

THE ROLES OF COLONIZATION AND SUCCESSION IN THE RECLAMATION OF MINE SITES¹

by

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Abstract It is of advantage to the reclamationist to have some conceptual understanding of natural succession, and even more important to have a practical knowledge of the climax vegetation and natural successional processes in the region where he or she works. Factors that can limit succession on reclaimed land include lack of appropriate seed source, unsuitable soil conditions, and climatic or microclimatic factors. The use of natural successional processes is not incompatible with a certain amount of management, and measures that can be used to initiate or enhance succession include the use of physical site stabilization or a nurse crop, an enhanced native seed source, or the use of minimal soil amelioration. An understanding of seed ecology, patch dynamics and the role of soil microorganisms are also invaluable to the reclamationist. The extensive literature on colonization and succession, both on untreated and treated wastes of various types and in various climates, is reviewed.

The concept of succession

The concept of ecological succession has been at the heart of ecological thinking since the time of Clements (1916, 1936). According to Clementsian thinking, succession is an autogenic process, in which vegetation develops on a formerly bare substrate as a sequence of plant communities, each one altering the environment such that it favours the one that follows, culminating in a relatively steady-state - the climax. This concept of succession came to be known as "Relay Floristics" (RF).

Egler (1954) introduced another concept of succession, which suggested that the species composition early in the successional process can have a great influence on the final composition. This concept, which would be especially applicable to secondary successions such as those following industrial disturbance, was known as Initial Floristic Composition (IFC). A lesson on the importance of "initial composition" can be learned from the Mount St. Helen's eruption, where "late successional" species such as hemlock and true fir became established on the debris slide within a year (Dale, 1992). Similarly, Bellairs and Bell (1992) found that initial species composition largely determined vegetation development on sand-mined soils in Western Australia.

Connell & Slatyer (1977) presented two further models of succession, the "tolerance" model and the "inhibition" model. The tolerance model incorporates both the RF and the IFC approaches, since it proposes that vegetational change is the result of the superior success of the species best able to make use of the available resources. These species will normally include both "pioneers" and species already established.

In the context of revegetation, the tolerance model is likely to include a third component - the species sown or planted by the reclamationist. The model is particularly relevant in the case of revegetated land, in view of the use of fertilizers as a tool in implementing revegetation and in managing revegetated land. A plant community is the result of the interaction between the ecological tolerance of the species having the opportunity to become established and the sites available for colonization (Gleason, 1926), and the reclamationist often has the opportunity to manage one or both of these factors.

Connell and Slatyer's second model, that of "inhibition", emphasizes the IFC factor, in that it postulates that the early colonists are able to keep invaders out, especially if allelopathy (the production of chemical toxins) is involved. The whole question of the role of allelopathy and other physiological factors in succession require more attention by researchers (Bazzaz, 1979). In relatively mesic sites in arctic Alaska, Billings and Peterson (1980) suggest that the early colonists inhibit later arrivals, rather than facilitating them, and Brenner *et al.* (1984) hypothesize that dense stands of *Lotus corniculatus* (Birdsfoot Trefoil) or *Coronilla varia* (Crown Vetch) might inhibit colonization of surface mine wastes by native species.

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According to Cargill & Chapin (1987), the facilitation model is much more likely to apply on low-nitrogen substrates, where the earliest colonists may be symbiotic nitrogen fixers such as *Alnus* spp. (Alders), *Dryas drummondii* (Mountain Avens) or members of the pea family. The Bradshaw group in the U.K. have emphasized the importance of nitrogen buildup by legumes, whether native or exotic, in promoting the establishment of other species. On nutrient-poor china clay wastes in Cornwall, the clovers introduced in the seed mixture were supplemented by the "ingression" of several other leguminous species (Dancer *et al.*, 1977; Marrs *et al.*, 1980).

Whatever the concept of succession, the process can be seen to depend on certain factors that are categorized as follows by Cargill & Chapin (1987):

- 1) Life history characteristics of each species, such as dispersal abilities, growth rates, life span and reproductive behaviour
- 2) Physiological attributes of each species, such as tolerance of low levels of nutrients, light or water. Bazzaz (1979) has contrasted the physiological attributes of early and late successional species in his review on the physiological ecology of succession.
- 3) The way in which each species modifies the habitat by shading, nutrient and water consumption, deposition of leaf litter, etc.
- 4) Interactions of the above that determine the competitive and/or mutualistic relationships among species.

Bradshaw (1983) has broken down the overall process into two components: (a) **colonization** and (b) **ecosystem development**, and has applied these processes specifically to derelict land. He considers the process of **colonization** to consist of four sub-processes:

- (1) Immigration of those species that have appropriate dispersal mechanisms
- (2) Selection of pre-adapted species
- (3) Selection of those **capable** of adaptation
- (4) Slow growth in an open environment where there is a lack of competition

He also considers **ecosystem development** to have four major components:

- (1) Colonization by appropriate species
- (2) Accumulation of nutrients in plants and soil
- (3) Changes in soil structure, resulting from plant and animal activity
- (4) Reduction of any toxicity that may have existed

Bradshaw (1984) distinguishes between "restored" and "replacement" ecosystems, and suggests that a "restored" ecosystem has a balance between structure and function which is similar to that of the original ecosystem, whereas most "replacement" ecosystems are simpler in structure although potentially more productive.

Why should reclamationists be interested in succession?

Reclamationists are often engineers, agronomists or foresters by training, although the number of ecologists entering the field is increasing. One would expect the ecologist to have special insights into the process of revegetation, but sometimes this still excludes the recognition of natural revegetation processes. Jeffrey *et al.* (1974), in a paper tantalizingly entitled "Ecological approach to mining waste revegetation", do not even mention succession or natural recolonization! Fortunately this attitude is changing, as exemplified by Skaller's (1981) paper entitled "Vegetation management by minimal intervention: working with succession". Bradshaw (1987a), while acknowledging that the self-healing properties of ecosystems weakens the argument that we have to fully understand the ecosystem before we can repair it, suggests that the rate of achievement of successful restoration can be taken as a criterion of our understanding of the system.

Revegetation often involves the establishment of a vegetation type that is quite different from the "climax" vegetation of the area, thereby "working against nature", especially if the species used are exotics. MacMahon (1987) makes the point that the process of succession on disturbed land is biome-specific, suggesting that the appropriate approach to restoration of a site might be very much dependant on the climate and the climax vegetation in that area. It is clearly beneficial for the natural processes to be working in parallel with the revegetation technology, and to use what Skaller (1981) calls "minimal intervention". It is then to the reclamationist's advantage to have some knowledge of the local climax vegetation, and of the successional processes that normally occur following disturbance. To quote Niering (1987): "Plant community dynamics and vegetation management are intricately interrelated,

and an understanding of the basic processes involved in vegetation change is essential for the sound manipulation of plant communities".

Unlike Davis *et al.* (1985), who suggest that, in the short term, the twin goals of achieving maximum cover and maximum diversity in revegetation may be incompatible, the present author is of the opinion that, with careful "minimal intervention", they may be made less so. In the Sudbury Land Reclamation Program (Winterhalder, 1985, 1987, 1988 a & b), the use of minimal amelioration and minimal seeding rates makes for a lean, diverse edaphic environment, with sparse initial cover, which is very suitable for colonization by a diversity of species, and probably by a diversity of genetic variants of some of the species.

The observation of natural primary succession in an area, or in an area similar to that being reclaimed, may teach functional as well as floristic lessons. An excellent example can be seen in the work by Crocker & Major (1955), in their study of soil development in relation to succession on glacial till at Glacier Bay, Alaska. Here, *Alnus crispa* (Green Alder) forms dense thickets at an intermediate stage of succession, having a profound effect upon the organic carbon and nitrogen buildup in the soil. Eventually, the climax species *Picea sitchensis* (Sitka Spruce), *Tsuga heterophylla* (Western Hemlock) and *Tsuga mertensiana* (Mountain Hemlock) supersede the shrubs (Cooper, 1931). A similar lesson can be learned from the natural ecology of the leguminous tree *Robinia pseudo-acacia*, which is a vigorous pioneer colonist in the early regeneration of cleared or disturbed hardwood forest in the southern Appalachians (Boring & Swank, 1984). Its tendency towards a growth decrease and possible mortality after ten to twenty years suggest that it might play the useful role of soil stabilization and soil humus and nitrogen buildup before giving way to native woody species.

Knowledge of the normal successional dynamics in the area may influence not only the revegetation procedures themselves, but also the operations that will influence the final physical conformation of the site, whether they be pre-reclamation site preparation or even the mining and waste-disposal procedures themselves. Van Haveren & Cooper (1992) studied placer tailings in the Birch Creek watershed, interior Alaska, with the goal of promoting natural plant succession. They showed that depth to water table is the overriding variable in the establishment of the native, floodplain-colonizing shrub *Salix alaxensis* (Feltleaf Willow), because the seed dispersal period of the willow occurs at the driest period of the growing season. If some thought

had been given to the matter during the mining period, and the tailings disposal carried out accordingly, it is possible that the intervention required, such as topdressing or site regrading, would have been greatly reduced.

Harper (1987) has suggested that the restoration ecologist can test the various hypotheses on succession by the appropriate use of manipulation. For example, an attempt could be made to "bypass" some of the normal seral stages by soil amelioration (simulating the effects of the previous seral stage according to the relay floristics hypothesis), or by planting species that are usually "later colonists" or have a poor dispersal mechanism. In Sudbury's land reclamation program, the three native pines (*Pinus banksiana* - Jack Pine, *P. resinosa* - Red Pine and *P. strobus* - White Pine) are introduced within the first few years following treatment, since they are slow natural colonizers, presumably because of the lack of an appropriate seed bed. They are planted in small groups in order to avoid the appearance of a plantation, and it is hoped that they will form a seed source for future colonization. Luke *et al.* (1982) have gone further than this, in that they include the seeds of tree species normally forming a later stage in succession in the original treatment, but with rather variable success.

Knowledge of the "strategy" adopted by each potential colonist can also be very helpful. Several plant ecologists have attempted to categorize plant species according to their strategies. MacArthur & Wilson (1967) spoke of "r-selected species" which produce abundant seeds and are short-lived and "K-selected species" which allocate more of their resources to survival and competitive ability and less to reproduction. Grime (1977, 1979) expanded the concept to three components, in which R-selected species (like r-selected species) are ruderals, colonizing temporary, disturbed habitats. Grime's C-selected species allocate maximum resources to growth, and are therefore highly competitive, while his S-selected species allocate resources to maintenance, and are highly stress-tolerant. Rather than categorizing species, Van Hulst (1978) has categorized habitats on the basis of two criteria - "fertility" and "stress". The combination of the two former approaches with the latter could have great predictive potential.

It seems that we shall never be able to entirely remove the "probabilistic" components of succession on disturbed land as suggested by Bradshaw (1987b), but our knowledge of ecosystem dynamics and function will certainly help to hasten the reconstruction process.

Factors limiting colonization and succession on disturbed land

A discussion of factors limiting colonization will occur throughout the text, and only a few examples will be given here. The critical limiting factors can be categorized under the following broad headings:

Lack of appropriate seed source

Prach (1986) considered transport of seeds or other propagules to coal-waste dumps in Czechoslovakia to be a key factor in unassisted revegetation, but Archibold (1980), using seedtraps consisting of trays filled with sterilized potting soil, found that an adequate seed rain did not ensure vegetation establishment on strip-mine spoils in Saskatchewan. A similar study at a limestone quarry at Marulan, Australia (Archibold, 1984) indicated the presence of an adequate seed rain, but demonstrated a low success rate based on the seed rain. Using the same seed trap technique on the smelter-denuded soils of Trail, British Columbia, Archibold (personal communication¹) obtained results suggesting that lack of seeds is a major factor limiting colonization at that site, although several tree and shrub species with wind-dispersed seeds were present within reasonable distance of barren soils (e.g. *Populus tremuloides*, *Salix scouleriana*, *Betula papyrifera*). However, the technique may not be applicable in all environments, since Winterhalder, using the same technique on Sudbury's smelter-denuded soils, failed to trap seeds of species that readily colonized small plots that had been detoxified by limestone application (Winterhalder, 1983).

Seed size and dispersal technique often play an important role in the colonization sequence, with the smaller, wind-dispersed species colonizing first (Fenner, 1987). Hall (1957) found that woody plant colonization of coal pit heaps in North Staffordshire, England, was less on the north and east sides of the coalfield, and he explained it on the basis of the prevailing south-west winds.

The time of year of the last disturbance of a site in relation to the time of year seeds of a certain species are available and capable of germination can be critical, as pointed out by Keever (1983), in relation to old-field succession. In the case of mined land, it may be the timing of the amelioration rather

than that of the disturbance that is critical. On the Sudbury barrens, where limestone is used as a "trigger factor" (Winterhalder, 1983), the situation may be somewhat more complex. For example, for maximum establishment of poplars or willows, it is necessary that there be a juxtaposition of limed ground, a sparse growth of seeded grasses and legumes, a good wind and moist weather and soil during the short period of seed dispersal and seed viability. Leisman (1957) has made a similar point with respect to the establishment of *Populus tremuloides* and *P. balsamifera* on iron range spoil banks in Minnesota, and also points out that aspens only produce good seed crops every four or five years.

Soil conditions

Soil conditions can limit colonization and succession in a number of ways, and these limiting conditions can be physical, chemical, or even biological. In a study of problem spoil banks in Illinois, Lindsay & Nawrot (1981) stress the fact that density of natural vegetation is more dependent on the minesoil than on time.

The changes in soil physical characteristics that occur during disturbance, such as compaction, may divert or obstruct the "normal" progress of succession or interfere with the establishment of native species, as shown by Burrows (1986) and Enright & Lamont (1992) in sand mine rehabilitation in Australia.

Turning to soil chemical characteristics, soil nutrient status is important in defining the course of succession, not only from the point of view that there may be some selection of colonizing species related to their nutritional strategies, but in terms of nutrient capital limitations.

Climatic and microclimatic factors

In climates with severe winter temperatures, the degree of insulation by leaf litter is of great importance. Courtin (personal communication²) has suggested that patch enlargement of *Betula papyrifera* (White Birch) "oases" in the open, stunted woodland found on acid, metal-contaminated soils in the Sudbury area, may be dependent on the development of a leaf litter or moss cover to prevent frost heaving or needle ice formation.

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How can natural succession be encouraged?

This topic will be dealt with throughout the text, and only a few examples will be given in this section. The options can be categorized as follows:

Use of physical site stabilization

To quote Brenner *et al.* (1984), "Reclamation should, therefore, be designed to stabilize the site, while encouraging the invasion of both woody and herbaceous vegetation". Stabilization can be carried out in several ways, one of which is purely physical, by the use of a brush cover or mulch. If the mulch is made of native vegetation, then it serves a double purpose, in that it also provides a seed source.

Use of an enhanced seed source

The introduction of a seed source additional to the natural seed bank and seed rain might seem incompatible with "natural succession", but it can be used, like the other procedures described, to give the process a head start. The use of native plant materials as a mulch has already been mentioned. A more radical approach is the use of native topsoil, but as a source of propagules rather than as a growth medium. However, since there is a fine distinction between the two uses of topsoil, the topic is discussed in a wider context here.

If topsoil is carefully separated from overburden and returned to the surface following mining, it can act as a valuable source of seeds and vegetative propagules (McGraw, 1980; Tacey & Glossop, 1980). Bellairs and Bell (1992), working on sand-mined sandplain soil in Western Australia, found that a native vegetation mulch and native topsoil were more effective as a native seedling source than broadcast seed.

Both Farmer *et al.* (1982) and Wade & Thompson (1990) found forest topsoil to be an effective agent in the re-introduction of native species to mined land. Glass (1989), in his review of the role of seed banks in restoration and management, 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 is therefore advisable, even if it is only feasible to use a small amount as a seed source and microbial inoculum.

The retention of topsoil is particularly important in arctic tundra. Gartner *et al.* (1983) showed that the

seedbank of *Eriophorum vaginatum* and *Carex bigelowii* in Alaskan tussock tundra was restricted to the surface organic horizon.

Use of minimal soil amelioration

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 *A. scabra* (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). Figures 1 & 2 show the colonization of a patch of the metal-tolerant moss *Pohlia nutans* by birch seedlings following surface limestone application.



Figure 1. One metre-square plot on bare area with partial *Pohlia* cover, six km southwest of the Falconbridge smelter, just prior to limestone application (August, 1979).

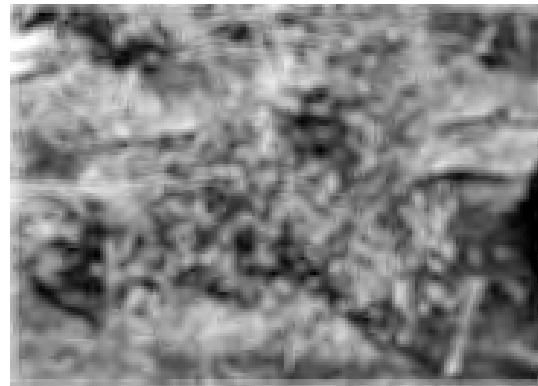


Figure 2. Same plot in June, 1985, showing establishment of *Betula papyrifera* seedlings.

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 *Populus tremuloides* seedlings. Hedin (1992) refers to this phenomenon as the elimination of a "colonization bottleneck".

In the majority of Sudbury's land regional land reclamation sites, minimal amelioration is followed by minimal seeding with a grass-legume mixture. The need to leave space for colonization is stressed by Polster (1989), and it is important that the herbaceous cover produced by seeding be relatively sparse. Brown & Chambers (1989), working in the alpine ecosystems of the Beartooth Mountains in Montana, conclude that the interests of increased rates of succession are best served by a reduced rate of application of a seed mixture that includes species with low nutrient requirements or nitrogen-fixing symbionts, together with a moderate application of nutrients.

Use of a nurse crop

A nurse crop can serve several purposes, including surface stabilization and microclimate modification, as well as acting as a seed trap. For example, Brenner & Goughler (1981) have shown that the use of *Sorghum vulgare* (Sorghum) as a cover crop during reclamation of surface coal mines in Pennsylvania provides an excellent seed bed for invading native species, and is superior to either *Avena sativa* (Oats) or *Lolium perenne* (Perennial Rye) for this purpose.

Colonization of untreated industrial wastes and contaminated soils

Most documented cases of natural colonization of industrial wastes and contaminated soils came about by default, at a time when there was neither legal nor moral requirement for reclamation, and controlled experiments on the topic are rare. An interesting exception to this is the study of three relatively innocuous industrial or urban substrates - "land-fill soil", "commercial topsoil" and a fine sandpit sand - by Rebele (1992) in Berlin. One-metre-square plots containing the substrates were set up in an experimental garden, and colonization tracked over a five-year period. Not surprisingly, the main determinants of succession were the type of substrate and the initial floristic composition (as represented by the seed bank). An interesting trend that arose from Rebele's work, and one that could be of importance in revegetation and in the management of revegetated

land, is the tendency for succession towards a woody (more "advanced") stage of succession to occur more rapidly on nutrient-poor (sandy) substrates. Certainly the effects of the deliberately minimal amelioration that is employed in the treatment of acid, metal-contaminated soils in the Sudbury area (Winterhalder, 1987) support the hypothesis that might be based upon such a tendency.

On some industrial sites, natural revegetation will occur spontaneously when the site is left untreated. On a site that is not highly stressed, normal "pioneer" species may colonize, followed by natural succession towards the climax. On more stressed sites, the colonists will be plants that are adapted to the particular type of stress. In this case, the result is often a monospecific or low-diversity community, which is less than desired, such as the pure sward of metal-tolerant *Deschampsia caespitosa* (Tufted Hairgrass) that can develop in the Sudbury area, Ontario.

Because of the wide diversity of materials upon which unassisted colonization has been documented, they will be divided into somewhat arbitrary categories.

Coal wastes and strip mines

One of the characteristics of coal wastes is the frequent presence of pyrite, and a tendency to acid-generation. Possibly the earliest report of colonization of a mine waste in North America is that by Croxton (1928), who documented, in a very perceptive way, the colonization of coal strip-mined land in Illinois. He described the development of a weedy stage dominated by *Polygonum pennsylvanicum* (Smartweed), replaced within two to five years by *Melilotus alba* (White Sweet-Clover). The two major woody species, *Populus deltoides* (Cottonwood) and *Platanus occidentalis* (Sycamore), gradually gained dominance, and eventually showed signs of developing a closed canopy. He noted that on more acid soils, the Smartweed phase was maintained longer, and that below pH 4.5 vegetation failed completely. He concluded that succession on the more acid sites was largely allogenic rather than autogenic.

The pH on a coal-waste tip is often quite variable. On a tip in Scotland described by Kimber *et al.* (1978), different degrees of pyrite oxidation had occurred, along with burning and waterlogging in some areas. Acid areas (pH<4.0) had *Agrostis tenuis* (Rhode Island Bent) as its major colonist, with grasses *Deschampsia caespitosa* (Tufted Hairgrass) and *Holcus lanatus* (Yorkshire Fog), forbs *Epilobium angustifolium* (Fireweed), *Rumex* spp. (Sorrels) and

Tussilago farfara (Coltsfoot), and moss *Ceratodon purpureus*, with no woody species represented. Areas above pH 4.0, however, had many more species, including shrubs *Vaccinium myrtillus* (Whinberry) and *Salix* spp. (Willows). Birch (*Betula* sp.) had also colonized the less acid sites. Species representation on burned sites was intermediate between the two.

Down (1973) found that vascular plants began to colonize coal wastes in Somerset, England after 12 years, at which time the pH, having dropped to below 3.0 in the first five years, was beginning to rise again, and was close to 4.0 (Down, 1975). By 178 years, the pH had risen to 6.7. Down (1973) was particularly impressed by the high percentage of hemicryptophytes (68-79%) invading the wastes, 31.8% of which were rosette plants, and he suggests that rosette-forming species should be used in reclamation seed mixtures.

Brown and Southwood (1987), in their discussion of secondary succession in general, suggest that a herb-grass to woody plant sequence is typical in temperate sites. This model applies quite well on European coal tip sites. Brierley (1956) described succession on pit heaps in the Nottinghamshire-Derbyshire coalfield of England, and made some interesting observations on the way in which plants achieved stabilization. Two of the pioneer species, *Deschampsia flexuosa* (Wavy Hairgrass) and *Epilobium angustifolium* (Fireweed), had a tendency to build up a ledge of rock fragments behind the tussock, eventually creating terraces. *Betula verrucosa* (Birch) then became established on the terraces.

Hall (1957) also described succession on colliery spoil heaps in a number of English coalfields, where a pioneer herb-grass cover gave rise to a grass sward approximately 15 years after abandonment. By 30-40 years, a *Betula* woodland had developed, followed by the establishment of *Quercus* (Oak) and *Crataegus* (Hawthorn) after 50 years. Many of the south Lancashire colliery wastes studied by Molyneux (1963) were even older - up to eighty-four years - but woody plants (*Quercus robur* (Oak), *Rubus fruticosus* (Blackberry) & *Sambucus nigra* (Elderberry)) were rare, the commonest species being *Agrostis gigantea* (Redtop³), *Deschampsia flexuosa* (Wavy Hairgrass) *Hieracium* spp. (Hawkweeds) and *Epilobium angustifolium* (Fireweed).

³ This is one of the few examples of *Agrostis gigantea* being described as a colonizer of disturbed land, although it is an excellent reclamation species on Sudbury, Canada's acid, metal-contaminated soils, and metal-tolerant ecotypes have also been found in Sudbury (Hogan *et al.*, 1977).

Titlyanova & Mironycheva-Tokareva (1990) describe very rapid colonization of non-toxic coal-mining spoils in western Siberia. *Melilotus albus* (White Sweet Clover) acted as a first-year pioneer, and dominated for the first three years. Several "weedy" species, including *Agrostis gigantea* (Redtop), peaked in the fourth year and rapidly declined, while "meadow" species such as *Poa pratensis* (Kentucky Blue Grass) and *Trifolium repens* (White Clover) became dominant in the later stages of succession. Woody species were lacking in this succession, presumably because the climax vegetation in the area is a mesophytic forb-grass meadow.

The Brown & Southwood model (1987), involving heavy colonization by annual grasses and herbs in the first year, rarely applies in North America, unless a topsoil covering is used. In east-central Illinois, Karr (1968) found that grasses (mostly *Poa pratensis* - Kentucky Bluegrass) did not become important on strip-mined land until woody vegetation was well established. Not only are grasses rarely the first colonists, but bryophytes such as the mosses *Dicranella heteromalla* and *Ceratodon purpureus*, which occur as disjunct or highly localized species on coal spoils in southern Iowa, do not "prepare the way" for vascular plants (Carvey *et al.*, 1977), as they may be observed to do in more humid climates, but require prior stabilization of the substrate and protection from erosion.

Some old strip-mined areas, abandoned before legislation required reclamation, have developed a vegetation that is structurally similar to the local climax, although they may not be so rich floristically. Skousen *et al.* (1988) have studied the colonization of lignite mine sites from one to fifty years since abandonment in the Post Oak (*Quercus stellata*) savannah area of east-central Texas. Woody plants colonized as early as five years after mining, but shrub and tree cover did not become substantial until twenty to thirty years post-mining. By fifty years, the site was dominated by multi-layered vegetation similar in species composition to the surrounding native stands. Glenn-Lewin (1979), in his study of abandoned strip mines from five to thirty-eight years of age in Iowa, found extensive colonization by woody plants, but suggested that there was no simple successional scheme. Rather, he suggested that the stands had developed individually (Glenn-Lewin, 1980), dominant species including *Populus deltoides* (Cottonwood), which seems to be a constant feature as a dominant woody species on abandoned spoils in the western interior coal province (Rogers, 1951). Cottonwood has also been described as a dominant of abandoned spoils in east-central and

southern Illinois (Karr, 1968; Hansen & Warnock, 1978), and both Hansen & Warnock (1978) and Smith and Klimstra (1987) note that such spoils show little indication of succession towards the oak-hickory climax of the area. Indeed, Cottonwood is sometimes accompanied by *Platanus occidentalis* (Sycamore), more typically a bottomland species, as where it colonized a mined bottomland site in Ohio only two years after mining (Merz & Plass, 1952).

On unreclaimed bituminous coal mine spoils in central Pennsylvania, Bramble & Ashley, (1955) listed *Populus tremuloides* (Trembling Aspen), *P. grandidentata* (Large-toothed Aspen) and *Prunus pensylvanica* (Pin Cherry) as the dominant woody colonizers, with *Acer rubrum* (Red Maple) present but less important. After thirty-five years, *Rubus allegheniensis* (Blackberry) dominates the shrub layer, with some *Comptonia peregrina* (Sweet Fern), *Rhus typhina* (Staghorn Sumac), *R. glabra* (Smooth Sumac) and *Salix humilis* (Prairie Willow). Hedin (1988) studied twenty non-re-soiled bituminous strip mines in northwestern Pennsylvania, ranging from twelve to forty-one years after abandonment. The most important woody colonists were once more *Populus tremuloides* (Trembling Aspen) and *P. grandidentata* (Large-toothed Aspen), with *Acer rubrum* (Red Maple) and *Prunus serotina* (Black Cherry) being more sporadic. Cornwell (1971) painted a very similar picture of anthracite mining spoils in Pennsylvania, where most of the first colonizers were trees, although a number of grass and herb species did occur. The most acid-tolerant tree species proved to be *Betula populifolia* (Gray Birch), less acid-tolerant tree species being *Populus tremuloides* (Trembling Aspen), *P. grandidentata* (Large-tooth Aspen) and *Betula lenta* (Black Birch). Important shrubs were *Comptonia peregrina* (Sweet Fern) and *Rubus allegheniensis* (Blackberry), while important grasses were *Danthonia spicata* (Poverty Grass) and *Panicum depauperatum*.

Orphan strip mine sites in Kentucky described by Kiernan *et al.* (1983) are colonized by woody pioneer species such as *Robinia pseudo-acacia* (Black Locust), *Liquidambar styraciflua* (Sweet Gum), *Cornus florida* (Flowering Dogwood) and *Sassafras albidum* (Sassafras), much as might be expected as a result of some other form of disturbance in this area.

Descriptions of strip-mine colonization in the prairie zone are rare, but in southeastern Saskatchewan, forty-year old strip-mined land in the lignite coalfields shows interesting differences between the colonization of the ridges and the interridge areas (Jonescu, 1979). Ridge slopes were 50% or less covered with vegetation, with a prairie grass (*Agropyron trachycaulum* - Slender

Wheatgrass) being the most important. Apart from native *Artemisia frigida* (Pasture Sage) and *Grindelia perennis* (Gumweed), most of the species were weedy. Thirty-four species were found both on the ridges and in the surrounding prairie. In the interridge areas, the first colonists were *Hordeum jubatum* (Foxtail Barley) and *Kochia scoparia* (Summer-Cypress). There were forty-seven species in common between interridge and prairie, the prairie itself supporting seventy-four species.

High-sulphide metalliferous tailings

Sulphide ore tailings usually acidify with age, as a result of the oxidation of the sulphides to give sulphuric acid, and they normally remained uncolonized if untreated. The Beattie gold and copper tailings in Québec are unusual in having a pH range from 1.9 to 8.7, and Gagnon & Crowder (1984) found that after thirty years, cover types varied from bare, through herbaceous stands dominated by *Equisetum palustre* (Marsh Horsetail), to shrub stands dominated by *Populus balsamifera* (Balsam Poplar) or *P. balsamifera* and *Salix* spp. (Willows).

Low sulphide metalliferous tailings

The silver-zinc-lead-cadmium tailings at Elsa, Yukon are circumneutral, but still quite metal-toxic, and colonization does not occur spontaneously. When flooded, however, marsh plants can colonize, and Blundon (1984) found *Carex aquatilis* (a sedge), *Juncus castaneus* (a rush) and *Equisetum arvense* (Field Horsetail) growing in submerged tailings at this site.

Taconite and other iron mine wastes

The residues left after mining iron as taconite are relatively innocuous, compared to those involving sulphide ores, and Tryon & Markus (1953) have described eighty-five to one hundred and nine-year old iron ore spoils in northern West Virginia, which are dominated by oaks. Leisman (1957) studied natural colonization of spoil banks consisting mostly of overburden and lean ore dumps of coarse taconite in Minnesota, treating a series of spoil banks up to 51 years of age as a chronosequence. He found a uniform pattern of succession, in which the earliest invaders were ruderals, followed very soon by *Populus tremuloides* (Trembling Aspen) and *P. balsamifera* (Balsam Poplar), with root suckering playing a major role in their spread. There was a grassy understory, chiefly *Poa pratensis* (Kentucky Bluegrass), and in some areas the grassland

dominated, with isolated patches of trees. The best development of Aspen-Balsam Poplar woodland was on the coarse lean ore banks, where the understory was sparse. Leisman suggests that the coarse-textured substrate and the micro-habitats that it offered, together with the sparse competing understory, contributed to their success. By analogy with colonization of stony slopes in the Sudbury area, the present author would support this hypothesis, and add to it the role that coarse materials play in creating turbulent wind flow and in trapping wind-born seeds.

Gravel pits and quarries

Gravel pits and quarries present a unique situation in that they do not involve toxic materials. However, they usually present a very sheltered environment, and they often contain a pond if worked down to the water table. For this reason, their value as wildlife habitat or as recreational land has long been appreciated. In the United Kingdom, seventy-five old mineral workings, many of them pits and quarries, have been declared Sites of Special Scientific Interest (Johnson, 1978). In 1982, a symposium was held in Crookston, Minnesota on the wildlife value of gravel pits, and the resulting proceedings (Svedarsky & Crawford, 1982) form a useful source of information on the colonization of pits, both by plants and by animals. Many points of view, conveniently summarized by Swanson (1982) are presented on the degree of management required to enhance diversity and wildlife habitat in abandoned gravel pits, including abandonment to natural processes. For example, Higgins (1982) describes a thirty-five to forty year old pit in North Dakota which has been colonized by *Populus deltoides* (Cottonwood), and several willow species (*Salix discolor*, *S. amygdaloides*, *S. rigida* and *S. petiolaris*), as well as *Symphoricarpos occidentalis* (Snowberry), *Elaeagnus commutata* (Silverberry) and *Rosa woodsii* (Western Wild Rose).

Fly Ash

Fly ash (pulverized fuel ash), the finely-divided ash remaining after the burning of pulverized coal in electrical generating plants, is often used as a component of concrete, but much of it is disposed of as a slurry into lagoons (Bradshaw & Chadwick, 1980). Shaw (1992) has reported on colonization of an abandoned fly ash lagoon in England over a period of 7 - 24 years. Colonization began with pioneer ruderals such as *Cirsium arvense* (Thistle) and *Tussilago farfara* (Coltsfoot), followed after 10-15 years by *Salix* and *Betula* scrub. By 25 years, most

pioneer species were shaded out by the *Salix-Betula* woodland.

In Tennessee, Gonsoulin (1975) describes a colonization sequence on alkaline fly ash beginning with a total of eight species and domination by *Conyza canadensis* (Horseweed) and *Bromus inermis* (Smooth Brome) in the first six months, followed by a total of twenty species and domination by *Bromus inermis*, *Andropogon virginicus* (Broom Sedge) and *Populus deltoides* (Cottonwood) by the third year, and finally a total of twenty-five species and domination by *Solidago* spp. (Goldenrods), *Melilotus alba* (White Sweet Clover), *Populus deltoides*, *Salix interior* (Sandbar Willow) and *Salix nigra* (Black Willow) by the eighth year. Gonsoulin suggests that the reason for the *Populus* and the *Salix* being the first woody colonists may be their adaptation to moist, alkaline soils. In the opinion of the present author, however, the success of these two genera in colonizing moist industrial wastes has much to do with the plentiful production and wind dispersal of seeds.

Lime wastes

The chemical nature of the substrate can clearly influence the species that colonize. Whereas on fly ash, with its moderate phosphorus content, several leguminous species are colonizers (Shaw, 1992), colonizers on lime wastes in Cheshire, England (Lee & Greenwood, 1976) were phosphorus-limited and legumes were scarce. However, the lime-rich deposit at Witton supported a diverse and fascinating vegetation, including species typical of coastal dune slacks such as *Salix repens* (Creeping Willow) and *Dactylorhiza incarnata* (Early Marsh Orchid), as well as other rather rare orchid species. As pointed out in the discussion of gravel pit succession and in Hodgson (1982), abandoned workings can have conservation value, sometimes, as in this case, because of the specific chemical characteristics of the wastes.

Blast furnace slag and other alkaline wastes

Alkaline Leblanc Process wastes in the Croal-Irwell valley in northwestern England have developed a rich calcicolous flora, including the orchids *Dactylorhiza fuchsii* (Common Spotted Orchid), *D. incarnata* & *D. purpurella* (Northern Marsh Orchid) (Gemmell, 1977). There are indications that the herbaceous plant community on the wastes will eventually undergo succession towards a hawthorn-willow scrub.

Bentonite clay

Bentonite clay, which is extensively surface mined on the Northern Great Plains, produces a spoil material that is saline and of low fertility, with high levels of expanding lattice clay minerals and low water infiltration properties. Nevertheless, certain salt-tolerant native species can colonize it spontaneously, the commonest being the annual forb *Atriplex suckleyi* (Scurfless Saltbush or Rillscale), sometimes accompanied by *Sarcobatus vermiculatus* (Black Greasewood) or *Hordeum jubatum* (Foxtail Barley) (Sieg *et al.*, 1983; Smith *et al.*, 1986).

Contaminated soils

Contaminated soils differ from industrial waste deposits in that they can, to varying degrees, retain some of the characteristics of the original soils. They may also retain a partial seed source, whether it be a seed bank or, more commonly, a seed-rain originating from nearby unaffected areas or survivors on the site itself.

The benefits of the retention of soil characteristics can be seen on the acid, metal-contaminated soils of the Sudbury area (Winterhalder, 1984), where variable amounts of organic matter have escaped erosion. These relic organic deposits form a ready nutrient source, especially when the metal toxicity preventing the colonization by non-tolerant plants is eliminated by liming.

It should not be forgotten that colonization and "succession" are not the only dynamic processes taking place during the recovery of a damaged ecosystem. Genetic selection in the actual species may also be taking place, the implications of which are thoroughly discussed by McNeilly (1987). On soils that are toxic in nature due to extremes of pH or to elevated metal levels, colonization by tolerant species, or of ecotypes of normally non-tolerant species that have evolved tolerance, often occurs. As long ago as 1934, Prat observed the colonization of an abandoned copper mine in Silesia by *Silene dioica* (Catchfly). Some plants show metal-tolerance at the species or subspecies level (e.g. the zinc-tolerant Violet *Viola calaminaria* and the Pennycress *Thlaspi alpestre* ssp. *calaminaria* of Europe), while others show the selection of metal-tolerant ecotypes from otherwise non-tolerant species. In 1952, Bradshaw discovered that the *Agrostis tenuis* (Rhode Island Bent) colonizing an old lead mine in Wales was a lead-tolerant ecotype, and later *A. stolonifera* (Creeping Bent Grass), *A. canina* (Velvet Bent

Grass), *Festuca rubra* (Red Fescue), *F. ovina* (Sheep Fescue), *Anthoxanthum odoratum* (Sweet Vernal Grass) and *Holcus lanatus* (Yorkshire Fog) were all shown capable of producing metal-tolerant ecotypes (Gemmell, 1977).

On the barren, acid, copper- and nickel-contaminated soils of the Sudbury, Ontario mining and smelting region, the first colonizer is the moss *Pohlia nutans*, which has been shown by Beckett (1986) to be metal tolerant. Mosses are often the first green plants (apart from algae) colonizing new substrates, since spores are readily carried by the wind. The first vascular colonizers on the barrens near the active Copper Cliff and Falconbridge smelters are *Agrostis scabra* and *Deschampsia caespitosa* (Figure 3) and where a seed source is nearby, *Betula pumila* (Dwarf Birch), normally a wetland species, moves up the barren mineral slopes (Figure 4). Near the Coniston smelter, which has been inactive since 1972, *Betula papyrifera* (White Birch) seedlings are beginning to colonize barren soil (Figure 5), and *Deschampsia flexuosa* (Wavy Hair Grass) is moving in around the larger "relict" birches and the birch seedlings that are becoming established.



Figure 3. *Deschampsia caespitosa* colonizing a barren site near Copper Cliff smelter, 1984



Figure 4. *Betula pumila* colonizing a barren hillside near the Copper Cliff smelter.



Figure 5. *Betula papyrifera* colonizing barren ground near the inactive Coniston smelter

As pointed out by McNeilly (1987), a knowledge of evolutionary processes in plants can be just as valuable to the restorationist as a knowledge of ecology, but McNeilly cautions that our knowledge should be used with understanding and respect if we are to retain the integrity of natural plant populations.

Table 1 summarizes some examples of vascular colonizers of acid, metal-contaminated land in Ontario:

TABLE 1

VASCULAR COLONIZERS OF ACID, METAL-CONTAMINATED SOILS IN NORTHERN ONTARIO

| SPECIES | LOCALITY | REFERENCE | STRESS | STAGE IN SUCCESSION |
|-------------------------------|----------------------|----------------------------|---------------------|---|
| <i>Agrostis gigantea</i> | Sudbury Ontario | Hogan <i>et al.</i> , 1977 | High Cu, Ni | Primary colonizer |
| <i>Agrostis scabra</i> | Sudbury, Ontario | Archambault, 1991 | Low pH, high Cu/Ni | Primary colonizer |
| <i>Betula pumila</i> | Sudbury, Ontario | Roshon, 1988 | Low pH, high Cu/Ni | Primary colonizer |
| <i>Deschampsia caespitosa</i> | Sudbury, Ontario | Cox & Hutchinson, 1981 | Low pH, high Cu/Ni | Primary colonizer |
| <i>Deschampsia flexuosa</i> | Wawa, Ontario | Personal observation | Low pH | Primary colonizer |
| | Sudbury, Ontario | Archambault, 1989 | Low pH, high Cu/Ni* | Follows <i>Betula papyrifera</i> colonization |
| <i>Hordeum jubatum</i> | Sudbury Ontario 1985 | Rausser & Winterhalder, | High Cu/Ni** | Primary colonizer |
| <i>Poa compressa</i> | Sudbury Ontario 1985 | Rausser & Winterhalder, | High Cu/Ni | Primary colonizer |

*Archambault was unable to show a difference in copper or nickel tolerance between populations from metal-contaminated soils and other acid soils. *D. flexuosa* is known to be a very acid-tolerant species.

**On the Coniston roastbed, the pH was between 6.5 & 7. In spite of Cu content between 1,000 and 3,000 ppm and Ni content between 50 & 1,500 ppm, the *Hordeum* was not metal-tolerant.

Subarctic and arctic sites

The arctic tundra, with its short growing season and other growth limitations, constitutes a challenge to the reclamationist, but natural colonization of disturbed substrates, while slow, can occur. Younkin (1974) found that two grasses, *Arctagrostis latifolia* and *Calamagrostis canadensis*, which normally constitute no more than 2% of the ground cover in tundra in the North West Territories of Canada, invade disturbed areas very rapidly, while Bliss & Wein (1972) found the same species playing the same role following fire. On the Mackenzie Delta, N.W.T, Bliss & Wein describe *Arctagrostis latifolia* var. *latifolia*, *Calamagrostis canadensis* and *Poa lanata* as minor species in dwarf shrub-sedge-heath hummock tundra, yet active colonizers of disturbed ground, natural or otherwise. *Calamagrostis canadensis*, along with *Eriophorum angustifolium*, is also able to exploit the deeper layer of thawed soil that results from vehicle track compression (Chapin & Shaver, 1981), whereas *E. vaginatum* is not. Presumably a relatively slow return to the original vegetation would follow such an invasion by native graminoids, but at least the invader would be a native and a stabilizer, and one might recommend the use of *A. latifolia* and *C. canadensis* in a native seed mixture on the Alaskan arctic tundra where there is no seed bank and where the seed rain is sparse. The need to seed may even be eliminated by the use of judicious fertilization of the neighbouring undisturbed tundra, which enhances the seed rain by stimulating flowering and therefore seed production by *Eriophorum vaginatum* (Chapin & Chapin, 1980).

Kershaw & Kershaw (1987) found a total of four hundred and thirty-three taxa colonizing eighty borrow pits of various age and varying microclimates in northwestern Canadian tundra sites, eighteen of these species being found in all major categories of age and environment. Included were the grasses *Arctagrostis latifolia* and *Poa arctica*, the leguminous forb *Hedysarum alpinum*, forbs *Epilobium angustifolium* and *E. latifolium*, shrubs *Betula glandulosa*, *Empetrum nigrum* and several willow species, and the tree *Populus balsamifera*. There were also several mosses and lichens, as well as the horsetail *Equisetum arvense*. The most vigorous colonist overall was the willow *Salix alaxensis*. Johnson (1987) stresses the fact that, in the case of gravel pits, there is some choice in location, and the pit can be located in such a way as to enhance revegetation. In a choice between upland and riparian sites, the riparian environment offers the advantage of a nearby source of plants well adapted to disturbance. On the negative side, disturbance of riparian gravels can adversely affect fish populations.

Studies of succession on natural substrates can clearly be helpful in understanding or facilitating successional restoration of disturbed sites. For example, Cargill & Chapin (1987) found *Salix alaxensis*, along with *S. interior*, to be an early successional species on silt bars on floodplains in interior Alaska, and to be followed by *Populus balsamifera*, (Balsam Poplar), with heavier-seeded *Alnus tenuifolia* (Alder) and *Picea glauca* (White Spruce) colonizing more slowly. Grazing by snowshoe hare and moose speeds up the elimination of the willow from mid-successional alder thickets, while the spruce, with its longer life span, survives to dominate in the later stages, where it takes advantage of the soil nitrogen built up by the alder. As pointed out by Cargill and Chapin (1987), such a succession illustrates all three models of succession

Cargill & Chapin (1987) make the point that succession is likely to occur rapidly and without assistance in mesic disturbed sites, especially if some of the organic mat remains or is returned to the surface, and that the sowing of exotic grasses might actually inhibit the establishment of native plants. Cases have been described in which non-native grasses inhibited invasion by native grasses of gravel pads in arctic Alaska, probably by tying up much of the nutrient pool (Johnson & Van Cleve, 1976), and Gartner *et al.* (1983) point out that, in the context of arctic disturbances, exotic species usually require repeated heavy fertilization, whereas native species do not.

In contrast, the invasion of xeric sites by native plants may be facilitated by sowing or planting, especially if symbiotic nitrogen fixers are used, and in exposed disturbed tundra sites Cargill & Chapin (1987) recommend the low-density sowing of exotic grasses known to have poor survival or competitive ability in the arctic environment, as a short-lived nurse crop.

Colonization of treated industrial wastes and contaminated soils

As pointed out by Polster (1989), and discussed in the section on minimal soil amelioration, it is often desirable to modify site conditions in some way in order to facilitate the establishment of invading species. This can be done by making physical, chemical or biological modifications to site conditions.

For example, once iron tailings in New York state were stabilized with Switchgrass (*Panicum virgatum*), Mitchell & Richards (1980) found that indigenous woody species such as Trembling and Large-toothed Aspen and Grey Birch colonized. They

noted the necessity (and relative difficulty) of establishing a sparse grass cover that will stabilize the tailings but will not compete. In northern Ontario, both on the copper-nickel Inco tailings in Sudbury (Peters, 1984) and the uranium tailings in Elliott Lake (Kalin & Smith, 1984), White Birch and Trembling Aspen became established some years after grassing. Mitchell & Richards (1980) discuss the approach of using grass to encourage woody colonization from both the practical and philosophical points of view, and conclude by referring to the degree of tolerance and ecological perspective that will be required for its social and political acceptance. This lack of tolerance is a major factor contributing to the relatively rare use of successional revegetation.

In arid areas, reliance on natural colonization might be considered as impractical, but Smith (1984) has reported the colonization of treated bentonite spoils by the desert shrub *Sarcobatus vermiculatus* (Black Greasewood) in the western United States. Sindelar (1979) found that vegetation established on abandoned surface mined land in southeastern Montana almost 50 years previously varied from site to site. Two sites with a sandy loam spoil differed in that one was dominated by *Artemisia cana* (Silver Sagebrush), *A. dracunculus* (False Tarragon Sagewort) and *Bromus tectorum* (Cheatgrass), with only 7% cover by perennial grasses, while the second showed almost 50% cover by perennial grasses. A possible factor in the difference in development could have been grazing history, pointing to the possible need for some management in certain cases of "natural" revegetation.

The plants that colonize the acid, metal-contaminated soils of Sudbury, Ontario, "triggered" by the surface application of ground dolomitic limestone (Winterhalder, 1988b), are predominantly wind-dispersed species. The "trigger" mechanism described by Winterhalder can be interpreted as the phenomenon described by Van Hulst (1978), in which autogenic change in a high-stress environment is much more important than in a low-stress environment. Figure 6 shows a previously-barren site, with relict *Betula papyrifera* (White Birch) and *Quercus borealis* (Red Oak) one year after treatment, with a grass-legume cover dominated by *Agrostis gigantea* (Redtop). Figure 7 shows the same site six years later, in which the grassed area has been extensively colonized by White Birch.

White Birch is not the only species to colonize treated land, and Figure 8 shows the major colonizing species, ranked by mean Cover/Frequency Index (Relative Cover + Relative Frequency / 2), and based on 1,684

1m² quadrats in 45 transects on land treated between ten and fourteen years previously.

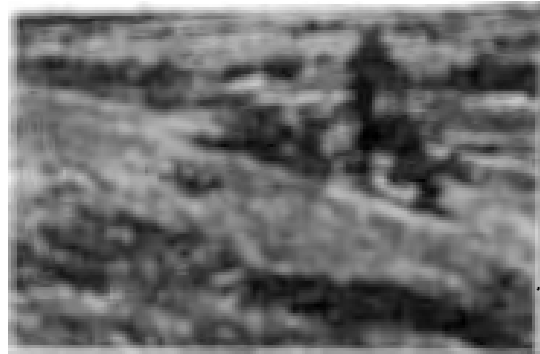


Figure 6 Grassed site near Coniston in 1980, showing scattered "relict" White Birch and Red Oak.

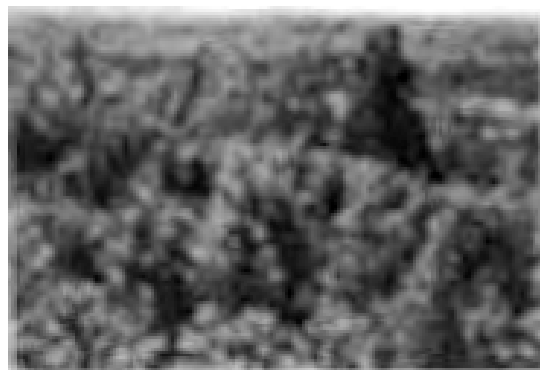


Figure 7. The same site in 1986, showing colonization of grassed area by White Birch.

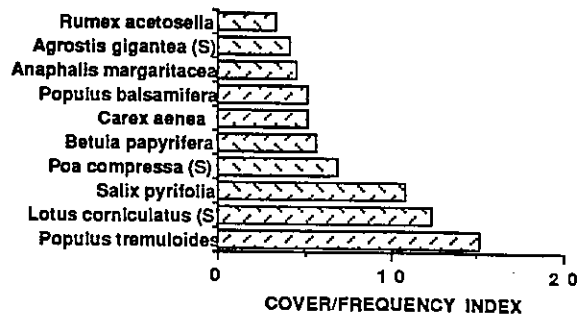


Figure 8. Cover/Frequency Indices of the ten highest-ranking species on revegetated Sudbury barrens. Species marked (S) were seeded, others are volunteers.

The difference between successional processes on limed and unlimed Sudbury soils can be strikingly shown by measuring the importance of native species across the limed-unlimed boundary. Figures 9-11 show such transects near Coniston, where *Betula papyrifera* (White Birch) is already beginning to

colonize untreated land, but *Populus tremuloides* (Trembling Aspen), *Salix humilis* (Pussy Willow), the nitrogen-fixing shrub *Comptonia peregrina* (Sweet Fern) and the native wildflower *Anaphalis margaritacea* (Pearly Everlasting) need the stimulus of limestone application before they do so.

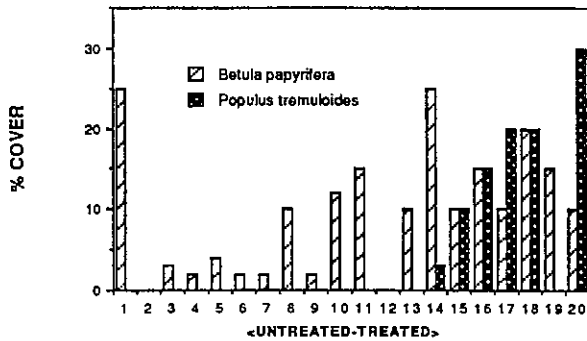


Figure 9. Percent cover of *Betula papyrifera* (White Birch) and *Populus tremuloides* (Trembling Aspen) across the liming boundary.

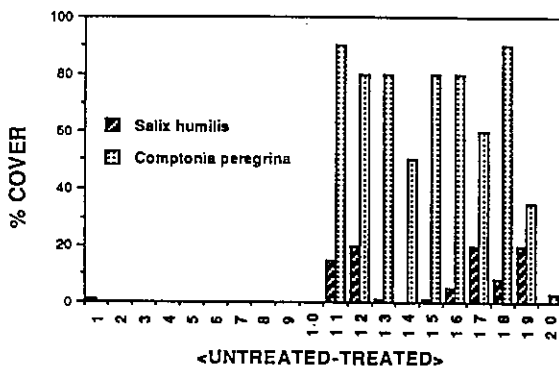


Figure 10. Percent cover of *Salix humilis* (Pussy Willow) and *Comptonia peregrina* (Sweet Fern) across the liming boundary.

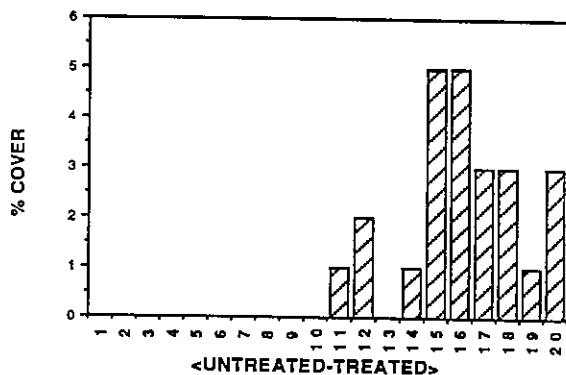


Figure 11. Percent cover of *Anaphalis margaritacea* (Pearly Everlasting) across the liming boundary.

Biondini *et al.* (1985) tested the hypothesis that fertilization practices and soil thickness over oil shale wastes can have a "long-term" effect on succession and ultimate species composition in northwestern Colorado, although the five-year span of their experiment was hardly adequate in the context of the length of natural seral change. They did find some differences, with fertilized plots becoming dominated by native grasses and unfertilized plots by non-native leguminous forbs. This result was not unexpected in view of the nitrogen-fixing potential of the dominant forb, *Medicago sativa* (Alfalfa). It would be particularly interesting to continue such a study to the point at which (it is hoped) the shrub component of the climax community (*Artemisia tridentata* - Sagebrush) colonized.

The present author's experience with acid, metal-contaminated soils in the Sudbury area is that the differences in species composition between areas treated with different ameliorants decreases as "succession" continues. As shown in Figure 12, 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 *Lotus corniculatus* (Birdsfoot Trefoil) is interesting, since it peaks, then falls off as the canopy develops.

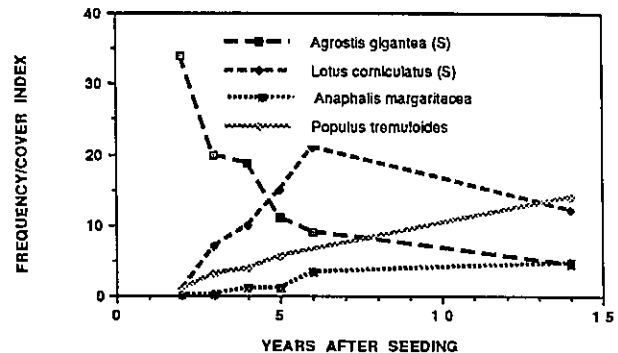


Figure 12. Change in Cover/Frequency Index of four species (two seeded, two volunteer) over fourteen years following reclamation of acid, metal-contaminated Sudbury soils.

Even planted woody species can have an effect on later colonization. Larson & Vimmerstedt (1988) found that a number of woody species colonized thirty-year old mined lands in east-central Ohio that had previously been planted with trees, and some interesting patterns emerged. Subplots planted with *Robinia pseudo-acacia* (Black Locust) contained high numbers of *Prunus serotina* (Black Cherry) volunteers, while subplots planted with *Pinus strobus* (White Pine) had the fewest volunteers, except on calcareous clay minesoil, where *Fraxinus americana* (White Ash) was plentiful.

There are frequent reports of *Robinia pseudo-acacia* (Black Locust) stands providing a favourable environment for colonization by other woody species (e.g. Ashby *et al.*, 1980, in Indiana, Missouri and Kansas). Smith & Klimstra (1987) report the invasion of a thirty-five year old Black Locust plantation in Illinois by *Prunus serotina* (Black Cherry), *Acer negundo* (Box Elder) and *Ulmus rubra* (Slippery Elm).

Are reclamation by succession and reclamation by seeding or planting incompatible?

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). 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. 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 *Betula papyrifera* (White Birch) and *Populus tremuloides* (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.

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. Hunt (1986) actually found that agronomic species encroached on native species on taconite tailings in Wisconsin, and he suggests that species selection is critical in directing a successional trajectory. While this is true, attention should also be paid to fertilization level. On sand-mined New Zealand dunes, the introduced European sand-binding marram grass *Ammophila arenaria* tends to inhibit the return of the threatened native sand-binding sedge *Desmoschoenus spiralis*, and it is the conclusion of Partridge (1992) that sand-mining should cease.

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 *Lotus corniculatus* (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.

A constructive way of exploiting natural tendencies towards spontaneous colonization is to employ 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. A modification of this approach is under investigation on the revegetated Sudbury barrens at this time, especially with respect to the introduction of understory species characteristic of the plant community targeted. The pioneer species are introduced in large blocks of their own soil, so that seedlings or propagules of associated species are introduced with them. Figure 13 illustrates a transect across such a "nucleated" barren site in Sudbury; it shows the spread of *Arctostaphylos uva-ursi* (Bearberry) from blocks of soil transplanted onto the site ten years previously.

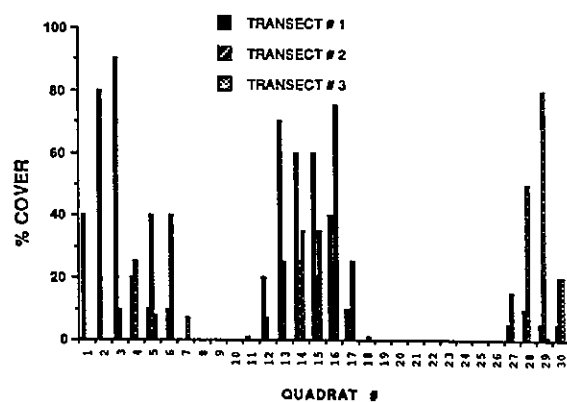


Figure 13 Percent cover of Bearberry in transects across original planting rows, showing spread from original "nuclei".

The importance of seed banks and seed rain in successional reclamation

The presence of a dormant seed bank in topsoil that is returned after surface mining can be critical in re-establishing native vegetation, whether or not amelioration and/or seeding or planting follow topsoil replacement. Nevertheless, the seed rain can be just as important as the seed bank, if not more so. Certainly Iverson & Wali (1982a & b) found that the most prevalent colonizers after reclaiming with topsoil - *Kochia scoparia* (Summer Cypress), *Setaria viridis* (Green Pigeongrass) and *Salsola collina* (Russian Thistle) - were not present in the seed bank. However, several other species that were in the seed bank became established more slowly, e.g. *Hedeoma hispida* (Rough Pennyroyal), *Artemisia ludoviciana* (White Sage), *A. frigida* (Pasture Sage) and *A. absinthium* (Wormwood). Although the *Kochia* dominated the stand in the first two years, acting as a nurse crop for the seeded *Agropyron* spp., it declined after this, apparently due to autotoxic allelopathy. Iverson & Wali (1987) have suggested a management technique to speed up the replacement of *Kochia* by native perennial grasses - the mowing of the *Kochia* just before seed set.

On the Sudbury barrens, there appears to be small resident seed bank, but most of the seed source is from the seed rain.

Species richness and diversity - one of the goals of successional reclamation

Traditional revegetation techniques tend not to achieve high species diversity, not only because few species are seeded or planted, but because high fertilization rates lead to a dense cover that acts to exclude colonizers. Indeed, some of the most floristically rich plant communities are nutrient-poor (Green, 1972; McNaughton, 1968). In the Sudbury Regional Land Reclamation Program, a conscious attempt is made to use minimal amelioration. Furthermore, the manual method of limestone application ensures a mosaic of soil pH and base content, and the resultant environmental mosaic makes for both floristic and genetic diversity, especially with respect to metal tolerance. A homogenous, rich application of limestone and fertilizer might result in the loss of metal-tolerant races of grasses through competition.

Patchiness of successional processes

Niering (1987) has developed an excellent flowchart that incorporates the several concepts of succession in

a holistic way. He suggests that the replacement of the term "climax" by "steady state" or "relative stability" would "permit a more flexible way of looking at the physiognomic, historically conditioned mosaic of relatively stable cover types on a diversity of sites within a given vegetation zone or biotic system." His reference to a mosaic of a diversity of types reflects his landscape ecology perspective - one that is very valuable to the reclamationist, who should be thinking in terms of creating a "patchy" reclaimed site rather than a homogenous one if he or she has ecological interests at heart.

Natural revegetation of disturbed land is inevitably a patchy process, and the role of the patches can be quite important, especially from the point of view of "nucleation" phenomena (Yarranton & Morrison, 1974; Miller, 1978), as discussed earlier. Barnes & Stanbury (1951) describe the colonization of mica china clay residues in England, which begins with the alga *Zygonium ericetorum*, followed by the moss *Hypnum schreberi*, then the herbaceous annual *Spergularia rubra* (Sand Spurrey). Then come the rush *Juncus effusus* (Soft Rush) and the grass *Agrostis tenuis* (Rhode Island Bent), which form persistent patches that slowly spread, becoming colonized by other species as this occurs, and eventually coalescing. The spatial pattern of colonization of abandoned surface coal mines in Missouri has been studied by Game *et al.* (1982), using aerial photography over a sixteen-year period, followed by image analysis. They found that the colonizing plants formed patches that grew at a uniform rate, while new patches were also formed; finally the patches coalesced to form a complete cover.

The ultimate goal of successional revegetation - the "climax"

The term "climax" is just as controversial and fraught with misunderstanding as is the term "succession". Not only are there several different concepts of "climax", from Clements' monocl意思 (which states that only one truly climax vegetation type exists per climatic zone), through Tansley's polyclimax (which states that Tansley's "climatic climax" is only one of several possible climaxes, which depend on other environmental variables such as soil or topography), to Whittaker's idea that the climax is a pattern of many vegetation types. Indeed, Patterson (1986) has actively campaigned against the use of the term "climax" by foresters to avoid confusion.

Because of the importance of the Initial Floristic Composition factor, it is likely that, even in the long term, uniquely post-disturbance and/or post-

reclamation plant communities may persist into the "climax". Niering (1987) gives an example of a fortuitously established thicket of Nannyberry (*Viburnum lentago*) that has persisted in a stable form for 55 years in Greenwich, Connecticut. In contrast to this, dense stands of Pin Cherry (*Prunus pensylvanica*) that appear after clear-cutting northern hardwoods in New England are eventually replaced by forest hardwood species. The persistence of stable patches of trees or shrubs that resist tree colonization is probably an important feature in ensuring both species and habitat diversity, and may create the edge effect required for many wildlife species.

The vegetation mosaic formed on seeded sites on the Sudbury barrens, resulting both from microtopography of the site and the patchy manual limestone application, contrasts favourably with the often monospecific stands formed after liming without seed application. The coincidence of the presence of colonizable soil, suitable weather conditions and the time of seed dispersal can be important in seeds with limited viability, as shown by Stergios (1976) in *Hieracium aurantiacum*. The synchronism of a good seed year, the presence of a recently-treated area with a bare stony surface or an open grass cover, and moist weather and suitable winds during the short period of seed dispersal and seed viability, is especially important to the establishment of aspen in the Sudbury area, and may explain some of the patchiness of its distribution.

It is clear that the processes of colonization and change in biotic communities following disturbance and rehabilitation are critical, yet they are not fully understood. It would therefore be beneficial if reclamationists were to follow the advice of Gross (1987), who argues for the incorporation into restoration projects of experimental studies designed to test specific hypotheses.

From a functional point of view, the goal of revegetation is a functional, self-perpetuating ecosystem, and Miller (1987) has suggested that reclamation research should be organized around an attempt to reestablish an entire system and get it working again. Although "allowing nature to take its course" through the process of natural succession will, in the long run, achieve this goal, it is often desirable to speed up the process by supplying or managing a range of biotic and abiotic components for nature to work upon. Thus, the use of a native plant mulch, the return of native topsoil or the transplantation of blocks of native soil complete with plants and microorganisms (the "nucleation" approach), are examples of strategies that can expedite the achievement of the ultimate goal.

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