The spread of gray birch (*Betula populifolia*) in eastern Quebec: landscape and historical considerations

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Abstract: The understanding of recent changes of the spatial distribution of tree species occurring in agricultural landscapes is essential to realistically predict future positions of the range limit of tree species. In Quebec (Canada), it has recently been suggested that gray birch (*Betula populifolia* Marsh.) is spreading rapidly eastward. We tested the hypothesis that this tree migration is strongly facilitated by human activities. Herbarium specimens, historical landscape reconstructions, botanical surveys in mined peatlands and old fields, and dendrochronological data were used to reconstruct past and recent distribution limits of gray birch in the study area (Bas-Saint-Laurent region). Gray birch has been present in the Bas-Saint-Laurent region since at least 1945. However, herbarium specimens and botanical surveys indicate that gray birch individuals were scarce before 1970. The introduction of gray birch in the Bas-Saint-Laurent region seems to be associated with peat mining activities. All mined peatlands located between Rivière-Ouelle and Isle-Verte were colonized by gray birch, but only 11% of old fields surveyed contained at least one gray birch individual. This suggests that the spread of an early successional tree species in an agricultural landscape is facilitated more by the presence of a few large patches favorable to the growth of the species (mined peatlands) than by numerous small patches (old fields). The recent expansion of gray birch populations in the Bas-Saint-Laurent region could be a major concern for peat mining companies because massive invasions of gray birch in abandoned mined bogs may impede successful restoration of these ecosystems.

Key words: *Betula populifolia*, gray birch, Quebec, peatland, old field, landscape ecology.

Résumé : L’étude des changements récents de la répartition spatiale des espèces arborescentes dans les paysages agricoles est essentielle pour prédire, de façon réaliste, la position future des limites de répartition des arbres. Au Québec (Canada), on a remarqué récemment que l’aire de répartition du bouleau gris (*Betula populifolia* Marsh.) s’agrandit rapidement vers l’est. Nous avons testé l’hypothèse que cet agrandissement de l’aire de répartition est fortement facilité par des activités humaines. Pour reconstituer l’évolution de l’aire de répartition du bouleau gris dans la région d’étude (Bas-Saint-Laurent), nous avons utilisé des spécimens d’herbier, étudié l’historique des paysages et échantillonné (dendrochronologie) des bouleaux sur le terrain (tourbières exploitées, champs agricoles abandonnés). Le bouleau gris est présent dans le Bas-Saint-Laurent depuis au moins 1945. Toutefois, les spécimens d’herbier et les études botaniques antérieures indiquent que le bouleau gris y était rare avant 1970. L’introduction du bouleau gris dans le Bas-Saint-Laurent semble être associée aux activités d’extraction de la tourbe. Toutes les tourbières exploitées entre Rivière-Ouelle et l’Isle-Verte sont colonisées par le bouleau gris, ce qui est le cas de seulement 11 % des champs abandonnés. Ceci suggère que la migration d’une espèce arborescente de début de succession dans un paysage agricole est davantage facilitée par la présence de quelques grandes parcelles favorables à la croissance de l’espèce (tourbières exploitées) que par celle de nombreuses petites parcelles (champs abandonnés). L’expansion récente du bouleau gris dans le Bas-Saint-Laurent constitue un problème potentiel pour les compagnies de tourbe puisque des invasions massives de bouleaux dans les tourbières exploitées pourraient empêcher la restauration des sites.

Mots clés : *Betula populifolia*, bouleau gris, Québec, tourbière, champ agricole abandonné, écologie du paysage.

Introduction

Tree migration processes (sensu Sauer 1988) have recently attracted the attention of plant ecologists, because range limits of many tree species are expected to change in response to future global climate warming (Davis and Zabinski 1992; Lenihan and Neilson 1995). During the last major period of tree migration (late Pleistocene – early Holocene epochs: 18 000 – 6000 years BP), most tree species colonized deglaciated regions at rapid rates (10–300 km/century; Davis 1981; Huntley and Birks 1983; Ritchie and MacDonald 1986; Delcourt and Delcourt 1987). Recent models integrating paleoecological data and tree life histories have shown that these rates could not be achieved by a diffusion process, i.e., a simple “step-by-step” movement of the range limit resulting from local, short-distance seed dispersal (Clark 1998; Clark et al. 1998). Long-distance seed dispersal

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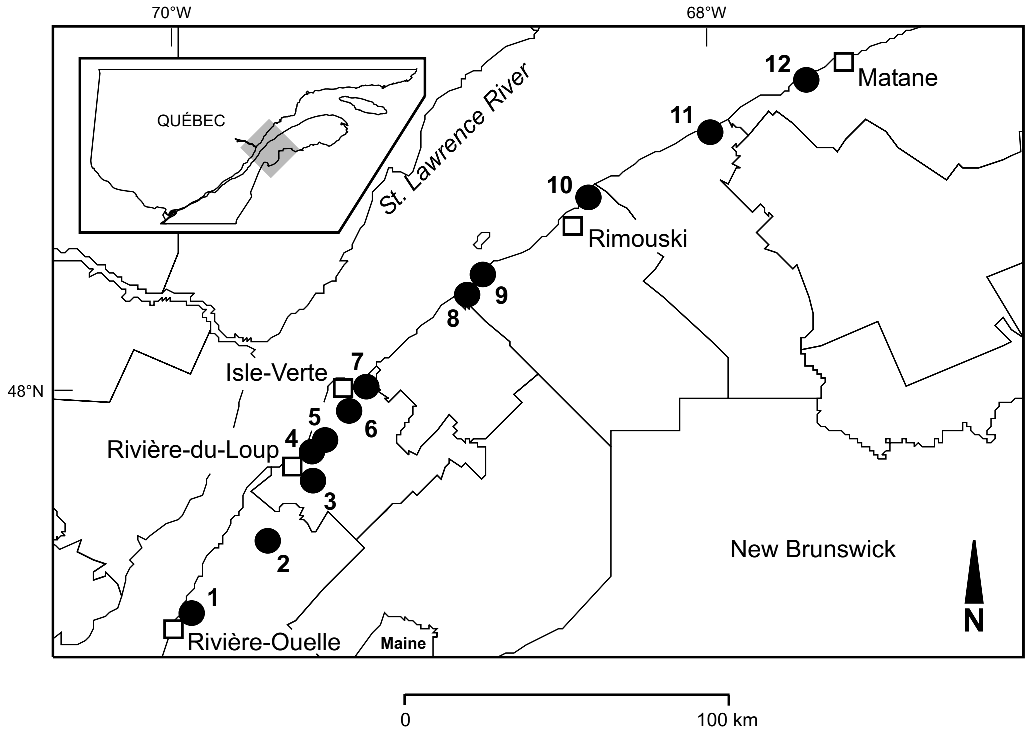
Fig. 1. Study area. (●) Mined peatland; (1) Rivière-Ouelle; (2) Saint-Alexandre; (3) Rivière-du-Loup; (4) Leparc; (5) Cacouna; (6) Coteau-du-Tuff; (7) Isle-Verte; (8) Porc-Pic; (9) Saint-Fabien; (10) Pointe-aux-Pères; (11) Mitis; (12) Saint-Ulric; (□) city. Subdivisions are municipal regional counties.



seems to be a much more efficient mechanism allowing rapid spread of tree species.

The late Pleistocene – early Holocene tree migration was realized in an environment almost devoid of anthropogenic disturbances, at least in North America. Tree spread was limited only by natural factors, such as seed barriers (mountains, large lakes, etc.) or the absence of animal vectors. Migrating plants are today confronted with landscapes largely modified by man: fragmented forests, large cultivated plains, big cities, etc. It is likely that plant migration processes are strongly affected by such man-made landscapes or structures. The understanding of recent changes of the spatial distribution of tree species occurring in agricultural landscapes is thus essential to realistically predict the change in the range of temperate tree species.

One common tree species in agricultural landscapes of northeastern North America is gray birch (*Betula populifolia* Marsh.). This successional species has a wide ecological range. It is common on rocky or sandy open woods, old fields, waste places and cutovers, and along roads and drainage ditches (Meilleur et al. 1994; Farrar 1996; Furlow 1997). This is one of the most common tree species bordering woodlots in agricultural areas of southern Quebec (Boutin and Jobin 1998). It is able to grow on many types of soils, from sandy to organic, and from well to poorly drained (Bouchard and Maycock 1978; Bergeron et al. 1988). This species may form almost pure stands on highly disturbed habitats, such as burned or mined peatlands (Lévesque and Millette 1977; Jean and Bouchard 1987; Lavoie and Rochefort 1996) or coal mine spoils (Pratt 1986).

In his recent book, Farrar (1996) suggested that gray birch populations are spreading westward and northward in abandoned agricultural fields. However, no data are given to substantiate this assertion. In Quebec (Canada), it has been suggested that gray birch is rapidly spreading eastward (Lavoie and Rochefort 1996). According to Rousseau (1974), the northeastern limit of this tree species was located, in 1965, in the Rivière-Ouelle area (Fig. 1). Some individuals were recently (1994) discovered as far as Isle-Verte, 90 km eastward (Lavoie and Rochefort 1996). This implies a rapid migration rate of more than 200 km/century. In this study, we examined how this species is able to migrate so fast in a landscape (agricultural plain of the Bas-Saint-Laurent region) with very few patches favorable to the growth of gray birch. We tested the hypothesis that this tree migration is strongly facilitated by human activities, especially peatland mining. Herbarium specimens, historical landscape reconstructions using aerial photographs, botanical surveys, and dendrochronological data were used to reconstruct past and recent distribution limits of gray birch in the study area.

Study area

The study area is located in the Bas-Saint-Laurent region, on the south shore of the St. Lawrence River, eastern Quebec (Fig. 1). More precisely, it is located in the agricultural plain, bordered at the northwest by the St. Lawrence River and at the southeast by the Appalachian foothills, between Rivière-Ouelle (47°27′N, 69°58′W) and Matane (48°48′N, 67°39′W). This plain is a narrow (4–10 km) and low-altitude (0–150 m) strip of sand, silt, and clay surficial marine deposits (Fulton 1995). The region was deglaciated about 12 000 years BP but was then submerged by the Goldthwaith Sea. On the plain, the vegetation cover was established shortly after marine regression, about 9500 years BP. Pollen and macrofossil data indicated that modern vegetation developed after 8000 years BP (Richard et al. 1992). On mesic and xeric sites, this vegetation is composed mainly of sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britt.), and balsam fir (*Abies balsamea* (L.) Mill.) forests (Grondin 1996). Large ombrotrophic peatlands are common in wet depressions and are dominated by black spruce (*Picea mariana* (Mill.) BSP), ericaceous shrubs and *Sphagnum* species (Gauthier and Grandtner 1975).

The European colonization of the Bas-Saint-Laurent region began at the end of the 17th century. At Rivière-Ouelle, Rivière-du-Loup, and Matane (Fig. 1), the first settlers established in 1672, 1683, and 1688, respectively (Laberge 1993; Morin 1993*a*). The colonization of the southwest of the study area was rapid. By 1720, all agricultural land bordering the St. Lawrence River was occupied. In 1815, almost all good agricultural land of the plain surrounding Rivière-Ouelle was cleared for cultivation (Laberge 1993). In the Rivière-du-Loup and Matane regions, the colonization was slow between 1683 and 1810; however, the population expanded rapidly in the first half of the 19th century because of a shortage of agricultural lands in southern Quebec (Morin 1993*b*). Around 1830, half of the land bordering the St. Lawrence River was cleared for cultivation near Cacouna, 8 km east of Rivière-du-Loup (Bouchette 1832). Almost all forests of the plain surrounding Rivière-du-Loup were transformed into agricultural land at the end of the 19th century (Fortin 1993). Today, the landscape of the plain between Rivière-Ouelle and Matane is composed mainly of agricultural land with scattered small woodlots and old fields. Because of the scarcity of woodlots, forest harvesting is now a marginal activity in the region. Large peatlands are still major components of the Bas-Saint-Laurent region, but most of them are mined for the production of horticultural peat. Many smaller peatlands (50–200 ha) were mined between 1940 and 1970; several are today abandoned (Desrochers et al. 1998). Most of them are naturally revegetated by bog plant species, and gray birch is frequently found on those abandoned bogs (Lavoie and Rochefort 1996).

Methods

Herbarium specimens and botanical surveys

To reconstruct the past and recent range of distribution of gray birch in Quebec, we collected information on all herbarium specimens of gray birch and of a closely related hybrid (*Betula ×cœrulea* Blanch.) sampled in the province. Herbarium specimens were requested from a total of 24 herbaria, i.e., 9 from Quebec (MT, MTMG, QFA, QSA, QUE, SFS, UQAM, UQAR, UQTR), 5 from Ontario (CAN, DAO, OAC, QK, TRT), 2 from New Brunswick (NBM, UNB), and 8 from the United States (BH, BKL, CM, GH, MASS, MICH, NY, VT), respectively. Each herbarium specimen was checked for possible misidentification, and we noted the specimen number, species, sampling location, year of sampling, and habitat characteristics. For each location, one specimen (gray birch only) per decade was chosen. Data on selected specimens were incorporated into a geographical information system (MapInfo,® MapInfo Corp., Troy, N.Y.) to reconstruct precisely the evolution of the range of distribution of gray birch during the 20th century. Furthermore, literature on botanical surveys conducted in the Bas-Saint-Laurent region was carefully consulted for any mention of gray birch in the study area.

Peatlands

Since gray birch is common in mined peatlands in the Bas-Saint-Laurent region, all mined bogs located between Rivière-Ouelle and Matane (Fig. 1, Table 1) were visited during summer 1997 to detect the presence of this species and to find the oldest individual at each site. The mining history of the bogs was reconstructed using aerial photographs (1930–1995) and archive documents from peat companies. In small peatlands (500 ha), we covered the perimeter of all mined sections, since most birch individuals grow close to the edges of mined sites (D. Campbell, unpublished data). We also examined all drainage ditches where old individuals are likely to be found since they were less susceptible to be removed during peat extraction activities (M. Girard and C. Lavoie, unpublished data). In the Rivière-du-Loup peatland (3375 ha), we concentrated our survey in the oldest mined sections, i.e., those harvested before the advent of mechanical peat extraction (ca. 1965–1970). In the Rivière-Ouelle peatland (1655 ha), gray birches were very numerous (thousands of individuals). Consequently, since our intention was to find the oldest individual of the peatland, we only visited sampling sites where gray birch was detected during a botanical survey conducted in the bog in 1965 (Gauthier 1967).

In each peatland (or in the selected sampling sites of the Rivière-du-Loup and Rivière-Ouelle bogs), every gray birch >2 m height was sampled. The individual was positioned using a global positioning system (GeoExplorer II; Trimble Navigation Ltd., Sunnyvale, Calif.). Herbarium specimens were taken to prevent misidentification with *Betula ×cœrulea* Blanch. and *Betula pendula* Roth, an Eurasian species very similar to gray birch and widely used as an ornamental in North America (Catling and Spicer 1988; DeHond and Campbell 1989). We revisited some bogs during early spring 1998 to confirm the identification of problematic individuals, since the number of preformed staminate catkins is a good character to discriminate gray birch from other birch species (DeHond and Campbell 1989). A cross section of the trunk of each sampled individual was taken using a small (24 cm) increment borer, as close as possible to the collar. In the laboratory, tree rings were counted on the fine-sanded cross sections. In bogs with no individual >2 m height, all gray birches were sampled (herbarium specimen and tree rings).

Old fields

Gray birch is a tree species usually found in old fields. To determine whether gray birch spread occurred only in mined peatlands or also in abandoned agricultural fields or pastures, we visited old fields of the study area (during summer 1998). Old-field patches are very numerous in the agricultural plain of the Bas-Saint-Laurent region (more than 900 patches between Rivière-Ouelle and Matane); therefore, only those located between Rivière-Ouelle and Isle-Verte were visited (i.e., between the presumed species limits in 1965 and 1994, respectively). Recent old-field maps from the Ministère de l'Agriculture et de l'Alimentation du Quebec (C. Morneau, unpublished) were used to randomly choose old fields to be visited. Sixty-three old-field patches were selected (Fig. 2, Table 2); their perimeters totalled 100 km. For the purpose of this study, the perimeter of an old field was more important than its area, since gray birches are more common at the edge of old fields and woodlots than in the core area (Boutin and Jobin 1998). The perimeter of the old field and each path and drainage ditch inside the abandoned patch were examined. Gray birches were sampled as for peatlands.

To date the year of abandonment of agricultural activities, we divided the area of each old field into five equal parts. In each part, we selected the tree individual with the biggest diameter at breast height (visually estimated). Only early successional tree species were selected: balsam poplar (*Populus balsamifera* L.), trembling aspen (*Populus tremuloides* Michx.), white birch (*Betula papy-*

Table 1. Mined peatlands sampled in the Bas-Saint-Laurent region, Quebec.

Peatland	Latitude (N)	Longitude (W)	Altitude (m)	Area (ha)	Distance from Rivière-Ouelle (km)	Beginning of mining activities (year)	End of mining activities (year)	Sampling effort (h)	No. of *Betula populifolia* sampled	Oldest *Betula populifolia* tree ring (year)
Rivière-Ouelle	47°28′	69°57′	15	1655	5	1935	Still mined	7	26	1945
Saint-Alexandre	47°39′	69°40′	105	455	30	1962	Still mined	5	13	1962
Rivière-du-Loup	47°48′	69°30′	100	3375	60	ca. 1940	1962 (sampled sector)	17	6	1962
Leparc	47°52′	69°30′	75	93	65	1962	1967	9	26	1945
Cacouna	47°54′	69°27′	85	175	70	1942	1963–1975	50	67	1960
Coteau-du-Tuff	47°58′	69°22′	65	51	80	1948	1970–1975	5	3	1970
Isle-Verte	48°02′	69°18′	35	157	90	1935	1965–1980	11	9	1964
Porc-Pic	48°16′	68°56′	90	190	125	1944	Still mined	4	—	—
Saint-Fabien	48°19′	68°52′	115	192	130	1944	Still mined	4	—	—
Pointe-aux-Pères	48°30′	68°28′	25	502	170	1940	Still mined	4	—	—
Mitis	48°40′	68°01′	70	76	200	1988	1995	1	—	—
Saint-Ulric	48°48′	67°39′	30	365	230	1939	Still mined	4	—	—

rifera Marsh.), white spruce (*Picea glauca* (Moench) Voss), and of course, gray birch. The tree was cored using the same small increment borer used for gray birch (as close as possible to the collar) and tree rings were counted on the fine-sanded cross section. The aging of an early successional tree individual gives only a minimum estimate of the year of abandonment of agricultural activities. There is usually a delay of 5–20 years between field abandonment and invasion of tree species (Pickett 1982; Inouye et al. 1987; Girard 1990; Vankat and Snyder 1991).

All collected gray birch specimens are stored in the Louis-Marie Herbarium (QFA) of Université Laval. Nomenclature follows Farrar (1996) for trees and shrubs and Scoggan (1978–1979) for other plant species.

Results

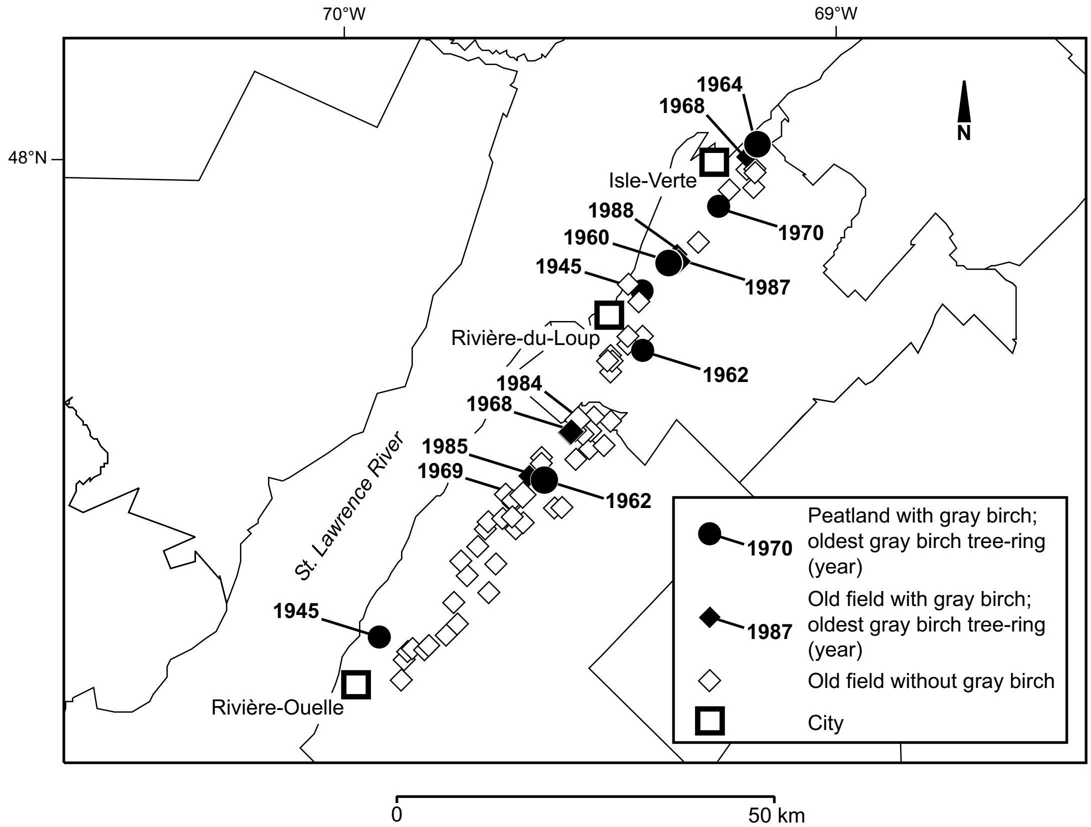
Herbarium specimens and botanical surveys

A total of 785 herbarium specimens (including those collected in this study) were carefully examined. Data from 259 selected specimens were used to reconstruct precisely the recent evolution of the range of distribution of gray birch in Quebec (Fig. 3). The oldest specimens were sampled in Nicolet (46°13′N, 72°37′W) and Montréal (45°30′N, 73°36′W) regions in 1864 and 1874, respectively. The oldest herbarium specimen from the Quebec City area was sampled in 1905. Few gray birches (16) were sampled before 1930. However, at the beginning of the century, the species was certainly present all along the St. Lawrence River between Montréal and Quebec City, and also in the Eastern Townships (near the U.S. border) and the Laurentides (north of Montréal) regions.

Several botanical surveys were conducted in southern Quebec during the 1930s and 1940s. Herbarium specimens collected during these decades indicate that the gray birch range roughly corresponded to the area inundated by the Champlain Sea 11 000 years ago (Dyke and Prest 1987). This correspondence has also been noted for the same species in Ontario (Catling and Spicer 1988). Not much change occurred in the spatial distribution of gray birch in Quebec between 1950 and 1970, but some range extensions were noted south and east of Québec City. However, it is important to note that the reconstruction of the distribution range of gray birch populations before 1970 might be strongly influenced by the lack of collections. According to herbarium specimen data, the northeastward extension of the species range (from Québec City to Isle-Verte) occurred during the last three decades of the 20th century.

Major botanical surveys were conducted in the Bas-Saint-Laurent region during the 20th century (Table 3). For example, in the Rivière-du-Loup county and Témiscouata county (near New Brunswick), the vegetation of more than 120 sites sampled in 1964 was carefully described by Lemieux (1964); no gray birch specimen was found in this study. Gauthier (1967) sampled the vegetation of five ombrotrophic peatlands between Rivière-Ouelle and Matane in 1965; gray birch was found only in the Rivière-Ouelle bog. Other phytosociological studies were conducted in the Rivière-du-Loup county between 1965 and 1967 (Blouin and Grandtner 1971); once again, no gray birch specimen was reported. Since gray birch is an easily detectable tree species, it seems unlikely that this species was common in the Bas-Saint-Laurent region before 1970.

Fig. 2. Sampling sites located between Rivière-Ouelle and Isle-Verte, eastern Quebec. (●) Mined peatland with gray birch; (◆) old field with gray birch; (◇) old field without gray birch; (□) city. For each site with gray birch, the oldest gray birch tree ring is indicated. Subdivisions are municipal regional counties.



Peatlands

Gray birch populations were found within each mined peatland located between Rivière-Ouelle and Isle-Verte (Figs. 1 and 2, Table 1). All gray birches established after the beginning of peat mining activities (especially during the 1960s), except in the Leparc peatland where six individuals established between 1945 and 1956. However, these individuals were located along a very old drainage ditch, probably dug in the mid-1940s. No gray birch was found in mined bogs east of Isle-Verte.

Old fields

We found gray birch individuals in only 7 of the 63 old fields visited (Fig. 2, Table 2). These sites were never located very far from mined peatlands (Saint-Alexandre, Cacouna, Isle-Verte). Surprisingly, no gray birch was found in old fields located near the Rivière-Ouelle peatland, although gray birch is common in disturbed parts of the bog since at least 1945. The oldest gray birch individuals from old fields were always younger than those growing in nearby peatlands.

Discussion

Gray birch has been present in the Bas-Saint-Laurent region since at least 1945 (Rivière-Ouelle and Leparc peatlands). However, herbarium specimens and botanical surveys conducted in the region during the 1960s indicate that gray birch individuals were scarce before 1970. The introduction of gray birch in the Bas-Saint-Laurent region seems to be associated with the beginning (Saint-Alexandre) or the abandonment (Rivière-du-Loup, Cacouna, Coteau-du-Tuff, Isle-Verte) of peat mining activities. Several peatlands were progressively abandoned at the end of the 1960s and during the 1970s because they were too small to be economically harvested with new peat mining techniques (tractor-drawn vacuum machines). An abandoned peat deposit is dry, highly susceptible to erosion, acid (pH 3–5), nutrient-poor, and devoid of a seed bank. Few plants are able to grow on this kind of soil (Lavoie and Rochefort 1996). In this context, low competition and harsh environmental conditions seem to favor opportunistic species like gray birch. For example, in the Cacouna bog, gray birch was one of the rare species to invade rapidly (2 or 3 years) bare peat surfaces after their abandonment (Lavoie and Rochefort 1996). In the Farnham bog (southern Quebec), gray birch massively invaded bare peat surfaces after the abandonment of mining activites in 1929, although the species was probably not present inside the peatland before the disturbance (Lavoie et al. 1995).

Gray birch probably invaded the Bas-Saint-Laurent region from the southwestern part of the province of Quebec, along the St. Lawrence River. There are some populations in New Brunswick and Maine, near the Quebec border (H. Hinds and C. Campbell, personal communications), but it seems unlikely that gray birches of the Bas-Saint-Laurent region originated from these populations. Lavoie (1984) found only one gray birch specimen in the entire Témiscouata county (located between the Rivière-du-Loup county and New

Table 2. Old fields sampled in the Bas-Saint-Laurent region, Quebec.

Old-field No.	Latitude (N)	Longitude (W)	Altitude (m)	Area (ha)	Perimeter (km)	Distance from Rivière-Ouelle (km)	Vegetation (main tree or shrub species)	Sampling effort (h)	Oldest tree-ring sampled (year)	No. of *Betula populifolia* sampled	Oldest *Betula populifolia* tree ring (year)
5	47°25′	69°55′	200	5.3	1.3	3	*Picea glauca*	0.5	1945	—	—
10	47°27′	69°55′	20	3.2	0.8	4	*Alnus incana* ssp. *rugosa*, *Cornus stolonifera*	1.0	1980	—	—
12	47°27′	69°54′	20	7.5	2.1	5	*Cornus stolonifera*, *Picea glauca*	0.5	1945	—	—
15	47°27′	69°54′	20	14.6	2.6	6	*Alnus incana* ssp. *rugosa*, *Cornus stolonifera*	1.0	1946	—	—
19	47°27′	69°53′	90	3.0	0.8	7	*Betula papyrifera*	1.0	1975	—	—
20	47°27′	69°52′	80	2.1	0.6	7	*Alnus incana* ssp. *rugosa*, *Betula papyrifera*, *Populus tremuloides*	1.0	1980	—	—
25	47°28′	69°52′	55	6.7	0.6	8	*Rubus idaeus*	0.5	1995	—	—
30	47°28′	69°51′	75	12.6	1.7	10	*Populus tremuloides*	1.0	1982	—	—
31	47°28′	69°50′	70	5.2	1.5	10	*Populus tremuloides*	1.0	1958	—	—
38	47°29′	69°49′	80	2.9	0.8	12	*Populus balsamifera*	0.5	1972	—	—
46	47°31′	69°50′	30	5.5	1.4	14	*Picea glauca*	1.0	1975	—	—
52	47°31′	69°46′	130	5.3	1.1	18	*Abies balsamea*, *Betula papyrifera*	1.0	1967	—	—
54	47°32′	69°48′	50	16.1	3.5	17	*Betula papyrifera*, *Populus tremuloides*	1.0	1963	—	—
59	47°34′	69°49′	20	3.3	0.8	18	*Alnus incana* ssp. *rugosa*	0.5	1938	—	—
68	47°33′	69°45′	110	8.7	1.7	21	*Alnus incana* ssp. *rugosa*, *Betula papyrifera*	1.5	1958	—	—
73	47°34′	69°47′	80	1.8	0.6	21	*Alnus incana* ssp. *rugosa*	1.0	1958	—	—
78	47°36′	69°46′	95	4.4	1.0	23	*Picea glauca*	1.0	1946	—	—
80	47°36′	69°46′	95	7.2	1.9	24	*Betula papyrifera*	0.5	1993	—	—
88	47°36′	69°45′	110	5.6	1.2	26	*Populus balsamifera*, *Populus tremuloides*	1.0	1970	—	—
89	47°36′	69°43′	120	8.2	1.7	26	*Populus tremuloides*	0.5	1988	—	—
95	47°37′	69°43′	105	23.3	4.0	27	*Abies balsamea*, *Picea glauca*	1.5	1943	—	—
96	47°37′	69°44′	100	1.8	0.5	27	*Rubus idaeus*	0.5	1993	—	—
97	47°36′	69°42′	135	8.3	1.4	27	*Abies balsamea*, *Betula papyrifera*	1.5	1978	—	—
99	47°38′	69°44′	135	19.6	3.0	28	*Alnus incana* ssp. *rugosa*, *Cornus stolonifera*	1.0	1975	—	—
102	47°38′	69°43′	120	1.5	0.5	28	*Abies balsamea*, *Picea glauca*	0.5	1923	—	—
103	47°38′	69°44′	110	3.7	0.9	28	*Alnus incana* ssp. *rugosa*, *Cornus stolonifera*	0.5	1973	—	—
108	47°38′	69°42′	120	5.2	1.0	30	*Abies balsamea*, *Betula papyrifera*	1.5	1969	3	1969
111	47°37′	69°38′	155	13.1	3.2	31	*Betula papyrifera*	1.0	1936	—	—
113	47°39′	69°42′	125	5.3	1.1	32	*Picea glauca*, *Populus tremuloides*	1.5	1962	8	1985
115	47°37′	69°39′	160	3.0	0.8	32	*Populus tremuloides*	1.0	1977	—	—
118	47°40′	69°41′	120	4.8	1.2	34	*Alnus incana* ssp. *rugosa*, *Picea glauca*	1.0	1929	—	—
122	47°41′	69°41′	120	5.0	1.0	35	*Picea glauca*, *Populus tremuloides*	1.0	1942	—	—

Table 2. (*concluded*).

Old-field No.	Latitude (N)	Longitude (W)	Altitude (m)	Area (ha)	Perimeter (km)	Distance from Rivière-Ouelle (km)	Vegetation (main tree or shrub species)	Sampling effort (h)	Oldest tree-ring sampled (year)	No. of *Betula populifolia* sampled	Oldest *Betula populifolia* tree ring (year)
125	47°41′	69°37′	140	13.3	2.6	38	*Betula papyrifera*, *Populus tremuloides*	1.0	1954	—	—
127	47°41′	69°37′	140	19.4	3.4	38	*Populus tremuloides*	1.5	1968	—	—
132	47°41′	69°36′	140	11.2	1.9	39	*Populus tremuloides*	1.0	1964	—	—
136	47°43′	69°37′	110	4.1	1.3	40	*Populus tremuloides*	2.0	1968	10	1968
138	47°42′	69°37′	115	40.1	3.8	40	*Picea glauca*, *Populus tremuloides*	1.0	1969	—	—
140	47°42′	69°36′	130	17.0	1.8	41	*Populus tremuloides*	0.5	1977	—	—
145	47°43′	69°37′	110	7.8	1.2	41	*Betula populifolia*	1.0	1984	5	1984
147	47°42′	69°36′	125	14.3	2.4	41	*Populus tremuloides*	1.0	1981	—	—
150	47°41′	69°34′	140	11.2	2.3	41	*Populus tremuloides*	1.0	1984	—	—
153	47°43′	69°35′	120	1.6	0.5	43	*Betula papyrifera*, *Populus balsamifera*	0.5	1987	—	—
156	47°43′	69°33′	125	6.6	2.3	44	*Picea glauca*	0.5	1951	—	—
186	47°47′	69°33′	110	4.2	0.9	50	*Rubus idaeus*	0.5	1993	—	—
188	47°47′	69°34′	135	6.6	1.1	50	*Picea glauca*	1.0	1979	—	—
190	47°47′	69°33′	130	5.8	2.1	51	*Picea glauca*	1.5	1950	—	—
195	47°48′	69°33′	140	2.4	0.7	51	*Picea glauca*	1.0	1949	—	—
201	47°48′	69°32′	105	6.4	1.4	53	*Picea glauca*	1.0	1974	—	—
203	47°49′	69°32′	115	31.7	2.6	54	*Picea glauca*, *Populus tremuloides*	1.5	1980	—	—
206	47°49′	69°30′	95	20.0	1.9	55	*Populus tremuloides*	1.5	1979	—	—
223	47°52′	69°31′	75	3.1	0.8	59	*Betula papyrifera*, *Populus balsamifera*, *Populus tremuloides*	1.0	1929	—	—
230	47°53′	69°32′	15	9.6	1.8	60	*Alnus incana* ssp. *rugosa*, *Populus tremuloides*	1.5	1968	—	—
232	47°54′	69°26′	85	7.9	1.4	66	*Alnus incana* ssp. *rugosa*, *Cornus stolonifera*	1.5	1976	1	1987
235	47°55′	69°26′	75	4.4	1.2	67	*Betula papyrifera*, *Populus tremuloides*	1.5	1952	1	1988
238	47°56′	69°24′	85	2.6	2.1	70	*Populus tremuloides*	1.0	1962	—	—
253	47°59′	69°21′	60	8.4	1.8	76	*Populus tremuloides*	1.0	1939	—	—
258	48°00′	69°19′	55	3.5	1.0	80	*Betula papyrifera*, *Populus tremuloides*	1.0	1980	—	—
266	48°00′	69°19′	40	6.3	1.2	81	*Alnus incana* ssp. *rugosa*, *Betula papyrifera*	0.5	1980	—	—
267	48°01′	69°19′	25	7.2	2.1	80	*Alnus incana* ssp. *rugosa*	1.0	1973	—	—
268	48°01′	69°19′	35	6.7	2.0	81	*Betula papyrifera*, *Picea glauca*	0.5	1978	—	—
271	48°01′	69°19′	35	6.5	1.2	82	*Alnus incana* ssp. *rugosa*, *Populus balsamifera*, *Populus tremuloides*	1.0	1967	—	—
273	48°02′	69°19′	30	4.6	1.4	82	*Alnus incana* ssp. *rugosa*, *Populus tremuloides*	1.5	1968	2	1968
278	48°02′	69°18′	35	10.9	1.6	84	*Populus tremuloides*	1.5	1992	—	—

Fig. 3. Gray birch herbarium specimens (●) sampled in Quebec before 1930, 1950, 1970, and 1999, respectively. Shaded area is the region sampled in this study (Bas-Saint-Laurent). Subdivisions are municipal regional counties.

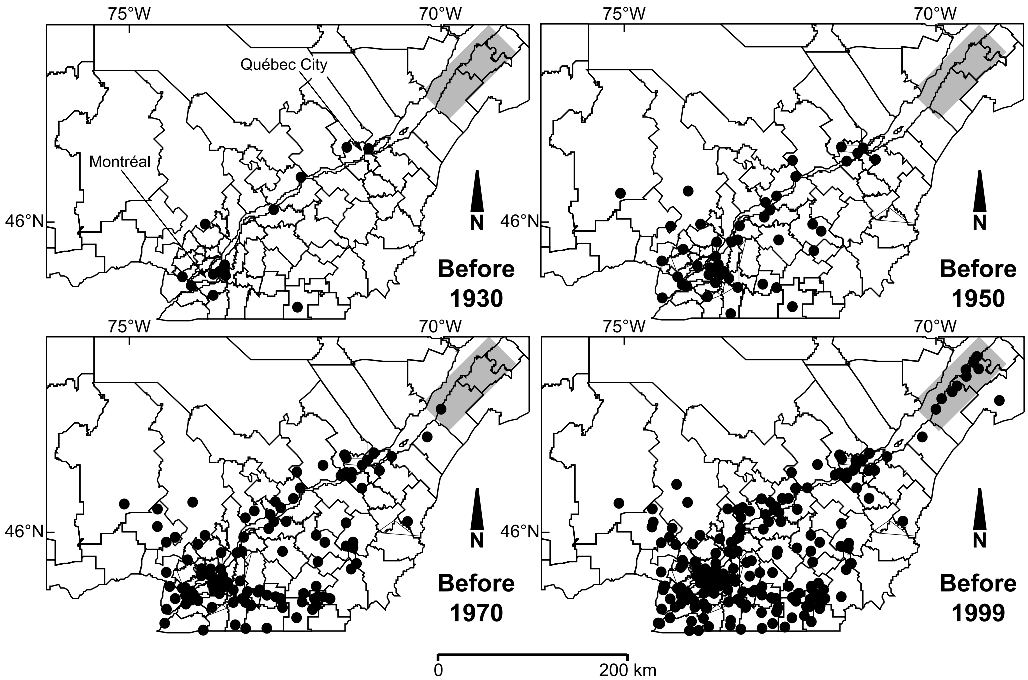


Table 3. Botanical surveys conducted in the Bas-Saint-Laurent region during the 20th century.

Reference	Area covered	Notes about *Betula populifolia*
Marie-Victorin (1916)	Bas-Saint-Laurent and Témiscouata; Rivière-du-Loup and Cacouna peatlands were visited	No mention
Dechamplain and Lepage (1941)	Bas-Saint-Laurent	No mention
Dansereau and Raymond (1948)	Bas-Saint-Laurent and Gaspésie; Saint-Fabien peatland was visited	No mention
Scoggan (1950)	Bic region (Saint-Fabien) and Gaspésie	No mention
Lepage (1963)	Bas-Saint-Laurent	No mention
Lemieux (1964)	Bas-Saint-Laurent, Témiscouata and Gaspésie	No mention
Gauthier (1967)	Bas-Saint-Laurent (peatlands)	Some individuals in the Rivière-Ouelle peatland; no mention in the Rivière-du-Loup, Saint-Arsène, Pointe-aux-Pères and Saint-Ulric bogs
Blouin and Grandtner (1971)	Rivière-du-Loup (county)	No mention
Zoladecki (1984)	Cap Enragé, Bic provincial park (Saint-Fabien)	No mention
Fortin and Belzile (1996)	Bic provincial park (Saint-Fabien)	No mention
Lavoie and Rochefort (1996)	Cacouna peatland	Gray birch populations inside mined sections abandoned in 1975

Brunswick and Maine) during a botanical survey conducted in 1975 and 1976. At that time, gray birch populations were already well established in the Bas-Saint-Laurent region. However, the expansion of gray birch range east of Rivière-Ouelle was not a “step-by-step” movement resulting from local, short-distance seed dispersal. Some bogs (e.g., Leparc) were colonized by gray birch long before other bogs or old fields located nearer Rivière-Ouelle. It seems that long-distance seed dispersal favored the establishment of gray birch in the study area. For example, wind dispersal of seeds on the snow cover is probably a very efficient dispersal mechanism for gray birch, especially in an agricultural plain almost devoid of obstacles (Matlack 1989). No gray birch individual was detected in mined peatlands east of Isle-Verte. However, numerous *Betula pendula* individuals were found in abandoned sections of the Pointe-aux-Pères bog, probably accidently introduced from a nearby golf course. *Betula pendula* and *B. populifolia* have similar ecological requirements; both species are reported to invade mined peatlands (Catling and Spicer 1988). This suggests that mined bogs located east of Isle-Verte, although suitable for the growth of gray birch, are still too far from main seed sources to be colonized by this tree species.

Whatever the migration route or the dispersal vector, it is noteworthy that all mined peatlands located between Rivière-Ouelle and Isle-Verte were colonized by gray birch

Table 4. Landscape structure of the Bas-Saint-Laurent agricultural plain between Rivière-Ouelle and Isle-Verte, Quebec.

Landscape object	No. of patches	Total area covered by all patches (ha)	Mean area covered by a single patch (ha)
Woodlot	506	13 226	26
Old field	356	3 857	11
Peatland	20	6 963	348
Agricultural field	—	51 306	—

Note: Data are from Ministère des Ressources naturelles du Québec (1 : 20 000 maps) for woodlots and agricultural fields, from Ministère de l'Agriculture et de l'Alimentation du Québec (C. Morneau, unpublished) for old fields, and from Buteau (1989) for peatlands.

but that only 11% of old fields surveyed contained at least one gray birch individual, although this species is usually found in old fields. Old fields and woodlots (other potential establishment sites for gray birch) are very numerous (more than 850 patches) in the St. Lawrence agricultural plain between Rivière-Ouelle and Isle-Verte (Table 4). However, most patches are very small (mean area 11–26 ha). On the other hand, peatlands are not very numerous (20), but most of them are large (mean area 348 ha) and disturbed by mining activities. This suggests that the spread of an early successional tree species such as gray birch in an agricultural landscape would be facilitated more by the presence of few large patches favorable to the growth of the species than by numerous small patches. This is consistent with ecological models showing that, in heterogeneous agricultural landscapes, larger patches have greater exchange of dispersing organisms (Gustafson and Gardner 1996; van Dorp et al. 1997). Furthermore, for wind-dispersed tree species, Greene and Johnson (1995) have calculated that in fragmented landscapes with a mean woodlot size of 10 ha, colonization of a woodlot by a tree individual (coming from another woodlot as a seed) is a rare event: about every 50 years for common tree species and every 1000 years for rare species. Of course, gray birch is not a woodlot species; most individuals grow in open environments exposed to stronger winds (higher dispersal potential). However, the study of Greene and Johnson (1995) suggest that dispersal of tree species in fragmented landscapes is problematic.

The recent expansion of gray birch populations in the Bas-Saint-Laurent region could be a major concern for peat mining companies. Many vacuum-mined peatlands should be restored in the next decades. Massive invasions of gray birch in abandoned peatlands, as observed in Cacouna and Rivière-Ouelle bogs, may have a detrimental effect on the water table (Heathwaite 1995) and impede successful restoration attempts of a living *Sphagnum* layer. Thus, further studies on the ecological impact of gray birch invasions in abandoned peatlands are required.

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