

Understory vegetation of boreal tree plantations: Differences in relation to previous land use and natural forests

Sophie Gachet^{a,*}, Alain Leduc^a, Yves Bergeron^b, Thuy Nguyen-Xuan^b, Francine Tremblay^b

^a *Chaire Industrielle CRSNG-UQAT-UQAM en Aménagement Forestier Durable, Université du Québec à Montréal, C.P. 8888 Succ. Centre-Ville, Montréal, Que. H3C 3P8, Canada*

^b *Chaire Industrielle CRSNG-UQAT-UQAM en Aménagement Forestier Durable, Université du Québec en Abitibi-Témiscamingue, 445 Boul. de l'Université, Rouyn-Noranda, Que. J9X 5E4, Canada*

Accepted 5 January 2007

Abstract

The aim of this study was to evaluate if and how the previous land use (here: agriculture versus forest) has influenced the floristic composition now observed in the understory of jack pine plantations of Abitibi-Témiscamingue (North-Eastern Canada). Floristic inventories were conducted in jack pine plantations which had been established on forest sites after logging and on sites previously utilized for agriculture. These were compared to one another and to inventories conducted in natural forests and on agricultural sites which had not (not yet) been planted with trees (old fields). The vegetation community composition of the sites is analysed using several multivariate techniques. Results show that the flora of plantations on old agricultural fields is markedly different than that of plantations established on sites which were previously forested and that the two types of plantation are unlikely to become floristically the same before the anticipated harvest time. Comparing old and young plantations and old fields in light of natural forests sites, we show that the previous land-use is a key determinant of future compositional differences in plantations. This must be considered when we evaluate the impact of establishing plantations on sites with different land-use histories.

© 2007 Elsevier B.V. All rights reserved.

Résumé

Le but de cette étude est d'évaluer dans quelle mesure l'utilisation du sol a pu influencer la composition floristique observée aujourd'hui dans le sous-bois de plantations de pin gris en Abitibi-Témiscamingue (nord-ouest du Québec). Des inventaires floristiques ont été effectués dans des plantations établies sur d'anciennes friches agricoles et sur d'anciennes friches forestières. Une comparaison (à l'aide d'analyses multivariées) est faite entre les sous-bois de chaque type de plantation, ainsi qu'avec ceux de sites présentement en friche et de forêts naturelles. Nos résultats montrent que la flore du sous-bois de plantations réalisées sur d'anciennes terres agricoles est très différente du sous-bois de plantations réalisées en sites forestiers. Les deux types de sites ont ainsi peu de chances de se ressembler dans le futur, surtout compte tenu des délais d'exploitation. L'historique d'utilisation du sol est donc un facteur déterminant qui explique les différences de composition floristique dans le sous-bois des plantations, ce qui doit être pris en compte dans l'évaluation des impacts de plantations réalisées dans ces environnements fort différents.

© 2007 Elsevier B.V. All rights reserved.

Keywords: Biodiversity; Flora; Multivariate analysis; Ecological value; Old fields; Site conversion

1. Introduction

In a sustainable forest management context, biological diversity concerns have become a component that cannot be

ignored in regional forest planning. The new forestry laws in Quebec (MRNFP, 2004) include biological diversity issues. Thus, it is urgent to provide forest managers with appropriate tools that will enable them to quantify the impact of current establishment practices on the integrity of ecosystems. One of the major concerns is the capacity of managed ecosystems (such as plantations) to maintain biodiversity (Whitehead, 1982; Roberts and Gilliam, 1995). Indeed, the conversion of natural forests into plantations is generally seen as a loss of biodiversity, although knowledge of the real impacts is limited

* Corresponding author. Present address: Muséum National d'Histoire Naturelle, CNRS UMR 7179, 4 rue du Petit Château, 91800 Brunoy, France.

E-mail addresses: gachet@mnhn.fr (S. Gachet), leduc.alain@uqam.ca (A. Leduc), yves.bergeron@uqat.ca (Y. Bergeron), nguyenxt@hotmail.com (T. Nguyen-Xuan), francine.tremblay@uqat.ca (F. Tremblay).

(Barbour et al., 1997). However, the planting of trees is often needed after clear-cut harvesting when the pre-established regeneration is absent or too weak to ensure the recovery of a forest stand as, for instance is the case after harvesting a jack pine stand.

In the Abitibi-Temiscamingue region of Quebec (Eastern Canada), the natural forest has been harvested since the beginning of the 20th century, first to create agricultural lands (hay) and then for lumber, which has become a major economic resource in the region. More recently, rural depopulation (in the 1980's) has left many agricultural lands abandoned (approximately 100 000 ha), posing the problem of their future management. Many of these old fields have subsequently been planted back into forests (afforestation). At the same time it has also been a common practice in the last 25 years to replant commercially harvested natural forests (reforestation).

Our question was whether we should consider these two plantation types as representing a similar threaten for the biodiversity. Is it conceivable to create plantations that could be comparable to natural forests in terms of biodiversity? The current fragmentation of forested landscapes leads to an important loss of species diversity (Vellend, 2004), partly because of the difficulties forest-species have re-colonizing these sites. It is influenced by the distance from propagule sources (combined with the forest age: Verheyen et al., 2003). This in turn depends on the nature of the surrounding landscape matrix and the neighbouring communities (Honnay et al., 2001). The intrinsic dispersal ability of species, such as their dispersion vector or persistence in a seed bank is key to regeneration dynamics in these situations. The aim of this article is to examine the impact of previous land-use (afforestation versus reforestation) of plantations on the understory community, taking into account several plant traits, and using natural forests as a reference of the potential natural system (Kimmins, 1997), in terms of the understory vegetation composition.

2. Methods

2.1. Study area

The study area was located in the Abitibi-Temiscamingue region, more specifically in the vicinity of Lake Duparquet (48°30'N, 78°14'W). This region is part of the northern Clay Belt of Quebec and Ontario, a large physiographic region created by lacustrine deposits left after the maximal extension of the proglacial lakes Barlow and Ojibway. The main surficial deposit is silt, clay and varved sand originating from the proglacial lake Ojibway. The following sites were chosen from within a total area of 1000 km²: 20 jack pine (*Pinus banksiana* Lambert) plantations on old fields (afforestation), 19 jack pine plantations on logged forests (reforestation) and 14 old fields (no plantation established). Both types of 'old fields' had previously been cultivated for fodder. Those on which there was no plantation establishment were open lands with a few trees (like *Salix* sp.); they varied in the time since abandonment (11 sites were more than 20 years old, four were between 10 and 16

years old) but ages were not considered separately in analysis. For the two plantation types, half of the sites were between 8 and 15 years old, and the other half were between 15 and 30 years old. The age of the stands was determined by questioning landowners and taking cores of several trees. Based on their ages, we identified four groups of plantations: young afforestations (YA), old afforestations (OA), young reforestations (YR), and old reforestations (OR). We were careful to select sites with similar abiotic conditions in terms of climate, topography, bedrock and soil type. The pedological properties (texture, drainage, slope) were assessed in the field following Saucier et al. (1994), and the depth of humus was also measured. Data (soil as well as flora) were all collected from June to August 2003.

2.2. Floristic data

In each old field and plantation, 15 plots (1 m²) were placed each 15 m along a U-shaped transect (lengths: 100 + 50 + 100 m). Inside each plot, an exhaustive inventory (presence/absence) of the vascular vegetation was made; thus, the list of species in each site is the sum of its 15 plots. We followed the nomenclature of Gleason and Cronquist (1991). Data from 10 sites in natural forests from previous studies conducted in the same area, using the same protocol (Bergeron et al., 1985; L egar e et al., 2001) were also available and used in our analyses.

Life-history traits are the most intuitive characteristics that can be used to describe species functional differences in ecosystems: in our study, we will take into account several traits, coming from the floristic database TOPIQ (Traits Of Plants In Quebec: Aubin et al., 2007), chosen for the information they can bring to understanding vegetation dynamics: growth forms *sensu* Raunkiaer, means of seed dispersal (by wind, animal, etc.), origin (exotic or native to Quebec), and flowering period (spring, summer, etc.).

2.3. Statistical analysis

By the end of the fieldwork, we obtained the following data matrices:

- *Matrix X*. For 53 sites: four 'site' characteristics (texture, drainage, slope, humus depth) and previous land-use (afforestation, reforestation, or old field - we do not have this information for the natural forests).
- *Matrix Z*. For 63 sites (20 afforestations + 19 reforestations + 14 old fields + 10 natural forest): presence/absence of 181 species (combined data for 15 plots per site).

In a first step, we tested for the homogeneity of site conditions within the compositional gradient. We used a Canonical Correspondence Analysis (Ter Braak and Šmilauer, 1998) on the matrix Z together with the disjunctive version of the matrix X (containing the variables we originally wanted to control *via* site choice: slope, soil texture, humus depth and drainage). This analysis allowed us to verify if these site

conditions could be responsible for any observed variation in understory composition among sites. The statistical significance of each of the variables in the X matrix was assessed by permutation tests (Monte Carlo permutations with 199 runs).

Secondly, the understory composition of the sites was characterized by their position (sample score) on the ordination axes obtained from a Correspondence Analysis (CA). We compared the contribution of different types of species to each end of the first CA axis using χ^2 -test. We tested for significant differences between stand origins and ages (NF, OF, YA, OA, YR, OR) using a distance-based Redundancy Analysis (db-RDA) (Legendre and Anderson, 1999): (i) matrix of ecological similarity values among all the samples was built from the species-sites matrix, using the Jaccard distance measure; (ii) the experimental design (here: the landuse) is translated in a “dummy matrix”; (iii) both matrices are then analysed with a RDA, and a permutation test under reduced model (499 runs) is done, testing for differences among groups by an approximate *F* statistic.

The Shannon index of species diversity was calculated for all the sites, using the abundance version of the matrix Z (except for natural forests, where abundances were not available).

All analysis were completed on XLSTAT software (Addinsoft, 2005), except the CCA and the db-RDA, performed using CANOCO version 4.5.

3. Results

3.1. Abiotic conditions

Testing each of the four site variables individually, the CCA (not shown) revealed that none of them were significantly related to species composition, according to the permutation tests under a reduced model. There was a slight but non-significant drainage difference, which suggested that old fields had slightly poorer drainage. However, overall, we considered our site conditions as sufficiently similar to undertake further (more detailed) analyses comparing composition among plantation types.

3.2. Compositional analyses

The reforestation sites were more diverse than the afforestation sites or old fields, as assessed by the Shannon index (Table 1). Reforestation sites shared 50% of their species with the natural forests.

In terms of species composition, old fields and afforestations were the most similar. The histogram of eigenvalues (not shown) from the CA presents a large number of axes associated

with weak eigenvalues, except for the first axis which represents 12% of the total variability: this implies that one gradient dominated variation in understory composition. Fig. 1 shows the separation among sites and species in ordination space. Based on the db-RDA comparing the six different stand types (NF, OF, YA, OA, YR, OR) there were significant differences among stand types ($F = 4.39$; $p = 0.002$), and the first axis is the most significant (eigenvalue = 16.5%; $F = 11.29$; $p = 0.002$). The first axis of the CA (accounting for 12% of the variation in the species data) separated the site types in two groups (Fig. 1a): sites with a forest past (natural forests and reforested sites) versus those with an agricultural past (afforested sites and old fields). The fourth axis seems to be related to a “forest maturation” gradient for the sites on the negative side of axis F1 in that natural forests separated from old reforestation which separated from young reforestation. No separation among afforestation types (young versus old) and old fields was apparent on the positive side of axis 1.

Table 2 presents the contribution of species of different life history types to each side of the first axis, with species classified according to the following traits (from Aubin et al., 2007): growth form *sensu* Raunkiaer, seed dispersal, species origin, and flowering period. We can observe major differences between the negative side, which was associated with natural forests and reforestation sites, and the positive one, which was associated with afforestation sites and old fields. Species classified according to “Raunkiaer type” show large and significant differences between sites with an agricultural past (YA, OA and OF) where the classes “geophytes”, “hemicryptophytes” and “therophytes” are present with the highest proportion (essentially because of grasses: *Agropyron repens*, *Poa pratensis*, *Phleum pratense*, etc.), and those with a forest

Table 2
Sum of the contribution of different types of species to each side of the first axis in the CA

	Negative side of first CA axis	Positive side of first CA axis
Raunkiaer types		
Phanerophytes	13.22	0.68
Therophytes	0.09	2.55
Chamephytes	6.48	1.90
Geophytes	7.30	15.83
Hemicryptophytes	12.88	35.32
Origin		
Indigenous	39.90	26.74
Exotic	0.08	29.56
Dispersion		
Animal	15.07	13.84
Wind	11.98	11.27
Flowering period		
Spring	24.21	8.75
Summer	11.62	38.77

Species are categorized by Raunkiaer type, origin of species, seed dispersal and flowering period (see Appendix A). In italics are the non-significant differences (χ^2 -test). The negative side of the axis is the “forest one” (natural forests, old and young reforestation sites), the positive side is the “agricultural one” (old field, young and old afforestations) (see Fig. 1).

Table 1
Shannon index (mean per site and standard deviation) in reforestation sites (old: OR; young: YR), afforestation sites (old: OA; young: YA) and old fields (OF)

	OR	YR	OA	YA	OF
Mean	4.69	4.63	4.27	4.12	4.16
S.D.	0.23	0.23	0.23	0.24	0.29

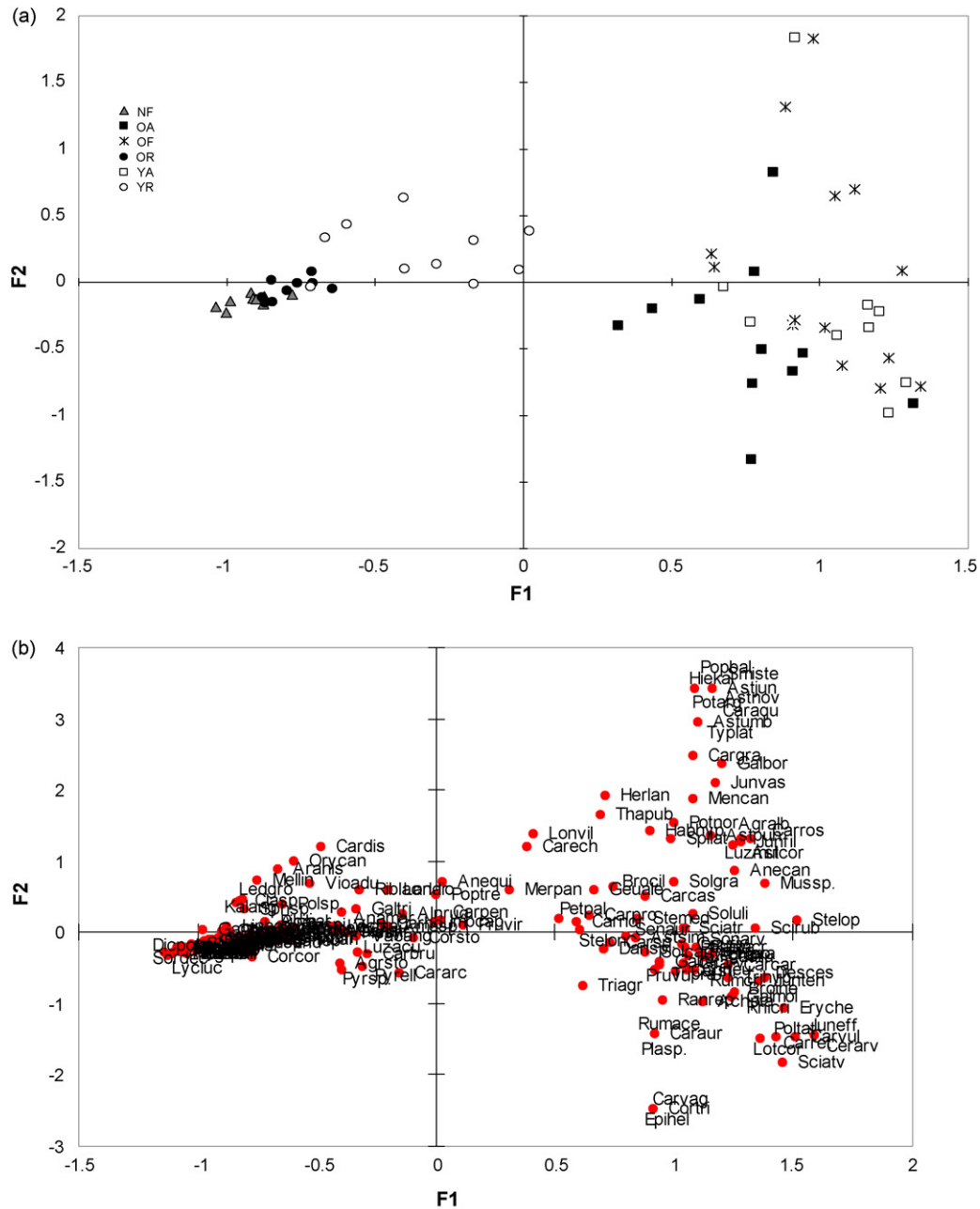


Fig. 1. Graph of the first two axes of the CA ($F_1 = 12\%$; $F_2 = 5\%$) calculated on the matrix Z (63 sites \times 181 species, species presence-absence data). (a) Location of sites in ordination space; NF: natural forests; OA: old afforestations; OF: old fields; OR: old reforestations; YA: young afforestations; YR: young reforestations. (b) Location of species in ordination space. Species codes are in the Appendix A.

past (YR, OR, NF) where woody plants (“chamephytes” and “phanerophytes”, like *Abies balsamea*, *Corylus cornuta*, *Betula papyrifera*) are more numerous. Not surprisingly, there were significantly more exotic species associated with the YA, OA and OF sites than the YR, OR and NF; nevertheless, there are the same number of indigenous species in the two stand origin types. On the other hand, no differences were found in relation to seed dispersal: species with animal and wind vectors were equally represented in each side. The trait “flowering period” shows two classes: “spring flowering” species were more common in sites with a forest origin (for example *Coptis groenlandica*, *Trientalis borealis* or *Clintonia borealis*); and

“summer flowering” species characterised sites with an agricultural past (species like *Lactuca biennis* or *Anaphalis margaritacea*). These patterns are further illustrated by examining the placement of the species in the ordination (Fig. 1b).

4. Discussion

Our results indicate that the understory of planted forests is influenced by previous land-use; this is especially clear when stands of different origin are compared with the understory of natural forests. Many authors have observed that previous

land-use may have a long-term impact on the floral assemblage (e.g. Bellemare et al., 2002; Gerhardt and Foster, 2002; Flinn and Vellend, 2005). It is confirmed in our sites, which were planted relatively recently (maximum 30 years); thus, it is not surprising to detect the influence of their agricultural past. Much longer ago, these agricultural plantations originally had a forest past, which no doubt influenced the present conditions: we can consider this past as an “historical print”. Our results from the afforestation sites demonstrate that the agricultural period was long enough to destroy this historical print, while this print is still visible on the reforestation sites.

Indeed, the reforestation sites had an understory closer to the plant assemblage found in natural forests, despite the disturbance caused by the harvest of the natural trees and the re-planting of jack pine, following a short time after the harvest. There are several explanations for this situation. First, the seedbed or propagules of previous forest species are probably still present and active. Moreover, as reforestation sites are often located in a forest matrix, dispersal from the untouched forests is possible. Finally, on reforestation sites soils were more lightly disturbed than on the afforestation sites: the harvest generally occurred during winter, with minor risks of soil compaction. In the agricultural-past sites, the soil was plowed before establishing the trees plantation. All these factors likely allowed the reforestation sites to quickly recover a “close-to-nature” understory.

On the contrary, fields are very simplified ecosystems: in plantations with an agricultural past, the cultivation has significantly reduced plant diversity (congruent with Flinn and Vellend, 2005), and probably the seed bank diversity also (Bossuyt and Hermy, 2001). In addition, repeated plowing may have promoted leaching of nutrients in these sites that were never or only slightly fertilized (and only with N–P–K). Many causes might explain the differences in the floristic assemblage. For example, in zoochorous species (often found in forest) seeds are generally large and moist, which promotes dispersal (Héroult and Honnay, 2005). However, moist seeds have a short life expectancy in the soil (Bakker et al., 1996), and few of these taxa are present in the seed bank. Thus, their ability to recolonize is low, especially if the animal guild they depend on is not present (Prodon and Lebreton, 1994). However, dispersal types cannot explain the strong difference in composition between sites with a forest-past and an agricultural-past, even though we notice a tendency (but not significant) of increasing frequency of animal-dispersed species in the sites with a forest past. Another factor influencing floristic composition in these sites is the regional species pool. The agricultural-past sites are in a predominantly agricultural matrix and this likely allows open-site exotic species to maintain themselves (these species are often noticed in agro-forest areas: Grime, 1979). These species have several means of dispersal helping them to colonize the ecosystem (anemochorous plants, for example), as noticed by Graae and Heskejaer (1997) or McIntyre et al. (1995). In addition, they are plastic enough to adapt themselves to forested sites, especially in the first years after plantation where the sparse canopy allows these species to maintain themselves (Lepart and Escarré, 1983; Augusto et al., 2001).

The impact of forest management on biodiversity is often examined from a temporal perspective, together with dynamics of the forest canopy (Deconchat, 1999). In contrast, the major difference in floristic composition observed in our sites is the separation between sites with a forest past and those with an agricultural past, which may be considered a gradient of “naturalness” (*sensu* Peterken, 1997). The clear separation that exists between the indigenous summer-flowering hemicryptophytes and the indigenous phanerophytes may reflect the aging and maturation of the forest ecosystem in these sites, since the forest-past sites seem to move more quickly towards natural forest. On the other hand, time (maturation) does not seem to decrease differences between the sites with an agricultural-past and those with a forestry past (since old agricultural-past sites are still very different from reforestation, even the youngest ones), even though the canopy is increasingly closed in both cases. This suggests some “specialization” of the plant assemblages and a strong impact of the previous land-use (Verheyen et al., 2003).

Our plantations are relatively young, thus we only can distinguish the initial trends. Several authors (for example Parker et al., 1994; Norton, 1998) have noticed that older plantations are more similar to native forest communities than younger ones. Indeed, our oldest reforestation sites were the ones most similar to the natural forests, considering their floral assemblage. The afforestations were the most different, but the oldest afforestation sites are close to the younger reforestation sites. This suggests that, with time, the “naturalness” of the afforested sites will tend to increase; but as emphasized by Flinn and Vellend (2005) forest plant recolonization may take centuries (or require active restoration). Ferns et al. (1992) spoke about an “economical optimum”, which often is reached earlier than the “ecological optimum” and this forms the basis of concern. Actually, in our case, if these plantations are harvested just as the trees reach maturity, it will probably not be possible to obtain a “close-to-natural” forest: the afforestation sites are unlikely to have a very “natural” understory by that time. Our results suggest that it will be different for the reforestation sites, which appear to become closer to natural forests with time.

Even though plantations are usually considered far from natural forests, they can still play a role in biodiversity conservation (Hartley, 2002), and many authors have proposed management solutions to mediate the impact of plantations that take into account factors, like light site-preparation (which minimized the destruction of what we called the “historical print”), various rotation periods, or uneven-aged harvesting systems (Carey and Johnson, 1995; Fries et al., 1997).

Finally, our results show that the understory community which develops in old fields (that are upwards of 20 years old) is quite dissimilar from a natural forest understory community, and the afforestation sites are still quite close to old fields. So, the establishment of plantations on these old fields does not represent a loss to the ‘natural’ land base. In contrast, it may facilitate development of the sites to a more ‘natural’ condition of biodiversity. Thus plantations established on agricultural sites should not be evaluated by forest managers with the same criteria as plantations implemented in natural forest, since it takes much more than planting trees to make a forest.

Acknowledgements

This work was supported by the FQRNT (Fonds Québécois de la Recherche sur la Nature et les Technologies). Many thanks to

Sandrine Pavoine, Joël Guiot and Lucero Mariani for statistical comments, and to Nicole Fenton for improvements of the English language. We are also very grateful to Ellen Macdonald for her precious global help during the editorial process.

Appendix A

List of plant species and their codes (as in Fig. 1). Each species is characterised with four traits (coming from the database TOPIQ: Aubin et al., 2007): biological types *sensu* Raunkiaer (P: phanerophytes; H: hemicryptophytes, G: geophytes; CH: chamephytes; T: therophytes); origin (status in Quebec: IN: indigenous; EX: exotic), seed dispersal (W: dispersed by wind; A: dispersed by animals; AU: autochory); and flowering period (SPR: spring; SUM: summer). NR: not recorded; NA: not applicable. Traits are not recorded for taxa not identified to species (i.e., noted “sp.”).

Code	Genus	Species	Raukiaer	Status	Dispersal	Flowering
Abibal	<i>Abies</i>	<i>balsamea</i>	P	IN	W	SPR
Acespi	<i>Acer</i>	<i>spicatum</i>	P	IN	W	SPR
Achpta	<i>Achillea</i>	<i>ptarmica</i>	H	EX	W	SUM
Actrub	<i>Actaea</i>	<i>rubra</i>	G	IN	A	SPR
Agralb	<i>Agrostis</i>	<i>alba</i>	H	EX	AU	SUM
Agrrrep	<i>Agropyron</i>	<i>repens</i>	G	EX	NR	SUM
Agresto	<i>Agrostis</i>	<i>stolonifera</i>	H	EX	AU	SUM
Alncri	<i>Alnus</i>	<i>crispa</i>	P	IN	W	SPR
Alnrug	<i>Alnus</i>	<i>rugosa</i>	P	IN	W	SPR
Amesp.	<i>Amelanchier</i>	sp.				
Anamar	<i>Anaphalis</i>	<i>margaritacea</i>	H	IN	W	SUM
Anecan	<i>Anemone</i>	<i>canadensis</i>	G	IN	W	SPR
Anequi	<i>Anemone</i>	<i>quinquefolia</i>	G	IN	W	SPR
Apoand	<i>Apocynum</i>	<i>androsaemifolium</i>	G	IN	W	SUM
Arahis	<i>Aralia</i>	<i>hispida</i>	CH	IN	A	SUM
Aranud	<i>Aralia</i>	<i>nudicaulis</i>	H	IN	A	SPR
Astcor	<i>Aster</i>	<i>cordifolius</i>	H	IN	W	SUM
Astjun	<i>Aster</i>	<i>junciformis</i>	H	IN	W	SUM
Astnov	<i>Aster</i>	<i>nova-angliae</i>	H	IN	W	SUM
Astpun	<i>Aster</i>	<i>puniceus</i>	H	IN	W	SUM
Astsim	<i>Aster</i>	<i>simplex</i>	H	IN	W	SUM
Astumb	<i>Aster</i>	<i>umbellatus</i>	H	IN	W	SUM
Athfil	<i>Athyrium</i>	<i>filix-femina</i>	H	IN	W	SUM
Betpap	<i>Betula</i>	<i>papyrifera</i>	P	IN	W	SPR
Brasp.	<i>Brachytecium</i>	sp.				
Brocil	<i>Bromus</i>	<i>ciliatus</i>	H	IN	NR	SUM
Broine	<i>Bromus</i>	<i>inermis</i>	H	EX	NR	SUM
Caraqu	<i>Carex</i>	<i>aqualitis</i>	G	IN	NR	SPR
Cararc	<i>Carex</i>	<i>arctata</i>	H	IN	NR	SPR
Caraur	<i>Carex</i>	<i>aurea</i>	G	IN	NR	SPR
Carbru	<i>Carex</i>	<i>brunnescens</i>	H	IN	NR	SPR
Carcar	<i>Carpinus</i>	<i>caroliniana</i>	P	IN	W	SPR
Carcas	<i>Carex</i>	<i>castanea</i>	G	IN	NR	SPR
Cardew	<i>Carex</i>	<i>deweyana</i>	H	IN	NR	SPR
Cardis	<i>Carex</i>	<i>disperma</i>	H	IN	NR	SPR
Carech	<i>Carex</i>	<i>echinata</i>	H	IN	W	SPR
Cargra	<i>Carex</i>	<i>gracillima</i>	G	IN	NR	SPR
Carhou	<i>Carex</i>	<i>houghtoniana</i>	G	IN	NR	SUM
Carint	<i>Carex</i>	<i>interior</i>	H	IN	NR	SPR
Carlep	<i>Carex</i>	<i>leptonervia</i>	H	IN	NR	SPR
Carnor	<i>Carex</i>	<i>normalis</i>	H	IN	NR	SPR
Carped	<i>Carex</i>	<i>pedunculata</i>	H	IN	NR	SPR
Carpen	<i>Cardamine</i>	<i>pensylvanica</i>	H	IN	NR	SPR
Carpro	<i>Carex</i>	<i>projecta</i>	H	IN	NR	SPR
Carret	<i>Carex</i>	<i>retrorsa</i>	H	IN	NR	SUM
Carros	<i>Carex</i>	<i>rostrata</i>	G	IN	NR	SUM
Carsp.	<i>Carex</i>	sp.				
Carsti	<i>Carex</i>	<i>stipata</i>	H	IN	A	SUM
Carvag	<i>Carex</i>	<i>vaginata</i>	G	IN	NR	SPR
Carvul	<i>Carex</i>	<i>vulpinoidea</i>	G	IN	NR	SPR
Cerarv	<i>Cerastium</i>	<i>arvense</i>	CH	IN	NR	SPR

Appendix A (Continued)

Code	Genus	Species	Raukiaer	Status	Dispersal	Flowering
Chrleu	<i>Chrysanthemum</i>	<i>leucanthemum</i>	H	EX	W	SUM
Cinlat	<i>Cinna</i>	<i>latifolia</i>	H	IN	NR	SUM
Cirarv	<i>Cirsium</i>	<i>arvense</i>	H	EX	W	SUM
Clasp.	<i>Cladina</i>	sp.				
Clibor	<i>Clintonia</i>	<i>borealis</i>	G	IN	A	SPR
Copgro	<i>Coptis</i>	<i>groenlandica</i>	H	IN	NR	SPR
Corcan	<i>Cornus</i>	<i>canadensis</i>	H	IN	A	SUM
Corcor	<i>Corylus</i>	<i>cornuta</i>	P	IN	A	SPR
Corsto	<i>Cornus</i>	<i>stolonifera</i>	P	IN	A	SPR
Cortri	<i>Corallorhiza</i>	<i>trifida</i>	G	IN	W	SPR
Cypaca	<i>cypripedium</i>	<i>acaule</i>	G	IN	W	SPR
Danspi	<i>Danthonia</i>	<i>spicata</i>	H	IN	NR	SUM
Desces	<i>Deschampsia</i>	<i>cespitosa</i>	H	IN	A	SUM
Dicpol	<i>Dicranum</i>	<i>polysetum</i>	NA		NA	NA
Dicsp.	<i>Dicranum</i>	sp.				
Dielon	<i>Diervilla</i>	<i>lonicera</i>	P	IN	NR	SPR
Drydis	<i>Dryopteris</i>	<i>disjuncta</i>	G	IN	W	SUM
Dryspi	<i>Dryopteris</i>	<i>spinulosa</i>	H	IN	W	SUM
Epihel	<i>Epipactis</i>	<i>helleborine</i>	G	EX	W	SUM
Eryche	<i>Erysimum</i>	<i>cheiranthoides</i>	T	EX	NR	SUM
Galbor	<i>Galium</i>	<i>boreale</i>	H	IN	NR	SUM
Galmol	<i>Galium</i>	<i>mollugo</i>	H	EX	NR	SPR
Galtet	<i>Galeopsis</i>	<i>tetrahit</i>	T	EX	NR	SUM
Galtri	<i>Galium</i>	<i>trifidum</i>	H	IN	NR	SUM
Gauhis	<i>Gaultheria</i>	<i>hispidula</i>	CH	IN	A	SPR
Geuale	<i>Geum</i>	<i>aleppicum</i>	H	IN	NR	SPR
Geuriv	<i>Geum</i>	<i>rivale</i>	H	IN	A	SPR
Goopub	<i>Goodyera</i>	<i>pubescens</i>	G	IN	W	SUM
Habhyp	<i>Habenaria</i>	<i>hyperborea</i>	G	IN	W	SPR
Herlan	<i>Heracleum</i>	<i>lanatum</i>	G	IN	NR	SPR
Hiekal	<i>Hieracium</i>	<i>kalmii</i>	H	IN	NR	SUM
Impcap	<i>Impatiens</i>	<i>capensis</i>	T	IN	E	SUM
Juneff	<i>Juncus</i>	<i>effusus</i>	G	IN	A	SUM
Junfil	<i>Juncus</i>	<i>filiformis</i>	G	IN	NR	SUM
Junten	<i>Juncus</i>	<i>tenuis</i>	H	IN	NR	SUM
Junvas	<i>Juncus</i>	<i>vaseyi</i>	H	IN	NR	SPR
Kalang	<i>Kalmia</i>	<i>angustifolia</i>	CH	IN	NR	SPR
Lacbie	<i>Lactuca</i>	<i>biennis</i>	H	IN	W	SUM
Larlar	<i>Larix</i>	<i>laricina</i>	P	IN	W	SPR
Ledgro	<i>Ledum</i>	<i>groenlandicum</i>	CH	IN	NR	SPR
Linbor	<i>Linnaea</i>	<i>borealis</i>	CH	IN	NR	SUM
Loncan	<i>Lonicera</i>	<i>canadensis</i>	P	IN	A	SPR
Londio	<i>Lonicera</i>	<i>dioica</i>	P	IN	NR	SPR
Lonhir	<i>Lonicera</i>	<i>hirsuta</i>	P	IN	NR	SPR
Lonvil	<i>Lonicera</i>	<i>villosa</i>	P	IN	A	SPR
Lotcor	<i>Lotus</i>	<i>corniculatus</i>	H	IN	E	SUM
Luzacu	<i>Luzula</i>	<i>acuminata</i>	H	IN	NR	SUM
Luzmul	<i>Luzula</i>	<i>multiflora</i>	H	IN	A	SUM
Luzpar	<i>Luzula</i>	<i>parviflora</i>	H	IN	A	SUM
Lycann	<i>Lycopodium</i>	<i>annotinum</i>	CH	IN	W	SUM
Lycla	<i>Lycopodium</i>	<i>clavatum</i>	CH	IN	W	SUM
Lycluc	<i>Lycopodium</i>	<i>lucidulum</i>	CH	IN	W	SPR
Lycobs	<i>Lycopodium</i>	<i>obscurum</i>	CH	IN	W	SUM
Mellin	<i>Melampyrum</i>	<i>lineare</i>	T	IN	NR	SUM
Mencan	<i>Menispermum</i>	<i>canadense</i>	H	IN	NR	SUM
Merpan	<i>Mertensia</i>	<i>paniculata</i>	H	IN	NR	SPR
Mitnud	<i>Mitella</i>	<i>nuda</i>	H	IN	NR	SPR
Monuni	<i>moneses</i>	<i>uniflora</i>	H	IN	NR	SUM
Mussp.	<i>Bryophytes</i>	sp.				
Oryasp	<i>Oryzopsis</i>	<i>asperifolia</i>	G	IN	NR	SUM
Orycan	<i>Oryzopsis</i>	<i>canadensis</i>	G	IN	NR	SUM
Osmcin	<i>Osmunda</i>	<i>cinnamomea</i>	G	IN	W	SUM
Oxamon	<i>Oxalis</i>	<i>montana</i>	H	IN	E	SUM
Petpal	<i>Petasites</i>	<i>palmatum</i>	G	IN	NR	SPR
Phaaru	<i>Phalaris</i>	<i>arundinacea</i>	G	IN	A	SUM

Appendix A (Continued)

Code	Genus	Species	Raukiaer	Status	Dispersal	Flowering
Phlpra	<i>Phleum</i>	<i>pratense</i>	H	EX	A	SUM
Picgla	<i>Picea</i>	<i>glauca</i>	P	IN	W	SPR
Picmar	<i>Picea</i>	<i>mariana</i>	P	IN	W	SPR
Pinban	<i>Pinus</i>	<i>banksiana</i>	P	IN	W	SPR
Plasp.	<i>Plantago</i>	sp.				
Pleshr	<i>Pleurozium</i>	<i>shreberi</i>	NA		NA	NA
Poapra	<i>Poa</i>	<i>pratensis</i>	G	EX	AU	SUM
Polcil	<i>Polygonum</i>	<i>cilinode</i>	H	IN	NR	SUM
Polsp.	<i>Polytrichum</i>	sp.				
Poltat	<i>Polygonum</i>	<i>tataricum</i>	H	EX	NR	SUM
Popbal	<i>Populus</i>	<i>balsamifera</i>	P	IN	W	SPR
Poptre	<i>Populus</i>	<i>tremuloides</i>	P	IN	W	SPR
Potarg	<i>Potentilla</i>	<i>argentea</i>	H	EX	NR	SUM
Potnor	<i>Potentilla</i>	<i>norvegica</i>	H	IN	NR	SUM
Prupen	<i>Prunus</i>	<i>pensylvanica</i>	P	IN	A	SPR
Pruvir	<i>Prunus</i>	<i>virginiana</i>	P	IN	A	SPR
Pruvul	<i>Prunella</i>	<i>vulgaris</i>	H	IN	NR	SUM
Pteaqu	<i>Pteridium</i>	<i>aquilinum</i>	G	IN	W	SUM
Pyrell	<i>Pyrola</i>	<i>elliptica</i>	H	IN	NR	SUM
Pyrsp.	<i>Pyrola</i>	sp.				
Ranacr	<i>Ranunculus</i>	<i>acris</i>	H	EX	A	SUM
Ranrep	<i>Ranunculus</i>	<i>repens</i>	H	EX	A	SUM
Rhicri	<i>Rhinanthus</i>	<i>crista-galli</i>	T	EX	NR	SPR
Ribgla	<i>Ribes</i>	<i>glandulosum</i>	P	IN	NR	SPR
Riblac	<i>Ribes</i>	<i>lacustre</i>	P	IN	NR	SPR
Ribri	<i>Ribes</i>	<i>triste</i>	P	IN	A	SPR
Rumace	<i>Rumex</i>	<i>acetosella</i>	H	EX	W	SUM
Rumcri	<i>Rumex</i>	<i>crispus</i>	H	EX	A	SUM
Samcan	<i>Sambucus</i>	<i>canadensis</i>	P	IN	A	SUM
Samrac	<i>Sambucus</i>	<i>racemosa</i>	P	IN	A	SPR
Schpur	<i>Schizachne</i>	<i>purpurascens</i>	H	IN	NR	SPR
Sciatr	<i>Scirpus</i>	<i>atrocinctus</i>	H	IN	NR	SPR
Sciatv	<i>Scirpus</i>	<i>atrovirens</i>	H	IN	A	SUM
Scirub	<i>Scirpus</i>	<i>rubrotinctus</i>	G	IN	NR	SUM
Senaur	<i>Senecio</i>	<i>aureus</i>	H	IN	NR	SPR
Smiste	<i>Smilacina</i>	<i>stellata</i>	G	IN	NR	SPR
Solcan	<i>Solidago</i>	<i>canadensis</i>	H	IN	W	SUM
Solgra	<i>Solidago</i>	<i>graminifolia</i>	H	IN	W	SUM
Solmac	<i>solidago</i>	<i>macrophylla</i>	H	IN	NR	SUM
Soluli	<i>Solidago</i>	<i>uliginosa</i>	H	IN	NR	SUM
Sonarv	<i>Sonchus</i>	<i>arvensis</i>	H	EX	W	SUM
Sorame	<i>Sorbus</i>	<i>americana</i>	P	IN	A	SPR
Sordec	<i>Sorbus</i>	<i>decora</i>	P		A	SPR
Sphsp.	<i>Sphagnum</i>	sp.				
Spilat	<i>Spiraea</i>	<i>latifolia</i>	P	IN	NR	SPR
Stegra	<i>Stellaria</i>	<i>graminea</i>	CH	EX	NR	SPR
Stelon	<i>Stellaria</i>	<i>longifolia</i>	H	IN	NR	SPR
Stelop	<i>Stellaria</i>	<i>longipes</i>	H	IN	NR	SUM
Stemed	<i>Stellaria</i>	<i>media</i>	T	EX	AU	SUM
Stros	<i>Streptopus</i>	<i>roseus</i>	G	IN	A	SPR
Taxcan	<i>Taxus</i>	<i>canadensis</i>	P	IN	W	SPR
Thapub	<i>Thalictrum</i>	<i>pubescens</i>	H	IN	NR	SUM
Triagr	<i>Trifolium</i>	<i>agrarium</i>	T	EX	NR	SPR
Tribor	<i>Trientalis</i>	<i>borealis</i>	G	IN	NR	SPR
Trihyb	<i>Trifolium</i>	<i>hybridum</i>	H	EX	A	SUM
Triptra	<i>Trifolium</i>	<i>pratense</i>	H	EX	NR	SUM
Trisp.	<i>Trillium</i>	sp.				
Typlat	<i>Typha</i>	<i>latifolia</i>	G	IN	W	SUM
Vacang	<i>Vaccinium</i>	<i>angustifolium</i>	P	IN	A	SPR
Vacmyr	<i>Vaccinium</i>	<i>myrtilloides</i>	P	IN	A	SPR
Vibcass	<i>Viburnum</i>	<i>cassinoides</i>	P	IN	A	SPR
Vibedu	<i>Viburnum</i>	<i>edule</i>	P	IN	A	SPR
Vibri	<i>Viburnum</i>	<i>trilobum</i>	P	IN	A	SPR
Vioadu	<i>Viola</i>	<i>adunca</i>	H	IN	A	SPR
Viosp.	<i>Viola</i>	sp.				

References

- Addinsoft, 2005. www.xlstat.com.
- 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 (2).
- Augusto, L., Dupouey, J.-L., Picard, J.-F., Ranger, J., 2001. Potential contribution of the seed bank in coniferous plantations to the restoration of native deciduous forest vegetation. *Acta Oecol.* 22, 87–98.
- Bakker, J.P., Poschlod, P., Strykstra, R.J., Bekker, R.M., Thompson, K., 1996. Seed banks and seed dispersal: important topics in restoration ecology. *Acta Bot. Neerl.* 45 (4), 461–490.
- Barbour, R.J., Johnston, S., Hayes, J.P., Tucker, G.F., 1997. Simulated stand characteristics and wood product yields from Douglas-fir plantations managed for ecosystem objectives. *For. Ecol. Manage.* 91, 205–219.
- Bellemare, J., Motzkin, G., Foster, D.R., 2002. Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. *J. Biogeogr.* 29, 1401–1420.
- Bergeron, Y., Bouchard, A., Camiré, P., Gangloff, P., 1985. Les types et les phases écologiques: relations fonctionnelles sol-végétation. Université d'Ottawa, pp. 41–55.
- Bossuyt, B., Hermy, M., 2001. Influence of land use history on seed banks in European temperate forest ecosystems: a review. *Ecography* 24, 225–238.
- Carey, A.B., Johnson, M.L., 1995. Small mammals in managed, naturally young- and old-growth forests. *Ecol. Appl.* 5, 336–352.
- Deconchat, M., 1999. Exploitation forestière et biodiversité. Thesis of Univ. Paul Sabatier, Toulouse, France, p. 191.
- Ferns, P.N., Cowie, R.J., Weir, A.G., 1992. Managing conifer plantations for the benefit of granivorous birds and mammals. *Aspects Appl. Biol.* 29, 83–88.
- Flinn, K.M., Vellend, M., 2005. Recovery of forest plant communities in post-agricultural landscapes. *Front. Ecol. Environ.* 3, 243–250.
- Fries, C., Johansson, O., Pettersson, B., Simonsson, P., 1997. Silvicultural models to maintain and restore natural stand structures in Swedish boreal forests. *For. Ecol. Manage.* 94, 89–103.
- Gerhardt, F., Foster, D.R., 2002. Physiographical and historical effects on forest vegetation in central new England, USA. *J. Biogeogr.* 29, 1421–1437.
- Gleason, H.A., Cronquist, A., 1991. *Manual of Vascular Plants of Northeastern United States and Adjacent Canada*. New York Botanical Garden Press.
- Graae, B.J., Heskjaer, V.S., 1997. A comparison of understorey vegetation between untouched and managed deciduous forest in Denmark. *For. Ecol. Manage.* 96, 111–123.
- Grime, J.P., 1979. *Plant Strategies and Vegetation Processes*. John Wiley & Sons, Chichester.
- Hartley, M.J., 2002. Rationale and methods for conserving biodiversity in plantation forests. *For. Ecol. Manage.* 155, 81–95.
- Héroult, B., Honnay, O., 2005. The relative importance of local, regional and historical factors determining the distribution of plants in fragmented riverine forests: an emergent group approach. *J. Biogeogr.* 32, 2069–2081.
- Honnay, O., Verhaeghe, W., Hermy, M., 2001. Plant community assembly along dendritic networks of small forest streams. *Ecology* 82, 1691–1702.
- Kimmins, J.P., 1997. *Forest Ecology: A Foundation for Sustainable Management*, 2nd ed. MacMillan Publishing.
- Légaré, S., Bergeron, Y., Leduc, A., Paré, D., 2001. Comparison of the understorey vegetation in boreal forest types of southwest Quebec. *Can. J. Bot.* 79, 1019–1027.
- Legendre, P., Anderson, M., 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecol. Monogr.* 69 (1), 1–24.
- Lepart, J., Escarré, J., 1983. La succession végétale, mécanismes et modèles: analyse bibliographique. *Bull. Ecol.* 14, 133–178.
- McIntyre, S., Lavorel, S., Tremont, R.M., 1995. Plant life-history attributes: their relationship to disturbance response in herbaceous vegetation. *J. Ecol.* 83, 31–44.
- MNRNP, 2004. *La gestion des forêts du domaine de l'État*. ISBN 2-550-41135-8.
- Norton, D.A., 1998. Indigenous biodiversity conservation and plantation forestry: options for the future. *N. Z. For.* 43 (2), 34–39.
- Parker, G.R., Kimball, D.G., Dalzell, B., 1994. Bird communities breeding in selected spruce and pine plantations in New Brunswick. *Can. Field-Nat.* 108, 1–9.
- Peterken, G.F., 1997. Concepts of naturalness. In: *Naturalité et forêts d'Europe*, Conseil de l'Europe, Strasbourg.
- Prodon, R., Lebreton, J.D., 1994. Analyses multivariées des relations espèces-milieu: structure et interprétation écologique. *Vie et Milieu* 44, 69–91.
- Roberts, M.R., Gilliam, F.S., 1995. Patterns and mechanisms of plant diversity in forested ecosystems: implications for forest management. *Ecol. Appl.* 5, 969–977.
- Saucier, J., Berger, J., D'Avignon, H., Racine, P., 1994. Le point d'observation écologique. *Journal. Gouvernement du Québec, Ministère des Ressources Naturelles*.
- Ter Braak, C.J.F., Šmilauer, P., 1998. *Canoco* 4, 351 pp.
- Vellend, M., 2004. Parallel effects of land-use history on species diversity and genetic diversity of forest herbs. *Ecology* 85, 3043–3055.
- Verheyen, K., Honnay, O., Motzkin, G., Hermy, M., Foster, D.R., 2003. Response of forest plant species to land-use change: a life-history trait-based approach. *J. Ecol.* 91, 563–577.
- Whitehead, D., 1982. Ecological aspects of natural and plantation forests. *For. Abstr.* 43, 73–92.