Volume 255, issues 5–6, 5 April 2008
ISSN 0378-1127
ELSEVIER

Forest Ecology and Management

Available online at www.sciencedirect.com
ScienceDirect
Forest Ecology and Management 255 (2008) 1637–1646
Forest Ecology and Management
www.elsevier.com/locate/foreco

Post-agricultural forests: Landscape patterns add to stand-scale factors in causing insufficient hardwood regeneration

Loïc D'Orangeville *, André Bouchard, Alain Cogliastro

Institut de recherche en biologie végétale (IRBV), Université de Montréal, Jardin botanique de Montréal,
4101 Sherbrooke E., Montréal, Québec H1X 2B2 Canada

Received 18 May 2007; received in revised form 21 November 2007; accepted 21 November 2007

Abstract

Over the last century, the northeastern United States and eastern Canada have witnessed gradual abandonment of unproductive agricultural land types. This major shift in land-use management has released numerous sites, which are now dominated by early-successional forests. Continued anthropogenic disturbance and isolation of these plant communities within an agricultural mosaic should compromise their natural regeneration, but few studies have addressed these issues. We sampled 28 former farmlands that were within 3 agroforested landscapes in southwestern Quebec (Canada) and which were characterised by a closed canopy of pioneer tree species. We measured regeneration of valuable hardwoods to quantify the relative effects of stand factors and landscape patterns on that regeneration.

Our results suggest that the persistence of high-value forests in such agricultural landscapes is jeopardised, due to a problem of recovery for hardwoods at the stand scale. Diversity and abundance of tree seedlings was low; 56.5% of the plots contained no valuable hardwood regeneration >30 cm in height. Furthermore, only 10.9% of all plots contained more than one valuable species. GIS and multivariate analyses revealed two distinct successional alternatives, which varied with the degree of agricultural footprint of the stand and landscape. Only one path led to valuable hardwood forests, although with very few valuable species. Regeneration was insufficient when seedling availability from nearby forest patches was limited, but it was enhanced under particular soil conditions and structure of stands, which could help guide management practices in these ecosystems.

Keywords: Tree regeneration; Post-agricultural forest; Agroforested landscape; Past land-use; Spatial scales; Seed dispersal

1. Introduction

North America continues to experience net loss of forested lands through urban expansion and agricultural conversion, but the northeastern United States and eastern Canada have witnessed the opposite trend, which has been attributed to the gradual abandonment of marginal cultivated lands (Smith et al., 2004). Many old-field sites are now dominated by early-successional forest species (Motzkin et al., 1996; Bouchard and Domon, 1997). These post-agricultural stands are an important component of agroforested landscapes, and their development has followed complex successional paths, which are influenced by historical land-use and environmental context (Flinn and Vellend, 2005). Various studies of agroforested ecosystems at the species, community and landscape level have stressed the disturbed nature of such secondary forest communities, because abiotic factors typically fail to explain their species composition (Meilleur et al., 1994; de Blois et al., 2001). In these human-dominated ecosystems, deterministic factors such as species ecology and stand structure have combined with stochastic factors such as agricultural legacy and herbivory to create a complex canvas for species establishment and growth in young forests.

These new habitats are of growing interest for the study of interactions between agricultural history and present-day plant communities, especially for herbaceous understory plants of north-temperate deciduous forests (Flinn and Vellend, 2005). However, our understanding of the specific controls underlying the colonisation of tree species in post-agricultural forests is far from reaching that of forest herbs. Nevertheless, the decline of certain valuable hardwood species raises the need for such understanding. Northern red oak (*Quercus rubra* L.), for example, has become less abundant in eastern North America, since this species is neither an aggressive coloniser nor

---

* Corresponding author. Tel.: +1 514 872 2054; fax: +1 514 872 2235.
E-mail address: loic.dorangeville@ville.montreal.qc.ca (L. D'Orangeville).

0378-1127/$ – see front matter © 2007 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2007.11.023

shade-tolerant and slow-growing (Crow, 1988). Hence, its adaptations to fire or heavy cutting were not advantageous in agricultural landscapes. Factors behind red oak decline will not necessarily explain the decline of other valuable hardwoods. Apart from their common timber interest and major economic value, valuable hardwoods do not represent a homogenous ecological group. However, all of these species are representative of the regional bioclimatic communities. From a management perspective, some researchers have concluded that natural tree regeneration alone cannot assure the persistence of post-agricultural stands (Tappeiner et al., 1997). Few studies have indeed reported cases of poor natural tree regeneration in these communities (Harmer et al., 1997; Fike and Niering, 1999). Species that are adapted to forest ecosystems characterised by small-scale disturbance and gradual change might be unable to persist in landscapes subject to a heavy human footprint (Matlack, 1994; Motzkin et al., 1996).

Natural regeneration of young post-agricultural forests was the main focus of this study. Although some tree species produce far-dispersed seeds, many others may be negatively affected in their dispersal and recruitment by the impacts of agricultural history on environmental conditions and availability of seed sources. Is natural regeneration in successional species sufficient to replace the actual overstory? How do the environmental conditions and the spatial patterns of the landscape add up to control the regeneration patterns? Answering those questions appears very relevant in the wake of a general rise in the proportion of secondary forests (Neef et al., 2006). We examined the problem from a large-scale vantage point by analysing numerous stands distributed across three agroforested landscapes. Specific objectives were (i) to measure the level of regeneration in valuable hardwoods in these communities and (ii) to quantify the relative effects of stand-scale factors, namely stand structure and soil profiles, together with the effects of landscape-scale patterns on that regeneration.

2. Methods

2.1. Study region

The study was conducted in three Regional County Municipalities (RCMs), which were located in the southernmost part of the Province of Quebec (Canada). The three RCMs (Haut-Saint-Laurent, Acton and Brome-Missisquoi) reflected a gradient of agricultural intensity and forest cover persistence (Fig. 1). Their respective forested areas occupied 27.8, 41.4 and 58.7% of the total land surface area, including a significant number of young forests that were dominated by early-successional tree species of low commercial value (Soucy-Gonthier et al., 2003).

The RCMs form part of the Montérégie region, a territory that is almost entirely divided among small private owners. The region is bounded on the south by New York and Vermont (USA) and by the St. Lawrence River on the north (Fig. 1). The western and eastern boundaries are formed by the province of Ontario and the Eastern Townships, respectively. The region belongs to the Nordic temperate sub-zone of northeastern North America and has a humid continental climate with hot summers and cold winters. It 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 bioclimatic domain, whereas Acton and Brome-Missisquoi are located in the maple-basswood bioclimatic domain (Robitaille and Saucier, 1998). Climate is relatively homogenous among the three municipalities, with a mean annual temperature around 6 °C and seasonal temperatures averaging −10 °C in January and 20 °C in July (Environment Canada, 2004).

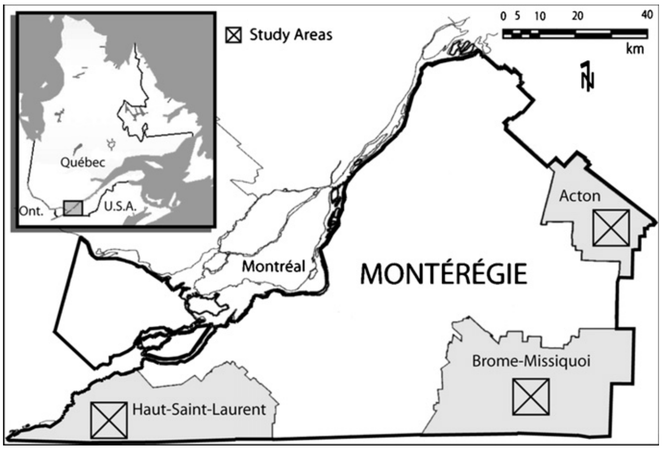


Fig. 1. Location of study areas in the Montérégie region.

Mesic sites in the sugar maple-bitternut hickory domain were dominated by sugar maple (*Acer saccharum* Marsh.), followed by bitternut hickory (*Carya cordiformis* [Wangenh.] K. Koch), American basswood (*Tilia americana* L.), white ash (*Fraxinus americana* L.) and American beech (*Fagus grandifolia* Ehrh.). Disturbed sites were colonised by red maple (*Acer rubrum* L.), grey birch (*Betula populifolia* Marsh.) and trembling aspen (*Populus tremuloides* Michx.) (Meilleur et al., 1994). Climax vegetation of Brome-Missisquoi is also dominated by sugar maple, along with American beech, hop hornbeam (*Ostrya virginiana* [P. Mill.] K. Koch), white ash, eastern hemlock, black cherry (*Prunus serotina* Ehrh.) and American basswood (Bouchard and Maycock, 1978).

2.2. Selection of study sites

In order to rapidly locate the stands of interest inside such vast sampling areas, three recent high spatial resolution satellite images (IKONOS-2) were analysed. After a detailed image processing (Delage et al., 2005), followed by visual interpretation, classification and field validation, all stands that were at least 0.5 ha in area and which were dominated by intolerant hardwoods were identified. Three additional criteria, which were acquired from provincial forest maps, enabled us to limit our sampling to sites with good to imperfect drainage, low slope gradients (<4%), and sufficient soil depth (>25 cm). Potential stands were validated in the field to ensure the dominance of shade-intolerant hardwoods and to determine whether the forests were sites that had truly been abandoned. Landowners were interviewed to verify that all study sites had a history of clearing for cultivation or pasture, and to obtain sampling permission. Thus, 28 stands were selected, according to the following criteria: they were characterised by a closed canopy of shade-intolerant hardwoods; they ranged from 0.5 to 5 ha; and they were evenly apportioned among the three study areas.

2.3. *Stand sampling*

Systematic sampling of the stands took place during the summers of 2004 and 2005 along transects. The number of transects and quadrats were proportional to the size of the stand, with 2–4 evenly distributed transects per site, and 15–35 circular quadrats (5 m^2) spaced at 5 m intervals. There were a total of 595 quadrats for the 28 sites. The presence of seedlings with a diameter at breast height (DBH, 1.37 m) $<$ 1 cm was recorded for each quadrat in one of two categories: below and above 30 cm of height. We combined data for seedlings of white and green ash, since the two species are common to the study region and difficult to distinguish from one another at this stage. For consistency's sake, we also combined these two species for sapling and tree classes.

Point quarter method (Mueller-Dombois and Ellenberg, 1974) was used to measure composition and species relative importance on one in two quadrats for saplings (1 cm $<$ DBH $<$ 5 cm), trees (DBH $>$ 5 cm) and shrubs (DBH $>$ 1 cm). Briefly, the species DBH (cm) and distance (m) were recorded within the four quarters of each quadrat for the individual that was nearest to the quadrat centre; these data were used to calculate species densities and basal areas. We also measured canopy openness at each sample point (average of four measurements at breast height) with a spherical densitometer (Model-C, Forest Densitometers, Bartlesville, OK, USA). Four to six dominant trees were cored on each site to estimate time since abandonment, while avoiding veteran trees which could have been present when the properties were being farmed.

Soil samples (about 150 g taken at 15–20 cm depth) were taken from two quadrats on each transect. The soils from the same site were composited in the field to produce a single bulk sample for analysis. Subsamples of these composite samples were used for textural analysis (sand, silt and clay fractions), using the hydrometer method (Boyoucos, 1962). Results show that studied soils vary from sandy clay loams to clay loams. Bulk pH was determined electrometrically from 2:1 water and soil suspensions, revealing an average pH of 5.7 (S.D. = ±0.9). In terms of on-site measurements, surface stoniness was visually estimated (% cover) along the transects. Also, the thickness of organic and mineral horizons was determined, and used in conjunction with other features observed in 70-cm deep soil pits, one excavated per transect, to determine soil drainage class.

2.4. *Spatial analysis*

Land-use numerical maps, created from IKONOS-2 images, were analysed using SIGIS 2.55 (Géomatique SIGISCO Inc., Montreal, QC) to study the relationship between regeneration and the spatial context of the stand. First, site surface and perimeter length were measured to reflect the intensity of edge-effects on regeneration (Murcia, 1995). Second, distance to the closest forest patch was calculated. Finally, buffer zones of varying radius (60, 100, 160 and 250 m) from the perimeter of each stand were built to measure relative abundance of forest patches in the neighbourhood. The radii were chosen to reflect dispersal capacity of the main tree species in this region (Battaglia et al., 2002). Inside each buffer zone, the total area covered by forest patches was divided by total buffer zone area to provide an adequate index of forest cover.

2.5. *Data compilation*

Dendrochronological analysis of tree cores allowed us to date the stands from the time of abandonment. The observed values gave a minimal age estimate, since there is typically a delay between the point at which fields are abandoned and the period of tree invasion. While differences among samples within the same site were small (pooled S.D. = ±4.1 years), the maximal value was taken as the stand age.

Indices of relative density (DE), frequency (FR) and basal area (BA) were calculated from the point-quarter data. These indices were used in two distinct analyses: a specific analysis, where (DE + FR + BA)/3 enabled us to calculate relative importance values (IV) for each species of trees, shrubs and saplings (Barbour et al., 1999); and a structural analysis where indices were calculated for the vegetation layers (all species merged) of shrubs, saplings and trees.

A stocking index (SI) was generated to quantify regeneration success. Stocking indices measure the amount of natural regeneration that is capable of replacing the dominant tree layer. These indices have been used for decades in silvicultural management to evaluate the necessity of intervention during stand development (Gingrich, 1967). Stocking can be limited to seedlings or it can include saplings, with these indices expressed as a number of individuals or proportion of regenerated area relative to pre-established norms (Gingrich, 1967). This norm, above which the stand is considered to be well stocked, can vary depending on the goals of the stakeholder and thus constitutes the most subjective aspect of stocking indices. Since this study was set in a forest management framework to strike a chord with forest stakeholders, we used methods recommended by the Quebec government where regeneration success is measured as the percentage of quadrats in which one species or a given group of species was present and where a stocking value superior to 60% is considered sufficient (Ministère des Ressources naturelles et de la Faune du Québec, 2006).

We distinguished two cohorts of seedlings for estimating the SI, i.e., $>$30 and $<$30 cm in height, since these two groups are subject to different ecological constraints. Mortality of seedlings in their first few years can be very high due to competition, disease and herbivory, for example. Older seedlings, where height likely reflects ontogeny, are less sensitive to these high mortality risks and account for the future dominant trees of the stand (Tappeiner et al., 1997). Also, since only the seedling layer showed a shift in species composition (see Section 3) from intolerant hardwoods to high-value hardwoods, the SI excluded saplings, which were largely dominated on our sites by intolerant hardwoods. The SI were computed for every species and for two groups of species, viz., high-value hardwoods and 'other tree species', where high-value hardwoods consisted of species with high commercial value listed for tree planting in the southern forests of Quebec (Dumont, 1997).

2.6. Statistical analysis

Three explanatory matrices were constructed to partition variation in seedling 'regeneration', i.e., abundance, composition and distribution, into independent components of (i) spatial, (ii) edaphic and (iii) structural nature (Borcard et al., 1992). GIS-based variables composed the spatial matrix (i), stoniness, pH, texture and drainage composed the soil matrix (ii), while structural matrix (iii) included canopy openness, stand age and major species ($IV > 5\%$). This variation partitioning was performed using a series of partial redundancy analyses (RDA) on standardised matrices, where species abundance data were Hellinger transformed (Legendre and Gallagher, 2001). Briefly, the Hellinger transformation can be applied to presence–absence data as well as the abundances of species, as this transformation makes community composition data containing many zeros suitable for analysis by linear methods like RDA (Legendre and Gallagher, 2001). Although redundancy analysis uses a linear model to explore relationships between the explanatory and response variables, there was no reason why changes in species assemblages should necessarily have been linearly related to changes in environmental variables (Makarenkov and Legendre, 2002). Therefore, prior to the RDA, we included quadratic, cubic and logarithmic functions of each explanatory variable (except the IV) in the three explanatory matrices. Then, we used a forward selection procedure in a regression model to identify a subset of predictor variables within each explanatory matrix that could significantly and independently predict regeneration. That subset was used for the RDA. Significance was tested with 9999 permutations of residuals under reduced model at $P < 0.05$. Species IVs were excluded from variable selection, since these variables account for a stand structure that should be considered as a whole. Kendall's non-parametric correlations (t) were used to explore the relationships between environmental factors and abundances of the main hardwood seedlings. Instead of using individual tree species, we included the relative frequency and basal area for each structural layer taken as a whole (i.e., shrub, sapling and tree) to express the relationship between stand structure and seedling abundance. All multivariate analyses were generated using R Software (R Development Core Team, Vienna, AUS) and univariate analyses were done using JMP IN 5.1 (SAS Institute Inc., Carry, USA).

3. Results and discussion

3.1. Insufficient regeneration of valuable tree species

The canopy and sub-canopy layers were dominated by a high density of pioneer species of low commercial value, indicating that a majority of stands had reached the thinning stage (Kozlowski, 2002). Grey birch was dominant, accounting for 48.6% of tree density and 36.3% of sapling density (Fig. 2). Second in abundance, the shade-intolerant trembling aspen possesses excellent seed dispersal and establishment ability, accounting for 16.6% of tree density and 16.7% of sapling density (Fig. 2). Grey birch and trembling aspen were also found in the understory, but they were outperformed in this stratum by red maple, white and green ash, and black cherry. Red maple differed from the other understory dominant hardwoods in that it was also abundant in the canopy. White and green ash may have established relatively shortly after red maple, since they were found among the saplings (relative density = 9.5%). Sugar maple, American elm (*Ulmus americana* L.), American hornbeam (*Carpinus caroliniana* Walt.), northern white-cedar (*Thuja occidentalis* L.), black ash

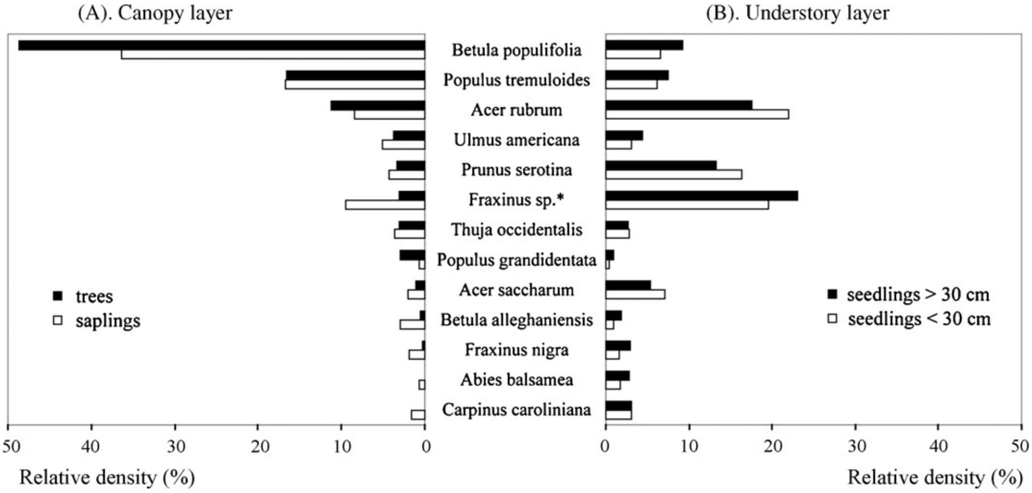


Fig. 2. Species composition in the canopy (A) and understory (B) layers. *Fraxinus* sp. includes *F. americana* and *F. pennsylvanica*. Composition of species is measured as relative densities of the main tree species (>2%) in all 28 stands.

(*Fraxinus nigra* Marsh.), balsam fir (*Abies balsamea* [L.] P. Mill.), and yellow birch (*Betula alleghaniensis* Britton) were also present in the seedling layer, but with less than 10% relative density for the two height classes (<30 and >30 cm) (Fig. 2).

In our study, all of the species that massively colonised the understory, resulting in a SI > 60% in one of the stands (Table 1), were anemochores (i.e., species with wind-dispersed seeds), except for the black cherry, which is mainly dispersed by birds. Plants with these dispersal modes are well adapted to agricultural landscapes, as seed can travel over cultivated areas and colonise abandoned patches (Foster and Gross, 1999; Holl, 1999). Seedlings of white and green ash, sugar maple, black cherry and American elm were present in many stands, reflecting a great dispersal capacity, as well as species of lower commercial value like red maple, trembling aspen and grey birch (Table 1). Other species, with short dispersal ranges, were only found on very few sites. Barochores (such as oak, hickory and walnut) were rare or absent from the seedlings layer. They produce slow-dispersal seeds well adapted to stable forests of late succession and such life-history traits do not seem favoured in post-agricultural stands of an average of 30 years of age (S.D. = ±11.7 years) within fragmented landscapes.

Only 9 of the 28 stands that we sampled showed overall stocking for high-value species ≥60%, while 13 others had stocking <40%. Also, 56.5% of the sample plots (S.D. = ±5.2%) did not contain seedlings of any valuable tree species taller than 30 cm (Table 1). Of the remaining 43.5% of the plots, few contained more than one high-value species. In fact, only 10.9% of all plots contained more than one high-value species. Based on these results, it can be stated that levels of valuable hardwood regeneration are low for a strong proportion of post-agricultural stands. Identifying and analysing the barriers to successional regeneration success is an essential step towards understanding the successional trajectories and management possibilities for such stands.

Table 1
Regeneration stocking of the main tree species

Seedlings > 30 cm of height	% F (S.D.)	N sites ($N > 60\%$)	% F_{MAX}
High-value hardwoods			
Fraxinus L.[a]	27.2 (5.9)	19 (7)	93.3
Prunus serotina Ehrh.	15.6 (4.1)	21 (2)	75.0
Acer saccharum Marsh.	6.4 (2.7)	11 (0)	56.3
Ulmus americana L.	5.2 (1.3)	16 (0)	28.0
Betula alleghaniensis Britt.	2.2 (1.1)	2 (0)	30.0
Tilia americana L.	1.0 (0.9)	3 (0)	20.0
Quercus macrocarpa Michx.	0.2 (1.2)	1 (0)	6.3
Other species			
Acer rubrum L.	20.7 (4.7)	18 (2)	75.0
Betula populifolia Marsh.	10.9 (2.0)	18 (0)	33.3
Populus tremuloides Michx.	8.9 (2.4)	15 (0)	45.8
Carpinus caroliniana Walt.	3.7 (3.0)	4 (1)	81.3
Fraxinus nigra Marsh.	3.5 (2.6)	4 (0)	50.0
Abies balsamea (L.) P. Mill.	3.4 (1.6)	3 (0)	45.0
Thuja occidentalis L.	3.2 (2.6)	4 (1)	68.8
Populus balsamifera L.	1.3 (0.5)	6 (0)	10.0
Populus grandidentata Michx.	1.2 (1.3)	2 (0)	33.3
Tsuga canadensis (L.) Carr.	0.7 (0.5)	2 (0)	11.8
Ostrya virginiana (P. Mill.) K. Koch	0.5 (0.4)	3 (0)	6.7
Prunus pensylvanica L. f.	0.5 (0.3)	1 (0)	8.6
Carya cordiformis (Wangenh.) K. Koch	0.5 (0.4)	3 (0)	6.7
High-value hardwoods group	43.5 (5.2)	28 (9)	–
Other species group	47.7 (4.7)	28 (8)	–
All species	68.6 (3.8)	28 (16)	–

Only tree species with $\%F > 1\%$ for at least one seedling size group are shown. F (frequency): quadrats with the presence of one species or at least one of the group species/sum of quadrats × 100; S.D.: standard deviation; F_{MAX}: maximal frequency; N sites: number of sites colonised; $N > 60\%$: number of sites showing a frequency > 60% for stocking.

[a] *Fraxinus* L. includes *Fraxinus americana* and *F. pennsylvanica*.

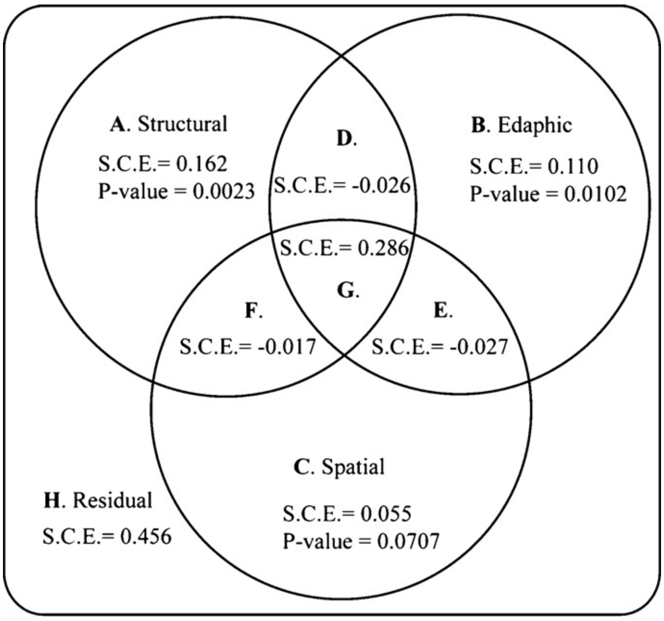
3.2. A wide range of barriers to regeneration

Our results showed that stand-scale factors, particularly stand structure and soils, were most important for the resilience of hardwood forests in temperate agroforested landscapes. Nevertheless, multivariate analysis revealed that landscape pattern was also an important determinant by its upstream effect on seed dispersal (Fig. 3).

Stand structure appeared to be more influential than other groups of variables, since it explained 16.2% of variation in seedling abundance and composition, while controlling for soil and spatial variables (Fig. 3). Taken separately, soil variables explained 11.0% of seedling abundance and composition, while spatial context explains 5.5% of variation in the seedling data set. The negative value of some fractions indicates the groups of variables have opposite effects. Statistical tests of partial RDAs for soil and structure are highly significant, while the test of spatial data set reveals a more important probability of type I error ($P = 0.0707$).

Our results showed a great part of the regeneration scheme (28.6%) is explained by the joint effect of all three data sets. This indicates a strong influence common to all factors which could express the legacy of past land-use and its joint effect on soils, stand structure and landscape. Indeed, the geographical patterns of agricultural land-use are conditioned by initial soils and topography, as areas with steeper slopes or lower-lime soils, for instance, tend to remain forested (Pan et al., 2001; Flinn et al., 2005). Successional stands having similar soils could then show similar land-use patterns and thus spatial contexts. In the same way, similar soils will influence the productivity of the stand and also its structure in similar ways. In other words, current regeneration patterns could result, in good part, from initial site context rather than land-use itself.

All variables that were included in the regressions explained 54.5% of seedling species abundance, while 45.6% of variation remained unexplained. Similar percentages of unexplained variation have been found in other studies using this modelling approach (Borcard et al., 1992; Maestre et al., 2003). Unexplained variation may be due to a complex number of causes of mortality, such as browsing, which influence the seedling bank patterns but are difficult to measure. The study



RDA on part of the data	set of variables tested	Sum of all canonical eigenvalues
1. ADFG	Structural	0.406
2. BDEG	Edaphic	0.343
3. CEFG	Spatial	0.298
4. ABDEFG	Structural and edaphic	0.489
5. ACDEFG	Structural and spatial	0.434
6. BCDEFG	Edaphic and spatial	0.382
Global RDA		
7. ABCDEFG	Structural, edaphic and spatial	0.544

*S.C.E. = Sum of all canonical eigenvalues
*R.D.A. = Redundancy analysis

Fig. 3. Variation partitioning of the seedling matrix. Variation partitioning shows the respective contributions of stand structure, soil conditions and spatial context. Fractions tested on residuals (perm = 9999).

region is known to host a high density of white-tailed deer (*Odocoileus virginianus*) of up to 16 individuals/km^2 of forested habitat (Société de la Faune et des Parcs du Québec, 2002). Studies show that high browsing pressure on tree seedlings and saplings could have affected tree regeneration abundance, although the amount of browsing at one site is highly variable, as it can depend on deer density, seedlings abundance and palatability, and availability of alternative food sources (Rooney and Waller, 2003). Furthermore, selective browsing could have affected seedlings composition to a certain degree, but we assume that this process was not exclusively detrimental to the group of valuable hardwoods which were the main focus of this study.

The regression model that was used here did not allow us to specify the direction of the relationships (i.e., a positive or negative influence). A RDA biplot is shown in Fig. 4 to properly detail those relationships. The forest structure variables that were included in the regression model contained log-transformed canopy openness ($R^2 = 0.162$; $P < 0.001$) and the quadratic term for stand age ($R^2 = 0.087$; $P < 0.01$). Canopy openness was more strongly associated with seedling regeneration than was stand age. Three edaphic variables significantly explained species regeneration attributes: mainly soil pH ($R^2 = 0.300$; $P < 0.001$), followed by visible stoniness ($R^2 = 0.060$; $P < 0.01$) and the cubic term for A-horizon thickness ($R^2 = 0.056$; $P < 0.05$). Organic-horizon (LFH) thickness, drainage and soil texture are not significant. Since all stands in our study were restricted to particular range of soil drainage classes, we expected that this variable would not be significant. The spatial variables that were included in the regression model measured the abundance of forested areas within radii of 60 m ($R^2 = 0.061$; $P < 0.05$) and 100 m ($R^2 = 0.289$; $P < 0.001$) of each stand. Stand area, perimeter length and distance to the closest forest patch, however, were found not to be significant.

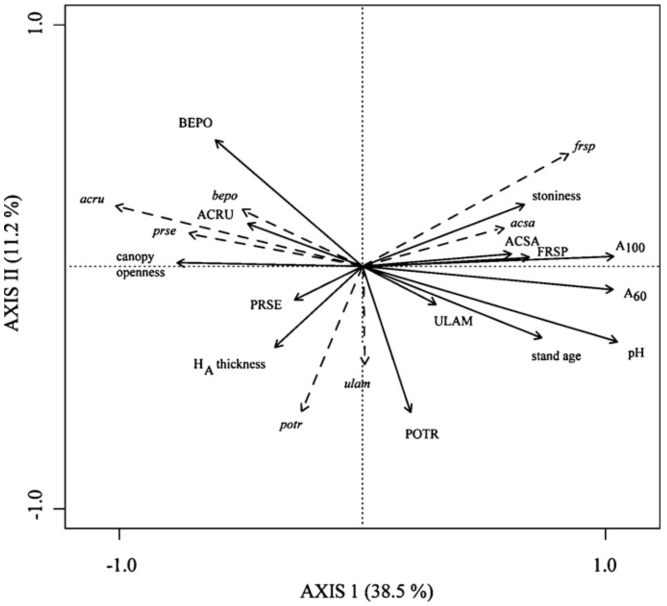


Fig. 4. RDA biplot of seedling species and environmental variables. Dashed arrows are understory regeneration; solid arrows are significant abiotic variables ($P < 0.05$) and main canopy species (IV > 5%). Values next to the axis captions show the fractions of variance accounted by that axis; $F = 2.907$ and $P = 0.0001$ after 9999 permutations under reduced model. ACRU: red maple; PRSE: black cherry; POTR: trembling aspen; ULAM: American elm; FRSP: white and green ash; ACSA: sugar maple; BEPO: grey birch; H_A = A-horizon thickness; A_{60} and A_{100} = forest abundance at radii of 60 and 100 m, respectively, around the stand.

3.3. A landscape-scale perspective: scarcity of seed sources

Location and abundance of forest patches in the landscape were found to be significant, contrarily to size or shape characteristics of the stand (Fig. 4). Our results showed that the abundance of neighbouring forest patches within a radius of 60 m, and especially within 100 m, was a more significant factor than simple proximity of a forest patch. The abundance of neighbouring forests could increase the chances for the presence of seed-bearing trees of valuable species. Forest patches are seed sources that shape stand composition according to the dispersal capabilities of their constituent species (Dzwonko, 1993; Matlack, 1994). Indeed, the majority of sampled tree species have corresponding seed dispersal ranges and modes (i.e., anemochores), except for black cherry seeds, whose dispersal varies depending on their bird consumer ecology (Burns and Honkala, 1990). Since the regression model of RDA excluded collinear variables, the two significant radii likely expressed the dispersal capabilities of different tree species. The significance was lost at greater distances, i.e., when radii extended to 160 or 250 m.

Regeneration of sugar maple, together with that of white and green ash, was significantly correlated with the abundance of neighbouring forest patches ($t > 0.400$, $P < 0.001$, in all cases), while seedlings of black cherry, red maple and grey birch are favoured in contrasting landscapes that consisted of scarce forest patches (Fig. 4; Table 2). Sugar maple was sensitive to seed source abundance, since it has a short dispersal range, produces no seed banks and has a germination rate of more than 95% (Burns and Honkala, 1990). Though red maple shows an identical dispersal mode, it is favoured in heavily cultivated landscapes (Fig. 4; Table 2). This species has been known to demonstrate a greater dispersal range than sugar maple; its seedlings can thus occupy more isolated landscapes with less competition. As for black cherry, its seedling abundance showed a weak and not significant negative correlation with the abundance of forested area in the landscape (Table 2), because its seeds can travel to far distances and it produces very abundant and long-lived seed banks (Auclair and Cottam, 1971). In fact, this species has been considered in Europe as an invasive (Starfinger et al., 2003). Its regeneration is thus not correlated to short-term seed production.

3.4. A stand-scale perspective: two successional pathways, one leading to high-value hardwood forests

Seedling species in the regeneration formed two distinct successional groups. The first group was associated with younger stands that had more open canopies and which showed a heavy agricultural footprint. It consisted of red maple, grey birch and black cherry. The second group was associated with older stands with more closed structure, which were on less acidic, stonier soils. These stands were less disturbed and contained sugar maple as well as white and green ash (Fig. 4).

The two groups of species were at opposite ends of Axis I (Fig. 4), which accounted for 38.5% of explained variance and showed a strong relationship with canopy openness and, to a lesser degree, stand age. In the first group, red maple was abundant because of its ability to colonise very early-successional stands ($t_{\text{age}} = -0.297$, $P < 0.05$), in contrast to sugar maple ($t_{\text{age}} = 0.101$) and white or green ash ($t_{\text{age}} = 0.267$, $P < 0.1$; Table 2). This species is considered an early-successional opportunist, showing strong fecundity and germination rate (Abrams, 1998). Our correlation analysis highlighted the proclivity for red maple to occupy open stands ($t_{\text{openness}} = 0.300$, $P < 0.05$) in strong contrast to stands with a well-developed tree layer ($t_{\text{Trees BA}} = -0.210$) (Table 2). From the correlation analyses for black cherry, we found that its seedlings were influenced less by stand structure, and more by soil and spatial factors (Table 2). Seedlings of pioneer species such as red maple, grey birch and black cherry, can dominate shade-intolerant hardwood communities of young and open-structured stands by using a strategy of rapid growth when sufficient light is present to overcome woody and herbaceous competition (Beckage et al., 2000). This strategy was possible under the canopy of pioneer species (Fig. 4), since light attenuation by these trees is low (Canham et al., 1994).

The second group lay at the other end of Axis I, where later successional species were more abundant, among dominant pioneer species. Sugar maple showed diametrically opposite ecological traits to red maple by having greater seedling abundance in relatively more mature successional stands with a more closed canopy ($t = -0.199$) and a prominent tree layer of 25.2 m^2/ha average basal area ($t = 0.179$) (Table 2). This species has favoured a strategy of survival rather than one of opportunism (DeLucia et al., 1998). Ash seedlings showed a similar ecology to sugar maple: a strong association with a prominent tree layer ($t = 0.421$, $P < 0.01$), with older stands

Table 2
Correlations between environment and seedling abundances

Parameters	Sugar maple	White and green ash	Black cherry	Red maple
Structure				
Trees BA	0.179	**0.421*****	−0.055	−0.210
Trees FR	−0.079	0.104	−0.123	0.114
Saplings BA	0	−0.064	−0.177	0.113
Saplings FR	−0.055	−0.034	−0.123	0.032
Shrubs BA	0.153	**0.243***	0.011	−0.198
Shrubs FR	0.207	0.214	−0.125	**−0.456*****
Canopy openness	−0.199	**−0.416*****	0.066	**0.300****
Stand age	0.101	**0.267***	−0.033	**−0.297****
Soil				
A-horizon thickness	−0.176	**−0.311****	−0.141	**0.251***
Stoniness	**0.280***	**0.454*****	−0.064	**−0.281***
pH	**0.405*****	**0.483*****	**−0.282****	**−0.572*****
Landscape				
Forest abundance at $r = 60$ m	**0.432*****	**0.545*****	−0.114	**−0.533*****
Forest abundance at $r = 100$ m	**0.452*****	**0.534*****	−0.086	**−0.454*****

Bold values underline the strongest correlations: $^{*}P \leq 0.1$, $^{**}P \leq 0.05$ and $^{***}P \leq 0.01$ after Kendall correlation test. Only the most abundant species of seedlings > 30 cm of height are used BA = Basal area; FR = Frequency.

(most regeneration was in stands averaging 42 years), and a more closed canopy ($t = -0.416$, $P < 0.01$) (Table 2). Shade-tolerant hardwood seedlings were associated with relatively older stands where a more closed canopy may inhibit heavy competition (Canham et al., 1990). Furthermore, chances can improve as time progresses for propagules to reach the stand and germinate, and for soils to improve from past land-use (Kalisz, 1986). The negative relationship between these species and canopy openness confirmed the relatively later opening of their establishment window. Seedlings of sugar maple, and white and green ash were most abundant in stands of an average canopy openness of 5.6%. This is no surprise since those species have an intermediate to high shade tolerance and prefer fertile and humid soils favoured by closed canopies (Burns and Honkala, 1990).

Numerous studies have highlighted the importance of soil pH for the survival and growth of hardwood regeneration (Cogliastro et al., 2003; Herault et al., 2004) as well as species composition and diversity (Kozlowski et al., 1991). In our study, the two successional pathways could be differentiated by correlations of soil pH with seedlings abundances (Table 2); these correlations were negative for opportunistic species like black cherry ($t = -0.282$, $P < 0.05$) and red maple ($t = -0.572$, $P < 0.01$), which were abundant on acidic soils (mean pH 4.9 for black cherry and 4.0 for red maple), and positive for sugar maple ($t = 0.405$, $P < 0.01$) and ashes ($t = 0.483$, $P < 0.01$), which were mostly found on neutral soils. There is a significant negative correlation between A-horizon thickness and soil pH ($t = -0.289$, $P < 0.05$; see Fig. 4). A-horizon thickness has been related to the efficiency of organic matter cycling, which is linked to microbial activity, which is itself favoured by higher soil pH (Schreffler and Sharpe, 2003).

Although soil pH could have influenced seedling establishment by controlling for nutrient availability, our results show that geographical patterns of land-use were closely linked to soil acidity. Previous studies have shown that agriculture typically increases soil pH, and, as trees regrow, soils typically gain acidity and lose base cations (Myster, 2004). In our study, however, higher soil pH was associated with stony sites (Fig. 4), while modern agricultural land-use is associated with stone-free areas. Typically, the majority of mature forests in the region of study are limited to stony glacial deposits, while the more productive marine clay deposits are monopolised by agriculture (Pan et al., 1999). The stony glacial deposits are mainly situated on a dolomitic bedrock containing high concentrations of calcium and magnesium, raising the soil pH. This suggests that stony sites, with higher pH, are located inside less disturbed landscapes than stands with stone-free acidic soils, and that contrasting edaphic conditions could account for distinct land-use histories. Spatially dependant seed dispersers like sugar maple and white or green ash would be correlated to stony and pH-neutral soils in part because of the underlying landscape pattern it represents. Indeed, a significant Kendall correlation confirms the association of pH-neutral soils and forest abundance in the landscape at radii of 60 and 100 m ($t = 0.605$ and 0.585, respectively, $P < 0.001$ for both).

This study could not take into account all possible barriers to high-value hardwood regeneration. Browsing can be a decisive factor in agricultural landscapes, although it is hard to measure (Horsley et al., 2003). Also, this study did not directly measure herbaceous competition, but instead used related factors such as canopy openness. However, the results of variation partitioning showed that a significant portion (54.4%) of factors controlling regeneration in the studied stands has been taken into account.

4. Conclusions

The results discussed in this paper raise some questions about the persistence of high-value forests in human-dominated landscapes, in relation to the quality of goods and services that they are expected to provide in answering the needs of a growing human population (Hobbs et al., 2006). As they are dominated by intolerant hardwoods, the diversity and abundance of valuable tree seedlings in these young forests has shown to be low. At the stand level, results point out two distinct successional alternatives according to the intensity of historical land-use. Only one of these pathways can lead to valuable hardwood forests, although they are likely to contain very few valuable species. In the light of these results, should we consider some of these stands degraded? Numerous degraded forests have been reported to prevent tree establishment because of the dominance of shrubs and herbs (DeSteven, 1991a,b; Gill and Marks, 1991; Myster, 1993; Benjamin et al., 2005), or to block succession because of exotic species invasions (Fike and Niering, 1999; Zimmerman et al., 2000). None of these elements of degradation, as defined by the Convention on Biological Diversity (CBD, 2001), have been observed here; indigenous trees outperformed herbs and shrubs in a relatively short time span and no exotic vascular plants were found (L. D'Orangeville, unpublished data). However, a deficiency of valuable regeneration was observed, suggesting a successional slowdown that extended the intermediate stages which precede the occurrence of resilient and valuable mature forests. Multivariate analysis revealed that stand-scale factors accounted for most of the regeneration abundance and diversity, but landscape patterns also affected the upstream availability of seedlings. Although soils and stand structure can definitely influence the regeneration, it has been often emphasised that succession slowdowns in degraded stands are related to floral and faunal impoverishment (Dobson et al., 1997). In this case, it was most likely that low regeneration was initiated by low seedling availability from nearby forest patches and then enhanced by particular soil conditions or stand structure. Hence, the root of the problem is found at the landscape scale rather than the stand scale. We believe such landscape perspectives should be considered as a necessary addition to the assessment of site degradation.

Proper management of these communities, with a view towards creating species-rich mature stands, could contribute substantially to the value-added wood products industry, improvements in environmental quality, and forest conservation in the region. Landscapes where seedling availability is jeopardised underscore the need to introduce species to quicken succession and increase the value of these young forests. Indeed, areas used for cultivation and pasture have been estimated to double before 2050, intensifying the pressure on global forest ecosystems (Perrings et al., 2006). It will then become necessary to intervene in such stands so they can recover the main functions, structure and productivity associated with natural forests. Underplanting to promote and enrich regeneration of abandoned agricultural lands has already aroused a great deal of interest (Cogliastro et al., 2006; Fournier et al., 2006; Paquette et al., 2006). Red oak, sugar maple, yellow birch and white ash account for more than 80% of hardwood production in Quebec nurseries, followed by bitternut hickory, bur oak (*Quercus macrocarpa* Michx.), white oak (*Q. alba* L.) and black cherry. Such programs are generally in place to favour plantations in open fields. In addition to this objective, we believe these programs could also be oriented towards enrichment of existing low-value stands, located inside isolated landscapes where seed dispersal is hardly probable. The species listed above, and others, are well suited for underplanting, notably red oak, which was absent from the surveyed stands, and yellow birch, represented by a low 2.2%. When natural regeneration is present, however, proper management of the advance regeneration that is already in place should be promoted for obvious economic reasons. Furthermore, natural regeneration has certain obvious ecological advantages over underplanting, in that genetic specificity and variability are maintained and the naturally regenerating species are generally better adapted to soil conditions than introduced provenances or other tree species.

Acknowledgements

We are grateful to Stéphane Daigle for his advice on data analysis. We also thank Nicolas Soucy-Gonthier and Marc Delage for their work on satellite image interpretation, and whose results we used. We thank William F.J. Parsons for helpful comments on the manuscript, and two anonymous referees for providing constructive reviews. We thank our technical staff (Valérie Haf-Gagné, Mélodie Boulet and Frédéric Boivin). This work was supported by the FQRNT (Action concertée Fonds forestier), the PMVRMF (Programme de mise en valeur des resources du milieu forestier)—Volet II Montérégie to Alain Cogliastro and a grant to André Bouchard from the Natural Sciences and Engineering Research Council of Canada.

References

Abrams, M.D., 1998. The red maple paradox: what explains the widespread expansion of red maple in eastern forests? Bioscience 48, 355–364.

Auclair, A.N., Cottam, G., 1971. Dynamics of black cherry (*Prunus serotina* Erhr.) in southern Wisconsin oak forests. Ecological Monographs 41, 153–177.

Barbour, M.G., Burk, J.H., Pitts, W.D., Gilliam, F.S., Schwartz, M.W., 1999. Terrestrial Plant Ecology, 3rd ed. Addison Wesley Longman, Menlo Park, California, p. 649.

Battaglia, L.L., Minchin, P.R., Pritchett, D.W., 2002. Sixteen years of old-field succession and reestablishment of a bottomland hardwood forest in the Lower Mississippi Alluvial Valley. Wetlands 22, 1–17.

Beckage, B., Clark, J.S., Clinton, B.D., Haines, B.L., 2000. A long-term study of tree seedling recruitment in southern Appalachian forests: the effects of canopy gaps and shrub understories. Canadian Journal of Forest Research 30, 1617–1631.

Benjamin, K., Domon, G., Bouchard, A., 2005. Vegetation composition and succession of abandoned farmland: effects of ecological, historical and spatial factors. Landscape Ecology 20, 627–647.

Borcard, D., Legendre, P., Drapeau, P., 1992. Partialling out the spatial component of ecological variation. Ecology 73, 1045–1055.

Bouchard, A., Domon, G., 1997. The transformations of the natural landscapes of the Haut-Saint-Laurent (Québec) and their implications on future resource management. Landscape and Urban Planning 37, 99–107.

Bouchard, A., Maycock, P.F., 1978. Les forêts décidues et mixtes de la région appalachienne du sud québécois. Naturaliste canadien 105, 383–415.

Boyoucos, G.J., 1962. Hydrometer method improved for making particle size analysis of soils. Agronomy Journal 54, 464–465.

Burns, R.M., Honkala, B.H. (Eds.), 1990. Silvics of North America: 1. Conifers; 2. Hardwoods. Agriculture Handbook 654. U.S. Department of Agriculture Forest Service, Washington, p. 877.

Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., White, P.S., 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Canadian Journal of Forest Research 20, 620–631.

Canham, C.D., Finzi, A.C., Pacala, S.W., Burbank, D.H., 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. Canadian Journal of Forest Research 24, 337–349.

CBD, 2001. Convention on Biological Diversity. http://www.biodiv.org.

Cogliastro, A., Benjamin, K., Bouchard, A., 2006. Effects of full and partial clearing, with and without herbicide, on weed cover, light availability, and establishment success of white ash in shrub communities of abandoned pastureland in southwestern Quebec, Canada. New Forests 32, 197–210.

Cogliastro, A., Gagnon, D., Daigle, S., Bouchard, A., 2003. Improving hardwood afforestation success: an analysis of the effects of soil properties in southwestern Quebec. Forest Ecology and Management 177, 347–359.

Crow, T.R., 1988. Reproductive mode and mechanisms for self-replacement of northern red oak (*Quercus rubra*)—a review. Forest Science 34, 19–40.

de Blois, S., Domon, G., Bouchard, A., 2001. Environmental, historical, and contextual determinants of vegetation cover: a landscape perspective. Landscape Ecology 16, 421–436.

Delage, M., Soucy-Gonthier, N., Marceau, D., Nicaise Mezui, L., Cogliastro, A., Bouchard, A., 2005. Détection et caractérisation des friches pour leur mise en valeur forestière en Montérégie. Institut de recherche en biologie végétale. Réseau Ligniculture Québec. Département de géographie de l'Université de Montréal, Montréal, p. 55.

DeLucia, E.H., Sipe, T.W., Herrick, J., Maherali, H., 1998. Sapling biomass allocation and growth in the understory of a deciduous hardwood forest. American Journal of Botany 85, 955–963.

DeSteven, D., 1991a. Experiments on mechanisms of tree establishment in old-field succession: seedling emergence. Ecology 72, 1066–1075.

DeSteven, D., 1991b. Experiments on mechanisms of tree establishment in old-field succession: seedling survival and growth. Ecology 72, 1076–1088.

Dobson, A.P., Bradshaw, A.D., Baker, A.J.M., 1997. Hopes for the future: restoration ecology and conservation biology. Science 277, 515–522.

Dumont, M., 1997. Le reboisement avec des feuillus: une option judicieuse sur les terres privées. Direction de l'assistance technique, ministère des Ressources naturelles, Québec, p. 20.

Dzwonko, Z., 1993. Relations between the floristic composition of isolated young woods and their proximity to ancient woodland. Journal of Vegetation Science 4, 693–698.

Environment Canada, 2004. Climate normals 1971–2000. http://www.climate.weatheroffi-ce.ec.gc.ca/climate_normals/index_e.html.

Fike, J., Niering, W.A., 1999. Four decades of old field vegetation development and the role of *Celastrus orbiculatus* in the northeastern United States. Journal of Vegetation Science 10, 483–492.

Flinn, K.M., Vellend, M., 2005. Recovery of forest plant communities in post-agricultural landscapes. Frontiers in Ecology and Environment 3, 243–250.

Flinn, K.M., Vellend, M., Marks, P.L., 2005. Environmental causes and consequences of forest clearance and agricultural abandonment in central New York, USA. Journal of Biogeography 32, 439–452.

Foster, B.L., Gross, K.L., 1999. Temporal and spatial patterns of woody plant establishment in Michigan old fields. American Midland Naturalist 142, 229–243.

Fournier, A., Bouchard, A., Cogliastro, A., 2006. Artificial regeneration of hardwoods in early successional shrub communities using two clearing intensities and herbicide application. Northern Journal of Applied Forestry 24, 184–191.

Gill, D.S., Marks, P.L., 1991. Tree and shrub seedling colonization of old fields in central New York. Ecological Monographs 61, 183–205.

Gingrich, S.F., 1967. Measuring and evaluating stocking and stand density. Forest Science 13, 38–53.

Harmer, R., Kerr, G., Boswell, R., 1997. Characteristics of lowland broadleaved woodland being restocked by natural regeneration. Forestry 70, 199–210.

Herault, B., Thoen, D., Honnay, O., 2004. Assessing the potential of natural woody species regeneration for the conversion of Norway spruce plantations on alluvial soils. Annals of Forest Science 61, 711–719.

Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A., Epstein, P.R., Ewel, J.J., Klink, C.A., Lugo, A.E., Norton, D., Ojima, D., Richardson, D.M., Sanderson, E.W., Valladares, F., Vilà, M., Zamora, R., Zobel, M., 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. Global Ecology and Biogeography 15, 1–7.

Holl, K.D., 1999. Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. Biotropica 31, 229–242.

Horsley, S.B., Stout, S.L., deCalesta, D.S., 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. Ecological Applications 13, 98–118.

Kalisz, P.J., 1986. Soil properties of steep Appalachian old fields. Ecology 67, 1011–1023.

Kozlowski, T.T., 2002. Physiological ecology of natural regeneration of harvested and disturbed forest stands: implications for forest management. Forest Ecology and Management 158, 195–221.

Kozlowski, T.T., Kramer, P.J., Pallardy, S.G., 1991. The Physiological Ecology of Woody Plants. Academic Press, San Diego, p. 657.

Legendre, P., Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. Oecologia 129, 271–280.

Maestre, F.T., Cortina, J., Bautista, S., Bellot, J., Vallejo, R., 2003. Small-scale environmental heterogeneity and spatiotemporal dynamics of seedling establishment in a semiarid degraded ecosystem. Ecosystems 6, 630–643.

Makarenkov, V., Legendre, P., 2002. Nonlinear redundancy analysis and canonical correspondance analysis based on polynomial regression. Ecology 83, 1146–1161.

Matlack, G.R., 1994. Plant species migration in a mixed-history forest landscape in eastern North America. Ecology 75, 1491–1502.

Meilleur, A., Bouchard, A., Bergeron, Y., 1994. The relation between geomorphology and forest community types of the Haut-Saint-Laurent, Quebec. Vegetatio 111, 173–192.

Ministère des Ressources naturelles et de la Faune du Québec, 2006. Méthodes d'échantillonnage pour les inventaires d'intervention (inventaire avant traitement) et pour les suivis des interventions forestières (après martelage, après coupe et années antérieures)—exercice 2006–2007. MRNFQ, Québec, p. 178.

Motzkin, G., Foster, D.R., Allen, A., Harrod, J., Boone, R.D., 1996. Controlling site to evaluate history: vegetation patterns of a New England sand plain. Ecological Monographs 66, 345–365.

Mueller-Dombois, D.R., Ellenberg, H., 1974. Aims and Methods of Vegetation Ecology. John Wiley & Sons, New York, p. 547.

Murcia, C., 1995. Edge effects in fragmented forests: implications for conservation. Trends in Ecology and Evolution 10, 58–62.

Myster, R.W., 1993. Tree invasion and establishment in old fields at Hutcheson Memorial Forest. Botanical Review 59, 251–272.

Myster, R.W., 2004. Post-agricultural invasion, establishment, and growth of neotropical trees. Botanical Review 70, 381–402.

Neef, T., Lucas, R.M., Roberto dos Santos, J., Brondizio, E.S., Freitas, C.C., 2006. Area and age of secondary forests in Brazilian Amazonia 1978–2002: an empirical estimate. Ecosystems 9, 609–623.

Pan, D., Domon, G., de Blois, S., Bouchard, A., 1999. Temporal (1958–1993) and spatial patterns of land use changes in Haut-Saint-Laurent (Quebec, Canada) and their relation to landscape physical attributes. Landscape Ecology 14, 35–52.

Pan, D., Domon, G., Marceau, D., Bouchard, A., 2001. Spatial pattern of coniferous and deciduous forest patches in an Eastern North America agricultural landscape: the influence of land use and physical attributes. Landscape Ecology 16, 99–110.

Paquette, A., Bouchard, A., Cogliastro, A., 2006. Survival and growth of underplanted trees: a meta-analysis across four biomes. Ecological Applications 16, 1575–1589.

Perrings, C., Jackson, L., Bawa, K., Brussaard, L., Brush, S., Gavin, T., Papa, R., Pascual, U., De Ruiter, P., 2006. Biodiversity in agricultural landscapes: saving natural capital without losing interest. Conservation Biology 20, 263–264.

Robitaille, A., Saucier, J.P., 1998. Paysages régionaux du Québec méridional. Les Publications du Québec, Québec, p. 220.

Rooney, T.P., Waller, D.M., 2003. Direct and indirect effects of white-tailed deer in forest ecosystems. Forest Ecology and Management 181, 165–176.

Rowe, J.S., 1972. Les régions forestières du Canada. Service canadien des forêts. ministère de l'Environnement, Canada, p. 172.

Schreffler, A.M., Sharpe, W.E., 2003. Effects of lime, fertilizer, and herbicide on forest soil and soil solution chemistry, hardwood regeneration, and hardwood growth following shelterwood harvest. Forest Ecology and Management 177, 471–484.

Smith, W.B., Miles, P.D., Visage, J.S., Pugh, S.A., 2004. Forest resources of the United States, 2002. Gen. Tech. Report NC-241. USDA Forest Service, North Central Forest Experiment Station, St. Paul, p. 137.

Société de la Faune et des Parcs du Québec, 2002. Plan de développement régional associé aux ressources fauniques de la Montérégie. Direction de l'aménagement de la faune de Montréal. de Laval et de la Montérégie, Longueuil, p. 143.

Soucy-Gonthier, N., Marceau, D., Delage, M., Cogliastro, A., Domon, G., Bouchard, A., 2003. Détection de l'évolution des superficies forestières en Montérégie entre juin 1999 et août 2002 à partir d'images satellitaires Landsat-Tm. Agence forestière de la Montérégie. Institut de Recherche en Biologie Végétale, Montréal, p. 34.

Starfinger, U., Kowarik, I., Rode, M., Schepker, H., 2003. From desirable ornamental plant to pest to accepted addition to the flora? The perception of an alien tree species through the centuries. Biological Invasions 5, 323–335.

Tappeiner, J.C., Lavender, D., Walstad, J., Curtis, R.O., DeBell, D.S., 1997. Silvicultural systems and regeneration methods: current practices and new alternatives. In: Kohm, K.A., Franklin, J.F. (Eds.), Creating a Forestry for the 21st Century. The Science of Ecosystem Management. Island Press, Washington, pp. 151–164.

Zimmerman, J.K., Pascarella, J.B., Aide, M.T., 2000. Barriers to forest regeneration in an abandoned pasture in Puerto Rico. Restoration Ecology 8, 350–360.