FACTORS AFFECTING VEGETATION DYNAMICS ON ACID, METAL-CONTAMINATED SOILS OF THE SUDBURY AREA

Keith Winterhalder

Biology Department, Laurentian University

ABSTRACT

The primary factor affecting vegetation dynamics on Sudbury's barren soils is their acidic, aluminum-, copper- and nickel-toxic properties, although certain plant species avoid the problem through genetically-based metal-tolerance. The soil can be detoxified sufficiently to initiate colonization by the surface-application of ground limestone, the dolomitic variety being more effective at certain sites. The drought-vulnerability of seedlings, resulting from toxicity-engendered root growth limitation, is exacerbated by enhanced frost action resulting from the lack of leaf litter. Phosphorus deficiency can be a problem on sandy valley-bottom soils, but most barren soils contain a substantial reservoir of phosphorus and nitrogen in the form of residual organic matter. Both rhizobial and actinorhizal species play an important role in dynamics, and it is likely that the role of mycorrhizae is critical, although more research is required on the latter topic. The seed availability factor is rarely limiting; while the seed bank is small, in most sites the seed rain of light, wind-dispersed seeds is adequate to colonize soil detoxified by liming. The process of "succession" can follow one of three different routes, depending on whether the barrens are left untreated, treated with limestone only, or treated with limestone and a grass-legume seed mixture.

Introduction

Sudbury lies at the southern edge of the Precambrian Shield, in Rowe's (1972) Great Lakes - St. Lawrence Forest Region, which is transitional between the coniferous forest to the north and the deciduous forest to the south. Prior to the advent of the mining and smelting industry in 1883, the area was characterized by extensive stands of red pine (*Pinus resinosa*) and white pine (*Pinus strobus*). One hundred years of logging, fire, soil erosion and enhanced frost action, as well as sulphur dioxide fumigation and copper, nickel and iron particulate fallout from the region's three smelters, have severely damaged the Sudbury landscape (Winterhalder, 1984), giving rise to 10,000 hectares of barren land which form concentric zones around the three smelters. Soils on the slopes have a stony covering that is the result of the combined action of frost-heaving and erosion on the glacial till-derived soil. Extensive rock outcrops also occur, on which shallow pockets of soil can be found, while in the valleys areas of boulder clay alternate with a fine sandy-silty alluvium. On valley sites that once supported a spruce bog or a cedar swamp, barren peatland now remains.

Until recently, the only plants found at "barren" sites were relict individuals of woody species that had survived the stresses responsible for the loss of the original vegetation. Tree species falling into this category were mostly white birch (*Betula papyrifera*), red maple (*Acer rubrum*) and red oak (*Quercus borealis*) in drier sites and trembling aspen (*Populus tremuloides*) in moister areas. While the former three species took on a coppiced form, with suckers arising from the base of a stool, the aspens existed as clonal patches arising from root suckers. Relict shrubs included the common blueberry (*Vaccinium angustifolium*), wild currant (*Viburnum cassinoides*) and red elderberry (*Sambucus pubens*). More recently, metal-tolerant plants, which will be discussed later, have begun to colonize the barrens.

Surrounding the barrens was a 36,000 hectare zone of stunted, semi-barren woodland, characterized by patches of bare soil between the relict, coppiced white birch, red maple and red oak (Amiro and Courtin 1981).

Soil characteristics conformed with the vegetation zones described above, showing a pattern of decreasing pH and increasing copper and nickel content as the three smelters were approached (Winterhalder 1975).

No attempt was made to revegetate the barrens until 1969, because it was believed that the only factor directly limiting the re-establishment and growth of plants was atmospheric quality. However, the announcement by Inco Ltd. in 1969 of its intention to construct a 381 metre smokestack stimulated the Ontario Department of Lands and Forests and Laurentian University to initiate a joint experimental tree-planting programme on a barren site near Coniston and in a stunted, partially-barren red oak woodland near Skead. When the trees on the barren site showed almost total mortality, it was suspected that the direct impact of atmospheric SO_2 was not responsible, and the question of the possible existence of limiting factors other than the direct effect of air pollutants was raised. A number of candidate environmental factors, falling into physical, chemical and biotic categories respectively, were considered, some of which proved to be important, others of which were later abandoned.

Atmospheric Sulphur Dioxide As A Potentially Limiting Factor To Plant Growth

Dreisinger & McGovern (1964) showed that, under Sudbury field conditions, acute SO_2 injury to vegetation could occur when the following concentrations were equalled or exceeded:

0.95 ppm SO_2 for 1 hour	0.35 ppm SO_2 for 4 hours
0.55 ppm SO_2 for 2 hours	0.25 ppm SO_2 for 8 hours

If any one of these conditions was met in daylight hours from mid-May to mid-October, then the fumigation was termed a Potentially Injurious Fumigation. In a later Ministry of the Environment report, Dreisinger & McGovern (1969) drew pollution zones onto a map of the Sudbury area, based on mean levels of SO_2 from 1953-1967 (Figure 1). The most severely impacted zone formed an ellipse running from southwest to northeast of the Falconbridge smelter, surrounded by a less severe elliptical zone that encompassed the Coniston and Copper Cliff smelters. The zones of vegetation damage of Struik (1973) (Figure 2) are similar, except that in this case each of the three smelters is surrounded by its own ellipse of barren ground.

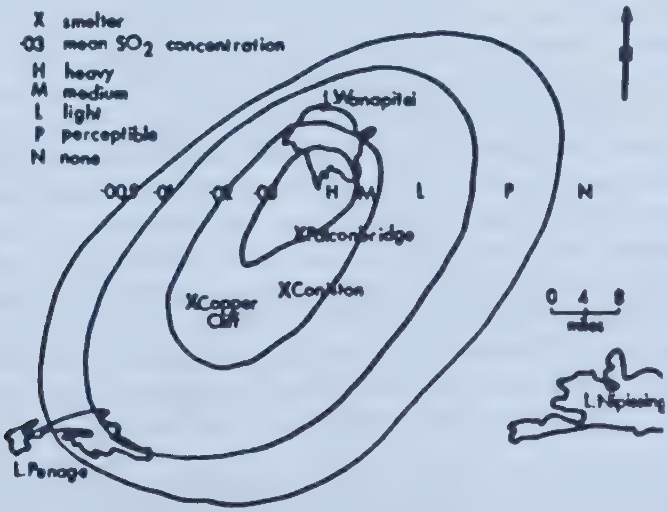

Figure 1: *Pollution zones in the Sudbury area, based on mean levels of SO_2 from 1953-1967 (Dreisinger & McGovern 1969).*

Although the deleterious effect of sulphur dioxide emissions on aquatic environments in the wider Sudbury area have been clearly demonstrated (e.g. Beamish & Harvey 1972), effects on the terrestrial environment are much more difficult to monitor. When an area is already denuded, it is not easy to obtain direct evidence of the direct effect of atmospheric pollution.

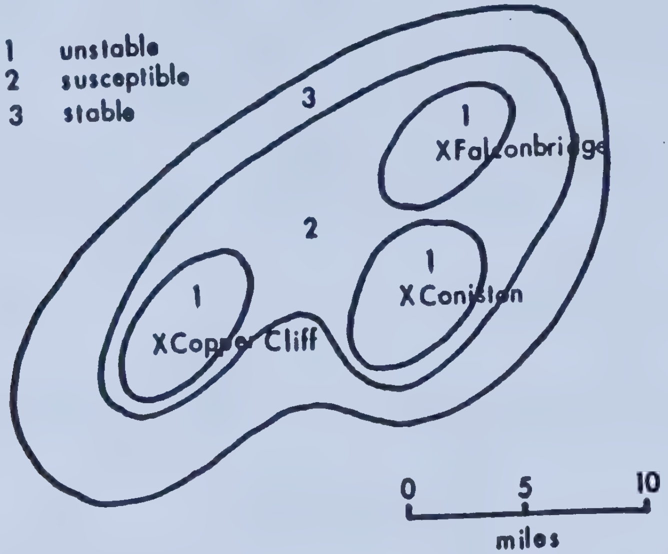

Figure 2: *Zones of "site and vegetational stability", based on aerial photographs taken in 1970 (Struik 1973). "Unstable" sites were barren, "susceptible" sites were semi-barren and "stable" sites were "normal".*

In the 1970s, the Ontario Ministry of the Environment published a series of annual reports on direct SO_2 damage to such species as poplars and birches, and photographic evidence of the sensitivity of white pine to sulphur dioxide was obtained by the Department of Lands and Forests in August, 1968, when sulphur dioxide fumes drifted further southwest than usual, and burned stands of white pines in the Lake Penage area. The Laurentian University/Ontario Lands & Forests "Sudbury Environmental Enhancement Programme" (SEEP) set up experimental transplants of potted white pine in areas of high SO_2 pollution in 1969, but results did not support the hypothesis that high SO_2 fumigation was the factor limitng tree growth. To quote an early progress report (Department of Lands & Forests 1973): "The potted stock trials have demonstrated that the role of recent injurious fumigations of sulphur dioxide has been over-estimated. Most certainly vegetative dieback and soil acidification has resulted from the presence of noxious gases, but at the present time, a much more critical factor responsible for limiting vegetative re-invasion and development is the hostile, impoverished soil medium, in so far as seed germination is possible but initial rooting is curtailed". It was later acknowledged that it is very difficult to measure the "subtle" effects of atmospheric sulphur dioxide on vegetation (J. Negusanti, Personal Communication[1]), and the Ontario Ministry of the Environment turned its attention to measuring the effects of acid precipitation on vegetation by the use of long-term monitoring plots through the Acid Precipitation in Ontario study (APIOS) (Ministry of the Environment 1991).

The ineffectiveness of sulphur dioxide pollution as an agent of permanent denudation is confirmed by studies on old roast bed sites. Early methods of roasting in open beds (Laroche *et al.* 1979) has often been blamed for the creation of the barrens, but as demonstrated by Turcotte (1981), the only roast bed sites that are currently surrounded by

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1 Mr. John Negusanti, Phytotoxicology Section, Ministry of the Environment & Energy, 199 Larch Street, Sudbury, Ontario P3E 5P9.

barrens are those in which there is also an old smelter site nearby. It seems that the roast beds produced large amounts of sulphur dioxide, but relatively little particulate metal.

When soil samples were taken in 1969 from each of the Dreisinger & McGovern (1969) pollution zones, chemical analysis showed a mean pH of around 4.0 in the "heavy" zone, around 4.5 in the "medium" zone and around 4.8 in the "light" zone, with soil copper and nickel levels showing a similar trend in relation to fumigation zones (Winterhalder 1975).

Figure 3 (Balsillie *et al.* 1978) shows the striking reduction in Potentially Injurious Fumigations that occurred in 1972 as a result of the closure of the Inco smelter at Coniston and the pyrrhotite sintering plant at Falconbridge, limitation of SO_2 output from the Inco iron ore recovery plant to 250 tons/day, and the introduction of the 381 metre "superstack" at the Inco Copper Cliff smelter, as well as a striking reduction in SO_2 tonnages emitted by both companies. It was expected that the improvement in atmospheric purity would give rise to a rapid improvement in existing vegetation and spontaneous recolonization of the barrens. As discussed below, any recovery has been limited and slow, confirming the hypothesis that soil properties were a more critical factor in the suppression of colonization than air quality. It is clearly true that the occurrence of numerous injurious fumigations during a season will prevent a tree from reaching its full growth potential, and the improved growth observed since 1972 in previously stunted birches and poplars in the moderately-affected zone is partly the result of improved atmospheric quality. In general, however, it is the indirect and historic effect of atmospheric chemistry, by way of the soil medium, that has been the major limiting factor.

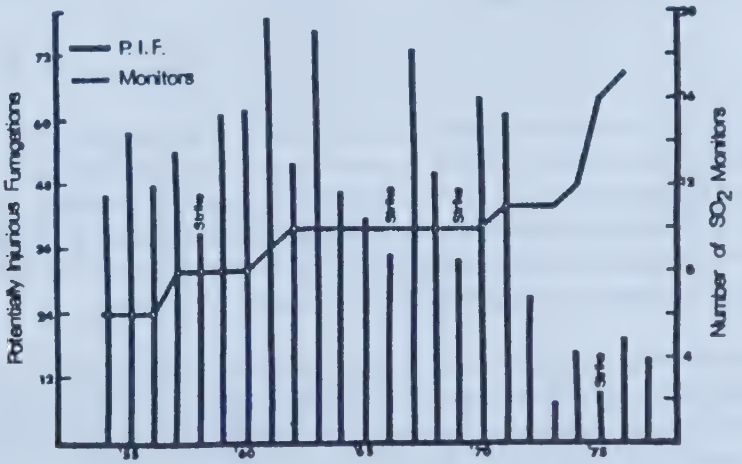

Figure 3: *Number of Potentially Injurious Fumigations occurring in the Sudbury area (Balsillie et al. 1978).*

Soil-based Limiting Factors

Tree-planting trials on the barrens by the Laurentian University-Department of Lands & Forests "Sudbury Environmental Enhancement Programme" (SEEP) in 1969 and 1970 resulted in almost total mortality. Bioassay trials (Hutchinson & Whitby 1974, Whitby and Hutchinson 1974, Winterhalder 1974, Balsillie *et al.* 1978) showed restriction of seed germination and inhibition of root growth to a degree closely related to the distance from the smelters. Roots of seedlings germinated in soil from the barrens show an immediate cessation in growth when the soil is contacted, and the seedling develops a mass of stubby roots on top of the soil. Once the soil dries out, the seedling dies of drought. In cases where roots are able to penetrate the soil, they do not develop root hairs.

Even in 1993, there are barren areas in the field that support no plant growth, or where growth is limited to metal-tolerant species.

Soil Chemistry

pH and associated effects

The pH of mineral soils collected from hilltops and slopes in a south-southeast transect from the Copper Cliff smelter in the 1970s ranged from 3.3 at 2 km distance to 3.9 at 34 km (Freedman & Hutchinson 1980), and Sudbury soils were not only found to be depressed from the normal pH of 4.5-5.5 to pH 3.2-4.4, but the titratable acidity was found to be very high (2.5-6 meq/100g) and the base saturation from 1-5% (Balsillie *et al.* 1978). Extremes of soil acidity that have been recorded near the Coniston smelter include 2.4 (Hazlett *et al.* 1983) and 2.2 (Hutchinson & Whitby 1974).

The direct effects of low pH on plants are often less deleterious than the indirect effects, and in a highly acidic soil that contains aluminosilicate minerals such as clays, aluminum ions will be present at a phytotoxic concentration. For example, Roshon (1988) found total "available" aluminum levels of around 400 $\mu g/g$ in several acidic Sudbury-area soils.

Furthermore, the acidity of the soil solubilizes the copper and nickel that has accumulated in the soil from atmospheric fallout, contributing to its phytotoxicity.

Metal contamination

In most "normal" soils, the average total copper content ranges from 15 to 40 $\mu g/g$ (average = 20 $\mu g/g$) (Aubert & Pinta 1977), whereas Hazlett *et al.* (1983) found a copper content of 9700 $\mu g/g$ in a soil 0.4 km from the Coniston smelter, while even 3 km from the Copper Cliff smelter, Freedman & Hutchinson (1980) described a soil containing 3700 $\mu g/g$ copper in its organic horizon. Toxicity symptoms often appear at "available" copper levels between 25 and 50 $\mu g/g$, the symptoms becoming more severe as the pH drops, whereas Roshon (1988) found Sudbury-area soils with "available" copper ranging from 300 - 900 $\mu g/g$ in her study.

In most temperate and boreal soils, the total nickel content ranges from 20 - 30 $\mu g/g$, whereas Hazlett *et al.* (1983) found a nickel content of 6960 $\mu g/g$ in a soil 0.2 km from the Coniston smelter, while 3 km from the Copper Cliff smelter, Freedman & Hutchinson (1980) described a soil containing 3000 $\mu g/g$ nickel in its surface horizon.

Metal-metal, pH-metal and limestone-metal interactions

Experiments on the germination and early growth of *Agrostis gigantea* (redtop), an important revegetation grass in the Sudbury area, suggests that the root growth inhibitory effects of copper and nickel interact in a synergistic fashion, i.e. they enhance each other's phytotoxic effect, giving a total toxicity that is more than the sum of the toxicities of the individual elements. On the other hand, the interaction between nickel and aluminum is antagonistic, the aluminum "protecting" the plant from increased nickel concentrations (Winterhalder 1983).

The effectiveness of limestone application in detoxifying the barren soils appears at first glance to indicate a simple case of a single limiting factor (i.e. low pH). As an environmental factor, however, pH rarely operates alone. Even Dansereau's (1966) "Law of Factorial Control", which distinguishes the limiting or "discrepant" factor from general holocoenotic effects of the environment, does not fully fit the circumstances that exist in the Sudbury barrens soils. We have a case here of an apparent single factor possessing its own particular suite of dependant and interacting subfactors, a sort of "oligocoenosis".

There are a number of mechanisms that could be postulated to explain the detoxification of Sudbury soils by ground dolomitic limestone. In a case where the soil is fully neutralized, it is possible that the toxic metal has been precipitated as a carbonate or a hydroxide. In many cases, however, it is not necessary to raise the pH of a soil to more than around pH 5 to achieve detoxification. The hydroxylation of the trivalent aluminum ion as the pH is increased by liming is almost certainly a factor, but it does not fully explain detoxification, since theoretically the copper ions could still be active inhibitors of root growth. A possible role of both calcium and magnesium ions in the dolomitic limestone employed is in the competitive exclusion of metal ions from the root-hair's exchange complex. The calcium may also play a role in improving membrane integrity.

It may be that magnesium plays yet another role, not as yet understood (Figure 4).

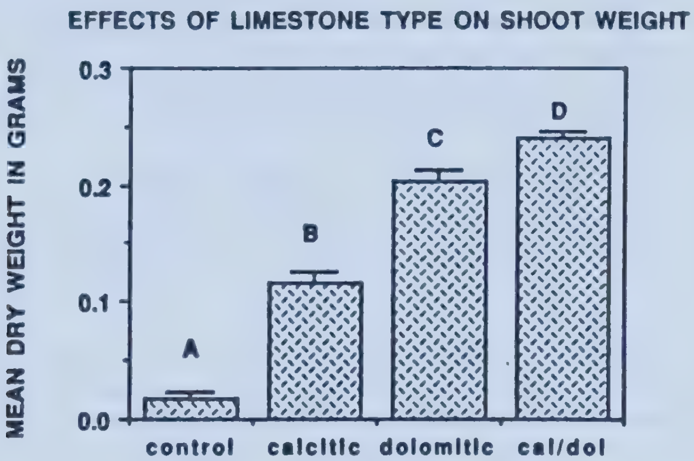

Figure 4: *Effect of limestone type on shoot weight in Mung beans grown on a barren soil from the Falconbridge area.*

Figure 4 shows that mung bean seedlings grown in certain Sudbury barren soils, especially those near the Falconbridge smelter, grow well when limed with dolomitic limestone, but relatively poorly when limed with calcitic limestone. It is hypothesized that this differential effect is the result of induced magnesium deficiency under calcitic limestone treatment and/or of antagonism between magnesium and nickel under dolomitic limestone treatment.

Soil nitrogen and phosphorus

Early field experiments, carried out on the sandy flood plain of Coniston Creek, indicated that soil phosphorus deficiency became a secondary limiting factor to plant growth once the soil was detoxified with limestone (Figure 5). It was later found that plant growth could be initiated and maintained for several years on stony slopes without the addition of phosphorus fertilizer, and it was hypothesized that there was a substantial capital of phosphorus, presumably in the form of phytin (inositol hexaphosphate) and its derivatives, in the "fossil" organic matter derived from the pre-denudation vegetation. Preliminary studies suggest that there is indeed a correlation between soil phosphorus and organic matter content.

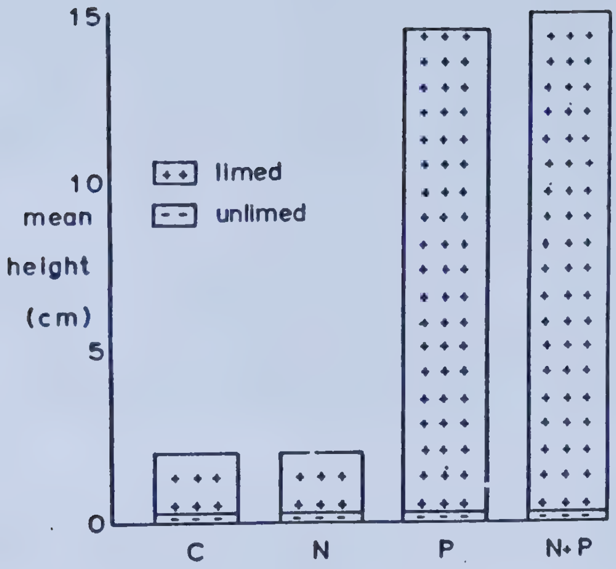

Figure 5: *Effects of lime-phosphorus-nitrogen interaction on the growth of redtop seedlings on sandy Coniston soil, showing that there is no response to phosphorus until the soil is limed, whereas there is no significant response to nitrogen under any treatment.*

Most plants growing on these barren soils seem to possess V-A mycorrhizae (Blundon, 1976), assisting them in obtaining what little soil phosphorus is present. Furthermore, the use of limestone as a soil ameliorant itself assists in the release of phosphorus (Fransen 1991).

Over a period of many years, more phosphorus will undoubtedly be slowly released to the system by the weathering of undecomposed stones in the glacial till, as well as through breakdown of the exfoliating bedrock material. Nevertheless, the total phosphorus "capital" in soil and parent material can limit the type of plant community that will ultimately occupy a site (Beadle & Burges 1949), and in the relatively short term, edaphic factors may prevent the development of the full climatic climax vegetation-type.

Since nitrogen fixation is a biological process, it is dependant on the presence of an ample supply of phosphorus, and preliminary studies (Winterhalder 1987) show a modest correlation between total soil phosphorus content and soil nitrogen measured by the Kjeldahl technique, which is primarily a measure of organic nitrogen.

Native symbiotic nitrogen fixers in the original pine forests of the Sudbury area were probably very rare, and were almost certainly confined to actinorhizal genera such as *Alnus* spp. (green & speckled alder) and *Comptonia peregrina* (sweet fern). Sweet fern can be found as relict plants or stands on barren sites, but it spreads actively once the soil is limed.

<u>Soil calcium and magnesium</u>

Lozano & Morrison (1981), in discussing the mineral nutrition of woody plants in the Sudbury area, suggested that not only calcium but also magnesium deficiency might become a problem once the metal toxicity was eliminated. Although there is so far no direct evidence of either calcium or magnesium deficiency in the soils, the effect of calcitic limestone on mung beans described above suggests a possible induced magnesium deficiency when the calcium:magnesium balance is altered by calcite application. It is a therefore a fortunate circumstance that the limestone most readily available in Sudbury, from Little LaCloche Island or from Michigan, is dolomitic in nature.

Soil Physical Characteristics

Some of the soils in the Sudbury area present physical problems to plant growth. Probably the most difficult soils are the boulder clays, which take on a gully-eroded, "badland" aspect. These soils do not lend themselves to the surface liming and seeding approach, but are an ideal site on which to plant black locust (*Robinia pseudo-acacia*). The fine silty sands of some of the creek valleys and other lowlands are equally unreceptive to the manual approach, but respond well to the use of light agricultural machinery such as the chain harrow. In fact they lend themselves to a similar treatment to that which is customary for local mill tailings (Peters 1984), which they resemble with respect to particle size distribution. At the other textural extreme are the gravelly soils of the Skead-airport area, which support a sparse oak forest. Here, the free-draining soil and the moisture-consuming trees make the establishment of a grass cover, apart from the native wavy hairgrass (*Deschampsia flexuosa*), difficult.

The loamy soils of the slopes, with their stony mantle, form an excellent seed bed and ameliorant trap, the stones forming a protective mulch. Although frost heaving and needle ice formation are common on these soils, the enhanced root growth that follows liming allows for the stabilization of the heaved areas by plant roots, while the cracks formed by frost action can be beneficial in creating "safe sites" in which seeds and ameliorants can lodge.

Soil Microbiota

Soil microbiota are just as important to vegetation development as are higher plants although, as Parkinson (1978) points out, very few land reclamation projects incorporate soil biological studies into an integrated research programme.

Soil algae are often the first primary producers to colonize mined land, on which they can act as stabilizers and and begin to build up fertility (Booth 1941). Many of the Cyanobacteria, formerly known as blue-green algae and still most conveniently considered with the algae in their role as primary producers, are nitrogen fixers, and they can play an important role in soil nutrient buildup. However, on the acid, metal-contaminated land in the Sudbury area, Maxwell (1991) found that chlorophytes such as the acid-tolerant *Chlamydomonas acidophila*, shown by Twiss (1990) to possess copper-tolerant strains in the Sudbury area, and *Chlorella saccharophila* also recognized (Hutchinson *et al.* 1981) as a metal-tolerant alga, were the main algal inhabitants of the Sudbury barren soils, and that cyanobacteria did not begin to colonize until the soil had been partly neutralized by the surface application of ground dolomitic limestone. She also found evidence that the cyanobacterial inoculum was brought onto the site on the limers' boots. In the Sudbury area, the cryptogamic mat that is often characteristic of barren soils is typically composed of moss protonemata (especially those of *Pohlia nutans*), rather than the more usual filamentous algae.

Other free-living nitrogen-fixers include the bacterium *Azotobacter*. An *Azotobacter*-like bacterium capable of growing on a nitrogen-free agar medium has been isolated from Sudbury barren soils, and nitrogenase activity in this organism has been demonstrated in agar culture by the widely-used acetylene reduction technique. Neverthless, neither the author nor de Catanzaro (1983) has been able to demonstrate nitrogenase activity in the soils themselves, and it is possible that the organisms do not fix nitrogen under soil conditions.

It is likely that, in the case of a tolerant grass such as tufted hairgrass, certain bacteria intimately associated with the roots (the rhizosphere) are nitrogen fixers. In fact, the genus *Azospirillum*, which grows right on the root surface (the rhizoplane), are preferentially associated with grasses (Hubbell & Haskins 1984).

With respect to symbiotic nitrogen fixation, the only native symbiotic nitrogen fixer that survives sporadically on the barrens is the actinorhizal shrub known as sweet fern. Following liming, sweet fern spreads rapidly. Unfortunately, the native alders (speckled alder - *Alnus rugosa*, and green alder - *A. crispa*) do not readily volunteer on treated land, despite their winged propagules. A native actinorhizal shrub from Manitoulin Island, soapberry (*Shepherdia canadensis*), has been successfully transplanted onto revegetated barrens, where it produces fruits, but does not so far show evidence of spreading. Another Manitoulin Island species, bearberry (*Arctostaphylos uva-ursi*), has not only been established succesfully by transplant, but is spreading vigorously by vegetative growth and, to a limited extent, by seed. Although not confirmed, this species is suspected of being actinorhizal (Sprent 1979).

In view of the lack of appropriate native symbiotic nitrogen fixers, two herbaceous legumnious species are used as part of the revegetation seed-mixture: Alsike clover (*Trifolium hybridum*) and birdsfoot trefoil (*Lotus corniculatus*). Blundon (1976) compared nodulation of two species of *Trifolium* on limed and unlimed barren soils. She found that nodulation did not occur on unlimed soils, but that liming increased nodulation to 20%. In general, nodulation of Alsike clover and birdsfoot trefoil on revegetated land is excellent. In more difficult sites, such as the boulder clay "badlands" mentioned above, a small leguminous tree native to the Appalachians, black locust, is used with great success.

Nitrogen is not the only plant nutrient for which the soil microbiota play an important role. It is not, therefore, surprising that mycorrhizal associations can be quite critical to the recolonization of disturbed lands, as shown by Schramm (1966) on anthracite wastes in Pennsylvania, and it is likely that V-A mycorrhizal associations, especially if in combination with rhizobial associations, can assist in the accelerated rehabilitation of industrial wastelands (Daft & Hacskaylo 1976, Khan 1978). Indeed, Daft & Nicolson (1969) have suggested that vesicular-arbuscular (V-A) mycorrhiza may have evolved as a response to the need for more efficient extraction of phosphorus. Furthermore, V-A mycorrhizal fungi are not only important in the phosphorus nutrition of the host plant, but they also play a role in soil aggregation, and McIlveen (Balsillie *et al.* 1978) showed that the aggregation of soil particles less than 0.05 mm diameter into particles greater than 0.05 mm in diameter was reduced by 20% in the vicinity of the Sudbury area smelters at a time when no plants (and therefore no V-A mycorrhizae) were present.

Although McIlveen (Balsillie *et al.* 1978) showed a decrease in the numbers of soil fungi and bacteria in the vicinity of the smelters, as well as a restriction in the degree of colonization of roots of oxeye daisy (*Chrysanthemum leucanthemum*) and devil's paintbrush (*Hieracium aurantiacum*) by V-A fungi, some degree of infection with V-A mycorrhizae is almost universal in the plants colonizing the Sudbury barrens, and Blundon (1976) has found that grasses invading barren soils in the Sudbury area readily become V-A infected.

It therefore seems likely that V-A mycorrhizae can re-establish quickly on a relatively sterile substrate through the transport of spores into the area by wind, rain, animals etc., so that the inoculum is not a limiting factor in the revegetation of Sudbury soils, but it is clearly advantageous to have a ready-made inoculum in the soil, and part of the rationale of the transplantation of blocks of soil from target plant communities onto revegetated Sudbury barrens is the introduction of the appropriate symbionts. Indeed, Reeves *et al.* (1979) have found that mycorrhizae are frequently absent in the early stages of succession on disturbed sites, and they hypothesized that the provision of mycorrhizal inoculum might enable the succession to "skip" one or more stages.

Ectotrophic mycorrhizae almost certainly play a role in the survival and colonization of woody species on the barrens. Jones & Hutchinson (1986) have shown that mycorrhizal paper birch seedlings grow better than non-mycorrhizal seedlings when subjected to toxic levels of nickel, and that seedlings infected with *Scleroderma flavidum* grow better than those infected with three different species of *Laccaria*. On the other hand, growth of mycorrhizal seedling exposed to toxic copper levels was significantly less than that of non-mycorrhizal seedlings.

Soil fauna play an important role in litter decomposition and nutrient cycling (Hutson 1980), and they may become critical elements in the reestablishment of a functioning ecosystem on mined land. In the acid, metal-contaminated soils of the Sudbury region, Behan-Pelletier & Winterhalder (unpublished manuscript) found only three oribatid mite species on barren soils, but this increased to thirteen species a few years following revegetation. Semi-barren soils, with intermediate pH and copper and nickel levels, supported thirty-three species of oribatid, but still far fewer than in undisturbed Ontario forests. Although the fauna of the semi-barren communities that surround the barrens form a source of immigrant mites for the revegetated barrens, there would be some benefit in using the "nucleation" approach, discussed above, as an additional source both of soil fauna and soil microflora.

Although comparisons have not, as yet, been made between the ground beetles of barren and revegetated land in Sudbury, a preliminary study (Winterhalder & Goulet, unpublished data[2]), shows that recently revegetated land supports forty-six species of ground beetle.

PLANT-BASED LIMITING FACTORS

Differential Metal Tolerance of Plants

The degree of metal tolerance itself can be regarded as a limiting variable, interacting as it does with the degree of toxicity of the soil. Dansereau's (1966) 9th "Law of Ecology", the "Law of Ecesis", suggests that "the resources of an occupied environment will first be exploited by organisms with high tolerance and generally with low requirements". Since the initiation of atmospheric improvement in 1972, a number of species or ecotypes of species having these characteristics have begun to colonize previously barren soils, the first noted being *Agrostis scabra* (tickle grass), which was seen to colonize experimental plots that had been fertilized but not limed, a treatment that was not an adequate detoxifier for the purpose of establishing agronomic grasses (Winterhalder 1974). Although tickle grass still colonizes large expanses of moist valley-bottom soil, it is only a weak perennial, and it often does not persist. Tickle Grass was later found to have evolved metal-tolerance (Archambault 1991).

The most notable of the colonizing grasses is tufted hairgrass (*Deschampsia caespitosa*), shown by Cox & Hutchinson (1980) to be multiple-metal-tolerant. An interesting and unique consequence of the dual phenomena of persistence of "relicts" and metal tolerance of grasses is a "savanna woodland" of clonal trembling aspen with an understory of tufted hairgrass that can be found in the Coniston Creek valley.

Other species in which enhanced metal tolerance has been reported are redtop (Hogan *et al.* 1977), Canada bluegrass - *Poa compressa* (Rauser & Winterhalder 1985) and a shrub known as dwarf birch -*Betula pumila* var. *glandulifera* (Roshon 1988).

It is notable that both tufted hairgrass and dwarf birch continue to spread aggressively after the soil has been limed, even if it is also seeded with grasses. This may be explained by the fact that neither species is a true acidophile, dwarf birch being characteristic of fens rather than bogs, and tufted hairgrass normally being found on circumneutral or alkaline soils. In contrast, a known acidophile that occasionally colonizes barren soils, but one upon which no tests of metal tolerance have so far been carried out, is sheep sorrel (*Rumex acetosella*).

Barren peatlands near the Coniston smelter have shown extensive colonization from the edges, with a rush (*Juncus brevicaudatus*), wool sedge (*Scirpus cyperinus*) and rattlesnake grass (*Glyceria canadensis*) being the major colonizers. All of these species should be investigated for enhanced metal-tolerance, as should the dryland sedge *Carex aenea*, which colonizes moderately contaminated soils.

Following colonization by species that are clearly outstanding in their metal-tolerance, we find a second set of plants that are able to colonize those acid, metal-contaminated soils that have spent a number of years free of atmospheric pollutant input, and have shown a consequent rise in pH of at least one unit since the early 1970s. Such soils are found close to the Coniston smelter, and they are currently undergoing colonization by white birch. So far there

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2 Dr. H. Goulet, Biosystematics Research Institute, Ottawa, Ontario.

is no evidence that, like dwarf birch, this species possesses metal-tolerant ecotypes, and it is likely that its ability to colonize these moderately toxic soils is the result of the phenotypic plasticity of the species. Another colonist that probably does not involve genetic selection for metal tolerance is wavy hairgrass, which is beginning to move in to form an understory under the relict and newly-colonized white birches. A preliminary study (Archambault 1989) did not show any difference in copper and nickel tolerance between plants from the Sudbury barrens and those at Wawa, where copper and nickel levels are not elevated, although the soil is acidified. It is therefore suggested that its ability to colonize may once again be due to phenotypic plasticity and to its well-known acidophily (Scurfield 1954).

The ability of a species to survive as a relict specimen does not necessarily indicate tolerance at the seedling stage, although it may give the species a head start in terms of colonization following soil amelioration. Amongst the tree species, red oak, red maple, white birch and trembling aspen are the commonest relicts. The survival of the trempling aspen is probably largely due to its ability to form root suckers, the relicts usually occurring as clonal patches on lowland sites, rather than as individuals, and they do not display conspicuous foliar symptoms of stress. They produce copious seeds, but the seeds do not germinate unless the soil is limed.

White birch relicts, on the other hand, occur as coppiced individuals that show a mid-season marginal chlorosis of the earlier leaves, although the leaves that are produced late in the season are green and do not show premature chlorosis. A possible explanation of this phenomenon could be soil moisture stress when the soil is still cold, or calcium-magnesium imbalance, as discussed earlier.

The relict red maples show distinct foliar symptoms of stress in the form of premature reddening, and each coppiced individual undergoes progressive "regressive dieback", in which less and less leaf biomass is produced each year. Each of the stems surrounding the base or "stool" eventually dies, and is replaced by a smaller stem. Ultimately all meristematic sites for suckering are used up, and the individual dies. Individuals continue to produce seeds throughout this prolonged period of dieback, and the seeds germinate normally, but quickly develop a red coloration and do not progress beyond the first foliar-leaf stage. The interaction of the red maple seedling with the soil is clearly very different from that which occurs in the case of white birch. There is some evidence of partial recovery of regressing maples following liming, but evidence is not conclusive. As mentioned previously, there is also some preliminary evidence that magnesium deficiency (or magnesium-calcium imbalance) may be a factor in the decline of red maple, but other possible causes such as lack of mycorrhizal infection require attention.

Competition as a Limiting Factor

Although it would be incongruous to consider plant competition as a potential limiting factor in the revegetation of bare soil, it must be considered as a factor once revegetation measures such as seeding or tree-planting have been employed. Competition, usually from grasses, can form a barrier to colonization and succession on many reclamation sites, as well as competing with planted trees for light and nutrients (Bradshaw & Chadwick, 1980), and forming a winter habitat for bark-gnawing rodents. In the Sudbury land reclamation program, the use of low seed and fertilizer rates, probably assisted by the stony soil, seems to have eliminated the competition factor.

A striking example of the need to consider the relative merits of seeding and natural colonization with care is seen at Mount St. Helen's. Immediately after the eruption in 1980, the Soil Conservation Service aerial-seeded 32,000 hectares with non-native grass and legume seeds, in an attempt to stabilize the surface. Unfortunately, the grass cover did little to prevent erosion, but attracted mice that killed many of the existing conifers by chewing the bark during the winter (Dale 1992). Furthermore, the dense cover of birdsfoot trefoil helped to reduce the success of native species. Following the Mount St. Helen's experience, the Soil Conservation Service has established native plant nurseries to provide seeds of native species.

Microclimatic Factors

As part of the Laurentian University-Department of Lands & Forests SEEP study, a comparison was made in 1969-70 of the microclimate on an open barren site near Coniston and an open scrub oak forest near Falconbridge. Surface wind velocities on the barrens were approximately twice those in the woodland, and they had a beneficial cooling effect on surface soil temperatures. On the bare, open patches within the scrub forest, temperatures exceeded the thermal death point (about 47°C) on several days in the early summer.

Courtin[3] (personal communication) has suggested that the slowness with which vegetation cover is spreading onto the barren areas between the birches of the semi-barren communities is due to a microclimate effect. While frost action is extreme in the barren areas, the area under each tree forms an "oasis" by virtue of the insulating effects of the leaf litter.

Seed Availability Factors

On the Sudbury barrens, there appears to be small resident seed bank, but most of the seed source is from the seed rain. This is in contrast to the situation described by Archibold (1978), who studied similar barrens created by the smelting of sulphide ore in Trail, British Columbia. He concluded that the limiting factor to recolonization at Trail was lack of seed rain, and he demonstrated this by soil-tray experiments (personal communication[4]). Trays filled with sterilized potting soil were countersunk into the barren soil surface, but no native species grew when the trays were returned to the greenhouse, although several tree and shrub species with wind-dispersed seeds were present within reasonable distance of barren soils (e.g. trembling aspen, *Salix scouleriana*, white birch). However, the present author's experience with such seed trays in the Sudbury area (unpublished data) suggests that they are a poor indicator of seed rain compared to the technique that utilizes limed plots of native soil, as described by Winterhalder (1983). The difference between the two sites may have had something to do with climatic or microclimatic factors, or else were a reflection of the technique used.

Both the limed plot approach and seed traps consisting of paper plates covered with sticky Tree Tanglefoot have demonstrated that there is a significant seed rain on the Sudbury barrens. However, the seeds trapped are normally of light, wind-dispersed species, and it is to be expected that species with larger, heavier seeds will be slower to colonize, even when the soil is no longer toxic. An exception is seen in the case of the bird-dispersed blueberry, which readily colonizes limed land and, more recently, unlimed land. Also, occasional red and white pine seedlings can be found on barren land, some distance from the nearest seed source; in this case the means of seed transportation is as yet unknown.

The collection of native seed was carried out in 1978 as part of the Regional Municipality of Sudbury's Land Reclamation Program, but was discontinued since it was considered by the RMS to be uneconomical. There were certainly some beneficial results, especially with respect to wavy hairgrass, in that it was possible to introduce this grass in advance of its normal associate, white birch, which colonized immediately following treatment. In general, however, most of the more easily-collected and -sown species are able to colonize naturally without assistance.

One method of decreasing the limiting nature of the seed rain is by the transplanting of sods of soil and plants from natural communities, so that the plants can act as a seed source. The use of sods also introduces a small seed bank. Glass (1989), in his review of the role of seed banks in restoration and mangement, points out that the seed bank in a plant community often shows a lack of close correspondence to the above-ground vegetation, and may contain species from earlier stages in succession. The use of some soil from a plant community that is the climax for the area, in the form of sod transplants, is therefore highly desirable.

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3 Dr. G.M. Courtin, Department of Biology, Laurentian University

4 Dr. O.W. Archibold, Department of Geography, University of Saskatchewan, Saskatoon, Canada S7N 0W0.

This method of exploiting natural tendencies towards spontaneous colonization is a modification of the principle of "nucleation". In their study of the Grand Bend sand dunes on Lake Huron, Yarranton & Morrison (1974) noticed that individuals of certain pioneer species such as *Juniperus virginiana* (red cedar) formed nuclei for the initiation of patches of other "persistent" species that spread and eventually coalesced. Miller (1978) suggested that such an approach might be taken in revegetation, in that selected "pioneer" species could be planted in clumps, then the "persistent" species introduced into the clumps once the pioneers are well established.

The modification of this approach which is under investigation on the revegetated Sudbury barrens at this time emphasizes the introduction of understory species characteristic of the plant community targetted. The pioneer species are introduced in large blocks of their own soil, so that seedlings or propagules of associated species are introduced with them.

Sometimes the selection of species that appears as a result of this approach is quite surprising, and plants introduced through the transplantation of soapberry and bearberry include *Juniperus communis* (juniper), *Picea glauca* (white spruce), *Fragaria virginiana* (wild strawberry), *Satureja vulgaris* (wild basil), *Senecio pauperculus* (balsam ragwort), *Smilacina stellata* (starry false Solomon's seal) and several species of *Aster* (asters) and *Solidago* (goldenrods).

THE IMPORTANCE OF TIMING AS A LIMITING FACTOR

The complexity of the interacting group of factors that control colonization is well illustrated by considering the establishment of one of the more important woody colonists, the trembling aspen. Once the seeds are ripened, the first constraint arises from the relatively short longevity of poplar seeds under natural conditions (Young & Young 1992). The seeds have to be dispersed to what Harper (1977) calls a "safe site", at which the seeds can germinate and seedlings can establish, while they are still viable. Wind direction and force will be important in carrying the seeds, and so will the presence of some turbulence in depositing them. Upon reaching the site, the correct surface conditions will be necessary for germination, including a fairly open plant cover like that seen in the first spring following treatment. If insufficient moisture is present during the short viability period, there will be no seedling establishment. For this reason, areas treated in different years may end up with very different patterns and densities of woody plant cover, despite similar overall conditions.

THE HOLOCOENOTIC ACTION OF POTENTIALLY LIMITING FACTORS

It is important to realise that environmental factors do not act independently, but interact, often involving positive or negative feedbacks. While it is not possible to show these interactions schematically, an attempt has been made (Winterhalder 1984) to show that a number of different factors are responsible for the Sudbury barrens (Figure 6).

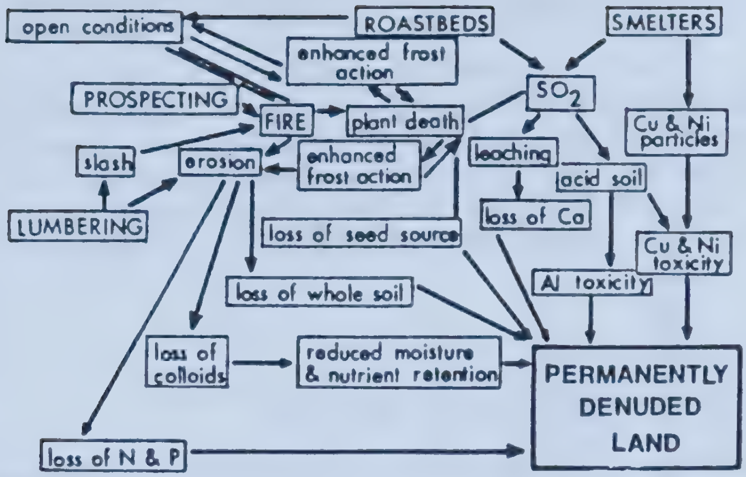

Figure 6: *A simplified representation of some of the major factor interactions leading to the formation of barren land.*

BREAKING THE CYCLE - THE TRIGGER FACTOR CONCEPT

The simple act of surface-applying ground dolomitic limestone creates positive feedback loops throughout the system. In fact, the Sudbury Regional Land Reclamation Program is an excellent example of the use of minimal amelioration as a "trigger factor" (Winterhalder, 1983), or what Skaller (1981) calls "minimal intervention". It was first noted by Winterhalder (1974), that minimal treatment of acid, copper- and nickel-contaminated soils in the Sudbury area led to rapid colonization, in which tickle grass seedlings became established after ameliorating the soil either with fertilizer or with limestone. Later, the role of manual surface liming of these soils in initiating colonization became known as a "trigger factor" (Winterhalder, 1983).

Hedin & Hedin (1990) and Hedin (1992) have described a very similar phenomenon on coal strip-mine spoils in Pennsylvania, where the surface application of limestone, fertilizer and wood chips stimulates the establishment of trembling aspen seedlings. Hedin (1992) refers to this phenomenon as the elimination of a "colonization bottleneck".

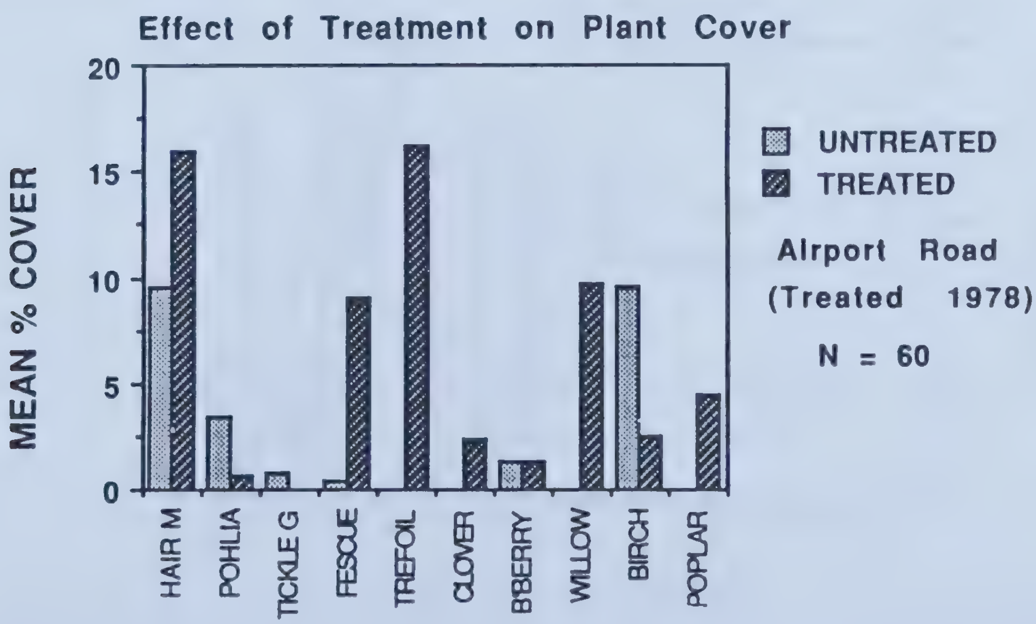

Figure 7: *Distribution of plants in relation to soil pH, 14 years after treatment.*

When limestone is applied manually from a bag, it is inevitable that it will be distributed in a patchy fashion, so to some extent a mosaic ensues, in which the degree of liming varies from zero to optimal or even excessive. This is probably beneficial, since it leads to a more random spacing of plants than an even cover would, as well as creating an environmental mosaic that will favour diversity both in terms of species and genetic biotypes. Some preliminary studies have indicated that a certain amount of selection of species with respect to pH has already occurred (Figure 7).

FACTORS CONTROLLING THE DYNAMIC PATH - THE INFLUENCE OF THE TYPE OR TREATMENT APPLIED

The process of "succession" on barren lands can follow one of three different routes, depending on whether the barrens are left untreated, treated with limestone only, or treated with limestone and a grass-legume seed mixture.

When left untreated, colonization is by metal-tolerant plants such as tufted hair grass, tickle grass and dwarf birch, although in the vicinity of the Coniston smelter, which has been inactive for 20 years, white birch is currently showing vigorous colonization and growth.

The importance of the dynamic processes that can occur following treatment was first appreciated in 1974 when a three-hectare sandy barren site in the Coniston Creek valley was grassed with Canada bluegrass, which is rhizomatous and forms an open sward. Within a year, there was noticeable colonization by other grass species such as redtop, legumes such as cow vetch (*Vicia cracca*), native "wildflower" species such as pearly everlasting (*Anaphalis margaritacea*) and woody species like trembling aspen.

The different dynamic path taken by the vegetation on adjacent areas, and the distinct line that demarcates treated and untreated areas, can be illustrated by a site west of Coniston, where a transect from untreated to limed-only shows the initiation of shrub growth on the limed side, with a much stronger stimulation of the native nitrogen-fixing sweet fern than of willow (Figure 8), presumably due to the sweet fern's ability to fix its own nitrogen. In Figure 9, however, it is interesting to note that, whereas poplar and willow establishment are stimulated by liming, the reverse is true of white birch, probably due to the competitive disadvantage at which the poplar and willow place the birch.

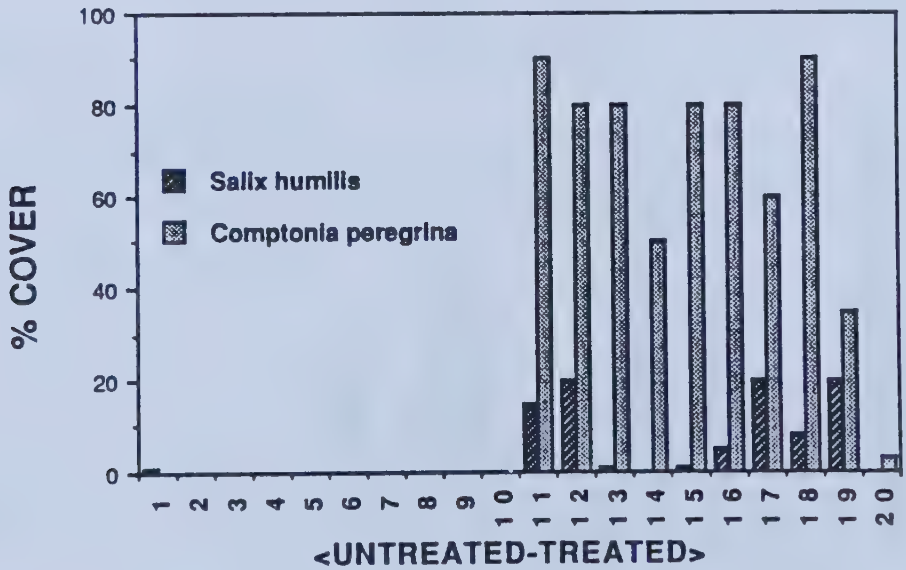

Figure 8: *Transect across liming boundary west of Coniston.*

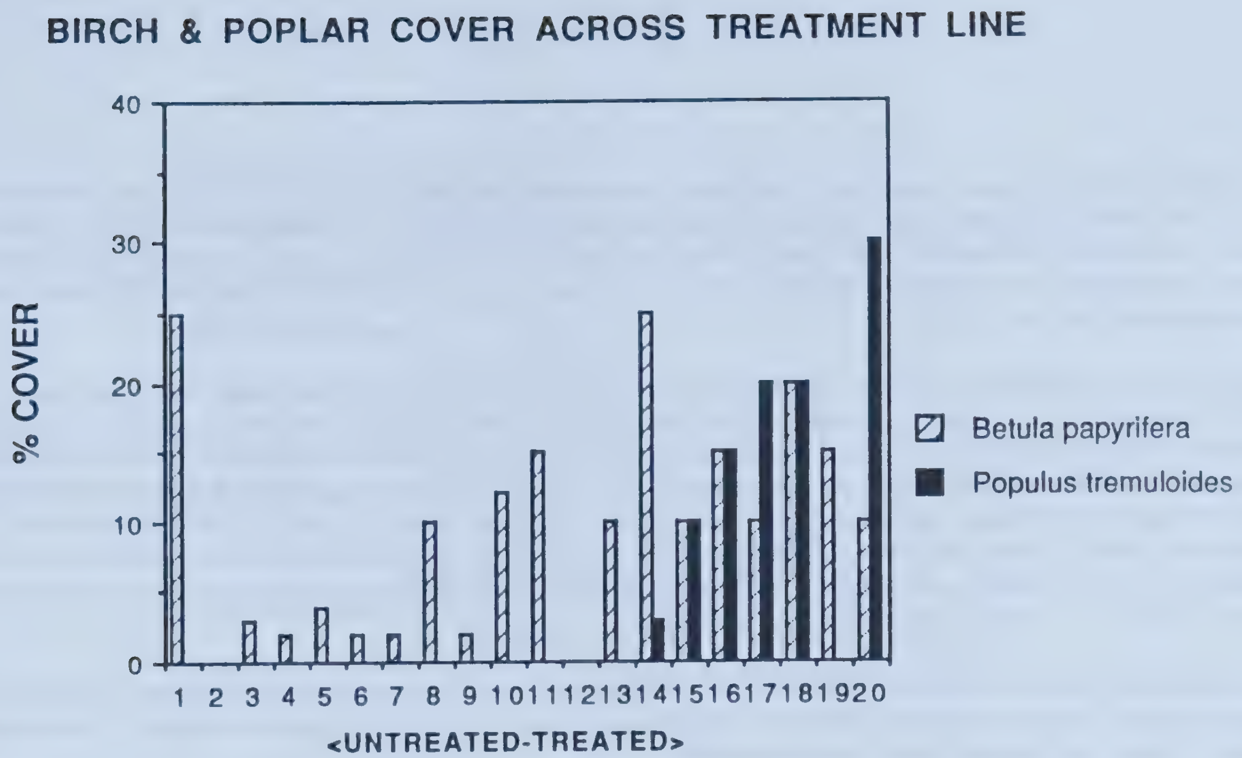

Figure 9: *Transect across liming boundary northwest of Falconbridge.*

As a result of the trigger factor effect described earlier, it is not necessary to use a grass-legume seed mixture to achieve revegetation following liming, and the seed rain is a sufficient source of seeds to achieve a good cover of birch, polar and willows within a few years. At a site near Hannah Lake, one area was limed, fertilized and seeded, while the other was limed only. Whereas the seeded area showed modest colonization by wood species, that of the limed site was much more extensive (Figure 10).

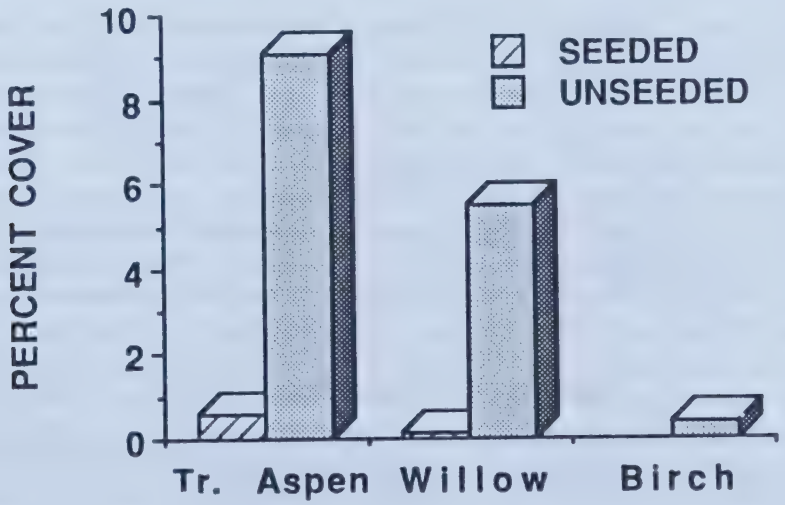

Figure 10: *Percent cover of woody plant seedlings on seeded and unseeded plots.*

It could be argued that the use of a seed mixture, and the concomitant introduction of alien species, is neither necessary nor desirable. Nevertheless, there are at least three advantages to the use of a seeding step. Firstly, there is a very rapid establishment of plant cover, which not only stabilizes erosion-prone sites, but also gives an immediate aesthetic improvement that is gratifying to operational and funding agencies. Secondly, the introduction of a nitrogen-fixing legume is clearly benefical to the mineral nutrient status of the developing ecosystem. Thirdly, the woody species develop in a more patchy fashion on the seeded sites, giving rise to the spatial diversity that is both ecologically and aesthetically desirable, whereas on unseeded sites the woody plants tend to form dense, homogeneous thickets.

Despite the three different colonization trajectories that occur between untreated land, limed and seeded land, and limed-only land, it is interesting to note that the type of liming material and/or fertilizer (if any) that is used on limed and seeded sites has little effect on colonization. Indeed, variations in seeding rates and even in species composition of the seed mixture do little to influence the process of colonization, although it seems inevitable that the presence of leguminous species in the mixture will have a long-term effect on the structure and function of the plant-soil system. Indeed, the use of black locust in some sites may also influence colonization, since there are frequent reports of black locust stands providing a favourable environment for colonization by other woody species (e.g. Ashby *et al.* 1980, in Indiana, Missouri and Kansas).

As shown in Figure 11, there is a tendency for the importance of introduced species to decrease and of native species to increase with time after treatment. The pattern shown by nitrogen-fixing birdsfoot trefoil is interesting, since it peaks, then falls off as the canopy develops.

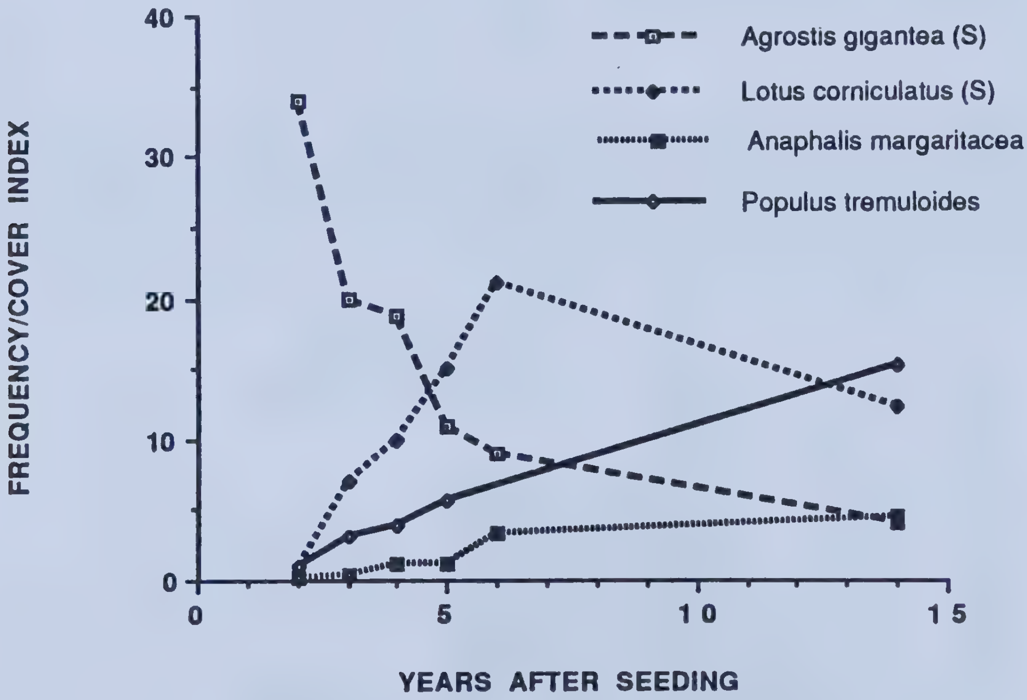

Figure 11: *Change in Cover/Frequency Index of four species (two seeded, two volunteer) over fourteen years following reclamation of acid, metal-contaminated Sudbury soils.*

Figure 12, showing the relative importance of the "top ten" species, illustrates the fact that the plant community that results from the revegetation procedure contains components derived from the seed mixture, the seed rain and any metal-tolerant plants already on site. Even planted woody species can have an effect on later colonization.

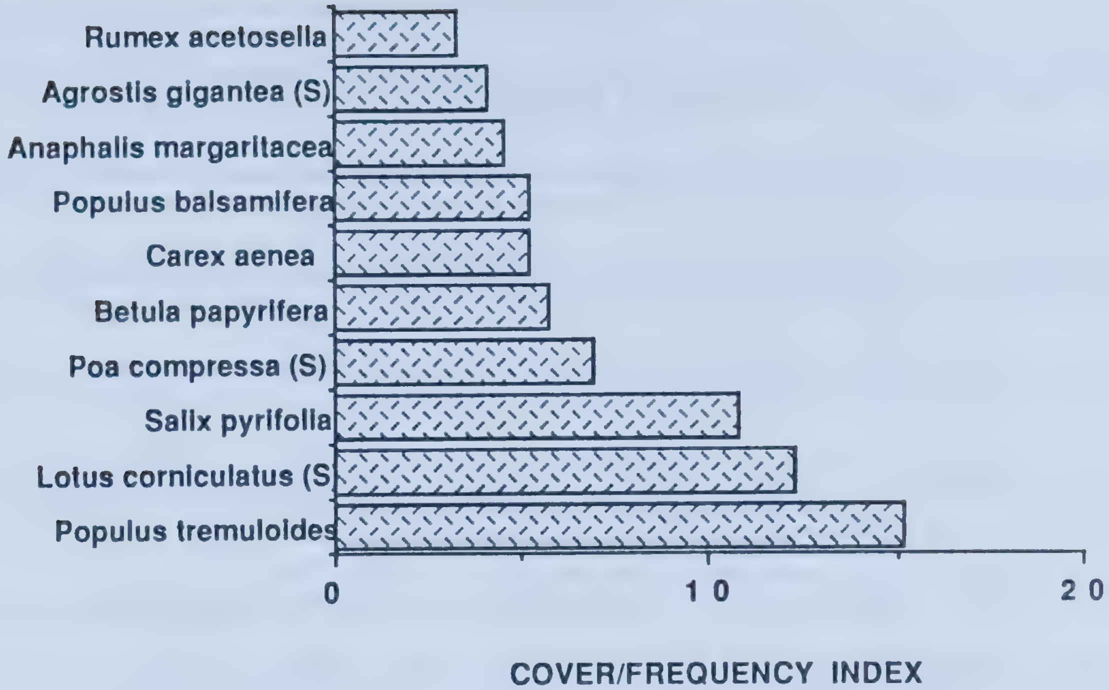

Figure 12: *The "top ten" species in terms of Cover-Frequency Index after ten to fourteen years. (Species labelled (S) are derived from the seed mixture).*

SUCCESSIONAL REVEGETATION AND THE "NURSE CROP" EFFECT

Seeding or planting and natural colonization or "succession" are by no means mutually exclusive. The whole concept of the "nurse crop", widely used in revegetation, is based on the idea of one species facilitating the establishment of another more desirable and usually longer-lived one (the Relay Floristics model of succession). It is traditional in northern Ontario to use a cereal species such as fall rye (*Secale cereale*) as a nurse crop (Peters 1984), but on the Sudbury barrens, this has been found unnecessary, partly because of the presence of a stony mantle on most sites, which acts as a seed trap. The most commonly touted function of the nurse crop is microenvironmental improvement, with reduction of evapotranspiration and increased snow cover in cold climates as examples of benefits. However, another benefit of a nurse crop, so long as the cover is not too dense, is its function as a seed trap. On uranium mine tailings in Elliott Lake, Ontario, Kalin & Smith (1984) have shown that the spontaneous establishment of white birch and trembling aspen has only occurred where there is some grass cover. While it is possible that both grasses and trees may be kept out of other sites by soil properties, it is almost certain that the grass has played a role in trapping the wind-blown seeds of the two tree species. On the Sudbury barrens, the primary factor facilitating colonization following liming is soil detoxification, but the seed rain is made more effective by the presence of a herbaceous cover that creates turbulent air flow over the surface, leading to the deposition and trapping of seeds. Colonization by woody plants is therefore assisted in a number of ways by the presence of the cover introduced by seeding, and the grass-legume cover can thus be interpreted as a nurse crop in relation to the native colonizing species.

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ACKNOWLEDGEMENTS

These proceedings are the result of dedication and commitment of many people including members of the Canadian Land Reclamation Association, technical contributors, other associations and government bodies. The contribution of these groups to the 1993 Annual Meeting is gratefully acknowledged.

In particular, we would like to recognize the financial assistance provided by;

Aggregate Producers' Association of Ontario
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Citation

The citation of this document in all references is;

1993 Canadian Land Reclamation Association
Annual Meeting, Lindsay, Ontario, August 11th - 13th

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