

# Demographic Analysis of Tree Colonization in a 20-Year-Old Right-of-Way

**CHARLES MERCIER**  
**JACQUES BRISON**  
**ANDRÉ BOUCHARD\***

Institut de recherche en biologie végétale  
 Université de Montréal and Jardin botanique de Montréal  
 4101 est, rue Sherbrooke  
 Montréal, Québec  
 Canada H1X 2B2

**ABSTRACT** / Past tree colonization dynamics of a powerline-right-of-way (ROW) corridor in the Haut-Saint-Laurent region of Quebec was studied based on the present age distribution of its tree populations. This colonization study spans 20 years, from 1977 (ROW clearance) to 1996. The sampled quadrats were classified into six vegetation types. Tree colonization dynamics were interpreted in each type, and three distinct patterns were identified. (1) Communities adapted to acidic conditions were heavily colonized by *Acer rubrum*, at least for the last 12 years. (2) Communities adapted to mesic or to hydric conditions were more intensely colonized in the period 1985–1987 than in the following 9 years; this past success in tree colonization may have been caused by herbicide treatments,

which could have facilitated tree establishment by damaging the herbaceous and shrub vegetation. (3) Cattail, vine-raspberry, and reed-dominated communities contained few tree individuals, with almost all trees establishing between 1979 and 1990; those three vegetation types appear as the most resistant to tree invasion in the ROW studied.

This study supports the need for an integrated approach in ROW vegetation management, in which the selection of vegetation treatment methods would depend on the tree colonization dynamics in each vegetation type. Minimizing disturbances inflicted on ROW herbaceous and shrub covers should be the central strategy because disturbances jeopardize natural resistance to future tree invasion, except in communities adapted to acidic conditions where the existing vegetation does not prevent invasion by *A. rubrum*. Many trees are surviving the successive cutting operations by producing new sprouts each time, particularly in communities adapted to mesic and hydric conditions. In these cases, mechanical cutting should be replaced by a one-time stump-killing operation, to avoid repeated and unsuccessful treatments of the same individuals over time.

Powerline right-of-way (ROW) corridors are disturbed ecosystems that offer challenges in vegetation management. To guarantee free access to the powerline as well as safety for electricity transport, ROW communities have to be kept in an early successional state, reasonably free of tall tree stems. This vegetation control has generally been achieved using herbicide and/or mechanical, nonselective treatments (Carvell 1976, Bramble and others 1987, Luken 1990).

The use of nonselective herbicide applications in ROW management has been criticized at least since the 1950s (Egler 1958). As an alternative, plant scientists have proposed selective herbicide application to remove unwanted tree stems while allowing the development of a low-growing plant cover that interferes with tree establishment (Bramble and others 1990). The potential role of certain plant communities in slowing tree invasion has been documented

for shrubs (Niering and Goodwin 1974, Dreyer and Niering 1986, Bramble and others 1990, Meilleur and others 1994b, Berkowitz and others 1995) and herbaceous cover (White 1965, Grime 1973, Bazzaz 1996, Davis and others 1998)

In ROW management research, the ecologically based strategy of using selective mechanical and/or herbicide methods in conjunction with low-growing plant communities that slow tree invasion has been defined as Integrated Vegetation Management (IVM) (McLoughlin 1997, Morrow 1997). Compared to earlier nonselective ROW management methods, IVM takes advantage of ecological interactions between ROW vegetation and invading trees. The implementation of IVM requires an understanding of what happens when trees invade a ROW, i.e., the dynamics of ROW tree colonization.

Mechanisms involved in the resistance of plant communities to tree invasion have received a lot of attention from plant scientists: above- and belowground competition (Burton and Bazzaz 1991, 1995, Gill and Marks 1991, Putz and Canham 1992), seed and seedling predation by small mammals (Ostfeld and Canham

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\*Author to whom correspondence should be addressed.

1993, Bramble and others 1996, Manson and others 1998), plant litter effects (Facelli 1994, Myster 1994), and allelopathy (Tillman 1987, Monk 1983, Byrnes and others 1993). So far, studies focusing on the long-term dynamics of ROW tree invasion in different plant communities have been rare. Hill and others (1995) used a demographic empirical model to quantify the long-term net effect of different ROW communities on invading tree populations. However, they did not describe the actual long-term dynamics of the ROW, in which invading tree individuals interact with ROW vegetation in changing conditions due to successional processes and periodical vegetation treatments. One possible way to describe tree invasion dynamics is to carry out a static demographic study of tree populations found in the ROW: their past colonization dynamics can be interpreted from their present-day age structure (Rankin and Pickett 1989).

The goal of our study is to interpret the history of tree invasion in a ROW that was created in 1977 in southern Quebec. To achieve this goal, we classified the vegetation of the ROW and interpreted the age distributions of the tree species in relation with this classification to address the following questions:

1. What are the most common tree species invading the ROW?
2. Can we identify patterns of tree invasion dynamics in the various vegetation types of the ROW?
3. Did the type of vegetation management practices (cutting or herbicide) influence the present age structure of ROW tree populations?
4. How can a better understanding of the long-term dynamics of tree invasion improve vegetation management?

## Study Site

The powerline under study occupies a corridor in the Municipalité régionale de comté du Haut-Saint-Laurent. The MRC is located in the southwest of Quebec province, and is bordered by the St. Lawrence River to the north and the state of New York (USA) to the south (Figure 1).

The bedrock is mainly composed of Potsdam sandstone in the southern part and of Beekmantown dolomite in the northern part, which are the main elements found in regional moraine deposits. Gley and organic soils are predominant in the marine plain, whereas eluvial brown soils and podzols occupy the moraines.

The region has a humid continental climate with cool summers. The annual average temperature is 6.1°C in Huntingdon (elevation: 75 m above sea mean

level) with an average temperature of  $-10^{\circ}\text{C}$  in January and  $20.8^{\circ}\text{C}$  in July. The region under study is located within the Maple-Hickory region (Grandtner 1966), which is part of the deciduous forest of the Great Lakes and St. Lawrence River system (Rowe 1972). Mesic forests are generally dominated by *Acer saccharum*, with *Fagus grandifolia*, *Tsuga canadensis*, *Ostrya virginiana*, and *Tilia americana*. Forests growing on poorly drained soils or open sites are mostly dominated by *Fraxinus pennsylvanica* and *Acer rubrum* (Meilleur and others, 1994a, 1994b). *Acer saccharinum* can grow on more fertile and poorly drained sites (Rowe 1972), while *Pinus strobus*, *A. rubrum*, *Populus tremuloides*, and *Betula populifolia* are the main dominant species on xeric sites (Meilleur and others 1994a).

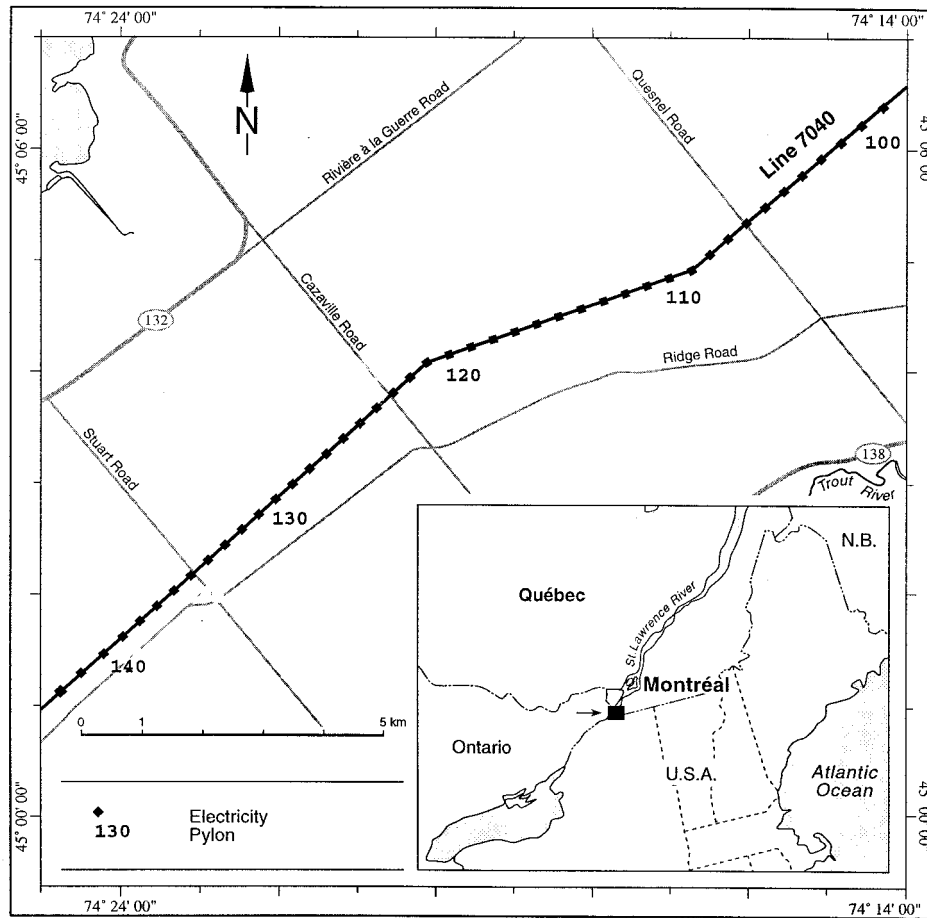
Since the beginning of the 19th century, profound transformations by human colonization have taken place in the Haut-Saint-Laurent territory. The result is a complex mosaic, where the plains are used for agriculture and forests colonize the moraine deposits. The later decrease in agricultural land use on those deposits led to an increase in the area occupied by forests (Bouchard and Domon 1997).

In 1977, a 60 m-wide strip was cleared for the construction of the transmission line that was brought into service in 1978. Since then, three herbicide treatments (1978, 1981, 1984) and four mechanical cutting treatments (1987, 1990, 1993, 1996) were performed to manage tree invasion. A survey done in 1986 showed that the area of the corridor is mainly occupied by mixed early successional herbaceous and/or shrub communities (75%) and agricultural fields (15%) (Meilleur and Bouchard 1989). In the ROW sections that were selected for this study, bordering forests form a mosaic of the following vegetation types: late successional maple-hickory forest (*A. saccharum* with *Fraxinus americana*, *O. virginiana*, *F. grandifolia*, *Carya cordiformis*, *T. canadensis*) and early successional *Populus* and/or *Betula* stands in mesic soils; mixed woods containing variable combinations of *F. pennsylvanica*, *Betula alleghaniensis*, *Fraxinus nigra*, and/or *Quercus macrocarpa* in hydric soils. *A. rubrum* and *Thuja occidentalis* are ubiquitous in ROW border forests-although the former reaches a higher-abundance in hydric soils. The topography of the corridor is predominantly flat, with occasional gradual slopes.

## Methods

### Sampling Sites

Field sampling was carried out from June to August 1997 within a 20-km portion of the ROW. We



**Figure 1.** Location of the powerline right-of-way in the study area.

located on a map several ROW sections that had a forest edge on both sides, with the objective of focusing our study where the tree-invasion process was the most intense due to the proximity of seed-bearing trees. Eleven sampling sites of varying sizes were thus selected, between pylon number 99 and pylon number 141 of the electricity powerline 7040 of Hydro-Québec (Figure 1).

In each site, we sampled in transects perpendicular to the ROW corridor. The transects were located 50 m apart from one another, and they each consisted of three 5-m-by-5-m quadrats: one in the center, under the powerline, and the two others on each side, near the forest edges. Overall, we sampled 175 quadrats.

#### Vegetation Classification

In every quadrat, we estimated the percentage area covered by each herbaceous and shrub species using the following semiquantitative scale: 1 = 0–1%, 2 = 1–5%, 3 = 5–15%, 4 = 15–25%, 5 = 25–50%, 6 = 50–75%, 7 = 75–100%. We identified 178 plant species

during the sampling period. To minimize the effect of uncommon species in our analysis, we rejected all species occurring in three quadrats or less. The final data matrix for classification of ROW vegetation included 133 species. Botanical nomenclature follows Marie-Victorin (1995) and Gleason and Cronquist (1991).

In the analysis, we first used Simil 1.01 software from the Progiel R. statistical package (Legendre and Vaudor 1991) to compute a similarity matrix. We chose the Steinhaus similarity index ( $S_{17}$ ) because it is well suited to data measured on a semiquantitative scale and because it assigns an equal weight to every species (Legendre and Legendre 1984). Then, based on the similarity matrix, the clustering method UPGMA (Unweighted Pair-Group method using Arithmetic Averages) was utilized to partition the 175 quadrats in a small number of vegetation types. We then used the software IndVal  $\beta$  (Dufrêne and Legendre 1997) to assign indicator species to each vegetation type of the classification. This characterization using indicator species allows direct field recognition of the vegetation types.

### Tree Abundance and Age Distribution

All tree stems located inside each quadrat were identified at the species level, harvested by cutting the roots, and tagged. A few adjustments and restrictions apply to tree sampling. First, the species *F. americana* and *F. pennsylvanica* were identified as *Fraxinus* sp. given the frequent difficulty involved in identifying them at a young age and/or in a multistem form created by previous cutting treatments. Second, the freshly germinated tree seedlings (less than 1 year old) were not recorded because their presence in a given site is dependent on the sampling date; a site sampled at the beginning of the summer could have been free of tree seedlings because germination had not yet taken place. Third, we decided not to include individuals belonging to vegetatively propagating species such as *Populus* sp. and *Prunus pennsylvanica*. They were numerous (~250 stems) but mostly concentrated in five quadrats. Because the goal of the present study is to understand tree colonization dynamics through seed invasion and seedling establishment in different plant communities, the *Populus* and *Prunus* clones were not considered because their invasion process follows a different dynamic. The root suckers are nutritionally linked to parent trees, so their survival in a given quadrat is clearly less influenced by the plant community in which they grow (Richard 1973). A large number of root suckers concentrated in a given quadrat can inhibit or facilitate the subsequent establishment of other tree species, but in our study, those uninvestigated effects are limited to less than 3% of the sampled sites.

We harvested a total of 1797 tree individuals. For each of them, we manually or mechanically sawed a slice at base level, then sanded it. We counted the growth rings and estimated the age of each individual, which was put in one of the eight following age classes: 1–3 years, 4–6 years, 7–9 years, 10–12 years, 13–15 years, 16–18 years, 19–21 years, and more than 21 years. The first seven classes cover the entire lifespan of the ROW, from its creation in 1977 to the sampling year in 1997. The eighth age class is an indication of the number of trees that are older than the powerline and therefore were able to survive the clearing operation and seven subsequent treatments.

The effect of vegetation type on individual tree abundance was tested separately for each of the seven post-1977 age classes using Kruskal-Wallis nonparametric tests, one per age class. If that general test was significant, individual differences between pairs of vegetation types were tested with Tukey-Kramer HSD test of multiple comparisons using rank-coded data.

Spatiotemporal tree dynamics was analyzed by build-

ing and interpreting two age distributions for each vegetation type identified in the ROW. The first distribution shows the proportion of individuals (relative abundance) present in each age class. The second distribution shows the proportion of the total number of quadrats where a given age class is present; it illustrates whether a given age class is restricted to a few quadrats or dispersed in most of the quadrats belonging to a given vegetation type. Both distributions appear in the same graph, thus allowing a weighting of the relative abundance of a given age class according to its spatial dispersion in the quadrats.

## Results

### Vegetation Classification

The clustering analysis led to the partition of the 175 quadrats into six unequally represented vegetation types. Each type is defined by a list of indicator species (Table 1).

*Communities adapted to mesic conditions (type M)* are the most common type in the sampled portion of the ROW: they represent 95 quadrats out of a total of 175. They are a mosaic of grassy and herbaceous prairies composed predominantly of *Poa pratensis*, *Fragaria americana*, *Daucus carota*, *Asclepias syriaca*, *Aster cordifolius*, *Pastinaca sativa*, interrupted by pure or mixed islands of *Rubus alleghaniensis*, *Zanthoxylum americanum*, and *Crataegus* sp.

The five other vegetation types all share several common species adapted to more hydric conditions. The predominant ones are two ferns, *Onoclea sensibilis* and *Thelypteris palustris*, and the shrubs *Cornus stolonifera* and *Spiraea alba*. Each of the vegetation type is also defined by its own indicator species.

*Communities adapted to hydric conditions (type H)* represented by 39 quadrats, are characterized by a few species with low indicator values, in the genera *Carex* and *Scirpus*. This type is more practically defined by the presence of the species common to hydric conditions (*O. sensibilis*, *T. palustris*, *C. stolonifera*, *S. alba*) combined to the absence of indicator species associated with the four vegetation types described below.

*Communities adapted to acidic conditions (type A)* are the third type in representation (14 quadrats out of 175). They are a mosaic of herbaceous communities mixed with shrub islands and are characterized by several species that can naturally grow in acidic soils: *Aronia melanocarpa*, *Ilex verticillata*, *Ledum groenlandicum*, *Osmunda cinnamomea*, *Osmunda regalis*, *Rubus canadensis*, *Spiraea tomentosa*.

The last three types are less common in the sampled

Table 1. Six vegetation types identified in the ROW and their indicator species

Vegetation types	Number of quadrats	Indicator species
Communities adapted to mesic conditions	95	<i>Poa pratensis</i> , <i>Fragaria</i> spp., <i>Rubus allegheniensis</i> , <i>Daucus carota</i> , <i>Asclepias syriaca</i> , <i>Aster cordifolius</i> , <i>Zanthoxylum americanum</i> , <i>Crataegus</i> spp., <i>Pastinaca sativa</i> .
Communities adapted to hydric conditions	39	<i>Carex</i> sect. <i>Ovales</i> , <i>Scirpus atrovirens</i> , <i>Carex lurida</i> , <i>Scirpus cyperinus</i> .
Communities adapted to acidic conditions	14	<i>Aronia melanocarpa</i> , <i>Rubus canadensis</i> , <i>Spiraea tomentosa</i> , <i>Maianthemum canadense</i> , <i>Ilex verticillata</i> , <i>Solidago gigantea</i> , <i>Osmunda regalis</i> , <i>Ledum groenlandicum</i> , <i>Osmunda cinnamomea</i> .
Cattail-dominated communities	13	<i>Typha</i> spp., <i>Galium palustre</i> , <i>Eupatorium maculatum</i> , <i>Aster puniceus</i> , <i>Lythrum salicaria</i> .
Vine-raspberry communities	8	<i>Clematis virginiana</i> , <i>Rubus occidentalis</i> .
Reed-dominated communities	6	<i>Phragmites australis</i> .

ROW section and are overly dominated by one or two species. The *cattail-dominated communities* (type C, 13 quadrats) and the *reed-dominated communities* (type R, 6 quadrats) are characterized by dense populations of *Typha* sp. and *Phragmites australis*, respectively, in which other species are present but occur as scattered individuals or patches. Finally, the *vine-raspberry community* (type V, 8 quadrats) is a unique association between the shrub *R. idaeus* and the vine *Clematis virginiana*.

#### Tree Species Distribution

The majority of the 1797 tree individuals harvested is composed of midsuccessional or intermediate shade tolerance species, the main ones being *A. rubrum* (37.3%), *F. americana*, and *F. pennsylvanica* (25.4% together) (Table 2). *A. rubrum* strongly dominates in communities adapted to acidic conditions (type A), but is also represented with a lesser importance in all other types. *F. americana* and *F. pennsylvanica* are found in every type except type A. Overall in the ROW, typical pioneer (*Betula populifolia*, *B. papyrifera*) or late-successional species (*A. saccharum*, *T. canadensis*, *F. nigra*) are poorly represented.

#### Tree Age Distribution

There are differences in tree abundance among the six vegetation types (Table 3), with significantly more young trees (1–3, 4–6, and 7–9 years age classes) in the communities adapted to acidic conditions than in the five other vegetation types. This pattern is weaker in the 10–12 and 13–15 years age classes, where significant differences remain between some pairs of types, but not enough to show a clear difference between type A and the five others. In the oldest age classes (16–18 and 19–21 years), the multiple tests show no significant difference between vegetation types. In addition to the broad differences described above, the demographic

tables constructed for each vegetation type revealed other trends.

In the communities found in acidic conditions, the age distribution illustrates that abundance in a given class is inversely proportional to tree age, a relationship that is consistent with a relatively stable tree establishment and mortality rates over time (Figure 2A). Also, in the three younger age classes (1–3, 4–6, and 7–9 years), the invasion process is spatially widespread, reaching 80–90% of the quadrats belonging to this vegetation type. Thus, in communities found in acidic conditions, tree colonization is not only more abundant, as shown by statistical tests, but also more spatially widespread. In the other five vegetation types, the maximum proportion of quadrats that contain trees seldom exceeds 65%.

The age distributions of all five other vegetation types depart from the dynamic pattern described above. In the communities adapted to hydric conditions, the main distinctive element is a sharp peak both in relative abundance (>30%) and in the proportion of quadrats that contain trees (>60% of the quadrats), located at the 10–12 years age class (Figure 2B). In the communities adapted to mesic conditions (Figure 2C), a weak peak is present in the proportion of quadrats that contain trees, in the 10–12 year and 13–15 year age classes (50–55% of the quadrats), which resembles the situation identified in the communities adapted to hydric conditions (type H). The relative abundance follows a different pattern: first, an increase from the 19–21 year to the 10–12 year age classes; and second, an almost stable section between the 10–12 year and the 1–3 year age classes. Despite the two weak peaks observed, the overall tree age structure in the communities adapted to mesic conditions is balanced among classes, with no relative abundance value going above 20%. In both communities of hydric and mesic condi-

Table 2. Main tree species found in the ROW and their abundance in each vegetation type.

Tree species	Relative abundance in each vegetation type (%)						Relative abundance in the ROW (n = 1797)
	M (n = 890)	H (n = 251)	A (n = 573)	C (n = 30)	R (n = 14)	V (n = 7)	
<i>Acer rubrum</i>	7.9	21.1	91.3	20.0	28.6	28.6	37.3
<i>Fraxinus americana</i> + <i>F. pennsylvanica</i>	38.3	39.8	0.5	6.7	50.0	14.3	25.4
<i>Carya cordiformis</i>	12.0	0.4	0.5	0	0	0	6.2
<i>Thuja occidentalis</i>	7.0	16.3	0.3	6.7	0	0	6.0
<i>Betula populifolia</i>	3.0	9.2	6.8	6.7	0	0	5.9
<i>Ostrya virginiana</i>	10.3	0.8	0	0	0	0	5.2
<i>Acer saccharum</i>	6.7	0.4	0.2	0	0	0	3.5
<i>Prunus serotina</i>	5.4	0.4	0.2	0	0	14.3	2.9
<i>Ulmus americana</i>	2.1	4.8	0	13.3	0	42.9	2.1
Other species*	7.1	6.7	0.2	46.6	21.4	0	5.5

The letters refer to the vegetation types: M = communities adapted to mesic conditions, H = communities adapted to hydric conditions, A = communities adapted to acidic conditions, C = cattail-dominated communities, R = reed-dominated communities, V = vine-raspberry communities.

\*In decreasing order of abundance: *Juglans cinerea*, *Tilia americana*, *Betula alleghaniensis*, *Quercus macrocarpa*, *Fraxinus nigra*, *Carpinus caroliniana*, *Betula papyrifera*, *Abies balsamea*, *Larix laricina*, *Tsuga canadensis*, *Ulmus thomasi*, *Pinus strobus*.

Table 3. Differences in tree abundance between vegetation types

Vegetation types	Number of quadrats	Age class (in years)						
		1-3	4-6	7-9	10-12	13-15	16-18	19-21
M	95	[0-0-3]a	[0-0-3]a	[0-0-3]a	[0-1-5]abc	[0-1-3]ab	[0-0-2]a	[0-0-2]a
H	39	[0-0-6]a	[0-0-2]a	[0-0-3]a	[0-1-4]bc	[0-0-2]ab	[0-0-2]a	[0-0-1]a
A	14	[0-18-62]b	[0-6-17]b	[0-4-24]b	[0-2-11]c	[0-1-6]b	[0-0-2]a	[0-0-1]a
C	13	[0-0-1]a	[0-0-1]a	[0-0-5]a	[0-0-2]a	[0-0-3]ab	[0-0-1]a	[0-0-0]a
V	8	[0-0-1]a	[0-0-0]a	[0-0-0]a	[0-0-1]ab	[0-0-0]a	[0-0-0]a	[0-0-0]a
R	6	[0-0-1]a	[0-0-0]a	[0-0-2]a	[0-0-2]abc	[0-0-0]a	[0-1-2]a	[0-0-0]a

The tests are performed for every age class. The numbers in square brackets are respectively: the 1st decile, the median, and the 9th decile of the distribution of the number of tree individuals per quadrat. For a given age class, vegetation types identified by the same letter are not significantly different. Abbreviations are: M = communities adapted to mesic conditions, H = communities adapted to hydric conditions, A = communities adapted to acidic conditions, C = cattail-dominated communities, V = vine-raspberry communities, R = reed-dominated communities.

tions, many older individuals are resproutings of *Fraxinus* sp. that survived several treatments.

In the three other vegetation types, type V, type C, and type R communities, tree invasion is very low, resulting in irregular age distributions with multiple peaks and zero values due to low absolute numbers (Figure 2D, E, F). There are two trees in eight quadrats for type V, 2 trees in 13 quadrats for type C, and 1 tree in 6 quadrats for type R.

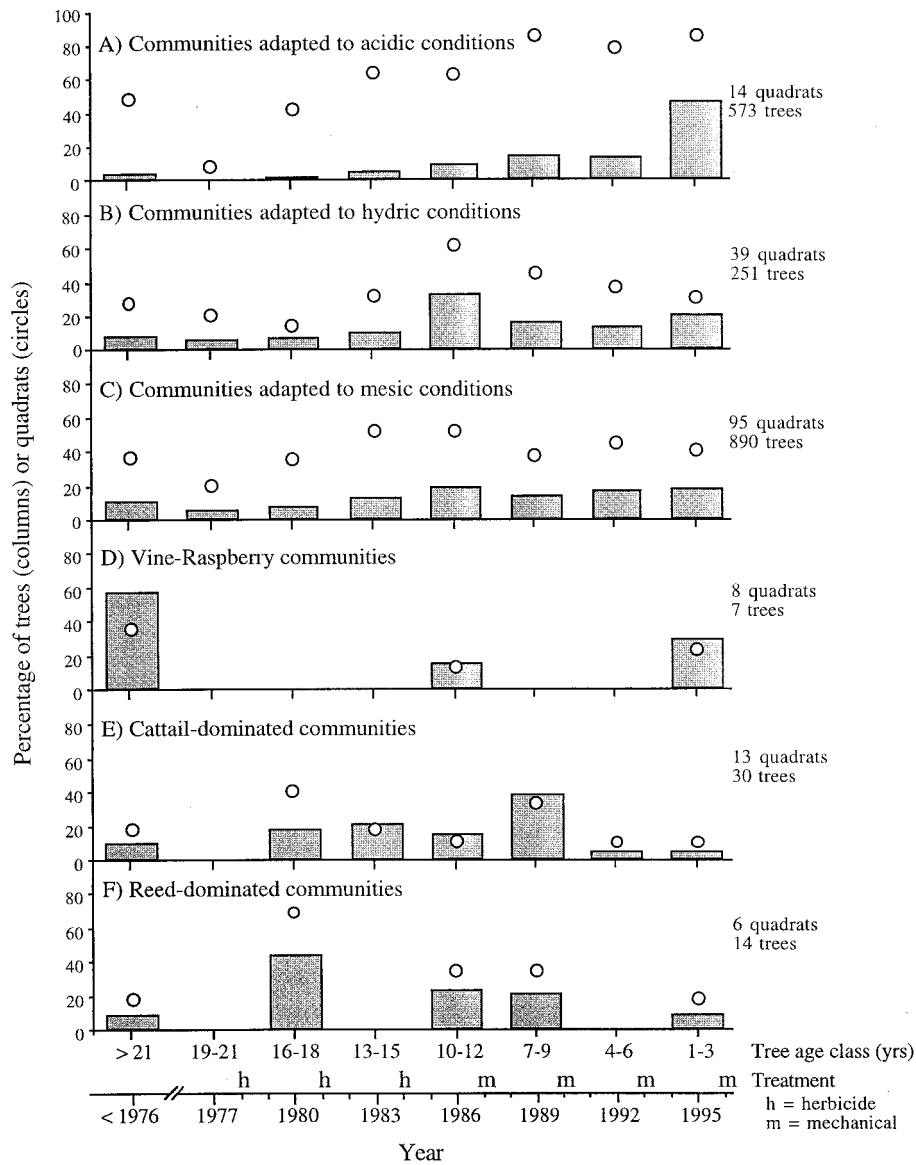
## Discussion

### Tree Species Distribution in the ROW

Pioneer tree species are present in low proportion in the ROW (Table 2). It is unlikely that this low abundance is due to unsuccessful seed dispersal, because *Betula* and *Populus* species are well distributed in the ROW bordering forests and they have light seeds that are dispersed by wind over long distances (Burns and

Honkala 1990). Our explanation is that the plant communities presently found in the ROW do not offer good establishment conditions for pioneer tree species. Their typical seedbed, mineral soil relatively free of herbaceous or shrub cover (Farmer 1997), is relatively rare in the ROW corridor. Canham (1993) made the same observation and interpretation in a ROW study in the state of New York.

The dominance of the ROW tree vegetation by *A. rubrum*, *F. americana*, and *F. pennsylvanica* in this study has been reported elsewhere in eastern North America: the province of Ontario (Brown 1994) and the states of New York (Hill and others 1995) and Pennsylvania (Byrnes and others 1993). More specifically, their abundance can be linked to several relevant life-history and physiological characteristics. *A. rubrum* reaches sexual maturity at a young age (less than 10 years), produces wind-dispersed seeds annually with bumper crops once every 2 years, can adapt its root system to various soil



**Figure 2.** Age-class distributions of tree populations in the six ROW vegetation types. For a given class, the grey bars indicate relative tree abundance and the empty circles (O) illustrate the percentage of quadrats that contain trees. Each bar and each circle covers a 3-year age class but is centered on the middle year. The class >21 years (<1976) includes trees established before the creation of the ROW (1977). On the right-hand side, the total numbers of quadrats and of trees in each vegetation type are presented. The years of mechanical and chemical vegetation treatments are indicated at the bottom of the graph.

types (hydric, dry, or mesic conditions), is capable of stump sprouting and shows herbicide resistance (Burns and Honkala 1990). *F. americana* and *F. pennsylvanica* have intermediate shade tolerance and can sprout readily when cut (Burns and Honkala 1990). Those characteristics play an important role in the predominance of these three species in the ROW over the pioneer and late-successional species.

*Fraxinus* species are restricted to communities

adapted to mesic and hydric conditions. *A. rubrum* is ubiquitous in the ROW but abundant only in communities adapted to acidic conditions. *A. rubrum* is known to have a wide tolerance to pH and soil conditions, but in the Haut-Saint-Laurent region, it reaches its maximum importance value in organic acidic soils (Bergeron and others 1988). In addition to ecological preferences, the observed patterns for *Fraxinus* sp. and *A. rubrum* may partially be due to higher seed sources

from bordering forests (Brisson and others 1997). These wind-dispersed species with intermediate seed mass do not disperse over long distance. They can invade the ROW in the zones bordered by forests where they naturally occur. In the studied ROW, unpublished presence/absence data shows that *A. rubrum* is present in the border of every vegetation type, whereas *F. americana* and *F. pennsylvanica* were not observed in the forest bordering communities adapted to acidic conditions.

#### High Red Maple Invasion in Communities Adapted to Acidic Conditions

Communities adapted to acidic conditions are the only ones that show a tree-age distribution consistent with a continuous and relatively stable establishment, mainly of *A. rubrum*, with a large number of young seedlings and progressively fewer older stems. Yet *A. rubrum*, despite the characteristics that makes it a prolific invader (Burns and Honkala 1990), is a poor competitor (Abrams 1998). Berkowitz and others (1995) have already demonstrated the importance of plant competition in ROW invasion dynamics. The high density and continuous establishment of *A. rubrum* suggest that competitive pressure exerted on trees by herbaceous and shrub covers is less intense in communities adapted to acidic conditions than elsewhere in more resource-rich conditions of the ROW.

#### Decreasing Colonization over Time in Communities Adapted to Hydric or Mesic Conditions

Understanding tree colonization dynamics in communities adapted to hydric (type H) or mesic (type M) conditions is important for vegetation management purposes in the studied ROW because they include 71% of the total 175 quadrats that were sampled. In communities adapted to hydric conditions, the number of recently established tree individuals is lower than the number of older tree individuals, strongly suggesting that tree colonization has been more abundant at some point in the past than at the time of sampling. In communities adapted to mesic conditions, numbers of individuals in age classes 1–3, 4–6, 7–9, and 10–12 years are approximately similar. This pattern is also more likely the result of a higher tree establishment rate at some point in the past rather than a constant tree establishment rate combined with a zero mortality rate. A near-zero mortality rate for trees established in the ROW is not probable given the combined mortality pressure from man-made (vegetation control) as well as natural causes. As an example of annual natural mortality rate, Hill and others (1995) report values ranging from 0.071 to 0.308 for tree seedlings over 1 year old,

an estimate that does not even include mortality caused by vegetation control treatments.

In communities adapted to hydric conditions, the peak in age class 10–12 years indicates a period of successful tree establishment that occurred in 1985–1987, immediately after the last chemical treatment applied to the ROW in 1984. Such a temporal sequence suggests that the peak might have been caused by the chemical treatment, which affects not only the targeted trees but also the surrounding shrub and herbaceous vegetation, creating holes in the vegetation cover and opening short-term windows for tree colonization. In contrast, mechanical treatments are more selective, only affecting the targeted tree. Luken and others (1994) have assessed several methods of vegetation management using herbicides, and they concluded that they had a negative effect on nontarget vegetation. In a study comparing the survival and growth of planted tree seedlings in intact versus cleared ROW plant communities, Berkowitz and others (1995) found that tree seedlings generally grow and survive better when the surrounding vegetation is cleared. The decrease in relative abundance and spatial dispersion observed from age class 10–12 years to age class 1–3 years in communities adapted to mesic conditions may thus be the result of the vegetation layer being progressively more resistant to tree invasion. This interpretation of age-classes may also be consistent with the age distribution in communities adapted to mesic conditions. Although the effect of chemical treatment on tree invasion needs further investigation through experimental studies, our results support the idea that damaging ROW vegetation can facilitate tree colonization.

#### Low Tree Colonization in Type V, Type C, Type R Communities

Recent tree colonization is very low in the vine-raspberry, cattail-dominated, and reed-dominated community types. Some characteristics of plant species found in those three types could inhibit the germination of tree seeds and/or the initial survival of tree seedlings.

In the vine-raspberry community, *C. virginiana*, an herbaceous vine growing in moist soils (Gleason and Cronquist 1991), dominates aerial cover and is often associated with the shrub *R. idaeus*. Both species form a dense vegetation cover from 0.5 to 1.5 m tall that seems to effectively prevent light from reaching the soil surface. This factor, as well as competition for water and nutrients, could explain the almost zero abundance observed in age classes ranging from 1–3 year to 19–21 years. A similar vine-dominated vegetation type (involving the vines *Celastrus orbiculatus* and *Vitis labrusca*) that



interferes with successional development has been reported in southeastern Connecticut (Fike and Niering 1999).

Both in the cattail-dominated and the reed-dominated community types, the wet conditions are highly unfavorable for germination of many tree species. In addition, the vegetation itself may inhibit tree germination. For example, in the cattail-dominated communities, the low abundance in the two younger age classes (1–3 years and 4–6 years) is likely due to the thick leaf litter, which interferes with tree seed germination. Also, *Typha* sp. forms a dense network of rhizomes (Grace and Wetzel 1998) possibly involved in inhibitory interactions with tree seedlings. The age distribution indicates that some tree colonization did occur before the 1991–1996 period, possibly because the *Typha* sp. understory was either less well developed at that time or damaged by chemical treatments. In the reed-dominated community type, *Phragmites australis* grows in very dense populations. It has the capacity to aggressively invade and dominate a given site by vegetative reproduction (Ricard 1996). Soil is covered by a thick layer of dead stems that accumulate and have the potential of preventing tree establishment (Marks and others, 1994). Like in the cattail-dominated communities, some tree invasion occurred between 1978 and 1990, possibly because the reed community was less densely developed or damaged by herbicides.

## Conclusion

Through the analysis of the static age distributions of tree populations in six different vegetation types, three distinct patterns were identified: (1) an intense and continuous tree invasion in communities adapted to acidic conditions; (2) a lower tree colonization that peaked in the 1985–1987 period following the last herbicide application and that decreased since in communities adapted to hydric or to mesic conditions; (3) a very low tree invasion, particularly in the 1991–1996 period, in vine-raspberry, cattail-dominated, and reed-dominated community types.

For ROW vegetation, mortality involves human causes (chemical and mechanical treatments) in addition to natural factors (environmental conditions, interspecific plant competition, herbivory, etc). Although static age distributions can not provide direct information on past mortality in tree populations, they can lead to a better understanding of the tree invasion process, and allows to make hypotheses on factors important for tree establishment. We found evidence that tree invasion in the ROW is a complex process influenced by historical (past history of the site, type and sequence of

treatments) and ecological factors (vegetation type, environmental variables).

The three dynamic patterns identified support the need for an integrated approach in ROW vegetation management, in which the selection of treatment methods would depend not only on cost efficiency and practical feasibility but also on the tree colonization dynamics that occur in a given ecological type. More specifically, on the basis of the ROW portion studied here, we can make the following recommendations:

1. In the majority of the ROW portion sampled, new establishment is moderate to low. Therefore, minimizing disturbances inflicted on ROW plant communities should be the central strategy because it preserves their natural resistance to future tree invasion. Nonselective mechanical or herbicidal methods should be avoided. As there is some evidence that herbicide drift can damage spots of ROW vegetation and favor tree establishment, selective mechanical treatments should be maintained. Monitoring and research can determine the appropriate frequency of treatment for each community type.
2. In the communities adapted to acidic conditions, periodical selective mechanical treatments will always be necessary due to the intense and continuous tree invasion and the little resistance of the vegetation to tree establishment.
3. In all vegetation types of the ROW, we observed significant tree survival and resprouting despite periodical treatments at 3-year intervals. For these individuals, mechanical cutting should be replaced by a one-time stump-killing operation, to avoid repeated and unsuccessful treatments of the same individuals over time.

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