

Optimizing Hardwood Reforestation in Old Fields: The Effects of Treeshelters and Environmental Factors on Tree Seedling Growth and Physiology

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Abstract

Strong competition for water is largely recognized as the main factor explaining the resistance of herbaceous old fields to tree invasion. Therefore, site preparation as well as chemical and mechanical vegetation control are recommended when establishing hardwood tree plantations on such sites, but those methods are sometimes socially or ecologically inappropriate. The main objective of this study was to analyze whether treeshelters could improve early tree growth in herbaceous old fields, when mulching alone is used to partially control herbaceous competition. Our results indicate that treeshelters can facilitate tree growth in those conditions but that this was not caused by an improvement of tree water relations. Rather, it appeared to be related to an optimization of light levels inside the shelter, where light intensity was low enough to

lead to a photosynthetic system less costly to maintain due to a greater specific leaf area but high enough to have no adverse effects on photosynthetic rates. Although treeshelters increased tree growth when surrounding herbaceous vegetation was low (either height or standing biomass), allowing high light levels, they reduced growth when surrounding vegetation was high and blocked a substantial quantity of light. Therefore, environmental factors such as light availability need to be considered to optimize the success of hardwood plantations when treeshelters are used in recently abandoned agricultural fields.

Key words: *Acer saccharinum*, facilitation, *Fraxinus pennsylvanica*, hardwood silviculture, microtopography, *Quercus macrocarpa*, water relations.

Introduction

In eastern North America, marginal agricultural land is abandoned and allowed to follow secondary succession (Lepers et al. 2005). This socioeconomic phenomenon leads to the formation of “novel ecosystems” (Hobbs et al. 2006), which offer opportunities for forest restoration (Bouchard & Domon 1997), and a number of projects have already been established (e.g., Cogliastro et al. 1997a; King & Keeland 1999; Stanturf et al. 2000). In this region, low-growing plant communities that are resistant to tree invasion are frequently observed following agricultural abandonment (Pound & Egler 1953; Niering & Egler 1955; Benjamin et al. 2005). For this reason site preparation as well as chemical or mechanical vegetation control are recommended for the establishment of hardwood tree plantations on recently abandoned fields, whether for restoration or production purposes (e.g., Davies 1985; Cogliastro et al. 1990). However, those methods can sometime be socially or ecologically inappropriate, and in

many regions of the world, such as the province of Québec (Canada), herbicide use has been banned for forestry (Gouvernement du Québec 1995). Therefore, there is a need to develop alternative strategies for the establishment of hardwood plantations in herbaceous fields.

Following recent theoretical work on the interplay of competition and facilitation in plant communities (Callaway & Walker 1997; Holmgren et al. 1997; Brooker & Callaghan 1998), restoration ecologists are now searching for novel ways to optimize tree establishment using pioneer vegetation instead of suppressing it, as to maximize facilitation and minimize competition (Castro et al. 2002; Gomez-Aparicio et al. 2004; Padilla & Pugnaire 2006). This is also the rationale behind techniques such as planting under shelterwoods (Paquette et al. 2006) or partial clearing in shrub thickets (Cogliastro et al. 2006). However, in recently abandoned fields, it is largely recognized that the interaction between tree seedlings and pioneer vegetation is strongly competitive (Berkowitz et al. 1995), mainly for soil water (Burton & Bazzaz 1995; Davis et al. 1998). On such sites, improvement of tree establishment through positive interactions with vegetation is thus difficult or even impossible. On the other hand, it might be possible to “artificially facilitate” tree establishment on such sites by improving their water relations, in order to counteract some of the competitive effects of herbaceous vegetation.

Such “artificial facilitation” of tree growth in abandoned fields has been obtained with mulching, which

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increases soil water availability around trees (Truax & Gagnon 1993; Cogliastro et al. 1997b). However, mulched trees still encounter belowground competition from surrounding herbaceous plants, as an increase in herbaceous biomass around the mulch has often been observed (Davies 1985; Truax & Gagnon 1993; Cogliastro et al. 1997b). Consequently, the positive impacts of mulching seem to be primarily due to a reduction of soil evaporation, which benefits both the tree and the surrounding vegetation, and not to a reduction of competition per se.

In addition to mulching, treeshelters could potentially facilitate tree seedling establishment in herbaceous communities. Treeshelters, which were first made popular by Tuley (1985) and are largely used to protect tree seedlings from herbivores (e.g., Stange & Shea 1998; Ward et al. 2000; Sweeney et al. 2002), can increase tree seedling growth, especially height growth (Davies 1985; Tuley 1985; Potter 1988). Treeshelters generally reduce light availability (Sharew 2005), and some authors have linked their positive effects on growth to an improvement of tree water relations due to a reduction of solar radiation (Bellot et al. 2002) or to an increase in the boundary-layer resistance to water vapor (Kjelgren 1994; Kjelgren et al. 1994). Interestingly, it appears that these mechanisms are similar to those associated with the facilitation of tree seedling establishment under the canopy of nurse-plants (i.e., isolated trees) in herbaceous communities (Callaway & Walker 1997; Holmgren et al. 1997).

Based on this model, treeshelters, like nurse-plants, could either have positive or negative effects on tree growth, depending on whether light or water is the main factor limiting tree establishment (Holmgren et al. 1997). Furthermore, because distinct resource heterogeneity occurs even in old fields with uniform vegetation and little topographic relief (Kelly & Canham 1992), the effect of treeshelters could also shift from positive to negative along subtle resource gradients within a single field. However, no study has yet considered how microenvironmental factors can influence the effect of treeshelters on tree growth. In this study, we wished to answer the following questions:

- (1) Can tree shelters facilitate growth of tree seedlings planted in herbaceous old fields, when only mulching is used?
- (2) What is the relative impact of treeshelters and environmental factors on tree growth, allometry, and water relations?
- (3) How does the effect of treeshelters on tree growth vary along different environmental gradients within a single field?

Methods

Study Area and Site Selection

The study area was located within the Parc national des îles-de-Boucherville (lat 45°N, long 73°W), an 8-km²

archipelago located in the Saint-Lawrence River near the city of Montréal (Québec, Canada). The region is characterized by 2,109 degrees-days above 5°C, and mean temperatures of the warmest (July) and coldest (January) months of 20.5 and -10.4°C, respectively (MSC 2006). Mean annual precipitation is 1046 mm, 25% of which falling as snow (MSC 2006). Most of the islands within the park have been cultivated since the end of the seventeenth century (Giroux 1986), and about one-third of the park is still under cultivation. Although the park was originally created to protect riparian habitats on the islands, park authorities have since reclaimed land that was under lease to farmers, in an effort to restore forested ecosystems.

The study site was a recently abandoned (2 years) agricultural field (6 ha) where vegetation was composed mostly of a dense herbaceous cover of *Solidago canadensis*, with *Cirsium arvense*, *Agropyron repens*, and *Trifolium pratense* also being common. No woody species were present on the site. Prior to abandonment, sweet corn was grown without the use of persistent herbicides (e.g., atrazine, simazine) because these are not allowed in the park. Surficial materials were composed of fluvial and marine deposits overlaying black shist (Utica group). Soils were a loam (47% silt, 43% sand, 11% clay; Laliberté, unpublished data), which can be classified as a humic gleysol (SCWG 1998). Drainage was moderate to imperfect. Topography was mainly flat, with a slight depression in the middle of the field. Absolute difference in elevation between the highest and lowest position was 2.9 m. In June 2004, water table was 70 cm deep in lower areas of the study site.

Experimental Design

The experimental design was a complete randomized block design, with three blocks that were each composed of two plots (treeshelter versus control). Blocks were spread across the field and separated by around 100 m. Plots were 25 × 25 m, oriented along a north-south axis. In each plot, three native hardwood species were planted at the beginning of June 2004: *Acer saccharinum*, *Fraxinus pennsylvanica*, and *Quercus macrocarpa*. Those species were selected from the main tree species found in an 8-ha woodland that bordered the study site. They were also well adapted to the edaphic conditions of the study site, according to Cogliastro et al. (1997a). All tree seedlings were produced at the Berthier nursery of Québec Ministry of Natural Resources. *Acer saccharinum* (1 + 0)¹ and *F. pennsylvanica* (1 + 0) were container produced, whereas *Q. macrocarpa* (2 + 0) was field produced (bare-root seedlings). Each plot contained 30 *A. saccharinum*,

¹First number = number of growing seasons prior to pricking out in the nursery. Second number = number of growing seasons following pricking out. The sum of those two numbers indicates total seedling age.

30 *F. pennsylvanica*, and 22 *Q. macrocarpa* seedlings. Spacing between seedlings was 2×2 m.

In treeshelter plots, each tree was planted inside a 1.5-m high polyethylene (2×2 -mm mesh) treeshelter (Freegro[®], Prince-Rupert, British Columbia, Canada), whereas in control plots no treeshelters were used. The treeshelters used in this study transmitted 40% of photosynthetic photonic flux density (PPFD) of full sun (Laliberté, unpublished data). Control plots were surrounded by a 2.5-m-high wire fence to prevent damage by White-tailed deer (*Odocoileus virginianus*), which are abundant in the study area. No fencing was used for treeshelter plots because treeshelters themselves efficiently prevent deer herbivory (Stange & Shea 1998).

No site preparation was done prior to planting, and no herbicides were used throughout the study. However, plastic mulch (1×1 m) was used around each seedling, regardless of treatment (treeshelter or control). This was considered essential in order to reach acceptable survival and growth rates because of the very dense herbaceous cover present on the study site (Fig. 1). All seedlings were also protected against rodents with spiral plastic protectors (TIMM Entreprises Ltd., Milton, Ontario, Canada).

Data Collection

Height and collar diameter were recorded for each seedling directly after planting (June 2004), and measured again in September 2004 and 2005. Prior to planting, 30 extra seedlings per species (randomly selected) were used

to calculate allometric regression equations to predict dry shoot and root biomass of all planted seedlings from their initial height and collar diameter.

During the 2005 summer, a number of environmental variables were measured on a randomly selected sample of 15 seedlings per species per plot (270 seedlings total). For each of those seedlings, soil water (% volume) was measured three times (May, June, and July 2005) using time-domain reflectometry (ML2X probe; ΔT Devices, Cambridge, United Kingdom). Available photosynthetic photonic flux density at 30 cm (%PPFD_{30cm}) height and at the top of the seedling crown (%PPFD_{tree}) was measured two times (June and July 2005) with Li-190 probes (Li-Cor Biosciences, Lincoln, NE, U.S.A.), following the methodology described by Parent and Messier (1996). Red: far-red ratio was also measured at 30 cm (R/FR_{30cm}) and at the top of seedling crown (R/FR_{tree}) in July 2005, using a SKR-110 probe (Skye Instruments, Powys, United Kingdom). For trees inside treeshelters, %PPFD_{tree} and R/FR_{tree} took in account the combined effects of surrounding vegetation and treeshelters on light levels, whereas %PPFD_{30cm} and R/FR_{30cm} measured only the effect of surrounding vegetation.

Between 29 and 31 August 2005, for a subsample of five randomly selected trees per species per plot (selected from the 15 trees per species per plot described above), two 25×50 -cm quadrats were placed along the mulch, in which surrounding herbaceous biomass was cut to ground level and split into four different groups: (1) *S. canadensis*; (2) *A. repens*; (3) *C. arvensis*; and (4) other species. The



Figure 1. Tree seedlings in treeshelter (A) and control plots (B) at the end of the 2005 growing season. (A) After two growing seasons, this *Fraxinus pennsylvanica* seedling has grown past the treeshelter, which was 1.5 m high. Surrounding herbaceous vegetation is composed primarily of a dense *Solidago canadensis* cover. Plastic mulch (1×1 -m) has been used at the base of the tree but cannot be seen in this picture. (B) *Acer saccharinum* seedling in a control plot, at the same date. Surrounding herbaceous vegetation is also composed of *S. canadensis*. Again, the 1×1 -m plastic mulch cannot be seen on the picture because it has been grown over by vegetation. (Photos by E. Laliberté, September 2005)

first three groups corresponded to the most abundant species on the study site, as determined from percent cover and biomass data. Herbaceous biomass was dried in a greenhouse for 3 weeks and then weighed. Mean height of surrounding herbaceous was also estimated on 29 August 2005.

Leaf stomatal conductance (g), predawn leaf water potential (Ψ_{am}), and leaf water potential (Ψ_{pm}) were measured after warm and dry spells (3–4 days without a significant rain event and afternoon temperatures around 30°C) in June and July 2005. Leaf stomatal conductance from one mature, subterminal, and sun-exposed leaf was measured (on the same 15 trees per species per plot) from 12:00 to 15:00, using a steady-state porometer (PMR-1; PP Systems, Hertfordshire, United Kingdom). For seedlings inside treeshelters, a small window was cut at the desired height in order to allow measurement of g without disturbing micro-environmental conditions inside the shelter, and the window was taped back afterward (e.g., Kjelgren 1994). In July and August 2005, Ψ_{am} (03:00–06:00) and Ψ_{pm} (12:00–15:00) were each measured once per species using a pressure chamber (model 600; PMS Instrument Co., Albany, OR, U.S.A.), following the methodology described by Turner and Long (1980) and Boyer (1995). Leaf water potentials were measured on the same subsample (five trees per species per plot) that had been used for herbaceous biomass.

At the end of two growing seasons (mid-September 2005), but prior to leaf shed, aboveground biomass of each tree from the larger sample (15 trees per species per plot) was harvested, dried for 2 weeks in a greenhouse, and then oven dried at 50°C for 72 hours. Prior to this, three leaves per tree (one at the top of the crown, one in the middle, and one at the bottom) were taken for leaf area measurements (MK2 Area Meter; ΔT Devices). Those leaves were dried and weighed, and specific leaf area (SLA) was calculated. Dry root biomass was also evaluated, but for *F. pennsylvanica* only, because of limited time and resources. To do so, half of the root system from five trees per plot was carefully dug up by hand. Roots were then washed, oven dried at 50°C for 72 hours, and the resulting dry weight was multiplied by two in order to give an estimate of the whole root system. Finally, aboveground dry biomass from all harvested trees was partitioned into leaves, stalks, branches, and trunk, which were individually weighed. Relative height growth rate (RGR_H), as well as diameter (RGR_D), aboveground biomass (RGR_{AB}), belowground biomass (RGR_{BB} ; *F. pennsylvanica* only), and total biomass (RGR_{TB} ; *F. pennsylvanica* only) were calculated using Equation 1:

$$RGR_X = \frac{\ln(X_f) - \ln(X_i)}{t} \quad (1)$$

where X_f and X_i were, respectively, final (mid-September 2005) and initial (June 2004) height, diameter, aboveground biomass, belowground biomass, or total biomass, whereas t was the duration of the experiment in years (in

our case, 2). For each tree that had been harvested, a number of allometric ratios were also calculated: leaf weight ratio (LWR = total leaf weight on total seedling aboveground biomass), leaf area ratio (LAR = total leaf area on total seedling aboveground biomass), height:diameter ratio (H/D), and branch weight:trunk weight ratio (B/T). Root weight ratio (RWR = root weight on total seedling biomass) was also calculated for *F. pennsylvanica*.

In July 2005, elevation, latitude, and longitude of each tree were measured using a high-precision differential GPS (Radian IS; Sokkia Corporation, Kanagawa, Japan), with a mean error of ± 1.5 cm. Using these data, as well as data from 780 additional points, a digital elevation model of the study site was created, from which a slope model was also obtained. This was done using SIGIS software (SIGISCO, Inc., Montréal, Québec, Canada).

Data Analysis

A mixed analysis of variance (ANOVA) model was used to test for the effects of treeshelters on relative growth rates, allometric ratios, and water relations. Because previous analyses had shown significant ($p \leq 0.05$) treatment \times species interactions (results not shown), species were analyzed individually. These interactions were due to the fact that *F. pennsylvanica* generally reacted strongly to the treatment (mainly growth), whereas *Q. macrocarpa* did not. All tests were performed with 9,999 permutations of residuals under a reduced model (Anderson & ter Braak 2003). Because factor “treatment” had a low number of possible permutations (<100), Monte-Carlo asymptotic p values were used instead of permutational p values for this factor (Anderson 2001). Analyses were performed using PERMANOVA software (Anderson 2005).

Canonical redundancy analyses (RDA) were used to analyze the relative effects of environmental variables and treatment on all response variables (growth, allometry, water relations). Species were analyzed individually and response variables were standardized to make them dimensionally homogenous (Legendre & Legendre 1998). Treatment factors (treeshelter and control) were coded as orthogonal dummy variables (Draper & Smith 1981). Forward selection (at $\alpha = 0.1$) of explanatory variables was used, and all tests were performed using 9,999 permutations of residuals under a reduced model. In order to assess the potential effects of surrounding vegetation on tree growth and physiology, three variables (surrounding vegetation biomass, surrounding *S. canadensis* biomass, and height of surrounding vegetation) were added as supplementary (i.e., passive) variables if they had been left out in the forward selection procedure. This was done to illustrate their correlation with other variables. To account for the blocked structure of the experiment, permutations were restricted within blocks, which were used as covariables. Analyses were performed with CANOCO (ter Braak & Smilauer 2002), and unbiased adjusted R^2 values (R_a^2) were calculated a posteriori (Peres-Neto

et al. 2006). R_a^2 values, which correct for the artificial increase of explanatory power due to the mere addition of predictors, were calculated following Equation 2:

$$R_a^2 = 1 - \frac{n - 1}{n - p - 1} (1 - R^2) \quad (2)$$

where n is the number of samples, p the number of predictors, and R^2 the standard canonical coefficient of determination (Peres-Neto et al. 2006).

To test the effect of treeshelters on tree growth along different environmental gradients (soil water, light availability, surrounding vegetation height, and surrounding herbaceous biomass) analysis of covariance (ANCOVA) was used. Again, species were analyzed individually. In these analyses, we were specifically interested in the presence of a significant ($p \leq 0.05$) “treatment \times covariable” interactions in ANCOVA, which indicated that the effect of treeshelters differed along the gradient, relative to the control. In the presence of a significant interaction, we tested individual regression lines (i.e., for each treatment) at $\alpha = 0.05$. Analyses were performed using JMP (SAS 2003). Pearson correlation coefficients between covariables were also calculated and tested by permutation (9,999 random permutations of one of the two vectors).

Results

Treeshelters significantly improved height growth (RGR_H) of *Acer saccharinum* and *Fraxinus pennsylvanica*, as well as

above- (RGR_{AB}) and belowground biomass growth (RGR_{BB}) of *F. pennsylvanica* (Table 1). Treeshelters had no growth effect on *Quercus macrocarpa*. Treeshelters increased H/D of *F. pennsylvanica*, increased SLA or LAR of all species, while decreasing LWR of *Q. macrocarpa* (Table 1). In general, treeshelters had no effect on water relations, although they significantly decreased midday g of *Q. macrocarpa* and predawn water potential (Ψ_{am}) of *F. pennsylvanica* (Table 1).

The RDA models (Fig. 2), which were all significant ($p \leq 0.01$), explained between 12.2 and 49.5% (R_a^2) of the variation of all response variables (e.g., RGRs, allometric ratios, and water relations). *Quercus macrocarpa* was the species that was the least influenced by the treatment and the environment, whereas *F. pennsylvanica* was the most influenced one (Fig. 2). For each species, treatment (i.e., treeshelter and control) was selected in the forward selection procedure (at $\alpha = 0.1$). The correlations between the orthogonal treatment vectors (treeshelter versus control) and the different response variables were consistent with the results from ANOVA (Table 2). For example, the “treeshelter” vector was strongly positively correlated with SLA and LAR in all species (Fig. 2), while ANOVA had shown that treeshelters significantly increased SLA and/or LAR (Table 2). In addition, light quality (R/FR_{tree}) was strongly positively correlated with growth, especially diameter and aboveground biomass relative growth rates (and belowground biomass growth rate for *F. pennsylvanica*) (Fig. 2). Light quality (R/FR_{tree}) was negatively correlated to the quantity of surrounding herbaceous vegetation, expressed either by height of vegetation (H_{Herb}) or biomass (W_{Herb}) (Fig. 2). Surrounding

Table 1. Growth, allometric ratios, and water relations of *Acer saccharinum*, *Fraxinus pennsylvanica*, and *Quercus macrocarpa* in treeshelter and control plots.

	<i>Acer saccharinum</i>		<i>Fraxinus pennsylvanica</i>		<i>Quercus macrocarpa</i>	
	Treeshelter	Control	Treeshelter	Control	Treeshelter	Control
Growth						
RGR _D (mm mm ⁻¹ yr ⁻¹)	1.59 ± 0.22 ^a	1.61 ± 0.23 ^a	1.64 ± 0.25 ^a	1.57 ± 0.19 ^a	1.29 ± 0.20 ^a	1.40 ± 0.18 ^a
RGR _H (cm cm ⁻¹ yr ⁻¹)	2.91 ± 0.41^a	2.61 ± 0.37^b	3.02 ± 0.36^a	2.55 ± 0.28^b	2.32 ± 0.50 ^a	2.25 ± 0.34 ^a
RGR _{AB} (g g ⁻¹ yr ⁻¹)	2.74 ± 0.67 ^a	2.60 ± 0.65 ^a	2.89 ± 0.71^a	2.29 ± 0.61^b	1.68 ± 0.74 ^a	1.87 ± 0.54 ^a
RGR _{BB} * (g g ⁻¹ yr ⁻¹)	—	—	2.57 ± 0.42^a	2.31 ± 0.54^b	—	—
RGR _{TB} * (g g ⁻¹ yr ⁻¹)	—	—	2.79 ± 0.48 ^a	2.25 ± 0.50 ^a	—	—
Allometric ratios						
SLA (m ² /kg)	23.44 ± 2.88 ^a	18.58 ± 2.24 ^a	25.01 ± 3.85^a	18.38 ± 2.96^b	21.33 ± 7.99^a	15.48 ± 2.27^b
LAR (m ² /kg)	7.16 ± 1.49^a	6.10 ± 0.98^b	6.12 ± 1.54 ^a	4.90 ± 1.11 ^a	6.64 ± 2.63^a	5.57 ± 1.60^b
LWR (%)	30.65 ± 5.67 ^a	32.91 ± 4.18 ^a	24.36 ± 4.30 ^a	26.60 ± 3.86 ^a	31.79 ± 10.35^a	35.76 ± 7.78^b
H/D (cm/mm)	9.78 ± 2.23 ^a	7.03 ± 1.70 ^a	10.56 ± 2.86^a	6.84 ± 1.81^b	6.90 ± 3.21 ^a	5.40 ± 1.97 ^a
B/T (%)	10.32 ± 9.41 ^a	12.17 ± 9.07 ^a	5.22 ± 5.88 ^a	4.12 ± 6.24 ^a	13.83 ± 11.75 ^a	17.72 ± 14.67 ^a
RWR* (%)	—	—	34.52 ± 4.67 ^a	42.35 ± 6.52 ^a	—	—
Water relations						
g (mmol [m ²] ⁻¹ second ⁻¹)	133.0 ± 46.3 ^a	155.1 ± 64.6 ^a	187.2 ± 94.8 ^a	429.7 ± 288.3 ^a	179.3 ± 96.3^a	332.4 ± 188.3^b
Ψ_{am} (MPa)	-0.47 ± 0.08 ^a	-0.39 ± 0.22 ^a	-0.68 ± 0.12^a	-0.47 ± 0.06^b	-0.36 ± 0.12 ^a	-0.23 ± 0.11 ^a
Ψ_{pm} (MPa)	-1.25 ± 0.21 ^a	-1.11 ± 0.60 ^a	-1.58 ± 0.32 ^a	-1.43 ± 0.29 ^a	-1.01 ± 0.41 ^a	-0.98 ± 0.42 ^a

Values are $\bar{X} \pm SE$. For each species and each variable, means of each column followed by different subscript letters (in bold) are significantly different at $p \leq 0.05$ according to ANOVA.

*Measured on *F. pennsylvanica* only.

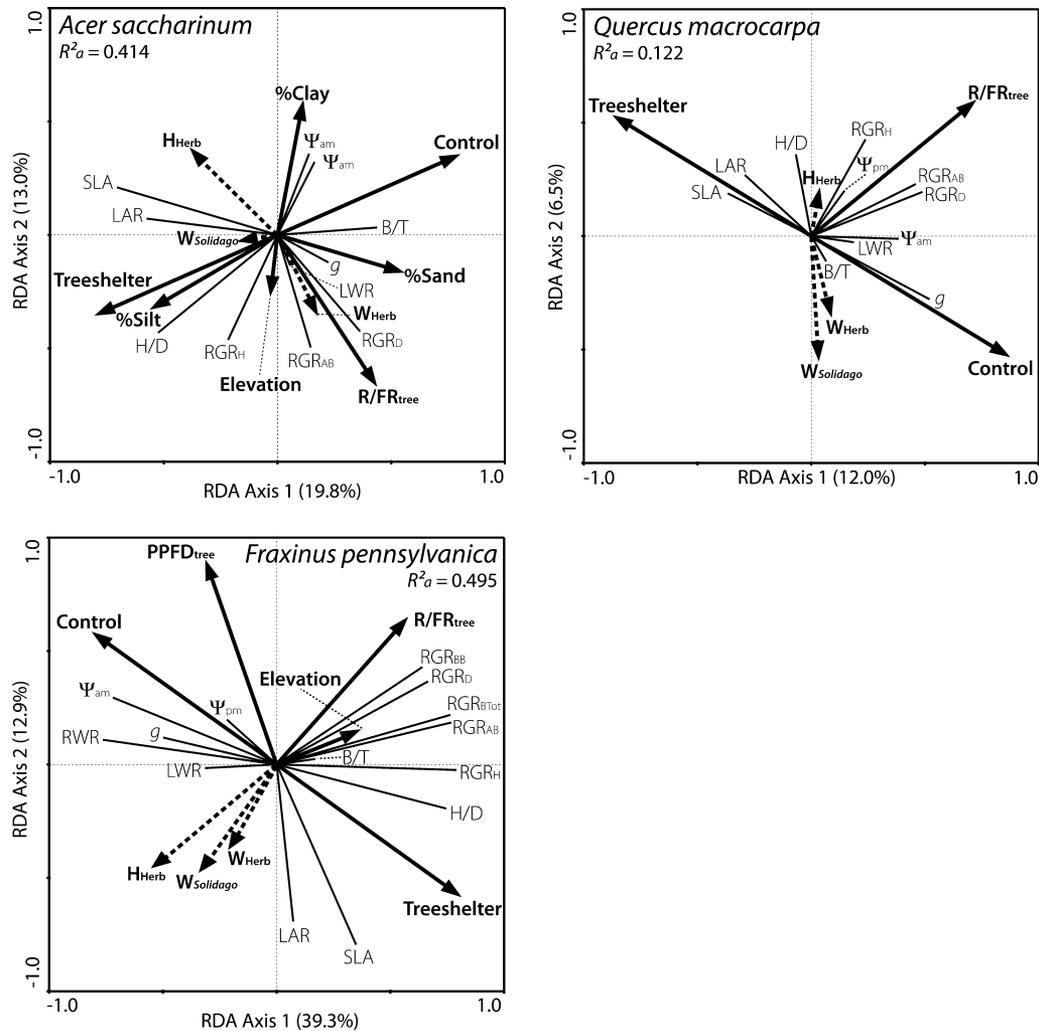


Figure 2. Canonical redundancy (RDA) biplots illustrating the effects of environmental factors and treatment (treeshelter versus control) on tree growth, allometric ratios, and water relations. All models are significant ($p \leq 0.01$). Percent variation explained by each canonical axis is indicated on the biplots. Unbiased adjusted R^2 values (R^2_a) were calculated a posteriori. Biplot scores are represented following type II scaling (correlation biplot). Arrows indicate explanatory variables (environmental factors or treatment) that were included in the model after forward selection ($\alpha = 0.1$), whereas lines (without arrows) indicate response variables. Dashed arrows are supplementary explanatory variables (variables related to surrounding herbaceous vegetation only) that were not included in the model and are shown on the biplots to indicate their correlation with other variables. RGR_{BTot} , relative total biomass (above- and belowground) growth rate; %Clay, percentage of clay in soil; %Sand, percentage of sand in soil; %Silt, percentage of silt in soil.

herbaceous biomass of *Solidago canadensis* ($W_{Solidago}$) was negatively correlated with growth of *F. pennsylvanica* and *Q. macrocarpa* but weakly correlated to growth of *A. saccharinum* (Fig. 2). However, all variables related to surrounding vegetation were never selected in the forward selection procedure and are only shown on Figure 2 as supplementary variables. Finally, elevation, which was strongly negatively correlated with soil water ($r = -0.614$, $p < 0.001$), was also positively correlated with growth of *A. saccharinum* and *F. pennsylvanica* but not of *Q. macrocarpa*.

The effect of treeshelters on growth varied along certain environmental gradients, as indicated by significant treatment \times covariable interactions in ANCOVA (results not shown). It should be noted, however, that the different

covariables used in ANCOVA were all significantly ($p \leq 0.001$) intercorrelated (Table 2). Although treeshelters increased RGR_D of *A. saccharinum*, compared to the control, when soil water was high (i.e., above 25% vol.), they inhibited RGR_D when soil water was lower (Fig. 3). Treeshelters also increased height growth (RGR_H) of *A. saccharinum* when surrounding vegetation was below 1.5 m high, but inhibited RGR_H when surrounding vegetation was higher (Fig. 4); a similar relationship was obtained with aboveground biomass growth (RGR_{AB}) of *Q. macrocarpa* (Fig. 5). Finally, height growth (RGR_H) of *F. pennsylvanica* was greater in treeshelters when surrounding herbaceous biomass was below 6.0 kg/m², but the opposite was observed above that level (Fig. 6).

Table 2. Pearson correlation matrix of the five environmental covariables used in ANCOVA.^a

	H_2O_{soil}	H_{Herb}	W_{Herb}	%PPFD _{30cm}	R/FR _{30cm}
H_2O_{soil}	—	—	—	—	—
H_{Herb}	-0.405*	—	—	—	—
W_{Herb}	-0.356*	0.380*	—	—	—
%PPFD _{30cm}	0.536*	-0.832*	-0.627*	—	—
R/FR _{30cm}	0.535*	-0.743*	-0.634*	0.906*	—

H_2O_{soil} , soil water.

^aCorrelation coefficients were tested by permutation (9,999 permutations of one of the two vectors).

* $p \leq 0.001$.

Discussion

Our results showed that the establishment of hardwood trees in an herbaceous old field can be facilitated by the use of treeshelters, when mulching is solely used to control herbaceous vegetation. In this study, treeshelters improved height growth of *Acer saccharinum* and *Fraxinus pennsylvanica*, as well as above- and belowground biomass growth of *F. pennsylvanica*, but had no effect on the growth of *Quercus macrocarpa*. Because deer were excluded from control plots in this study, the positive effects of treeshelters on growth could not be attributed to protection from browsing, contrary to previous studies where deer significantly impacted the growth of unprotected seedlings (Stange & Shea 1998; Taylor et al. 2006).

Moreover, positive impacts of treeshelters on growth were not linked to an improvement of tree seedling water relations. Indeed, they either had no effect on leaf stomatal conductance (g) or leaf water potential (Ψ_{am} or Ψ_{pm}), or negatively influenced them. Treeshelters decreased g of *Q. macrocarpa*, as well as Ψ_{am} of *F. pennsylvanica*. However, those negative

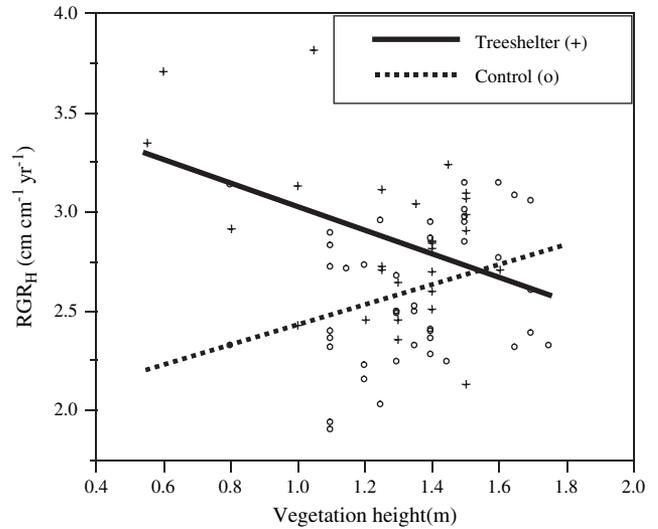


Figure 4. Effect of surrounding vegetation height on RGR_H of *Acer saccharinum* in treeshelters versus control. Regression slopes are significantly different ($p \leq 0.05$) according to “treatment \times covariable” in ANCOVA. Each individual regression line is significant ($p \leq 0.05$).

influences were not an indication of water stress, even though g or Ψ were measured during warm spells, following at least three days without precipitation. For example, various genotypes of *F. pennsylvanica* have been shown to tolerate Ψ values around -1.5 to -2.0 MPa without adverse effects to photosynthesis (Abrams et al. 1990); values quite lower than the mean Ψ_{am} observed in this study for this particular species in treeshelters (-0.49 MPa).

The presence of negative influences of treeshelters on water relations, or the absence of effect on them, is

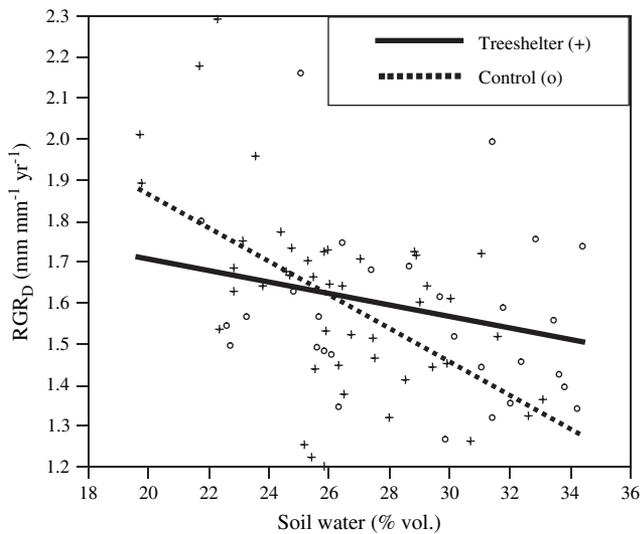


Figure 3. Effect of soil water on RGR_D of *Acer saccharinum* in treeshelters versus control. Regression slopes are significantly different ($p \leq 0.05$) according to “treatment \times covariable” in ANCOVA. Each individual regression line is significant ($p \leq 0.05$).

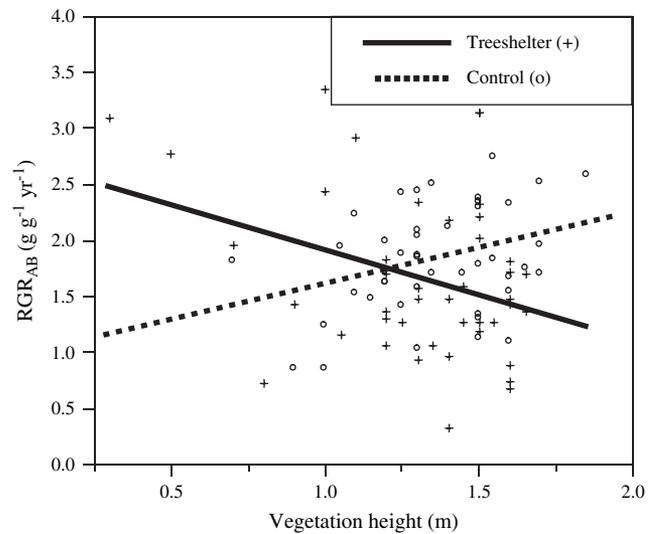


Figure 5. Effect of surrounding vegetation height on RGR_{AB} of *Quercus macrocarpa* in treeshelters versus control. Regression slopes are significantly different ($p \leq 0.05$) according to “treatment \times covariable” in ANCOVA. Each individual regression line is significant ($p \leq 0.05$).

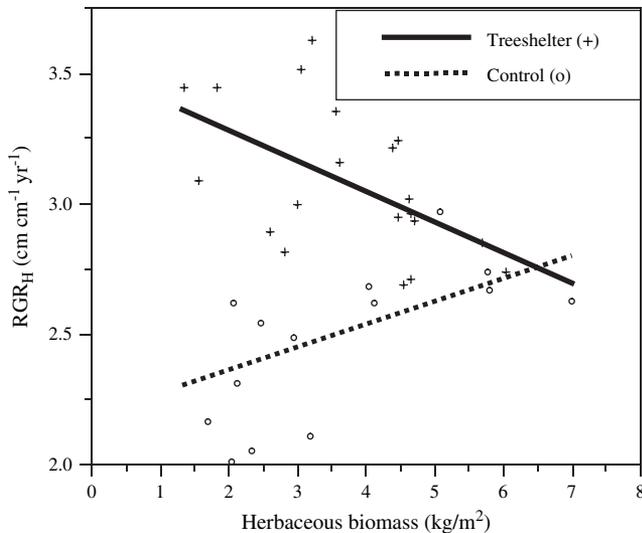


Figure 6. Effect of surrounding herbaceous biomass on RGR_H of *Fraxinus pennsylvanica* in treeshelters versus control. Regression slopes are significantly different ($p \leq 0.05$) according to "treatment \times covariable" in ANCOVA. Each individual regression line is significant ($p \leq 0.05$).

contrary to the results of other studies that had shown that treeshelters could increase g (Kjelgren 1994; Bergez & Dupraz 1997; Kjelgren et al. 1997; Kjelgren & Rupp 1997a) and Ψ_{pm} (Kjelgren & Rupp 1997a; Kjelgren et al. 2000). A decrease of Ψ_{am} , but without any effect on Ψ_{pm} , has also been previously observed (Kjelgren 1994; Kjelgren & Rupp 1997b). Those studies, however, were conducted in warmer and drier regions than our study area (Utah, western U.S.A., and Montpellier, southern France), where water deficit might have been a crucial factor limiting tree establishment.

In this study, it appears that water limitation was unlikely, even though tree seedlings were surrounded by dense herbaceous vegetation (4 kg/m^2 , mean dry weight). In fact, tree growth was generally greater on elevated sites (differential of 2.9 m) where soil water was lower. Furthermore, mean Ψ_{am} and Ψ_{pm} measured during warm and dry spells did not indicate water stress in any of the three species planted. Therefore, although competition for soil water between tree seedlings and herbaceous vegetation is largely recognized as the main factor limiting tree growth and survival in herbaceous communities (Gordon & Rice 1993; Davis et al. 1998), this was not observed in this study, and different factors can be put forward to explain this situation. First, mulching could have increased soil humidity around trees, as it has been previously observed in similar conditions (Cogliastro et al. 1997b). Second, the relatively high water table could have maintained fairly high soil water levels through capillarity (Foth 1984). Soil water levels below 20% volume have rarely been measured, even during warm and dry periods. Finally, precipitation at the study site during the 2004 and 2005 growing seasons (May to September) was 5.2 and 24.5% higher than the 1971–2000 mean values

(MSC 2006). Those three factors combined could have lessened the competitive impact of herbaceous vegetation on tree establishment by increasing water availability, as it has been demonstrated by Davis et al. (1998).

We suggest that the positive impacts of treeshelters on growth observed in this study were primarily the result of leaf morphological adaptations that can be attributed to the reduction of light intensity. Treeshelters increased SLA and/or LAR of the three species planted: adaptations that are commonly observed in plants exposed to lower light levels (Young & Smith 1980; Björkman 1981). Increases in SLA in lower light levels can be attributed to reductions in mesophyll cell layers (Pons 1977; Björkman 1981), nonstructural carbohydrates (Waring et al. 1985), as well as phenolic compounds (Waring et al. 1985; Mole & Waterman 1988). A higher SLA and LAR is associated with a lower respiratory burden per unit leaf area (Lambers & Poorter 1992). However, seedlings inside treeshelters were exposed to a lower light intensity, which could potentially lower photosynthesis. Therefore, the overall effect of treeshelters on tree growth (facilitation or inhibition) would be mainly determined by their impact on carbon budget: if the reduction of "carbon costs" (i.e., lower respiratory burden due to higher SLA and LAR) was greater than the potential reduction of "carbon gains" (i.e., lower photosynthesis due to lower light), treeshelters would then facilitate growth, whereas the opposite relationship would inhibit it.

Maximum photosynthesis (A_{max}) of seedlings of *A. saccharinum* is attained at a PPFD of around $1,200 \mu\text{mol m}^{-2} \text{ second}^{-1}$ (Peterson & Bazzaz 1984), whereas it is reached around $400 \mu\text{mol m}^{-2} \text{ second}^{-1}$ for *Q. macrocarpa* (Hamerlynck & Knapp 1994). Bartlett and Remphrey (1998) have found that there was little increase in above-ground growth of *F. pennsylvanica* seedlings above 40% PPFD of full sun. Because mean PPFD in the open, on a sunny summer day, is around $1,600 \mu\text{mol m}^{-2} \text{ second}^{-1}$ in our region (Routhier & Lapointe 2002), and because treeshelters used in this study let 40% of PPFD through (Laliberté, data not shown), we can estimate that they transmitted $640 \mu\text{mol m}^{-2} \text{ second}^{-1}$ of PPFD on a sunny day. Therefore, it can be assumed that PPFD levels inside treeshelters did not limit photosynthesis of *F. pennsylvanica* or *Q. macrocarpa*, although for *A. saccharinum*, $640 \mu\text{mol m}^{-2} \text{ second}^{-1}$ corresponds to 70% of the A_{max} of 1-year seedlings (Peterson & Bazzaz 1984). Consequently, the positive impacts of treeshelters on growth that were observed in this study appear to be linked to an optimization of light levels inside the shelter, where light intensity was reduced enough to increase SLA and/or LAR, but high enough to have no, or few, adverse impacts on photosynthesis. This could explain the positive impacts of treeshelters on the growth of *A. saccharinum* (RGR_H) and *F. pennsylvanica* (RGR_H , RGR_{AB} , RGR_{BB}). Our results, however, showed that treeshelters had no effect on the growth of *Q. macrocarpa*; yet, it should be noted that the belowground growth (RGR_{BB}) was not measured. It is

possible that, for this species, the potential improvement of its carbon budget in treeshelters led mostly to belowground growth gains. During the first years of establishment, *Q. macrocarpa* seedlings invest a large part of their carbon resources toward the development of a deep and extensive root system (Weaver & Kramer 1932; Bragg et al. 1993).

Even though our study site appeared to be relatively homogenous (e.g., similar vegetation composition, low topographic relief), environmental heterogeneity played an important role on tree establishment. For example, microtopography influenced growth of *A. saccharinum* and *F. pennsylvanica*, which was higher on elevated areas. Light quality (R/RF_{tree}), which was influenced by surrounding herbaceous vegetation height and standing biomass, also appeared to be a limiting factor to tree growth for all species. Indeed, our results showed that tree growth was generally lower when surrounding vegetation was high (either height or standing biomass), likely mainly because of competition for light resources. However, other factors may have been involved in the interference between herbaceous vegetation and tree seedlings. For example, previous studies have suggested that *Solidago* species may inhibit tree seedling establishment through competition for soil nitrogen (Burton & Bazzaz 1995) and allelopathy (Horsley 1977; Fisher et al. 1978). There is evidence that plants are most susceptible to allelopathy under wet conditions (Fischer 1978; Ito et al. 1998), which may partly explain the poorer growth observed in lower areas with higher soil water for *A. saccharinum* and *F. pennsylvanica*. However, our experimental design does not allow us to directly test these hypotheses because we are unable to uncouple these potential sources of interference from competition for light.

In addition to the effect of environmental heterogeneity on tree growth, our results showed that the effect of treeshelters (facilitation or inhibition) could vary along gradients of soil water, as well as surrounding vegetation biomass and height. Those environmental variables, however, were all highly significantly intercorrelated. Soil water was positively correlated to light availability (quantity, %PPFD_{30cm} and quality, R/FR_{30cm}) and negatively correlated to surrounding herbaceous biomass and height. Light quantity (%PPFD_{30cm}) and light quality (R/FR_{30cm}) were also strongly positively correlated. Hence, trees planted in areas with higher soil water were surrounded by less herbaceous vegetation and thus were exposed to higher light levels. Because herbaceous vegetation on our study site was dominated by *Solidago canadensis*, which grew up to 1.8 m high (Laliberté, unpublished data), a dense cover of this species around tree seedlings could block a significant amount of light. Overall, treeshelters appear to have facilitated tree growth when surrounding vegetation was low (i.e., high light availability), while inhibiting growth when surrounding vegetation was high (i.e., lower light levels).

Those results are consistent with our “light optimization” model inside treeshelters, based on a balance

between a reduction in carbon costs and carbon gains. In general, treeshelters had positive impacts on tree growth when light levels were sufficient, but when surrounding herbaceous vegetation was important, competition for light became a crucial factor. This likely led to a reduction of carbon gains in treeshelters (i.e., lower photosynthesis) greater than the reduction of carbon costs (i.e., higher SLA and/or LAR), thus leading to poorer growth in treeshelters than the control. Our results are similar to those of Bardon et al. (1999), who attributed growth reductions of underplanted *Quercus rubra* in treeshelters to insufficient light levels in the understorey. However, light transmission between different treeshelter models is variable (Sharew 2005), and care must then be taken in selecting a proper model for a particular situation.

In summary, although treeshelters have been shown to improve tree establishment in water-limited environments (Kjelgren 1994; Kjelgren et al. 1994, 2000; Bellot et al. 2002), our results show that when water is a not limiting factor, treeshelters can still facilitate tree growth. In that case, positive impacts of treeshelters on growth can be mainly attributed to an optimization of light levels, which lead to an improvement in the carbon budget of the seedling. Treeshelters may not be adequate where surrounding vegetation is expected to block a substantial quantity of light. Therefore, environmental factors such as light availability need to be considered to optimize the success of hardwood plantations when treeshelters are used in recently abandoned agricultural fields.

Implications for Practice

- Treeshelters can improve hardwood tree establishment in herbaceous old fields, when mulching is solely used to control herbaceous vegetation.
- Environmental heterogeneity in recently abandoned fields can greatly influence tree seedling growth, even when such fields appear to be relatively homogenous (e.g., similar vegetation composition, low topographic relief). Furthermore, environmental heterogeneity can influence the effect of treeshelters on tree growth (facilitation or inhibition).
- Treeshelters will only show positive effects on tree growth if surrounding vegetation does not block too much light.
- Practitioners should ensure that the light transmission characteristics of the treeshelter model used, as well as light levels transmitted by surrounding vegetation, are sufficient for the tree species planted.

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