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Effect of Predation, Competition, and Facilitation on Tree Survival and Growth in Abandoned Fields: Towards Precision Restoration

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Received: 8 September 2018; Accepted: 1 November 2018; Published: 7 November 2018

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Abstract: Tree seedlings planted in abandoned agricultural fields interact with herb communities through competition, tolerance, and facilitation. In addition, they are subject to herbivory by small mammals, deer or invertebrates. To increase the success of forest restoration in abandoned fields and reduce management costs, we should determine which species are tolerant to or facilitated by herbaceous vegetation and those which require protection from competition and predation. Eight native tree species were planted in plots covered by herbaceous vegetation, plots where herbaceous vegetation was removed, and plots where seedlings were surrounded by an organic mulch mat. Half of the seedlings were protected against small mammal damage. Results showed that two non-pioneer and moderately shade-tolerant species (yellow birch and red oak) were inhibited by herbaceous vegetation. Birch species were particularly affected by small mammal predation. No effects of predation or herbaceous competition were observed for conifer species. Rather, herbaceous vegetation had a positive effect on the survival and the height growth of tamarack (*Larix laricina*). None of the tested herb communities had a stronger competitive effect on tree growth than another. Restoration of abandoned fields using multi-tree species should be designed at the seedling scale rather than at the site scale to account for different tree responses to predation and competition as well as variable site conditions. An approach resembling precision agriculture is proposed to lower costs and any potential negative impact of more intensive vegetation management interventions.

Keywords: tree plantation; abandoned agricultural field; predation; competition; tolerance; facilitation; precision restoration

1. Introduction

Facilitation has been proposed as a possible restoration tool for woody species [1,2]. It is well known that facilitation effects on growth are generally restricted to less favorable environments [3]. However, facilitation may occur in productive systems such as mesic temperate habitats [2,3]. Indeed, positive effects of herbaceous cover on tree emergence and survival have been previously observed in temperate-zone abandoned fields, whereby the presence of herbaceous vegetation reduced frost heaving, heat and desiccation stresses on tree seedlings [4–7].

Usually, the improvement in emergence, survival, growth, or fitness of young trees (facilitation) is assisted by nurse shrubs and trees rather than herbaceous neighbors [2,8]. Dense herbaceous communities colonizing abandoned agricultural fields may inhibit the establishment and growth of numerous tree species for many years [9,10]. Competition for soil water from herb species is recognized as a primary factor affecting tree survival and growth, although when water is not limited, herbaceous vegetation may have no perceptible effect on tree seedlings (tolerance) [5,11–14].

The relationship between herbaceous plants and tree seedlings is influenced by the functional characteristics of trees and herbs. Pioneer tree species have a greater proportion of deep roots, higher cumulative root length and number of root apices than non-pioneer species, allowing them to explore a larger volume of soil and to be better adapted to water and nutrient limited sites [15,16]. Moreover, pioneer species can rapidly outgrow the vegetation layer due to their faster growth rates, although their establishment may be limited by herbaceous vegetation, whereas moderately to highly shade-tolerant species establish better under herb cover but grow more slowly [17–19]. On the other hand, some herb communities are known to be stronger competitors than others. With their high root/shoot ratio, their clonal growth form, their ability to produce tillers and spread rapidly, grasses are generally stronger competitors than forbs [2,20,21]. However, some forb species that form dense communities (e.g., *Solidago* and *Aster* sp.) may compete with tree seedlings or inhibit them via the production of allelopathic compounds, although allelopathy remains mainly hypothetical [11,22,23].

In addition to its variable direct effect on different species of tree seedlings, herbaceous vegetation cover may increase rates of small mammal predation by sheltering them from larger predators [6,24,25]. Rabbits and voles, as well as deer and invertebrates may cause serious damage to tree seedlings, but the severity of herbivory depends on predator density, tree species, the season, the presence of a vegetative cover, the area of tree plantation, and the distance to neighboring woodlands [6,26–30].

Due to predation and competition, most tree plantation projects on abandoned fields have used protection against predation as well as some form of control of herbaceous vegetation [31–34]. Mechanical control, such as plowing, has been used to reduce herbaceous competition, but this can also slow down site restoration by eliminating natural regeneration, disturbing the soil, and decreasing organic matter, microbial activity, and mycorrhizal diversity [35–37]. Light mechanical treatments, such as mowing and shallow cultivation, have also been used, but their effects fade rapidly [38,39]. Despite their lower efficiency in controlling root competition by herbaceous plants, plastic and weed cloth mulch mats are often used as they decrease competition for light, increase soil temperature and moisture, and are more socially acceptable than herbicides [40–43]. However, using non-biodegradable mulching materials, or plastic spiral protectors and tree-shelters against predation could be costly since it is necessary to return to the planting site after a few years to remove these materials.

The main goal of this research was to test whether the success of restoration of abandoned agricultural fields using multi-tree species could be improved through a greater understanding, at the tree species level, of the effects of predation, competition, and facilitation on tree survival and growth. More specifically, we addressed the following questions: (1) Are tree species or tree functional groups affected differently by small mammal predation and herbaceous competition? and (2) Is growth of various tree species influenced differently by various herb groups and soil moisture? We hypothesized that: (1) survival of moderately to highly shade-tolerant species is not negatively affected by herbaceous vegetation; but that (2) the growth of these non-pioneer species is more strongly affected by competition than are pioneer species; (3) competition effects on tree growth increase with the abundance of *Solidago* and *Aster* species that surround tree seedlings; and (4) conifers are less affected by small mammal predation than hardwoods.

2. Materials and Methods

2.1. Study Site

The study was conducted in a peri-urban area of Montréal (Québec, Canada), in the agricultural zone of Laval (45°40′ N; 73°43′ W). The dominant regional forest is sugar maple—hickory and the climate is humid continental. Average annual temperature, recorded at the Montréal Pierre Elliott Trudeau weather station (45°28′ N; 73°45′ W), is 6.8 °C with monthly means of 21.2 °C in July and −9.7 °C in January, the warmest and the coldest months (means were calculated for the

1981–2010 period) [44]. Annual precipitation is 1000 mm, of which around 20% falls as snow [44]. From 2010 to 2012, the average annual temperature was 8.2 °C and the average annual precipitation was 1134 mm [45]. The experiment was carried out in three abandoned agricultural fields. Field #1 (surface area ≈ 9000 m^2) is separated from field #2 (≈23.000 m^2) by a ditch bordered by eastern cottonwood (*Populus deltoides* Marsh.) trees. These two fields are situated on the south side of a 3.5 ha forest composed of silver maple (*Acer saccharinum* L.), black ash (*Fraxinus nigra* Marsh.), green ash (*Fraxinus pennsylvanica* Marsh.), eastern cottonwood (*Populus deltoides* Marsh.), and eastern white cedar (*Thuja occidentalis* L.) trees. Field #3 (≈9000 m^2) is located on the north side of this forest.

The abandoned fields had a similar past land use with grains and vegetables having been cultivated for more than 25 years until the early 2000s. Following this agricultural period, the sites were colonized by ruderal herbaceous species and were mown once or twice a year, until the fall preceding the experiment (2009). The vegetation was principally dominated by grass species (*Poaceae* spp. and *Cyperaceae* spp.), *Solidago*, *Trifolium*, *Sonchus*, and *Aster* species. *Daucus carota*, *Taraxacum officinale*, *Cirsium* spp., *Arctium* spp., and *Erigeron* spp. were also common. Total ground coverage by all species was around 65% in each field at the time of planting. Mowing prevented tree and shrub establishment, but ash (*Fraxinus* sp.) seedlings colonized the sites as soon as mowing ceased, i.e., in the first summer (2010) following planting.

The surface deposit is a mix of glacial (till) and marine deposits. Soil is an orthic melanic brunisol type [46]. Fields #1 and #2 and the majority of field #3 are covered by a stony clay loam that is moderately well-drained, while the remainder of field #3 is a well-drained clay loam [46]. Topography is mainly flat although there are slight depressions. The experimental design (see below) was included in a restoration project of the abandoned fields using more than 15,000 tree and shrub seedlings (height < 1 m) planted from June to August 2010, at least 2 m from experimental plots.

2.2. Experimental Design

The study took place between the end of May 2010 and the end of September 2012. Trees were also measured in June 2015, but no vegetation treatment (weeding or mowing) was done between 2012 and 2015. Four 40.5 m × 27 m experimental blocks were established at least 25 m from mature trees and roads, along an east-west axis: one in field #1 (surface area of ≈1 ha), two in field #2 (23 ha), and one in field #3 (1 ha). Experimental blocks were divided into six subplots following a split-plot design where the main factor was "protection" (plastic spirals against small mammals vs. no protection) and the subplot factor was "vegetation" (VG, intact herbaceous vegetation; M, mulch mats; BS, bare soil). Eight tree seedlings of eight species were randomly planted (within each subplot) for a total of 192 trees per species. Species that were used in the experiment are native to the area and represent a gradient of growth rates and shade tolerances (Table 1). The chosen species were: paper birch (*Betula papyrifera* Marsh.), yellow birch (*Betula alleghaniensis* Britt.), tamarack (*Larix laricina* (Du Roi) K. Koch), red pine (*Pinus resinosa* Ait.), northern red oak (*Quercus rubra* L.), red ash (*Fraxinus pennsylvanica* Marsh.), red maple (*Acer rubrum* L.) and sugar maple (*Acer saccharum* Marsh.).

Container-produced tree seedlings were obtained from the Berthier nursery (Berthierville, QC, Canada) of the Ministère des Fôrets, de la Faune et des Parcs du Québec and were delivered in cold-storage. All tree seedlings were container-produced (initial sizes are provided in Table 1). Hardwood species were one year old, while conifer species were two years old. Seedlings were kept in a dark cool room (≈15 °C) until manual planting from 28 May to 11 June 2010. Seedlings were planted at 1.5 m spacing and were watered once after planting.

One-third of the tree seedlings were planted directly in the herbaceous vegetation (VG) which was less than 20 cm high at the time of planting. Another third of the tree seedlings were surrounded by a 50 cm × 50 cm × 8−10 mm organic mulch mat (M) made of coconut fiber (Biomat, Multi-formes Inc., La Guadeloupe, QC, Canada) installed immediately following planting. Mats were affixed to the ground surface with four U-nails. Finally, the remaining tree seedlings were planted on bare soil (BS). Before planting, herbaceous vegetation was cut to ground level with a gasoline-powered weed cutter. A herbicide (Roundup® concentrate, glyphosate 143 g/L; 100 mL diluted in two liters of water, 25 L/ha) was applied covering a 50-cm radius at each location where seedlings were to be planted. Tree seedlings were planted one week after herbicide application. From July 2010 to September 2012, the vegetation was regularly hand-weeded to maintain bare soil conditions in a 30- to 35-cm radius around each tree. In rows between bare soil seedlings, vegetation was mowed with the weed cutter to prevent the herbaceous vegetation from exceeding 20 cm in height.

In July 2010, half of the tree seedlings were protected from small mammals (e.g., voles, rabbits, etc.) using plastic spiral protectors (TIMM Enterprises Ltd., Milton, ON, USA) 35 cm in length, affixed to the ground with a U-nail. If trees were shorter than 50 cm, plastic protectors were cut to an appropriate length for seedling size. Seedlings affected by predation before the installation of the protectors (<2%) were excluded from the analyses.

2.2.1. Survival and Growth

Tree survival and signs of mammal predation were evaluated every spring and fall from fall 2010 to fall 2012 as well as in June 2015. Seedlings were identified as live (no sign of predation), damaged live or damaged dead by voles (i.e., gnawed stem, removed bark near the ground, or gnawed roots), damaged live or damaged dead by rabbits (i.e., clean-cut edges), damaged live or damaged dead by deer (i.e., rough-torn edges) [24,27]. Tree mortality due to small mammal predation may also be inferred when mortality rates for unprotected seedlings were greater than for seedlings protected with a plastic spiral protector.

Height and diameter were measured every fall (2010−2012) and in June 2015. Height was measured as the distance between the soil surface and the apical meristem while diameter was measured 5 cm above the soil surface. The relative growth rate (RGRX) of height or diameter was calculated using the formula:

$$\mathrm{RGRX} = \frac{\ln(X2) - \ln(X1)}{T2 - T2}$$

where $X1$ corresponds to seedling height or diameter in year $T1$, $X2$, height or diameter in year $T2$.

2.2.2. Foliar Measurements

Foliar predation by invertebrates was estimated for all tree seedlings in September 2011. When more than 30% of leaves showed signs of invertebrate predation (such as sawfly damage), the seedling was classified as being affected by invertebrate predation. Further foliar measurements were made between 15−23 August 2012 on two trees per species randomly chosen in each subplot among those having a minimum of 25 leaves (if not possible, trees having the highest number of leaves were chosen). This minimum number of leaves per individual was required for foliar analyses. Leaves and needles were placed between wet paper towels and were kept moist and cool until laboratory analysis. Specific leaf area (SLA) was only measured for leaves of the following species: paper birch, red maple, yellow birch, red oak and sugar maple. Specific leaf area was measured following the method described by Cornellissen et al. [47]. Ten healthy leaves, or the maximum number of healthy leaves, if there were less than ten leaves, were scanned the day of collection. Leaf area was calculated using the Winfolia software (Régent Instruments, QC, Canada). All leaves and needles were dried at 70 °C for at least 48 h before their mass was measured or before grinding. Specific leaf area was calculated as the total one-sided area of fresh leaves divided by their oven-dried mass and was expressed in $\mathrm{mm}^2\ \mathrm{mg}^{-1}$. Leaves were finely ground with a vibratory pulverizer (Fritsch, Idar-Oberstein, Germany). Between each sample, the pulverizer was cleaned with a vacuum and rinsed with ethanol (70%). Concentrations of nitrogen (leaf N) were analyzed on a Leco CNS−2000 (LECO, St-Joseph, MO, USA) in the laboratory at the Canadian Forest Service's Laurentian Forestry Centre.

Table 1. Characteristics of the eight tree species planted for this restoration experiment.

Common Name	Scientific Name	Mycorrhizal Association	Successional Status	Growth Rate	Shade Tolerance	Initial Mean Height (cm)	Initial Mean Diameter (mm)
Tamarack	*Larix laricina* (Du Roi) K. Koch	EM	Pioneer	Rapid	1	38.7	6.8
Red pine	*Pinus resinosa* Aiton	EM	Pioneer	Rapid	1.9	25.9	5.9
Paper birch	*Betula papyrifera* Marsh.	EM	Pioneer	Rapid	1.5	30.1	4.0
Red ash	*Fraxinus pennsylvanica* Marsh.	AM	Pioneer	Rapid	3.1	33.8	4.8
Red maple	*Acer rubrum* L.	AM	Pioneer	Rapid	3.4	62.3	6.9
Northern red oak	*Quercus rubra* L.	EM	Non-pioneer	Moderate	2.8	41.8	5.7
Yellow birch	*Betula alleghaniensis* Britt.	EM	Non-pioneer	Slow	3.2	37.0	3.8
Sugar maple	*Acer saccharum* Marsh.	AM	Non-pioneer	Slow	4.8	53.0	5.6

AM: arbuscular mycorrhizal species; EM: ectomycorrhizal species; Successional status and growth rate [48,49]; Shade tolerance scales range from 0 (not tolerant) to 5 (maximum tolerance) [50].

2.2.3. Soil Water Content and Light

Environmental measurements were taken on two seedlings per species randomly selected in each subplot. Soil water content (SWC) was measured three times in the summer of 2011 with a TDR-200 probe (Spectrum Technologies Inc., Plainfield, IL, USA), using 12-cm rods. The first measurements were taken on 10 June, two days after a 10-mm rainfall, but the 9 preceding days had been without rain (Environment and Climate Change Canada, 2013b). The second measurements were taken on August 17th, one day after 11 mm of rain and three days after 22 mm of rain. The third measurements were taken on August 23rd, one day after 3 mm of rain and 2 days after 40 mm of rain (Environment and Climate Change Canada, 2013b). Soil water content was also estimated on 21 September 2012, three days after a 21-mm rainfall (Environment and Climate Change Canada, 2013b). Photosynthetic photon flux density (%PPFD) was measured using point quantum sensors (LI-COR Inc., Lincoln, NE, USA) at a height of 30 cm on the south side of each seedling. Measurements were taken at the end of July 2011, on cloudy days, following the method described in Messier and Puttonen [51].

2.2.4. Herbaceous Vegetation

On 17 August 2011, herbaceous biomass was measured around one randomly chosen seedling per species in each herbaceous vegetation and mulch mat subplot. After the first year, some herb plants began to pierce the organic mulch mats or grow through the crack in the middle of the mulch mats. All plants inside a 50 × 25 cm plot installed on the east side of the selected seedling were cut to ground level and placed in a paper bag. Samples were air dried at 25 °C until there was no further loss of mass due to humidity and then weighed to estimate above-ground biomass of the surrounding vegetation. On 23 July 2012, in herbaceous vegetation subplots, an inventory was taken of herbaceous vegetation beside the same two seedlings randomly chosen for SWC. All herbaceous species in a 50 × 25 cm plot were identified and their percent cover was evaluated. The species were grouped into five herb communities: Graminoids (grasses), *Solidago* spp. such as *Solidago rugosa*, *Asteraceae* spp. such as *Sonchus arvensis*, *Fabaceae species* (legumes) such as *Trifolium repens*, and *Apiaceae* mainly dominated by *Daucus carota*. More than 95% of the species identified fit into these groups.

2.3. Statistical Analysis

Seedling mortality was evaluated using Chi-squared tests. We first compared mortality rates between experimental factors (protection, vegetation, and protection × vegetation) from fall 2010 to fall 2012 and in the spring of 2015. We then compared mortality rates due to predation by small mammals (data combined from 2010 to 2012) between the vegetation treatments. Repeated measures of analyses of variance (ANOVAR) and univariate analyses of variance (ANOVA), based on the two-way split-plot design, were performed for each species to evaluate the effects of protection and vegetation treatments on seedling height and diameter, leaf nitrogen (N), SLA, and SWC. Species were analyzed individually because there were significant ($p < 0{,}05$) treatment × species interactions (results not shown), meaning that species reacted differently to the treatments. Herbaceous biomass and light (%PPFD) were only compared between herbaceous vegetation and mulch mat subplots with ANOVAs. Student and Tukey tests were used as post-hoc tests. Log transformations were used when data were not normal. A multiple regression was used to estimate the effects of SWC, average herbaceous cover height, and percentage cover of each herb community on the height and diameter relative growth rates (RGR) of each tree species. All statistical analyses were performed using JMP 10.0 (software from SAS).

3. Results

3.1. General

With the exception of paper birch, seedlings of the pioneer species had less mortality than did non-pioneer species. After five seasons of growth (spring 2015), mortality rates varied from 3% for red ash to 61% for yellow birch seedlings, all treatments combined (Figure 1). Pioneer species such as tamarack, paper birch, and red ash had the highest height and diameter growth between the fall of 2010 and spring of 2015, whereas the non-pioneer species red oak had the lowest growth (Figure 2).

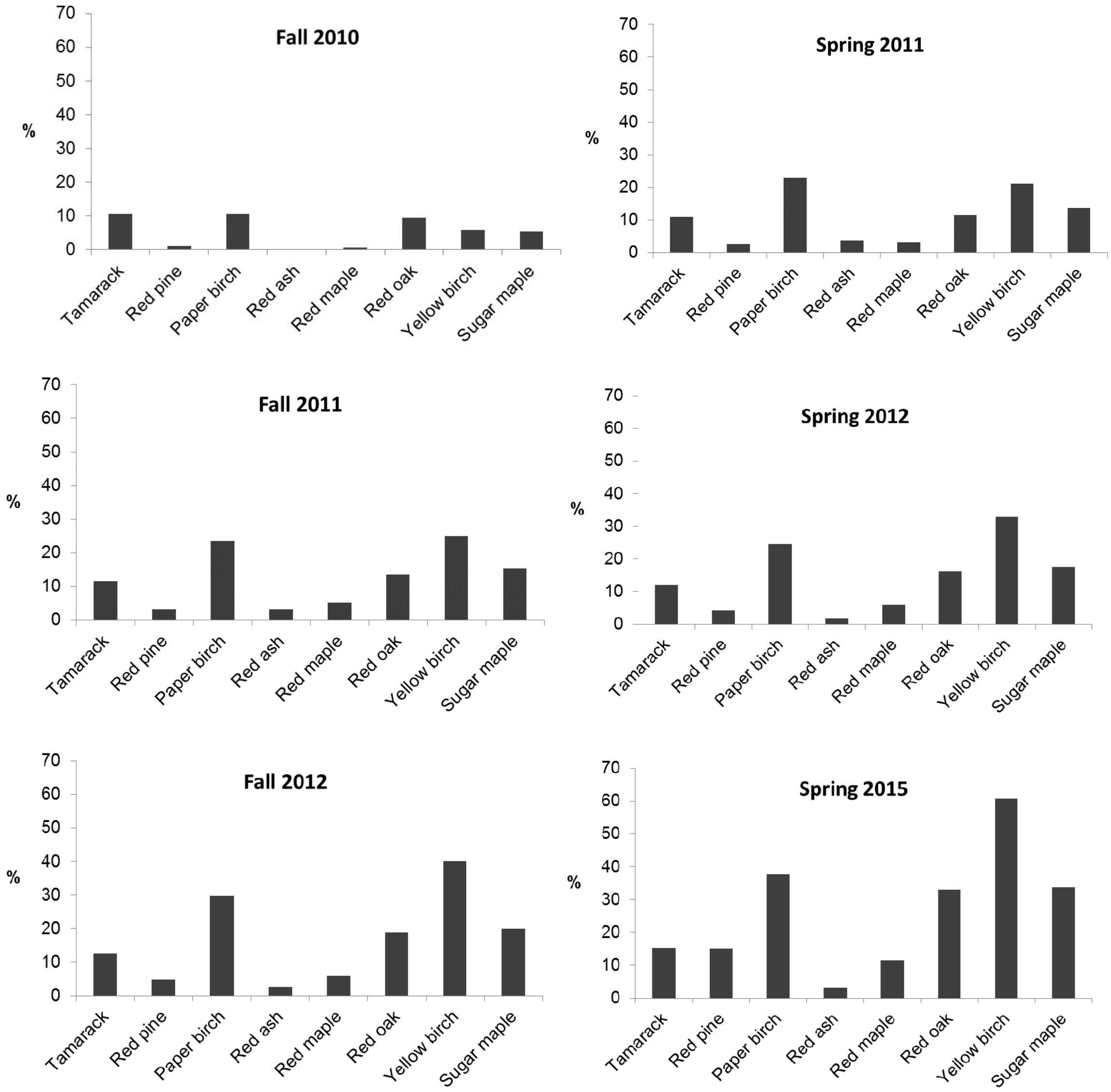
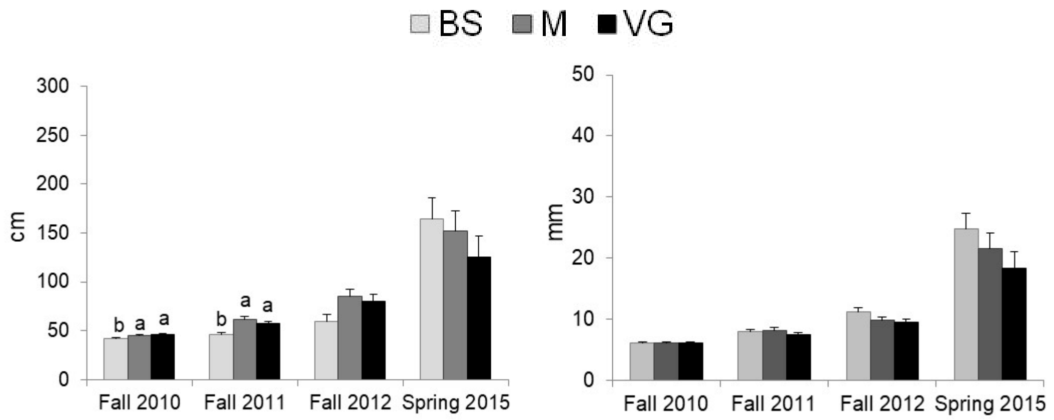
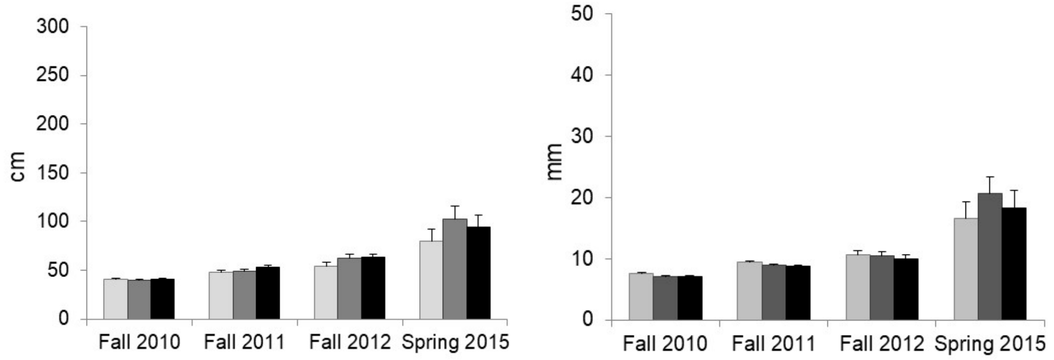


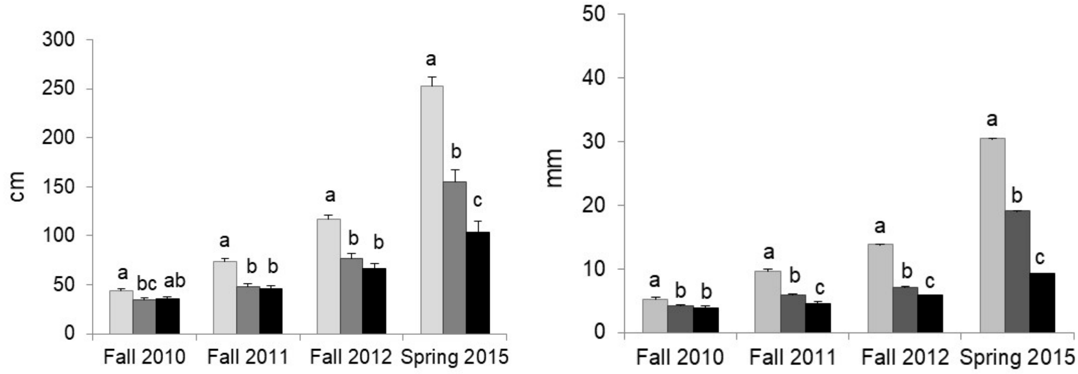
Figure 1. Rates of seedling mortality (all treatments combined) as a function of tree species in fall 2010, spring 2011, fall 2011, spring 2012, fall 2012, and spring 2015.



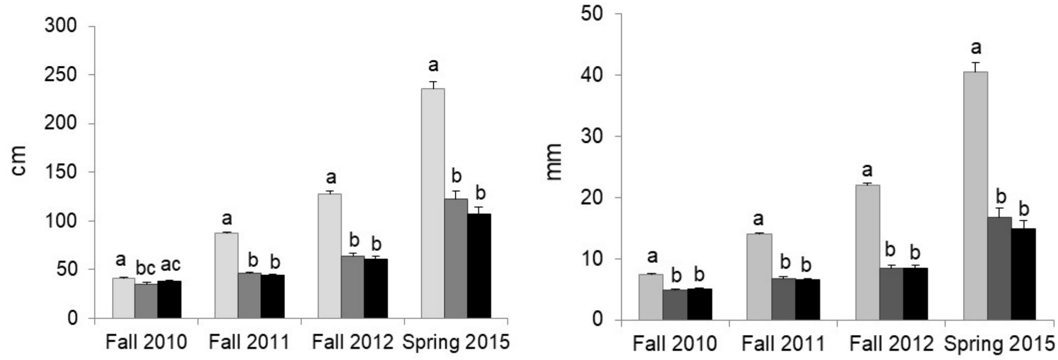
(**a**) Tamarack



(**b**) Red pine

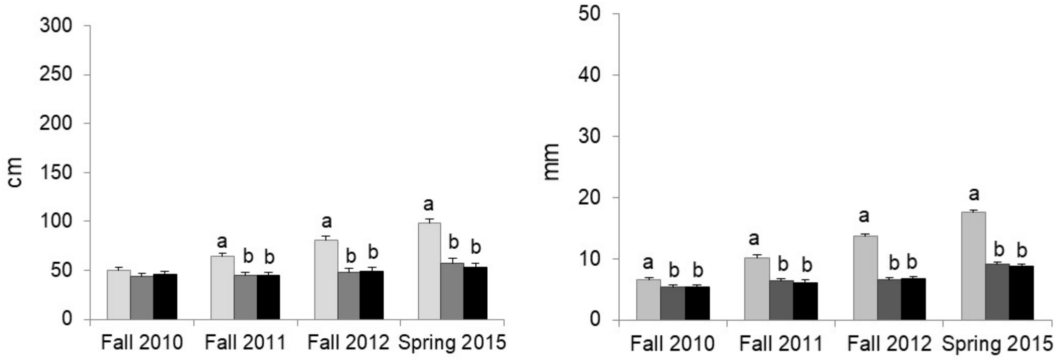


(**c**) Paper birch

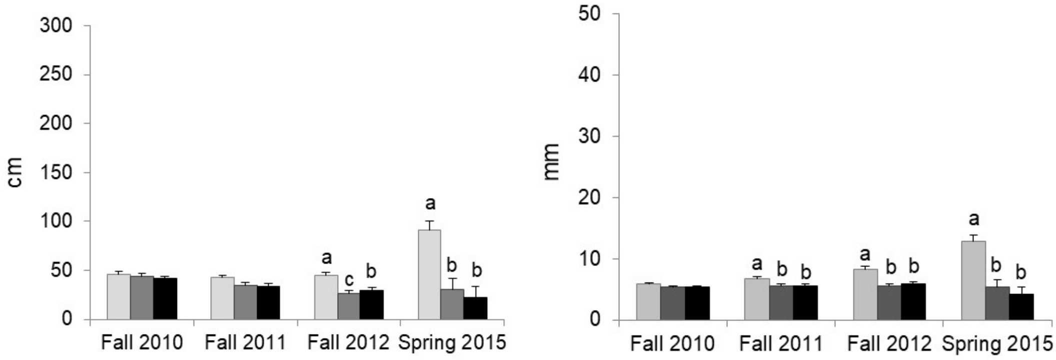


(**d**) Red ash

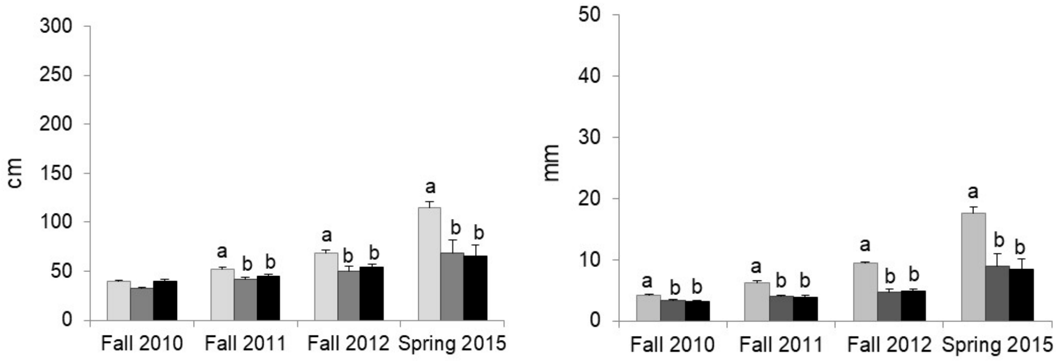
Figure 2. *Cont.*



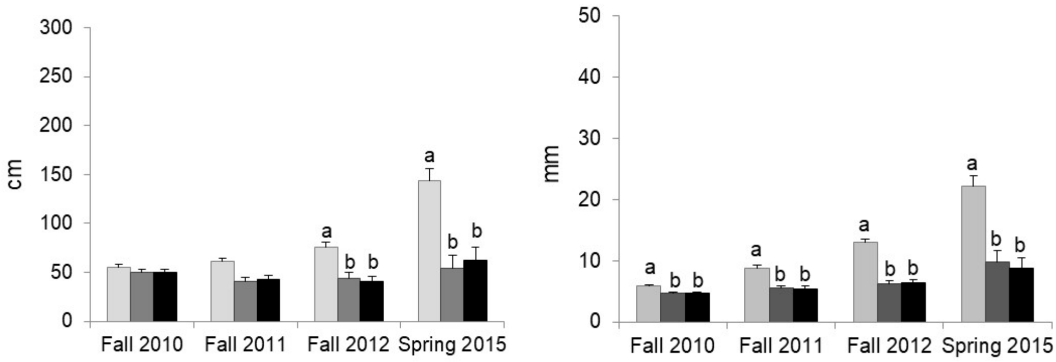
(**e**) Red maple



(**f**) Red oak



(**g**) Yellow birch



(**h**) Red oak

Figure 2. Height and diameter of seedlings (least-squares means and SE) growing in bare soil subplots (BS; light grey), surrounded by mulch mat (M; medium grey) or in vegetation subplots (VG; black), from autumn 2010−2012 and in spring 2015.

3.2. Predation and Herbaceous Vegetation Effects on Tree Survival and Growth

Mortality due to predation was generally higher for non-pioneer species than for pioneer species, with the exception of paper birch (Tables 2 and 3). In fact, both birch species had mortality rates double that of the next most vulnerable species (Figure 1, Table 3). Many birch seedlings were dead after the first winter with their mortality being principally related to predation, although competition also affected yellow birch survival (Table 2). Yellow birch (17%), paper birch (15%), red oak (7%), and sugar maple (6%) seedlings showed more signs of lethal small mammal damage than other species (Table 3). The vegetation control treatments also had a significant impact on predation rates in the most vulnerable species. Seedlings of both species in the birch genus surrounded by a mulch mat were more affected by small mammal damage than seedlings growing in vegetation (Table 3; $\chi^2 = 23.153$, $p \leq 0.0001$). However, birch seedlings in both of these treatments were more susceptible to predation than bare soil seedlings ($\chi^2 = 15.634$, $p = 0.0004$).

Mortality due to predation of the non-pioneer species, red oak, and sugar maple, was also inferior or did not occur in bare soil subplots (Table 3; $\chi^2 = 11.544$, $p = 0.0031$; $\chi^2 = 10.050$, $p = 0.0066$, respectively). Effects of predation on red maple mortality were observed in the spring of 2015 survey (Table 2; $\chi^2 = 8.202$, $p = 0.0042$), but between 2010 and 2012 only 2% of dead seedlings showed small mammal damage (Table 3). The use of plastic spiral protectors did not have much of an influence on tree growth with the exception of a positive effect on red oak height from the second growing season onward ($p < 0.03$). The size of unprotected red oak seedlings significantly decreased due to leader mortality or the appearance of a new stem following small mammal damage. In fact, this decline in size was noted in more than 50% of red oak seedlings when all treatments were combined.

In general, predation by rabbits caused two times more seedling mortality than predation by voles (4.2% and 2.0% of seedling mortality, respectively). Both species of birch seedlings (14.3% for yellow birch and 11.5% for paper birch) were most affected by rabbit predation while red oak was the species preferred by voles (5.9%). Mortality due to small mammal damage was observed on some protected seedlings of yellow birch (5.5%), paper birch (2%), and red oak (1%). For these individuals, voles cut roots under the spiral protector while rabbits cut stems above the protector. Some red ash seedlings (3%) snipped by rabbits or voles produced new stems the year following predation, explaining the decrease in mortality rates in 2012 (Figure 1).

Herbivory by deer was negligible, only five seedlings (0.3%) died due to deer predation. Foliar herbivory by invertebrates was also minor (4% of tree seedlings, in total) and did not vary between treatments. Conifer species were not affected by any kind of herbivory.

Table 2. Predation, competition, and facilitation effects estimated from the results obtained from the different experimental treatments on tree seedling mortality from fall of 2010 to spring of 2015.

Species	Factor	Fall 2010	Spring 2011	Fall 2011	Spring 2012	Fall 2012	Spring 2015
Tamarack	Protection						
	Vegetation	Facilitation *	Facilitation *	Facilitation *	Facilitation *	Facilitation **	Facilitation **
Red pine	Protection						
	Vegetation						
Paper birch	Protection		Predation in VG*		Predation **	Predation **	
	Vegetation					M < BS = VG *	Competition ***
Red ash	Protection						
	Vegetation						
Red maple	Protection						Predation **
	Vegetation						Competition **
Red oak	Protection	Predation **			Predation **	Predation **	
	Vegetation		Competition **	Competition **	Competition ***	Competition ***	Competition ***
Yellow birch	Protection		Predation ***	Predation ***	Predation ***	Predation ***	
	Vegetation		Competition **	Competition **	Competition **	Competition ***	Competition ***
Sugar maple	Protection			Predation in VG *			
	Vegetation	Facilitation *		Facilitation if Protection * M < BS = VG if No Protection *	M < BS = VG *		M < BS = VG **

BS: tree seedlings growing in bare soil subplots, M: surrounded by organic mulch mat, VG: or in intact herbaceous vegetation. Blank spaces mean mortality did not differ between treatments. Predation means mortality is higher for seedlings unprotected against small mammals. Competition means mortality is lower when trees are growing in bare soil (BS > M = VG or BS > VG > M). Facilitation means mortality is lower when trees are growing in herbaceous vegetation (BS = M < VG or BS < M = VG). *p*-value: * < 0.05; ** < 0.01; *** < 0.001.

Table 3. Tree mortality (%) due to predation compared between vegetation treatments (evaluated using signs of lethal small mammal damage on unprotected and protected seedlings, data compiled from Spring 2010 to Autumn 2012), tree mortality in Autumn 2012 compared between protection treatments, and tree mortality in Spring 2015 (total).

Species	Mortality Due to Predation (2010–2012)				% Dead Seedlings (Fall 2012)		% dead Seedlings (Spring 2015)
	Bare Soil	Mulch Mat	Herbaceous Vegetation	Total	Unprotected	Protected	
Tamarack	0	0	0	0	6.8	5.8	15.2
Red pine	0	0	0	0	0.5	4.2	15.1
Paper birch	1.1 a	8.9 b	4.7 c	14.7	20.4 a	9.4 b	37.7
Red ash	0	2.1	0	2.1	2.1	0.5	3.1
Red maple	0	0.5	1.6	2.1	4.2	1.6	11.5
Red oak	0 a	2.6 b	4.2 b	6.8	13.6 a	5.2 b	33.2
Yellow birch	0.5 a	10.1 b	6.4 c	17.0	27.5 a	12.7 b	60.8
Sugar maple	0 a	3.7 b	2.1 b	5.8	12.1	7.9	33.5

Bare soil: seedlings growing in a bare soil, Mulch mats: surrounded by organic mulch mat, Herbaceous vegetation: or in intact herbaceous vegetation. Means for each species were tested using ANOVA and then compared using Tukey tests following ANOVA. Means of each row followed by different letters are significantly different at $p < 0.05$.

In general, the survival of pioneer species was not affected by herbaceous competition except at the end of the experiment for paper birch and red maple seedlings (Table 2). Nevertheless, competition effects were seen on the growth of hardwood pioneer species which was usually higher in bare soil (Figure 2). The conifer species were either tolerant of or facilitated by the presence of the vegetation layer. Red pine mortality (<5% within the first 3 years), height, and diameter did not vary with any treatment at any time (Table 2, Figure 2b). Mortality of tamarack seedlings occurred principally within the first growing season following planting in bare soil or in mulch mat subplots (Figure 1a, Table 2). No effects of herbaceous vegetation were observed on tamarack diameter, but tamarack seedlings growing in bare soil were smaller than those surrounded by mulch mat or in herbaceous vegetation, after the first (F-test = 9.7673; $p = 0.0118$) and the second (F-test = 13.4052; $p = 0.0061$) growing seasons (Figure 2a). After three years, this relationship was only marginally significant ($p = 0.0922$) and it was not significant by the spring of 2015 ($p = 0.4503$).

Herbaceous vegetation also showed some evidence of facilitation on sugar maple survival (Table 2). After the first growing season, sugar maple mortality was higher in bare soil ($\chi^2 = 6.330$, $p = 0.0422$) whereas after the second growing season, sugar maple mortality was lower in vegetation, but only for seedlings protected against predation ($\chi^2 = 6.344$, $p = 0.0419$). Seedling mortality of the other two non-pioneer species was, on the contrary, lower in bare soil subplots (Table 2). The growth of non-pioneer species was greater in bare soil (Figure 2).

No benefit of the organic mulch mats on tree survival was observed in this experiment. Mulch mats had effects comparable to or more negative than herbaceous vegetation (Table 2, Figure 2). In the second summer, herb biomass (47 g) growing through the organic mulch mats (F-test = 2.7507, $p = 0.1958$) and %PPFD at 30 cm high (60%; F-test = 0.7491, $p = 0.4504$) were not different from herb biomass and %PPFD in intact vegetation (65 g and 69%, respectively). By the end of the experiment (five growing seasons), many mulch mats were almost completely decomposed.

After five years, survival of all pioneer species seedlings growing in herbaceous vegetation was higher than 75%, except for paper birch (Figure 3a). Excluding red maple, they all had a height growth increment of more than 30 cm (Figure 3b). By contrast, non-pioneer species seedlings surrounded by vegetation had a lower survival and height growth rate.

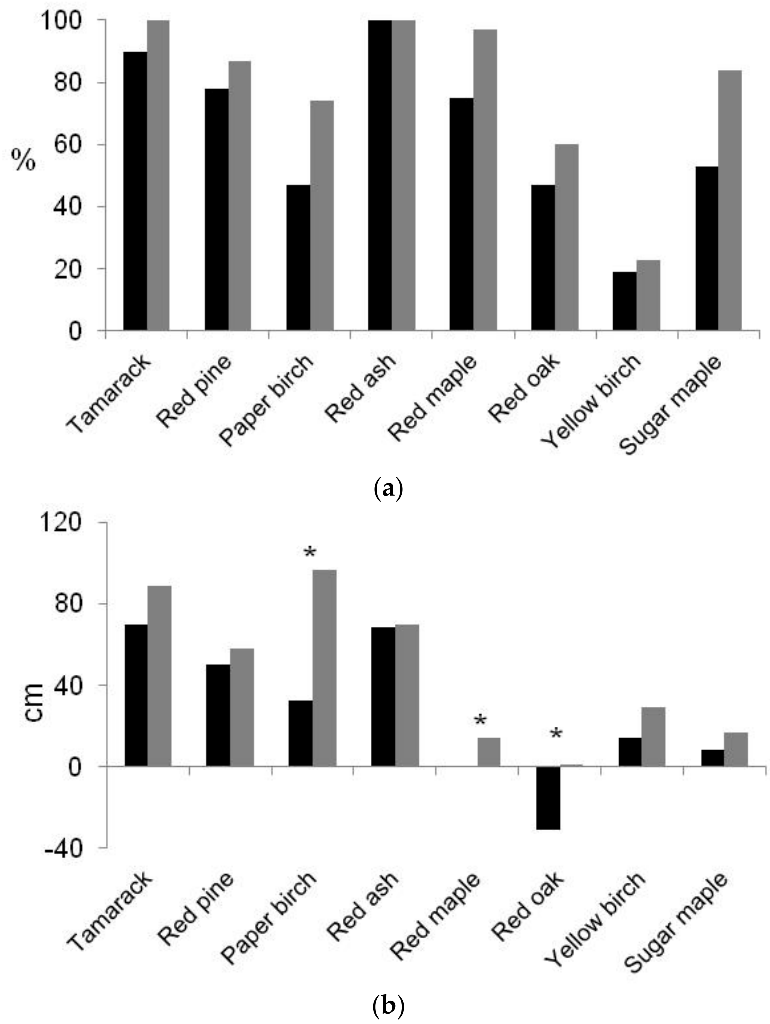


Figure 3. Differences of (**a**) survival rates in spring 2015 and (**b**) height growth increment (2010–2015) for seedlings growing in herbaceous vegetation. Black bars: seedlings unprotected against small mammal predation. Grey bars: seedlings protected. (* $p < 0.05$, two-sample *t*-test).

3.3. Foliar Attributes, Soil Water Content, and the Influence of Herb Communities

All hardwoods, except yellow birch, had more leaves ($p < 0.01$) and a lower specific leaf area (SLA) ($p < 0.03$) in bare soil subplots (SLA was not measured for red ash and conifers). Nitrogen (N) in conifer needles or in birch leaves was not affected by the presence or absence of herbaceous vegetation (Table 4). Leaf N was, however, higher in bare soil for the three endomycorrhizal (AM) tree species: red ash (F-test = 47.9526; $p = 0.0002$), red maple (F-test = 11.8862; $p = 0.0081$), and sugar maple (F-test = 55.9883; $p = 0.0001$). More seedlings with superficial bare roots were observed in bare soil subplots for all species, except paper birch and sugar maple (Table 4).

Soil water content (SWC) did not vary between vegetation treatments in either 2011 or 2012. Further, it did not influence the relative growth rate (RGR) of seedlings growing in herbaceous vegetation (Table 5). The relative growth rate (RGR) of red maple and conifer species was positively related to the height of the herbaceous layer. In general, no specific herb community influenced tree growth, other than *Solidago* species which had a negative effect on red ash and red maple growth (Table 5). Grasses had a marginally significant positive effect ($p < 0.10$) on tamarack growth (Table 5).

Table 4. Vegetation treatment effects on leaf nitrogen (N) and rooting (%).

Species	Leaf Nitrogen (N)			Superficial Bare Roots		
	BS	M	VG	BS	M	VG
Tamarack	1.91	1.46	1.43	11.6 x	1.7 y	2.3 y
Red pine	1.02	1.07	0.97	12.8 x	1.1 y	2.7 z
Red ash	2.30 a	1.43 b	1.62 b	8.1 x	0 y	3.8 z
Paper birch	2.28	1.84	1.93	3.4	0.7	0.7
Red maple	1.68 a	1.16 b	1.23 b	10.4 x	0.6 y	2.7 y
Yellow birch	1.95	1.86	1.79	6.1 x	0 y	0 y
Red oak	1.68 a	1.11 b	1.24 ab	9.2 x	0.6 y	1.8 y
Sugar maple	1.68 a	1.13 b	1.22 b	1.8	0	2.4

For each variable, means of each row followed by different letters are significantly different at $p < 0.02$.

Table 5. Results of multiple regressions of height and diameter relative growth rates (RGR) (fall 2010–fall 2012) in relation to soil water content, average herb height, percentage cover of grasses, *Solidago*, *Asteraceae*, *Apiaceae*, and *Fabaceae* (legumes) species.

Species		Adjusted R^2	Soil Water Content	Herb Height	Grasses	*Solidago* spp.	*Asteraceae* spp.	*Apiaceae* spp.	*Fabaceae* spp.
Tamarack	RGR_{Height}	0.30		0.03 * (+)	0.09 (+)			0.09 (−)	
	$RGR_{Diameter}$	0.28		0.01 * (+)	0.08 (+)				0.03 * (+)
Red pine	RGR_{Height}	*0.39*		0.06 (+)					
	$RGR_{Diameter}$	0.14		0.02 * (+)					
Paper birch	RGR_{Height}	−0.07							
	$RGR_{Diameter}$	−0.13							
Red ash	RGR_{Height}	0.11							
	$RGR_{Diameter}$	0.20				0.02 * (−)			
Red maple	RGR_{Height}	*0.36*		0.004 **(+)		0.04 * (−)			
	$RGR_{Diameter}$	0.31		0.02 * (+)		0.09 (−)			
Red oak	RGR_{Height}	*0.40*					0.04 * (−)		0.02 * (−)
	$RGR_{Diameter}$	−0.05							
Yellow birch	RGR_{Height}	0.03							
	$RGR_{Diameter}$	−0.26							
Sugar maple	RGR_{Height}	−0.16							
	$RGR_{Diameter}$	−0.11							

Only significant effects ($p < 0.05$) and marginal effects ($p < 0.10$) are presented. Positive (+) or negative (−) effects. p-value: * < 0.05; ** < 0.01.

4. Discussion

4.1. Predation

Compared to other studies, predation by deer and small mammals was relatively low, probably due to predation being determined by both the environment and predator densities [26,27,32,52]. Tree species preferences also differed from other studies. For instance, rabbits and voles can potentially inflict damage on pine seedlings in fields or forests [6,52,53], but none of our conifer species exhibited any signs of herbivory. Differences in seedling size, growth rate, density of resin droplets on the stem, the presence of specific monoterpenes in the bark, and palatability are among the factors that have been proposed to explain species and seedling preferences of herbivores [25,26,53]. In our study, birch species were the most vulnerable to small mammal damage, particularly by rabbits. These species were also the smallest at the time of planting (Table 1) and had the smallest diameters, at least in the first two years of growth (Figure 2). By the fifth year of growth, red maple was the only species affected by predation and was amongst the species with the smallest end of experiment diameters

(Table 2, Figure 2). These results suggest that seedlings with small diameters are more vulnerable to small mammal damage.

Predation occurred just as frequently, or even more frequently, with mulch mats than the vegetation layer treatment. Mulch mats appear to offer the same protective benefits to small mammals against their predators as does an herbaceous cover. Mulch mats and the vegetation layer allow voles to feed and move safely beneath cover, whereas for rabbits, the presence of mats may make the young tree seedlings more visible than in the vegetation cover.

4.2. Competition, Tolerance, and Facilitation

Generally, tree mortality was not as affected by herbaceous competition as tree growth. Herbaceous vegetation increased the mortality of four hardwood species (Table 2), whereas growth of all hardwoods was negatively affected by competition (Figure 2).

Contrary to what we expected to see and to what has been observed in the tropics [17–19], the survival of the two moderately shade-tolerant, ectomycorrhizal and non-pioneer species was negatively affected by herbaceous competition. By contrast, slight effects of facilitation were identified for the survival of sugar maple, the species with the highest shade-tolerance [50], consistent with what Berkowitz et al. [7] had observed. Survival and growth of conifer species were not negatively affected by herbaceous vegetation (tolerance), while positive effects were observed on survival and height growth of tamarack seedlings. These positive effects suggest that facilitation does not only occur in harsh conditions such as dry environments [54–56].

The lack of competition effects on survival may be related to the low competition for water. Indeed, no differences in soil water content (SWC) were observed among the different treatments and no effect of SWC on relative growth rates was found for any species. However, herbaceous vegetation may have reduced heat and desiccation stresses in the uppermost few centimeters of soil; reductions that benefited tamarack which has a shallow root system [57]. In the first two growing seasons, few heat wave (>30 °C) events were observed [45]. Tamarack is one of the species (together with red pine) that has a low specific root length (SRL) [58]. It develops roots that are shorter and thicker than any of the hardwoods that were tested. Conifers probably developed a better root system in herbaceous vegetation than in bare soil. The positive effects of herbaceous vegetation on tree survival have been previously observed in other mesic habitats, including facilitation of pine seedlings in temperate-zone abandoned fields, but facilitation effects on growth, such as those that were observed for tamarack, are rare [2,3,5,6]. Similarly, seedling heights of hybrid larch (*Larix* × *marschlinsii* Coaz) planted for a boreal reforestation project were positively related to vegetation cover [59].

While the growth of hardwoods was influenced by competition, only endomycorrhizal (AM?) tree species had a higher leaf N in bare soil subplots. Furthermore, *Solidago* species exerted negative effects on red maple and red ash growth. Burton and Bazzaz [11] also observed lower foliar N for ash seedlings that were growing in *Solidago* patches. In abandoned agricultural fields, forbs and many grass species decrease the rate of N accumulation in the soil [60]. Frequent mowing in the rows of bare soil subplots promoted the legume species, *Trifolium*, from the second growing season onward, which could have increased soil N availability [60]. The explanation may also be related to mycorrhizae. Arbuscular mycorrhizal fungi do not promote tree N acquisition when N availability is low, in contrast to ectomycorrhizal fungi [61,62]. Contrary to what we expected, no herb community seemed to be a stronger competitor than another except for the few negative effects of *Solidago* species on tree growth. The vegetation surrounding the tree seedlings was composed of multiple herbaceous species which may have diluted any allelopathic effects that might occur in pure dense communities of *Solidago* and *Asteraceae* [11,22].

Tree species can be considered to be tolerant to herbaceous vegetation if they have high survival rates, even if growth is reduced, because many of the seedlings will eventually outgrow the vegetation layer [5,63]. Thus, we suggest that conifer species and red ash are tolerant to herbaceous vegetation because they had a high survival rate (>75%) and a height increment of more than 50 cm after five years in vegetation subplots. As expected, pioneer species had a higher growth rate than non-pioneer species, except for the moderately shade-tolerant red maple which had a survival rate higher than 75%. Due to a low survival rate (19% for yellow birch) and a low or negative growth rate (for red oak), we consider these two EM moderately shade-tolerant and non-pioneer species to be inhibited by the herb cover which had both direct and indirect (via predation) effects (Figure 3).

5. Conclusions

In this restoration experiment of an abandoned mesic field using multi-tree species, soil water content did not differ between treatments and did not affect tree growth. However, tree species responded differently to predation and herbaceous vegetation. Therefore, when planting trees in abandoned fields, specific treatments could be used according to the characteristics of the tree species and variable site conditions. Such an approach is inspired by the principles of precision agriculture for increasing efficiency and decreasing environmental and economic costs. Many definitions of precision agriculture have been proposed since its inception in the 1980s, but Gebbers and Adamchuk [64] (2010, p. 828) summarized it as “a way to apply the right treatment in the right place at the right time”.

With this in mind, we propose that precision restoration requires the application of the right treatment to the right species at the right place. For instance, on our study sites, conifer species could be planted without controlling for competition and small mammal predation, as they were highly tolerant to or facilitated by herbaceous vegetation and unaffected by herbivory. Nevertheless, herbivory may vary with the environment, predator density, and the diversity of species used. Hardwood pioneer species could also be planted directly into herbaceous vegetation, although paper birch should be protected against small mammal damage. Planting seedlings with a diameter greater than 5 cm could also decrease vulnerability to predation, but this should be further tested. For large-seeded species, such as northern red oak, direct seeding could be a better approach than planting, given that their emergence and survival are not affected by herbaceous competition [65,66], but large-seeded species could be more affected by seed predation [4,67]. A better knowledge of the effect of various factors on different hardwood and conifer species under various site conditions could be used to recommend tree species that require the least amount of protection and vegetation control. Such an approach could be applied to other types of ecosystems, such as forests and industrial wastelands, to reduce costs and improve success rates.

Author Contributions: A.S.-D., D.K., and C.M. conceived and designed the experiment, A.S.-D. collected and analyzed the data, A.S.-D., D.K., and C.M. wrote the paper.

Funding: This study was funded by the National Science and Engineering Research Council in Canada (NSERC, Ottawa, Canada), the Fonds Québécois de la Recherche sur la Nature et les Technologies (FQRNT, Québec, Canada), WSP (GENIVAR Inc.) and the NSERC/Hydro-Québec Research Chair on Tree Growth.

Acknowledgments: We are grateful to the numerous field assistants and occasional contributors to sampling and weeding, particularly: Philippe-Olivier Boucher, Kasia Richer-Juraszek, Sophie Carpentier, Nathan Probst, Christophe Jenkins, Chantal Cloutier, Yann Gauthier, Étienne St-Hilaire, Matthias Schwetterlé, Olivier Lafontaine and Mathieu Messier. We would like to thank also Stéphane Daigle for advice on data analyses. We are thankful to the city of Laval for their collaboration and the use of their land in this research study. We acknowledge the collaboration of Dominic Senecal (WSP) in this study. We are also thankful to three anonymous reviewers for their comments and advice on the manuscript.

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

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