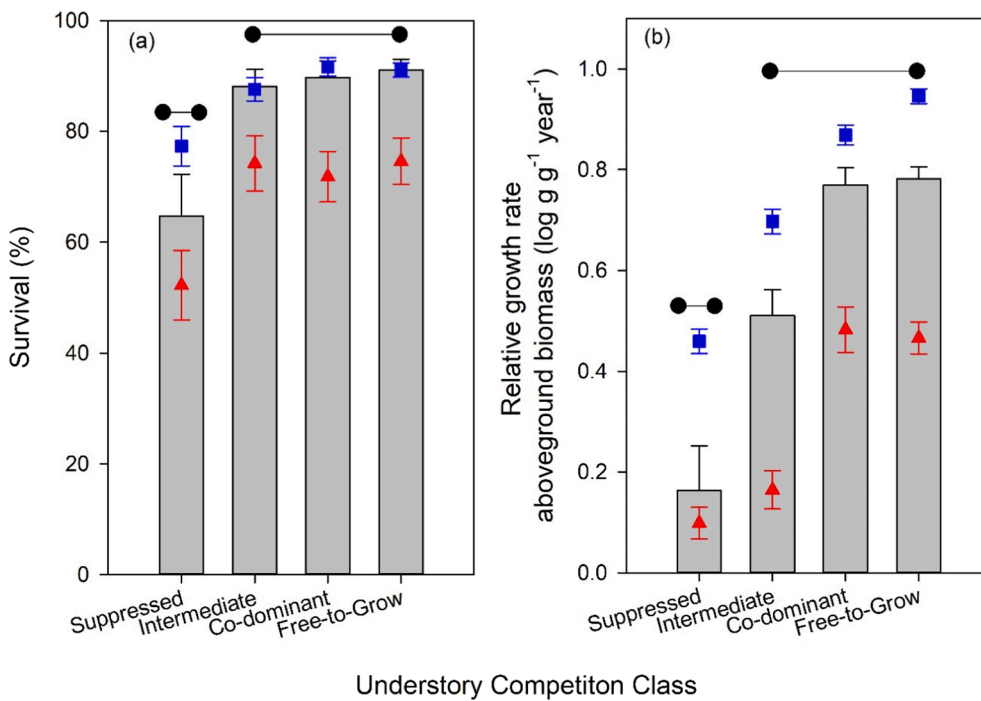
Fig. 3. The relationship between understory vegetative competition with (a) four-year survival and (b) growth in terms of relative growth rate in aboveground biomass. Data for American chestnut seedlings are presented using vertical bar plots with horizontal bars that denote groups of chestnuts that are not significantly different (p < 0.01). Additionally, performance of assisted population expansion and assisted range expansion groups are presented using square (blue) and triangle (red) boxplots, respectively. For clarity, any statistical differences among assisted migration groups are withheld, but are reported in the text.
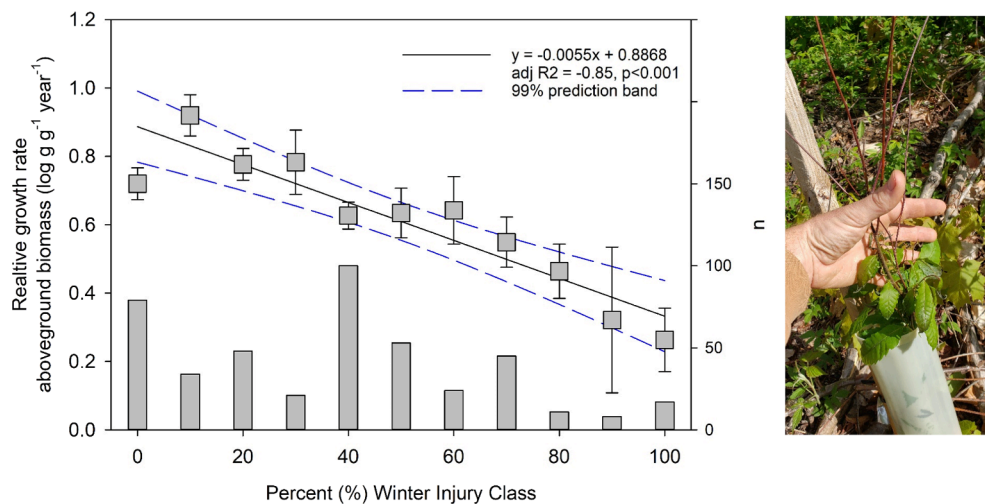
Fig. 4. LEFT: The effect of percent shoot winter injury (three-year mean) on American chestnut seedlings in terms of relative growth rate in aboveground biomass (boxplots and linear regression) and the number of individuals affected (n; bars). RIGHT: Picture depicting winter shoot injury and associated dieback on an American chestnut seedling.

endogenous factors such as vegetative competition at the local site and minimum winter temperatures that control the establishment of plantings within the context of efforts aimed at both climate change adaption and restoration.

In our experiment, we demonstrate the four-year response of American chestnut seedlings planted approximately 1200 km north of parent source and 100 km north of the species' known historical range (representative of an assisted migration trial) performed better than other species classified as assisted range expansion (a proxy for source transfer distance). Moreover, the American chestnuts tested here frequently performed as well or better than those classified as assisted population expansion, species which are presumably more closely adapted to local conditions. In fact, based on ranked performance between growth and survival, American chestnut was the second-best ranking species tested (out of six possible rankings) in this

experiment, and was the only assisted range expansion species that scored highly in our combined ranking procedure. The other assisted range expansion species, black birch and bitternut hickory, two deciduous species with different functional attributes than American chestnut (see Table 2), were ranked lowest. We therefore reject our first hypothesis that American chestnuts would perform similarly to assisted range expansion species planted outside of their native range. Although this finding was unexpected, the results do support recent forecasted northward shifts in habitat suitability of American chestnut (Barnes and Delborne 2019; Noah et al. 2021) and provide additional justification for future restoration and reintroduction efforts that consider northward expansions of the species.

Gailing and Dananelson (2017) reported that compared to the mean centroid of American chestnuts, comparatively high allelic diversity is found in populations in Ontario, Canada and northwest of the

Appalachian range. Their findings suggest that historical long-distance dispersal likely occurred, likely owing to movement from Indigenous Peoples (Abrams and Nowacki 2008), illustrating the species' capacity to disperse and persist outside of its core range. The American chestnuts used in this experiment represented one of the longest transfer distances from parent seed source of any species tested in the experiment (approximately 1200 km), a distance well outside of those suggested from seed transfer guidelines under "ideal" conditions (up to 200 km north or 100 m in elevation (see Pedlar et al., 2012; Gray and Hamann, 2013)). Despite this long-distance transfer, American chestnut seeds derived central to their range were capable of establishment as seedlings well outside of their historic range, at least in the near term. Besides differences in initial germination rates among backcrosses, presumably owing to genetic variability conferred by the last American chestnut parent for each type, the intra-species response among chestnut backcrosses was relatively uniform. These findings further illustrate the potential adaptability of chestnuts seedlings to perform well under long-distance transfers and assisted migration trials, particularly during the seedling establishment period which is a critical bottleneck for the recruitment of future forests (Ibáñez et al. 2007; Canham and Murphy 2016). Still, the long-term performance of these chestnuts remains uncertain, as numerous biophysical feedbacks (e.g., vegetative competition, canopy closure, extreme winter minimums, changes in insulative snowpack) could possibly and dramatically alter plant response with changes in ontogeny. Additionally, American chestnuts are susceptible to other diseases such as root rot (*Phytophthora cinnamomic* Rands), which is common in southern portions of its range, but is expected to move northward as climate warms (Gustafson et al. 2022), potentially generating a need for additional blight resistant planting material originating from various seed zones. Nevertheless, given that limited viable biological and genetic material remains from post-blight chestnuts, particularly along the northern extent of its range (Van Drunen et al. 2017), our study demonstrates the flexibility of long distance transfers of chestnuts seedlings originating central to its range where biological and genetic legacies still remain.

Although the American chestnut backcrosses tested here showed promise for restoration and assisted migration relative to other species planted, several factors influenced seedling performance, namely understory vegetation competition, cumulative winter injury, and to a lesser extent the microrefugia (areas with favorable microclimate that support local persistence under otherwise difficult conditions) offered by residual woody overstory vegetation, gap edges, and predation protection that supported germination in the initial planting site. Therefore, these results support our second hypothesis that seedling performance is bounded by local biophysical factors. The influence of interference interactions between planted seedlings and understory competition on seedling survival and growth are well documented (George and Bazzaz 1999; Royo and Carson 2006). Using preliminary outcomes from the same NEASCC experiment, Clark et al., (2021) described this process in the context of "ecological memory" (see also, Johnstone et al., 2016), or the successional mechanisms in forests that may resist efforts to introduce new species or transition ecosystem composition. In the context of American chestnut planting efforts, either in the form of reintroductions as part of restoration efforts or as assisted migration components used to expand populations and ranges, we also demonstrate the negative relationship that understory vegetative competition can have on chestnut performance. For foresters seeking to strengthen the capacity for seedlings to overcome competition or other factors, it is possibly that the role of ontogeny (sown seeds versus nursery transplants) may improve this response (Clark and D'Amato in press). For instance, while we observed an initial positive growth response for chestnut seedlings sown from seed, it is likely that this may be improved by planting more mature seedling stock.

Although American chestnut seedling survival, growth, and photosynthetic response were limited by local vegetative competition, our findings generally support those reported elsewhere that chestnuts perform well or better compared to many hardwood species in competitive environments, particularly the assisted range expansion species we tested (Belair, Saunders, and Bailey 2014; Joesting, McCarthy, and Brown 2007). In mixed species forests like the northern hardwoods tested in this study where light is a limiting factor, performance is also likely mediated by species-specific functional traits. For instance, the slow initial growth rates for red spruce and hemlock are likely offset by higher shade tolerance, while rapid growth of aspen are associated with lower shade tolerances. Additionally, tradeoffs can exist linked to seedling life history strategies that prioritize rapid aboveground growth (higher growth, lower survival) versus belowground allocation into rooting structures (lower growth, higher survival; Canham et al. 1999; Kobe 1997). During the forest establishment stage, the functional traits associated with shade tolerance or growth strategies can also drive near- and long-term performance of species, and ultimately the capacity to persist. For seedlings grown under competitive environments, American chestnut exhibited a similar LCP as some locally present, future-climate adapted species that are shade tolerant (e.g., red maple LCP = 35.8 $\mu mol \cdot m^{-2} \cdot s^{-1}$), yet maintained a similar response to some species of intermediate shade tolerance grown under open conditions (e.g., northern red oak LCP = 48.9 $\mu mol \cdot m^{-2} \cdot s^{-1}$; Kubiske and Pregitzer 1996). In a similar four year field trial, Knapp et al. (2014) tested the physiological response of American, Chinese, and three generations of hybrid chestnuts (B1F3, B2F3, and B3F3). The authors found that B3F3 chestnuts (like those tested in our experiment) displayed the same photosynthetic capacity as true American chestnuts, whereas all other hybrids with Chinese chestnut genes had significantly lower capacity. These results suggest that the outcomes from our work closely represent the silvical response for true American chestnut planted in situ in forested settings. Combined, our results illustrate the flexibility of American chestnut to maintain growth and photosynthetic capacity under varying levels of competition, while simultaneously exhibiting an ability to capitalize on open grown environments — traits which may contribute to a competitive edge for this species to establish and persist. Nevertheless, it will be important to track growth and survival of American chestnuts during successive forests stages, as canopy closure will reduce available light and increase local competition, potentially altering the long-term response of this species.

As species are moved increasingly outside of their ranges, the risk of site and climate maladaptation and phenological mismatches likely increases concordantly (Aitken et al. 2008). For instance, wild American chestnut are commonly associated with well-drained soils typically found on sand plains and dry ridges, with decreased long-term performance on more mesic, or nutrient-rich soils (like those tested in our experiment; Wang et al. 2013). Yet perhaps one of the greatest factors limiting long-distance transfers of American chestnuts derived for the center of its range and migrated into northern latitudes may be the extreme temperature sensitivity of the species. As demonstrated in the few studies of chestnut performance in northern latitudes (Gurney et al. 2011; Saielli et al. 2014; Schaberg et al. 2022), cold weather minimums appear to strongly control chestnut performance. For instance, evidence from these field trials show potential for the establishment of American chestnut at its northern range limits but reveal challenges due to climate maladaptation under extremely colder temperatures. This vulnerability to the cold can lead to freezing injury and shoot dieback, frequently resulting in a shrub-like growth form for afflicted seedlings, yet this may be moderated by the depth of insulative snowpack. Our study supports these findings and likewise demonstrated lower survivorship and biomass growth associated with repeated elevated levels of winter injury. The high rates of cold-induced dieback on the seedlings examined suggest a potential maladaptation to the site. Therefore, breeders should continue to incorporate trees originating from northern range limits into disease resistant breeding efforts to develop climate-appropriate material that reflects that region. Although climate projections forecast a general warming trend in annual temperatures (IPCC 2022), the potential for increased extreme weather events such as

pronounced cold air minimums or the replacement of insulating snow-pack with more freezing rain (Swanston et al. 2018; Janowiak et al. 2018) may elevate the risk of damage to cold weather sensitive plant parts.

Although winter injury resulted in dynamic growth and multi-stem growth forms of chestnuts, American chestnut seedlings sustained high biomass growth rates during the experiment, relative to other species tested. Other studies have also demonstrated rapid growth in American chestnuts (Jacobs and Severeid 2004; Jacobs, Selig, and Severeid 2009), particularly when compared to like hardwood species and traits that historically co-occurred with chestnuts (e.g., northern red oak, bitternut hickory). Among the potential ecological and adaption benefits generated from American chestnut restoration and assisted migration plantings, the high biomass growth accumulation rates associated with this species may also provide climate change mitigation benefits due to high rates of aboveground carbon gains. Furthermore, American chestnut wood is highly rot resistant (Ronderos 2000), so that these carbon gains may be particularly long-lasting and consequential for detrital carbon pools (Jacobs, Selig, and Severeid 2009; Gustafson et al. 2017). Although this study focused on the seedling stage of this species, making long-term forecasts limiting, it is possible that a co-benefit of American chestnut planted for climate adaptation may be that they also contribute to a greenhouse gas mitigation strategy. Therefore, future monitoring of these adaptation plantings is important to determine if these long-term outcomes are realized.

5. Conclusions and management implications

Forest tree species composition throughout eastern North America are forecasted to shift as climate warms, potentially leading to new and novel assemblages. Simultaneously, efforts to support vulnerable, underrepresented, or degraded foundational species and their ecosystem functions have been pursued (Palik et al. 2021; Rhodes 2022). Here, we demonstrate that American chestnut seedlings planted within a combined restoration and assisted migration framework exhibit a positive four-year growth and survival response, illustrating potential for future restoration and adaptation initiatives. Nevertheless, important endogenous factors such as local site vegetation and extreme winter temperature minimums bounded the species' response. Additional factors aiding in the establishment and persistence of this restoration species include the need for planting material originating from various seed sources at northern range limits. The results from our experiment may be modified (for all species tested) if seed sources were better optimized to match local (or future) climate. Yet given limited tree nursery capacity in the region to target climate adapted sources, this experiment represents the current conditions that a forester would experience. While American chestnut seedlings planted far outside of parent ranges exhibit maladaptive traits (in the form of winter injury) under current conditions, it is possible that site conditions may become more favorable for these individuals in the long term as climate change advances, provided they are not limited by other biophysical factors. Additional factors associated with protections from herbivory and planting microsite location lead to higher levels of growth and survival—with greater performance of those seedlings grown in open conditions relative to suppressed environments under woody overstory vegetation and along gap edges. As such, forest managers may need to consider post planting maintenance such as competition control during seedling establishment, as well as the potential for growth reductions and mortality in regions experiencing low winter temperatures. As for the latter, it is possible that winter injury may continue to hinder future American chestnut restoration until the climate becomes more favorable, or more northernly disease resistant chestnuts are developed. Still, managers may alleviate the most deleterious effects of winter injury by avoiding planting in cold areas (e. g., higher elevations, cold air drainage, etc.) and focusing on locations protected from excessive wind and exposure.

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.

CRediT authorship contribution statement

Peter W. Clark: Conceptualization, Methodology, Formal analysis, Investigation, Visualization, Writing – original draft. **Alissa J. Freeman:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft. **Anthony W. D'Amato:** Conceptualization, Methodology, Resources, Writing – review & editing, Supervision, Funding acquisition. **Paul G. Schaberg:** Conceptualization, Methodology, Resources, Writing – review & editing. **Gary J. Hawley:** Conceptualization, Resources, Writing – review & editing. **Kevin S. Evans:** Conceptualization, Resources, Writing – review & editing. **Christopher W. Woodall:** Conceptualization, Resources, Writing – review & editing, Funding acquisition.

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.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120505.

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