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Overstory and understory resource competition variably influences conversion of introduced conifer plantations to native hardwoods

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ABSTRACT

Restoration of native hardwood forests through tree planting may provide significant ecological and economic benefits, but reforestation in natural forests and afforestation on open field sites is challenging. Conversion of existing plantations of introduced conifers to hardwoods may provide an alternative opportunity for restoration. In the Midwest US, large areas of mature, introduced pine (*Pinus* spp.) plantations exist that have little economic and ecological value. These stands may provide ideal sites for planting of native hardwood species that have similar site preferences to pine. We sought to determine optimal management strategies for converting pine plantations by manipulating overstory canopy density and understory competition. We underplanted American chestnut (*Castanea dentata* (Marsh.) Borkh.) and northern red oak (*Quercus rubra* L.) seedlings in three overstory canopy treatments: control, shelterwood, and clearcut. Understory competition was either controlled or not through two growing seasons. After three growing seasons, oak performed best in the clearcut and chestnut in the shelterwood, reflecting variation in the species' shade tolerance. Chestnut height and root collar diameter (RCD) were double that of oak, and chestnut leaf N content increased with light availability while oak did not, which can be explained by the species' different adaptive strategies in biomass allocation. Both species had highest photosynthesis in the clearcut. Chestnut seedlings had significantly higher RCD in weeded clearcut and shelterwood plots, and oak in weeded clearcut plots. Weeding in the uncut control plots was ineffective because shade limited competition. Our results indicate that pine plantations offer suitable habitat for these hardwood species and provide insight regarding their growth strategies. Pine shelterwoods and clearcuts are each viable silvicultural conversion options for chestnut and oak if understory competition is controlled.

1. Introduction

Native and non-native *Pinus* species are among the most widely planted tree species worldwide and remain dominant in many regions of Asia, Europe, and North America (Messier et al., 2022). They are used frequently because of their ease of establishment and relatively high growth and productivity rates under a range of site conditions. Pine monocultures, however, typically provide fewer ecosystem services outside wood production, and are associated with lower resilience against disturbance and less biodiversity compared to native mixed forest types (Felton et al. 2016).

In contrast, native hardwood forests may provide important economic and ecological benefits and there is high interest in hardwood restoration in areas that have experienced significant forest cover loss due to conversion to agriculture, urban development, or commercial conifer plantations (Kenk and Guehne, 2001, Zerbe and Kreyer, 2007, Messier et al., 2022). Simultaneously, many native hardwood forest tree species have decreased in abundance or become threatened by introduced pests and pathogens (Jacobs et al., 2023), invasive species (Collier et al. 2002), ungulate browsing (Petersson et al. 2019), and human-mediated fire suppression (Abrams, 1992; Russell et al. 2001).

In many regions where native hardwoods are a significant component of natural forests, extensive stands of monocultural conifer plantations co-occur, sometimes consisting of introduced (non-native) species. In many locations of Asia, Europe, and USA, for example, pines (*Pinus* spp.) were extensively planted 40–150 years ago to counteract soil erosion from over-farming, to build up standing volumes of wood, attract wildlife, and reduce streamflow (Swank and Miner, 1968,

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Spathelf and Ammer, 2015).

In the Midwestern US, eastern white pine (*Pinus strobus* L.), red pine (*Pinus resinosa* Aiton), and shortleaf pine (*Pinus echinata* Mill) were selected for plantation establishment because they were the only tree species available in nurseries at the time (Dumroese et al. 2005), despite that these species are mainly outside of their native range in this region. Introduced conifer plantations comprise about 60,000 ha in Illinois, Indiana, and Ohio (USDA Forest Service 2013). There is little incentive for landowners to manage and maintain these stands as there is virtually no market for softwood species within these states because there are no softwood mills and cost of transportation exceeds net profit (Spelter et al. 2007).

These stands may, however, provide ideal sites for planting of native hardwood species that are of restoration concern and have similar site preferences to pine (Aughanbaugh 1934; Zhou et al. 1998; Hartman et al. 2005; Johnson et al. 2009; Lesko and Jacobs 2018). Native oak species (i.e., *Quercus rubra* L., *Q. alba* L., *Q. velutina* Lam.), for example, have strong versatile timber and are considered ecosystem drivers (Ellison et al. 2005; Johnson et al. 2009), yet oak regeneration is in decline due to factors reducing its competitive ability against other species (Lorimer, 1984; Johnson et al. 2009). Historically, American chestnut (*Castanea dentata*) had similar economic and ecological importance to oaks but was effectively eliminated as a canopy trees species during the early-1900s due to the accidental importation of the chestnut blight fungus (*Cryphonectria parasitica* (Murrill) Barr) from Asia (Steiner et al. 2017). Breeding programs to introduce blight resistance into American chestnut have motivated research to develop silvicultural strategies for reintroduction (Jacobs 2007; Jacobs et al., 2013; Montague et al. 2022).

Manipulating the overstory canopy to optimize understory light availability represents an important silvicultural prescription for successful conversion of conifer plantations to hardwoods (Löf et al. 2007, Lesko and Jacobs 2018). An ideal overstory canopy treatment will increase understory light availability and alter the forest microenvironment while limiting competition and protecting seedlings from abiotic and biotic disturbances (Dey et al. 2012). Oak and chestnut artificial regeneration (and natural regeneration for oaks) have both been grown under shelterwoods/partial canopy removal (Löf et al. 2010; McCament and McCarthy, 2005; Clark et al. 2012; Belair et al. 2014; Vrska et al. 2016). Oaks range from low to intermediate shade tolerance, and chestnuts are believed to have intermediate to high shade tolerance, so planting in partial shade provides sufficient light (20–50 %) for these species to establish (Gottschalk, 1994; Dey and Parker, 1996; Joesting et al. 2007). Additionally, control of understory competing vegetation, whether by herbicides or manually, is often critical to the success of trees planted following overstory removal. Even low levels of woody and herbaceous competition can substantially reduce seedling growth by competing for soil moisture and resources and reducing light infiltration (Sloan et al. 2016; Belair et al. 2014).

This study was designed to assess the effects of overstory and understory stand manipulation in conversion of introduced pine plantations to two native hardwood species, including northern red oak (*Quercus rubra* L.) and American chestnut. Our objectives were to: i) determine the effects of pine overstory canopy reduction on underplanted seedling growth and physiology; ii) assess the influence of understory vegetation control and interactions with overstory canopy reduction on seedling performance; iii) compare the growth and physiology of underplanted oak and chestnut.

2. Methods

2.1. Site description

The experiment was conducted at Purdue University forest properties, including Cunningham (40°14'59.5"N, 86°49'51.2"W) and Martell (40°26'13.2"N, 87°02'13.2"W), near West Lafayette, IN, USA, in the Central Hardwood Forest region (Supplemental Fig. 1). Both sites contained stands of eastern white pine (*Pinus strobus* L.) about 50–60 years old by tree ring analysis. At both sites, the pines were originally planted onto open, abandoned agricultural land. Prior to the original land clearing, the sites consisted of oak-forests typical of 79 % of the total forest land in the region (Brandt et al., 2014). Soils at Martell are well-drained Richardville silt loam, and soils at Cunningham include well-drained Richardville and Rockfield silt loams (NRCS, 2014). All soils were glacial till and loess derived. Both sites receive an average precipitation of 937 mm year^{-1}. Average annual temperature is 10.4°C, warmest in July at mean 23°C and coolest in January at mean −4°C (NCDC, 2012). The understory coverage of the pine plantations prior to planting was comprised of 42 % native forbs (i.e., *Pilea pumila* (L.) A. Gray, *Erigeron* spp. L., *Polygonum virginianum* (L.) Gaertn., and *Phytolacca americana* L.), 20 % vines (*Toxicodendron radicans* (L.) Kuntze and *Parthenocissus quinquefolia* (L.) Planch.), 18 % woody vegetation (*Ulmus* spp. L., *Sassafras albidum* (Nutt.) Nees, *Prunus serotina* Ehrh., *Rubus* spp. L., *Lindera benzoin* L., and *Asimina triloba* (L.) Dunal.), 3 % ferns, and the remainder was 8 % woody debris and 9 % bare ground. Additional site information and photos can be found in Lesko (2017).

2.2. Experimental design

Three eastern white monocultural pine plantations were selected to create three replicate blocks, two at Martell and one at Cunningham (Supplemental Fig. 1). The three stands were 111 × 193 m (Martell block 1), 88 × 124 m (Martell block 2), and 119 × 164 m (Cunningham block 3). Plantations were each divided into whole plots in north–south orientation (to provide minimum shading among plots) equaling one-third of the stand and randomly assigned to overstory canopy modification treatments including uncut control, clearcut, and shelterwood. We selected approximately a third of the area in the middle of each whole plot, about 25 × 20 m, to establish our experimental planting plots (described below). For the first-stage shelterwood plot, reduction of the overstory was done by removing half of the overstory pines by cutting every other tree in already-existing rows, alternating every other tree. The mean pre-treatment basal area of the plantation was 81.3 (± 15.3) m^2 ha^{-1}, which is very dense but within range of published information for unthinned white pine stands (Dierauf and Scrivani, 1995) and representative of many residual pine stands in this region that were never thinned and growing on high quality soils. Resulting mean basal area after the shelterwood establishment cut was 55.5 (± 3.6) m^2 ha^{-1}. In the clearcut plot, all the overstory pines were removed. No pines were removed in the uncut control plot. Overstory canopy treatments were installed between February and May 2014 by chainsaw felling and extraction with tractor-mounted winch. All midstory trees were removed post-harvest to reduce confounding from midstory differences. These same pine stands and overstory canopy plots were used in another study (Lesko and Jacobs 2018), but the plots in this study were physically separated from those in the other trial.

We obtained 225 northern red oak and 207 American chestnut bareroot (1+0) seedlings from the Indiana Department of Natural Resources State Tree Nursery in Vallonia, IN. For American chestnut, some of the seedlings planted were pure American chestnut while others were BC_3F_2 backcross hybrids. The hybrids carry and express mostly American chestnut genes, so differences between the hybrid and pure American chestnut were expected to be marginal and are reflective of the genetic sources to be used for reintroduction (Diskin et al. 2006; Worthen et al. 2010; Knapp et al. 2014). Each whole plot (about 25 × 20 m) in each of the three overstory treatments at each replicate block was planted in June 2014 with 25 northern red oaks and 22 American chestnuts. Planting was done manually with 2 × 2 m spacing and random intermixing of the species, and there was a 5-m buffer between seedlings and the edge of the plot.

Planted seedlings were subjected to competition control treatments. During the first year (2014), we weeded all plots monthly. In the 2015 and 2016 growing seasons, overstory canopy plots were divided into two subplots and randomly assigned to a weeded or unweeded treatment. There were approximately equal numbers of surviving chestnuts and oaks in each subplot. One row of seedlings within the dividing line was kept as a buffer zone, and these seedlings were not included in analyses. We removed herbaceous vegetation and stump sprouts in the weeded subplots down to 0–20 cm height with brush saws, loppers, and hand-pulling monthly during the growing season. While chemical weed control using herbicides is operationally standard for forestry in this region, hand weeding was used to ensure consistency across the weeding treatments and to avoid potential damage to experimental seedlings from herbicide. Fencing (2 m high and at least 50 cm from seedlings) was installed around every planted area to impede deer herbivory.

The experiment was arranged as a split-split plot design with three factors in full combination: species (two levels), overstory canopy treatment (three levels), and post-planting competition control (two levels).

2.3. Environmental measurements

Photosynthetically active radiation (PAR, μmol photons $m^{-2}s^{-1}$) was measured between late July and early August 2014 in 47 (25 oak + 22 chestnut) points per plot. We measured PAR between 11:00 and 14:00 h at a height of about 80 cm, the height of an average seedling at time of planting, with a light ceptometer (AccuPAR model LP-80, Decagon Devices, Pullman, WA). In 2015 we measured PAR for one third of the points.

Soils were sampled August 2014, October 2015, and both August and October 2016 to observe possible seasonal soil nutrient differences. In 2014, we took 15 samples per plot (5 m apart) as five transects. In 2015 and 2016, we took nine samples per plot (8 m apart) for three transects. Cores were taken in an evenly spaced grid pattern. Mineral soil was collected to a depth of 20 cm with a 2.54 cm diameter tubular soil sampling probe (Oakfield Apparatus Co., Oakfield, WI). At a laboratory, soil moisture for each sample was determined by loss of mass between fresh and dry weight after drying in a drying oven set at 68°C for 48 h. Dried soil cores were sifted through a 2-mm sieve. For analysis, composite samples from each transect were sent to Brookside Laboratories, Inc. (New Bremen, OH). Total exchange capacity (TEC), a soil fertility parameter which measures both anion and cation exchange capacity, and the cation saturations, were measured according to Ross (1995), and pH by the methods of McLean (1982). Nitrogen was measured several ways, first as estimated nitrogen release (ENR), or the amount of N released annually through organic matter (OM) decomposition. OM was quantified using the loss on ignition methods of Schulte and Hopkins (1996). Total nitrogen (N) was quantified using combustion (McGeehan and Naylor, 1988). Available nitrate (NO_3^-) and ammonium (NH_4^+) were measured using extraction with potassium chloride (Dahnke, 1990). Remaining nutrients (phosphorus (P), potassium (K), sulfur, calcium (Ca), magnesium (Mg), sodium (Na), boron (B), iron (Fe), manganese (Mn), copper (Cu), zinc (Zn), and aluminum (Al)) were measured as Mehlich III extractables (Mehlich, 1984).

2.4. Plant performance measurements

Survival, height, and root collar diameter (RCD) were measured at the beginning and end of each growing season during 2014–16. Height was measured to the nearest 0.5 cm, and RCD to the nearest 0.5 mm. We considered seedlings that died back but later continued growing to be alive, and measured height and RCD of the new shoots. Incidences of herbivory and stem gnawing were noted. Height-diameter ratio (Ht:Di) was calculated as the ratio of height to RCD.

Gas exchange (net photosynthesis rate (CO_2 assimilation), stomatal conductance, transpiration) was measured in mid to late summer 2015 and 2016, sampling the same seedlings within years. Three seedlings of each species in each of the subplots were randomly chosen. For each seedling, the youngest fully formed healthy leaf was measured. Measurements took place on two days between 10:00 and 12:30 h, with a portable infrared gas exchange analyzer (IRGA; LI-XT 6400, LI-COR Inc., Lincoln, NE, USA). Carbon dioxide at 400 μmol and flow at 500 μmol s^{-1} were held constant in the IRGA. Light levels and temperature in the LI-XT LED light source and inside the chamber were set at the average PAR and temperature for each overstory canopy treatment as determined by PAR and temperature daytime summer measurements on all three sites and plots therein recorded via a light ceptometer and data loggers, respectively. Mean (± SE) PAR and temperature values from these measurements were 1739 (±62.8) μmol m^{-2} s^{-1} and 26.6 (±0.2) °C for the clearcut, 824 (±93.61) μmol m^{-2} s^{-1} and 25.9 6 (±0.1) °C for the shelterwood, and 456 (±66.6) μmol m^{-2} s^{-1} and 24.9 (±0.1) °C for the uncut control. Additional measurements were made to create light curves in 2016, and each seedling was subjected to all three combinations of PAR and temperature corresponding to the values measured for the three overstory canopy treatments. Negative conductance and transpiration values were removed from the analysis. WUE was calculated as the ratio between rate of photosynthesis (A) and rate of transpiration (E).

Pre-dawn plant moisture stress (PMS) was measured on the same seedlings sampled for photosynthesis, with a pressure bomb (PMS company instrument, Corvallis, Oregon). All measurements were taken between 00:00 and 05:00 in late summer on nights at least three days since any precipitation in 2015 and 2016, twice per year. From each seedling, a healthy recently mature leaf was measured. Sampled leaves were collected and dried in an oven at 65°C for 72 h, weighed, and ground into powder with a constructed ball mill, a vortexer-centrifuge combination. Leaf nitrogen (N) was measured on an elemental analyzer (Costech ECS 4010, Costech Analytical Technologies, Inc., Valencia, CA). Acetanilide standards were used for calibration and quality control checks were run every 10 samples. Leaf nitrogen content, N percent concentration in a leaf multiplied by the leaf's weight, was calculated in 2015 and 2016.

2.5. Statistical analysis

Independent variables included species, overstory canopy treatment, and weeding treatments, though species were analyzed as separate populations of interest. Dependent variables were survival, height, RCD, measures of gas exchange, PMS, foliar nitrogen, soil, and PAR. Each overstory canopy treatment in each replicate plot was designated as an experimental unit, and individual seedlings comprised sampling units for analyses involving seedling responses. A linear mixed effects model with repeated measures was used; site was set as a random effect and fixed effects were overstory canopy treatment and weeding treatment. Measures of gas exchange were analyzed with PAR-temperature combination as an additional main effect for the 2016 growing season when seedlings were subjected to three combinations. Tests for normality and homoscedasticity of residuals were conducted, and when results were not normal, log and square root transformations were employed. ANOVA ($p<0.05$) was used to detect significant differences among treatments and when significant, we used Tukey's HSD test to assess pairwise comparisons ($\alpha=0.05$). Interactions were also tested for significance. Seedlings that exhibited dieback due to vole herbivory, brush cutter damage, or other reasons were removed from analysis. All tests were done in R 3.1.2 (R Core Team, 2014).

3. Results

3.1. Environment parameters

PAR was greatest in the clearcut, intermediate in the shelterwood, and least in the uncut control during both 2014 and 2015 (all $p<0.001$; Fig. 1a). Neither weed competition control nor the interaction of overstory canopy and competition control treatments resulted in a

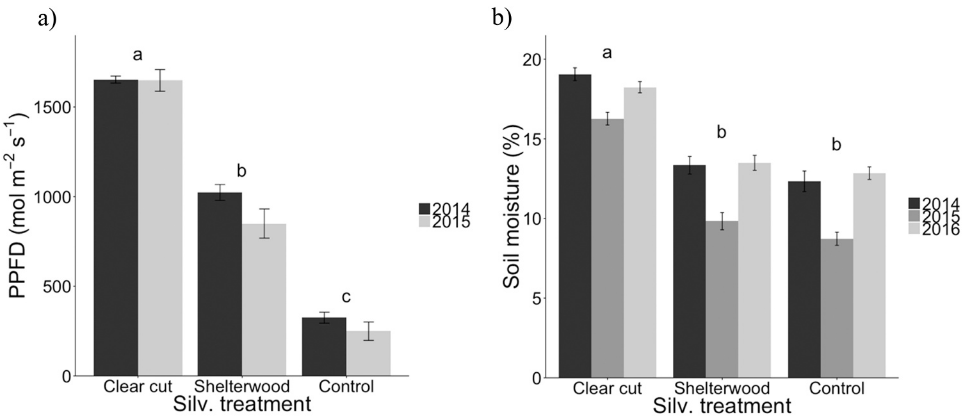

Fig. 1. a) PAR (photosynthetically active radiation) ± standard error in 2014 and 2015 growing seasons; each year was analyzed separately. Different letters indicate significant differences among treatments per Tukey's HSD (α=0.05). b) Percent soil moisture ± standard error, mean of 2014–2016 growing seasons; each year was analyzed separately. Different letters indicate significant differences among treatments according to Tukey's HSD (α=0.05).

significant difference in PAR in 2015.

The relationships between the soil moisture of overstory canopy treatments remained the same each year: clearcut treatments had greater soil moisture than shelterwood and uncut control ($p<0.001$; Fig. 1b). There was no statistically significant difference between weeding treatments. There was a significant canopy-weeding treatment interaction in 2015 ($p=0.019$; data not shown).

Mean pH ranged from 4.3 to 4.5 across sites, with no significant differences in pH between the overstory canopy treatments (Table 1).

Table 1
Soil characteristics (mean ± standard error), including pH, organic matter, and total exchange capacity (sum of cation and anion exchange capacity). Nitrogen (N) was measured as NH_4+ (ammonium), NO_3- (nitrate), and estimated N release. Ratio of ammonium to nitrate was also calculated. Different letters indicate significant differences among treatments per Tukey's HSD (α=0.05). P=phosphorus, K=potassium.

Chemical char.	Year	Clearcut	Shelterwood	Uncut Control
pH	2014	4.43 (±.13)	4.41 (±.15)	4.25 (±.04)
	2015	4.42 (±.11)	4.43 (±.06)	4.57 (±.04)
	2016	4.27 (±.04)	4.23 (±.03)	4.33 (±.04)
Organic matter (%)	2014	3.16 (±.31)	2.82 (±.25)	2.58 (±.20)
	2015	3.06 (±.43) a	2.00 (±.14) b	2.04 (±.16) b
	2016	2.93 (±.14) a	2.27 (±.08) b	2.31 (±.11) ab
Total exchg. capac.	2014	10.31 (±1.26)	6.78 (±.51)	8.39 (±.68)
(meq/100 g)	2015	10.19 (±.61) a	7.66 (±.49) b	8.82 (±.86) ab
	2016	9.35 (±.54) a	6.55 (±.34) b	7.65 (±.51) ab
NH_4+ (ppm)	2014	4.79 (±.57)	4.03 (±.76)	7.28 (±2.28)
	2015	3.49 (±.77)	3.41 (±1.08)	3.21 (±.57)
	2016	1.28 (±.18) b	1.98 (±.3) ab	2.97 (±1.38) a
NO_3- (ppm)	2014	1.87 (±.35) b	3.46 (±.40) a	2.59 (±.52) ab
	2015	18.5 (±3.33) a	8.2 (±1.79) b	8.53 (±2.14) b
	2016	11.8 (±1.18)	9.57 (±1.35)	10.02 (±1.44)
$NH_4+:NO_3-$	2014	2.56	1.16	2.81
	2015	0.19	0.42	0.376
	2016	0.11	0.21	0.296
Est. N release	2014	86.83 (±4.11)	82.42 (±3.71)	78.54 (±3.88)
(kg/ha)	2015	85.31 (±5.45) a	67.13 (±3.16) b	68.13 (±3.61) b
	2016	85.68 (±2.26) a	73.23 (±1.76) b	74.22 (±2.36) b
P (ppm)	2014	42.87 (±4.54)	42.27 (±2.9)	48.73 (±4.28)
	2015	29.22 (±3.57)	32.78 (±3.34)	35.22 (±4.1)
	2016	30 (±2.63)	28.22 (±2.11)	34.56 (±3.24)
K (ppm)	2014	85.07 (±7.85) a	63.00 (±3.56) b	63.87 (±2.32) b
	2015	72.22 (±5.99)	70.56 (±9.07)	79.00 (±8.06)
	2016	70.22 (±5.58)	61 (±5.39)	70.67 (±4.86)

Organic matter ranged from 2 % to 3 % and was significantly higher in the clearcut than the other treatments in 2015 and 2016 (both $p<0.001$; Table 1). Total exchange capacity (TEC) was 6–11 meq/100 g; loams generally contain 15–30 meq/100 g. Total exchange capacity was significant each year ($p<0.02$), and clearcut soil TEC was higher than the other treatments (Table 1). In 2015 and 2016, estimated nitrogen release (ENR) differed significantly across treatments ($p<0.001$) and clearcut areas had significantly higher ENR than the other treatments (Table 1). Nitrate (NO_3-) ranged from 1 to 20 ppm, and ammonium (NH_4+) 1–7 ppm. The NO_3- relationship between canopy treatments was different every year and there was no significant difference in NH_4+ (Table 1). Ammonium:NO_3- ratio decreased each year. Phosphorus ranged from 28 to 50 ppm, and there was a significant effect of canopy treatment in 2016 ($p=0.047$; Table 1). The K range for the soils was 60–90 ppm. Potassium was significant in 2014 ($p<0.001$) and was higher in the clearcut than the other treatments (Table 1). The observed range of Ca was 300–500 ppm, and 15–45 % saturation (Supplemental Tables 1 and 3). The observed range for Mg was 50–100 ppm and 4–20 % saturation (Supplemental Tables 1 and 3). Overstory canopy treatment was significant (both $p<0.01$) for both Ca and Mg in 2014 and 2016, and the clearcut treatment values were significantly higher than the others (Supplemental Table 1). Copper, manganese, zinc, sodium, and sulfur results can be found in Supplemental Table 1.

3.2. Seedling growth response

Survival was high for both species (84 % on average) through the three growing seasons. For both northern red oak and American chestnut seedlings, there was a significant effect of overstory canopy and weeding treatments after three growing seasons (Table 2), but no statistical differences between treatments were detected.

At planting, mean American chestnut seedling height was 66.4

Table 2
Main effects of silvicultural/overstory canopy treatment, weed (competition control) treatment, and their interaction using repeated measures of time. For silvicultural/overstory canopy treatment, measurements are from spring 2014-fall 2016, and for weed treatment and the interaction, measurements are from spring 2015-fall 2016.

	Effect	Height (cm)	RCD (mm)	Survival (%)
Chestnut	Silv. treatmt.	**<0.001**	**<0.001**	**0.037**
	Weed treatmt.	0.065	**<0.001**	**0.003**
	Silv × Weed	0.051	0.094	0.960
Oak	Silv. treatmt.	**<0.001**	**<0.001**	**<0.001**
	Weed treatmt.	0.399	**<0.001**	**0.013**
	Silv × Weed	**0.002**	**<0.001**	0.100

(±1.3) cm, and northern red oak was 57.3 (±0.9) cm. After three growing seasons, mean chestnut height was 242.9 (±8.0) cm, and oak was 119.7 (±4.2) cm. Overstory canopy treatment significantly affected American chestnut seedling height (p<0.001), with seedlings in the shelterwood treatment taller than in the control or clearcut; and those in the clearcut taller than in the control (Table 2; Fig. 2). There was no effect of weeding or the interaction between canopy and weeding treatments on height for chestnut (Table 2). The interaction between canopy and weeding treatments was significant for oaks (P=0.002), with clearcut seedlings taller than uncut control seedlings regardless of weeding treatment, and no differences between the clearcut and shelterwood regardless of weeding. Seedlings in the shelterwood were taller than the uncut control only with weeding (Table 2; Fig. 2).

At planting in spring 2014, mean American chestnut seedling RCD was 6.7 (±0.1) mm and northern red oak RCD was 6.5 (±0.1) mm. After three growing seasons, mean seedling RCD was 27.1 (±1.1) mm for chestnut and 13.8 (±0.5) mm for oak. For chestnut seedlings, there was a significant effect of overstory canopy (p<0.001) and weeding treatments (p<0.001) but no interaction between canopy and weeding treatments (Table 2). After three growing seasons, chestnut seedling RCD was greatest in the shelterwood treatment, significantly more than in the clearcut and uncut control; and clearcut seedlings had

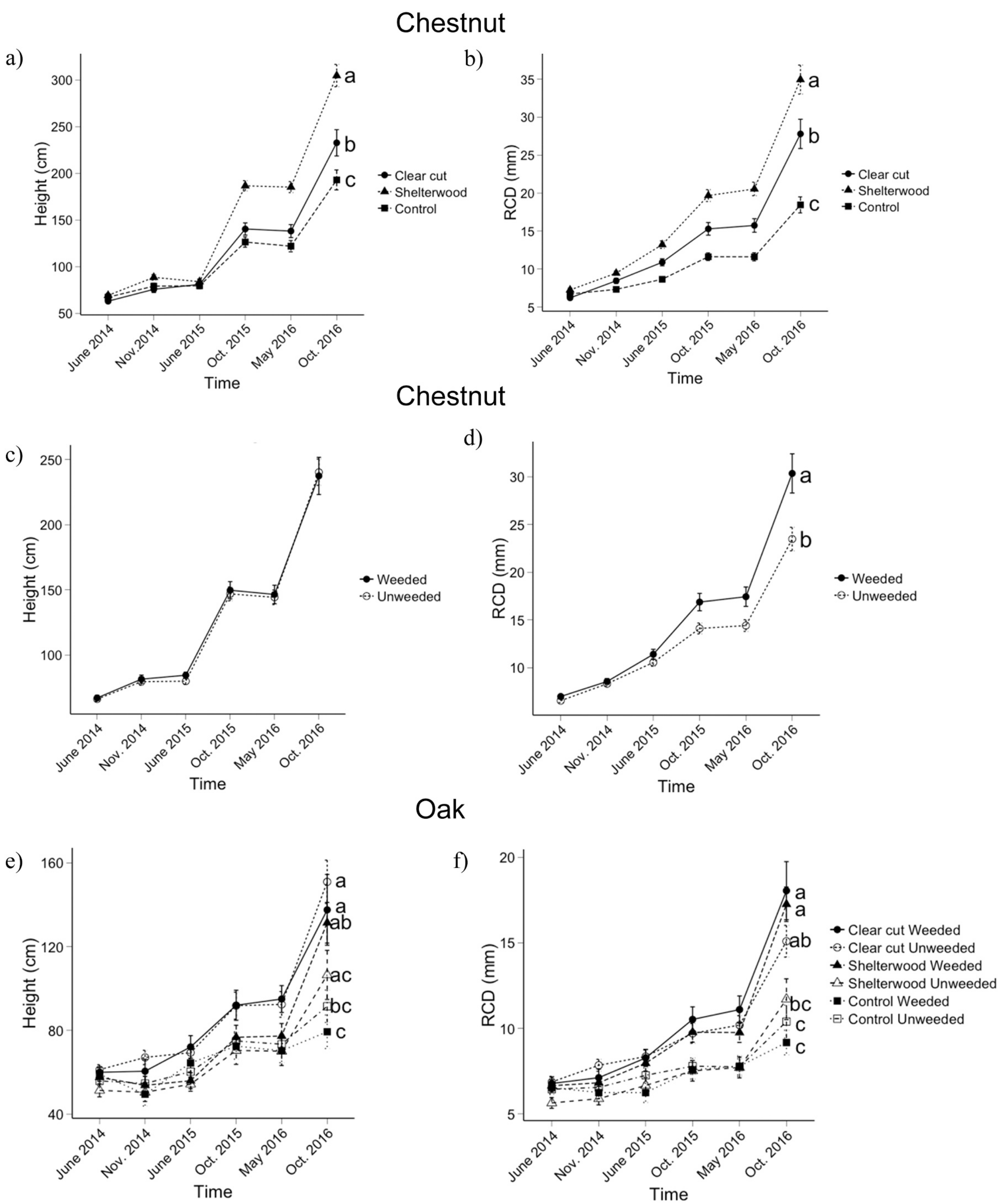

Fig. 2. Height and RCD ± standard error as affected by silvicultural/overstory canopy and weeding treatments. Different letters indicate significant differences among treatments per Tukey's HSD (α=0.05). Chestnut silvicultural/overstory canopy treatment effect on height (a) and RCD (b), chestnut weed treatment effect on height (c) and RCD (d), and oak overstory canopy-weed treatment effect on height (e), and RCD (f).

significantly greater RCD than the control (Fig. 2). Seedlings grown in the weeded treatment had significantly greater RCD than those in unweeded treatments (Table 2; Fig. 2). For northern red oak seedlings, the interaction between canopy and weeding treatments was significant ($p<0.001$, Table 2). Clearcut seedlings had greater RCD than the uncut control seedlings, regardless of weeding treatment. The clearcut treatment also had significantly greater RCD than the shelterwood unweeded treatment, regardless of weeding treatment. Shelterwood seedlings had significantly greater RCD than uncut control seedlings only with weeding treatment. The shelterwood weeded treatment had significantly greater RCD than the shelterwood unweeded treatment (Table 2; Fig. 2).

3.3. Seedling physiological response

For chestnuts in 2015, effect of overstory canopy treatment was significant for photosynthesis ($p<0.001$, Table 3); chestnuts in the clearcut treatment had higher assimilation than those in the uncut control and shelterwood (Fig. 3). There was no difference in photosynthesis between weeding treatments. Overstory canopy treatment also had a significant effect on stomatal conductance ($p=0.036$) and transpiration ($p<0.001$); with clearcut treatment seedlings having higher values than shelterwood and uncut control treatments (Table 3, data not shown). In 2016, there was a significant interaction between canopy and weeding treatments for photosynthesis ($p=0.015$, Table 3). Seedlings in the clearcut and shelterwood treatments had significantly higher photosynthesis than those in the uncut control when weeded (Fig. 3). But seedlings in the unweeded clearcut and shelterwood treatments did not differ from those in the unweeded control (Fig. 3). For conductance, canopy treatments were significant ($p<0.001$) with the control treatment seedlings having lower conductance than those in the clearcut and shelterwood, though the interaction of canopy and weeding treatments was marginally significant ($p=0.041$, Table 3, data not shown). The effect of overstory canopy treatment was significant for transpiration ($p<0.001$) with the control treatment seedlings having lower transpiration than those in the clearcut and shelterwood (Table 3, data not shown). When PAR-temperature combination was analyzed as a main effect for chestnuts in 2016, effect of overstory canopy treatment, PAR-temperature combination, and canopy-weeding treatment interaction were significant for photosynthesis, stomatal conductance, and transpiration (Supplemental Table 2). However, no statistical difference was detected between any treatments. Light response curves for chestnut photosynthesis in 2016 reflected treatment differences (Supplemental Fig. 2).

Overstory canopy treatment significantly affected northern red oak stomatal conductance ($p=0.004$) and transpiration ($p<0.001$), but not photosynthesis in 2015 (Table 3). There was not a significant difference between treatments for conductance, but clearcut leaves transpired significantly more than shelterwood and uncut control (data not shown). In 2016, effect of overstory canopy treatment was significant for oak seedling photosynthesis, stomatal conductance, and transpiration (all $p<0.001$, Table 3). Photosynthesis was significantly lower in seedlings in the uncut control treatment compared to shelterwood and clearcut (Fig. 3). Additionally, clearcut oak seedlings had greater conductance than uncut control, and clearcut and shelterwood leaves transpired more than uncut control (data not shown). When PAR-temperature combination was analyzed as a main effect for oaks in 2016, overstory canopy treatment had a significant effect on photosynthesis, stomatal conductance, and transpiration though no significant differences were detected between overstory canopy treatments (Supplemental Table 2). Seedlings subjected to the high PAR-temperature combination photosynthesized and transpired more than those subjected to the low combination ($p=0.020$). Light response curves for oak photosynthesis in 2016 also reflected treatment differences (Supplemental Fig. 2).

No treatments or their interaction had a significant effect on oak WUE in either year, or on chestnut WUE in 2015. Overstory canopy and weeding treatments significantly affected WUE of chestnut seedlings in 2016 (Table 3), but with no statistical difference between treatments.

For chestnut seedlings, overstory canopy treatment and canopy-weeding treatment interaction significantly affected plant moisture stress in 2015, but with no statistical differences between treatments (Table 3). For northern red oak seedlings in 2015 there were no significant treatment effects. Overstory canopy treatment effect was significant in 2016 but no statistical differences were detected between treatments (Table 3).

3.4. Foliar nitrogen

Foliar nitrogen concentration differed significantly among overstory canopy treatments for chestnut ($p=0.010$) and oak ($p<0.001$) in 2015, but not 2016 (Table 3). Seedlings in the clearcut had lower leaf N concentration than those in the shelterwood and uncut control for both species (data not shown). Neither overstory canopy treatment, weed control treatment, or their interaction had a significant effect on leaf concentration for either species in 2016 (Table 3).

Overstory canopy treatment significantly affected chestnut leaf nitrogen content in 2015 ($p=0.005$, Table 3), but there were no significant pairwise comparisons. Canopy treatments were again significant for chestnut in 2016 ($p<0.001$, Table 3), with leaves in the uncut control treatment having lower N content than those in the clearcut or

Table 3
LMM model testing the effects of light (df=2), weeding (df=1), and their interaction on American chestnut (a) and northern red oak (b) photosynthesis (A), stomatal conductance (g), transpiration (E), and WUE (water use efficiency; A/E), PMS (plant moisture stress; ψ), and leaf nitrogen concentration. Leaf N concentration was also measured in 2014, and effect of silvicultural/overstory canopy treatment was significant for both species (both $p<0.001$).

2015	Effect	A	g	E	WUE	PMS	Leaf N (%)	Leaf N (mg/leaf)
Chestnut	Silv. treat.	**<0.001**	**0.036**	**<0.001**	0.687	**0.043***	**0.010**	**0.005**
	Weed treat.	0.429	0.656	0.686	0.497	0.385	0.772	0.179
	Silv × Weed	0.114	0.185	0.212	0.707	**0.027**	0.150	0.119
Oak	Silv. treat.	0.586	**0.004**	**<0.001**	0.530**	0.607	**<0.001**	0.389
	Weed treat.	0.569	**0.006**	0.134	0.749	0.431	0.949	0.406
	Silv × Weed	0.138	0.369	0.594	0.220	0.374	0.906	0.085
2016	**Effect**	**A**	**g**	**E**	**WUE**	**PMS**	Leaf N (%)	Leaf N (mg/leaf)
Chestnut	Silv. treat.	**<0.001**	**<0.001**	**<0.001**	**0.001**	0.089	0.079	**<0.001**
	Weed treat.	0.367	0.514	0.884	**0.012**	0.810	0.733	0.405
	Silv × Weed	**0.015**	**0.041**	0.063	0.265	0.260	0.378	0.629
Oak	Silv. treat.	**<0.001**	**<0.001**	**<0.001**	0.430	**0.008**	0.645	0.988
	Weed treat.	0.509	0.506	0.452	0.907	0.403	0.516	0.729
	Silv × Weed	0.692	0.554	0.668	0.770	0.981	0.944	0.396

*=here the PMS was the average of two dates of measurement. For chestnut 2015, the second date did indicate a significant. Difference between light treatments.
**=for oak WUE in 2015, log transformation was required.

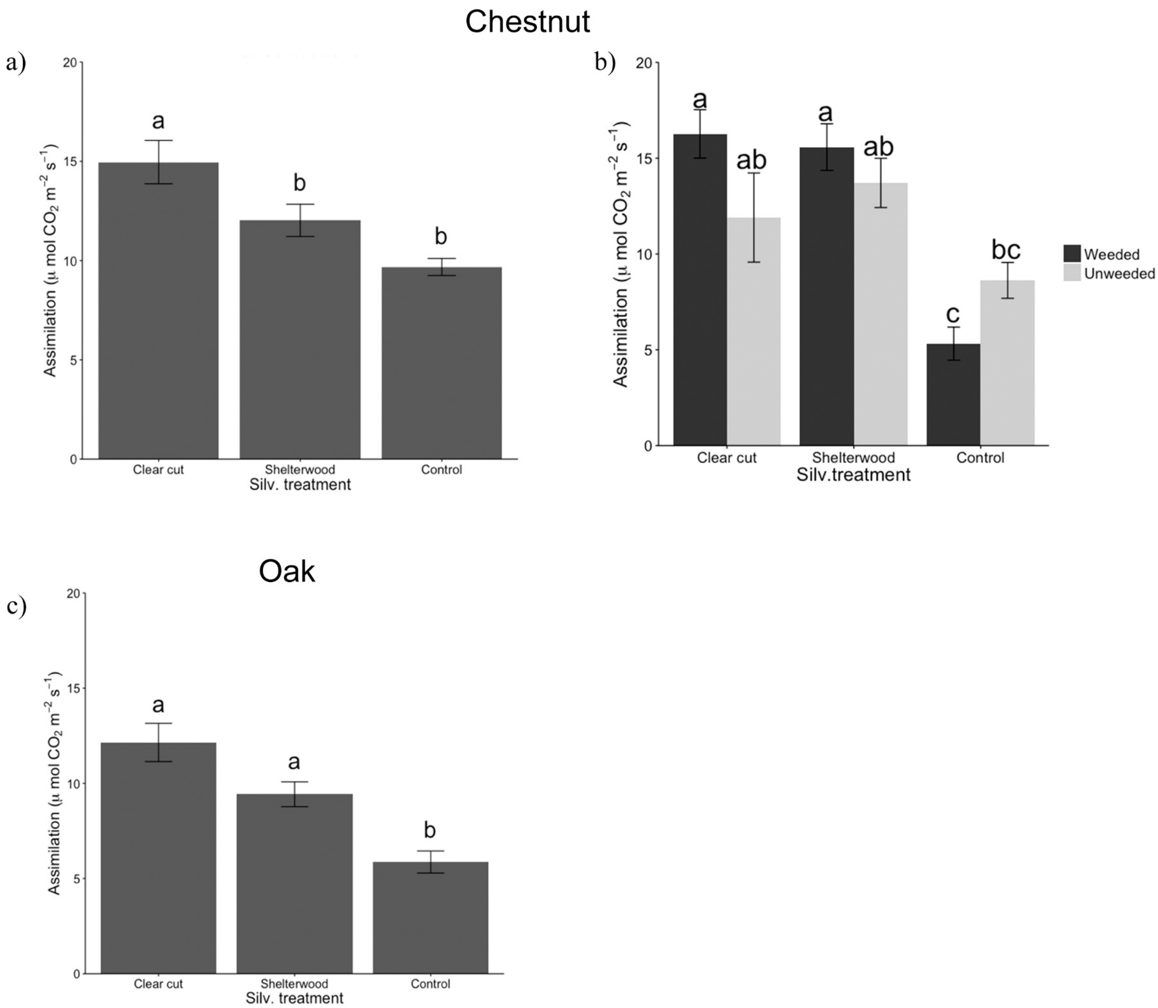

Fig. 3. Seedling photosynthesis at acclimated level of light ± standard error. Only significant results are shown (no significant effects in 2015 for oak, and no significant interaction for oaks in 2016 and chestnuts in 2015). Different letters indicate significant differences among treatments per Tukey's HSD (α=0.05). Chestnut photosynthesis in 2015 (a), chestnut photosynthesis in 2016 (b), and oak photosynthesis in 2016 (c).

shelterwood (data not shown). For oak, overstory canopy treatments were not significantly different for nitrogen content in either year. Weed control and overstory canopy-weeding treatment interaction were not significant (Table 3).

4. Discussion

4.1. Seedling response to overstory canopy treatments

American chestnut performed best in the shelterwood treatment as predicted. Several other studies have also observed higher rates of chestnut growth in intermediate light levels (McNab et al. 2003; McCament and McCarthy, 2005; Brown et al. 2014b). Anagnostakis (2007) found that chestnut seedlings grew better in 65 % shade than in full sun. Northern red oaks performed best in the clearcut treatment. Past studies have found similar results, and northern red oak is known to perform better in large canopy gaps and openings (Buckley et al. 1998; Morrissey et al. 2010). Both species had high survival (>84 %) exceeding that of operational hardwood plantings in Indiana (Jacobs et al. 2004), and there were no significant differences among treatments in survival.

Chestnuts in the clearcut treatment had consistently highest rates of photosynthesis during the second growing season in 2015 (Fig. 3). Other studies measuring chestnut gas exchange found greater net chestnut photosynthesis with increasing light availability (Wang et al. 2006; Joesting et al. 2007; Brown et al. 2014b). Oak photosynthesis was also significantly affected by overstory canopy in 2016, with uncut control seedlings having lower photosynthesis than the other treatments; microclimate measurements indicate this was largely due to PAR, not soil parameters. Stomatal conductance and transpiration of both species corresponded with growth and photosynthesis rates. For both species, photosynthesis in shelterwood and clearcut treatments was overall similar because both reached light saturation. Dey et al. (2008) reported that northern red oak reached saturation by 50 % canopy removal, ~550 μmol m^{-2} s^{-1} PAR, and here we found a saturation value of about 600–700 μmol m^{-2} s^{-1} PAR. Joesting et al. (2007) reported chestnut light saturation at 600 μmol m^{-2} s^{-1} and we found a similar saturation value of about 700–800 μmol m^{-2} s^{-1} PAR.

Leaf N concentration is directly linked to photosynthesis rates (Reich et al. 1998; Goodman et al. 2014). Nitrogen concentration in the three overstory canopy treatments was lowest in the clearcut treatment and highest in the uncut control for both species in 2015 (Table 3). Leaves of shaded seedlings allocate a greater proportion of leaf N to chlorophyll (Kubiske and Pregitzer, 1996). Higher leaf N concentration in the uncut control seedlings appears to contradict growth and photosynthesis results, in which clearcut and shelterwood seedlings outperformed uncut control seedlings. However, significantly higher chestnut leaf N content in the clearcut and shelterwood suggest that N dilution occurred in the faster growing seedlings of these treatments (Supplemental Table 4). Species with high rates of shoot growth such as chestnut exhibit strong correlation between leaf N content and light availability (Kaelke et al. 2001). Conversely, species like northern red oak that allocate more biomass to root growth exhibit no clear differences in leaf N content (Kaelke et al. 2001). The findings of this study agree with this past research (Supplemental Table 4).

4.2. Seedling response to weeding

Seedlings of both species responded to weed control with increased RCD but exhibited no height response. Diameter growth is often more responsive to vegetation control than height (Creighton et al. 1987; Miller et al. 1991; Jensen and Löf, 2017). Presumably, seedlings in the unweeded subplots allocated more biomass to height to compete with the tall herbaceous and woody competition (Grossnickle, 2012). Additionally, oak seedlings allocate more biomass to roots and root collar diameter in the absence of aboveground competition as an adaptation to surface fire and drought (Dey and Fan, 2009; Johnson et al. 2009). The same results were found in a similar study for northern red oak, but not for chestnut (Belair et al. 2014). Weed control did not have as much of an effect as overstory canopy treatment on seedling growth, possibly because the weed control treatment was not initiated until the start of the second growing season.

There was a significant height and RCD interaction between overstory canopy treatment and weed control treatment for oak but not for chestnut (though marginally significant; $p=0.094$ for RCD and $p=0.051$ for height, Table 2). This suggests that increased shade associated with canopy retention, such as in control or partial thinning, reduces understory vegetation growth, which in turn promotes seedling growth. Kolb et al. (1990) concluded the same in a similar examination of the relationship between shading and herbaceous cover.

The significant interaction of overstory canopy and weed control treatments in 2016 for chestnut seedling photosynthesis indicates that weeding positively influenced chestnut photosynthesis. Weed control was relatively more impactful in plots with more competition, i.e., clearcut. However, there was no significant impact of weeding on oak photosynthesis.

4.3. Seedling species comparison

Although we analyzed species separately, precluding statistical comparison between species, chestnut seedlings grew twice as quickly as oak, and had higher photosynthesis, leaf N concentration (2015 and 2016), and leaf N content (2015), corroborating results from past studies (Jacobs and Severeid 2004; Griscom and Griscom, 2012; Belair et al. 2014; Brown et al. 2014a; Lesko and Jacobs 2018). Chestnut has been called "an exception to the rule of environmental tradeoffs" with resource variation because it performs so well across a broad range of conditions (Latham, 1992).

Chestnuts performed best in the shelterwood, and oaks in the clearcut. Sufficient light availability is a critical factor for plant growth, so differences in PAR (clearcut> shelterwood> control; Fig. 1) explain much of the seedling growth variation between overstory canopy treatments. Our findings support chestnut's classification of having intermediate to high shade tolerance (Joesting et al. 2007, 2009; Wang et al. 2006).

Chestnut's dominance may be explained in part by its growth strategy. Much like tulip poplar (*Liriodendron tulipifera* L.) and red maple (*Acer rubrum* L.), it invests >70 % biomass in aboveground shoot growth, to decrease the likelihood of being overtopped (Latham, 1992; Groninger et al. 1996; Oliver and Larson, 1996). Oak (along with hickory (*Carya* spp.)), on the other hand, dedicates more biomass to belowground root growth (Johnson et al. 1986), surviving repeated understory disturbance until there is an opportunity to attain a canopy position (Johnson et al. 2009).

4.4. Seedling response to soils

Soil pH was acidic (mean 4.3–4.5, Table 1) which increases exchangeable soil Al, possibly leading to Al toxicity (Horneck et al. 2011). Low K and Ca and low base saturation percentages helped to explain the low pH (Supplemental Table 3). Potassium range for soils in this study was 60–90 ppm, and the normal range for K is 100–130 ppm for the total exchange capacity of these types of soils (Table 1; LaBarge and Lindsey, 2012). A typical cation saturation range for Ca is 40–80 %, and the observed range was 15–45 % saturation (LaBarge and Lindsey, 2012; Supplemental Table 3).

While many mesic tree species cannot tolerate these conditions, northern red oak and chestnut typically perform best in soils of pH 4–6 (Griffin, 1992; Rhoades, 2009; Johnson et al. 2009; Wang et al. 2013) and are adapted to the nutrient composition associated with low pH. Soil did not appear to be limiting. Chestnut sprouts are frequently observed in soils like those of this study (Paillet, 1988; Wang et al. 2013). Northern red oak also grows well in these somewhat poorer soils associated with pines (Johnson et al. 2009). Soil moisture was probably not limiting either, as PMS measurements did not reveal differences between treatments. Chestnuts performed best in the shelterwood, which had similar soil moisture to the uncut control where seedlings performed worst (Fig. 2). None of the soil nutrient results indicated that the uncut control treatment had lower nutrients than the other two canopy treatments, so this was likely not the reason for the reduced rate of growth and photosynthesis. Rather, soil in the uncut control was similar to that of the shelterwood (Table 1; Supplemental Table 1).

5. Conclusions and management implications

The results of this study suggest that a shelterwood or clearcut treatment would provide the most effective prescription for conversion of pine plantations to hardwoods. Similar results have been found in Europe, where large areas of Norway spruce (*Picea abies* L. Karst) have been converted to native broadleaves using shelterwood systems (Ammer et al. 2008). Underplanting into shelterwoods is also recommended for establishing oak regeneration in the eastern US (Dey et al. 2012). Shelterwoods of conifers can be unstable during major storm events (Löf et al. 2010), however, necessitating careful site selection and additional measures to stabilize the shelterwoods. For example, sites with less wind exposure may be prioritized, and forest edges facing the prevailing wind direction should remain uncut to protect the remainder of the stand from wind damage.

A shelterwood will promote less competition and therefore require less weed control compared to a clearcut. Reduction in understory competition led to an increase in seedling RCD, except in the uncut control plots where shade reduced weed competition. Weed control for at least one growing season is recommended, and weeding for more than one growing season adds further RCD benefits (Creighton et al. 1987; Jacobs et al. 2012) since competing vegetation height and cover regenerates rapidly in the seasons following treatment in this region (Jacobs et al. 2004). In this study, we used manual vegetation control rather than herbicide, but depending on objectives, herbicide could be similarly effective and a cheaper alternative although its use is controversial (Löf et al. 2012). Chestnut height and RCD were double to triple that of oak, and chestnut leaf N content increased with light availability while oak did not. These results can be explained by different adaptive strategies in biomass allocation between the two species; oak tends to allocate resources belowground and chestnut toward aboveground growth (Wang et al. 2006; Johnson et al. 2009).

American chestnut and northern red oak were well-suited to pine plantation characteristics, demonstrating pre-adaptation to the low pH and base saturation of cations of the soils. Pine plantation conversion thus represents a potential target site type for restoration of northern red oak and chestnut. Non-native pine plantations in the Midwestern US are unsustainable and non-profitable and will be replaced by natural regeneration of less valuable or invasive species, unless this opportunity is used to replace them with restoration of native hardwood species.

CRediT authorship contribution statement

Joshua Sloan: Writing – review & editing, Methodology, Conceptualization. **Jennifer Lesko:** Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Magnus Löf:** Writing – review & editing, Visualization. **Douglass Jacobs:** Writing – review & editing, Visualization, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

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.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122102.

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