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Ectomycorrhizal colonization on black spruce and jack pine seedlings outplanted in reforestation sites

B.J. McAFEE[1] and J.A. FORTIN
Centre de Recherches en Biologie Forestières, Faculté de Foresterie et Géodésie, Université Laval, Ste-Foy, Québec, Canada G1K 7P4. [1] *Present address: Plant Biotechnology Institute, National Research Council, 110 Gymnasium Road, Saskatoon, Saskatchewan, Canada S7N 0W9*

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Abstract

Six-week-old, mycorrhiza-free, bareroot jack pine and black spruce seedlings were outplanted in ten reforestation sites, situated between 45–48° latitude N and 69–74° longitude W, within the province of Quebec, representing diverse operational forestry disturbances and ecological conditions.

Two months after outplanting, root systems of black spruce seedlings had fewer mycorrhizae than those of jack pine seedlings. Ectomycorrhizal colonization on black spruce seedlings did not vary significantly with the reforestation site. Percent mycorrhizal colonization for these seedlings was positively correlated with seedling dry weight while with the jack pine seedlings, mycorrhizal colonization varied significantly with the outplanting site and there was no correlation between mycorrhizal formation and seedling dry weight.

Multiple linear regressions showed pH to be a determinant soil factor for mycorrhizal colonization for the two species. Drainage was the other influential factor affecting colonization of black spruce while organic matter accumulation was more important for jack pine.

Inoculation with selected ectomycorrhizal fungi could be more important for black spruce than for jack pine seedlings.

Introduction

In recent years mycorrhizal research has focused on the manipulation of specific ectomycorrhizal fungi to improve seedling survival and growth (Boyle *et al.*, 1987; Danielson *et al.*, 1984; Fortin *et al.*, 1987; Kropp and Fortin, 1987; Marx *et al.*, 1984). Large scale utilization of mycorrhiza technology depends upon an adequate demonstration of the advantages of inoculation. Field studies are necessary in order to gain an understanding of the ecology and management of ectomycorrhizal isolates. The survival of the outplanted fungus in competition with indigenous mycobionts as well as with other microorganisms and the effects of site edaphic and environmental factors must be considered.

How site disturbances modify soil and vegetation conditions and thus affect populations of indigenous ectomycorrhizal fungi is poorly understood. If mycorrhizal technology is to be incorporated into the reforestation system, it is important to determine under what conditions the indigenous mycorrhizal populations of the soil are too low to induce natural infection, and to know what soil and environmental conditions are most favourable to natural mycorrhizal infection.

Several researchers have reported diminished soil inoculum potentials following forest removal (Harvey *et al.*, 1980; Parke *et al.*, 1984; Pilz and Perry, 1984). Greenhouse bioassays using seedlings placed in soil cores (Perry *et al.*, 1982) determined that the ectomycorrhizal fungus, although present, diminished over time after clearcutting.

Scarification in clearcut sites in addition to altering soil temperatures and soil water tension (Plamondon *et al.*, 1980) tends to expose mineral soil in certain areas while in others there is an accumulation of organic matter. Organic matter has been reported to inhibit mycorrhiza formation (Alvarez *et al.*, 1979; Schoenberger and Perry, 1982) while other researchers have published that ectomycorrhizae develop better in humus and litter trays than in mineral soil (Fogel, 1980; Harvey *et al.*, 1980).

This study was designed to investigate the occurrence and abundance of ectomycorrhizal fungi associated with jack pine and black spruce seedlings in reforestation sites throughout the province of Quebec and to examine the various site conditions and environmental factors that are favourable for indigenous ectomycorrhizae colonization.

Materials and methods

Bareroot jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill.) BSP) were produced in containers composed of 67 cavities (IPL Inc., Bellechasse, Quebec). Prior to sowing, seeds were stratified at 5°C in running water for 3 days. The substrate consisted of a 75:25 v/v mixture of vermiculite: peatmoss respectively. Benomyl (Benlat, DuPont of Canada Inc., Mississauga, Ontario) was added to the substrate (0.066 mg/cavity) to control undesirable fungi at the time of sowing. Each seedling received respectively 1.00, 0.87 and 0.83 mg per plant per week, of N–P–K, using 15–30–15 fertilizer (Plant Products Co. Ltd., Bramalea, Ontario). This rich fertilization regime was selected in order to control contamination from any undesirable ectomycorrhizal fungi present in the greenhouse, as these quantities of N and P exceed the upper limits suggested by Gagnon *et al.* (1987) for successful mycorrhizal innoculation. Six weeks after sowing, seedlings were outplanted to the experimental field stations.

A thin metal wire support, placed in each cavity prior to the addition of the substrate, facilitated seedling extraction from the cavities and minimized root damage. Each root system was washed with a fine spray to remove any adhering substrate particles before transplantation. The soil was opened with a flat shovel and the root system was applied to the exposed soil profile, with minimal disturbance to the edaphic environment. In September, two months after outplanting, the soil was again opened with a flat shovel and the seedlings were removed. Mycorrhizal colonization was determined as a percentage of the short roots forming mycorrhizae per plant. Observations were carried out with the aid of a stereomicroscope. Ectomycorrhiza types were distinguished on the basis of color and morphology and the numbers of distinct ectomycorrhiza types in each plot were recorded. In cases where mycorrhiza formation was uncertain, freehand sections were examined for detection of mantle and Hartig net formation.

Within the province of Quebec, ten study sites, situated between 45–48° latitude N and 69–74° longitude W were selected (Fig. 1). These sites represented actual plantations or areas destined to be planted within 2 years. At each of the respective sites, 3 replicate plots, composed of 16 seedlings, were designated at random. Jack pine seedlings were outplanted in 6 different sites while the black spruce seedlings were placed in 5 other sites. At site 9, plots contained 16 spruce and 16 pine seedlings. Three random soil samples per plot at a depth of 20 cm were taken when the plots were established. After air drying and sieving, (2 mm) the pH (1:2 soil: H_2O), total Kjeldahl nitrogen, available phosphorus (Truog, 1930) and organic carbon (Walkley and Black, 1934) was determined. Cations of Al, Fe, K, Ca and Mg were extracted with NH_4NO_3 and analyzed by atomic absorption spectrophotometry. Drainage was qualitatively estimated as good or poor and was analyzed as a non-parametric variable.

An analysis of variance was carried out on the means of % mycorrhiza formation, seedling dry weight and the number of mycorrhiza types. Prior to analysis, data were tested with the Kolmogorov–Smirnov goodness of fit test for normality (Stephens, 1974) and the homogeneity of variances were examined with the Burr–Foster test (Anderson and McLean, 1974). Differences among means were evaluated with Duncan's multiple range test (Duncan, 1955). A correlation matrix, with Pearson correlation coefficients, was constructed to examine correlations between soil variables and seedling parameters. The relationship between percent mycorrhiza formation and the physicochemical properties of the soil was analyzed for each tree species using the RSQUARE procedure (SAS, 1982).

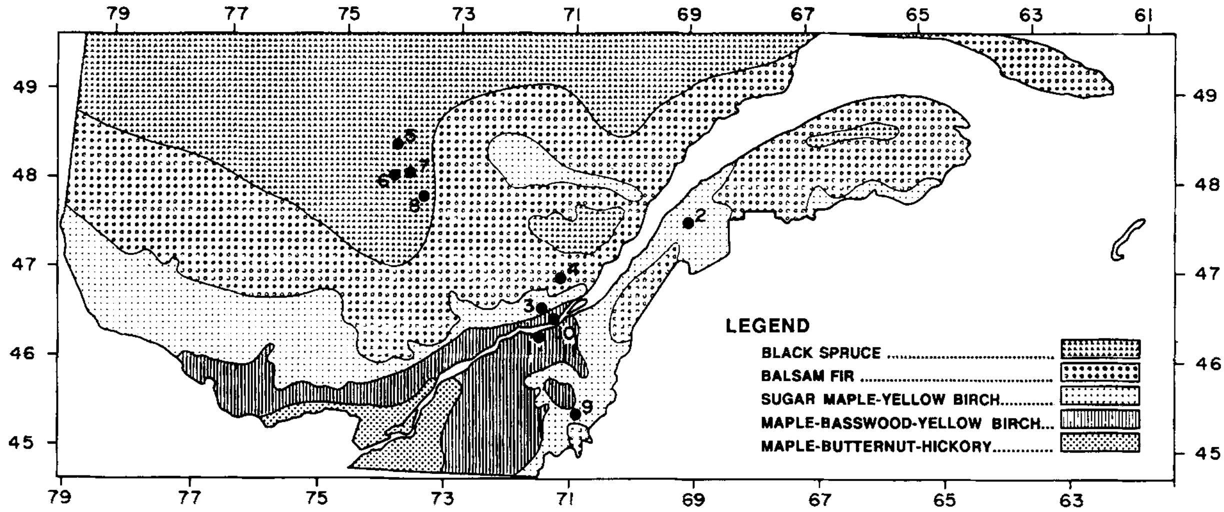

Fig. 1. Location of experimental plots in the forest regions of Quebec.

Results

The history of forestry operations as well as climatic, vegetational and pedological features varied with the site (Table 1). The 10 sites represented a broad range of conditions including experimental nursery plots on the campus of Laval university, abandoned farmland, a recently active landing as well as intensively forested areas where various different techniques of site preparation were used. Balsam fir-black spruce and sugar maple-yellow birch were the principle forest cover types represented at or surrounding the outplanting sites. The surficial 20 cm of the soil profile varied from well drained loams with abundant earthworm activity, associated with the converted farmland to the typical podzolic profiles in the harvested areas of the boreal forest. Most sites had 50% or more sand while organic matter content varied between 0.9% at Site 6, the rcent burn and 8.5% at the Montmorency Forest, where the organic debris was windrowed.

Nitrogen was the only soil element that varied significantly between sites (Table 2). The greatest silt content was at the more recently abandoned farmland, Site 1. This occurred with a significantly more basic pH (6.5) as compared to the most acidic site, the Montmorency Forest, where pH was 4.4.

Vegatation varied with plantation site disturbance: the landings being devoid of vegetation and the more recently abandoned farmland regenerating in grassland and small shrubs. Natural conifer regeneration in the harvested sites was prevalent in some sites but sparse in others where the ericaceous understory dominated. Distinguishing between the two sub-sites at Site 5, 10 years after scarification, the thick fruticose lichen carpet did not redevelop in Site 5a, but was replaced by a crustaceous species *Frapeliopsis granulosa* (Hoffm. (Lumbsch.)).

Two months after outplanting, mycorrhiza colonization on black spruce seedlings, ranging from 1.6% in the more recently abandoned farmland to 26.4% in the black spruce plantation, did not show significant differences with the outplanting sites (Table 3). Seedling dry weight varied significantly with the site, the more recently abandoned farmland, Site 1 and the landing, Site 2, yielding significantly lower dry weights (25.6 and 34.3 respectively) than the black spruce plantation (87.3), Site 9. Linear correlation tests showed a positive correlation between mycorrhiza colonization and black spruce seedling dry weight ($r = 0.72$).

Mycorrhiza colonization on outplanted jack pine seedlings varied with the outplanting site, (Table 3) the greatest colonization (77.3%) occurring on seedlings outplanted in site 7, the burned and scarified site, where there was a gap of 40 yrs between harvest and plantation. There was however, no

Table 1. Characterization of 10 conifer outplanting sites in the province of Quebec

Site, forest region and forest type	Soil features (Surficial 20 cm)	Dominant vegetation	History of forestry operations
1. St-Apollinaire (Lotbinière), maple—basswood	—well drained loam —extensive earthworm activity	—grassland —small shrubs	—Farmland abandoned in 1980, planted in 1981.
2. St-Cyprien (Rivière-du-Loup), maple—yellow birch	—Fibric surficial layer, up to 15 cm in depth, consisting of decomposing logging waste, resting on a poorly drained clayey deposit	—Absent —surrounded by mixed forest	—Landing active until 1986.
3. Val-Cartier (Quebec), maple-yellow birch	—well drained loam —extensive earthworm activity	—grassland with *Alnus* and *Rubus* regeneration	—Farmland abandoned ~20 yrs ago, natural regeneration has been continuously removed.
4. Montmorency Forest, balsam fir	—well drained podzol with pockets of organic matter accumulation resulting from scarification	—regeneration of *Rubus* and *Sambucus* —surrounding climax forest 60% *Abies* and 20% *Picea glauca*	—Climax forest cut in 1984. —Brush and logging debris uprooted, windrowed and planted in 1986.
5a. Lac Baillargé (Lac St-Jean west), black spruce	—disturbed podzolic profile —well drained	—Jack pine, black spruce with a *Vaccinium* understory on a crustaceous lichen carpet *Frapeliopsis granulosa*)	—10-yr-old jack pine plantation among black spruce stumps remaining after scarification.
5b. Lac Baillargé (Lac St-Jean west), black spruce	—Typical podzol with a 3—5 cm organic layer over a well developed Ae horizon, resting on a well drained sand	—Jack pine plantation with black spruce, an understory of *Kalmia* and *Vaccinium* on a thick carpet of *Cladina* spp.	—10-yr-old jack pine planted with a shovel among natural regeneration of black spruce.
6. Lac Frenette (Champlain), black spruce	—1—3 cm surficial layer of charred organic matter overlaying sand	—Natural black spruce and jack pine regeneration with an ericaceous understory on a carpet of *Polytrichium commune*	—Following a natural burn in 1983, the area was harvested in 1984, scarified the following year and planted in 1986.
7. Lac de l'intérieur (Lac St-Jean west), black spruce	—Typical podzolic profile with 2—7 cm organic layer, a well developed Ae layer over a well drained sand	—sparce natural regeneration of jack pine, black spruce, alder and birch on a thick carpet of *Vaccinium* and *Cladina*	—Jack pine plantation interspaced with alder; scarified, and planted in 1985, 40 yrs after harvesting.
8. Camp Windigo (Champlain), black spruce	—well drained with no distinct horizons	—absent	—Abandoned landing active from 1970—77, planted in 1985 with jack pine and alder. Organic matter was removed but not burned.
9. Lac Drolet (Frontenac), maple—bitternut hickory	—thin, poorly drained clay deposit over a glacial till	—Natural regeneration of fir, alder, birch and willow, annual grasses and forbs	—40-yr-old mixed forest, cut and scarified in 1980. Planted in black spruce and scotch pine in 1981.
10. Laval University (Quebec), maple—basswood	—well drained sandy loam with abundant earthworms	—annual grasses and forbs among alder and oak plantations	—nursery plots.

significant difference between mycorrhiza formation at this site and at site 5b (70.8%), the pine plantation established among natural regeneration, or at site 10 (66.6%), the university nursery. Mycorrhizal colonization was lowest in site 6 (52.3%), an area that was harvested, scarified and planted 3 years after a forest fire and at site 9 (53.0%), a 6-yr-old plantation, in a poorly drained

Table 2. Physico-chemical properties of soil samples taken from each site at 20 cm depth[a]

Site	K ($\mu g\, g^{-1}$)	P ($\mu g\, g^{-1}$)	N total (%)	pH (H_2O)	Silt (%)	Clay (%)	Sand (%)	Organic matter
1	8.7b	59.2a	0.19bcd	6.5a	20.6ab	11.6c	67.9ab	3.0ab
2	13.0ab	13.2a	0.17cd	5.3bcd	27.7ab	10.7c	61.7abc	4.9ab
3	7.9b	102.5a	0.23bc	5.6bc	43.4a	8.0cd	48.6bc	4.6ab
4	12.9ab	50.6a	0.30b	4.4e	19.0ab	8.7cd	72.3ab	8.5a
5a	2.0b	12.7a	0.04e	5.0cde	5.3b	10.0c	84.7a	1.3b
5b	2.5b	9.5a	0.12de	4.9de	8.3ab	6.0d	85.7a	2.0b
6	1.9b	29.6a	0.11de	5.3bcd	7.0ab	5.8d	87.2a	0.9b
7	4.4b	24.2a	0.12de	4.9de	27.0ab	7.8cd	62.2abc	3.9ab
8	11.0b	63.5a	0.02e	5.7b	10.7ab	5.4d	83.9a	1.6b
9	11.0b	71.8a	0.08de	5.5bcd	39.9ab	17.6b	42.6bc	1.1b
10	43.7a	15.3a	0.42a	5.0cde	15.8ab	26.9a	57.3abc	4.0ab

[a] Mean values of nine samples. Column means followed by the same letter are not significantly different at the 5% level.

clayey soil, planted directly after harvesting and scarification and in site 8 (54.7%), an abandoned landing, where the organic matter was removed but not burned.

Jack pine seedling dry weight (Table 3) also varied with site conditions, the greatest dry weight accumulation occurring in the nursery site (412.7) which was also one of the best sites for mycorrhizal formation. In the other two sites, (site 7, 5b) where mycorrhizal colonization was highest, seedling biomass was significantly lower (149.3 and 173.4 respectively). No correlations between mycorrhizal colonization and dry weight of jack pine seedlings were identified with Pearson correlation coefficients.

Data relating to the mean values of per cent mycorrhiza formation on black spruce and the mean values of soil physico-chemical properties were fit by the following linear regression equations:

% mycorrhiza formation (black spruce)

$$= -1.100 + 0.2788\,(\text{pH}) + 0.2312\,(\text{drainage})$$

$$p < 0.01, \text{f} = 8.7 \text{ at a c.v.} = 25.4, r^2 = 0.69.$$

A similar linear model related percent indigenous mycorrhiza formation on outplanted jack pine seedlings to soil variables.

% mycorrhiza formation (jack pine)

$$1.46 - 0.1732\,(\text{pH}) + 0.0321\,(\text{organic matter})$$

$$p < 0.001, \text{f} = 11.36 \text{ at a c.v.} = 13.0, r^2 = 0.59.$$

Table 3. Mycorrhiza formation and dry weight of jack pine and black spruce seedlings, two months after outplanting

Site	Mycorrhizae[a] (%) (short roots per plant forming mycorrhizae)	Types of indigenous mycorrhizae recognized[a]	Seedling dry wt[a] (mg)
Jack pine			
7	77.3a	2.00a	149.3c
5b	70.8ab	2.10a	173.4c
10	66.6ab	1.30a	412.7a
5a	65.4bc	2.00a	156.6c
8	54.7dc	2.40a	263.1b
9	53.0d	1.10a	194.0bc
6	52.3d	2.20a	215.0bc
Black spruce			
9	26.4a	0.60a	87.3a
3	23.3a	0.30a	62.3ab
4	21.5a	0.70a	50.5bc
2	5.2a	0.10a	34.3c
1	1.6a	0.02a	25.6c

[a] Mean values of 48 seedlings.

Discussion

Indigenous ectomycorrhiza colonization on barefoot jack pine seedlings, 2 months after outplanting, was generally good, being greater than 50% in all cases. The greatest mycorrhizal colonization (77.3%) was observed in site 7, a 2-yr-old jack pine plantation, planted in a characteristic podzol, 40 yrs after harvesting. Site 6 (52.3), and Site 9 (53.0), which were planted respectively in sand with a charred carbon layer and in a clayey deposit over till, had the lowest indigenous mycorrhizal colonization. Both of the latter sites were burned, scarified and planted within two years of harvesting. Parke *et al.* (1983) found a 40% reduction in mycorrhizal colonization in burned clearcuts and a field study in the boreal forest (McAfee and Fortin, 1986) showed that indigenous mycorrhizal populations decreased by more than 50% in a recent burn as compared with the undisturbed forest. Schroenberger and Perry (1982) found that the influence of burning affected mycorrhizae for at least 20 years and Harvey *et al.* (1980) observed that these burn induced changes eventually return to preburn levels. In our study 25% greater mycorrhizal colonization occurred in the 40-yr-old clearcut compared to the recent clearcut. Both of these sites, however, were burned at approximately the same time. These values for the recent clearcut, where there was little natural regeneration, approached those found in a mature jack pine stand in northern Quebec (76%) in a previous study (McAfee and Fortin, 1986). Ferrier and Alexander (1985) have observed that in the absence of hosts, ectomycorrhizal fungi remain active for up to nine months. The natural regeneration of the ectotrophic alder and dwarf birch may explain the presence of ectomycorrhizal inoculum in Site 7, 40 years after clearcutting.

Root exudates from ericaceous plants have been shown to inhibit some ectomycorrhizal fungi (Robinson, 1972). Brown and Mikola (1974) have described the alleopathic effects of fruticose lichens, especially from the genera of Cladonia, Cladina on mycorrhizal fungi. In our study sites, where extensive foliose lichen cover was extensive or ericaceous regeneration was abundant, we did not observe differences in indigenous colonization. Site 5a and 5b differed in the presence of a thick lichen carpet in site 5b, that had not yet developed in site 5a, 10 years after scarification. Mycorrhizal colonization in the two sites, however, was similar.

The original forest types or the varying ground cover did not influence the intensity of mycorrhizal colonization. Rather, the history of forestry operations on each site and their consequent effects on soil parameters such as pH, organic matter accumulation and drainage *etc.*, were more important.

The linear regression model identified pH as one of the soil variables influencing ectomycorrhizal colonization of jack pine and black spruce seedlings. The pH was positively correlated with mycorrhizal formation on black spruce while on jack pine, mycorrhizal formation increased with decreasing soil pH. It is generally accepted that ectomycorrhizal fungi are acidophilic (Hung and Trappe, 1983; Theodorou and Bowen, 1969) and enhanced ectomycorrhiza formation has been demonstrated with increased substrate acidity (Marx and Zak, 1965; Shafer *et al.*, 1985). The influence of soil factors is not only due to direct effects on the fungus. As jack pine is also an acidophilic species, the association of pH with mycorrhiza formation, that we observed, may be the result of a plant mediated process.

Organic matter was the other soil parameter selected in the linear model as significantly influencing mycorrhizal formation on jack pine seedlings. Tyler (1985) found that organic matter content and metal ion saturation percentage were the soil variables most influencing the distribution of macrofungi in beech forests in Sweden. He also noted that the frequency of mycorrhizal species sharply increased towards the most acid soils with well developed mor properties. Frankland and Harrison 1985) found positive significant relationships with mycorrhiza formation on Betula and soil pH and organic matter content in 25 soils from the UK. While several researchers have reported the effects of soil organic matter content on ectomycorrhizal formation (Harvey *et al.*, 1979; Kropp, 1982; Parke *et al.*, 1983), Harvey *et al.* (1987) have shown a strong site-specific relationship between soil organic components and mycorrhiza distribution in forest stands. Fortin (unpublished data) found that 40–50% of the mycorrhizae in jack pine stands in northern Quebec occurred in the organic horizons.

Scarification tends to create pockets of organic matter. If indeed ectomycorrhizal inoculum is associated with organic matter, it is normal then to find pockets of inoculum. We found this at several of our sites especially at the Montmorency Forest, where the organic matter accumulation was greatest. While many seedlings were non-mycorrhizal, some were intensely mycorrhizal, corresponding to the patches of organic matter. Although it was not possible in this study, an investigation of the effects of various types of scarification and broadcast burning on organic matter accumulation would provide further details on the ectomycorrhizal inoculum potentials in clearcut sites.

The other factor influencing indigenous colonization on black spruce seedlings was drainage; mycorrhizal infection increasing in the well drained sites. Drainage was certainly more important for black spruce than jack pine, as it was mostly black spruce that were outplanted in poorly drained sites. Browning and Whitney (1987) have reported a delay in initial infection on wet clayey sites although these authors outplanted jack pine rather than black spruce seedlings. Frankland and Harrison (1985) observed that mycorrhizal formation on Betula was lowest in two soils from poorly drained sites.

The university nursery was the most fertile site, having the highest quantities of N and K in the soil, whereas P did not vary significantly between any of the sites. This more fertile soil corresponded to the site with the greatest seedling dry weight but correlations showed that this fertility and the consequent greater dry weight was not attributed to greater mycorrhizal formation on jack pine seedlings. High N and P regimes (Gagnon *et al.*, 1987; Marx *et al.*, 1977) have been shown to inhibit or decrease mycorrhizal development. Tyminska *et al.* (1986) have shown that growth increases with ectomycorrhizal pine seedlings were not correlated with the intensity of ectomycorrhizal colonization. This was also true in our observations where mycorrhizal colonization was not significantly influenced by soil N or P.

Although we did not attempt to identify individual indigenous mycobiont spp. at each site, the number of different types per site was recorded. The presence of *Cenococcum geophilum* Fr., easily recognized by its distinctive black mantle and long, bristly emanating hairs, was noted at nearly all of the sites but was especially frequent at sites 8 and 6, respectively the landing, where the organic matter had been removed, and the recent burn. Frankland and Harrison (1985) related presence of *C. geophilum* to the percent organic matter in the soil. In the two sites in our study, where *C. geophilum* was more frequent, there were significant differences in organic matter accumulation. Also at site 6, the recent burn, the presence of 'beaded roots' which has been previously correlated with phosphorous deficiency (Frankland and Harrison, 1985) or related to the occurrence of *Mycelium radicis atrovirens* Melin (MRA) (Richard and Fortin, 1974) was noted. Our baiting plant bioassay method could be useful to investigate the presence of dermatiaceous ectendomycorrhizal fungi and of MRA in the charred layers of recent burns. No significant differences in the number of types at the various sites for either jack pine or black spruce was found. Browning and Whitney (1987) found that diversity in jack pine reforestation sites in northern Ontario, increased more over time in the same site rather than between sites.

Indigenous colonization on black spruce seedlings was relatively less than on jack pine seedlings, being especially low in the abandoned, primarily endomycorrhizal, agricultural soils. Inoculation, with particularly adapted fungi, in these soils devoid of inoculum, could be of great benefit to outplanted seedlings. Comparing colonization of jack pine and black spruce at site 9, a poorly drained clay deposit over till, where the two species were planted in the same plots, indigenous colonization was twice as intense on the jack pine root systems. However, for the jack pine, this was a relatively poor site, perhaps indicating the preference of this species for xeric sites, or simply that black spruce requires a longer time period to initiate mycorrhizal development or that black spruce has less sugar available for ectomycobionts. Wilson *et al.* (1987) stated that on outplanted *Picea sitchensis* (Sitka spruce) seedlings mycorrhiza formation with indigenous fungi was slow. In inoculation trials with a hyphal suspension of *Laccaria bicolor* 6, 9 and 12 weeks after inoculation, the % mycorrhiza formation was 0, 32, 64 and 7, 23, 40% respectively for jack pine and black spruce seedlings (Fortin *et al.*, 1987). Our low colonization values with black spruce could be due to a lag phase in colonization required by this species. That variation in growth response is related to levels of mycorrhizal colonization may indicate that a certain biomass must be attained before the black spruce seedlings can sustain ectomycobionts on the root systems.

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