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Ecological Factors Affecting White Pine, Red Oak, Bitternut Hickory and Black Walnut Underplanting Success in a Northern Temperate Post-Agricultural Forest

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Abstract: This study took place in southern Québec (Canada) where young stands of white ash and grey birch have been underplanted with white pine, red oak, bitternut hickory and black walnut. The establishment success of white pine and red oak was measured with and without tree shelters (to protect from deer). Ecological factors affecting the height growth of the four species were also measured for protected trees. After 6 years, the survival and total height of unprotected oak was 29% and 44.3 cm vs. 80.5% and 138.5 cm for protected oak. White pine was less affected by browsing (survival of 79.5 and 93.5%; height of 138.5 and 217.9 cm for unprotected vs. protected pine). Height of white pine was higher in the grey birch stands, while height of all hardwoods was higher in the white ash stands, which had better soil drainage, higher fertility, and an understory dominated by *Rubus* species. Total height of all hardwoods was significantly ($p < 0.05$) correlated with *Rubus* cover and with soil fertility. Pine and walnut height were strongly correlated ($p < 0.001$) to shelterwood structure (canopy openness or total basal area). Pine was less sensitive to variations in shelterwood characteristics, while black walnut showed high sensitivity. This study provides evidence that underplanting is suitable for black walnut assisted migration northward and for bitternut hickory restoration, despite soil conditions that were less favorable than in bottomland habitats mainly supporting these species in eastern Canada. Tree shelters offering protection from deer browsing and species-specific site selection are recommended for underplanting in the southern Québec region.

Keywords: tree shelter; deer browsing; hardwood restoration; assisted migration; enrichment planting; shelterwood; *Pinus strobus* L.; *Quercus rubra* L.; *Carya cordiformis* (Wangenh.) K. Koch; *Juglans nigra* L.

1. Introduction

In eastern North America, nut producing hardwoods (*Quercus*, *Juglans* and *Carya* spp.) and eastern white pine (*Pinus strobus* L.) are major components of temperate hardwood forest ecosystems for biodiversity, but also for the production of high-value timber [1–3]. In the southern Québec region (southeastern Canada), multiple ecological and human factors have contributed to the decline of these important species. Historically, white pine was among the first species to be overexploited following settlement, and therefore this species is now much less abundant than it used to be [4,5]. Early settlers also clearcut several butternut (*Juglans cinerea* L.) stands because this species was associated with high quality soils for agricultural use [4]. Besides, butternut is now threatened by the butternut canker (*Sirococcus clavigignenti-juglandacearum* Nair et al.), a virulent and deadly Asian fungal pathogen, which affects the species in all of its habitats [6].

The human control of forest fires is another factor that could have contributed to a reduction in the abundance of species that typically regenerate after fires including hickories, oaks and white pine [7–9]. Furthermore, in many regions of northeastern North America, the natural regeneration of several hardwood species and white pine is threatened by the overabundance of white-tailed deer (*Odocoileus virginianus* Zimm.), and changes in forest composition over the long-term are documented in areas supporting large deer populations [3,10–13]. Climate change is also expected to increase summer temperatures and lower soil water content in the southern Québec region, which could be detrimental to drought sensitive species, but potentially beneficial to drought tolerant species [14], including pines, hickories and oaks [15]. However, the migration of forest species into more suitable habitats is expected to occur at a slower rate than the rate of modification of regional climates [14], and the migration of bottomland species, such as hickories (*Carya cordiformis* (Wangenh.) K. Koch and *Carya ovata* (Mill.) K. Koch), may also be constrained by soil fertility factors in southern Québec [16].

Given the multiple past, present and future factors that will affect the regeneration and distribution of nut producing hardwoods and white pine, there is an urgent need to test restoration and/or migration strategies in the particular context of southern Québec. Field plantations have been often proposed for the restoration of white pine and nut producing hardwoods [17–19]. However, field plantations are often costly as they need site preparation (soil cultivation), intensive vegetation management (herbicide or mulch treatments) and tree pruning to achieve wood production objectives. In rural areas, the social acceptability of such plantations is often low because tree planting on cultivated land and old-fields competes with agricultural land use [20]. Furthermore, many stressors prevailing in open-field environments (high light, wind exposure, lack of mycorrhizal partners, herbaceous competitors, vole predation, etc.) can be detrimental to the planted species [18,21–23]. Although white pine has the ecophysiological capacity to become established in grasslands and old-fields [24], such environments increase its susceptibility to the pine weevil (*Pissodes strobi* Peck) and to the blister rust (*Cronartium ribicola* J.C. Fisch. ex Rabenh.) [25].

Underplanting (*i.e.*, enrichment or gap planting) in forest stands and tree plantations is a promising alternative to field plantations of oaks and white pine [3,25–32]. Such sylvicultural systems are often characterized by reduced abundance of grass species (Gramineae), which are strong competitors for nutrients and water [33]. Shelterwood environments can also contribute to hide seedlings from large herbivores such as deer [27], while being characterized by reduced populations of meadow voles, which are key consumers of tree seedlings in old-field habitats [22]. However, when deer populations are high in an area, tree shelters are generally required for successful underplanting [3,34]. Shelterwood environments can also increase the wood quality of more shade-tolerant species having high crown plasticity, by increasing height growth of the stem at the expense of lateral branch growth [35].

Past studies have identified several factors responsible for the success or failure of underplanting. For red oak (*Quercus rubra* L.) and white pine, two intermediate shade-tolerant species at the seedling stage [36,37], sufficient light availability in the understory is a critical factor to achieve optimal seedling development [25,30,31,34,38]. For oaks, the presence of shrubs (i.e., *Rubus* spp.) in the understory is believed to have an indirect facilitation effect on seedling growth by protecting trees from large herbivores and by eliminating other competing plants [34,39,40]. In terms of site selection, young early-successional stands of *Populus tremuloides* Michx. located on mesic fertile soils were found to be optimal for red oak [41]. Also, red oak tends to become established well in all topographic locations (*i.e.*, ridge, middle slope and valley) when underplanted [42]. Grey birch stands have equally been used for red oak underplanting, but such shelterwoods often have imperfect drainage conditions and poorly drained microsites [40,43], which are inadequate for red oak [44]. However, grey birch is often an associated forest cover species of white pine, which grows well on imperfectly drained sites [37]. In the understory, competition from shrubs and hardwoods is also an issue with white pine, given its slow growth rate at the seedling stage [37]. Initial competition from aspen suckers and later competition from shrubs and red maple (*Acer rubrum* L.) led to very high pine mortality in young thinned and unthinned aspen stands [45]. Conversely, mesic sites having a balsam fir mid-story prior to the shelterwood treatment were found to be adequate for white pine because they have reduced hardwood competition in the understory [46].

For species of the Juglandaceae very few studies have evaluated their potential in underplanting systems [28,47]. Moreover, limited information exists about the regeneration ecology of hickory species, especially at the northern limit of their range [9]. In southern Québec, only two hickory species are found (shagbark hickory, *C. ovata*, and bitternut hickory, *C. cordiformis*), but mostly in the bottomlands and on the moraine ridges of the St. Lawrence Valley where soil fertility is high [43,48,49]. Surprisingly, in both southern Québec and southern Ontario (Canada), poor growth and survival have been observed with bitternut and shagbark hickory in old-field plantations [17,50]. Yet, theory suggests that shelterwood cuts can be used to create advance hickory regeneration, but experimental evidence is lacking [51]. Observations made before 1935 further suggest that bitternut hickory had a wider distribution as it was frequently found in hilly landscapes of southern Québec where soil fertility is lower than in the St-Lawrence Valley [52]. Bitternut hickory individuals have been observed in different areas of the Precambrian Shield foothills (Outaouais and Laurentides regions in Quebec), where seepage increases soil moisture and nutrient availability on lower slopes [53,54]. This suggests that bitternut hickory could be suited for underplanting in upland habitats of southern Québec, providing soil richness and soil moisture are adequate.

Butternut is the sole species from the *Juglans* genus native to Québec, and it has been designated an endangered species following high mortality caused by the butternut canker [55]. Black walnut (*Juglans nigra* L.), which is native to nearby southern Ontario (Canada), has been suggested as a replacement species for butternut pending the development of resistant butternut hybrids or the identification of resistant individuals [41]. Black walnut is known for its high sensitivity to soil conditions, as it generally grows on deep, well-drained, nearly neutral pH, fertile and mesic soils [17,56,57]. Besides, black walnut generally requires very intensive and long-term weed control in old-field environments, otherwise growth stagnation may occur due to nitrogen limitation [58,59]. Compared to most hardwoods, black walnut flushes later in the spring and drops it leaves earlier in the fall, which allow herbaceous competitors to thrive for many years in the plantation understory [58,59]. This is a potential indication that black walnut may be more suitable in gap plantations where herbaceous competition is reduced. Yet, black walnut is relatively shade-intolerant [56], so competition for light by overstory trees may be an important growth-limiting factor in underplanting systems.

This study took place in southern Québec on a privately owned property where young stands of white ash and grey birch, originating from agricultural abandonment, have been underplanted with white pine, red oak, bitternut hickory and black walnut. In 1991, red oak had been successfully underplanted without protection from deer in such shelterwoods [27,41]. However, two decades ago, deer was less abundant than it had become when the present study was initiated in 2012 [60]. The first objective of this study was to evaluate if tree shelters are needed for the successful underplanting of white pine and red oak, two regionally important species. The second objective was to evaluate ecological factors, other than deer, affecting the height growth of underplanted white pine, red oak, bitternut hickory and black walnut after 6 years. Since red oak and white pine seedlings are heavily browsed in habitats supporting high deer populations [12,61], we hypothesized that both species will be responsive to the tree shelter treatment in terms of height growth and survival. We also hypothesized that black walnut will be the most responsive species to variations in shelterwood characteristics.

2. Materials and Methods

2.1. Study Site Description

The study site is located on the land of a Benedictine monastery at St-Benoît-du-Lac, in the Estrie administrative region of southern Québec, Canada (45°10′ N; 72°16′ W), a few km north of the Vermont (United States) border in the Appalachian geographic region (Figure A1). This 216 ha privately owned property has a 150 ha forested area composed of a complex mosaic of young and older successional stands, and some old growth stands, with most young stands originating from agricultural abandonment [41]. The study site is located on the western shore of Lake Memphremagog, a large lake (95.3 km^2) [62] within a wide north-south valley flanked by hills. Thick till generally underlays glacio-lacustrine deposits on these lakeside hills [63]. In the study area, forest ecosystems are dominated by hardwoods on mesic sites and by conifers on xeric and hydric sites [63]. The study area belongs to the sugar maple-basswood ecoregion of Québec [63], and more generally to the northern hardwoods forest ecosystem [64,65]. A continental subhumid moderate climate [63], with mean annual precipitation of 1260 mm and mean annual temperature of 5.3 °C, characterizes the study site [66].

In 2010, a vegetation analysis of the forested area was undertaken to identify the forest communities. Digital topographical and ecoforest maps, and aerial photos (orthophotos) were used. Using these sources of information and ArcGIS (Esri, Redlands, CA, United States), a set of parallel transects were used to determine the location of 71 permanent plots (20 m × 20 m), where vegetation, soil and site characteristics where measured. A Detrended Correspondence Analysis of the 71 forest vegetation plots was done and two community types presenting a high potential for white pine and hardwood underplanting where identified: (1) the White ash community type, which was located on mesic sites dominated by young forests regenerated on old-fields (average largest tree age = 47) and (2) the very young Grey birch-balsam poplar-elm community type that also has regenerated on old fields (average largest tree age = 40) (Figure 1). Mean total basal area (trees + saplings) was 30 m^2/ha for the White ash community type and 18 m^2/ha for the Grey birch-balsam poplar-elm community type. Additional details related to site description can be found in Truax et al. [41].

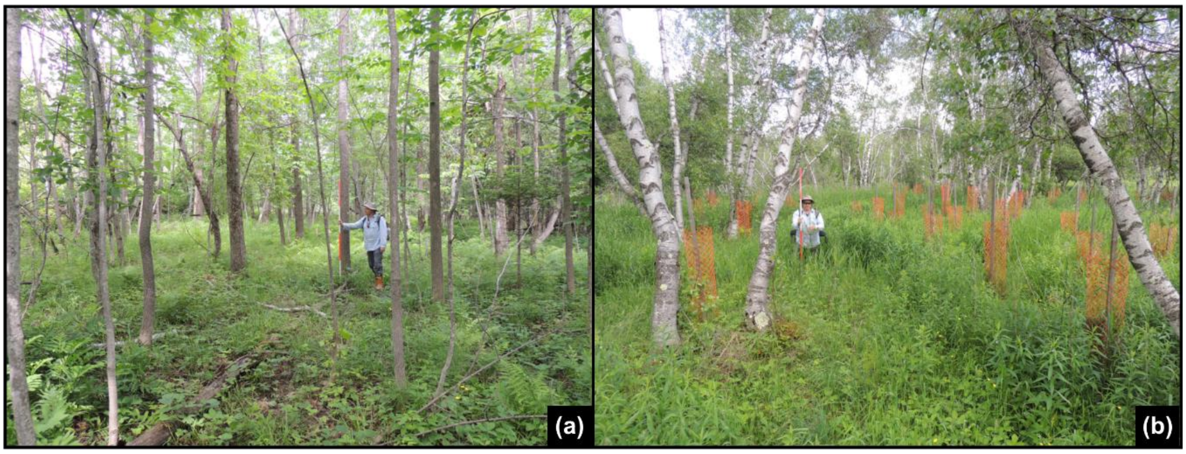

Figure 1. The two distinct forest community types used for underplanting: (**a**) the White ash community type and (**b**) the Grey birch-balsam poplar-elm community type.

2.2. Experimental Design

A complete randomized block design with 25 blocks and two factors (Tree species and Deer protection treatment) was established within the two selected forest community types. Among the 25 blocks, 8 were located in the White ash community type and 17 were located in the Grey birch-balsam poplar-elm community type. Each block measured 9 × 12 m and contained two species (red oak and white pine) and two deer protection treatments (a tree shelter treatment and a control treatment with no protection) for a total of 100 experimental plots (2 Tree species × 2 Deer protection treatments × 25 blocks). Each plot measured 4.5 × 6 m and contained 8 trees of a single species/treatment combination. In the middle of each plot, one bitternut hickory or one black walnut seedling was also planted, and these additional species were always protected with a tree shelter. Tree spacing was 1.5 × 2 m between all trees. Overall, the initial experimental design contained 400 red oak seedlings and 400 white pine seedlings, half of which were protected by tree shelters, but also 50 bitternut hickory seedlings and 50 black walnut seedlings, all protected by shelters. Figure 2 gives an overview of the experimental design.

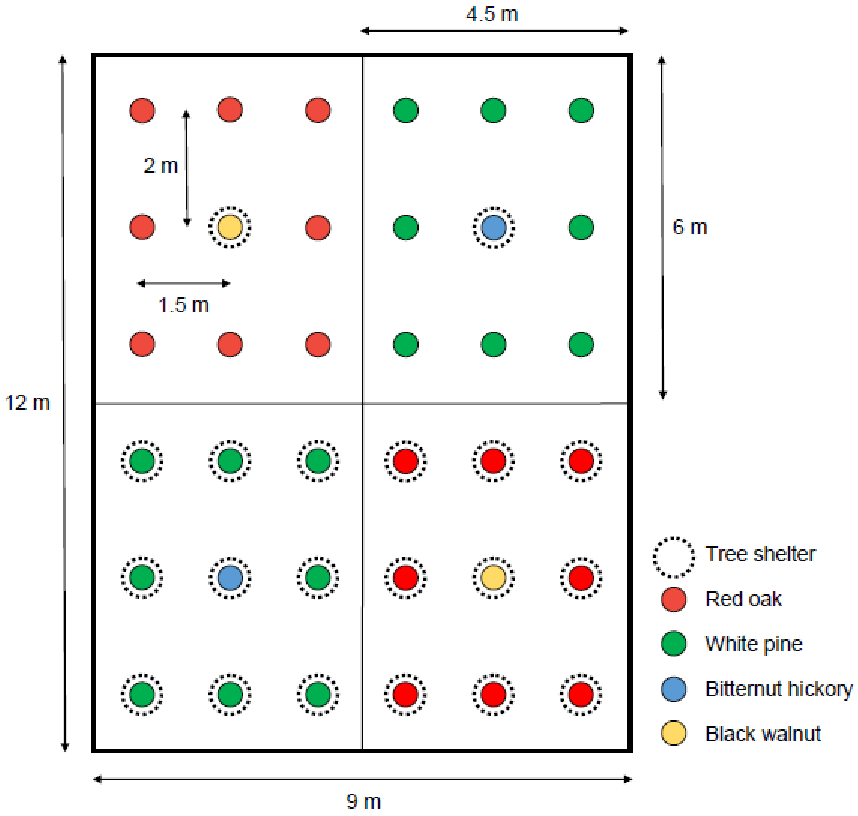

Figure 2. Schematic representation of a block with 4 experimental plots, one for each tree species (red oak or white pine)/deer protection treatments (tree shelter or control) combination. The position of each species/treatment combination was randomly assigned within each block. In the middle of each experimental plot, one bitternut hickory or one black walnut was planted and was protected with a tree shelter. The position of the two bitternut hickories and the two black walnuts within a block was always crisscrossed. The position of the first black walnut or bitternut hickory position was randomly assigned in the top left plot.

During the year preceding tree planting, a shelterwood cut was done in all blocks to increase light availability in the understory and remove overtopping trees located in the middle of the blocks. Large woody debris were also removed to facilitate the establishment of the experimental design. In early May 2012, all trees were planted manually and no vegetation treatment was done. Two-year-old bare root seedlings were used for red oak (2-0) and two-year-old container seedlings were used for white pine (2-0). One-year-old bare-root seedlings were used for bitternut hickory and black walnut (1-0). Height and basal diameter of seedlings at planting were respectively: 21 cm and 5.5 mm for white pine; 70 cm and 11.2 mm for red oak, 38 cm and 8.3 mm for bitternut hickory, and 48 cm and 9.8 mm for black walnut. Seedlings were provided by the Berthier nursery (Sainte-Geneviève-de-Berthier, QC) of the Ministère des Forêts, de la Faune et des Parcs (MFFP) of Québec.

During the week following tree planting, tree shelters were installed. Homemade tree shelters were conceived based on the model developed by Peter Kilburn (Model-K shelter), a private landowner who has successfully planted more than 5000 hardwoods on his property in southern Québec. The Model-K shelter was built using Vexar® construction plastic fence (MasterNet Ltd., Mississauga, ON, Canada), which has a mesh size of 5 × 5 cm. Fence sections approximately 1 m wide were cut, rolled and attached (using tie-wraps) to form a cylinder, which was then slid through a hardwood stake (2 m long above ground). Dimensions of the shelter were 120 cm in height by approximately 25–30 cm in diameter. The model-K shelter is ideal for underplanting because the large mesh size of the fencing material casts very little shade on the seedling compared to solid or small mesh-size commercial tree shelters developed for afforestation. As shown by Bardon et al. [67] the reduction in light availability caused by some commercial tree shelters can reduce the growth and survival of underplanted red oaks. The Model-K shelter can also be slid up on the wooden stake as tree height increases, which eliminates deer browsing of the main stem.

2.3. Measurements of Survival, Tree Growth and Deer Browsing

At the end of each growing season (except year 5), survival of each tree was recorded. In September of year 1 and 6 deer browsing on the main stem was evaluated for each living tree. Deer browsing data are expressed in percent data (number of browsed trees/number of trees alive × 100). In September of year 6, total tree height and basal diameter were measured on each living tree and DBH (1.3 m from ground-level) was measured when possible. For trees with no DBH, the simple cone volume formula was used to calculate stem volume [68]:

$$V = \pi\, D_B{}^2 H/12 \tag{1}$$

where V is the stem volume (cm^3), D_B is the basal diameter (cm) and H is the tree height (cm). For trees with a DBH value, the stem volume was measured by summing the volume of two stem sections (1) from basal diameter to DBH and (2) from DBH to tree tip. For stem Section 2, Equation (1) was used, but D_B was replaced by a DBH value and H was replaced by the height of the stem section from DBH to the tree tip. For stem Section 1, the following formula was used [69]:

$$V = \pi/12(D_1{}^2 + D_2{}^2 + D_1 D_2)\ L \tag{2}$$

where, V is the volume (cm^3) of a stem section, D_1 is the base diameter (cm) of the stem section, D_2 is the diameter (cm) at the top of the stem section, and L is the length (or height) of the stem section. Thus, the volume of stem Section 1 was measured by replacing D_1 by a basal diameter value, D_2 by a DBH value and L by 130 cm in Equation (2).

2.4. Measurements of Shelterwood Characteristics

Over the years it became obvious that the main factor affecting white pine and red oak growth and survival in the control treatment (no shelter) was deer browsing. Consequently, some ecological variables were only measured in the tree shelter treatment in order to evaluate which factors, other than deer, affect height growth. Descriptive statistics of ecological variables measured across the 25 blocks are presented in Table A1.

2.4.1. Overstory Structure and Composition

During summer 2012 (first growing season), residual basal area of all trees and saplings located within block boundaries was calculated using diameter at breast height (DBH, 1.3 m from ground-level) measurements. Since saplings (i.e., tree stems with DBH ranging 1.0–9.9 cm) were a minor component of the shelterwoods, their basal area was combined with the basal area of trees to form a single basal area index (i.e., total basal area) at the block level. Basal area was also calculated for dominant tree species (*Betula populifolia* Marsh., *Ulmus americana* L. and *Fraxinus americana* L.). In the center of each plot, hemispherical photographs were taken at the end of spring 2012. The camera was placed 90 cm above the ground level with its back always facing north. The same procedure was repeated once in the middle of the block position. Canopy openness data were obtained from hemispherical photographs using the software Gap Light Analyzer V 2.0 (Simon Fraser University, Vancouver, BC, Canada).

2.4.2. Relative Cover of Understory Vegetation

During August of the 6th growing season (2017), the relative vegetation cover in the understory was determined visually at the plot-level for the most abundant species, genera or functional group (i.e., *Rubus* spp., Gramineae spp., *Solidago* spp., *Carex* spp., *Fragaria virginiana* Duch., *Phalaris arundinacea* L. and *Onoclea sensibilis* L.). This sampling procedure was done only in plots of the tree shelter treatment.

2.4.3. Soil Characteristics

During summer 2012 (first growing season), a composite soil sample was collected in each plot (0–20 cm of depth). Soil samples were air dried and sieved (2 mm). Soil pH, clay, silt and sand content, percent organic matter, cation exchange capacity (CEC) and base saturation were determined by the Agridirect Inc. soil analysis lab in Longueuil (Québec). Methods used are those recommended by the Conseil des productions végétales du Québec [70]. The determination of soil pH was made using a 1:1 ratio of distilled water to soil. For particle size analyses, the Bouyoucos [71] method was used. Percent organic matter was determined by weight loss after ignition at 550 °C for 4 h. Cation exchange capacity and base saturation were calculated following the recommendations of the Centre de référence en agriculture et agroalimentaire du Québec [72], after Ca, K and Mg extraction with the Mehlich III method [73] and concentration determination using ICP emission spectroscopy [74]. Total soil C and N concentrations were determined by the combustion method at high temperature (960 °C) followed by thermal conductivity detection. These analyses were done by the CEF lab (Dr. R. Bradley and Dr. W. Parsons) at the University of Sherbrooke.

Soil macronutrient supply rates were determined using Plant Root Simulator (PRS^{TM}-Probes) technology from Western Ag Innovations Inc. (Saskatoon, SK, Canada). The PRS-probes consist of an ion exchange membrane encapsulated in a thin plastic probe, which is inserted into the ground with little disturbance of soil structure. Nutrient supplies observed with this method are strongly correlated with nutrients concentrations or stocks obtained with conventional soil extraction methods over a wide range of soil types [75]. On 22 June 2017 (6th growing season), four pairs of probes (an anion and a cation probe in each pair) were buried in the A horizon of each plot for a 41-day period. After probes were removed from the soil (2 August 2017), they were washed with distilled water, and returned to Western Ag Labs for analysis (NO_3, NH_4, P, K, Ca, Mg, S). Composite samples were made in each plot by combining the four pairs of probes. This sampling procedure was only done in red oak and white pine plots of the tree shelter treatment.

2.5. Statistical Analyses

2.5.1. Red Oak and White Pine Data

Main effects (Tree species and Deer protection treatment) and interaction effects (Tree species × Deer protection treatment) on measured variables were analyzed using two-way ANOVA in a fixed factorial design [76]. For survival data, the ANOVA was done with data from the 100 experimental plots (2 species × 2 treatment × 25 blocks = 100 experimental plots). However, for tree growth and main stem browsing data collected after 6 years, the ANOVA was done with data from only 21 blocks (84 experimental plots) given that no living red oak was found in the control treatment of 4 blocks. Following ANOVA, the normality of residuals was verified using the Shapiro-Wilk W-test. Survival data for year 4 were logit transformed to satisfy the ANOVA assumption of normality in residuals distribution [77]. However, all survival data are reported in percent values. Main effects or interaction effects were declared statistically significant for three levels of significance ($p < 0.05$, $p < 0.01$ and $p < 0.001$).

In this study, 8 blocks were located in the White ash community type and 17 blocks were located in the Grey birch-balsam poplar-elm community type (referred to as the Grey birch community in Tables). Thus, we evaluated if survival and height growth of white pine and red oak, in both treatments (deer protection and control), significantly differed between community types using Student's *t*-test. An individual *t*-test was done for each tree species/deer protection treatment combinations. Using the mean value at the block level for the different ecological variables (basal area, canopy openness, understory plant cover, soil characteristics), a *t*-test was also used to determine if ecological variables significantly varied between the two forest community types. All *t*-tests were run at an alpha level of 0.05.

To evaluate which ecological factors (measured as continuous variables) were significantly correlated with red oak or white pine total height after 6 years in the tree shelter treatment, a correlation matrix, with Pearson correlation coefficients (r), was used (Table A2). Linear and non-linear regressions between ecological factors and red oak or white pine height growth were then developed. Bivariate regression models were selected based on the normality of residuals distribution, which was evaluated using the Shapiro-Wilk W-test. Plot-level data were used for soil variables, understory plant cover variables and canopy openness, while block-level data where used for total basal area or species-specific basal area.

2.5.2. Bitternut Hickory and Black Walnut Data

The effect of tree species on growth and survival was analyzed using a one-way ANOVA in a fixed factorial design [76]. In each block, the two trees of a single species (bitternut hickory or black walnut) were considered as a plot in the ANOVA (see Figure 2). For survival data, the ANOVA was done with data from the 50 experimental plots (2 species × 25 blocks = 50 experimental plots). However, for tree growth data collected after 6 years, the ANOVA was done using data from only 23 blocks (46 experimental plots) given that no living black walnut was found in 2 blocks. We also evaluated if survival and height growth of bitternut hickory and black walnut significantly varied between forest community types using the Student *t*-test procedure for means separation. Using mean value at the block level for the different ecological variables, a correlation matrix, with Pearson correlation coefficients (r), was used to identify significant factors affecting height growth (Table A2). Linear and non-linear regressions between ecological factors and bitternut hickory or black walnut total height after 6 years were then developed. Models were selected based on the normality of residuals distribution, which was evaluated using the Shapiro-Wilk W-test. All statistical analyses were done using JMP 11 from SAS Institute (Cary, NC, United States).

3. Results

3.1. Effect of Tree Species and Deer Protection Treatments on Survival and Growth

For survival data of red oak and white pine, the two-way ANOVA showed significant ($p < 0.001$) Tree species × Deer protection treatment interaction effects for all years except year 1, where tree survival ranged 99%–100% across all species/treatment combinations (Figure 3a). After 6 years, the highest survival rate was observed for white pine in the shelter treatment (93.5%), while the lowest survival rate was observed for red oak in the control treatment (29%). Similar survival rates were observed for unprotected white pine (79.5%) and sheltered red oak (80.5%). Results from Figure 3a also show that tree mortality occurred gradually over the years for unprotected white pine and red oak. A significant Species effect on deer browsing of the main stem was observed for unprotected trees after 1 year, with 75% of red oak trees being browsed vs. only 0.5% for white pine (Figure 3b).

However, during the 6th growing season, deer browsing was recorded on about half of living trees for both species.

For growth data of red oak and white pine after 6 years, the two-way ANOVA showed significant Tree species and Deer protection treatment effects on total height, basal diameter and stem volume, but non-significant interaction effects (Figure 4). White pine growth was significantly higher than red oak growth across treatments, while the growth of sheltered trees was significantly higher than the growth of unprotected trees across species. After 6 years, the mean height of sheltered white pine and red oak was 217.9 cm and 138.5 cm, respectively, while the mean height of unprotected white pine and red oak was 146.3 cm and 44.3 cm, respectively. Stem volume of white pine was 55% higher in the shelter treatment compared to the control, while stem volume of red oak was 610% higher in the shelter treatment compared to the control.

For growth and survival data related to bitternut hickory and black walnut growing in tree shelters, the one-way ANOVA showed significant Tree species effects on survival rate, basal diameter and stem volume after 6 growing seasons (Table 1). While survival of black walnut was inferior to that of bitternut hickory (64% vs. 90%, respectively), stem volume of walnut was 5.5 times higher than stem volume of hickory. However, height growth of both species was similar after 6 years.

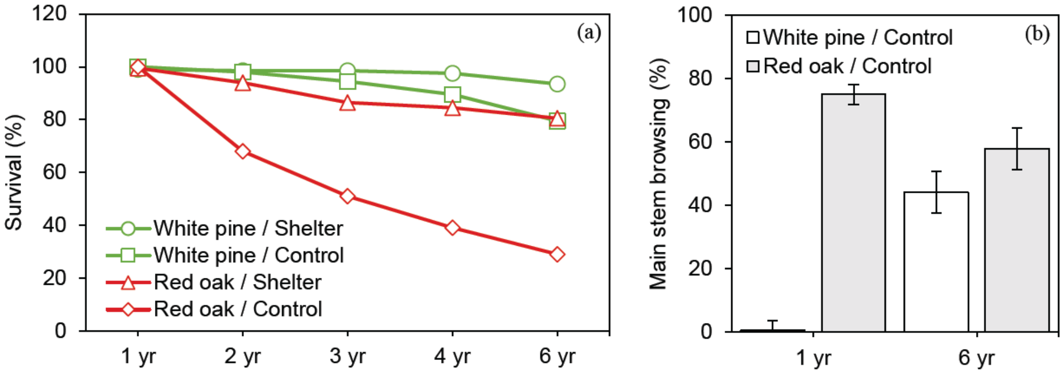

Figure 3. (**a**) Tree species × Deer protection treatment interaction effect on survival rate of underplanted red oak and white pine measured after 1, 2, 3, 4 and 6 years of growth in young forest stands. The interaction effect is significant ($p < 0.001$) for all years, except for year 1 ($p = 0.51$) and the standard error of the mean (SE) is 3.5% for year 6. (**b**) Tree species effect on deer browsing of the main stem of underplanted trees in the control treatment. The species effect on stem browsing is only significant for year 1 ($p < 0.001$).

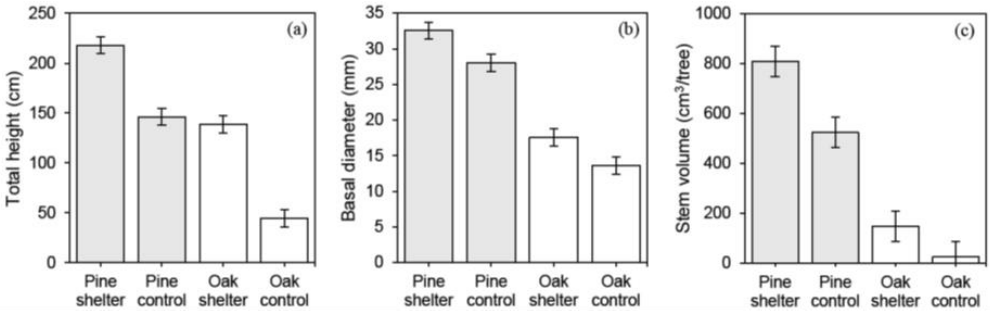

Figure 4. (**a**) Total height (**b**), basal diameter, and (**c**) stem volume of underplanted red oak and white pine in the tree shelter and control treatments (no deer protection) after 6 growing seasons in young forest stands. The interaction effect is not significant for total height ($p = 0.19$), basal diameter ($p = 0.81$) and stem volume ($p = 0.19$). The Species effect is significant at $p < 0.001$ for all variables. The Deer protection treatment effect is significant at $p < 0.001$ for total height and at $p < 0.01$ for basal diameter and stem volume. Pine = white pine and Oak = red oak.

Table 1. Tree species effect on survival, height, basal diameter, stem volume of underplanted bitternut hickory and black walnut after 6 growing seasons in young forest stands (all trees protected with shelters). SE = standard error of the mean.

Species	Survival (%)	Total Height (cm)	Basal Diameter (mm)	Stem Volume (cm^3/tree)
Bitternut hickory	90	162	16.4	158
Black walnut	64	171	27.6	862
SE	3.6	17	2.1	316
p-value	<0.001	0.74	<0.001	<0.05

3.2. Effect of the Forest Community Type on Ecological Variables, and on Tree Survival and Growth

Results from Table 2 show that the mean value of several ecological variables was statistically different between the White ash and Grey birch-balsam poplar-elm community types. Compared to the Grey birch-balsam poplar-elm community type, the White ash community type was characterized by a lower total basal area and canopy openness, but higher soil fertility in terms of soil NO_3 supply rate and CEC. The understory of the White ash community type was also characterized by a lower cover of Gramineae and *Solidago* species, but a higher cover of *Rubus* and *Carex* species.

After 6 years, the total height of the four tree species protected with tree shelters was statistically different between the two forest community types (Table 3). The three hardwood species were taller in the White ash community type, while white pine was taller in the Grey birch-balsam poplar-elm community type. In terms of magnitude, the total height of white pine was the least affected by the forest community type, while the total height of black walnut was the most affected (Table 3). After 6 years, the survival of sheltered white pine was also higher in the Grey birch-balsam poplar-elm community type (97.1% ± 2.4%) vs. the White ash community type (85.9% ± 3.4%), while the survival rate of sheltered hardwood species was not statistically different between forest community types.

For unprotected white pine, total height, survival and main stem browsing were also statistically different between the two forest community types after 6 years (Table 4). Unprotected white pines were taller, less browsed and had higher survival rate in the Grey birch-balsam poplar-elm community type, compared to the White ash community type. For unprotected red oak, total height, survival and stem browsing were not statistically different between the forest community types.

Table 2. Mean value (± standard error) of selected environmental variables in the two forest community types (N = 8 blocks in the White ash community type and N = 17 blocks in the Grey birch-balsam poplar-elm community type). All means are statistically different between community types at the α = 0.05 level following Student's *t*-test. d = days.

	Stand Structure		Soil		Understory Plants			
Community Type	Total Basal Area (m^2/ha)	Canopy Openness (%)	CEC (meq/100 g)	NO_3 Supply (µg/10 cm^2/41d)	Gramineae spp. (%)	*Rubus* spp. (%)	*Solidago* spp. (%)	*Carex* spp. (%)
White ash	10.8 ± 1.7	25.9 ± 1.8	18.5 ± 0.5	89.8 ± 13.6	5 ± 6	39 ± 4	25 ± 7	11 ± 2
Grey birch	16.3 ± 1.1	35.9 ± 1.2	16.4 ± 0.3	14.9 ± 9.3	26 ± 4	3 ± 3	45 ± 5	2 ± 1

Table 3. Mean total height growth (± standard error) after 6 years for underplanted tree species protected with tree shelters in the two forest community types (N = 8 plots in the White ash community type and N = 17 plots in the Grey birch-balsam poplar-elm community type for red oak, white pine and bitternut hickory. For black walnut, N = 8 plots in the White ash community type and N = 15 plots in the Grey birch-balsam poplar-elm community type. All means are statistically different between community types at the α = 0.05 level following Student's *t*-test.

Community Type	**Total Height of Sheltered Trees (cm)**			
	Red Oak	**White Pine**	**Bitternut Hickory**	**Black Walnut**
White ash	200.5 ± 23.1	192.8 ± 8.7	214.0 ± 20.0	287.9 ± 34.8
Grey birch	131.1 ± 15.9	230.4 ± 6.0	126.3 ± 13.7	108.0 ± 25.4

Table 4. Mean total height growth, survival rate and main stem browsing (± standard error) after 6 years for unprotected white pine in the two forest community types (N = 8 plots in the white ash community type and N = 17 plots in the Grey birch-balsam poplar-elm community type). All means are statistically different between community types at the α = 0.05 level following Student's *t*-test.

Community Type	**Unprotected White Pine**		
	Total Height (cm)	**Survival (%)**	**Stem Browsing (%)**
White ash	87.5 ± 14.1	59.4 ± 7.0	81.5 ± 6.7
Grey birch	163.5 ± 9.6	89.0 ± 4.8	34.5 ± 4.6

3.3. Relationships between Shelterwood Characteristics and Total Height after 6 Years for Red Oak, White Pine, Bitternut Hickory and Black Walnut Protected with Tree Shelters

For white pine, significant positive relationships were observed between canopy openness or the basal area of grey birch and total height, while soil CEC was found to be a significant negative predictor of total height (Figure 5). For red oak, significant positive relationships were observed between the cover of *Rubus* species or soil CEC and total height (Figure 6). For bitternut hickory, significant positive relationships were observed between the cover of *Rubus* species or soil NO_3 supply rate and total height, while a significant negative relationship was observed between the basal area of grey birch and total height (Figure 7). For black walnut, six ecological variables were found to be significantly correlated with total height (Figure 8). Soil NO_3 supply rate, soil CEC and the cover of *Rubus* species in the understory were positive predictors of walnut total height, while total tree basal area, the basal area of grey birch and the cover of Gramineae species in the understory were negative predictors of walnut total height (Figure 8).

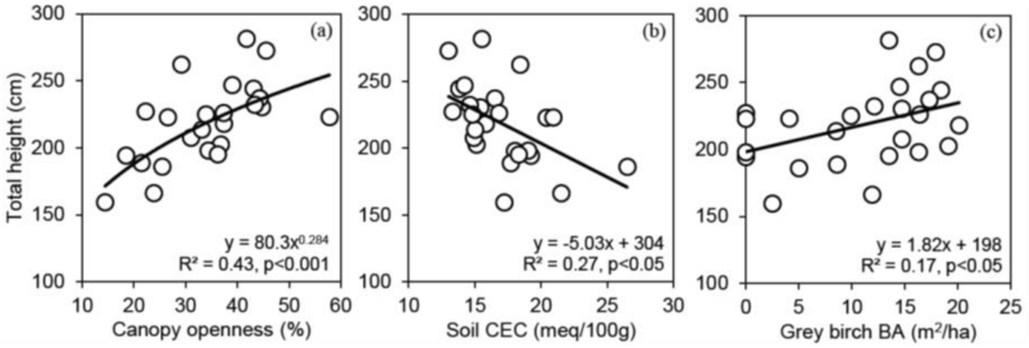

Figure 5. White pine (*Pinus strobus*) total height after 6 years in the tree shelter treatment as a function of (**a**) canopy openness, (**b**) soil cation exchange capacity (CEC) and (**c**) basal area (BA) of grey birch (*Betula populifolia*) in the overstory. N = 25 plots for each relationship.

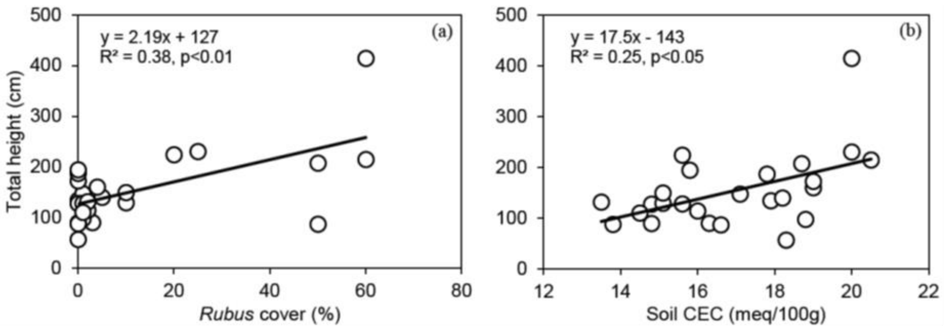

Figure 6. Red oak (*Quercus rubra*) total height after 6 years in the tree shelter treatment as a function of (**a**) cover of *Rubus* species in the understory and (**b**) soil cation exchange capacity (CEC). N = 25 plots for each relationship.

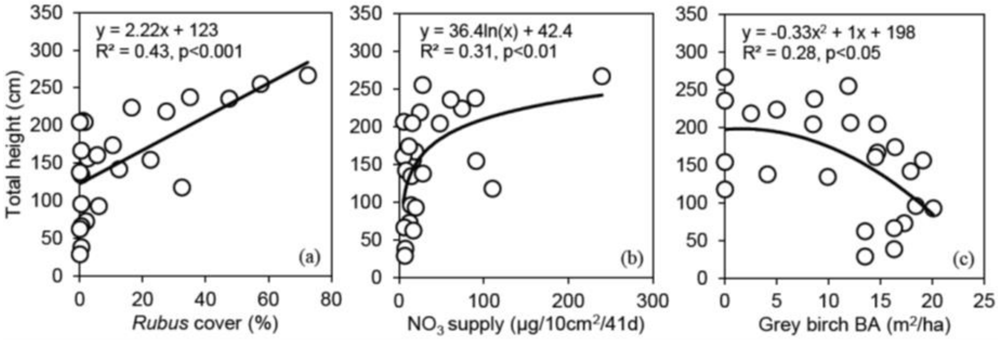

Figure 7. Bitternut hickory (*Carya cordiformis*) total height after 6 years as a function of (**a**) cover of *Rubus* species in the understory, (**b**) soil NO_3 supply rate and (**c**) the basal area (BA) of grey birch (*Betula populifolia*) in the overstory. N = 25 plots for each relationship.

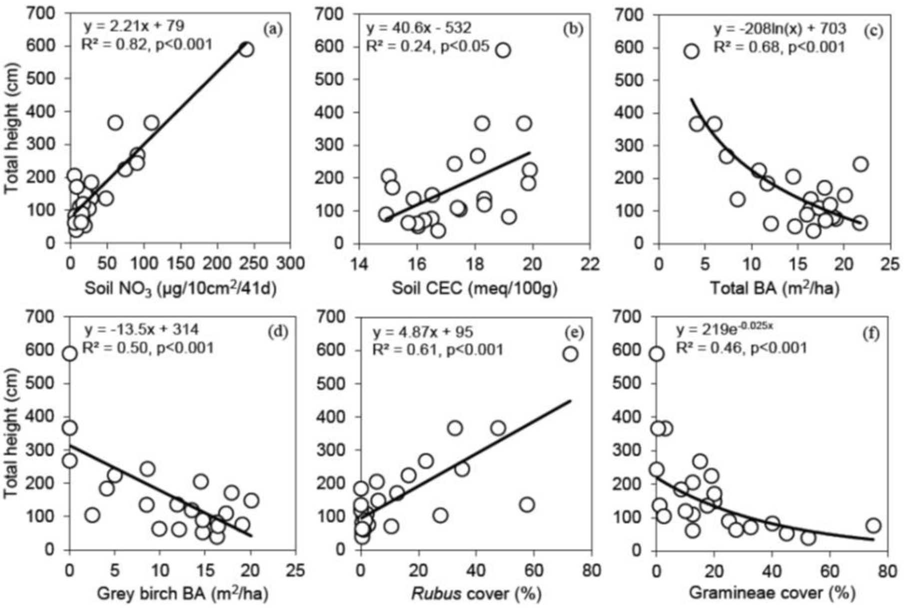

Figure 8. Black walnut (*Juglans nigra*) total height after 6 years as a function of (**a**) soil NO_3 supply rate, (**b**) soil cation exchange capacity (CEC), (**c**) total basal area (BA) of trees in the shelterwood, (**d**) basal area (BA) of grey birch (*Betula populifolia*) in the overstory, (**e**) cover of *Rubus* species in the understory and (**f**) total cover of grass (Gramineae) species in the understory. N = 23 plots for each relationship.

4. Discussion

4.1. Deer Impact on Red Oak and White Pine Survival and Growth

In northeastern North America, the overabundance of deer is a growing problem for the regeneration of several hardwood and coniferous species [3,10–12]. As hypothesized, the survival and growth of red oak and white pine were significantly decreased when these species were underplanted without tree shelters (Figures 3 and 4). Only 29% of unprotected red oaks survived after 6 growing seasons, and the average total height of survivors was lower (44.3 cm) than average seedling height at planting (70 cm). This contrasts with the high survival (80.5%) and total height (138.5 cm) achieved by red oak in the tree shelter treatment (Figures 3 and 4). Two decades ago, it was possible to achieve successful underplanting of red oak without tree shelters at the study site [27], however, this is no longer possible because of increased deer density.

For white pine, the impact of deer was less striking than for red oak (Figures 3 and 4). By the end of the first growing season, 75% of red oaks had their main stem browsed, while almost no deer browsing was observed on white pine seedlings (Figure 3b). Such a browsing pattern reflects the tendency of deer to browse heavily on deciduous species during the growing season, while conifers are more heavily browsed during the dormant season when other food sources are scarce [10]. Also, at planting, white pine seedlings were relatively small (21 cm of height) and less conspicuous in the understory vegetation, compared to taller red oak seedlings (70 cm). Small white pine seedlings were also protected by snow during the first winters (B. Truax, field observations). Thus, even though a similar proportion of red oaks and white pines had their main stem browsed during the 6th growing season (Figure 3b), the vulnerability of red oak to browsing was greater. However, browsing of white pine lateral branches in the control treatment remained severe despite that many 6 year-old trees had their terminal shoot above the browsing line (Figure 9a). Thus, even though pines had their lateral branches constrained in the tree shelters, this silvicultural treatment was highly efficient at increasing growth and survival (Figures 3, 4 and 9b). Furthermore, in the control treatment, no red oak was observed above the browsing line in June 2018 (7th growing season), which suggests that mortality induced by over-browsing will likely increase in the subsequent years.

Figure 9. (**a**) Heavy browsing on white pine lateral branches in the control treatment. (**b**) White pines in the tree shelter treatment growing in the Grey birch-balsam poplar-elm community type (6th growing season).

4.2. The Effect of Shelterwood Characteristics on Underplanted Tree Growth

After 6 years, the forest community type had an important effect on the total height of all hardwoods and white pine protected with tree shelters (Table 3). White pine was the only species with a higher total height and survival in the Grey birch-balsam poplar-elm community type (Table 3, Section 3.2, Figure 9b). White pine was also the species with the smallest total height difference between the two community types (Table 3), an indication of its wider ecological amplitude compared to the studied hardwoods.

Previous observations have shown that white pine grows well on imperfectly drained and lower fertility soils when no hardwood competition is present, with grey birch being an associated forest cover of this species [37,46]. White pine also has a very efficient nitrogen retention strategy, which allows its establishment in environments dominated by herbaceous vegetation, despite the strong competition for soil nitrogen [24,78]. Although white pine is intermediate in shade-tolerance [37], controlled and field experiments have shown strong positive relationships between canopy openness, gap size or light availability and seedling height or shoot biomass growth [79–81]. In this study the Grey birch-balsam poplar-elm community type had regenerated on an imperfectly drained old-field and was characterized by the lowest soil fertility, the highest canopy openness, an understory dominated by forbs and grasses, and the absence of hardwood competition in the understory and mid-story (Table 2). Thus, it is not surprising that white pine outcompeted the three hardwood species in the Grey birch-balsam poplar-elm community type since these hardwood species are very sensitive to competition from herbaceous species, and they generally require good drainage conditions and higher soil fertility to reach optimal growth [44,50,51,56,57,59,78]. Consistent with the community type effect observed on white pine growth, and previous knowledge about white pine ecology, the total height of this species in the shelter treatment was positively related to canopy openness and the basal area of grey birch, but negatively related to soil CEC (Figure 5). Also, because 17 of the 25 blocks of the experimental design were located in the Grey birch-balsam poplar-elm community type, it is not surprising that white pine had better overall growth and survival than red oak (Figures 3 and 4).

While canopy openness was strongly related to white pine total height in the shelter treatment ($R^2 = 0.43$, $p < 0.001$) (Figure 5a), no such significant relationship was observed between these two variables in the control treatment ($R^2 = 0.15$, $p = 0.06$). This suggests that deer browsing overrides the canopy openness effect on unprotected white pine growth, which contrasts with observations made in northern Wisconsin (United States) [81]. A possible explanation would be the potentially higher deer population density at our study site. Unprotected white pine also had significantly higher total height and survival in the Grey birch-balsam poplar-elm community type, with height and survival differences between the two community types being much larger for unprotected vs. sheltered pine (Tables 3 and 4). Because they had a slower height growth, white pines in the White ash community type were likely to be subjected to more intense and repeated browsing of their terminal shoots (Table 4).

In the northern hardwood forest ecosystem, red oak, bitternut hickory, black walnut and white ash are associated species in several habitats, while grey birch is generally not an associated forest cover of these species [44,49,51,53,54,56]. Accordingly, all hardwood species reached higher total height in the White ash community type (Table 3, Figure 10), where soil fertility was higher and the understory dominated by *Rubus* species, and not by grasses and forbs (Table 2). Consistent with this community type effect, the height of the three hardwood species was positively and significantly correlated with *Rubus* cover and with at least one soil fertility indicator (CEC or NO_3 supply rate), while bitternut hickory and black walnut total height was also negatively correlated with the basal area of grey birch in the overstory (Figures 6–8).

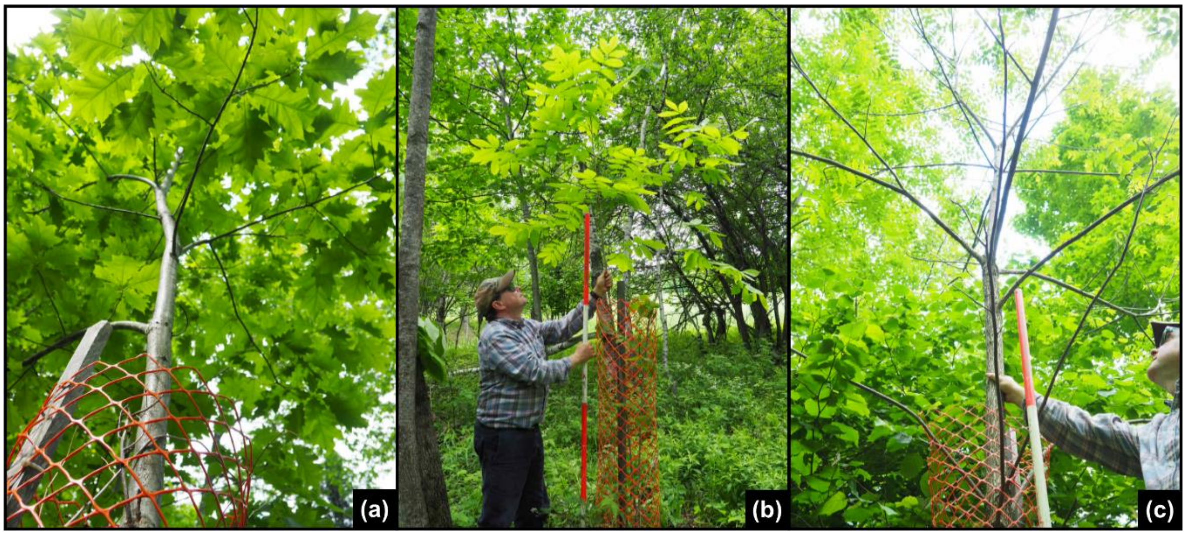

Figure 10. Underplanted hardwoods growing in the White ash community type at the beginning of the 7th growing season (early June 2018); (**a**) red oak, (**b**) bitternut hickory, and (**c**) black walnut.

Many authors have suggested that a moderate *Rubus* cover has a facilitating effect on underplanted oaks, because such a vegetation cover temporarily hides seedlings from large herbivores without being too competitive for light and nutrients [29,34,40]. Conversely, a dense *Rubus* cover under canopy gaps can interfere with red oak [81]. In this study, neither the height, the survival nor the main stem browsing of unprotected red oaks was statistically different between the two community types, which suggests little facilitating effect of *Rubus* in the White ash community type. At high deer densities, *Rubus* species are also severely browsed [13], potentially reducing their sheltering effects on hardwood seedlings. On the other hand, habitats supporting *Rubus* species regionally have fairly good soil drainage [82], and relatively high soil fertility in terms of NO_3 availability given that *Rubus* species are nitrophilous [83]. Such soil conditions are beneficial to the studied hardwoods [51,57], despite that red oak, black walnut and hickories have a slight preference for NH_4 uptake [84–86]. Being highly sensitive to grass competitors, the studied hardwoods [50,59,87,88] may also benefit from the reduction in herbaceous plant cover following understory colonization by *Rubus* species [81].

Among the studied species, black walnut is probably the most sensitive to competition for soil resources by herbaceous vegetation. A negative relationship ($R^2 = 0.46$, $p < 0.001$) between Gramineae cover in the understory and total height was observed for black walnut (Figure 8f), but not for the other hardwoods. The strong and steep negative relationship ($R^2 = 0.68$, $p < 0.001$) between total basal area and total height of black walnut (Figure 8c) is consistent with its shade-intolerance [56]. On the other hand, canopy openness or total basal area were not correlated with total height of red oak and bitternut hickory, suggesting that competition for light by shelterwood trees was not a strong factor affecting these moderately shade-tolerant species [9,36,51].

As hypothesized, black walnut was the most sensitive species to environmental conditions prevailing in the studied shelterwoods, with six ecological factors being significantly related to its total height after 6 years (Figure 8). Among trees growing in shelters, black walnut was also the species with widest total height difference between the two community types (Table 3), and the lowest survival rate (64%). Such results are consistent with the relatively narrow niche occupied by black walnut at the northern limit of its range, where it mostly regenerates in open forest habitats on rich soils of well-drained bottomlands [43].

A potential limitation of this study pertains to the physical constraint of the shelters on tree architecture and development. The use of fence enclosures around plots would have allowed unrestricted tree development, and a potentially more accurate quantification of ecological factors affecting growth.

4.3. Management Implications for Forest Restoration and Hardwood Species Migration

This study is the first to document the major impact of deer on underplanted red oak and white pine in the southern Québec region. Moreover, to our knowledge, few studies have documented the establishment success of underplanted black walnut and bitternut hickory in the northern hardwood forest ecosystem. Despite the fact that conclusions from this study where only drawn from a single site, several management implications should be considered in the context of forest restoration and tree species migration into more northern forest ecosystems.

Considering that high deer densities are now common throughout the southern Québec region [89], it is clear from this study that without protection from deer, red oak restoration in young forest ecosystems will be challenging (Figures 3 and 4). The deer browsing situation in the study area is of lesser concern for white pine, although the use of tree shelters resulted in a 14% increase in survival and a 49% increase in total height after 6 years. While underplanted white pine grows much slower than it does on clearcut sites [3], open sites produce pines with a large branch biomass, which adversely affects wood quality [25]. Moreover, open sites increase vulnerability to damaging agents such as the white pine weevil, which affects the terminal shoot and leads to excessive branching [25]. Large openings or 50% canopy cover are thus recommended to maintain good growing conditions (Figure 5a), early branch self-pruning, and reduced damages by the blister rust and the pine weevil [25]. In southern Québec, many grey birch stands have regenerated on imperfectly drained pasture sites and along riparian corridors located on farmland (B. Truax and J. Fortier, personal observations). These grey birch stands could be targeted for white pine restoration.

For the studied hardwoods, we found that the mesic White ash forest community type was a more suitable shelterwood than the grey birch stands. Thus, white ash stands could be targeted for hardwood restoration, as white ash is an important forest associate of many northern hardwood species [90]. Moreover, considering that the emerald ash borer (*Agrilus planipennis* Farmaire) will very likely continue to spread in southern Québec, canopy gaps created following white ash mortality could provide suitable light conditions for hardwood underplanting.

This study provides rare evidence that underplanting can be suited for bitternut hickory and black walnut, two species often growing poorly in open environments where the soil has been strongly disturbed (e.g., old-fields and mined land) [17,50,58,59,91]. In the province of Québec (Canada), bitternut hickory stands are mostly found in the St-Lawrence Valley and on the Precambrian Shield foothills [43,48,49,53,54]. However, bitternut hickory is not found in the mountain forests of northern New England (United States), just south of the study site (Figure 1A) [51]. Yet, this study supports the notion that this species has the potential to grow on mesic sites of the Québec Appalachians, as depicted by the distribution map of *Carya* species made by Marie-Victorin in the early 1900s [52].

It was recently proposed that migration of bitternut and shagbark hickory will be constrained by soil fertility in the province of Québec [16]. However, in the eastern United States, the recent landscape and stand scale analysis of Lefland et al. [9] has shown that dry, acidic, and nutrient-poor sites favor the establishment of hickories. Moreover, at the northern limit of its range, on the Precambrian Shield foothills of the Outaouais region (Québec), bitternut hickory has been found in association with red oak and white oak (*Quercus alba* L.) on steep slopes having thin, nutrient-poor and dry soil, with pH ranging 3.9–4.7 [53]. Thus, there is no reason why bitternut hickory should not be underplanted in the Appalachian region of southern Québec, especially in a context where soil water content of forest ecosystems is expected to decline regionally with climate change [14]. Additional studies are also needed to evaluate the growth potential of shagbark hickory (*Carya ovata*) in the study area given that bitternut and shagbark hickories are associates on upland sites [9,51].

This study provides the first evidence of establishment success of black walnut in forest ecosystems located northward of its natural range. Black walnut growth was correlated to numerous ecological factors (Figure 8), an indication that proper site selection will lead to successful underplanting. Being shade-intolerant, black walnut may require larger canopy gaps than red oak or bitternut hickory to maintain good growth potential at the juvenile stage. In southern Illinois (United States), black walnut planted in 20 m^2 clearcut gaps achieved more than 90% survival after 7 years, but annual herbaceous vegetation control was necessary to achieve good growth (height > 5 m) [92].

In southern Québec, many post-agricultural forests have little hardwood regeneration because of over-browsing and/or of a lack of seed sources in the surrounding landscape [89,93,94]. While such a situation is worrisome for forest ecosystem integrity and resilience, it creates ideal conditions to underplant oak and white pine, which are adversely affected by tall hardwood competition (>1.5 m) in the understory [37,45,46,95]. Moreover, as shown by Lucas et al. [96], increased nutrient inputs through deer fecal and urine deposits along with competition reduction caused by deer browsing, had a positive effect on the growth rate of mature red oak. Thus, if trees are protected by shelters, they will likely have good growing conditions in the post-agricultural forests of southern Québec.

The type of tree shelter (Model-K) used was well-suited for underplanting because very little light is intercepted by the fencing material (Figures 9b and 10). Smaller mesh size or opaque commercial tree shelters have been found to have little positive effect on white pine in open environments, and to even have negative effects on underplanted red oak [67,97]. Yet, the large mesh size (5 cm) of the fencing material allowed some leaves and branches to grow outside the shelter and therefore be browsed by deer. Besides, during the 6th growing season, we had to replace many rotten stakes. If not replaced in a timely manner, rotten stakes break with snow packing and wind, and the shelter falls on the ground with the tree it contains. Such an occurrence was observed in the spring of the 7th growing season in blocks exposed to the dominant wind (B. Truax and J. Fortier, field observations). Lifting up the fencing material on the wooden stake is also recommended to maintain protection of the terminal shoot. Freeze and thaw cycles, and probably deer collisions, also reduced the stability of the wooden stakes, which had to be hammered down on a few occasions during the 6 years of the experiment. Ideally, to reduce shelter maintenance, we recommend the use of metal stakes.

5. Conclusions

This study showed that the use of tree shelters against deer browsing was essential to successfully establish underplanted red oak in southern Québec, where deer densities above 20 individuals/km^2 are now common in many areas [89]. Unprotected white pine achieved satisfactory growth, but the use of tree shelters was clearly beneficial.

Distinctive growth response for white pine and hardwoods (growing in tree shelters) was observed between the two forest community types underplanted. White pine achieved higher total height in the Grey birch-balsam poplar-elm community type, while hardwoods reached higher total height in the White ash community type, which was characterized by a better soil drainage, higher soil fertility, and low herbaceous competition. The height growth of all hardwoods was positively correlated with at least one soil fertility indicator, and with the cover of *Rubus* species, while the height growth of white pine was negatively correlated to soil fertility and positively correlated to canopy openness. Across the two community types, white pine had the smallest growth variation, while black walnut had the largest. Moreover, black walnut had the largest number of ecological factors significantly correlated with its total height, with the strongest relationships being observed with shelterwood total basal area and soil NO_3. This suggests that site selection for underplanting should be species-specific.

Lastly, underplanting was found to be a suitable method for starting black walnut migration northwards and for bitternut hickory restoration. Within the global change context, additional studies are required to determine the optimal shelterwood environments for black walnut and hickories at, or beyond, the northern limit of their actual range, given their high-value for biodiversity and timber production. White ash mortality induced by the emerald ash borer may provide suitable shelterwood conditions to restore or introduce nut producing hardwoods.

Author Contributions: B.T. and D.G. conceived and designed the experiment. B.T., F.L. and M.-A.P. were involved in sampling design and field sampling. J.F., B.T., F.L. and M.-A.P. analyzed the data. J.F. wrote the first draft of the manuscript. B.T., D.G., and F.L. critically revised the manuscript.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

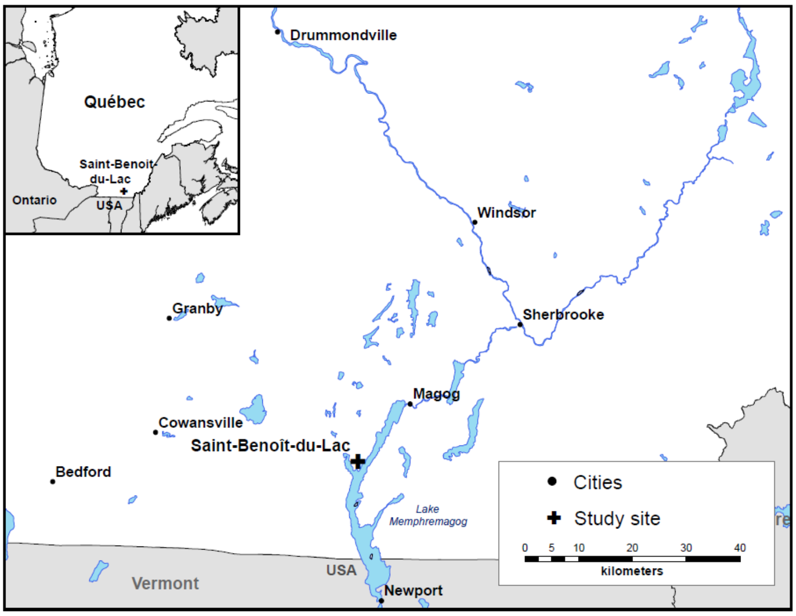

Figure A1. Study site location in southern Québec, Canada.

Table A1. Descriptive statistics for the ecological variables measured across all blocks. For each variable, descriptive statistics where obtained from block averages (N = 25 blocks).

Component	Variable [1]	Min.	Max.	Median	Mean	Std. dev.
Soil	pH	4.7	5.6	5.3	5.3	0.2
	CEC (meq/100 g)	14.3	19.9	16.7	17.1	1.7
	Base saturation (%)	31.0	58.7	45.4	45.3	8.1
	NO_3 (μg/10 cm^2/41d)	4.9	239.6	16.7	38.8	51.8
	NH_4 (μg/10 cm^2/41d)	3.0	39.0	4.4	5.9	7.0
	P (μg/10 cm^2/41d)	1.1	8.7	2.8	3.1	1.7
	K (μg/10 cm^2/41d)	7.4	92.4	26.4	34.1	22.3
	Ca (μg/10 cm^2/41d)	1561	2384	2095	2040	228
	Mg (μg/10 cm^2/41d)	286	567	432	430	64
	S (μg/10 cm^2/41d)	17	128	55	58	27
	Organic matter (%)	6.9	13.4	10.6	10.3	1.6
	C/N	9.4	12.0	10.8	10.8	0.7
	Clay (%)	0	62	26	30	13
	Silt (%)	18	83	44	44	11
	Sand (%)	0	58	29	26	11
Stand structure and composition	Canopy openness (%)	20.8	46.2	34.0	32.7	6.9
	Total BA (m^2/ha)	3.5	21.8	16.3	14.5	5.3
	Betula pop. BA (m^2/ha)	0	20.1	13.5	11.0	6.7
	Ulmus am. BA (m^2/ha)	0	11.8	0.0	1.2	3.1
	Fraxinus am. BA (m^2/ha)	0	10.8	0.0	1.0	2.6
Understory plant cover	*Rubus* spp. (% cover)	0	73	3	14	20
	Gramineae spp. (% cover)	0	75	15	19	18
	Solidago spp. (% cover)	8	80	38	38	21
	Fragaria virginiana (% cover)	1	45	18	20	13
	Carex spp. (% cover)	0	28	2	5	7
	Phalaris arundinacea (% cover)	0	33	5	9	10
	Onoclea sensibilis (% cover)	0	16	0	3	4

1. Abbreviations used in Table A1: CEC (cation exchange capacity), BA (basal area), pop. (*populifolia*), am. (*americana*), min. (minimum value), max. (maximum value), std. dev. (standard deviation), d (days).

Table A2. Correlation matrix between total height after 6 years for the four studied tree species and selected ecological variables.

Red oak	Total height	*Rubus* cover	Soil CEC				
Total height	**1.00**	**0.61**	**0.50**				
Rubus cover	**0.61**	**1.00**	**0.49**				
Soil CEC	**0.50**	**0.49**	**1.00**				
White pine	Total height	Canopy openness	Soil CEC	Grey birch BA			
Total height	**1.00**	**0.60**	**−0.52**	**0.41**			
Canopy openness	**0.60**	**1.00**	−0.29	**0.49**			
Soil CEC	**−0.52**	−0.29	**1.00**	**−0.40**			
Grey birch BA	**0.41**	**0.49**	**−0.40**	**1.00**			
Bitternut hickory	Total height	*Rubus* cover	Soil NO_3	Grey birch BA			
Total height	**1.00**	**0.65**	**0.48**	**−0.50**			
Rubus cover	**0.65**	**1.00**	**0.76**	**−0.62**			
Soil NO_3	**0.48**	**0.76**	**1.00**	**−0.70**			
Grey birch BA	**−0.50**	**−0.62**	**−0.70**	**1.00**			
Black walnut	Total height	Soil NO_3	Soil CEC	Total BA	Grey birch BA	*Rubus* cover	Gramineae cover
Total height	**1.00**	**0.91**	**0.49**	**−0.72**	**−0.71**	**0.78**	**−0.57**
Soil NO_3	**0.91**	**1.00**	**0.45**	**−0.67**	**−0.69**	**0.75**	**−0.43**
Soil CEC	**0.49**	**0.45**	**1.00**	**−0.42**	**−0.59**	**0.46**	−0.34
Total BA	**−0.72**	**−0.67**	**−0.42**	**1.00**	**0.76**	**−0.48**	0.40
Grey birch BA	**−0.71**	**−0.69**	**−0.59**	**0.76**	**1.00**	**−0.60**	**0.61**
Rubus cover	**0.78**	**0.75**	**0.46**	**−0.48**	**−0.60**	**1.00**	**−0.57**
Gramineae cover	**−0.57**	**−0.43**	−0.34	0.40	**0.61**	**−0.57**	**1.00**

Correlation coefficients (r) in bold are significant at $p < 0.05$.

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