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# Can plantations develop understory biological and physical attributes of naturally regenerated forests?

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## ABSTRACT

With an increasing proportion of natural forests being replaced by plantations, there is a need to determine their potential to fulfill ecological purposes other than wood production. This study evaluated the extent to which deciduous and coniferous plantations develop understory attributes comparable to those of naturally regenerated stands. A functional group approach was used to synthesise species responses in terms of their ecological traits. Multivariate analyses of ecological traits revealed 16 emergent groups that shared common traits associated with a similar life history strategy. Responses of these groups, understory structure, and understory environmental conditions to plantation types and stand stages were analyzed and compared to naturally regenerated stands. Clear associations of trait responses to stand developmental stages and plantation types emerged. Light-demanding and wind-dispersed species groups were associated with early-successional stages, while woody groups, ferns and ant-dispersed spring-flowering herbs were associated with late-successional stages. Analyses also revealed an indicator group associated with old naturally regenerated forest. The understory functional groups and environmental conditions of deciduous plantations converged toward those of old naturally regenerated forests. However, understory structure in deciduous plantations remained poorly developed and richness of the indicator group was low compared to unplanted stands. Conifer plantations, currently the most common plantation type in the northern hardwood biome, showed a completely different pathway of understory development. Modifications to current plantation management practices are proposed to help recreate or maintain natural understory biological and physical attributes.

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## 1. Introduction

Around 60,000 km<sup>2</sup> of primary forest are lost or modified annually by human interventions around the globe (FAO, 2007). In many regions, this marked loss of natural forests has been offset by the rapid increase in forested lands allocated to plantations (FAO, 2007). While plantations

provide tree cover and forest wood products, little is known about their potential to fulfill other ecological services typical of the ecosystems that they are replacing, such as the maintenance of biodiversity. The question has arisen therefore whether plantations can develop ecological attributes similar to naturally regenerated forest ecosystems over time.

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Conceptually, natural forests are complex adaptive systems dominated by native tree species that regenerate themselves naturally. They are composed of myriads of living organisms together with their abiotic environment, and are not subject to agricultural practices (Gardner-Outlaw and Engelman, 1999; Kimmins, 1997). Such forests exhibit connectivity among their components, are dynamic, and are self-organized into hierarchies and cycles (Levin, 1998; Holling, 2001). Their complexity is expressed at three levels of diversity: compositional, structural and functional (Noss, 1990).

In contrast to naturally regenerated forests, plantations are generally composed of one or several artificially established tree species, whose individuals are even-aged and regularly spaced (FAO, 2007). Many plantations are also made of genetically improved native tree species or fast-growing exotic species. They are typically managed on a relatively short rotation, which contrasts sharply with the longevity that characterizes natural forest components. From the perspective of wood production, plantations have been very successful, producing roughly half of the world wood products on less than 5% of the world's forest cover (FAO, 2007). However, with the increasing conversion of primary forests (i.e. natural forests never disturbed directly by human), and modified natural forests (i.e. managed forests that regenerate naturally; FAO, 2007) to plantations worldwide, the question has arisen as to what extent plantations that are managed for timber production can also provide some of the basic ecological attributes found in more natural forests, particularly the conservation of biodiversity (Evans, 1999; Kanowski et al., 2005; Stephens and Wagner, 2007).

At the same time, modernization of agriculture of the last century resulted in the abandonment of many agricultural lands. While natural revegetation often occurs rapidly on these lands, the resulting understory communities are generally considered as biologically impoverished relative to the original forest because of their (i) altered composition and poor richness of species with high conservation value (Flinn and Vellend, 2005; Singleton et al., 2001), and (ii) low forestry potential (Benjamin et al., 2006; D'Orangeville et al., 2008). In part because of negative societal perceptions of abandoned farmlands (Benjamin et al., 2007; Hunziker, 1995), these lands are often converted into agricultural fields or into plantations by rapid afforestation. Abandoned agricultural lands being a transitional stage, vegetation development greatly varies in time and space, from herb-dominated communities to communities dominated by shrubs and pioneer trees (Benjamin et al., 2005; Flinn and Vellend, 2005). Abandoned agricultural lands also vary according to their land use history, with succession on former pasturelands being quite different than that on cultivated fields or hay meadows (Benjamin et al., 2005; Flinn and Vellend, 2005; Stover and Marks, 1998). Among abandoned agricultural lands with various land use histories, pasturelands that have not experienced modern heavy machinery plowing hold particular potential for natural revegetation. This potential arises in part because they have preserved some of their original micro-topography and soil properties (Beatty, 2003) and may possess relict populations of forest herbs (Stover and Marks, 1998).

To address the question of the capacity of plantation to provide the basic ecological attributes of forest, one has to

first determine what makes a forest a fully self-sustaining and functional ecosystem. This has remained difficult to define due to the intrinsic spatial and temporal complexity of such ecosystems. Consequently, ecologists have sought to develop integrative tools that can take into account the complexity of forest ecosystems without having to put all of the pieces of the puzzle together. The ecological integrity concept, which can be defined broadly as the capability of an ecosystem to maintain a community comparable to that of a natural habitat for a given region (Karr and Dudley, 1981), provides a valuable framework for evaluating heavily modified systems such as plantations.

This study aimed at evaluating to what extent plantations can be compared to naturally established forests. To characterize the functionality of forest ecosystems, we used understory community development, in terms of its functional and structural attributes, as an indicator of the ecological integrity of the whole ecosystem. The understory flora is a suitable key element to evaluate ecological integrity of an ecosystem because of its high compositional, structural and functional diversity, its numerous interactions with different trophic levels, and its important role in ecosystem functioning (George and Bazzaz, 2003; Gilliam and Roberts, 2003; Nilsson and Wardle, 2005).

A plant functional type (PFT) approach was used in order to obtain a more synthetic view of the understory community, which was free of differences found at the species level (Lavorel et al., 1997). Based on universal vegetation traits rather than on site-specific vegetational composition, the PFT approach has been shown to greatly facilitate large scale studies or inter-regional comparisons (Cramer, 1997; Graae and Sunde, 2000; Aubin et al., 2007) and has been frequently used for the characterization of vegetation responses to human-induced change (e.g. Verheyen et al., 2003).

We compared assemblages of understory species in conifer and deciduous plantations established in the northern hardwood biome of eastern Canada. Until recently, plantations in temperate deciduous regions of Europe and North America were almost exclusively composed of monospecific conifer stands. Deciduous plantations have been slowly gaining in popularity but they are still marginal (Cogliastro et al., 2006), representing less than 10% of the planted trees in the deciduous zone of Quebec (MRNFP, 2006). Except for studies dealing with vegetation competition, very few studies have been conducted on understory development in North American plantations. Most studies on North American understory flora in plantations have been conducted in boreal forests and only account for conifer plantations (Swindel and Grosenbaugh, 1988; Ramovs and Roberts, 2005; Newmaster et al., 2006; Gachet et al., 2007). These studies observed a generally low abundance and diversity of native forest herbs in plantations. In Europe, Hérault et al. (2005) compared understories of Norway spruce plantations with those of natural deciduous forests and found that, functionally, conifer plantations' understories were completely different from natural deciduous stands. To our knowledge, studies from the temperate deciduous region of North America have neither characterized the understory development of coniferous plantations nor compared them with those of deciduous plantations.

Using the ecological traits of the understory flora, together with the structural and environmental conditions as indicators, we evaluated the potential of plantations to develop understory attributes of naturally regenerated stands. To do so, we first characterized understory traits responses to stand development stage in order to determine traits associated to early- versus late-successional stages. Second, we assessed differential understory development between conifer and deciduous plantations to determine which plantation type was most likely to develop attributes similar to naturally regenerated deciduous forests. Third, we compared plantations to naturally regenerated stands, to evaluate if planting abandoned agricultural sites accelerates the development of the native flora. From these results, we have suggested modifications to current management practices that promote the development of a functional understory in plantations.

## 2. Methods

Fifty-six plots were established within two areas of deciduous forest in the Great Lakes St. Lawrence forest region (Rowe, 1972) of southern Quebec, Canada (Fig. 1). The two areas were the Upper St. Lawrence (45°01'–45°08'N; 73°58'–74°21'W) and Drummondville (45°52'–46°01'N; 72°09'–72°35'W). Mean annual temperature across both areas is 5 °C and the growing season typically lasts 190–200 days (Robitaille and Saucier,

1998). Annual precipitation is slightly higher in the Drummondville area (1000–1100 mm) compared to the Upper St. Lawrence (900–1000 mm). Percent forest cover (including plantations) ranged from 28% for Upper St. Lawrence to 40% for Drummondville (Robitaille and Saucier, 1998). Naturally established, mature mesic forests in both regions are normally dominated by *Acer saccharum* in association with *Fagus grandifolia*, *Tilia americana* and *Ostrya virginiana*, and also with *Carya cordiformis* in the Upper St. Lawrence. *Fraxinus americana*, *A. rubrum*, *Populus tremuloides* and *Betula populifolia* are found on disturbed sites (Meilleur et al., 1994; Brisson and Bouchard, 2003). Small gaps created by tree senescence are characteristic of the natural disturbance regime in the region, while some large scale disturbances such as ice storm and wind throw are occasional events (Bouchard and Brisson, 1996).

In both regions, European settlement in the 19th century brought intense forest exploitation, first for wood and potash production, and subsequently for agriculture (Simard and Bouchard, 1996; Domon and Bouchard, 2007). In the last quarter of the 19th century, the Upper St. Lawrence area was nearly completely deforested and converted to different forms of agriculture (Domon and Bouchard, 2007). The Drummondville area had a slightly earlier settlement date than the Upper St. Lawrence region. Along the St. Francis River, where the large majority of our sampled plantations were located, small subsistence farms were mainly cultivating hay, with

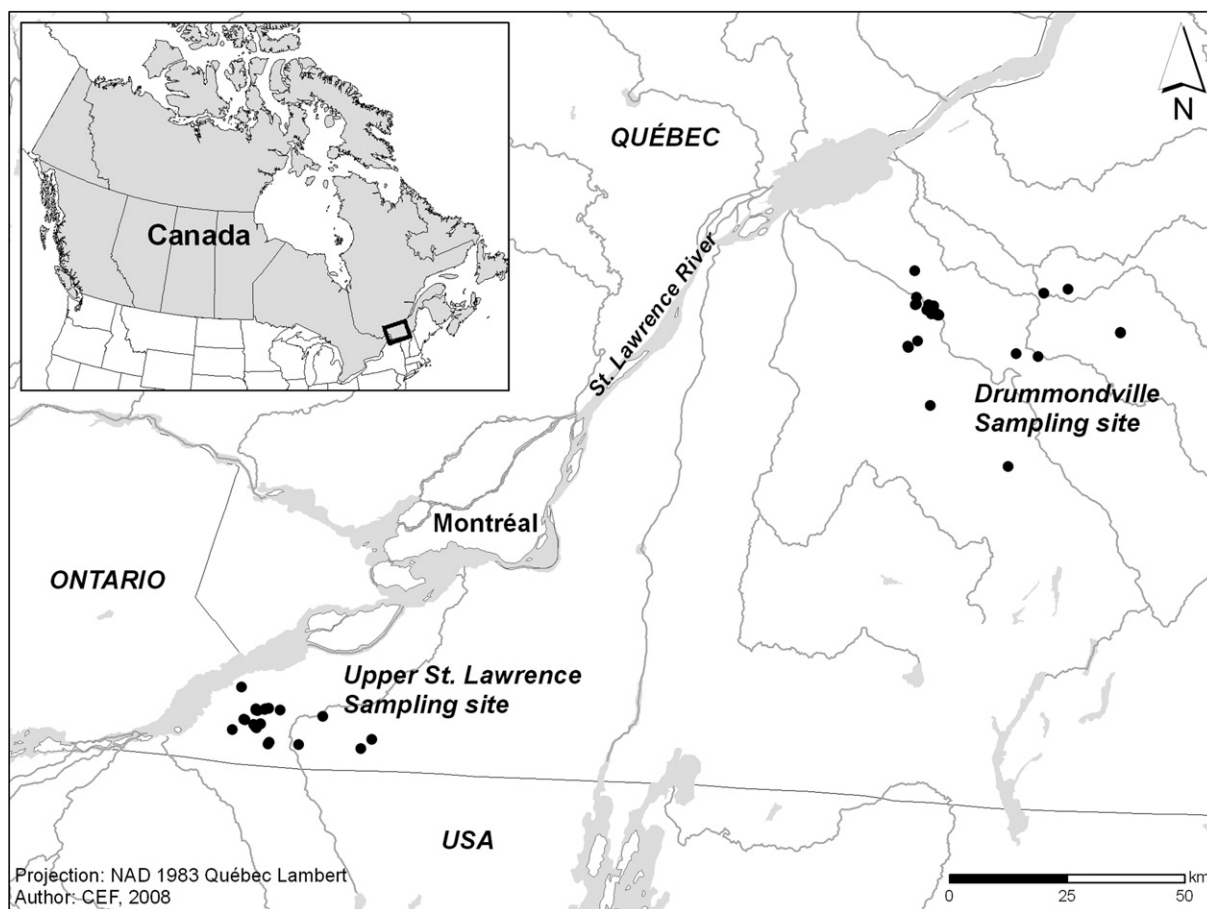


Fig. 1 – Location of the study sites.

small parcels of crops (corn, turnips and potatoes). Each of these farms had a portion of their land used as pasture. As in many other agricultural regions in Eastern North America, the traditional rural landscape changed during the 20th century towards intensive agriculture, resulting in the progressive abandonment of marginal agricultural lands (Bouchard and Domon, 1997; Domon and Bouchard, 2007). A proportion of these abandoned farmlands was converted to plantations, while others were left to regenerate naturally (Benjamin et al., 2006). Additionally in the Drummondville area, the Southern Canada Power company bought many pieces of land along the St. Francis River at the beginning of the 20th century with the intention of constructing a hydroelectricity dam. Since the dam was never built, the company decided to progressively convert these agricultural lands into plantations.

Soil deposits in both regions originate from the post-glacial Champlain Sea. In the Drummondville area, the deposits are mainly sand and reworked till (Robitaille and Saucier, 1998). This region principally lies on slate, limestone and sandstone bedrock of the Bourret, Bulstrode and Melbourne formations, and of the Shefford group (Tremblay and Bourque, 1991). The Upper St. Lawrence region lies on a bedrock of sandstone, dolomite and shale of the Postdam and Beekmantown groups (Globensky, 1987). Superficial deposits in this region are of two major types: morainal deposits in islets and ridges with stony soils on which forests and abandoned old fields are mainly found (including the sampled stands), and nutrient-rich marine clay deposits in the lowlands, where agricultural lands are now concentrated (Robitaille and Saucier, 1998; Domon and Bouchard, 2007).

### 2.1. Description of study plots

Fourteen polyculture deciduous (DP) and 18 monoculture conifer (CP) plantations were surveyed. They were compared with 24 naturally regenerated stands of an old field-deciduous forest succession of pasture origin, hereafter referred to as unplanted stands (UN). Stands from these three stand types were classified according to their stand stages: (O) open canopy, age 7–25 years, maximum tree height 3–8 m; (C) closed canopy, age 14–39 years, maximum tree height 8–17 m, complete canopy closure but immature stem; (M) mature canopy, 32–65 years, maximum tree height 14–24 m, economically mature stem; and for the unplanted stands (NAT) old naturally regenerated forest, over 100 years in age, a maximum tree height of 29 m and composed of tree species characteristic of mature mesic forests. These over 100 years pasture origin forests had been previously compared with unmanaged old growth forests in Aubin et al. (2007). They have been found to possess a similar understory assemblage, although slightly impoverished in spring geophytes and ferns.

Conifer plantations were composed of native red pine (*Pinus resinosa*), while deciduous plantations were composed of mixed native hardwoods (*Quercus rubra*, *Q. macrocarpa*, *Fraxinus americana*, *Betula alleghaniensis*, *A. saccharum*, *Prunus serotina*, *Juglans cinerea* and *J. nigra*). Natural regeneration in the unplanted stands consisted principally of *Ulmus americana*, *Prunus* spp., *Fraxinus* spp., and *A. saccharum*.

Plantations were located in or close to the “Forêt Drummond” in the Drummondville region, while unplanted stands

were located in the Upper St. Lawrence region. Because it is based on universal traits rather than on site-specific vegetation composition, the plant functional group approach allows this type of inter-regional comparison (Tsuyuzaki and del Moral, 1995; Graae and Sunde, 2000; Verheyen et al., 2003; Aubin et al., 2007).

We sampled one plot per stand and had six stands for each combination of stand type × stage, except for mature deciduous plantations, where it was not possible to find more than two stands owing to the rarity of old deciduous plantations. All stands were located on mesic, flat lands at similar elevation.

All investigated stands were of pasture origin. They all had visible signs of their past agricultural use, such as old barbed wire or large trees with broad, open-grown crowns. In both regions, pasture lands have experienced various degree of low intensity plowing in their land use histories, with occasional events of subsistence cropping or pasture enhancement with hay or leguminous plants. However, none had experienced modern heavy machinery plowing in their agricultural histories.

Site preparation for both deciduous and coniferous plantations included plowing and harrowing, with some supplemental drainage for few stands (see Table 1). A large proportion of these abandoned agricultural lands have been previously drained. Plastic mulches were installed for open and closed canopy deciduous plantations. Deciduous plantations received the most frequent and intensive silvicultural treatments, with pruning every 2–3 years in young stands, and thinning done every 10 years. In coniferous plantations, pre-commercial systematic thinning was done 20–25 years after planting. A selective thinning was performed every 10 years afterward. Mechanical, manual and/or chemical release treatments were periodically made on plantations when competitive vegetation was considered as an impediment to tree development. Table 1 should be consulted for more details on site preparation and maintenance.

Information on land use history for unplanted stands came from previous studies (Benjamin et al., 2005; Aubin et al., in press) and are based on the research amassed by a multidisciplinary team over the last 25 years (for more detail, see the synthesis of Domon and Bouchard, 2007). Information on plantation stands was provided by officials from the provincial forest ministry, from local forest agencies and from present or past land owners. Year of land abandonment and recent land use history was later validated through air photograph interpretation (1964–1966, 1975–1983). Table 1 should be consulted for more details on land use history.

### 2.2. Field sampling

A 25-m radius plot was established at the approximate center of each stand. All plots were located at least 25 m away from any openings and between 40 and 800 m from a forested area (mainly early-successional stands). These study plots were sampled three times from May to September 2003 for the Upper St. Lawrence region, and from May to September 2004 for the Drummondville area, to obtain floristic data for all species present during the growing season.

**Table 1 – Characteristics and stand history of sampled stands**

Stand type	N Plots	Stand history <sup>a</sup>	Forest cover <sup>b</sup>	Richness <sup>c</sup>
<i>Unplanted</i>				
Old naturally regenerated forest (NAT)	6	Around 1900: abandoned. Naturally regenerated	TH: 29 BA: 36.2 TD: 672	48
Mature canopy (UN-M)	6	1943–1971: abandoned. Naturally regenerated	TH: 14 BA: 14.5 TD: 743	68
Closed canopy (UN-C)	6	1964–1980: abandoned. Naturally regenerated	TH: 8 BA: 2.5 TD: 181	73
Open canopy (UN-O)	6	1978–1993: abandoned. Naturally regenerated	TH: 3 BA: 0.3 TD: 20	64
<i>Plantation – deciduous</i>				
Mature canopy (DP-M)	2	1954: plantation Site preparation: P (partial), H Maintenance: Ma (unknown frequency) Th (unknown frequency)	TH: 19 BA: 20.4 TD: 508	39
Closed canopy (DP-C)	6	1988–1991: plantation Site preparation: P, H, M Maintenance: Me or Ma (2 years after plantation and periodically when needed). Pr (each 2–3 years). Th (each 10 years).	TH: 12 BA: 11.9 TD: 1134	47
Open canopy (DP-O)	6	1990–1995: plantation Site preparation: P, H, M Maintenance: Me or Ma (2 years after plantation and periodically when needed). Pr (each 2–3 years).	TH: 8 BA: 1.6 TD: 243	57
<i>Plantation – conifer</i>				
Mature canopy (CP-M)	6	1940–1952: plantation Site preparation: P, H, D (?) Maintenance: Ma (unknown frequency). Th systematic 25–35% b.a. (20–25 years after plantation). Th selective 20–30% b.a. (30–35 years after plantation). Pr ?	TH: 24 BA: 39.8 TD: 625	51
Closed canopy (CP-C)	6	1979–1989: plantation Site preparation: P, H, 2 stands: D Maintenance: Ma or Ch (2 years after plantation and Ma periodically when needed). Fi when needed	TH: 17 BA: 30.8 TD: 1784	36
Open canopy (CP-O)	6	1993–1996: plantation Site preparation: P, H Maintenance: Ma or Ch (2 years after plantation and Ma periodically when needed). Fi when needed	TH: 5 BA: 0.1 TD: 9	45

a Stand history: Site preparation: P: plowing; H: harrowing; D: drainage; M: plastic mulches; ?: not confirmed. Maintenance: Pr: Pruning; Th: thinning; Me: mechanical release; Ch: chemical release; Ma: manual release; Fi: fill planting.

b Forest cover: TH: mean maximum tree height (m); BA: mean basal area (m<sup>2</sup>/ha), DBH > 5 cm; TD: Mean tree density (stems/ha), DBH > 5 cm.

c Mean richness of the entire plots.

We determined floristic composition using linear vegetation surveys. In each study plot, 52 circular points (15-cm radius) were systematically sampled along four 25-m transects. Vascular species within a sampling point were given an occurrence value of 1, for a possible total score of 52 when a species was present at all points. Species present in the plot, but not at any of the sampling points, were assigned an occurrence value of 0.5. The frequency of occurrence (%) of a given species was the proportion of points within a plot where that species occurred. All woody species with a DBH (diameter basal height) <5 cm and a height <5 m were included. Grasses, sedges and hawthorns (*Crataegus* spp.) were identified to genus only. Planted tree occurrences were recorded separately. We followed the nomenclature of Gleason and Cronquist (1991). To describe vertical structure, we sampled the vegetation as described above for every 50 cm in height, from the soil surface to the top of the understory vegetation (around 5 m; see Aubin et al., 2000 for further details).

Forest cover data were collected in each plot for tree composition, maximum tree height (m), basal area (m<sup>2</sup>/ha),

and the density of individuals (stem/ha) with diameters at breast height (DBH) >5 cm. To characterize understory environmental conditions, light availability and soil cover substrate were also quantified for the 52 sampling points in each plot. The percentage of above-canopy photosynthetic photon flux density (% PPF) was measured both at the ground level and at two meters above the ground, using a line-quantum sensor (LI-COR, Lincoln, Nebraska, USA). An average per plot was then calculated for both light measurements. Light measurements were taken under completely overcast sky conditions following the methods of Messier and Puttonen (1995) and Gendron et al. (1998). Soil cover substrate type was assigned to one of the following categories: grasses, herbs, deciduous shrub or tree leaf litter, conifer needles, mineral soil, rock, downed woody debris, and plastic mulch. If the sampling point had equal amount of two or more substrates, the point was divided accordingly. The frequency of occurrence (%) of a given substrate type was the proportion of points in a plot where that substrate type occurred.

### 2.3. Species ecological traits

Information on species ecological traits was obtained from the TOPIQ data base (Traits Of Plants In Quebec, see Aubin et al., 2007). Ten categorical traits and two quantitative traits were used in the present study (Table 2).

### 2.4. Data analysis

#### 2.4.1. Identifying emergent groups

Emergent groups (i.e., groups of species having similar biological traits) were identified separately for woody and herbaceous species following the hierarchical approach suggested by McIntyre et al. (1999) and Deckers et al. (2004). Not all classes of seed dispersal vectors, life cycle, foliage structure and flowering phenology traits were present in the woody species and therefore, they were omitted from the classification of the woody species subset (indicated with an asterisk in Table 2). No trait was omitted for the herbaceous species subset, except for Raunkiaer's phanerophyte forms.

To identify emergent groups, a Gower similarity coefficient was calculated separately for the woody and herbaceous subsets of the biological traits matrix. This coefficient can handle missing values, as well as quantitative and qualitative data (Legendre and Legendre, 1998). A hierarchical agglomerative clustering analysis, Ward's minimum variance method (Legendre and Legendre, 1998), was computed for these similarity matrices to classify species into groups. The cut off limit was determined subjectively after a visual screening of the dendrogram and according to our botanical knowledge.

#### 2.4.2. Assessing differences among stand types

We examined the relative occurrence of these groups between stand types and among the different stand stages using a procedure similar to Hérault et al. (2005) and Aubin et al. (2007). A matrix of the species group occurrences was calculated as the product of the transposed species data matrix (353 species  $\times$  56 plots, with percent occurrence data of each species) by the binary matrix of emergent groups (353 species  $\times$  16 emergent groups). This new matrix (56 plots  $\times$  16 emergent groups) was then standardized by dividing the occurrence of each group by the total occurrence for all the groups in each plot.

To compare the understory vegetation assemblage of each combination of stand type and stand stage (hereafter referred to as stand type  $\times$  stage) and with the old naturally regenerated forests, we performed principal components analysis (PCA) on the matrix of the relative occurrences of emergent groups. The PCA also allowed us to determine if there was an emergent group associated with the old naturally regenerated forest, our natural habitat benchmarks in this study. The mean relative occurrence and mean richness of this indicator group in the different stand type  $\times$  stage combinations were then compared with those found in the old naturally regenerated forests using a one-way ANOVA followed by a Dunnett two-sided post hoc test.

#### 2.4.3. Vertical understory stratification and understory abiotic conditions

We used the matrix of species occurrence, as determined for individual strata, to examine vertical occupancy of the under-

**Table 2 – Plant biological traits as compiled from the literature**

Trait	Code	Description
Raunkiaer life form	RAU	mg: mega or meso-phanerophyte ( $\geq 8$ m in height); mc: micro or nanophanerophyte (25 cm to 8 m); ch: chamaephyte (herb or shrub, bud between 1 mm and 25 cm above ground); h: hemicryptophyte (herb with bud at the ground surface)*; g: geophyte (herb with underground bud)*; t: therophyte (annual)*
Principal means of reproduction (21)	REP	1: seeds only; 2: vegetative propagation possible but mostly by seeds; 3: mostly by vegetative propagation
Foliage persistence	PFO	0: no; 1: yes
Foliage structure	SFO	For phanerophytes: ms: spread out stem; me: erect stem; mu: multi-stemmed; vi: vine For other life forms*: No stem: r: rosette or semi-rosette; g: graminoid; e: erect leaves With stem: el: erect leafy stem; de: decumbent stem; um: umbel-shaped stem; vi: vine Non-leafy stem: nl: saprophyte
Physical defences (e.g., thorns)	DEF	0: no; 1: yes
Flowering phenology	FPH	sp: spring; su: summer; sf: summer-fall
Color of flower	CFL	w: white; g: unattractive (green or brown); b: bright (red, yellow or blue); na: non applicable
Seed dispersal vector <sup>1</sup> (28)	DI	w: wind (anemochorous); ez: mammal ingestion (endozoochorous); zz: animal, carried externally (epizoochorous)*; an: insect, mostly ant (myrmecochorous)*; bi: bird ingestion (avichorous); hd: human dispersal: (anthropochorous)*; ex: ballasts or explosive discharge (ballistichorous)*
Seed size	SE	quantitative variable: <0.1–40 mm
Height	HT	quantitative variable: 6–3500 cm
Light requirement (9)	LI	1: intolerant; 2: mid tolerant; 3: shade tolerant
Status in Quebec	ST	0: native; 1: exotic

In parentheses: number of missing value. <sup>1</sup>For the seed dispersal vector, a species can have more than one class \*Omitted in the analysis of the woody species subset emergent groups.

story vegetation. Development of vegetation structure was characterised for each stand type × stage. To assess differences in pattern of vertical stratification among stand types × stages, a Friedman two-way analysis of variance by ranks was used, where the randomised blocks were the different strata (Siegel and Castellan, 1988). For each stratum, a rank was given to the different combination of stand type × stage. The cumulative rank of each stand type × stage was tested using Friedman's  $\chi^2$  statistic followed by Scheffé-type contrasts (Marascuilo and McSweeney, 1977).

To compare the understory abiotic conditions of each combination of stand types × stand stages, a PCA was performed on the environmental variables matrix.

When necessary, we performed a natural-logarithmic transformation on the dependent variables to ensure normality and homoscedasticity. A significance level of 0.05 was used. The XLStat program (Addinsoft, 2006) was used for all analyses.

### 3. Results

#### 3.1. Emergent group identification

A total of 84 woody species and 269 herbaceous species were recorded. Cluster analysis delineated six emergent groups for the woody species (Cut off limit at  $S = 0.63$ ) and nine for the herbaceous species ( $S = 0.77$ ). As grasses and sedges were not identified to species, they were assigned to an a priori group. For woody species (Table 3a), the first three groups were composed of micro or nanophanerophytes with multi-stemmed foliage structure reproducing mainly by vegetative propagation. These groups were: (W1) summer-flowering vines or shrubs dispersed by birds (avichorous); (W2) spring-flowering shrubs dispersed by birds or by mammal ingestion (endozoochorous); and (W3) low-stature shrubs that were also spring-flowering, but with small seeds dispersed by wind

(anemochorous). The last three woody groups were composed of trees (megaphanerophytes) which reproduced predominantly by seed: (W4) propagules dispersed by wind; (W5) propagules dispersed by bird or mammal ingestion; and (W6) coniferous trees.

For the herbaceous species (Table 3b), the following traits characterized the groups: (H1) exotic annuals, which were dispersed predominantly by mammal ingestion; (H2) exotic perennials, which were mainly wind-dispersed; (H3) summer-flowering species, which were mainly wind-dispersed and shade intolerant; (H4) summer-flowering species dispersed through mammal ingestion; (H5) late-flowering, wind-dispersed hemicryptophytes; and (H6) ferns and allies, which have distinct biological traits, along with other shade tolerant species with very small seeds (this group included a relatively large proportion of species with persistent foliage). The spring-flowering species were separated into: (H7) those dispersed through ingestion by animals or birds, which possessed the largest seeds and were shade tolerant; (H8) those that were dispersed by wind, carried externally by mammals (epizoochorous), or had no specialised vector (barochorous); and (H9) those whose propagules were dispersed by ants (myrmecochorous), and that were the shortest in height.

#### 3.2. Responses of emergent groups to stand types

The two PCA axes of the species groups relative occurrence illustrated the distribution of emergent groups among the different study plots ( $n = 56$ , Fig. 2). The first two axes that were extracted from principal components analysis explained 38% of the total variance (Fig. 2). The first principal component (F1) represented mostly a gradient of deciduous stand development, with open canopy stages (O) on the left and mature canopy (M) and old naturally regenerated forest stands (NAT) on the right sides of the ordination. This successional gradient was reflected in the location of the emergent groups

**Table 3a – Classification by species groups of woody species having similar biological traits computed from a cluster analysis done on the biological traits data matrix ( $n = 84$ )**

Traits	W1. Summer-flowering vines or shrubs	W2. Shrubs dispersed by bird	W3. Shrubs dispersed by wind	W4. Trees dispersed by wind	W5. Trees dispersed by mammal or bird	W6. Conifer trees
RAU	mc (mg)	mc	mc	mg	mg	mg
SFO	vi (mu)	mu	mu	(ms)	ms	me (ms)
REP	3, 2	3	3	2 (3)	2	2
LI	2	2	1	–	(2)	–
CFL	b g	b	b	g (b)	g	na
DI	bi	bi ez	w	w	ez bi	w ez
ST	0	0	0	0	0	0
SE	4.35	4.27	1.79	6.70	20.53	4.25
PFO	0	0	0	0	0	(1)
DEF	0	(1)	0	0	0	0
FPH	su	sp	sp	sp	sp	sp
HT	840	425	271	2317	2300	2480
Sp	<i>Parthenocissus quinquefolia</i> <i>Sambucus canadensis</i>	<i>Ilex verticillata</i> <i>Cornus sericea</i>	<i>Spiraea alba</i> <i>Myrica gale</i>	<i>Acer saccharum</i> <i>Ulmus americana</i>	<i>Carya cordiformis</i> <i>Juglans cinerea</i>	<i>Pinus resinosa</i> <i>Abies balsamea</i>
N	10	30	8	18	8	10

Cut off limit at  $S = 0.63$ .

See Table 2 for code definitions. Codes in parentheses indicate that this class is present but in lower proportion. Sp: characteristic species.

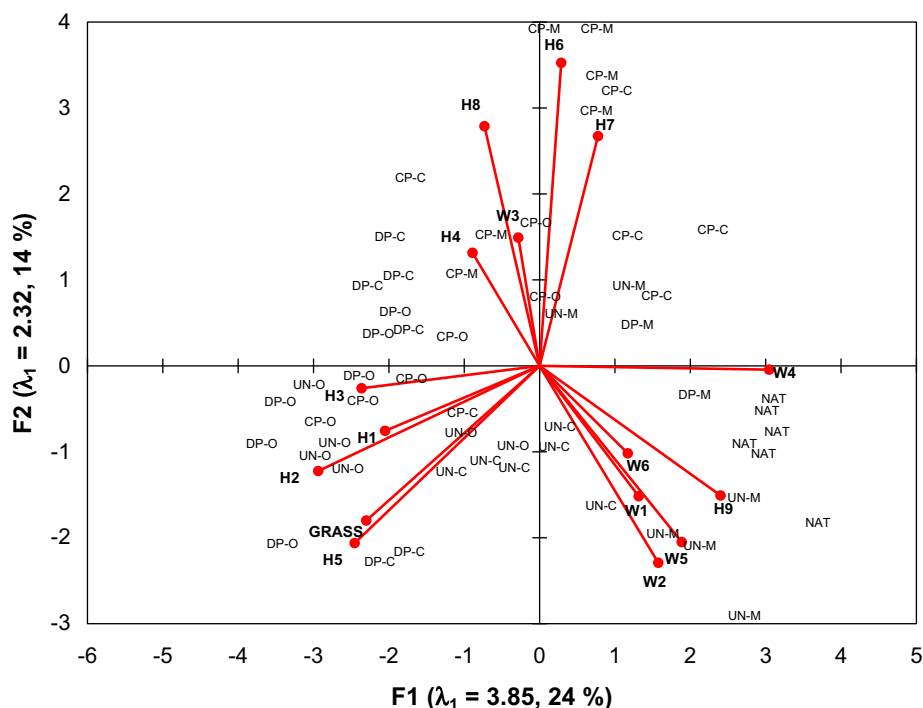
**Table 3b – Classification by species groups of herbaceous species having similar biological traits computed from a cluster analysis done on the biological traits data matrix (n = 270)**

Traits	H1. Introduced annuals	H2. Introduced perennials	H3. Summer-flowering herbs dispersed by wind	H4. Summer-flowering herbs dispersed by mammal	H5. Late-flowering herbs dispersed by wind	H6. Ferns and allies	H7. Spring-flowering herbs dispersed by mammal/bird	H8. Spring-flowering herbs dispersed by wind/gravity	H9. Short spring-flowering herbs dispersed by ant	Grass. Grass and sedges
RAU	t (h)	h	h (t)	h	h	h (g)	g h	h (g)	h g	h
SFO	–	(r)	el (r)	de el	el r	e	el de	–	r e	g
REP	1	(3)	–	3	–	3	3	3	3	3
LI	1	1	1 (2)	–	(1)	3	3	–	–	1 (2)
CFL	b (w)	b	b (w)	w	b	na	w b	w b	b w	g
DI	(ez)	(w)	(w)	ez	w	w ex	ez (bi)	(w zz) barochore	an (ex)	w (ez an)
ST	1	1	0	0	0	0	0	0	0	(1)
SE	2.03	2.56	2.68	2.15	1.34	0.27	3.30	2.43	2.46	1.5
PFO	0	0	0	0	0	(1)	0	(1)	0	0
DEF	0	–	0	(1)	0	0	0	0	0	0
FPH	su	su	su	su	su sf	su	sp	sp	sp	–
HT	96	94	131	144	143	116	114	82	29	–
Sp	<i>Chenopodium album</i> <i>Galeopsis tetrahit</i>	<i>Cirsium arvense</i> <i>Hieracium caespitosum</i>	<i>Anemone virginiana</i> <i>Lactuca canadensis</i>	<i>Rubus idaeus</i> <i>Galium palustre</i>	<i>Aster novaeangliae</i> <i>Solidago canadensis</i>	<i>Dryopteris intermedia</i> <i>Thelypteris noveboracensis</i>	<i>Smilacina racemosa</i> <i>Aralia racemosa</i>	<i>Cardamine dyphilla</i> <i>Hydrophyllum virginianum</i>	<i>Sanguinaria canadensis</i> <i>Asarum canadense</i>	<i>Poa pratensis</i> <i>Carex lurida</i>
N	18	43	65	19	18	26	20	41	19	85

Cut off limit at S = 0.77.

See Table 2 for code definitions. Codes in parentheses indicate that this class is present but in lower proportion. Sp: characteristic species.





**Fig. 2 – The first two axes of the PCA calculated on the emergent group relative occurrence matrix. Nat: old naturally regenerated forest; UN-M: unplanted mature canopy; UN-C: unplanted closed canopy; UN-O: unplanted open canopy; DP-M: mature deciduous plantation; DP-C: closed canopy deciduous plantation; DP-O: open canopy deciduous plantation; CP-M: mature conifer plantation; CP-C: closed canopy conifer plantation, CP-O: open canopy conifer plantation. See Table 3 for emergent group description.**

in the ordination biplot; pioneer species groups that were associated with open habitats (H1 to H5, and grass) were on the left-hand side of axis F1, while spring-flowering ant-dispersed herbs (H9) and woody species (W) associated with mature and old naturally regenerated stands were on the right. Conifer plantations (CP) tended to segregate from other stand types along the second axis (F2). Ferns (H6) and spring-flowering herbs that were dispersed by mammals or birds (H7), or by wind and gravity (H8), were located at the top of axis F2, while woody species (W) and late-flowering herbs (H5) were at the bottom. The ordination of the PCA components showed that the old naturally regenerated forest stands (NAT,  $n = 6$ ) formed a tight, homogeneous grouping that was separated from the other study plots ( $n = 50$ ), which in turn formed less distinct clusters. Old naturally regenerated forest stands had a high occurrence of woody groups (W) and of ant-dispersed spring-flowering herbs (H9), as well as a low occurrence of exotic groups (H1, H2), wind-dispersed summer- and late summer-flowering herbs (H3, H5), and grasses and sedges (GRASS). Unplanted mature canopy stands (UN-M) and deciduous plantation mature canopy stands (DP-M) had emergent group assemblages that were most similar to old naturally regenerated forest stands. The mean relative occurrence of emergent groups for each stand type  $\times$  stage has been provided in the [Electronic Appendix](#).

Ant-dispersed spring-flowering herbs (H9) were chosen as an indicator group, since they were associated with old naturally regenerated forests. We additionally compared the mean relative occurrence of this group in old naturally regenerated

forests (NAT) with those found in the different stand type by stages (One-way ANOVA, followed by Dunnett's tests). Deciduous plantations with a mature canopy (DP-M) were found to be the only stand type by stages not significantly different from the NAT reference site (Table 4).

The comparison of the mean richness of this indicator group (H9) in old naturally regenerated forest stands (NAT) with those found in the different stand type by stages revealed that unplanted stands with a mature canopy (UN-M) were the only stand type by stages not significantly different from the NAT reference site ( $P < 0.05$  One-way ANOVA, followed by a Dunnett's test; Table 4).

### 3.3. Understorey abiotic conditions

The two PCA axes of the abiotic conditions matrix illustrated light availability and substrate distribution among the different study plots ( $n = 56$ , Fig. 3). The first two components that were extracted by PCA explained 50% of variation in the environmental data. Moreover, the stand groupings for the abiotic variables (Fig. 3) mirrored the patterns depicted for the emergent groups in Fig. 2. The principal component F1 represented a gradient of stand development, with open canopy stages (O) on the left and mature canopy (M) on the right. The old naturally regenerated forests (NAT) formed a homogeneous group to the right. The different stand types separated along the second principal component, with the conifer plantations (CP) being located at the top of the axis F2 and the unplanted stands (UN) mostly located near the bottom. The primary

**Table 4 – Mean relative occurrence (%) of emergent groups and functional diversity (r: richness of each emergent group) of the ant-dispersed spring-flowering herbs group (H9) among stand types and stages**

Stand types	Stages	Occurrence (%)	Richness
NAT		17.1	5.8
UN	M	5.0	4.2 <sup>a</sup>
	C	4.6	3.3
	O	1.1	1.8
DP	M	7.6 <sup>a</sup>	2.0
	C	0.4	1.0
	O	0.1	0.2
CP	M	0.0	0
	C	0.3	0.3
	O	0.2	0.3

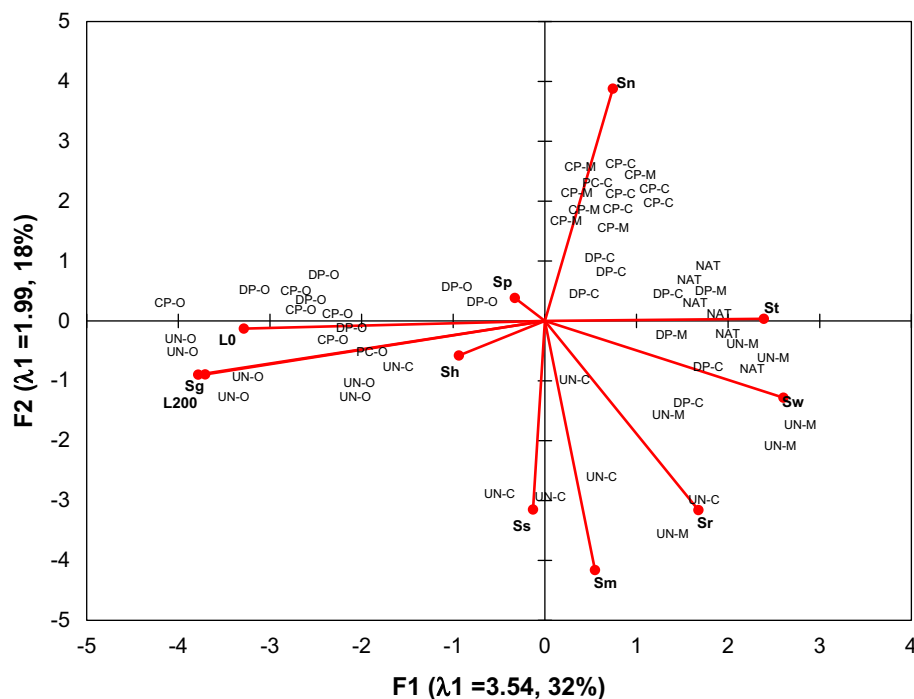
Nat: old naturally regenerated forest; UN: unplanted; DP: deciduous plantation; CP: coniferous plantation; M: mature; C: closed; O: open canopy.  
<sup>a</sup> Not significantly different from NAT at  $P < 0.05$  (One-way ANOVA followed by a Dunnett's test).

gradient (Axis 1) included light availability (L200, L0), and the decreasing occurrence of grass litter (Sg), while that of tree leaf litter (St) and downed woody debris (Sw) increased. The secondary gradient (Axis 2) highlighted the relative occurrence of needle substrate (Sn) versus mineral soil (Sm). Open

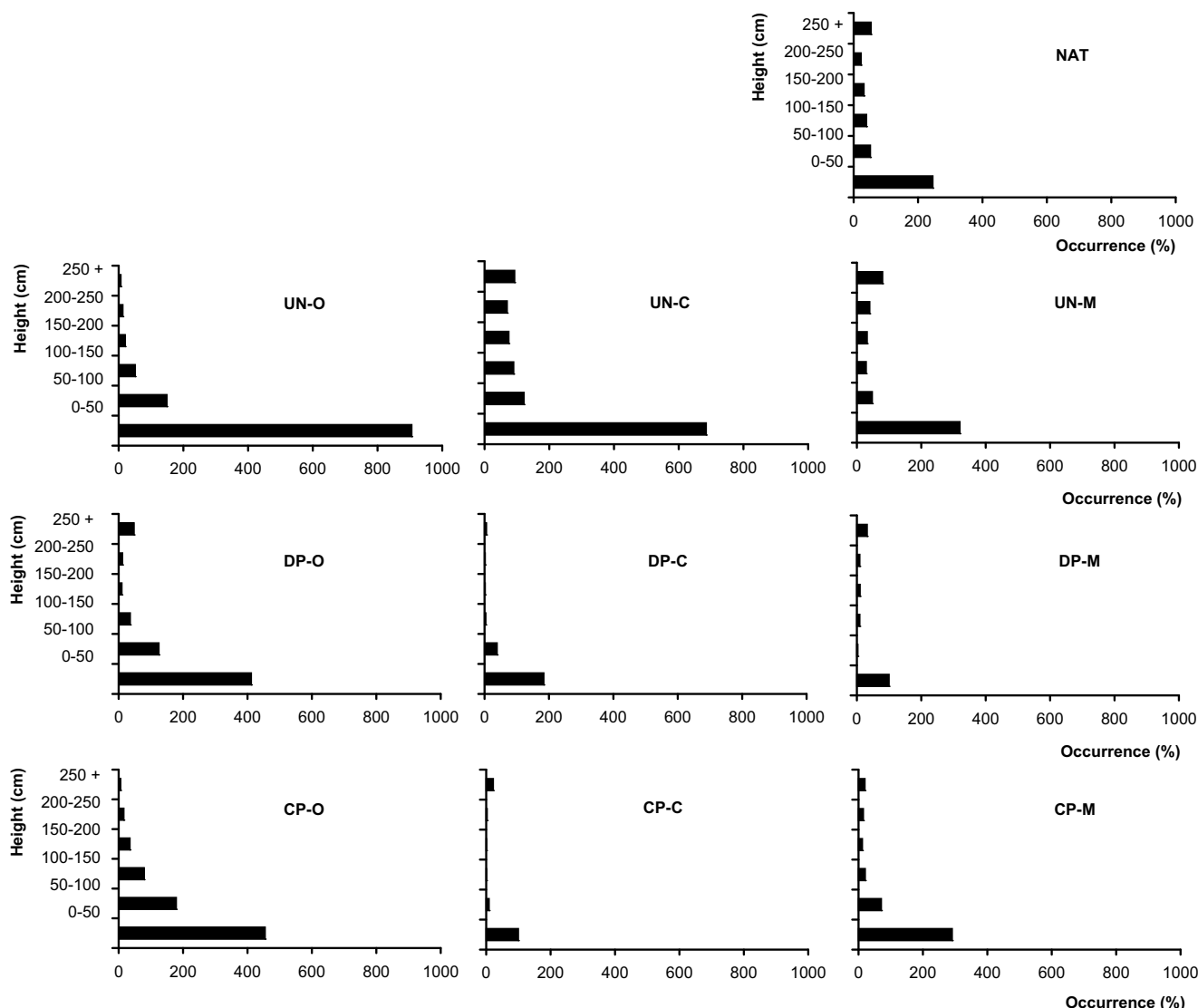
canopy stands (O) were all characterised by high light availability (L200, L0) and grass litter substrate (Sg). Important differences in soil cover substrate were observed among stand types for closed (C) and mature (M) canopy stands. Conifer plantations with a closed and mature canopy (CP-C, CP-M) were dominated by a needle litter. Unplanted stands with a closed canopy (UN-C) were characterised by a mixture of mineral soil (Sm), downed woody debris (Sw) and deciduous shrub leaf litter (Ss), while deciduous tree leaf litter (St) progressively gained dominance in unplanted mature canopy stands (UN-M). Deciduous plantations with a mature canopy (DP-M) possessed combinations of understory abiotic conditions that were most similar to the old naturally regenerated forests (NAT), with low light availability and a soil cover substrate dominated by tree leaf litter (St) and downed woody debris (Sw). Mean light availability and soil cover substrate types for each stand type  $\times$  stage are provided in the Electronic Appendix.

### 3.4. Understory vertical stratification

Vertical stratification of the vegetation was pronounced for all stand types (Fig. 4). The old naturally regenerated forests (NAT) had a well-developed low stratum (0–50 cm), little vegetation in the 50–200 cm stratum, and a moderate amount of vegetation in the  $\geq 250$  cm stratum. Vertical patterning of the vegetation differed significantly among stand types and stages (Friedman's test,  $\chi^2 = 177.94$ ,  $P < 0.0001$ , d.f. = 9). The



**Fig. 3 – The first two axes of the PCA calculated on the environmental variables. Nat: old naturally regenerated forest; UN-M: unplanted mature canopy; UN-C: unplanted closed canopy; UN-O: unplanted open canopy; DP-M: mature deciduous plantation; DP-C: closed canopy deciduous plantation; DP-O: open canopy deciduous plantation; CP-M: mature conifer plantation; CP-C: closed canopy conifer plantation, CP-O: open canopy conifer plantation. Environmental variables: Sg: grasses; Sh: herbs; Ss: deciduous shrub leaf litter; St: deciduous tree leaf litter; Sn: needle litter; Sm: mineral soil; Sr: rock; Sw: downed woody debris; Sp: plastic mulch; L0: light (% PFD) at forest floor; L200: light at 200 cm.**



**Fig. 4 – Cumulative occurrence of vegetation by vertical stratum for each stand type and stage. Nat: old naturally regenerated forest; UN-M: unplanted mature canopy; UN-C: unplanted closed canopy; UN-O: unplanted open canopy; DP-M: mature deciduous plantation; DP-C: close canopy deciduous plantation; DP-O: open canopy deciduous plantation; CP-M: mature conifer plantation; CP-C: close canopy conifer plantation, CP-O: open canopy conifer plantation.**

analysis separated the stands into 3 groups: (1) Unplanted closed canopy stands (UN-C) which possessed the most developed vertical patterning; (2) a group possessing a moderately developed understory that was composed of all open canopy stands (UN-O, DP-O, CP-O), of unplanted and coniferous plantations with mature canopy stands (UN-M, CP-M), and of the old naturally regenerated stands (NAT); and (3) a group possessing a low vegetation occurrence composed of deciduous plantations with closed or mature canopy (DP-C, DP-M) and of coniferous plantations with a closed canopy (CP-C).

#### 4. Discussion

Major differences were found in species trait responses among the two plantation types and in comparisons with unplanted stands. In order to assess if plantations could develop understory attributes similar to naturally regenerated forest

ecosystem, these differences in trait responses have to be discussed with regard to their temporal dynamics, and to the differential understory development among stand types.

##### 4.1. Species trait responses to stand developmental stages

Clear patterns in species trait responses did exist along stand developmental stages. Light-demanding and wind-dispersed species groups, such as grasses, exotics and summer- or late summer-flowering herbs, were predominant in open canopy stands. An understory that possess a high proportion of these groups could be described as being at an early-successional stage. Conversely, woody groups and ant-dispersed spring-flowering herbs were associated with mature canopy stands and old naturally regenerated forests. Many studies have associated ant-dispersed spring-flowering herbs with natural unmanaged forests or ancient forests (Bossuyt et al., 1999;

Scheller and Mladenoff, 2002; Aubin et al., 2007). Their slow growth and low colonization capacity have made them particularly sensitive to human disturbances (Bierzzychudek, 1982; Meier et al., 1995; Whigham, 2004). In contrast, the other forest herb groups contained species that are normally encountered in a wider range of forest types or are associated with forest edges (e.g., *Aralia nudicaulis* of the spring-flowering herb dispersed by mammal or bird group). The ant-dispersed spring-flowering herbs have been considered as having high conservation value and are used as an indicator of natural forests for the deciduous temperate biome (Keddy and Drummond, 1996; Hermy et al., 1999; McLachlan and Bazely, 2001; Aubin et al., 2007). This group thus was considered as our indicator group. An occurrence and a richness of this indicator group comparable to those of old naturally regenerated forest were used in this study as an indicator of the development of a mature understory.

#### 4.2. Differential understory development between deciduous and coniferous plantation

We noted contrasting differences in understory development between coniferous and deciduous plantations. At young stages, the understory assemblages and understory environmental conditions were quite similar between the two plantation types. However, they were radically different in mature canopy stands. Understory attributes were much more similar to old naturally regenerated forests in the deciduous plantations compared to the coniferous ones. In mature deciduous plantations, the proportions of the different emergent groups were similar to those of old naturally regenerated forests. The group of ant-dispersed spring-flowering herbs, which was our indicator group, also occurred in deciduous plantations with frequencies comparable to those of old naturally regenerated forests. However, the richness of this group was low and the understory structure of deciduous plantations was poorly developed when compared to old naturally regenerated forests. Understory development in conifer plantations followed a trajectory that differed greatly from deciduous plantations. Their understory vegetation assemblages were compositionally, structurally and functionally different from those of naturally regenerated or planted deciduous stands. Our indicator group (ant-dispersed spring-flowering herbs) decreased in its frequency of occurrence along stand stages in conifer plantations, and was absent from the mature canopy stage. Hérault et al. (2005) have also observed a low frequency of occurrence of spring geophytes in mature conifer plantations, together with contrasting floral assemblages between Norway spruce plantations and natural deciduous forests in Europe. In our study, the two measured understory environmental variables (light and soil cover substrate) were also radically different in coniferous plantations than in deciduous stands. These differences may have constrained the establishment of forest herbs associated with deciduous stands. For example, the acidic and nutrient-limited needle litter layer (Hunter, 1990; Augusto et al., 2002), together with cool and dark spring conditions found under conifer canopy compared to those of a deciduous canopy, may have inhibited the establishment of many spring-flowering herbs, which are known to be nutrient- and light-demanding during their short

spring time, above ground vegetative cycle (Lapointe, 2001; Whigham, 2004). At the species level, we did not find in this stand type any high conservation value species, such as orchids, associated with acidic litter.

#### 4.3. Differential understory development between planted and unplanted stands

For a similar stand stage, the understory of plantations was generally less developed than naturally regenerated stands, suggesting that traditional tree planting does not effectively promote the development of a mature and functional forest understory. Although they possessed a younger and smaller canopy stratum than plantations, the understory vegetation assemblage of unplanted stands was species-rich, with well-developed structure. These results suggest a good but undervalued potential for natural understory recovery in abandoned pasture lands. Bowen et al. (2007) have underlined a similar neglected potential for native forest fauna following natural restoration on abandoned agricultural lands.

The differences between planted and unplanted stands may be attributed to the intensity of the site preparation methods used in the planted stands. In these plantations, the heavy plowing equipments used may have profoundly altered some important features of the stand biological legacy (sensu Franklin et al., 2000). Site preparation in plantations, such as plowing or soil scarification, has been reported to have an important impact on biodiversity (Hartley, 2002). Such soil modification mainly destroys the established flora and reduces soil surface heterogeneity. The resulting uniformity of the soil surface can reduce habitat diversity and may impede forest herb establishment via environmental limitations and competition (Beatty, 2003; Flinn and Vellend, 2005; Flinn and Marks, 2007). Species such as ant-dispersed spring-flowering herbs may take a century to reestablish via seed dispersal (Scheller and Mladenoff, 2002; Flinn and Vellend, 2005; Flinn and Marks, 2007). Accordingly, retaining a proportion of the established flora in plantations (intentionally or not) has been reported to favor diversity and native vegetation recovery (Hartley, 2002).

Silvicultural treatments in plantations, such as thinning, pruning and weed control, have been reported to have an important impact on biodiversity (Hartley, 2002). Although not specifically tested in this study, they may have contributed to the divergence between unplanted and planted stands. Thinning generally promotes the development of the shrub and herb strata, and thus, has generally been perceived as a positive step for understory development (Parker et al., 2001; Thysell and Carey, 2001; Hartley, 2002). However, thinning has been known to disturb extant vegetation and the forest floor, to increase light availability, and to modify the microclimate (Hunter, 1990; Hansen et al., 1991; Moore and Allen, 1999). In fact, it has been reported to principally favor generalist (Hérault et al., 2005) and exotic (Parker et al., 2001; Newmaster et al., 2006) species. Many forest herbs are sensitive to competition with pioneer species, which is likely to occur following such types of disturbance (Meier et al., 1995), and are sensitive to desiccation following forest floor disturbance (Metzger and Schultz, 1981). Pruning probably had a similar, but less pronounced impact than thinning.

For its part, the impact of weed control on understory development will vary according to the technique used (chemical, mechanical or plastic mulch) and the success of the weed control. As stated by Hartley (2002), “the less perfectly that competing vegetation is eliminated from the stand the better, for most species”. Globally, weed control is likely to promote the establishment of species adapted to disturbance. This suggests that silvicultural treatments globally favor pioneer species, to the competitive disadvantage of forest herb specialists. Accordingly, while relative occurrence for groups associated with pioneer stage sharply decrease between open and closed canopy stages for unplanted and coniferous plantation stand types, we still observed a high relative occurrence for pioneer groups in closed canopy deciduous plantations (Fig. 2); this stand type received the most frequent and intensive silvicultural treatments (Table 1).

#### 4.4. Can plantations develop the understory attributes of a naturally regenerated forest ecosystem?

Planting a tree cover results in the rapid development of a forest structure that will be attractive for some wildlife species and which may indeed favor the development of forest herbs by creating understory environmental conditions comparable to a natural forest. The rapid creation of a tree cover has been shown to facilitate tree seedling growth and survival in many biomes (Paquette et al., 2006b) and has been suggested to have a positive global impact on biodiversity (Stephens and Wagner, 2007). However, our study did not show any evidence of an accelerated understory flora development in plantations compared to unplanted land of similar land use history. In fact, understory development in conifer plantations was very different from that found in naturally regenerated habitats dominated by temperate deciduous species in the region. These plantations might, however, be comparable to white pine (*Pinus strobus*) stands that were known to be more frequent in northern hardwood regions prior to intense harvesting in the 19th century (Simard and Bouchard, 1996; O’Keefe and Foster, 1998). However, in pre-colonial forests, white pine was mainly found scattered throughout the hardwood forest. Pure stands of pine were rare and confined to dry and poor sites (Brisson and Bouchard, 2006). The structure, composition and function of the understory found in monospecific conifer plantations are not representative of the conditions found in natural forests of the temperate deciduous biome. They should then be avoided, minimized and/or confined to localized poor soil conditions to preserve the ecological integrity of the biome. Conversion of such plantations into deciduous woodlands has become a major objective for forest management in Europe (Herault et al., 2005) and might become a preoccupation in North America with the continuing decline of natural forests.

Deciduous plantations developed understories that were compositionally, functionally and structurally similar to those of old naturally regenerated forests. However, they remained impoverished in terms of high conservation value species even after 50 years. Post-agricultural forests are known to take more than a century to recover their original understory composition (Matlack, 1994; Bossuyt et al., 1999; Flinn and Marks, 2007). The native forest flora faces both dispersal

and environmental constraints to its establishment in post-agricultural lands (Ehrlén and Eriksson, 2000; Nordén and Appelqvist, 2001; Flinn and Marks, 2007). Dispersal is known to limit the establishment of many forest herbs, especially those with short distance dispersal such as spring-flowering herbs that are dispersed by ants (Ehrlén and Eriksson, 2000; Flinn and Vellend, 2005). Environmental limitations have been less frequently documented, but these may be just as important as dispersal capacity in determining the establishment success of forest herbs (Nordén and Appelqvist, 2001; Flinn and Marks, 2007). For instance, many forest herbs and non-vascular species are reported to be unable to colonize a stand when suitable microhabitats, such as coarse woody debris or a particular microtopographic feature, are absent (Humphrey et al., 2002; Scheller and Mladenoff, 2002; Flinn and Marks, 2007). Similarly, some species are confined to low light environments where they have a competitive advantage (Collins et al., 1985).

A first step in the establishment, development and persistence of high conservation value forest herbs in plantations requires that understory environmental conditions similar to those of their natural habitat be attained. In our study, the two measured understory environmental conditions in mature canopy deciduous plantations corresponded to those of old naturally regenerated forests. Consequently, we suspect that dispersal limitation may have been the major factor impeding the establishment of high conservation value species in these stands. Restoration activities, such as plantation or seeding of these species may be the prescribed treatments in this case.

#### 4.5. How can development of a mature understory be promoted in plantations?

It is generally accepted that the main positive impact of plantations on global biodiversity is that high timber production on a small portion of the land can possibly allow the development of more protected areas and/or better forest management approaches that maximize nature conservation elsewhere on the landscape (Evans, 1999; Hartley, 2002; Messier et al., 2003). Furthermore, some authors have argued that it is possible to enhance other ecological services in plantations with little negative impact on timber production and with only minimal changes in plantation design and management (Hartley, 2002). Thus based on our results and our understanding of the ecology of natural temperate deciduous forests of eastern North America, one could enhance their conservation potential by: (1) favoring deciduous tree species instead of conifers; (2) preserving natural stand structural legacies by minimizing site preparation; (3) favoring silvicultural activities that preserve or recreate the prevailing environmental conditions and stand structural heterogeneity encountered in natural forest; (4) favoring longer rotations to allow sufficient time for the development of a mature understory community; and (5) reintroducing, when understory environmental conditions are favorable, forest herbs that have high conservation value and low seed dispersal capacity, for example, ant-dispersed spring-flowering herbs. Clearly, enrichment planting is a good alternative to conventional planting techniques since it would tend to preserve

understory community and stand legacies while ensuring good tree growth (Paquette et al., 2006a,b).

## 5. Conclusion

Although some limitations inherent to coarse synthesis have to be considered in the interpretation of this study, the approach used here gives a comprehensive and broadly applicable portrait of the ecological integrity of plantations. This study has shown that deciduous plantations and to a much lower extent, conifer plantations, can be a viable habitat for some native flora. However, we did not find any evidence that planting abandoned agricultural sites effectively accelerated the development of the native flora. This study even highlights the neglected potential of marginal lands as habitats for native flora. In fact, the success of natural restoration of the understory will be a function of the type of planted trees and presumably, of its associated activities. Important population attributes that were not studied here, such as fine scale species distribution patterns or genetic variability, might be different in plantations than in naturally regenerated stands. These modifications might have a profound impact both at the level of population stability and ecosystem processes.

Further research is needed to refine our understanding of understory development in plantations. A lack of knowledge about the ecological traits of many species has impeded our understanding of their responses to different environmental filters. In this study, the use of other important, but insufficiently documented ecological traits, such as seed longevity, soil chemistry requirements and interactions with mycorrhizae, herbivores and pollinators, would have substantially improved our understanding of understory development mechanisms. It is important to note that distance to a seed source (forest) was relatively small in our study, facilitating understory recovery. The spatial context is a major factor in determining the potential of a plantation to become a forest (Hartley, 2002).

The marked decline of natural unmanaged forest has prompted us to develop tools that quantify the ecological integrity of these human-created ecosystems, which could help us in managing them in such a way as to increase their naturalness. Therefore, in regions where the proportion of natural forest is low or declining, the goal of tree plantation should include a restoration objective as well as a timber objective.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.biocon.2008.07.007](https://doi.org/10.1016/j.biocon.2008.07.007).

## REFERENCES

- Addinsoft, 2006. XLStat-Pro version 2006.06, New York, USA.
- Aubin, I., Beaudet, M., Messier, C., 2000. Light extinction coefficients specific to the understory vegetation of the southern boreal forest (Québec). *Canadian Journal of Forest Research* 30, 168–177.
- Aubin, I., Gachet, S., Messier, C., Bouchard, A., 2007. How resilient are northern hardwood forests to human disturbance? An evaluation using a plant functional group approach. *Ecoscience* 14, 259–271.
- Aubin, I., Ouellette, M.H., Legendre, P., Messier, C., Bouchard, A., in press. Comparison of two plant functional approaches to evaluate natural restoration along an old-field-deciduous forest chronosequence. *Journal of Vegetation Science*.
- Augusto, L., Ranger, J., Binkley, D., Rothe, A., 2002. Impact of several common tree species of European temperate forests on soil fertility. *Annals of Forest Science* 59, 233–253.
- Beatty, S.W., 2003. Habitat heterogeneity and maintenance of species in understory communities. In: Gilliam, F.S., Roberts, M.R. (Eds.), *The herbaceous layer in forests of eastern North America*. Oxford University Press, New York, pp. 177–197.
- 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.
- Benjamin, K., Cogliastro, A., Bouchard, A., 2006. Potentiels et contraintes des friches agricoles dans une trame agroforestière: perceptions des propriétaires. Réseau Ligniculture Québec. Institut de recherche en biologie végétale, Montréal.
- Benjamin, K., Bouchard, A., Domon, G., 2007. Abandoned farmlands as components of rural landscapes: an analysis of perceptions and representations. *Landscape and Urban Planning* 83, 228–244.
- Bierzuchudek, P., 1982. Life histories and demography of shade-tolerant temperate forest herbs: a review. *New Phytologist* 90, 757–776.
- Bossuyt, B., Hermy, M., Deckers, J., 1999. Migration of herbaceous plant species across ancient-recent forest ecotones in central Belgium. *Journal of Ecology* 87, 628–638.
- Bouchard, A., Brisson, J., 1996. Domaine de l'érablière à caryer cordiforme. In: Bérard, J. (Ed.), *Manuel de foresterie*. Presses de l'Université Laval, Sainte-Foy, pp. 160–170.
- Bouchard, A., Domon, G., 1997. The transformation of the natural landscapes of the Haut-Saint-Laurent (Québec) and their implications on future resource management. *Landscape and Urban Planning* 37, 99–107.
- Bowen, M.E., McAlpine, C.A., House, A.P.N., Smith, G.C., 2007. Regrowth forests on abandoned agricultural land: a review of their habitat values for recovering forest fauna. *Biological Conservation* 140, 273–296.

- Brisson, J., Bouchard, A., 2003. In the past two centuries, human activities have caused major changes in the tree species composition of southern Québec, Canada. *Ecoscience* 10, 236–246.
- Brisson, J., Bouchard, A., 2006. The Haut-Saint-Laurent wilderness at the time of settlement based on Sellar's History. Part II: Forests and wetlands. *Chateauguay Valley Historical Society Annual Journal* 37, 29–45.
- 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.
- Collins, B.S., Dunne, K.P., Pickett, S.T.A., 1985. Responses of forest herbs to canopy gaps. In: Pickett, S.T.A., White, P.S. (Eds.), *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando, FL, pp. 217–234.
- Cramer, W., 1997. Using plant functional types in a global vegetation model. In: Smith, T.M., Shugart, H.H., Woodward, F.I. (Eds.), *Plant functional types: their relevance to ecosystem properties and global change*. Cambridge University Press, Cambridge, pp. 271–288.
- Deckers, B., Verheyen, K., Hermy, M., Muys, B., 2004. Differential environmental response of plant functional types in hedgerow habitats. *Basic and Applied Ecology* 5, 551–566.
- Domon, G., Bouchard, A., 2007. The landscape history of Godmanchester (Quebec, Canada): two centuries of shifting relationships between anthropic and biophysical factors. *Landscape Ecology* 22, 1201–1214.
- D'Orangeville, L., Bouchard, A., Cogliastro, A., 2008. Post-agricultural forests: landscape patterns add to stand-scale factors in causing insufficient hardwood regeneration. *Forest Ecology and Management* 255, 1637–1646.
- Ehrlén, J., Eriksson, O., 2000. Dispersal limitation and patch occupancy in forest herbs. *Ecology* 81, 1667–1674.
- Evans, J., 1999. Planted forests of the wet and dry tropics: their variety, nature, and significance. *New Forests* 17, 25–36.
- FAO, 2007. *State of the world's forest*, seventh ed. Food and Agriculture Organization of the United Nations, Rome.
- Flinn, K.M., Marks, P.L., 2007. Agricultural legacies in forest environments: tree communities, soil properties, and light availability. *Ecological Applications* 17, 452–463.
- Flinn, K.M., Vellend, M., 2005. Recovery of forest plant communities in post-agricultural landscapes. *Frontiers in Ecology and the Environment* 3, 243–250.
- Franklin, J.F., Lindenmayer, D., MacMahon, J.A., McKee, A., Magnuson, J., Perry, D.A., Waide, R., Foster, D., 2000. Threads of continuity: ecosystem disturbance, recovery, and the theory of biological legacies. *Conservation Biology in Practice* 1, 8–16.
- Gachet, S., Leduc, A., Bergeron, Y., Nguyen-Xuan, T., Tremblay, F., 2007. Understorey vegetation of boreal tree plantations: differences in relation to previous land use and natural forests. *Forest Ecology and Management* 242, 49–57.
- Gardner-Outlaw, T., Engelman, R., 1999. *Forest futures: population, consumption, and wood resources*. Population Action International, Washington, DC.
- Gendron, F., Messier, C., Comeau, P.G., 1998. Comparison of various methods for estimating the mean growing season percent photosynthetic photon flux density in forest. *Agricultural and Forest Meteorology* 92, 55–70.
- George, L.O., Bazzaz, F.A., 2003. The herbaceous layer as a filter determining spatial pattern in forest tree regeneration. In: Gilliam, F.S., Roberts, M.R. (Eds.), *The Herbaceous Layer in Forests of Eastern North America*. Oxford University Press, New York, pp. 265–282.
- Gilliam, F.S., Roberts, M.R., 2003. The herbaceous layer in forests of Eastern North America. Oxford University Press, New York.
- Gleason, H.A., Cronquist, A., 1991. *Manual of vascular plants of northeastern United States and adjacent Canada*, second ed. The New York Botanical Garden, New York.
- Globensky, Y., 1987. *Géologie des basses terres du Saint-Laurent*. Ministère de l'Énergie et des Ressources naturelles du Québec, Québec.
- Graae, B.J., Sunde, P.B., 2000. The impact of forest continuity and management on forest floor vegetation evaluated by species traits. *Ecography* 23, 720–731.
- Hansen, A.J., Spies, T.A., Swanson, F.J., Ohmann, J.L., 1991. Conserving biodiversity in managed forests. Lessons from natural forests. *Bioscience* 41, 382–391.
- Hartley, M.J., 2002. Rationale and methods for conserving biodiversity in plantation forests. *Forest Ecology and Management* 155, 81–95.
- Herault, B., Honnay, O., Thoen, D., 2005. Evaluation of the ecological restoration potential of plant communities in Norway spruce plantations using a life-trait based approach. *Journal of Applied Ecology* 42, 536–545.
- Hermy, M., Honnay, O., Firbank, L., Grashof-Bokdam, C., Lawesson, J.E., 1999. An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. *Biological Conservation* 91, 9–22.
- Holling, C.S., 2001. Understanding the complexity of economic, ecological, and social systems. *Ecosystems* 4, 390–405.
- Humphrey, J.W., Davey, S., Peace, A.J., Ferris, R., Harding, K., 2002. Lichens and bryophyte communities of planted and semi-natural forests in Britain: the influence of site type, stand structure and deadwood. *Biological Conservation* 107, 165–180.
- Hunter, M.L., 1990. *Wildlife, forests and forestry. Principles of managing forests for biological diversity*. Prentice Hall, Englewood Cliffs, NJ.
- Hunziker, M., 1995. The spontaneous reforestation in abandoned agricultural lands: perception and aesthetic assessment by locals and tourists. *Landscape and Urban Planning* 31, 399–410.
- Kanowski, J., Catterall, C.P., Wardell-Johnson, G.W., 2005. Consequences of broadscale timber plantations for biodiversity in cleared rainforest landscapes of tropical and subtropical Australia. *Forest Ecology and Management* 208, 359–372.
- Karr, J.R., Dudley, D.R., 1981. Ecological perspective on water quality goals. *Environmental Management* 5, 55–68.
- Keddy, P.A., Drummond, C.G., 1996. Ecological properties for the evaluation, management, and restoration of temperate deciduous forest ecosystems. *Ecological Applications* 6, 748–762.
- Kimmins, J.P., 1997. *Forest ecology. A foundation for sustainable management*, second ed. Prentice-Hall, New York.
- Lapointe, L., 2001. How phenology influences physiology in deciduous forest spring ephemerals. *Physiologia Plantarum* 113, 151–157.
- Lavorel, S., McIntyre, S., Landsberg, J., Forbes, T.D.A., 1997. Plant functional classifications: from general groups to specific groups based on response to disturbance. *Trends in Ecology and Evolution* 12, 474–478.
- Legendre, P., Legendre, L., 1998. *Numerical ecology*, second ed. Elsevier, Amsterdam.
- Levin, S.A., 1998. Ecosystems and the biosphere as complex adaptive systems. *Ecosystems* 1, 431–436.
- Marascuilo, L.A., McSweeney, M., 1977. *Nonparametric and distribution-free methods for the social sciences*. Brooks/Cole, Monterey, CA.
- Matlack, G.R., 1994. Plant species migration in a mixed-history forest landscape in eastern North America. *Ecology* 75, 1491–1502.

- McIntyre, S., Lavorel, S., Landsberg, J., Forbes, T.D.A., 1999. Disturbance response in vegetation – towards a global perspective on functional traits. *Journal of Vegetation Science* 10, 621–630.
- McLachlan, S., Bazely, D.R., 2001. Recovery patterns of understory herbs and their use as indicators of deciduous forest regeneration. *Conservation Biology* 15, 98–110.
- Meier, A.J., Bratton, S.P., Duffy, D.C., 1995. Possible ecological mechanisms for loss of vernal-herb diversity in logged eastern deciduous forests. *Ecological Applications* 5, 935–946.
- 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.
- Messier, C., Puttonen, P., 1995. Spatial and temporal variations in the light environment of developing scots pine stands: the basis for a quick and efficient method of characterizing light. *Canadian Journal of Forest Research* 25, 343–354.
- Messier, C., Bigué, B., Bernier, L., 2003. Using fast-growing plantations to promote forest ecosystem protection in Canada. *Unasylva* 54, 59–63.
- Metzger, F., Schultz, J., 1981. Spring ground layer vegetation 50 years after harvesting in northern hardwood forests. *American Midland Naturalist* 105, 44–50.
- Moore, S.E., Allen, H.L., 1999. Plantation forestry. In: Hunter, M.L. Jr. (Ed.), *Maintaining Biodiversity in Forest Ecosystems*. Cambridge University Press, New York, pp. 400–433.
- MRNFP, 2006. Ressources et industries forestières. Portrait statistique 2005–2006. Chapitre 5.6 reboisement. Ministère des ressources naturelles, de la faune et des parcs du Québec, Québec.
- Newmaster, S.G., Bell, F.W., Roosenboom, C.R., Cole, H.A., Towill, W.D., 2006. Restoration of floral diversity through plantations on abandoned agricultural land. *Canadian Journal of Forest Research* 36, 1218–1235.
- Nilsson, M.-C., Wardle, D.A., 2005. Understory vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. *Frontiers in Ecology and the Environment* 3, 421–428.
- Nordén, B., Appelqvist, T., 2001. Conceptual problems of ecological continuity and its bioindicators. *Biodiversity and Conservation* 10, 779–791.
- Noss, R.F., 1990. Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* 4, 355–364.
- O'Keefe, J., Foster, D.R., 1998. An ecological history of Massachusetts forests. *Arnoldia* 58, 2–31.
- Paquette, A., Bouchard, A., Cogliastro, A., 2006a. Successful under-planting of red oak and black cherry in early-successional deciduous shelterwoods of North America. *Annals of Forest Science* 63, 823–831.
- Paquette, A., Bouchard, A., Cogliastro, A., 2006b. Survival and growth of under-planted trees: a meta-analysis across four biomes. *Ecological Applications* 16, 1575–1589.
- Parker, C.P., Elliott, K.A., Dey, D.C., Boysen, E., Newmaster, S.G., 2001. Managing succession in conifer plantations: converting young red pine (*Pinus resinosa* Ait.) plantations to native forest types by thinning and underplanting. *Forestry Chronicle* 77, 721–734.
- Ramovs, B.V., Roberts, M.R., 2005. Response of plant functional groups within plantations and naturally regenerated forests in southern New Brunswick, Canada. *Canadian Journal of Forest Research* 35, 1261–1276.
- Robitaille, A., Saucier, J.-P., 1998. Paysages régionaux du Québec méridional. Les Publications du Québec, Québec.
- Rowe, J.S., 1972. Les régions forestières du Canada. In: Service des forêts. Environnement Canada, Ottawa.
- Scheller, R.M., Mladenoff, D.J., 2002. Understory species patterns and diversity in old-growth and managed northern hardwood forests. *Ecological Applications* 12, 1329–1343.
- Siegel, S., Castellan Jr., N.J., 1988. *Nonparametric statistics for the behavioral sciences*, second ed. McGraw-Hill, New York.
- Simard, H., Bouchard, A., 1996. The precolonial 19th century forest of the Upper St. Lawrence Region of Quebec: a record of its exploitation and transformation through notary deeds of wood sales. *Canadian Journal of Forest Research* 26, 1670–1676.
- Singleton, R., Gardescu, S., Marks, P.L., Geber, M.A., 2001. Forest herb colonization of postagricultural forests in central New York State, USA. *Journal of Ecology* 89, 325–338.
- Stephens, S.S., Wagner, M.R., 2007. Forest plantations and biodiversity: a fresh perspective. *Journal of Forestry* 105, 307–313.
- Stover, M.E., Marks, P.L., 1998. Successional vegetation on abandoned cultivated and pastured land in Tompkins County, New York. *Bulletin of the Torrey Botanical Club* 125, 150–164.
- Swindel, B., Grosenbaugh, L., 1988. Species diversity in young Douglas-fir plantations compared to old growth. *Forest Ecology and Management* 23, 227–231.
- Thysell, D.R., Carey, A.B., 2001. Manipulation of density of *Pseudotsuga menziesii* canopies: preliminary effects on understory vegetation. *Canadian Journal of Forest Research* 31, 1513–1525.
- Tremblay, P., Bourque, P.A., 1991. Carte Géo touristique. Géologie du Sud du Québec, du Bas-Saint-Laurent et de la Gaspésie. Direction générale de l'exploration géologique et minérale. Publications du Québec, Québec.
- Tsuyuzaki, S., del Moral, R., 1995. Species attributes in early primary succession on volcanoes. *Journal of Vegetation Science* 6, 517–522.
- Verheyen, K., Honnay, O., Motzkin, G., Hermy, M., Foster, D.R., 2003. Response of forest plant species to land-used change: a life-history trait-based approach. *Journal of Ecology* 91, 563–577.
- Whigham, D.F., 2004. Ecology of woodland herbs in temperate deciduous forests. *Annual Review of Ecology and Systematics* 35, 583–621.