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Unexpected seedling growth in the understory of post-agricultural forests from Eastern Canada

Loïc D'Orangeville · André Bouchard · Alain Cogliastro

Abstract
• *Introduction* The agricultural landscape in Eastern Canada has drastically changed in the last decades. Whilst certain forest communities are disappearing, post-agricultural forests are emerging from old fields colonized by fast-growing tree species.
• *Objective* The objective of this study was to assess the seedling establishment and growth patterns of deciduous angiosperms in regenerating 14 of these aggrading forests.
• *Results* Red maple and black cherry showed clear temporal windows of establishment about 10–20 years following old field colonization by trees, contrary to sugar maple, white and green ash. Also, height growth rates of red maple and phenotypic plasticity of sugar maple did not correspond to their shade tolerance ranks. In general, low growth rates were found for all tree species, suggesting that the presence of adverse conditions could slow down the domination of post-agricultural stands by later successional species.
• *Conclusions* These results underline the specificity of post-agricultural contexts and militate for the implementation of

adapted management strategies that could help in reversing the trend of decreasing mature forests worldwide.

1 Introduction

Following biophysical, anthropological and technological transformations, agricultural landscapes in Eastern Canada have drastically changed in the last decades. Numerous impacts have been observed including significant change in species relative abundances. For example, intensive cattle grazing has played a significant role in the appearance of white cedar stands (*Thuja occidentalis* L.) in the deciduous forests of southern Quebec (De Blois and Bouchard 1995). Whilst certain forest communities are disappearing, old fields are becoming increasingly colonized and dominated by fast-growing tree species, thus becoming post-agricultural forests (Flinn and Vellend 2005). In southern Quebec, these young aggrading forests are generally dominated by trembling aspen (*Populus tremuloides* Michx.) or grey birch (*Betula populifolia* Marsh.). Many stakeholders today are hoping that these new forests could someday produce the goods and services historically provided by the lost primary forests.

Using the current models of forest succession would lead us to predict the plant succession in post-agricultural forests in terms of species shade tolerance. The general model of shade tolerance that prevails today classifies the species according to their carbon assimilation strategy (Bazzaz 1979; Givnish 1988). According to this model, phenotypic plasticity and low-light height growth rate explain the shade tolerance of a given species (Canham 1988). However, a

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number of studies on shade tolerance in tropical and temperate regions suggest otherwise: shade tolerance, rather than being determined by the carbon assimilation capacity, could be defined by the capacity for a tree to retain its biomass and energy through traits such as low respiration rate or high leaf longevity (Kitajima 1994; Reich et al. 2003). Thus, as some studies already suggested, this theory underlies that the characteristics maximizing carbon gain in a light-limited environment, such as phenotypic plasticity or height growth rate, are not necessarily determining the shade tolerance of a species (Beaudet and Messier 1998; Paquette et al. 2007a). It is clear, however, that these characteristics still affect the successional dynamic of a forest ecosystem. The conditions associated with a successful dispersal of the seed to the old field, germination of the seed, survival and growth of the seedling change with time during an old field succession. Invasion and establishment are functions of the availability of adequate conditions and could depend on the removal of a barrier that had previously excluded a species from a site. Therefore, succession largely depends on the type of barrier and the availability of adequate conditions in space and time. Such conditions were formalized by some authors in the concept of a "window" (see Rankin and Pickett 1989) which represents regeneration opportunities and probabilities.

A previous study showed the major role of soil and landscape agricultural footprint on the successional trajectory of the stands, which could lead to a weakened resilience capacity (D'Orangeville et al. 2008). Using abundance and distribution data, it was concluded that seedling composition and abundance were insufficient to ensure the future of these stands. To follow up on these results, our main objectives in this study were to (1) detect the presence of temporal establishment windows for dominant species at the seedling stage and (2) compare growth and phenotypic plasticity of the species in relation with their known shade tolerance and growing strategies. We studied species in the understory that are predicted to constitute the next generation of dominant canopy trees, i.e. sugar and red maple (*Acer saccharum* Marsh. and *Acer*

rubrum L.), white and green ash (*Fraxinus americana* L. and *Fraxinus pennsylvanica* Marsh.) and black cherry (*Prunus serotina* Ehrh.; see D'Orangeville et al. 2008). On a scale of 0 (no tolerance) to 5 (maximal tolerance), sugar maple is very shade-tolerant (4.8±0.11), followed by red maple (3.4±0.23), green ash (3.1±0.11), and shade-intolerant white ash (2.5±0.21) and black cherry (2.5± 0.34; Niinemets and Valladares 2006). Three major parameters of secondary succession were measured: (1) the time frame of species establishment, (2) the height growth rate and (3) the phenotypic plasticity to light and neighbouring plant cover.

2 Materials and methods

2.1 Study region

The study took place in three regional county municipalities of the southernmost part of the Province of Québec (Canada)—Haut-Saint-Laurent (45°7′ N, 73°59′ W), Acton (45°40′ N, 72°33′ W) and Brome-Missisquoi (45°10′ N, 72°46′ W)—to reflect a gradient of agricultural intensity and forested cover. Their respective forest cover represents 28%, 41% and 59% of the total surface area, respectively (Soucy-Gonthier et al. 2003). The region is part of the deciduous forest region of the Great Lakes and St-Lawrence River system (Rowe 1972). Haut-Saint-Laurent is located in the maple–bitternut hickory (*A. saccharum–Carya cordiformis* [Wangenh.] K. Koch) bioclimatic domain, whereas Acton and Brome-Missisquoi are located in the maple–basswood (*A. saccharum–Tilia Americana* L.) bioclimatic domain (Grandtner 1966). Climate is relatively homogenous between the three municipalities (Table 1). The Haut-Saint-Laurent area is part of the St-Lawrence River bottomlands, a vast and flat marine plain of clay deposits heavily cultivated. Ridges and mounds of morainic deposits topped by brown forest soils can be found (Laplante 1959). Acton and Brome-Missisquoi areas have a high diversity of surface deposits, with varying land uses, where old fields bound agricultural and forested

Table 1 Climate means of the studied municipalities (Environment Canada 2004)

RCM	Weather station (coordinates)	T_{AN} (°C)	T_{SE} (°C)	R_{AN} (mm)	Degree days >5°C
Haut-St-Laurent	St-Anicet (45°7′ N, 74°21′ W)	6.5	January: −9.6 July: 20.9	989.2 (rain: 813)	2,136.2
Acton	St-Hyacinthe 2 (45°34′ N, 72°55′ W)	6.2	January: −10.5 July: 21.1	1,057.9 (rain: 856)	2,131.4
Brome-Missisquoi	Brome (45°10′ N, 72°34′ W)	5.3	January: −10.5 July: 19.4	1,266.7 (rain: 994)	1,872.7

T_{AN} mean annual temperature, T_{SE} mean seasonal temperature, R_{AN} mean annual precipitation.

areas. Mesic sites are generally dominated by sugar maple, along with bitternut hickory or American beech (*Fagus grandifolia* Ehrh.). However, an increasing proportion of sites presenting various degrees of disturbance are colonized by red maple, grey birch and trembling aspen (Meilleur et al. 1994).

2.2 Stand sampling

Using criteria acquired from provincial forest maps, we limited our sampling to sites of good to imperfect drainage, low slope gradients (<4%) and soil depth >25 cm. Fourteen post-agricultural stands were sampled in 2004 and 2005 using a systematic sampling protocol. Five stands were surveyed in each study region, except in Haut-Saint-Laurent where one site was excluded because of unforeseen harvesting. Stand area ranged from 0.5 to 5 ha (Table 2). Stands are dominated by shade-intolerant species, mostly grey birch and trembling aspen, as well as bigtooth aspen (*Populus grandidentata* Michx.; see Table 3), although individuals of later successional species are often found in the canopy. Soil texture varies from sandy loam to clay loam, soil acidity varies from pH values of 4.5–7.6 (Table 2), and regeneration stocking is generally low (D'Orangeville et al. 2008). Four to six dominant trees were cored at their base on each site using an increment borer whilst avoiding veteran trees which could have been present when the properties were being farmed. Ring counts from tree cores allowed us to date the stands from the time since abandonment. Main canopy tree ages span from 12 to 50 years (Table 2). These numbers give a minimal estimation of the duration of secondary succession since agricultural abandonment because there is typically a delay between the point at which fields are abandoned and the period of tree invasion.

The number of transects and plots was proportional to the size of the stand, with two to four evenly distributed transects per site. Eight to 20 circular plots per site, spaced at 10-m intervals along transects, were sampled, for a total of 147 plots distributed on 14 sites.

2.3 Measurements

Vegetation survey was done using plots of various radii according to plant forms and sizes. Herb strata were surveyed in 3.1-m^2 plots, seedlings with a diameter at breast height (DBH, 1.37 m) <1 cm in 12.5-m^2 plots, small shrubs (DBH<10 cm) and saplings (DBH<10 cm) in 28.3-m^2 plots, and trees and shrubs (DBH>10 cm) in 154-m^2 plots. Total understory cover and cover by morphological groups were visually estimated. The estimation, based on the vertical projection of the aerial parts of the plants on the ground, was made using a scale of plant cover: 5–15%, 15–25%, 25–50%, 50–75% and >75% ground cover. Morpho-

Table 2 Characteristics of studied stands including basal area and regeneration density

Stand name	Age[a] (years)	Size (ha)	Basal area[b] (m^2/ha)	Dominant species[c]	Regeneration density[d] (n/ha)	Soil pH[e]	Soil texture
Piette-25	12	1.8	19.2	*Betula populifolia*	7,000	5.3	Sandy loam
Daudelin-21	16	0.9	26.0	*Betula populifolia*	10,500	4.6	Loam
Boissé-3	19	0.5	24.0	*Populus tremuloides*	6,000	5.0	Loam
Grenier-1	20	1.6	16.0	*Betula populifolia*	3,000	4.7	Loam
Germiquet-2	21	0.6	17.0	*Betula populifolia*	2,300	4.8	Sandy loam
Chicoine-15	21	0.7	14.0	*Populus tremuloides*	5,100	6.6	Loam
Lemaire-24	24	5.0	26.0	*Betula populifolia*	5,360	5.9	Clay loam
Grenier-9	26	0.6	10.7	*Populus tremuloides*	2,000	5.1	Silt loam
Croteau-6	28	0.7	16.8	*Betula populifolia*	5,300	4.5	Loam
Westover-26	28	0.9	24.0	*Betula populifolia*	7,600	6.2	Loam
Cormier-28	33	2.2	26.6	*Populus tremuloides*	12,900	5.5	Loam
Boyer-12	44	0.9	41.0	*Populus grandidentata*	26,700	5.9	Sandy loam
Pivin-18	47	0.8	21.5	*Populus tremuloides*	14,400	7.6	Loam
McNair-16	50	0.9	18.3	*Populus grandidentata*	9,300	7.2	Silt loam

[a] Measured as time since tree establishment

[b] Basal area includes trees, saplings and shrubs

[c] Dominant tree species were chosen based on relative basal area

[d] Regeneration density values represent the number of seedlings of diameter<1 cm and height>20 cm per hectare, all species combined

[e] Soil analysis methods are detailed in D'Orangeville et al. (2008)

Table 3 Overstory composition of studied stands, expressed as the basal area of each tree species (diameter at breast height>10 cm) relative to the total tree basal area for each site

Stand name	Betula populifolia	Prunus serotina	Acer rubrum	Acer saccharum	Fraxinus sp.	Larix Laricina	Ulmus americana	Populus balsamifera	Populus grandidentata	Populus tremuloides	Tsuga canadensis	Abies balsamea	Thuya occidentalis
Piette-25	78.0	8.4	1.3	–	–	–	0.1	–	–	5.1	–	–	–
Daudelin-21	71.4	–	–	1.5	–	–	15.4	–	–	–	11.6	–	–
Boissé-3	13.3	–	–	–	–	–	–	–	–	86.7	–	–	–
Grenier-1	84.3	–	–	–	–	–	–	–	–	15.7	–	–	–
Germiquet-2	29.8	24.0	15.4	–	–	–	3.6	1.3	–	23.8	–	–	–
Chicoine-15	19.9	–	–	–	2.5	9.9	13.8	8.1	–	44.5	–	–	–
Lemaire-24	37.1	0.7	18.9	–	–	2.7	5.2	0.6	–	32.7	–	–	–
Grenier-9	47.6	5.8	5.1	–	–	–	10.6	–	–	15.4	–	–	–
Croteau-6	83.4	1.9	0.6	–	–	–	1.0	–	–	9.6	–	–	–
Westover-26	62.0	–	8.6	2.2	–	–	7.5	–	–	11.0	1.4	7.4	–
Cormier-28	14.0	3.5	13.3	–	18.5	–	1.3	–	–	46.6	–	–	–
Boyer-12	–	0.3	–	6.4	1.5	–	–	–	89.8	–	–	–	0.8
Pivin-18	–	–	–	0.4	19.0	–	1.5	–	–	56.4	–	–	–
McNair-16	–	–	–	0.7	5.2	–	–	–	31.9	31.3	–	–	17.1

Only species with basal area >5% on one site are shown

logical groups were defined as herbs, ligneous understory (DBH<1 cm), ferns and *Rubus* species. Finally, the height of the most abundant understory morphological group (in cover) was measured as the highest point of the group's canopy. Species DBH were recorded for trees, saplings and shrubs. Height and cover were also noted for shrubs of DBH<10 cm.

The BF2 type Sunshine Sensor (Delta-T Devices Ltd., Cambridge, UK) was used to measure diffuse available light (PAR; photosynthetically active radiation, micromoles per square metre per second). This device provides a good estimation of average seasonal available understory light under variable weather conditions, showing strong correlations ($r>0.9$; see Paquette et al. 2007b) with common methods of seasonal PAR estimation such as the overcast method (Messier and Puttonen 1995) and the hemispherical image analysis (Englund et al. 2000), as well as high accuracy (95% confidence limits of ±10 µmol m^{-2} s^{-1}). Measures of in situ PAR were taken in the middle of each circular plot only once. For each plot, three instantaneous point measurements were taken at 0.5, 1 and 2 m above ground using a levelled tripod. Using radio communications, simultaneous measures of incident open-field PAR were taken with another BF2 in a nearby field. The ratio of understory PAR over open-field PAR is the PAR ratio, or ratio of available light in the understory. A single value is then obtained by taking the average of the PAR ratios at 0.5, 1 and 2 m above ground for each plot. All sites were measured at the end of July 2005. The main sampling effort was aimed at seedlings above 20 cm in height to measure morphological variables. At the end of the growing season, seedlings above 20 cm in height were counted and identified. In every sampling plot, when present, up to two individuals per species per height class (20–30 cm, 31–50, 51–75, 76–100, 101–150 and 151+) were randomly chosen and their whole aboveground biomass harvested for laboratory investigations, for a total of 614 individuals. Of all harvested tree species, bur oak (*Quercus macrocarpa* Michx.) and yellow birch (*Betula alleghaniensis* Britton) specimens were discarded because of their low numbers. We combined data for white and green ash because the two species are common to the study region and difficult to distinguish from one another at this stage. Aboveground parts of the selected seedlings were used for biomass partitioning and morphological measurements, including a sample of three to five leaves from each seedling, depending on its height, randomly taken on a height gradient and set aside in a herbarium for leaf area measurements.

2.4 Laboratory analysis and data compilation

All collected seedlings were dried at 40°C for a full week; divided into main stem, secondary stems (including

petioles) and leaf components; and weighed in the laboratory. Individual leaf area of collected leaves was measured in the laboratory using an area meter (Delta-T area meter, Delta-T Devices Ltd.) and the samples weighed. Seedlings were aged by basal ring count in cross-sections at the root collar for every individual with binoculars ×40. To measure environmental effects on growth, mean annual height growth rate was calculated as seedling height divided by its age. The last growing season was subtracted from seedling height because harvesting took place before the end of the growing season. To measure environmental effects on morphology, a series of ratios were calculated based on biomass and leaf area measures. Growth type index (GTI), i.e. the ratio of branch mass on trunk mass; slenderness (H/D), i.e. height divided by diameter; leaf area ratio (LAR), i.e. total leaf area divided by total above-ground biomass; specific leaf area (SLA), i.e. the average of leaf area divided by leaf weight; and the ratio of non-photosynthetic tissue to photosynthetic tissue (NPT/PT). The relationships measured in this study between seedling morphology, growth and environmental conditions could have been affected by browsing, a stochastic phenomenon having a major impact on regeneration in agro-forested areas (Côté et al. 2004).

2.5 Statistical analysis

Data were analysed using the seedling as the experimental unit. Mean annual height growth rates were compared using honestly significant difference (HSD) tests (Tukey–Kramer). Temporal windows of establishment for each species were compared using a similar Tukey-type test for medians based on a comparison of the mean ranks. Data normality and homoscedasticity were tested prior to the HSD tests. To analyse growth responses to environmental factors, we integrated each response variable, successively, in a linear regression model, as well as all environmental variables (light and plant abundance), and applied a forward selection at $p=0.10$ (9,999 permutations) to identify

significant variables. A redundancy analysis (RDA) was then performed with the significant environmental variables and the response variables of all five species on stand-ardised response matrices. RDA significance was tested using 9,999 permutations on a reduced model.

Seedling morphological response to its environment is known to be strongly dependent on the development stage (Coleman et al. 1994). To measure the direct effect of the environment on seedling morphology, seedling size had to be taken into account. Thus, we partitioned the variance of each response matrix (one per species) using partial RDAs on standardised response matrices. Two environmental matrices were built: matrix A included seedling height and matrix B included environmental factors, namely available light as well as neighbouring plant height, basal area and cover. Each fraction was tested using 9,999 permutations. In addition, correlations between morphology indices and species heights were completed and tested using 9,999 permutations. All multivariate analyses were generated using R Software (R Development Core Team 2009) and univariate analysis were done using JMP IN 7.0 (SAS Institute, Cary, USA).

With the seedling as the experimental unit, site conditions or environmental factors other than those measured were not explicitly accounted for in the study design and statistical analysis. Whilst this limits the inference that can be made on the findings, our results still highlight the importance of certain parameters that are specific to post-agricultural contexts and help understand their successional dynamic in eastern North America.

3 Results

To compare growth and phenotypic plasticity among tree species, it was mandatory to ensure that stand structure and available light conditions were similar for each species. Results validate this premise (see Table 4, non-significant Tukey HSD tests). Mean levels of available light, i.e. the

Table 4 Forest structure and available light conditions associated with harvested seedlings (mean ± confidence interval at $\alpha=0.05$)

	Black cherry ($n=176$)	Red maple ($n=86$)	Sugar maple ($n=48$)	Ash species ($n=286$)
Mean PAR[a] (%)	4.9±0.7	5.9±1.1	6.2±1.7	4.9±0.9
Total basal area (m²/ha)	24.0±3.2	21.5±3.0	25.9±6.8	25.2±2.6
Shrub basal area (m²/ha)	0.7±0.4	1.0±1.0	0.5±0.4	0.9±0.5
Total understory vegetation cover (%)	78.4±4.5	74.1±6.7	75.4±9.6	77.0±4.3
Ferns cover (%)	24.0±7.7	18.0±7.2	21.8±13.2	29.6±8.2
Ligneous cover (%)	19.2±5.2	10.9±3.1	23.8±11.7	17.1±5.0
Herbaceous cover (%)	33.7±8.2	38.0±9.8	25.6±10.9	30.8±7.4
Rubus cover (%)	13.7±5.1	14.2±4.9	11.4±5.9	11.0±3.6

[a] Using Tukey HSD test, no significant differences were found between species at $p<0.05$ for any factor

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average of measures of light taken at 0.5, 1 and 2 m, range between 4.0% and 7.9% of PAR (95% confidence interval, CI), corresponding to basal areas between 32.7 and 18.5 m^2/ha (95% CI), respectively. The understory vegetation covers approximately 75% of the forest floor, the remaining 25% being rocks, woody debris, bryophytes and bare soil. A large part of the understory vegetation is composed of herbs (~30%) and species of the genus *Rubus* (~12%; Table 4), typical of young successional stands (Gill and Marks 1991).

3.1 Seedling establishment

Figure 1 shows relative abundances for seedlings of each species on a timescale beginning when the site was first colonized by trees (mainly birch and aspen). All species studied here produce good seed crops every 2 or 3 years
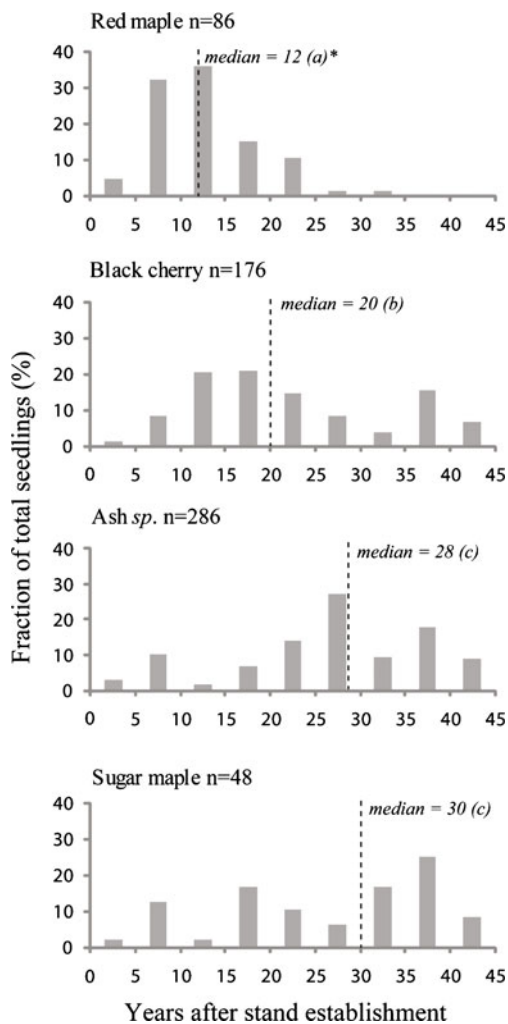

Fig. 1 Fraction of seedlings established as a function of time since stand initiation. *Letters* express the results of multiple comparison analyses (medians not sharing the same letter are different) for a global type I error of 0.05. Prior to multiple comparison analysis, a one-way ANOVA was performed, where $F=42.524$ and $p<0.0001$

(Burns et al. 1990). However, our results show for two out of four species a single abundance peak over more than 40 years of succession. Red maple establishment reaches its maximum abundance 12 years after the first pioneer trees and follows a normal distribution (Fig. 1). Black cherry reaches a first peak around 10–20 years for nine out of ten sampled sites, for a median age of 20 years since tree colonization. The tenth site shows a peak at around 40 years, which is a less representative value. Temporal windows of establishment for sugar maple and ash open statistically later than red maple and black cherry, with a median of 30 (SD=11.2) and 28 years (SD=10.7) after colonization by pioneer trees, respectively. The establishment window for sugar maple is vast and shows no single temporal peak (Fig. 1). In fact, seedling recruitment reaches peaks around 15–20 years, 30–35 years and, more commonly, 35–40 years after stand establishment. Ash seedlings present an intermediate picture, with a high peak of establishment 28 years after initiation of the stand, accompanied by much smaller peaks before and after (Fig. 1).

3.2 Regeneration height growth rates

Figure 2 shows mean annual height growth rates for seedlings since their germination. Large variation was observed for this variable. The varying ages and heights of seedlings, growing in various stands and environmental contexts, are likely responsible for this variation. In general, seedlings show slow height growth rates. Of the five species studied, black cherry is the fastest growing (10.0 cm $year^{-1}$, SD=7.2) whilst being the most shade-intolerant. Its average height growth rate is statistically higher than that of sugar maple (6.4 cm $year^{-1}$, SD=4.7) and ash (7.6 cm $year^{-1}$, SD=6.1; Fig. 2). Sugar maple is the most shade-tolerant and has the lowest average height growth rate. Trends indicate that ash has an average height growth rate slightly superior to sugar maple and inferior to red maple (8.1 cm $year^{-1}$, SD=8.6), two species more shade-tolerant than ash.

To assess competition effects, we examined relationships between seedling height growth rates, light availability, and height, cover and basal area (when possible) of plant groups, such as herbaceous species or shrubs. The results suggest that tree species can be separated into three groups (Fig. 3). Red maple is the only species whose height growth seems favoured in conditions of higher light availability, whereas black cherry's growth seems to be unaffected by the observed range of available light. Highest height growth rates of ash and sugar maple are associated with low-light conditions.

However, each species presents distinctive characteristics. Height growth of black cherry, although not correlated with available understory light, is negatively
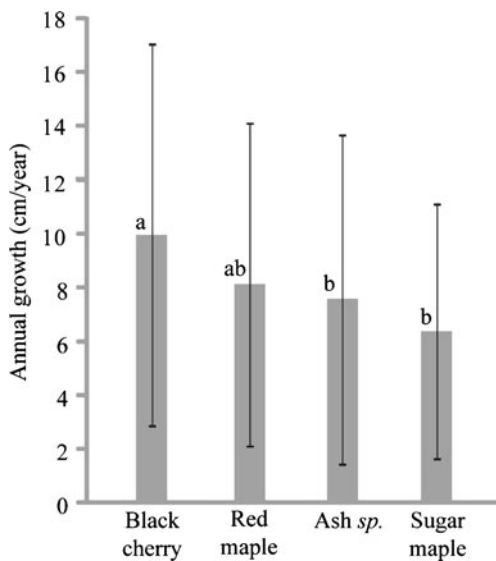
Fig. 2 Mean annual height growth rate of seedling species, as represented by seedling height divided by its age. ANOVA: $F=5.754$ and $p<0.001$. *Error bars* represent standard deviation from the mean. *Letters* express the results of multiple comparison analyses (means not sharing the same letter are different) for a global type I error of 0.05

correlated with the abundance of shrubs and ferns. At the same time, its height growth is positively associated with shade-intolerant herb and *Rubus* cover. In contrast with red maple, the highest height growth rates of sugar maple are associated with low-light contexts and a high understory cover. Furthermore, its growth seems positively correlated with the understory height. Just like sugar maple, ash growth is negatively correlated with available light. Figure 3 shows a positive association of ash seedlings with the presence of shrubs and a negative relationship with herbs and *Rubus* cover.

3.3 Phenotypic plasticity of seedlings

Many studies taking place in primary or weakly disturbed forests conclude that the degree of phenotypic plasticity for temperate hardwood seedlings is strongly affected by their height (Coleman et al. 1994; Delagrange et al. 2004). We first verified whether this assertion was true for post-agricultural forests. The analysis presented in Fig. 4 allows a quantitative assessment of the relative effect of the seedling's environment (light and plant abundance) and its height on seedling morphology. The results confirm the dominant influence of seedling height on seedling morphology in post-agricultural forests. Sugar maple has the strongest relationship, with 31% of its morphology explained by its height when controlling for the environmental variables (Fig. 4). Black cherry, red maple and ash follow with 21%, 17% and 17% of morphological variation explained by seedling height, respectively (Fig. 4).

When controlling for plant height, the influence of light and neighbouring plant groups is statistically significant for four out of five species and explains from 4% to 16% of the morphological variation. Sugar maple has the highest phenotypic plasticity (16%), followed by ash (8%). Black cherry has a lower phenotypic plasticity (5%), whilst the results for red maple are not significant. These trends suggest that levels of plasticity of the studied species could be counterbalanced by their height growth rates.

Significant relationships were found between seedling height and some morphological parameters (Fig. 5). For all species, LAR, SLA and NPT/PT varied significantly with seedling height. The modelled curves applied on the raw data show great differences in the ranges of coefficients of determination (R^2) depending on the morphological variable studied. LAR shows the highest R^2 ranges (0.28–0.42), NPT/PT is intermediate (0.11–0.18), whilst SLA has the lowest (0.05–0.09). The importance associated with these results should reflect those values. Throughout their vertical development, seedlings increase the relative amount of structural tissue (NPT/PT) over leaf tissue and furthermore reduce the fraction of total leaf surface and thickness relative to other aerial organs of the plant. This reduction of leaf mass and leaf thickness with ontogeny has been noted previously by Walters et al. (1993) in a controlled experiment, although light levels measured in our study were lower than those found in Walters et al. (1993).

Red maple had the lowest SLA and LAR throughout its vertical development, as well as a much higher NPT/PT ratio than any other species. Ash, cherry and sugar maple
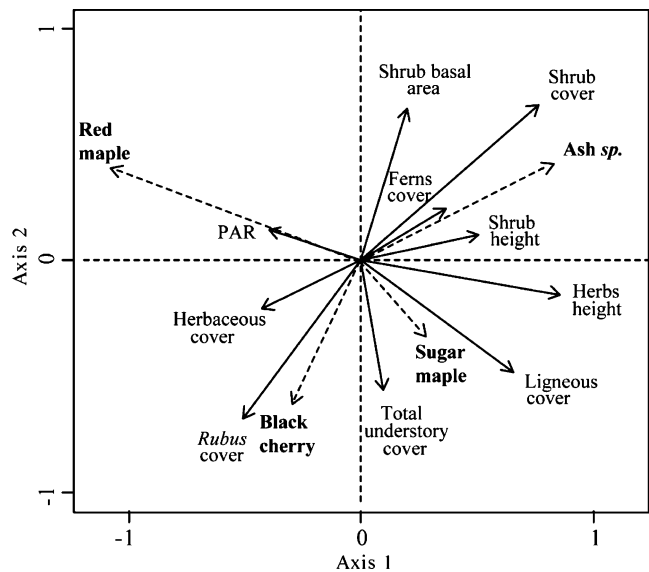

Fig. 3 Correlation biplot of a RDA of seedling species relative annual height growth (*dashed arrows*) and environmental variables (*solid arrows*); $F=6.56$ and $p=0.001$ after 9,999 permutations under reduced model. *PAR* photosynthetically active radiation

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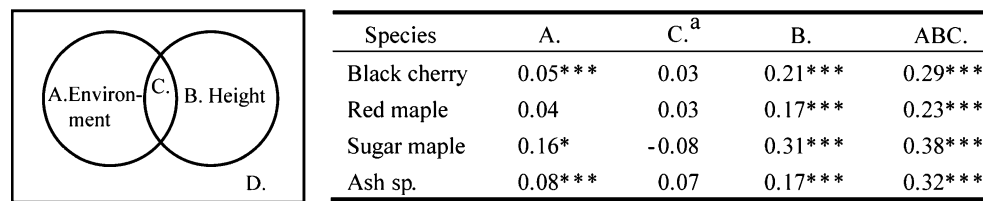| Species	A.	C.[a]	B.	ABC.
Black cherry	0.05***	0.03	0.21***	0.29***
Red maple	0.04	0.03	0.17***	0.23***
Sugar maple	0.16*	-0.08	0.31***	0.38***
Ash sp.	0.08***	0.07	0.17***	0.32***

Fig. 4 Variance partitioning (R^2) and partial RDA of the matrix of morphology variables showing the respective contributions of the environment (*A*) and of the seedling height (*B*), their common (*C*) and combined (*ABC*) effects. [a]The common fraction (*C*) cannot be tested. Fractions tested on residuals (perm=9,999).*$p<0.05$; **$p<0.01$; ***$p<$ 0.001; variables included in the environment matrix include PAR ratio as well as plant group height, cover and basal area. Morphology matrix includes GTI, LAR, SLA, H/D and NPT/PT; *D* represents the unexplained variation of the response data matrix

have very similar NPT/PT ratios. Ash species shows slightly higher LAR and SLA, followed by black cherry and sugar maple, suggesting that this species could allocate more energy to its leaves and produce more leaf area per unit mass.

4 Discussion

We found strong arguments for the existence of temporal windows of establishment for red maple and black cherry, although sugar maple regeneration does not seem to sustain specific temporal barriers, and ash species shows a series of establishment peaks difficult to categorize. Perhaps the fact that ash is a mix of two distinct species could help explain this result. In fact, a previous study conducted in North eastern USA found clear temporally separated periods of peak individual establishment for white ash (Palik and Pregitzer 1991). It is important to note that species dominating the regeneration layer were sometimes found in the overstory (Table 3). It is probable that they contributed in part to the introduction of seeds on site. However, the clear temporal peaks for black cherry and red maple argue for the existence of some barriers to the survival and growth of the seedlings, although the absence of temporal patterns for ash and sugar maple suggests otherwise. Many studies on old field secondary succession noted that tree invasion was unexpectedly slow (see Myster 1993). They generally explain the establishment delay measured for the second cohort of trees in post-agricultural stands with geographical and physical barriers to species invasion.

Seed-baring red maple, well adapted to many disturbance agents, is becoming more abundant in the landscapes of Eastern North America (Abrams 1998; Brisson and Bouchard 2003). Red maple often dominates the regeneration of secondary forests, although its establishment window varies by region (Peroni 1994; Rankin and Pickett 1989; Zaczek 2002). The invasiveness of black cherry is due in part to a different dispersal mode using birds and mammals—zoochory. It has allowed this species to estab-

lish rapidly inside forest patches and agricultural hedgerows of European landscapes. Black cherry is now considered in northwestern Europe (Belgium, the Netherlands, Germany and France) as very invasive (Verheyen et al. 2007). This dispersal mode contrasts with that of red maple whose seeds are dispersed by wind. In its natural habitat (Eastern North America), black cherry specializes in colonizing temperate forest gaps and is abundant in secondary successions (Auclair and Cottam 1971). The results from Phartyal et al. (2009) in Europe show that in stands where the species is abundant in the sapling and tree layer, there is no important seed bank formed in the soil. The same observation was made in North America, as black cherry favours a long-living seedling bank rather than a seed bank (Burns et al. 1990) because its seeds can only remain viable 3 years in the forest floor (Wendel 1977). This strategy is well adapted for the colonization of old fields and young post-agricultural stands because seed banks are usually scarce in old fields except for abandoned pastures. Seedling banks, however, as noted by Phartyal et al. (2009), illustrate a very efficient seed dispersal strategy, and the established seedlings have only to wait for favourable conditions to grow. Two factors could explain the lack of establishment window for sugar maple. First, seeds of sugar maple usually germinate the year following their production, whereas red maple, black cherry or ash seeds remain viable for longer periods of time (Marquis 1975). Second, the strong tolerance of sugar maple to shade and suppression may increase seedling survival after germination.

Although measures of annual height growth rates for seedlings in post-agricultural forests are very scarce, our height growth measures were low compared with other studies. In a Michigan old field dominated by bigtooth and trembling aspen, Palik and Pregitzer (1991) found higher average height growth rates, from 10 to 12 cm/year for red maple seedlings and from 12 to 20 cm/year for white ash. They also found no significant difference in height growth between the two species. In a study taking place in southern Quebec, height growth rates for planted 6-year-old black cherry seedlings under a canopy of grey birch were averaging 24.8 cm/year, whilst height growth rates for
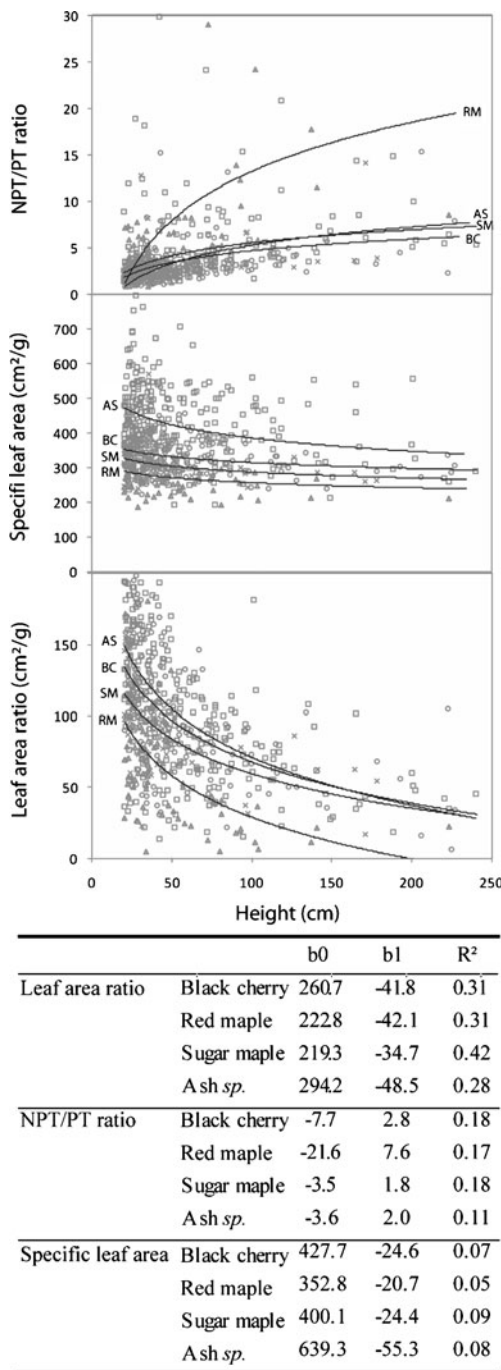
Fig. 5 Morphology of seedling species as a function of height (*H*). *AS* ash species (*square*), *BC* black cherry (*circle*), *RM* red maple (*triangle*), *SM* sugar maple (*cross*), *NPT/PT* non-photosynthetic tissue over photosynthetic tissue mass ratio. Equations are of the type $Y = b_0 + b_1(H) + \varepsilon$. Only significant relationships are plotted (p<0.05), with associated parameters given in the *inserted table*

		b0	b1	R²
Leaf area ratio	Black cherry	260.7	-41.8	0.31
	Red maple	222.8	-42.1	0.31
	Sugar maple	219.3	-34.7	0.42
	Ash *sp.*	294.2	-48.5	0.28
NPT/PT ratio	Black cherry	-7.7	2.8	0.18
	Red maple	-21.6	7.6	0.17
	Sugar maple	-3.5	1.8	0.18
	Ash *sp.*	-3.6	2.0	0.11
Specific leaf area	Black cherry	427.7	-24.6	0.07
	Red maple	352.8	-20.7	0.05
	Sugar maple	400.1	-24.4	0.09
	Ash *sp.*	639.3	-55.3	0.08

naturally regenerating sugar maple seedlings were averaging 21.5 cm/year (Paquette at al. 2007a). The explanations to the general low productivity of the studied species are not within the reach of this study: neither water nor soil nutrients could be measured as both resources could be

limiting growth, aside from available light (Burton and Bazzaz 1995). In fact, in a study comparing old field tree establishment in high- and low-fertility sites (Berkowitz et al. 1995), the authors found increased competition levels in high-fertility sites resulting in seedling growth rates similar to unproductive sites. Other stochastic factors such as browsing from white-tailed deer (*Odocoileus virginianus*) or eastern cottontail (*Sylvilagus floridanus*) could as well explain part of our results (Côté et al. 2004).

Although all the factors that could explain the growth patterns could not be taken into account, the significant relationships measured between seedling height growth rates and PAR availability generally correspond to the shade tolerance ranks of the five species, with the notable exception of red maple. As Abrams (1998) concluded in a review article on red maple ecology, red maple possesses characteristics of both shade-intolerant and shade-tolerant species. It can persist under very shady environments, whereas it can respond to canopy openings with above average growth rates. The strong negative correlation found between red maple height growth rate and the height of the understory layer confirms its ability to persist in low-light environments. The correlations between black cherry growth and different plant groups could be explained by unmeasured factors such as competition for water or nutrients, although the association with the thorny *Rubus* genus could give a certain degree of protection from browsing, as was suggested by Paquette et al. (2006) to explain similar results. The results suggest that the levels of available light are not limiting for the very shade-tolerant sugar maple. Of all species, sugar maple is represented by the shortest vector on the ordination biplot (Fig. 3), which could mean that it has a higher tolerance to variations in environmental conditions or that the factors affecting its growth have not been taken into account in this study (soil water and nutrients, pH, etc.). Because increases in available understory light favour an important herbaceous cover, ash growth is mostly affected by herbaceous competition. The presence of shrubs and their effect on available light could inhibit the establishment of a highly competitive herbaceous layer (Balandier et al. 2006) and indirectly favour shade-tolerant species such as ash seedlings.

Our results also show no consistent correlation between phenotypic plasticity and shade tolerance, this time because of sugar maple. The accepted theory states that shade-tolerant species should show reduced plasticity in order to save resources and tolerate low-light stress (Valladares and Niinemets 2008). Our results rather show that sugar maple is the most plastic of all the studied species. More research is necessary to better understand the link, if any, between phenotypic plasticity and shade tolerance of a species. This information would be extremely helpful for predicting the

evolution of post-agricultural forests because in the fragmented landscapes where they are found, the enlarging temporal gap between the establishment of early-successional and late-successional species could increase the importance of phenotypic plasticity in the succession of these communities.

We can conclude from these results that sugar maple compensates for its late establishment in post-agricultural forests with greater phenotypic plasticity than the other studied species as it allows the seedlings to maximize their survival in low-light environments. On the opposite, red maple grew best by establishing earlier and allocating more carbon to its ligneous structure compared with all other species, thereby increasing its growth because of higher PAR availability. In exchange, red maple displayed less phenotypic plasticity. Black cherry established quickly in post-agricultural stands, grew faster than ash and sugar maple, and seemed associated positively with certain plant groups such as herbs and *Rubus* species. As stated earlier, competition for resources not measured here (water or nutrients) could explain such behaviour. Ash is intermediate, showing a relative balance between establishment speed, height growth rate and phenotypic plasticity. Its high abundance in the regeneration layer (see Fig. 1) suggests that this intermediate strategy is also an efficient mean of survival in post-agricultural forest environments.

5 Conclusion

Our results show that characteristics associated with shade tolerance ranks of species are not the perfect tool to predict plant succession in post-agricultural forests. Height growth rates of red maple, relative to the other tree species studied, were much higher than expected for a shade-tolerant species, although this species is known to express a changing shade tolerance tributary of its development stage (Coleman et al. 1994). Also, sugar maple showed the highest phenotypic plasticity of all species, whilst shade-tolerant species generally tend to tolerate low-light stress by reducing their plasticity to save resources (Valladares and Niinemets 2008).

This study underlines the importance of certain parameters that are specific to post-agricultural contexts to understand their successional dynamic. For example, the isolation of a post-agricultural stand in an agro-forested mosaic generally delays the establishment of later species to the profit of opportunistic species. Indeed, only five species were sufficiently abundant for the needs of this study. Numerous tree species, typical in the study region, were scarce or absent from these communities. Furthermore, we measured low height growth rates that suggest the presence of adverse conditions that could slow down the domination

of post-agricultural stands by later successional species. These results militate for the implementation of adapted management strategies for post-agricultural forests in order to restore these abandoned farmlands back into mature forests.

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