



The potential effects of sexual reproduction and seedling recruitment on the maintenance of red maple (*Acer rubrum* L.) populations at the northern limit of the species range

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Abstract

Aim For this study, we wanted to evaluate the reproductive potential of northern red maple (*Acer rubrum* L.) populations to identify the possible factors responsible for the scattered distribution pattern of these northern populations.

Location Samara production and long-term establishment of seedlings were observed along a north–south transect crossing the transition zone between continuous and discontinuous stands of red maple (47°80′–49°27′ N) in western Quebec.

Methods Eleven populations of red maple were selected along a latitudinal gradient extending to the northern limit of the species. Seed traps were placed in each stand and distributed under the canopy of mature red maple trees. Seed abundance was tracked for 6 years from 1988 to 1993. Phenological observations were made in 1992 and 1993 at Roquemaure (Roq), a site located at the centre of the latitudinal gradient. Red maple trees were randomly selected within the population; counts of flower buds, pollinated buds and samaras produced were made in 1992–93. Samaras were collected from each branch immediately before dispersal and counted. During the summer of 1987, seedlings (< 1 cm d.b.h.) were collected and aged at each site in twenty 1 m² quadrants and age of the seedlings (< 1 cm d.b.h.) was determined by counting the annual scars left by terminal buds.

Results Samaras were produced even at the northern limit but large yearly variations were observed. Over the 6-year period we counted 3 years (1989, 1990, 1993) when samara production was high, and 3 years (1988, 1991, 1992) when production was low. Phenological observations indicate that the occurrence of spring frosts at the time of flower bud flushing could contribute to decreasing the abundance of seeds. The age structure of southern localities had a relatively constant production of seedlings, as indicated by an inverse J-shaped distribution. However, the five northernmost localities show sporadic recruitment.

Main conclusions Populations at the northern limit are maintained essentially through vegetative reproduction and infrequent sexual recruitment. Our results indicate that regeneration within established stands through sexual recruitment is possible in all of the populations we studied. This potential becomes very low at more northerly sites and sexual reproduction alone would be unlikely to ensure successful stand regeneration. Without major disturbances in those stands, shade tolerant conifer species such as balsam fir (*Abies balsamea*) or black spruce (*Picea mariana*) would readily dominate the canopy. The discontinuous distribution of red maple stands at the northern limit is the consequence of either a random colonization of few sites during a better climatic period or remnants of a much larger distribution that has been constrained because of climatic deterioration.

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Keywords

Northern limit, red maple, sexual reproduction, phenology, age structure, Quebec, Canada.

INTRODUCTION

Several factors have been suggested as the causes for the northern limits of tree species. These include climatic conditions, disturbance regimes, soil and nutrient status, competition or a combination of these factors; of these, climate, especially winter minimum temperature or growing season warmth are the most frequently cited (Sakai & Weiser, 1973; Oohata & Sakai, 1983; Woodward, 1987). The responses of trees to climatic conditions vary both among species and different stages of the life cycle (Woodward, 1987). For example, the contraction of the range of some species, such as *Pinus sylvestris* in northern Sweden or *Larix laricina* in northern Canada, during the cooler period of the 1960 and 1970s, is attributed to severe mortality of mature individuals (Payette & Lajeunesse, 1980; Agren *et al.*, 1983), while for *Betula pubescens* it seems more related to a lower probability of seedling establishment (Kullman, 1979, 1983).

Range limits may be associated with a specific limiting phase of the life cycle. A classic example is *Tilia cordata*, where the temperature sensitivity of pollen tube growth is responsible for the northern limit of regeneration of the species (Pigott & Huntley, 1978, 1980, 1981). However, no one particular stage of the life cycle can be identified as especially critical in controlling distribution of a species, although the progressive reduction of survival probabilities or production at a number of different stages is the most likely cause.

Red maple (*Acer rubrum* L.) is one of the most widely distributed tree species in eastern North America, with a range extending from Florida to Northern Quebec (Burns & Honkala, 1990). In the northern part of the range, the distribution is discontinuous. These populations are largely maintained through sprouting and are restricted to south facing slopes (James & Courtin, 1985; Lalonde, 1991). In the present study, we were interested in evaluating the reproductive potential of northern red maple populations to identify factors that would be responsible for the scattered distribution pattern of these northern populations. We hypothesized that the climate could adversely affect the species at a critical stage of reproductive development. Samara production and long-term establishment of the seedlings was assessed along a north-south transect extending across the transition between continuous and discontinuous stands of red maple.

METHODS

Site description

Eleven populations of red maple were selected along a latitudinal gradient extending to the species northern limit

(Fig. 1). The transect of sites extends across three bioclimatic regions (Thibault & Hotte, 1985), characterized by late successional stands of balsam fir and yellow birch in the south (Rem, Rol), balsam fir and white birch in the centre (Kek, Bou, Sab, Roq, Dup and Cal) and black spruce in the north (Fen, Pla, Col) (see Fig. 1 for complete site names and their locations). An ecological survey across these bioclimatic regions by the Quebec Ministry of Natural Resources shows the decreasing frequency of red maple from south to north. Red maple was present in 147 out of 346 samples (46%) in the south portion of the surveyed area, present in only 147 of 1282 samples (11%) in the central region and in only one sample (<1%) out of 1282 in the north [Ministère des Ressources naturelles du Québec (MRNQ), 1998, 1999a, b].

The entire area is located in the clay belt of northern Ontario and Quebec, a large physiographic region created by lacustrine deposits from proglacial lakes Barlow and Ojibway (Veillette, 1994). Red maple stands in the region are generally located on till deposits or rock outcrops (Lalonde, 1991). Although the soil characteristics where red maple stands are found are similar in the three bioclimatic regions (Lalonde, 1991), the availability of favourable surficial deposits changes from south to north (Table 1; MRNQ, 1998, 1999a, b). Clay and organic deposits are more prevalent in the north whereas rock and till deposits are more abundant in the south. The landscape topography is generally flat and uniform with low rolling hills, with elevations between 300 and 400 m. Altitudinal drop variations decrease from the south to the north (Table 1).

All the sampled stands were located on relatively well drained till deposits. At each site forest composition (Table 2) was assessed by establishing a total of 20 points based on the point-centred-quarter method (Mueller-Dombois & Ellenberg, 1974). The importance of values observed for each tree species were based on the average of the relative frequency, the relative density and the relative basal area for all of the species of trees in each different stand. The age of the red maple trees at each site was determined using an increment borer from a random sample of forty trees (with d.b.h. > 5 cm).

Based on 1951–80 climate normal from Meteorological Service of Canada (MSC) weather stations, annual temperature and precipitation decrease from the south of the area studied to north. Average annual temperature was approximately +1.6 °C at Remigny (near most southern sites) compared with 0.6 °C at La Sarre in the north. The mean of the temperatures of the coldest month measured at these same stations was between –17.4 and –18.5 °C and the July mean temperature was between 17.6 and 16.5 °C.

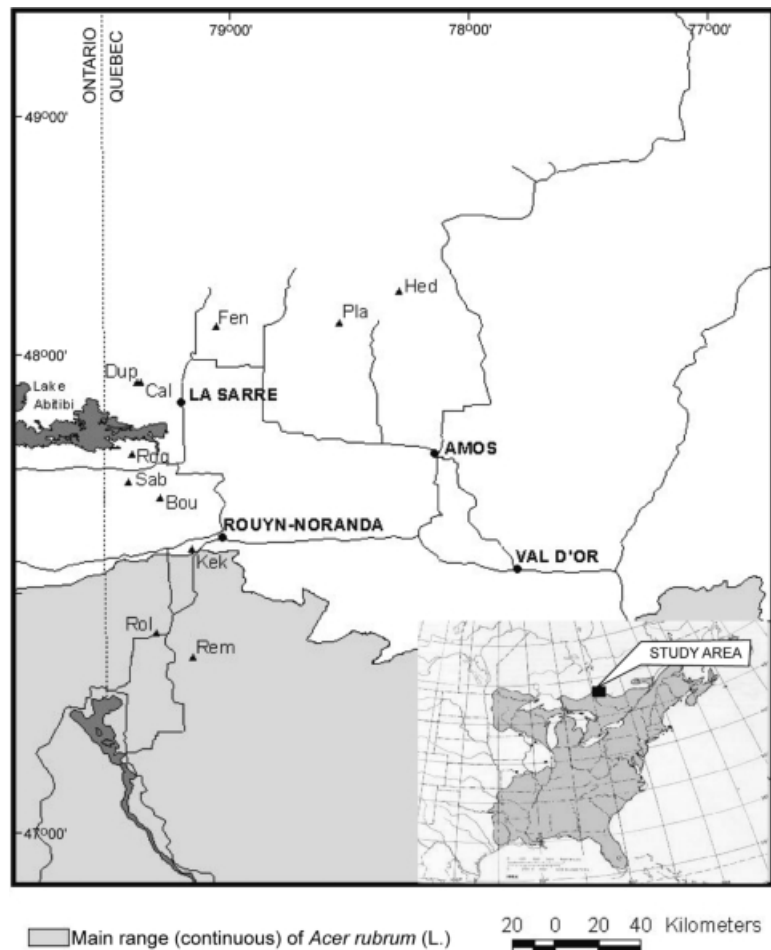


Figure 1 Location of the eleven red maple populations sampled in the Abitibi-Témiscamingue region in north-western Quebec. The selected sites are Remigny (Rem), Rollet (Rol), Collines Kekeko (Kek), Mont Bourniot (Bou), Mont Monsabrais (Sab), Roquemaure (Roq), Dupuy-La Reine (Dup), Calamite River (Cal), Mont Plamondon (Pla), Collines Hedge (Hed), Mont Fenouillet (Fen).

Mean annual precipitation was 937 mm at Remigny and 833 mm at La Sarre.

Seed traps

Twenty seed traps were placed and distributed under the canopy of the mature red maple trees in each stand. Traps were made of a grain bag supported by a metal ring located 60 cm above the ground with an approximate area of 0.25 m². Seed abundance was observed for 6 years, from

1988 to 1993. Annual seed production was correlated with climatic variables from nearby meteorological stations at Remigny (Rol, Rem), Kinojevis (Kek, Bou), Duparquet (Sab, Roq, Dup, Cal) and Joutel (Fen, Pla, Col).

Phenology

Phenological observations were made from 1992 to 1993 at Roquemaure (Roq), a site located at the centre of the latitudinal gradient. Thirteen trees were selected at random from within the population before flower bud break in 1992. Twenty-six branches were selected at random from these trees; counts of flower buds, pollinated buds and samaras produced were made in 1992–93. Observations were taken at regular intervals from May 11 until the end of June with samara dispersal. Samaras were collected and counted from each branch immediately before dispersal. A weather station was established at Roq (within 500 m of the red maple site) and the weather was monitored from early May to early October. The temperature and relative humidity sensors, Campbell Scientific 207 probes, were placed within a Stevenson screen 1.5 m above the surface. Rainfall was recorded with a tipping bucket. Local daily measures of

Table 1 Landscape characteristics of the bioclimatic regions in the south-north transect

	South	Central	North
Altitude (m)	299	308	294
Altitudinal drop (m)	35	28	19
Till and sand (%)	21	15	5
Clay (%)	34	52	73
Organic (%)	8	16	16
Rock (%)	23	10	3
Water (%)	14	6	3

Table 2 Site characteristics and trees importance values for the sampled stands. The importance value is defined as the average of the relative frequency, the relative density and the relative basal area

	Rem	Rol	Kek	Bou	Sab	Roq	Dup	Cal	Fen	Pla	Hed
<i>Abies balsamea</i>	24.49		29.62	9.4		1.73				1.67	2.78
<i>Acer rubrum</i>	40.76	51.07	50.37	34.14	28.97	3.46	5.24	18.94	9.25	3.67	2.78
<i>Acer saccharum</i>	12.36	1.43									
<i>Betula alleghaniensis</i>	5.85										
<i>Betula papyrifera</i>	2.73	40.95	10.81	24.76	33.1	7.53	22.57	20.19	42.5	82.81	46.7
<i>Picea glauca</i>				5.38	4.33		10.81			4.98	
<i>Picea mariana</i>				2.59	4.01	3.81	2.02		10.73		11.21
<i>Pinus banksiana</i>					28.01	81.74	4.11		33.62		22.84
<i>Populus tremuloides</i>		5.12	4.23	14.68	1.58	1.73	47.56	49.36			8.22
<i>Prunus pensylvanica</i>		1.43	4.98	5.82			4.31	6.09	3.91	6.87	2.42
Latitude	47°80'	47°83'	48°18'	48°38'	48°47'	48°58'	48°88'	48°89'	49°12'	49°13'	49°27'
Altitude (m)	330	335	375	412	350	340	310	320	390	400	412
Density (nb ha ⁻¹)	674	967	1296	1935	819	600	1558	1012	423	389	412
Basal area (m ² ha ⁻¹)	18.05	11.2	14.81	15.86	20.42	5.5	30.58	13.81	2.08	19.26	9.21
Mean stand age (years)	61	44	44	38	53	26	36	37	21	31	28

temperature and precipitation were recorded hourly using a Campbell Scientific CR10 data logger.

Seedlings

During the summer of 1987, seedlings (< 1 cm d.b.h.) were collected and aged at each site in twenty 1 m² quadrants located at the points used for forest composition sampling (see above). Age of the seedlings (< 1 cm d.b.h.) was determined by counting the annual scars left by terminal buds.

Data analysis

Seed production was correlated using the Pearson correlation coefficient with weather variables. Regressions were also used to evaluate possible effects of latitude, altitude, stand age, and basal area on seed and seedling abundance observed from quadrat data and forest sampling.

RESULTS

Seed production

Seed production varied greatly from year to year (Fig. 2). Over the 6-year period we observed 3 years (1989, 1990, 1993) when samara production was high, and 3 years (1988, 1991, 1992) when production was low. This pattern was common to all of the sites, although some were out of phase, such as Hed in 1991, and Rem and Roq in 1992. Seeds were produced at the southern sites for all 6 years of the study (Rem, Rol, Kek, Bou and Roq), in 5 years out of 6 at Fen, 4 years out of 6 at Sab, Dup, Cal and Hed, but in only a single year at Pla (Fig. 2).

Yearly variation in samara production had a negative correlation with the number of frosts occurring in May ($P < 0.01$) and a small positive correlation with precipitation (Table 3). Years of poor production were characterized

by either abundant or severe frosts in May. For example, at Duparquet (Dup) in 1991, a temperature of -7.5 °C was recorded on May 18 and at Kinojevis River the temperature dropped below 0 °C on 6 days during May. In contrast, the years of good samara production were characterized by either greater precipitation and little or no frost in May. In 1993 there was no frost in May.

Total seed production over the 6-year period correlated with latitude and stand age. However, while latitude had a significant correlation with seed production when the age of the stand is included in a regression model ($P < 0.05$), the age of the stand was not significant if latitude was included in the model ($P > 0.05$). These correlations were only valid for individual years as yearly variations are great. Neither altitude nor basal area in red maple had a significant correlation with seed production.

Seedlings

Seedlings were observed in all of the stands (Fig. 3) but their abundance decreased as the latitude increased (Table 4). The age structure for the southern localities showed a relatively constant production of seedlings, as suggested by an inverse J-shaped distribution, whereas the five northernmost localities exhibited sporadic recruitment. A negative correlation between latitude and 'the ratio of number of seedlings to seeds produced' indicates that for a given quantity of seeds, germination and establishment decreases with latitude.

Phenological observations

From the thirteen trees that were originally selected at Roq, seven produced only male flowers and six only female flowers. Samara production was thus followed on a total of thirteen branches on the six female trees. In 1992, samara production represented only 1–2% of the flowering potential. Of the 31–1056 flower buds per branch counted

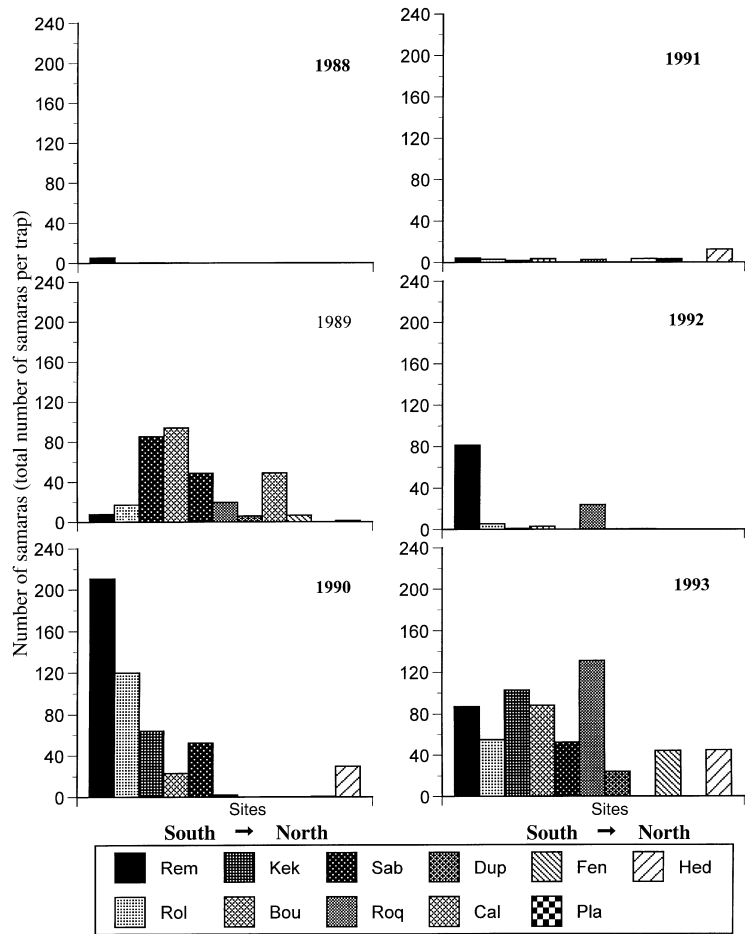


Figure 2 Number of seed (all traps combined) collected at each site from 1988 to 1993.

Table 3 Pearson correlation coefficient for the relationship between yearly samara production and key climatic factors at the Roquemaure site

Variable	Occurrence of frosts			Precipitation (mm)	
	May	June	May + June	May	June
Samara production	-0.5355**	-0.3485	-0.4313*	0.3010	0.3253

* $P < 0.05$; ** $P < 0.01$.

on 11 May, only 1–107 pollinated, of which 0–69 produced mature samaras (Table 5). Samara production was much higher in 1993, and between 10.6 and 84.1% of flower buds produced samaras.

DISCUSSION

Physiological constraints to sexual regeneration

This study clearly demonstrated the effect of latitude and climatic conditions, notably spring frosts, on seed production for northern red maple populations. Phenological observations suggest that severe spring frosts (below -6.0 °C) occurring during flower bud-break can significantly decrease seed abundance. At Roq in 1992, several frosts were recorded in May and there was a subsequent dramatic

decrease in the numbers of flower buds and pollinated buds. This suggests that the period available for pollination is critically related to the final number of samaras produced. But we were unable to establish a strict correlation between the northern limit of red maple and sexual reproduction, because red maple populations produce samaras even at the northern limit of the species range. Positive correlations between reproductive potential and high temperatures during the growing season have been reported for several species, but distribution limits are rarely explained by a single physiological constraint. Lack of a perfect match between sexual reproduction and the northern limit of red maple partially corroborates the conclusions of other studies on the northern limit of tree species. Red pine (Flannigan & Bergeron, 1998), Jack pine (Despots & Payette, 1992) and

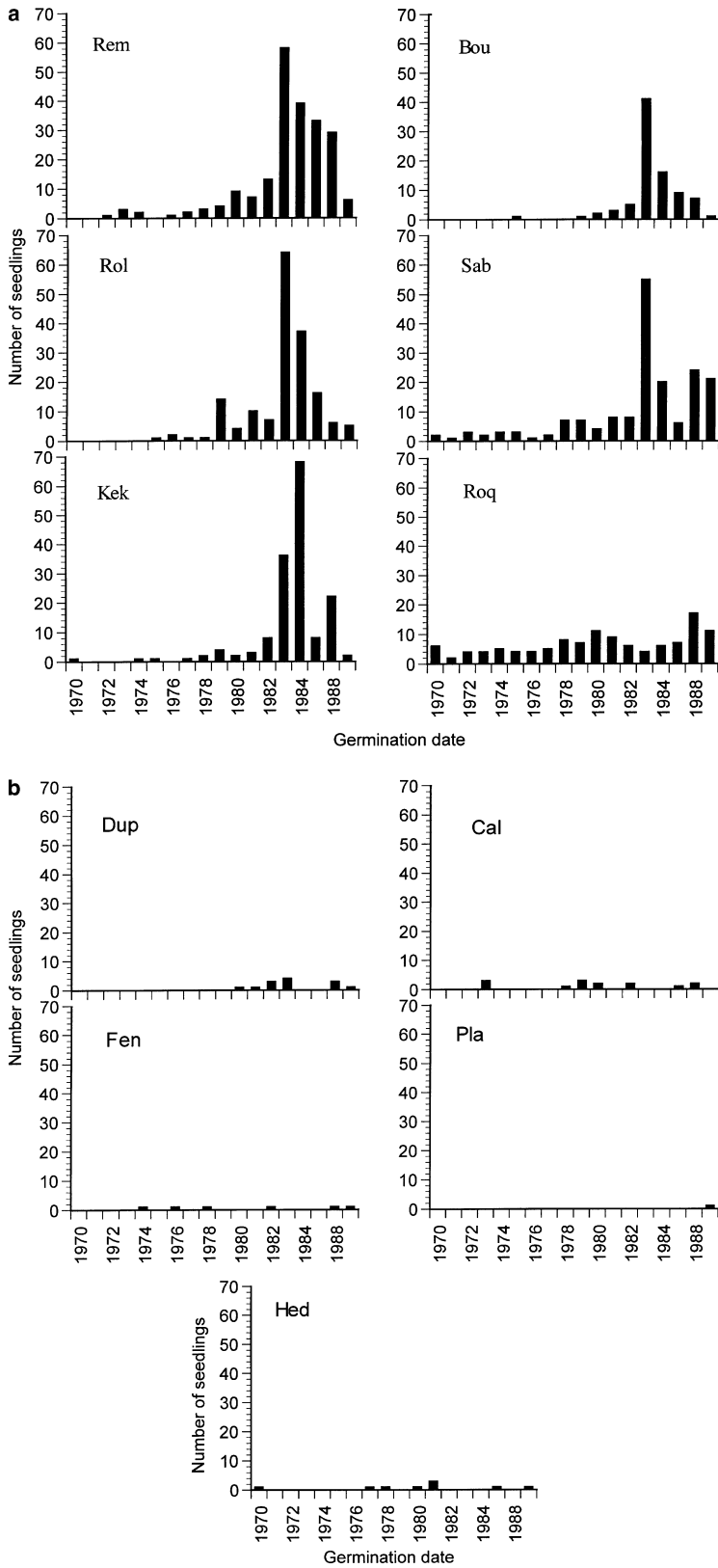


Figure 3 Age structures of red maple seedlings (< 1 cm d.b.h.) collected and aged at each site in twenty 1 m² quadrats located at the points used for the forest composition sampling. Age of seedlings (< 1 cm d.b.h.) was determined by counting the annual scars left by terminal buds. Red maple stands located: (a) in the southern part of the latitudinal gradient (Rem, Rol, Kek, Bou, Sab, Roq), (b) in the northern part of the latitudinal gradient (Dup, Cal, Fen, Pla, Hed).

Table 4 Person correlation coefficients for relationship between seed and seedling production and site factors for the period 1988–93 determined for thirteen sites on a north–south transect in Quebec

Variables	Latitude	Altitude	Mean age	Basal area
Seeds (1988)	−0.58	−0.26	0.67*	0.48
Seeds (1989)	−0.35	0.17	0.27	−0.09
Seeds (1990)	−0.81**	−0.27	0.81**	0.54
Seeds (1991)	0.21	0.38	−0.21	−0.01
Seeds (1992)	−0.55	−0.33	0.55	0.56
Seeds (1993)	−0.56	0.04	0.17	0.47
Seeds (all years)	−0.87***	−0.15	0.71*	0.57
Seedlings	−0.72**	−0.01	0.55	0.16
Ratio (seedlings/seeds)	−0.70*	0.00	0.50	0.09

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table 5 Phenological observations made at Roquemaure in 1992 and 1993

Year	Month	Date	Phenology	Number	Unfilled seeds	Filled seeds	Average weight of samaras (mg)	Germination (%)
1992	May	11	Bud active, still closed					
		13	Flower buds open	3735				
		25	Full development of female buds	327				
	June	15	Full development of samaras (still green)	371				
		21	Samaras collected at dispersal	252	203	49	10.5 (2.59)	67.5
1993	May	11	Bud active still closed					
		13	Reproductive buds open	6343				
		18	Female buds	6343				
		27	Full development of buds	6343				
	June	15	Full development of samaras (still green)					
		25	Samaras collected at dispersal	20,971	3508	16,788	12.97 (2.82)	61.8

Pitch pine (Meilleur *et al.*, 1997) all exhibit successful sexual reproduction at the limit of their range. In that respect, red maple clearly showed a progressive decrease in probability of sexual reproduction and seedling establishment as the latitude increases.

Effects on population dynamics

Our results indicate that regeneration within established stands through sexual recruitment is possible in all of the populations we studied. This potential becomes very low at more northerly sites and sexual reproduction alone would be unlikely to ensure successful stand regeneration. Without major disturbances in those stands, shade tolerant conifer species such as balsam fir (*A. balsamea*) or black spruce (*P. mariana*) would readily dominate the canopy. Although all the sampled red maple populations on this study were of post-fire origin (Lalonde, 1991), in the northernmost part of the latitude gradient, red maple stands (Dup, Cal, Fen, Pla, Hed) were characterized by an even-aged structure, while in the southern part (Rem, Rol, Kek, Bou, Sab, Roq) they proved to be of the uneven-aged type (Lalonde, 1991). Initial post-fire establishment was through stump sprouting and recruitment from seed was delayed until those trees were sufficiently mature to produce samaras. This suggests that in the northern sites (even-aged type), the stems are either killed

before reaching maturity or that low seed production does not allow for recruitment of new individuals between fires. In some cases, the harsh climate may limit the development of the main epicormic stem and the individuals have a shrubby stunted structure.

Low seed abundance and large interannual variations in seed production also limit the potential of northern populations to invade and colonize sites cleared by disturbances. Red maple has relatively large seeds with a short dispersal distance (Greene & Johnson, 1995), which when added to the low abundance of seeds will greatly diminish its capacity to invade other sites. Red maple seedlings are rarely observed in stands where mature trees are not already present (Bergeron *et al.*, 1983).

We therefore suggest that the maintenance of northern populations relies mainly on vegetative regeneration following a disturbance. Most mature red maples, especially in the central and northern populations, originated from stump sprouting following a fire (Lalonde, 1991; Babeux & Mauffette, 1994). Although Babeux & Mauffette (1994) have shown that stump sprouting is prolific even at the northern limit of the species, some stands may become locally extinct following a severe fire that kills the root system. This is particularly conceivable on the very shallow soils where red maple stands normally occur at these northern localities.

This is not to say that the northern limit of red maple is strictly controlled by a lack of sexual regeneration, e.g. in contrast with the northern limit of *T. cordata* in Europe for which a complete lack of sexual reproduction has been observed at its northern limit (Pigott & Huntley, 1978, 1980, 1981). However, the low level of sexual regeneration observed at the northern latitudes may limit the capacity of the species to maintain metapopulation dynamics at the landscape scale. Poor sexual regeneration limits the long-term maintenance of the species in local stands and reduces the possibility of colonizing any new sites available following a disturbance. In this context, a possible increase in fire severity and size in the transition zone between mixed and boreal forests (Heinselman, 1981; Gauthier et al., 2000) may contribute in limiting the northern extension of red maple populations. Greater fire severity and larger fires may lead to local extinction of populations and longer dispersal distances, both factors that will limit red maple distribution. In addition, the till deposits which constitute the most favourable habitat for red maple at these latitudes tend to decrease to the north (Table 1), which further limits the distribution of the species.

The discontinuous distribution of red maple stands at the northern limit is possibly the consequence of either a random colonization of few sites during better climatic periods or either remnants of a larger distribution that was subsequently constrained after climatic deterioration. Although specific data on red maple are not available, there is palaeoecological evidence that more meridional species such as *P. strobus* had larger distribution during a possibly warmer episode during the mid-Holocene (6000 yr BP) (Terasmae & Anderson, 1970; Jacobson & Dieffenbacher-Krall, 1995). Subsequent climatic deterioration associated with an increase in fire activity (Carcaillet et al., 2001) may have also lead to the present scattered distribution of remnant populations.

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REFERENCES

- Agren, J., Isaksson, L. & Zackrisson, O. (1983) Natural age and size of *Pinus sylvestris* and *Picea abies* on a mire in the inland part of Northern Sweden. *Holarctic Ecology*, **5**, 228–237.
- Babeux, P. & Mauffette, Y. (1994) The effects of early and late spring cuts on the sprouting success of red maple (*Acer rubrum* L.) in north-western Quebec. *Canadian Journal of Forest Research*, **24**, 785–791.
- Bergeron, Y., Bouchard, A., Gangloff, P. & Camiré, C. (1983) *La classification écologique des milieux forestiers d'une partie des cantons d'Hébertcourt et de Roquemaure*. Études Écologiques, No. 9, Université Laval St-Foy, 169 pp.
- Burns, R.N. & Honkala, B.H. (1990) *Silvics of North America*, Vols. 1 and 2. USDA Forest Service Agricultural Handbook, 654 pp.
- Carcaillet, C., Bergeron, Y., Richard, P.J.H., Fréchette, B., Gauthier, S. & Prairie, Y.T. (2001) Change of fire frequency in the eastern Canadian boreal forests during the Holocene: does vegetation or climate trigger the fire regime. *Journal of Ecology* (in press). **89**, 930–947.
- Despons, M. & Payette, S. (1992) Recent dynamics of jack pine at its northern distribution limit in northern Quebec. *Canadian Journal of Botany*, **70**, 1157–1167.
- Flannigan, M. & Bergeron, Y. (1998) Possible role of perturbations in shaping the northern distribution of *Pinus resinosa*. *Journal of Vegetation Science*, **9**, 477–482.
- Gauthier, S., De Grandpré, L. & Bergeron, Y. (2000) Differences in forest composition in two ecoregions of the boreal forest of Québec. *Journal of Vegetation Science*, **11**, 781–790.
- Greene, D.F. & Johnson, E.A. (1995) Long-distance wind dispersal of tree seeds. *Canadian Journal of Botany*, **73**, 1036–1045.
- Heinselman, M.L. (1981) Fire and succession in the conifer forests of the northern north America. *Forest succession, concepts and application, I* (eds D.C. West, H.H. Shugart and D.B. Botkin), pp. 374–406. Springer, New York, NY.
- Jacobson, J. & Dieffenbacher-Krall, A. (1995) White pine and climate change, insights from the past. *Journal of Forestry*, **93**, 39–42.
- James, G.I. & Courtin, G.M. (1985) Stand structure and growth form on the birch transition community in an industrially damaged ecosystem Sudbury, Ontario. *Canadian Journal of Forest Research*, **15**, 809–817.
- Kullman, L. (1979) Change and stability in the altitude of the birch tree line in the southern Swedis Scandes 1915–1975. *Acta Phytogeographica Suecica*, **65**, 121.
- Kullman, L. (1983) Past and present tree lines of different species in the Handolan Valley Central Sweden. *Tree line Ecology Proceedings of the Northern Quebec Tree-Line Conference* (eds P. Morissette and S. Payette), pp. 25–42. Centre d'études nordiques de l'Université Laval, Quebec Canada.
- Lalonde, D. (1991) *Distribution et dynamique des communautés d'Érable rouge à la limite nord de leur répartition en Abitibi, Québec*. MSc Thesis, Université du Québec à Montréal, Montréal, Canada.
- Meilleur, A., Brisson, J. & Bouchard, A. (1997) Ecological analysis of the northernmost population of pitch pine (*Pinus rigida*). *Canadian Journal of Forest Research*, **27**, 1342–1350.
- Ministère des Ressources naturelles du Québec (1998) *Rapport de classification écologique: sapinière à bouleau jaune de l'ouest*. Programme de connaissance des écosystèmes forestiers du Québec méridional. Gouvernement du Québec, Québec, Canada.
- Ministère des Ressources naturelles du Québec (1999a) *Rapport de classification écologique: sapinière à bouleau blanc de l'ouest*. Programme de connaissance des écosystèmes forestiers du Québec méridional. Gouvernement du Québec, Québec, Canada.

- Ministère des Ressources naturelles du Québec (1999b) *Rapport de classification écologique: Pessière à mousses de l'ouest*. Programme de connaissance des écosystèmes forestiers du Québec méridional. Gouvernement du Québec, Québec, Canada.
- Mueller-Dombois, D. & Ellenberg, H. (1974) *Aims and method of vegetation ecology*. Wiley, New York.
- Oohata, S. & Sakai, A. (1983) Freezing resistance and thermal indices with references to distribution of the genus *Pinus*. *Plant cold hardiness and freezing stress* (eds P.H. Li and A. Sakai), pp. 347–371. Academic Press, New York.
- Payette, S. & Lajeunesse, R. (1980) Les combes à neige de la rivière aux Feuilles (Nouveau-Québec): indicateurs paléoclimatiques holocènes. *Géographie Physique et Quaternaire*, **34**, 209–220.
- Pigott, C.D. & Huntley, J.P. (1978) Factors controlling the distribution of *Tillia cordata* the northern limits of its geographical range. I. Distribution in north-west England. *New Phytologist*, **81**, 429–441.
- Pigott, C.D. & Huntley, J.P. (1980) Factors controlling the distribution of *Tilia cordata* the northern limits of its geographical range. II. History in north-west England. *New Phytologist*, **84**, 145–164.
- Pigott, C.D. & Huntley, J.P. (1981) Factors controlling the distribution of *Tilia cordata* the northern limits of its geographical range. III. Nature and cause of seed sterility. *New Phytologist*, **87**, 817–839.
- Sakai, A. & Weiser, C.J. (1973) Freezing resistance of trees in North America in references to tree regions. *Ecology*, **54**, 118–126.
- Terasmae, J. & Anderson, T.W. (1970) Hypsithermal range extension of white pine (*Pinus strobus* L.) in Québec, Canada. *Canadian Journal of Earth Science*, **7**, 406–413.
- Thibault, M. & Hotte, D. (1985) *Les régions écologiques du Québec méridional (deuxième approximation)*. Service de la cartographie, Ministère de l'Énergie et des ressources du Québec, Québec. Carte Au 1:1 250 000.
- Veillette, J.J. (1994) Evolution and paleohydrology of glacial lakes Barlow and Ojibway. *Quaternary Science Reviews*, **13**, 945–971.
- Woodward, F.I. (1987) *Climate and plant distribution*. Cambridge Studies in Ecology. Cambridge University Press, Cambridge, UK.

BIOSKETCHES

The long-term objective of this research is to understand better the factors controlling the northern limit of mixed boreal forest. Some results are part of a master thesis by **Danielle Lalonde** who worked under the supervision of **Yves Bergeron**. Dr Bergeron's research focuses on forest ecosystem dynamics, primarily in boreal forests. He is Director of the NSERC/UQAT/UQAM Industrial Chair in Sustainable Forest Management. **Yves Mauffette** is a tree ecophysiologicalist working on plant–insect intersections. He is Director of the Inter University Forest Ecology Research Group (GREF-i). Francine Tremblay is a professor at the NSERC/UQAT/UQAM Industrial Chair in Sustainable Forest Management and is involved in projects on tree physiology and molecular biology.