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Differences in forest composition in two boreal forest ecoregions of Quebec

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Abstract. In order to describe and compare the post-fire succession patterns of the two ecological regions (mixed-wood and coniferous ecoregions) of northwestern Quebec, 260 forest stands were sampled with the point-centred plot method. The mixed-wood ecological region belongs to the *Abies balsamea-Betula papyrifera* bioclimatic domain whereas the coniferous ecological region belongs to the *Picea mariana*-moss bioclimatic domain. In each plot, tree composition was described, surficial deposits and drainage were recorded, and fire history was reconstructed using standard dendro-ecological methods. Ordination techniques (Correspondence Analysis and Canonical Correspondence Analysis) were used to describe the successional patterns of forest vegetation and to correlate them with the explanatory variables. The results showed the importance of surficial deposits, the time since fire and the ecoregion in explaining the variation of stand composition. *Abies balsamea* tends to increase in importance with an increase in time since fire, and this trend is more pronounced in the mixed-wood region. Even when controlling both for surficial deposits and time since fire, differences in successional trends were observed between the two ecoregions. As all the species are present in both ecoregions and as they are all observed further north, our results suggest that both the landscape configuration and fire regime parameters such as fire size and fire intensity are important factors involved in these differences.

Keywords: *Abies balsamea*; Balsam fir; Black spruce; Boreal forest; Chronosequence; Disturbance; Fire; *Picea mariana*; Succession.

Introduction

The vegetation dynamics of forest systems are controlled by numerous factors such as the available pool of species, the physical characteristics of the land, soil fertility, climate and disturbance regime characteristics (Major 1951). In the boreal forest of North America, several studies have shown the importance of abiotic factors such as surficial deposits, soils and/or moisture regimes in the understanding of vegetation composition and patterns (Bergeron & Bouchard 1984; Carleton & Maycock 1980; Jones et al. 1983). The importance of disturbances such as fire and insect outbreaks on boreal systems has also been recognized (Blais 1983; Morin 1994; Johnson 1979; Johnson 1992; Bergeron 1991; Bergeron et al. 1998; Pickett & White 1985; Kneeshaw & Bergeron 1998). In many boreal regions of Canada, fire is the most important disturbance affecting both vegetation composition and dynamics (Johnson 1992; Bergeron et al. 1998). However, the fire cycle varies considerably among different boreal regions, with a range of 50 - 500 yr (Johnson 1992; Foster 1983; Flannigan et al. 1998). With a short fire cycle, the high recurrence of fires may preclude succession with species replacement in the canopy (Dix & Swan 1971; Black & Bliss 1978; Johnson 1992). On the other hand, in regions where the fire cycle is longer, there is enough time between successive fires for the establishment of a second cohort of trees, resulting in species replacement (Foster & King 1986; Bergeron & Dubuc 1989; Bergeron & Charron 1994; Bergeron 2000). In the context of climate change, many studies have suggested that the fire cycle length is changing in many regions of the northern hemisphere (Flannigan et al. 1998 and references therein). Disturbance regime parameters such as cycle, interval length, and intensity are factors that may influence both the pool of available species for post-fire re-colonization and dynamics of forest stands (Pickett et al. 1987).

Within the forest ecosystem classification of Quebec, the continuous boreal forest zone is divided into two bioclimatic domains: the mixed-wood domain and the pure coniferous domain (Saucier et al. 1998). The mixed-wood domain, also called the *Abies balsamea-Betula papyrifera* domain, is characterized by the abundance of shade-intolerant hardwood species and *Abies balsamea*, whereas the pure coniferous domain, also called the *Picea mariana*-moss domain, is characterized by the importance of *P. mariana* and a lower importance of *Abies balsamea*. The main tree species present in the mixed-wood domain, however, are all

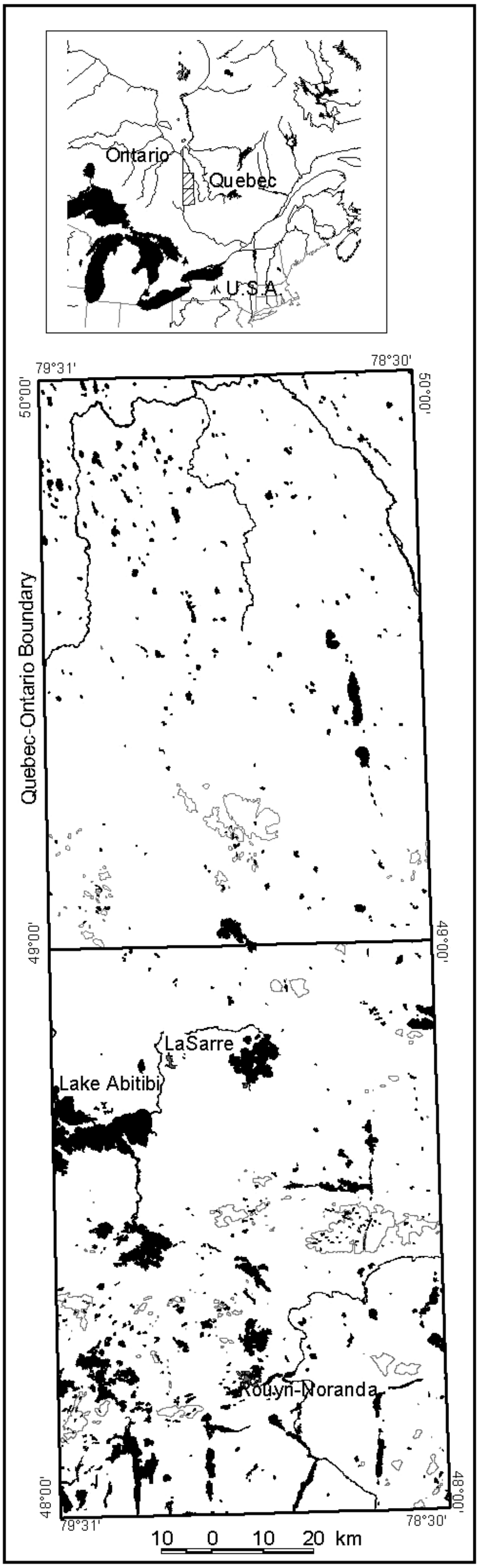

Fig. 1. Location map of the study area.

present in the coniferous region and are far from their northern limit of distribution.

Our goal within this study was to evaluate and compare post-fire succession trends of the forest vegetation in two adjacent ecoregions of the Quebec continuous boreal forest (Saucier et al. 1998). The objectives of the study were to compare succession trends among the two ecoregions, and to discuss the factors potentially responsible for the differences.

Study area

The study area (78° 30'-79° 30' W; 48° 00'- 50° 00' N) has a size of 15 000 km^2 and crosses two ecoregions in the continuous boreal forest area of Quebec. The two ecoregions (the Abitibi Lowland and the Lake Matagami Lowland) are located in the western section of the boreal forest of Quebec, at the border between Quebec and Ontario (Fig. 1). The ecoregions are land portions that have forest vegetation on mesic sites typical of the bioclimatic domain and are characterized by a particular configuration of land forms (Saucier et al. 1998). Roughly, the limit between the two ecoregions is located at 49°00'N (Fig. 1). The southern ecoregion (Abitibi Lowland) belongs to the *Abies balsamea-Betula papyrifera* bioclimatic domain and will be referred to as the mixed-wood ecoregion (Table 1). The northern region (Lake Matagami Lowland) belongs to the *Picea mariana*-moss bioclimatic domain and will be referred to as the coniferous ecoregion. Both regions are located within the Clay Belt of Ontario and Quebec, a large physiographic unit of clay deposits left by the proglacial Lake Ojibway (Vincent & Hardy 1977). In the coniferous ecoregion, the topography is generally flat, and the most important surficial deposit is organic soils (36% of the area) followed by clay deposits (29%) (Table 1). On the other hand, clay deposits are dominant in the mixed-wood ecoregion (45%) followed by organic deposits (18%). The southern part of the mixed-wood region is characterized by a rolling topography whereas the northern part is flat. The mean annual temperature, the number of degree days/year and the length of the growing season are all slightly higher in the mixed-wood ecoregion than in the coniferous region (Thibault & Hotte 1985; Saucier et al. 1998; Table 1).

Studies on the fire regime of the two ecoregions indicate that their fire cycles have not been different over the last 300 yr (Bergeron et al. 1997, in press). However, in both regions the fire cycle changed around 1850, which corresponds to the end of the Little Ice Age. Before 1850, the fire cycle was less than 100 yr, whereas after 1850 the cycles are extended (Table 1).

Material and Methods

Field sampling and dendro-ecological analysis

In order to define the post-fire succession trends, 260 sites in the study area (135 in the mixed-wood region and 125 in the coniferous region; Table 1) were visited during the summer of 1994 and 1995. Stands were selected as a function of accessibility, the absence of human disturbances, and the possibility of reconstructing the fire history. For these reasons, the number of stands sampled in each of the surficial deposits is not necessarily proportional to the percentage present in the ecological region (Table 1). In each stand, the point-centred plot method was used to characterize vegetation composition (Cottam & Curtis 1956). 10 points were placed at a distance of 10 m from each other. At each point, for the closest tree in each of four quadrants, the species and the diameter at breast height (DBH) classes (in 5-cm classes) were recorded. The type of surficial deposit, the slope and the drainage classes were also recorded. The date of the last fire was determined using the standard dendro-ecological approach (Arno & Sneck 1977). At each site visited, five disks or increment cores were collected preferentially from pioneer tree species, and a special effort was made to search for jack pine snags, to date previous fires. The fire date could be estimated within 5 yr. For jack pine snags, cross-dating was facilitated by the existence of a regional chronology (Dansereau & Bergeron 1993).

Data analysis

An importance value for each of the 11 tree species was compiled as follows:

$$\left[\textit{Relative density} \text{ of species A (\%)} + \textit{Relative basal area} \text{ of species A (\%)}\right]/2$$

where the *relative density* is the number of times that species A was recorded in the 40 quadrants (as a percentage), and *relative basal area* is the basal area covered by species A divided by the total basal area of the 40 measured trees in the stand (as a percentage).

In order to evaluate the factors responsible for the variation in forest composition, the importance values were used to compute two ordinations: one correspondence analysis (CA) and a canonical correspondence analysis (CCA). CA was used to represent the stands relative to each other and to compute correlations between the stand scores on the axis and the independent variables. CCA was computed using a forward selection of the independent variables in order to assess the importance of each variable in the explanation of the variation in forest composition. The downloading options for rare species was used. Finally, the same approach was used for each of the four main surficial deposits. Five different pathways were defined based on the species dominating the stand. In order to compare the vegetation dynamics of the two ecoregions, species with the highest importance values were considered as dominating species: *Pinus banksiana*, *Picea mariana*, *Betula papyrifera*, *Populus tremuloides* and *Abies balsamea*. For each 100-yr age class, the frequency of occurrence of each pathway was defined for each surficial geology type.

Finally, only for the organic stands (as the number of stands was sufficient in both regions), one stepwise

Table 1. General description of the two ecoregions. Numbers of stands in the surficial geology types and their percentages in the ecoregions are indicated.

		Mixed-wood ecoregion		Coniferous ecoregion	
		% in the region	No. of stands sampled / (%)	% in the region	No. of stands sampled / (%)
Rock		14	30 / (22)	6	7 / (6)
Clay		45	22 / (16)	29	10 / (8)
Till		5	21 / (15)	16	7 / (6)
Sand		11	15 / (11)	4	12 / (10)
Organic		18	33 / (24)	36	71 / (57)
Other / Non recorded		1	14 / (10)	0	18 / (14)
Water		6		8	
Mean annual temperature		0 - 2.5		–2.5 - 0	
Number of degree days/year		1220 - 1280		1100-1170	
Length of growing season		150 - 160		120-150	
Estimated length of fire cycle (year)					
	Total	158 (133 - 188)		182 (152 - 216)	
	1920 - 1999	316 (243 - 410)		398 (302 - 524)	
	1851 - 1920	106 (84 - 132)		133 (106 - 167)	
	< 1850	81 (64 - 103)		103(80 131)	

Table 2. Correlation (Correlation coefficient) values between the first two axis and the explanatory variables for the four main surficial deposits.

	Global			Rock			Clay			Sand			Org.		
Variable	rank[1]	Axis 1	Axis 2	rank	Axis 1	Axis 2	rank	Axis 1	Axis 2	rank	Axis 1	Axis 2	rank	Axis 1	Axis 2
Time	2	–312	–357	1	–114	–566	- - -	22	–39	1	–61	557	1	–379	5
Ecoregion	3	–464	–42	2	–486	106	1	–327	86	- - -	123	353	2	31	–193
Drainage 1	- - -	270	44	- - -	–96	17	- - -	–10	–187	- - -	–118	–169	- - -	- - -	- - -
Drainage 2	- - -	33	220	- - -	96	–17	- - -	–61	–140	- - -	32	216	- - -	- - -	- - -
Drainage 3	- - -	284	154	- - -	- - -	- - -	2	242	290	- - -	35	–44	- - -	110	–29
Drainage 4	- - -	68	212	- - -	- - -	- - -		–124	–116	- - -	–21	–146	- - -	- - -	- - -
Drainage 5	- - -	–197	–9	- - -	- - -	- - -	3	–226	–123	- - -	- - -	- - -	- - -	215	145
Drainage 6	- - -	–533	–331	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	–221	–115
Rock	- - -	293	20	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -
Till	- - -	200	90	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -
Clay	- - -	200	100	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -
Sand	4	–6	343	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -
Organic	1	–566	–337	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -	- - -

[1] rank : CCA Forward selection order of the variables with p to enter < 0.10

regression was computed per species with SAS (Anon. 1985) to define and compare the successional trends between the two ecoregions. The importance values of the species was the dependent variable used in these multiple regressions. The following independent variables (ER: ecological region, TSF: the time since fire (in 25 year classes), the log(TSF), TSF^2 and interactions (ER*TSF, ER*TSF^2, ER*log(TSF)) were used in the regressions.

Results

General ordination trends

An ordination (CA) with the importance values of the 11 species (using downweighting of rare species) and 260 stands was computed. The first axis expressed 27,8% (λ=0.630) of the variance in species composition whereas the second axis explained 23.7% (λ =0.539) of the variance. Correlations between the stand scores on the first two axes and the abiotic variables revealed that the ecoregion and the surficial deposit type (particularly sand and organic) had high correlations with the first axis, whereas the time since the last fire had an intermediate correlation with the first axis and the highest correlation with the second ordination axis (Table 2). A CCA with a forward selection procedure corroborated that vegetation composition is different on organic deposit stands as compared to all the other surficial deposit types (Table 2). Moreover, the time since fire is the second variable to enter in the model, the ecoregion is the third, whereas the sandy deposit type is the fourth variable to enter in the model.

In view of the significant effect of surficial geology type and the unbalanced sampling of the different surficial geology types in the two ecoregions, another ordination,

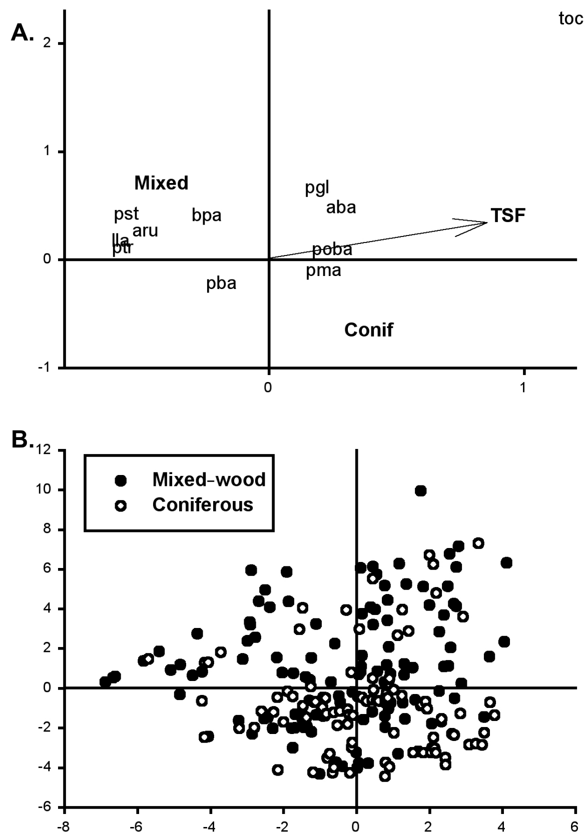

Fig. 2. Canonical Correspondence Analysis of the tree composition (importance values), with surficial deposit types and drainage as covariables of 260 stands of the mixed-wood and coniferous ecoregions of northwestern Quebec. **A.** Tree species and explanatory variables; **B.** Stands.

Aba = *Abies balsamea* Bpa = *Betula papyrifera*
Pba = *Pinus banksiana* Pgl = *Picea glauca*
Pma = *Picea mariana* Poba = *Populus balsamifera*
Ptr = *Populus tremuloides* Toc = *Thuja occidentalis*
Lla = *Larix laricina* Pst = *Pinus strobus*
Aru = *Acer rubrum* TSF = time since last fire
Mixed = centroid of the mixed-wood ecoregion
Conif = centroid of the coniferous ecoregion.

CCA, was performed where the analysis was constrained by surficial geology and drainage (Fig. 2). This analysis revealed that (1) the time since fire is strongly related to the first CCA axis and (2) that the differentiation as to ecoregion is a significant factor mainly associated with the second axis. The position of *Thuja occidentalis* at the far end of the first axis indicates that it is associated with a long time since fire. At the opposite side of the first axis we have species such as *Populus tremuloides* and *Larix laricina* which have the lowest scores (Fig. 2) showing their pioneer status. Both *Pinus banksiana* and *Picea mariana* are located on the negative side of axis 2, indicating their strong association with stands from the coniferous ecoregion. This graph also suggests that there are mainly two pathways observed in vegetation composition (1) with hardwoods starting succession and with an increasing amount of *Abies balsamea* over time; (2) with *Pinus banksiana* and *Picea mariana* as pioneers and with *P. mariana* becoming more abundant as time since fire increases. Moreover, Fig. 2 suggests that the mixed-wood ecoregion stands tend to have more shade-intolerant hardwood species whereas the coniferous region tends to have more stands dominated by *Picea mariana*. In fact, most (i.e. 81%) of the stands from the coniferous ecoregion are located at the negative side of axis 2, whereas many stands (i.e. 53%) of the mixed-wood ecoregion are located at the positive side. Using the procedure described by Borcard et al. (1992), we estimated that the surficial geology-drainage variables explain 12% of stand composition, while time since fire and location are responsible for 6.7%. Moreover, 6.6% of the variance is shared by the interaction among the two sets of variables.

Finally, when the analyses were computed independently for each surficial deposit, the results of the correlation calculations and the CCAs indicated that, on all surficial deposits except clay-till, time since fire contributes to the explanation of the observed variation among forest stands (Table 2). Moreover, in all surficial deposits, the location of stands is always an important factor in the explanation of vegetation composition.

Successional trends in stand composition for the main surficial deposits

Time elapsed since the last fire is the variable which contributed most to the explanation of the variation in forest composition among the 37 stands on rock outcrops (Table 2). Despite the fact that only seven sites belong to the coniferous region, significant differences can also be attributed to the ecoregion. On the rock outcrops of the coniferous region, succession after fire mainly starts with *Pinus banksiana*, while the importance of *Picea mariana* tends to increase with time since fire (Tables 3 and 4). On the other hand, the shade-intolerant hardwood species, mainly *Betula papyrifera* and, to a certain extent, *Populus tremuloides* are more

Table 3. Mean importance values and standard error *(*italics) for 11 tree species and the main surficial geology types (Geology) per 100-yr class.[1]

			Mixed-wood											Coniferous											
Geology	TSF	N	Pma	Pba	Bpa	Aba	Aru	Pgl	Ptr	Toc	Poba	Lla	Pst	N	Pma	Pba	Bpa	Aba	Aru	Pgl	Ptr	Toc	Poba	Lla	Pst
Rock	50	22	10.4	26.0	26.8	5.5	2.1	4.5	21.7	0.1	0.9	0.0	2.1	5	29.7	46.8	9.2	2.8	0.0	0.4	9.0	0.0	0.0	2.2	0.0
			14.6	*27.2*	*17.8*	*10.4*	*8.8*	*10.0*	*23.0*	*0.5*	*4.4*	*0.0*	*10.0*		*18.9*	*29.1*	*13.6*	*6.2*	*0.0*	*0.9*	*20.1*	*0.0*	*0.0*	*5.0*	*0.0*
	150	4	18.8	20.6	18.0	24.4	0.0	18.1	0.0	0.0	0.0	0.0	0.0	2	64.0	34.2	1.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
			13.3	*20.0*	*14.5*	*14.0*	*0.0*	*23.8*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*		*0.3*	*2.8*	*2.5*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*
	250	4	24.6	3.5	31.2	29.0	0.9	0.8	0.4	9.8	0.0	0.0	0.0												
			24.3	*7.1*	*12.7*	*20.2*	*1.8*	*1.0*	*0.9*	*19.5*	*0.0*	*0.0*	*0.0*												
Clay-Till	50	36	20.3	30.1	18.9	5.4	0.5	3.8	20.6	0.1	0.4	0.1	0.0	12	23.9	52.3	6.3	6.3	0.0	2.2	9.1	0.0	0.0	0.0	0.0
			24.4	*30.0*	*26.4*	*10.4*	*2.4*	*9.8*	*25.3*	*0.4*	*1.5*	*0.6*	*0.0*		*25.1*	*35.0*	*13.6*	*13.8*	*0.0*	*6.5*	*24.3*	*0.0*	*0.0*	*0.0*	*0.0*
	150	6	22.1	15.4	25.1	12.7	0.6	12.1	12.1	0.0	0.0	0.0	0.0	4	41.2	18.1	7.1	1.4	0.0	0.0	22.5	0.0	7.9	1.8	0.0
			21.4	*19.8*	*22.4*	*11.4*	*1.4*	*8.6*	*15.8*	*0.0*	*0.0*	*0.0*	*0.0*		*36.6*	*36.2*	*8.2*	*2.9*	*0.0*	*0.0*	*29.8*	*0.0*	*15.7*	*3.7*	*0.0*
	250	1	0.0	0.0	19.0	76.4	0.0	4.6	0.0	0.0	0.0	0.0	0.0	1	1.8	95.3	0.0	0.0	0.0	0.0	2.9	0.0	0.0	0.0	0.0
Sand	50	13	9.8	74.7	7.2	1.2	0.0	1.9	3.2	0.0	1.9	0.0	0.0	9	26.0	58.7	9.3	0.9	0.0	1.5	3.6	0.0	0.0	0.0	0.0
			20.6	*37.0*	*14.7*	*2.5*	*0.0*	*4.9*	*11.7*	*0.0*	*7.0*	*0.0*	*0.0*		*20.6*	*23.8*	*17.8*	*1.6*	*0.0*	*3.1*	*8.0*	*0.0*	*0.0*	*0.0*	*0.0*
	150	2	52.1	48.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3	45.5	20.8	6.0	22.8	0.0	0.0	5.0	0.0	0.0	0.0	0.0
			37.6	*37.5*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*		*27.5*	*19.5*	*10.3*	*39.5*	*0.0*	*0.0*	*8.6*	*0.0*	*0.0*	*0.0*	*0.0*
Organic	50	18	63.7	18.0	3.3	7.4	0.0	0.3	3.9	0.2	0.0	3.3	0.0	35	61.8	22.8	1.7	4.3	0.0	3.4	4.2	0.0	0.0	1.8	0.0
			27.3	*27.6*	*5.0*	*15.7*	*0.0*	*0.9*	*12.1*	*0.9*	*0.0*	*5.8*	*0.0*		*31.6*	*27.4*	*7.2*	*11.7*	*0.0*	*12.6*	*11.5*	*0.0*	*0.0*	*6.3*	*0.0*
	150	10	68.9	3.1	4.8	16.0	0.0	1.0	3.2	0.0	0.0	2.9	0.0	20	85.7	5.4	0.9	6.6	0.0	1.0	0.0	0.0	0.0	0.5	0.0
			25.4	*6.9*	*8.5*	*17.4*	*0.0*	*2.4*	*8.1*	*0.0*	*0.0*	*8.4*	*0.0*		*24.8*	*18.0*	*2.8*	*12.8*	*0.0*	*4.4*	*0.0*	*0.0*	*0.0*	*1.4*	*0.0*
	250	5	66.1	0.0	2.1	5.1	0.0	1.1	0.0	23.9	0.0	1.8	0.0	17	92.4	0.0	0.8	6.1	0.0	0.0	0.0	0.0	0.0	0.6	0.0
			46.3	*0.0*	*4.6*	*11.4*	*0.0*	*2.5*	*0.0*	*32.9*	*0.0*	*2.9*	*0.0*		*17.3*	*0.0*	*3.4*	*14.1*	*0.0*	*0.0*	*0.0*	*0.0*	*0.0*	*1.9*	*0.0*

[1] TSF = time since fire; N = number of stands; Pma = *Picea mariana*; Pba; *Pinus banksiana*; Bpa = *Betula papyrifera*; Ptr = *Populus tremuloides*; Aba = *Abies balsamea*; Aru = *Acer rubrum*; Pgl = *Picea glauca*; Toc = *Thuja occidentalis*; Poba = *Populus balsamifera*; Lla = *Larix laricina*; Pst = *Pinus strobus.*

Table 4. Comparison of the relative proportion of stands dominated by the five major species over a chronosequence of 250 years.

		Mixed-wood						Coniferous					
Geology	TSF[1]	*N*	Pma	Pba	Bpa	Ptr	Aba	N	Pma	Pba	Bpa	Ptr	Aba
Rock	50	22	9.09	36.36	31.82	22.73	0.00	5	20.00	60.00	0.00	20.00	0.00
	150	4	0.00	50.00	25.00	0.00	25.00	2	100.00	0.00	0.00	0.00	0.00
	250	4	25.00	0.00	25.00	0.00	50.00						
Clay-Till	50	36	19.44	33.33	25.00	16.67	5.56	12	25.00	50.00	8.33	8.33	8.33
	150	6	33.33	16.67	33.33	16.67	0.00	4	50.00	25.00	0.00	25.00	0.00
	250	1	0.00	0.00	0.00	0.00	100.00	1	0.00	100.00	0.00	0.00	0.00
Sand	50	13	7.69	76.92	15.38	0.00	0.00	9	33.33	55.56	11.11	0.00	0.00
	150	2	50.00	50.00	0.00	0.00	0.00	3	66.67	0.00	0.00	0.00	33.33
Organic	50	18	72.22	16.67	0.00	5.56	5.56	35	68.57	20.00	2.86	2.86	5.71
	150	10	90.00	0.00	0.00	0.00	10.00	20	95.00	5.00	0.00	0.00	0.00
	250	5	80.00	0.00	0.00	0.00	20.00	17	94.12	0.00	0.00	0.00	5.88

[1] TSF = time since fire; *N* = number of stands; Pma = *Picea mariana*; Pba = *Pinus banksiana*; Bpa = *Betula papyrifera*; Ptr = *Populus tremuloides*; Aba = *Abies balsamea*.

important in the mixed-wood ecoregion than in the coniferous one (Tables 3 and 4). Moreover, when looking at the successional trends (Table 3), we observed an increase in the importance of *Abies balsamea* with time since fire in the mixed-wood ecoregion only.

As stand compositions on clay and till deposits were similar, as indicated by the general ordination (Table 2), they were combined in the same ordination analysis. The CCA ordination revealed that forest composition on these 60 sites is mainly affected by the ecoregion, and by differences in drainage (Table 2). However, of the 60 stands on clay and till, only 12 were older than 100 yr, which may explain the low correlation of time-since-fire with the ordination axes. Some differences in successional trends can be observed between the mixed-wood region sites and the coniferous region sites (Table 3). Shortly after a fire, the importance of *Pinus banksiana* is greater in the coniferous region, whereas *Populus tremuloides* and *Betula papyrifera* are more important in the mixed-wood region. *Abies balsamea* and *Picea glauca* are increasing their importance with time since fire in the mixed-wood region whereas they are rare in the coniferous region (Table 3). The five main species are dominant in several stands in both ecoregions. However,

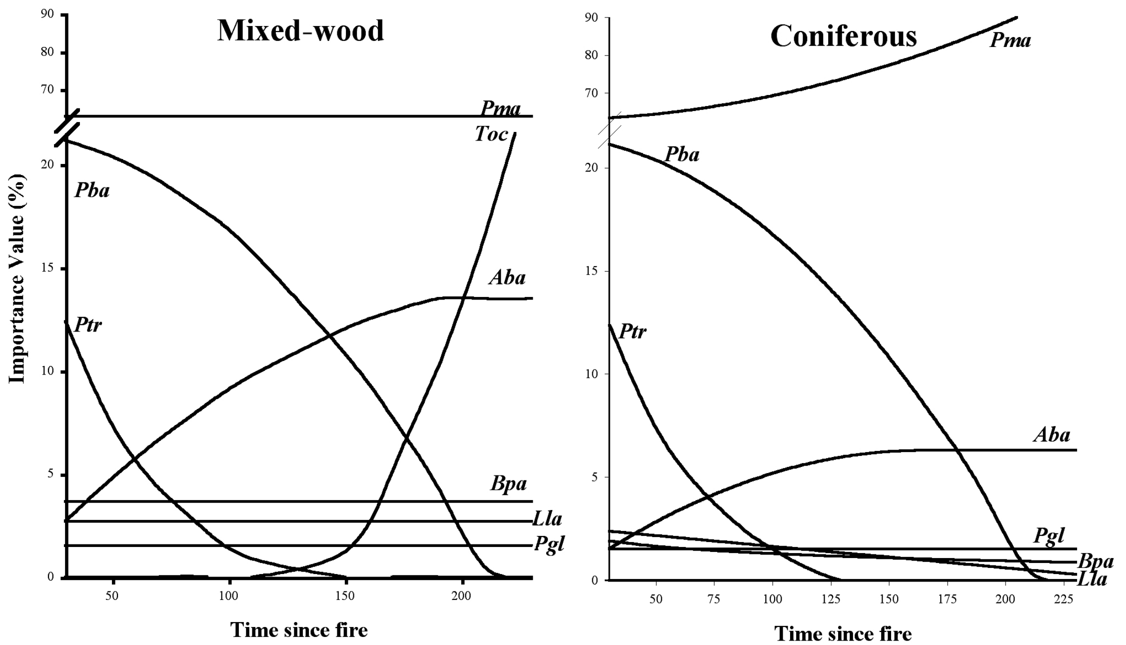

Fig. 3. Comparison of the successional trends on organic soils between the mixed-wood and coniferous ecoregions over a chronosequence of 250 yr. Note that the *y*-axis is interrupted.

stands dominated by *Betula* or *Abies* are scarcer in the coniferous ecoregion (Table 4) where both *Pinus banksiana* and *Picea mariana* dominate more frequently.

The analysis of stands located on sandy surficial deposits revealed that the time elapsed since the last fire is an important variable to explain variation in the composition of the 26 forest stands (Table 2). The importance of *Picea mariana* increases with time since fire in both ecoregions, while *Pinus banksiana* is more important in the mixed-wood ecoregion as compared to the coniferous one (Table 3). The majority of stands from the mixed-wood region are dominated by *Pinus banksiana* while in the coniferous region *Pinus banksiana* and *Picea mariana* dominate half of the stands respectively (Table 4).

The ordination of the 104 stands located on organic deposits indicates that time-since-fire is the most significant variable in the explanation of the variation in forest composition, followed by ecoregion (Table 2). The stands tend to be dominated by *Picea mariana* in both ecoregions over the entire time-since-fire sequence, but its importance value is higher in the coniferous region (Table 3). We have selected the organic deposits to assess the differences between the two ecoregions in vegetation dynamics using regression analysis techniques. The results showed that the importance value of *Picea mariana* tends to increase as time since fire increases in the coniferous region whereas it is somewhat more stable in the mixed-wood region (Fig. 3; Table 3). In both regions, there is an increase in the importance of *Abies balsamea* with time since fire, but the increase is larger in the mixed-wood region (Table 3; Fig. 3). Finally, both Table 3 and Fig. 3 suggest that the importance of *Thuja occidentalis* increases with time since fire in the mixed-wood region whereas the species is absent from the coniferous region.

Discussion

Our global analysis confirmed that surficial deposit and time-since-fire are two important variables explaining differences in vegetation composition among the 260 stands. Some species are more abundant on a particular surficial deposit. Among the pioneer species the importance of *Betula papyrifera* and *Pinus banksiana* is higher on drier surficial deposits (sand and rock) as compared with *Populus tremuloides*, which tends to be more abundant on the more mesic sites (clay and till deposits). Similar results have already been reported by others (Bergeron et al. 1983; Jones et al. 1983; Sims et al. 1990; Leduc et al. 1995). Moreover, stand composition is significantly different among different deposits, and the difference between organic deposits and the others is large. *Picea mariana* and *Larix laricina* are more dominant on organic deposits than on any other surficial deposit types. However, despite these differences, most species can be observed on any surficial deposit. Moreover, the differences in stand composition on different surficial deposits are in terms of species abundance rather than species exclusion, suggesting that there may be an interaction between the physical setting of the landscapes and fire regime parameters.

When controlling for surficial deposits, the results of correlation analysis and CCA indicated that time-since-fire is also a variable that helps explain the observed variation among forest stands (Table 2). On any surficial deposit type, most species appear to be present early after the fire as indicated by their importance values, which correspond to observations elsewhere (Johnson 1992; Johnson & Fryer 1989; Bergeron & Charron 1994; Bergeron & Dubuc 1989). However, the shade-tolerant species *Abies balsamea* and *Thuja occidentalis* show an increase in importance with time since fire. Long fire intervals (relative to average species longevity) in the same stand are no rare events in the studied system. In fact, 34% of the stands that were sampled have been exempted of fire for more than 150 yr. Our results therefore suggest that succession with some species replacement (in the mixed-wood region) can occur on sites where the interval between successive fires is longer than the longevity period of pioneer species, as reported by some authors (Bergeron 2000; Frelich & Reich 1995; Bergeron & Charron 1994; Bergeron & Dubuc 1989). Even in the coniferous region, where the species richness is lower, old *Picea mariana* stands may have also changed in terms of structure, from even-aged stands to uneven-aged stands, as the time since fire increases (Groot & Horton 1994; MacDonnell & Groot 1997; L. De Grandpré et al. 2000 (this issue)).

Potential causes for differences among successional trends between the two ecoregions

Even when controlling for time-since-fire and surficial deposit, differences among successional pathways and vegetation patterns between the two ecoregions were observed, as suggested by the CCA results. The differences in successional pathways between the two regions do not appear to be due to major differences in terms of climate as the major tree species are present in the two regions, far from their northern limit of distribution. Moreover, our data show that the five main species can be dominant in stands in both ecoregions, and on most surficial deposit types. If we first consider the organic deposits, our results indicate differences in vegetation dynamics among the two ecoregions, despite the fact that the same species pool is available. In fact, succession appears to be more diverse in the mixed-wood ecoregion, where shade-intolerant hardwood species and *Abies balsamea* are more important. In the coniferous ecoregion, large areas are occupied by organic surficial material, which is a favourable environment for *Picea mariana* (Sims et al. 1990). Our results show that the dominance of *Picea mariana* increases with time since fire in the coniferous region together with a very slow increase of *Abies balsamea* – as reported by others (Bergeron et al. 1983; Sims et al. 1990). On the other hand, on this surficial deposit in the mixed-wood region, the importance of *Picea mariana* is relatively stable over time and an increase in the abundance of *Abies balsamea* and *Thuja occidentalis* is observed with an increase in time since fire. Therefore, it seems that the re-invasion of stands by *Abies balsamea* takes more time and is more difficult in the coniferous region than in the mixed-wood zone. An explanation for this difference might be related to a paludification phenomenon, where the decomposition of organic material is slower under the cooler climate of the coniferous ecoregion (Økland 2000). This phenomenon may favour *Picea mariana* through its shading of *Abies balsamea* seedlings. On any surficial geology type in the coniferous region, a larger proportion of stands is dominated by *Picea mariana*, as compared to the mixed-wood ecoregion. One potential explanation for these differences is related to differences in the landscape configuration. The greater importance of the organic deposits in the coniferous region probably contributes directly to increasing the overall importance of *Picea mariana* in the landscape. Therefore, it may increase the potential for that species (*Picea mariana)* to re-invade burned sites on other surficial deposit types.

The landscape configuration of the coniferous ecoregion appears to be responsible for the occurrence of larger fires there than in the mixed-wood region. In fact, 12.5% of the 207 lightning fires that occurred in the coniferous region from 1972 to 1995 were larger than 100 ha as compared with only 1.3% of the 75 lightning fires that occurred in the mixed-wood region during the same period (data from the Direction de la conservation, MRNQ). Moreover, these facts are corroborated by the fire history work under completion by our group, where fires larger than 10 000 ha are more frequent in the coniferous region than in the mixed-wood one (Bergeron et al. unpubl.). The generally flat topography (Fig. 1) and the high proportion of organic surficial deposits that favours *Picea mariana* appear to be factors favouring the occurrence of large fires in the coniferous region as compared to the mixed-wood region (Turner & Romme 1994). Therefore, despite that both regions have faced the same fire cycles in the last 300 yr, the distribution of fire sizes appears to differ between them. The occurrence of large fires in the coniferous region may have resulted in fewer chances for re-colonization by *Abies balsamea, Picea glauca* and *Thuja occidentalis* after a fire, as these species are at a disadvantage when fires are extensive (Heinselman 1973; Bergeron & Dubuc 1989; Galipeau et al. 1997). On the other hand, the more rolling topography in the mixed-wood region, in which smaller fires are observed, may increase the chances of *Abies balsamea, Picea glauca* and *Thuja occidentalis* of being close to a recently burned site, which increases their chances of becoming established early after a fire. Moreover, stands with shade-intolerant hardwood species tend to have a bigger chance of meeting low-severity fires (Kafka et al. in press), which may also contribute to the distinction in successional trends between the two ecoregions.

Our results indicate that successional pathways are more diverse in the mixed-wood region than in the coniferous one. In the mixed-wood zone, the more frequent occurrence of shade-intolerant hardwoods appears to be favoured by disturbances other than fire. For instance, *Betula papyrifera* and *Populus tremuloides* are observed even in relatively old forests, mainly in the mixed-wood region (see Table 3). The mortality of *Abies balsamea* during spruce budworm outbreaks is favourable for the recruitment of these intolerant hardwoods (Kneeshaw & Bergeron 1996, 1998). As *Abies balsamea* is more important in the mixed-wood region, this may also contribute to the greater importance of intolerant hardwoods in this ecological region.

Conclusion

Our results suggest that under the current fire regime, directional succession may occur in both ecoregions. This phenomenon may be enhanced where the fire cycle tends to be extended as a result of climate change (Bergeron 1991; Bergeron et al. 1998, in press). Our results also show that a certain portion of the variation in vegetation composition cannot be attributed directly to the variables surficial deposit and time-since-fire. These results therefore suggest that landscape configuration is probably an important factor to be considered in the explanation of the differences in successional trends between the two ecoregions. In fact, landscape configuration can have a direct effect on vegetation succession through species preference and availability for re-colonization. Moreover, it is also important in controlling some fire regime parameters such as fire size or fire severity. Both these direct and indirect effects of landscape configuration may play an important role in the differences among successional trends between the two studied ecoregions.

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