Natural Inhibition as a Part of the Forest Ecosystem*

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ABSTRACT

Naturally occurring substances in several plants found in pine forests inhibit germination of jack pine seeds. These include sand cherry, black cherry, goldenrod, pussy willow and wintergreen. Others, including rice grass, june berry, bunch berry, star flower and red pine seem, at times, to stimulate jack pine seed germination.

Other plants, particularly reindeer lichens (Cladina stellaris) seriously retard seedling growth. This retardation is brought about by the inhibition of mycorrhizal fungi associated with jack pine roots and essential for proper mineral nutrition.

An explanation of the role of this inhibition in the forest-tundra biome is suggested. Possible silvicultural practices for management of this fragile ecosystem are put forth.

INTRODUCTION

The extremely uneven distribution of plants on a site is well illustrated in Pinus banksiana (jack pine) forests, where stands ranging from a few stems per acre to 1,000 or more per acre may be found within a few yards of each other. Groundcover plants show similar extremes of density. Irregular distribution of jack pine may result from differences in soil texture, available mineral nutrients, depth of water table, water-holding capacity, soil acidity, root competition, logging or fire history, slope exposure, microclimate, and seed dispersal. Since none of these factors adequately explained plant distribution in this study area, another possibility was investigated - the influence of naturally occurring, biologically active compounds on germination and growth. See Rice (1974).

LABORATORY GERMINATION TESTS

Jack pine seeds for all experiments were obtained from sites of active logging operations in northern Michigan. Only cones which had matured during the previous growing season were gathered. These cones were opened as seeds were needed by heating them in an oven at 150°F. All seeds were de-winged, and nearly all those which were without embryos or were damaged by insects were eliminated by floating them in diethyl ether. All viable seeds sank, and the brief ether treatment had no influence upon viability (Brown 1967a).

Water extracts of 55 plants commonly found in jack pine forests were used as the moistening medium for germinating seeds in the laboratory. Twenty grams dry weight of fresh material were reduced in a blender with sufficient water to produce 600 ml of liquid after the solids were removed by centrifugation (Brown 1967b).

The germination medium consisted of a 3/16-inch layer of perlite covered with filter paper and saturated with plant extract; distilled water was used

as a control. For each extract 20 jack pine seeds were placed on the filter paper in each of 10 petri dishes and the germination medium saturated with approximately 35 ml of extract. The dishes were then placed in a dark chamber controlled at 30 °C and 100% humidity and were removed briefly to light and room temperature daily for counting germination.

Table 1 lists those plants, extracts of which consistently inhibited germination at the 1% level using the student's t test of significance. Plants listed in Table 2 seemed to be somewhat inhibitory, but not at the 1% level consistently.

Table 3 is a listing of those plants which had no significant influence on jack pine seed germination in petri dish culture. A few plant extracts seemed to stimulate jack pine germination, but not consistently. They are listed in Table 4.

Since the hydrogen-ion concentration could conceivably influence germination, pH was determined for many of the extracts. There was no apparent relationship between pH of the medium and germination since pH of non-inhibitors ranged from 3.2 to 6.7 and that of the stimulators from 3.7 to 5.6, while that of inhibitors ranged from 4.9 to 6.3. These findings are in agreement with those of Maull (1963), who studied Pinus rigida Mill., and of Vaartaja (1957), who studied Pinus banksiana. Neither of these investigators found any significant relationship between seed germination and pH.

FIELD GERMINATION AND GROWTH TESTS

Plants used in the laboratory germination experiments were tested in a field situation. Eleven plants, three showing inhibiting properties in laboratory tests, six showing little or no influence, and two showing stimulating properties, were selected for study. Stands which were used were

as dense and as nearly pure as possible. In each "pure" plant cover type, four 1-meter square plots were laid out and subdivided into I/25-m^2 square plots. Before planting, the vegetation was clipped to a height of 1 to 2 inches and the soil surface scratched with a rake. Four seeds of jack pine were planted in each 1/25-m^2 plot (100/m^2 or 400/plant cover type). When the soil appeared dry, it was watered to eliminate differences due to moisture content. Watering was discontinued at the end of the first summer. Plants whose extracts consistently inhibited germination in the laboratory (Prunus pumila, Gaultheria procumbens, and Solidago juncea) also inhibited germination in the field. Of 400 seeds planted, only 14, 25, and 30 seeds germinated in the presence of these three plants respectively, as compared to 143, 144, and 222 in the case of Cornus canadensis, Pteridium aquilinum, and Pinus resinosa cover. Intermediate numbers germinated with Cladina rangiferina, Deschampsia flexuosa, Pleurozium scheberi, Epigaea repens, and Vaccinium angustifolium.

As a continuation of these studies, the growth of jack pines planted with nearly pure field stands of various ground cover species was recorded. All seedlings grew more or less normally except those in association with reindeer lichens. The seedlings grown in reindeer lichen cover attained an average height of only 7 cm in 7 years. When some of them were dug and examined for mycorrhizae, a few (10 to 20 per seedling) were found while on similar seedlings grown with other kinds of cover, many (over 100 per seedling) were found on each small tree. Ectomycorrhizal fungi, in particular, are known to be sensitive to substances released by plant roots or leached from plant material (Melin, 1925, 1946, 1953, 1963; Marks and Kozlowski 1973).

These observations suggested that jack pine growth is to some extent inhibited if the mycorrhizae are inhibited by water soluble substances in reindeer lichens. Leibundgut (1952) observed a somewhat similar inhibition

of mycorrhizae of Pinus silvestris, P. mugo, and Picea abies when he grew them with water extracts of Cladina spp.

These data gave good reason for more detailed studies on the effects of reindeer lichens on the growth of tree seedlings and in particular on mycorrhizal fungi. Because better facilities for conducting the research were available at the University of Helsinki and because reindeer lichens are much more abundant in Finland, I went there on a Fulbright Research Fellowship. There I conducted experimental studies with pure cultures of fungi and with synthesis cultures of mycorrhizae under axenic conditions. This work has been complemented with nursery plantings and some field observations in northern Finland where reindeer lichens are abundant in the forests. Since reindeer lichens are dominant ground cover plants in vast areas of the northern forests, their possible adverse influence on mycorrhizal fungi or tree seedings may have a great practical importance for forestry of these regions.

THE EFFECT OF LICHEN EXTRACTS ON FUNGI IN PURE CULTURE

Method

Water extracts of Cladina stellaris, C. arbuscula (sylvatica), C. rangiferina, and Cetraria islandica were prepared by blending an amount corresponding to 10 grams oven dry weight of undried fresh lichens with 100 ml of distilled water. In addition, humus from beneath them was also extracted by the same technique. These mixtures were filtered and centrifuged to remove solids. Then the centrifugate was put through a millipore filter to remove bacteria and fungus spores. This final filtrate was used

as a portion of the liquid in Hagem agar (Modess 1941):

KH_2PO_4	0.5 g	Glucose	5.0 g
NH_4Cl	0.5 g	Malt extract	5.0 g
$MgSO_4 7H_2O$	0.5 g	Agar	15.0 g
$FeCl_3$ (1% solution)	0.5 ml	H_2O	1000 ml

The agar was prepared with 1/2 enough water and cooled to 60° C; the other 1/2 of the water was then added as millipore filtered extract. This procedure was necessary to prepare sterile agar with a heat-labile extract (Brown and Mikola, 1974).

A total of 17 fungus species were used to inoculate petri dishes prepared with the above agar. Of the fungi tested, Fomes annosus is a well-known tree parasite. Collybia butyracea, C. dryophila, Marasmius androsaceus and Lepiota procera are litter-decomposing saprophytes, whereas all the other species are mycorrhizal. E-57 indicates an unidentified mycorrhizal species which commonly forms ectendotrophic mycorrhizae in forest nurseries (Mikola, 1965).

Inoculation of the petri dishes was performed by placing three 5 mm diameter agar inoculation pieces cut with a cork borer in each petri dish. Six or more replications were made. The control was a standard Hagem agar. The plates were incubated at room temperature from one to four weeks, depending on the growth rate of the fungus.

Growth of the fungi was measured by area of the colony outside the original inoculation piece. The results subjected to Student's "t" test are shown in Table 5. The levels of significance shown illustrate the degree of inhibition: .001 level indicates complete or almost complete inhibition while .01 or .05 indicate some growth of the fungus.

Results

Cladina stellaris was the most effective growth inhibitor of mycorrhizal fungi (Table 5). The lichen itself is a more effective inhibitor

than is the associated decaying humus (Table 6). Cladina arbuscula, C. rangiferina, and Cetraria islandica were less effective inhibitors than C. stellaris. This experiment compared reactions of different mycorrhizal fungi with each other, with humus decomposers, and with a pathogenic species (Fomes annosus). No consistency of any kind can be found. Among ecto-mycorrhizal fungi, Paxillus involutus, for instance, was inhibited by all lichens and humus extracts and Cenococcum graniforme by none of them. Other ectomycorrhizal fungi were intermediate between these extremes; occasionally stimulation could be observed. Strain E-57 was inhibited by several extracts. Among the saprophytic species, Collybia butyracea was unaffected or even stimulated while C. dryophila was inhibited by all the extracts. Of interest is Fomes annosus, which was almost completely inhibited by Cladina stellaris extract but stimulated by C. rangiferina, as was Boletus variegatus, a mycorrhizal fungus.

Thus, no generalization regarding relationships between mode of fungus nutrition and inhibition by C. stellaris or other lichens can be made. Little influence of lichen humus extracts is evident except on Paxillus involutus and to a lesser degree on Collybia dryophila and Marasmius androsaceus (Table 6).

THE EFFECT OF LICHENS ON THE PHOSPHORUS UPTAKE OF MYCORRHIZAE

After the results of the previous experiment had shown that Cladina stellaris and to a lesser extent other lichens inhibited many mycorrhizal fungi grown in pure culture, it became necessary to investigate whether or not the actual symbiotic relationship between fungus and tree was likewise affected. This was done by applying radioactive phosphorus to axenic synthesis cultures.

Method

120 ml test tubes were filled about 1/2 full of sterile silica sand and enough nutrient solution was added to nearly saturate the sand. A small test tube (15 ml) filled with sterile distilled water was placed in the center of each tube, to be used later for moistening the sand as it dried. The nutrient solution was prepared according to the following formula (Laiho 1970; Steward 1963; Hoagland 1948):

KH_2PO_4	0.5 g
$(NH_4)_2SO_4$	0.25 g
$(NH_4)_2HPO_4$	0.025g
$MgSO_4 7H_2O$	0.15 g
$CaCl_2$	0.05 g
NaCl	0.025g
Fe^{III}citrate (1% solution)	1.2 ml
H_3BO_3	2.86 mg
$MnCl_2 4H_2O$	1.81 mg
$CuSO_4\ 5H_2O$	0.08 mg
$ZnSO_4\ 7H_2O$	0.22 mg
$H_2MoO_4\ H_2O$	0.09 mg
Glucose	2.5 g
Thiamin	25 γ*
H_2O	1000 ml

*25 mg/1000 ml; 1 ml into this formula.

Scotch pine (Pinus silvestris) seeds were surface sterilized by soaking them for 5 minutes in 2% H_2O_2. They were then placed on sterile agar plates for germination. Two of the freshly germinated seedlings were placed in each test tube (with UV light for sterile conditions). To each of 100 test tubes, 10 ml of millipore filtered C. stellaris extract; into each of another 100 test tubes, 10 ml of C. rangiferina extract and into 100 more, 10 ml of Cetraria islandica extract. 100 controls each received 10 ml of sterile distilled water.

Each group of 100 was then divided into groups of 10 test tubes. Each group of 10 was inoculated with a pure culture of one of ten mycorrhizal fungi. Ten groups of controls were likewise inoculated. The eleventh group was the uninoculated control. Unfortunately, the experiment did not include uninoculated controls with lichen extracts added. All tubes were plugged with cotton.

The test tubes were randomized and placed in the greenhouse for six months. When the sand began to dry, the tube was tipped so that water ran out of the small tube in the center and moistened it again, thus watering the trees without contamination.

After six months, 10 UCi of ^{32}P in 5 ml of sterile distilled water were added to each test tube. After 48 hours, each seedling was carefully removed, washed in running water and taped on herbarium paper. A sheet of Saran Wrap was immediately put over the top and then an X-ray film placed on top and exposed for 20 hours. The area of exposure on the film was taken as a measure for the ^{32}P uptake. Although the correlation between the area of exposure and the actual amount of ^{32}P is not linear, in this case the method was considered sufficient to reveal relative differences in the ^{32}P uptake of different seedlings. The area of exposure on the film for each seedling was measured carefully with a planimeter with the knowledge that the high uptake areas are seriously underestimated.

In addition to the ^{32}P measurements, the length of stem, main root and needles were recorded for each seedling.

Results

Not all of the inoculated seedlings developed mycorrhizae. The results were calculated separately for mycorrhizal and nonmycorrhizal seedlings

(Table 7). In 55% of the inoculated seedlings, mycorrhizae were formed. The mycorrhizal root systems were significantly larger than the nonmycorrhizal ones, but stems and leaves were nearly equal in size.

Increased mineral nutrient uptake of mycorrhizal roots in comparison to nonmycorrhizal ones has been described by numerous investigators (for literature references, e.g., Bowen 1973). Greatly increased absorption of phosphorus, in particular, has been repeatedly shown by the use of ^{32}P (Kramer and Wilbur 1949; Harley and McCready 1950; Mejstrik and Benecke 1969). Likewise in this experiment the ^{32}P content in seedlings was significantly greater in the mycorrhizal than in the nonmycorrhizal plants.

In the mycorrhizal seedlings treated with C. stellaris extract the ^{32}P concentration was about the same as in the nonmycorrhizal seedlings and much less than in the mycorrhizal plants of all the other treatments. Seedlings grown with C. stellaris extract also showed a significant inhibition of root development when compared to mycorrhizal seedlings treated with the other lichen extracts and to the inoculated controls. Nonmycorrhizal seedlings treated with C. rangiferina and Cetraria islandica extracts showed a very low ^{32}P uptake. The uninoculated control (Table 7) has a good ^{32}P uptake.

These latter results are in agreement with Bjorkman (1942) and Voight (1971), for instance, who have stated that in fertile soils or nutrient solutions, little if any advantage is gained by mycorrhizal association. Here another dimension, the lichen extract, has been added and its influence upon nonmycorrhizal plants is obviously damaging. The ^{32}P uptake by mycorrhizal pine seedlings treated with C. rangiferina and Cetraria islandica extracts is significantly greater than is the ^{32}P uptake of nonmycorrhizal seedlings. But C. stellaris extract had an inhibitory influence throughout all treatments.

Table 8 expands upon some aspects of Table 7. It shows the average 32P uptake for all seedlings grown with each fungus under the influence of each extract. Again the reduction of the ability of seedlings to absorb ^{32}P in the presence of C. stellaris extract is well illustrated, but at the same time it is obvious that various mycorrhizal fungi do not behave in the same way. For example, Boletus variegatus is much inhibited by C. alpestris extract both in the ability to form mycorrhizae and in the ability of its symbiotic partner, the pine seedling, to incorporate ^{32}P. With C. rangiferina extract the percentage of mycorrhizal seedlings is more than 4 times higher and absorption of ^{32}P 6 times higher. Likewise, in the pure culture experiment, B. variegatus was inhibited by C. stellaris extract but stimulated by C. rangiferina (Table 5).

Of particular interest is Paxillus involutus, which in pure culture was inhibited by all lichen extracts tested. In the synthesis experiment, however, it formed vigorous mycorrhizae in all the other media, whereas C. stellaris completely inhibited the mycorrhiza formation of Paxillus involutus.

Lactarius repraesentaneus also deserves special attention. The fungus itself used in this investigation showed very poor growth. In spite of its poor growth, the fungus seemed to retard the growth of the host plant (Table 9) and the ^{32}P uptake. The seedlings inoculated with this fungus were easily distinguishable from most others by their uniformly unhealthy appearance and yellowish color. A balanced symbiosis of pine and L. repraesentaneus was not established in this experiment.

The figures in Table 8 indicate that the mycorrhizal fungi are not equally beneficial. This has previously been shown by numerous laboratory and field experiments although with somewhat inconsistent results (for literature references and summary of these experiments, see Mikola 1973, pp. 396-401). Table 8 also shows that different mycorrhizal fungi react

quite differently to lichen extracts. Thus, several species of mycorrhizal fungi growing with a symbiont would provide a broader range of adaptability to the biotic environment than would a single species. The advisability of introducing several efficient mycorrhizal fungi under conditions where trees have not grown such as Mikola (1969a and b), Braga and Myers (1967), Vega Condori (1964) and Bjorkman (1970) describe is substantiated.

Comparisons between different fungi in their ability to form mycorrhizae and to promote the phosphorus uptake and growth of the host plant are made in Table 9. In order to make these comparisons possible, all the different lichen extract treatments have been put together. The mycorrhizal fungi are listed according to their average efficiency of ^{32}P absorption, when both mycorrhizal and nonmycorrhizal seedlings are considered. The ^{32}P absorption of mycorrhyzal seedlings is significantly greater than that of non-mycorrhyzal seedlings in nearly all cases.

When only mycorrhizal seedlings are considered, ^{32}P absorption is quite consistent except for two fungi. The remarkable exceptions are Lactarius repraesentaneus and Cenococcum graniforme. As was stated previously, L. repraesentaneus somehow inhibited the host plant and this was also reflected in the ^{32}P uptake which was less than 50% of that of most other fungi. C. graniforme was not used as inoculum but occurred as a contaminant in six test samples of various treatments, the only contaminating fungus found in any treatment. As can be seen in Table 5, in pure culture C. graniforme was not influenced appreciably by any lichen extract tested. The root systems of the seedlings with C. graniforme mycorrhizae were much larger and had more numerous mycorrhizae than did those with any other treatment. The needles were larger, deeper green and more robust looking than were most of those in the other treatments. In total, this small accidental sample of C. graniforme gave the best

growth of any treatment. The obvious correlation of good growth is the exceedingly high ^{32}P absorption rate of 619 mm^2 as compared to the next highest of 301 by Paxillus involutus which grew well or to the lowest of 81 by Lactarius repraesentaneus which grew poorly. Although this material is limited, some comparison to the existing knowledge on Cenococcum graniforme can be made. Mikola (1948) observed that C. graniforme is not so sensitive to antibiotic substances as are most other mycorrhizal fungi. Because of its drought resistance and effectiveness in energy utilization it can form mycorrhizae under unfavorable conditions such as in dry soils or under a dense tree canopy (Mikola 1948; Worley and Hacskaylo 1959; Trappe 1964). Probably it also forms an effective barrier against attack by parasitic fungi, which function has been attributed to mycorrhizal fungi (Marx 1973). Reports on the symbiotic efficiency of C. graniforme are somewhat contradictory. Shemakhanova (1962), Park (1970), and Lamb and Richards (1971) obtained a remarkable growth promotion by inoculation with C. graniforme, whereas in the experiment of Lundeberg (1970) the same fungus suppressed the growth of pine seedlings through immobilization of exchangeable soil nitrogen.

Table 5 suggests that various fungal species may effect the growth of different organs of the seedlings in different ways. Thus, the best needle growth was obtained with Corticium bicolor and Cenococcum graniforme and the best stem growth with Paxillus involutus and Boletus luteus. Although the data are insufficient for any definitive conclusions, observations such as this suggest the use of mixed populations for mycorrhizal inoculation.

FIELD EXPERIMENT ON THE EFFECT OF GROUND COVER ON THE GROWTH OF THE SEEDLINGS

Method

Since the previous experiments were done in the laboratory, field validation of results was considered necessary. The forest nursery at

Suonenjoki (Central Finland) was chosen as the site for this experiment.

Paired 1 m^2 plots were laid out in the nursery and divided into 1/25 m^2 plots. C. stellaris was gathered from the surrounding forest and placed on one of the paired plots. Nylon fish net placed over the plots held the lichens in place. In each square meter plot, 25 one year old seedlings were planted. This was replicated 4 times for each of three kinds of seedlings, Pinus silvestris, Picea abies, and Betula verrucosa, a total of 100 seedlings of each species planted with lichens and 100 planted without lichens. All plots were sprinkled simultaneously when they became too dry. Plantings were made in mid-May and growth measurements taken in mid-July after 3-1/2 summers.

Results

Figure 1 shows that the growth and survival of both Pinus ylvestris and Picea abies are significantly reduced as a result of the C. stellaris treatment. In contrast, Betula verrucosa grew and survived equally well with and without the lichen treatment.

The poorer growth and survival of pine and spruce seedlings on C. stellaris plots can not be attributed solely in some substances leached from the lichen. Although the lichen cover may also affect the moisture, temperature and perhaps even nutrient conditions of the substrate, this field experiment corroborates the results of the laboratory studies on the inhibiting influence of C. stellaris on Pinus silvestris.

COMPLEMENTARY FIELD OBSERVATIONS

Laboratory and nursery experiments were complemented with field observations which were made in natural stands of Cladina stellaris where the influence of reindeer grazing was excluded. Such stands were found in a reindeer exclosure at Katkasuvanto, (Northwest Finland) and in the fenced Finland-Soviet Union border zone at Raja-Jooseppi, (Northeast Finland). Thousands

of seedlings per hectare were present in C. stellaris cover. As has been previously shown, C. stellaris has no influence upon the germination of pine seed. (Brown 1967b).

Eight years before we visited the site the border crossing highway was graded and the C. stellaris along the side, as well as all the other vegetation and pine seedlings were destroyed. New seedlings which looked much more robust were growing on this lichen denuded soil. Ten of these, not exceeding 30 cm in height and ten growing with C. stellaris were dug and taken to the laboratory where they were sectioned at ground level. Basal areas were measured, ages were determined and the number of mycorrhizal root tips were counted. The seedlings chosen for study were about average size for the C. stellaris cover but among the smallest on the denuded roadside. Distance between the collection points was about 1 meter and no soil differences were observable.

As is seen in Table 9, a tremendous difference exists in the growth of pine seedlings on a denuded roadside and in a dense C. stellaris vegetation. Again, the difference cannot be attributed solely to some antibiotic substances released from the lichen; elimination of competition might be a factor. Particularly noteworthy is the great difference in the number of mycorrhizae. Bjorkman (1942) suggests that light is a factor for mycorrhizal formation, but because the distance between the two sampling points at Raja-Jooseppi was only about one meter, light conditions were the same for both. Soil temperature could be a factor. Barnard and Jorgensen (1977) have demonstrated increased metabolic activity, especially of mycorrhizal roots, with a rise in temperature. Bare soil exposed to long hours of sunlight would be warmer than lichen covered soil and thus, both trees and fungi might grow more rapidly. However, the lichen almost surely exerts a direct harmful effect on the mycorrhizal fungi. Leibundgut (1952) observed inhibition of mycorrhizae by lichen vegetation.

The relationship between the density of C. stellaris cover and the growth of pine seedlings was also studied with vegetation analyses in the reindeer exclosure of Katkasuvanto. There, reindeer had been excluded for 25 years. 140 sample plots of 1 m^2 were laid out and the coverage of the dominant species rated on a scale from 0 to 5. The height of all seedlings in the sample plots was recorded. Plots were selected by throwing a 1 meter long stick in a predetermined direction and using it as the near edge of the plot.

Fig.] illustrates the relationships between the abundance of Arctostaphylos uva-ursi, C. ragiferina, and C. stellaris and the size of pine seedlings on these 140 plots. Each point on the graph represents at least 4 plots; some points represent up to 20 plots. This figure corroborates the previous data; where C. stellaris is abundant, growth of pine seedlings is retarded. While C. rangiferina would appear in this graph to be a stimulant to growth, it is not. Actually, it apparently also hinders growth of seedlings although to a smaller degree than does C. stellaris. Where C. rangiferina or Arctostaphylos uva-ursi was abundant, C. stellaris was almost or totally excluded. Thus, pine seedlings thrived best with A. uva-ursi which had no apparent influence on growth or on germination (Brown 1967 b; Brown and Mikola 1974).

The effect of elimination of lichens on the growth of pine seedlings is dramatically illustrated by the behavior of a local reindeer man. About 20 years ago a few reindeer were tethered to trees for one day. Pine seedlings are abundant all over the area but only around the trees where the reindeer had removed the lichen do they grow vigorously. Such examples of seedling growth are found in Lapland, as a result of the former practice of keeping female reindeer tethered to trees at the fawning season. After removal of the lichen its reestablishment takes a long time (Aakre 1966) during which a dense and vigorous thicket of pine seedlings can develop.

DISCUSSION

The laboratory and nursery experiments and field observations indicate consistently that lichens, Cladina stellaris in particular, exert a harmful effect on the growth of pine and spruce seedlings. One of the reasons for such an inhibition is most probably the release from the lichens of some toxic substances which affect adversely the mycorrhizal symbionts of the trees. The sensitivity of different species of mycorrhizal fungi to those substances varies considerably, and many saprophytic and parasitic soil fungi are affected as well. Paxillus involutus which was one of the most active mycorrhizal fungi, seems to be particularly sensitive to the antibiotic influence of C. stellaris. Since corresponding differences apparently exist in the sensitivity of mycorrhizal fungi against other antibiotic factors in soil, too, a mixed population of fungi may be preferable to a single or a few species for mycorrhizal inoculation (Mikola 1970). Then, if some species are inhibited by antibiotic substances present in the soil, others may be more resistant under prevailing conditions and may establish a balanced symbiosis with trees. Such a mixed population also corresponds better to natural conditions where several fungal species usually form mycorrhizae in the root systems of each single tree (Zak and Marx 1961).

The importance of toxic substances released from lichens for forestry practice is still unknown. Logically, if C. stellaris is destroyed or removed, its inhibiting influence will disappear. Cladina can be destroyed by fire. Burning is known to be very beneficial for the early growth of tree seedlings and therefore controlled burning has been widely practiced as a tool in reforestation. The beneficial effect of fire on seedling growth can he attributed, of course, to several factors, such as the elimination of competition, mobilization of nutrients, rise of pH, etc. Destruction of lichens and their inhibiting products can be added to those factors. As was suggested

previously, other plants may release toxic substances comparable with lichen antibiotics. The high temperature of burning also kills the mycorrhizal fungi near the soil surface and therefore somewhat delays the commencement of mycorrhizal infection of the seedlings, but once established, the mycorrhizae grow better than in unburned soil (Mikola et al. 1964).

Reindeer grazing can also destroy lichens effectively and in this respect is comparable with fire. Its strong promotion of seedling growth is hard to explain solely on the basis of elimination of competition; some other harmful effect of the lichen may have been eliminated at the same time. Again, the importance of the presence of inhibiting substances in lichens must be considered. Quite clearly, C. stellaris has the strongest inhibitory influence on mycorrhizal fungi and pine seedlings; C. arbuscula, C. rangiferina and Cetraria islandica have less effect.

An interesting analogy is found in the development of moist Hylocomium-Picea forests of northern Finland. There, with the advancing succession, biological processes slow down, organic matter accumulates and the growth of successive spruce generations gets poorer and poorer (Siren 1955; Harma 1961). It is not known, however, whether toxic excretions of some plants play any role in this process.

Stagnation of biological processes is, of course, contrary to the principles of sound forest management and should be avoided. Fire is known as an effective tool with which to accelerate soil biological processes through release of organically bound nutrients and, perhaps, also through destroying antibiotic factors. Controlled burning has been practiced with good success in the regeneration of old Hylocomium-Picea forests of northern Finland.

These findings have also their application in the lichen-dominated pine forests of northern Finland, although corresponding growth stagnation, as is known in moist spruce forests, has not been noticed in pine forests. A quite natural reason for that is the fact that wild fires have been much more

frequent on dry pine heaths than in moist spruce forests and, therefore, succession in the former has never advanced far enough. Effective control of fires, however, may change the situation. Prescribed burning does not belong to the silvicultural practices in lichen-pine forests, neither can it be recommended there in the future. Instead of that, reindeer grazing can be effectively used to combat the possible harmful effects of the lichens. Old pine forests with lichen vegetation should be heavily grazed immediately before final cutting. Then the ground would be effectively prepared for natural reproduction and the inhibiting effects of lichen on mycorrhizal fungi and tree seedlings would be greatly reduced. This system would also reduce the damage of young seedlings by reindeer, because after the cutting there would be very little food to attract reindeer to the area during the early years of seedling growth.

This subarctic forest biome well illustrates the continuity which must exist in any ecological system. A dynamic balance exists among the major components. Lichens apparently hold trees in check by retarding mycorrhizal growth. Reindeer, in turn, destroy dense lichen cover making rapid growth of mycorrhizal fungi and trees possible. Humans and other predators control reindeer population. Serious damage to any one component will adversely influence the others. Thus, sound reindeer husbandry and proper forestry practices are integral parts of the multiple-use management of this fragile natural system.

REFERENCES CITED

AAKRE, A. 1966. Harvesting of lichens in Nord-Osterdal. Specially the effects on natural pine reproduction. Meld. fr. Norges landbrukschgsk. 45, 20.

ANTI, T. 1974. Personal communication.

BARNARD, E. L. and J. R. JORGENSEN. 1977. Respiration of field-grown loblolly pine roots as influenced by temperature and root type. Can. J. Bot. 55: 740-743.

BJORKMAN, E. 1942. Uber die Bedingungen der Mykorrhizabildung bei Keifer and Fichte. Symb. Bot. Upsal. 6,2.

___ 1970. Mycorrhiza and tree nutrition in poor forest soils. Stud. For. Suec. 83.

BOWEN G. D. 1973. Mineral nutrition of ectomycorrhizae. In "Ectomycorrhizae" (G. C. Marks and T. T. Kozlowski, ec.) pp. 151-205.

BRAGA, G. E. and C. C. Myers. 1967. (Effect of mycorrhizae on the development of Pinus elliottii.) Silvicultura em Aso Paulo. 6: 261-271.

BROWN, R. T. 1967a. Separation of non-viable jack pine seeds by ether extraction. For. Sci. 13:84.

BROWN, R. T. 1967b. Influence of naturally occuring compounds on germination and growth of jack pine. Ecology 48: 542-546.

BROWN, R. T. and P. MIKOLA 1974. The influence of fruticose soil lichens upon the mycorrhizae and seedling growth of forest trees. Acta Forestalia Fennica 141: 1-23.

HARLEY, J. L. and C. C. McCready. 1950. Uptake of phosphate by excised mycorrhizal roots of beech. I. New Phytol. 49: 388-397.

HARMA, J. 1961. Bjorkens inflytande pa granens produktion. Norrl. skogsv. forb. tidskr., 288-290. (orig. in Russian, Les. Khoz. 1960.)

HOAGLAND, D. R. 1948. Lectures on the inorganic nutrition of plants. Chron. Bot., Waltham, Mass.

International Biological Program. 1971. Biochemical interaction among plants. Nat. Acad. Sci., Washington, D. C.

KRAMER, P. J. and K. M. Wilbur. 1949. Absorption of radioactive phosphorus by mycorrhizal roots of pine. Science 110: 8-9.

LAIHO, 0. 1970. Paxillus involutus as a mycorrhizal symbiont of forest trees. Acta For. Fenn. 106

LAMB, R. J. and B. N. Richards. 1971. Effect of mycorrhizal fungi on the growth and nutrient status of slash and radiata pine seedlings. Aust. Forest. 35, 1.

LEIBUNDGUT, H. 1952. Flechtenrasen als Hindernis fur die Ansamung. Schw. Zeitschr. f. Forstw. 103: 162-168.

LUNDEBERG, G. 1970. Utilization of various nitrogen sources, in particular bound soil nitrogen, by mycorrhizal fungi. Stud. For. Suec. 79.

MARKS, G. C. and T. T. KOZLOWSKI (editors). 1973. Ectomycorrhizae, their ecology and physiology. Acad. Press, Inc., New York. 444 pp.

MARX, D. H. 1973. Mycorrhizae and feeder root diseases. In "Ectomycorrhizae" (G. C. Marks and T. T. Kozlowski, ed.), pp. 351-382. Acad. Press. New York.

MAULL, T. W. 1963. Seed germination and establishment of Pinus rigida. An autecological study. Diss. Abstr. 23: 36-7-3608.

MEJSTRIK, V. and U. Beneke. 1969. The ectotrophic mycorrhizas of Alnus viridis (Chaix) D. C. and their significance in respect to phosphorus uptake. New Phytol. 68:141-149.

MELIN, E. 1925. Untersuchungen uber die Bedeutung der Baummykorrhiza. G. Fischer, Jena.

1946. Der Einfluss von Waldstreuextrakten auf das Wachstum von Bodenpilzen, mit besonderer Berucksichtigung der Wurzelpilze von Aaumen. Symb. Bot. Upsal. 8,3.

1953.. Physiology of mycorrhizal relations in plants. Ann. Rev. Plant Physiology 4: 325-346.

___ 1963. Some effects of forest tree roots on mycorrhizal Basidiomycetes. In "Symbiotic Associations" (P. S. Nutman and B. Mosse, ed.). pp. 125-145. Cambridge Univ. Press.

MIKOLA, P. 1948. On the physiology and ecology of Cenococcum graniforme especially as a mycorrhizal fungus of birch. Comm. Inst. For. Fenn. 36.3.

__ 1965. Studies on the ectendotrophic mycorrhiza of pine. Acta Forest. Fenn. 79.2.

1969a. Comparative observations on the nursery technique in different parts of the world. Acta Forest. Fenn. 98.

___ 1969b. Mycorrhizal fungi of exotic forest plantations. Karstenia 10: 169-176.

___ 1970. Mycorrhizal inoculation in afforestation. Int. Rev. Forest Res. 3: 123-196.

1973. Application of mycorrhizal symbiosis in forestry practice. In "Ectomycorrhizae" (G. C. Marks and T. T. Kozlowski, ec.), pp. 384-411. Acad. Press. New York.

1964. O. Laiho, J. Erikaenen and K. Kuvaja. The effect of slash burning on the commencement of mycorrhizal association. Acta Forest Fenn. 77,3.

MODESS, O. 1941. Zur Kenntnis der Mykorrhizabildner von Kiefer and Fichte. Symb. Bot. Upsal. 5, 1.

PARK, J. Y. 1970. Effect of field inoculation with mycorrhizae of Cenococcum graniforme on basswood growth. Canada Dept. of Fisheries and Forestry, Bi-m. Res. Notes 26: 27-28.

RICE, E. L. 1974. Allelopathy. Acad. Press, Inc. New York. 353 pp.

SHEMAKHANOVA, N. M. 1967. "Mycotrophy of woody plants." Isr. Program Sci. Transl., Jerusalem. (Orig. in Russian, Izd. Akad. Nauk. SSSR Moscow, 1962.)

SIREN, G. 1955. The development of spruce forest on raw humus sites in northern Finland and its ecology. Acta Forest. Fenn. 62. 4.

STEWARD, F. C. 1963. Plant physiology. 111. Inorganic nutrition of plants. Acad. Press, New York.

TRAPPE, J. M. 1964. Mycorrhizal hosts and distribution of Cenococcum graniforme. Llyodia 27: 100-106.

VAARTAJA, O. 1957. Damping off control by antibiotic plant substances. Bim. Progr. Rep., Div. For. Biol., Dep. Agr. Can. 13: 2.

VEGA CONDORI, L. 1964. Effect of mycorrhizae on the initial growth of tropical conifers. Turrialba 14: 151-155.

VOIGHT, G. K. 1971. Mycorrhizae and nutrient mobilization. In "Mycorrhizae," Misc. Publ. 1189, U. S. Forest Service, pp. 122-131.

WORLEY, J. F. and E. Hacskaylo. 1959. The effect of available soil moisture on the mycorrhizal association of Virginia pine. For. Sci. 5: 267-268.

ZAK, B. and D. H. Marx. 1964. Isolation of mycorrhizal fungi of individual slash pine. For. Sci. 10: 214-222.

TABLE 1. Germination of jack pine seeds in the presence of inhibitory plant leaf extracts.*

Species	Common name	pH of extract	Percentage germination after 14 days
Salix pellita	Pussy willow	6.2	9
Prunus pumila	Sand cherry	6.1	0
Prunus serotina	Black cherry	6.2	0
Gaultheria procumbens	Wintergreen	6.3	21
Solidago juncea	Goldenrod	5.0	9
Solidago uliginosa	Goldenrod	4.9	2
Control		7.0	82

*Revised from Brown 1967b.

TABLE 2. Plants whose water extracts sometimes inhibited jack pine seed germination.*

Species	Common Name	Plant part extracted
Boletus edulis	Bolete	Fruiting bodies
Cladonia cristalella	British soldiers	Entire plant
Sphagnum capillaceum	Peat moss	Entire plant
Populus tremuloides	Trembling aspen	Leaves
Populus grandidentata	Big tooth aspen	Leaves

*Revised from Brown 1967b.

Table 3. Plants whose water extracts do not inhibit germination of jack pin seeds.*

Species	Common Name	Plant parts extracted
Amanita muscaria	Fly amanita	Fruiting bodies
Cladina mitis)		
Cladina rangiferina)		
Cladina stellaris)	Reindeer lichens	Entire plants
Cladina uncialis)		
Cladonia gracilis	Spoon lichen	Entire plant
Polytrichum juniperinum	Hair cap moss	Entire plant
Polytrichum piliferum	Hair cap moss	Entire plant
Dicranum scoparium	Broom moss	Entire plant
Pleurozium schreberi	Red stem moss	Entire plant
Pteridium aquilinum	Bracken fern	Leaves
Picea mariana	Black spruce	Leaves
Pinus banksiana	Jack pine	Leaves and wood
Pinus strobus	White pine	Leaves
Andropogon scorparius	Little blue stem grass	Leaves
Calamagrostis canadensis	Blue joint grass	Leaves
Danthonia spicata	Poverty grass	Leaves
Deschampsia flexuosa	Hair grass	Leaves and stems
Carex pensylvanica	Sedge	Leaves and stems
Maianthemum canadensis	Canada mayflower	Leaves
Comptonia peregrina	Sweet fern	Leaves
Alnus rugosa	Alder	Leaves
Betula papyrifera	White birch	Leaves
Quercus rubra	Red oak	Leaves
Potentilla tridentata	3-leaf five finger	Leaves
Rubus recurvicaulis	Dewberry	Leaves
Acer rubrum	Red maple	Leaves
Arctostaphylos uva-ursi	Bear berry	Leaves
Chamaedaphne calyculata	Leather leaf	Leaves
Ledum groenlandicum	Labrador tea	Leaves
Epigaea repens	Trailing arbutus	Leaves
Vaccinium augustifolium	Blueberry	Leaves
Vaccinium myrtiloides	Blueberry	Leaves
Melampyrum lineare	Cow wheat	Leaves and stems
Campanula rotundifolia	Bluebell	Leaves and stems
Aster macrophyllus	Big leaf aster	Leaves
Hieracium aurantiacum	Orange hawkweed	Leaves and stems
Hieracium scabrum	Harsh hawkweed	Leaves and stems
Krigia biflora	Two-flowered dandelion	Leaves and stems

* Revised from Brown 1967b.

Table 4. Plants whose water extracts sometimes stimulated jack pine seed germination.*

Species	Common name	Plant part extracted
Pinus resinosa	Red pine	Leaves
Oryzopsis pungens	Rice grass	Leaves and stems
Amelanchier laevis	June berry	Leaves
Cornus canadensis	Bunch berry	Leaves and stems
Trientalis borealis	Star flower	Leaves and stems

* Revised from Brown 1967b.

TABLE 5. Action of lichen extracts on fungus growth. Figures show significance levels of inhibition or (+) stimulation (Student's t test). X indicates no influence, - indicates no test.*

FUNGUS	LICHEN EXTRACTS			
	Cladina stellaris	*C. arbuscula*	*C. rangiferina*	*Cetraria islandica*
Amanita muscaria	.001	X	X	X
A. rubescens	.001	X	X	.01
Cenococcum graniforme	X	X	X	X
Collybia botyracea	X	X	X	X
C. dryophylla	.001	.01	.001	.01
Corticium bicolor	.001	.05	.05	.001
E-57 (Ectendomycorrhiza)	.01	-	.05	.05
Fomes annosus	.001	-	+.001	.001
Laccaria laccata	.01	.01	.05	X
Lactarius representaneus	.001	-	-	-
Lepiota procera	.001	.001	.001	.001
Marasmius androsaceus	.001	.001	.001	.01
Paxillus involutus	.001	.001	.01	.001
Suillus bovinus	.05	.05	X	X
S. luteus	X	X	X	X
S. variegatus	.05	X	+.05	X
Tricholoma flavobrunneum	.001	X	X	X
T. imbricatum	.001	X	X	.05

*Revised from Brown and Mikola, 1974.

TABLE 6. Action of extracts from humus collected beneath lichen cover shown on fungus growth. Figures show levels of inhibition or (+) stimulation (Student's t test). X indicates no influence.*

	Cladina stellaris	*C. arbuscula*	*C. rangiferina*	*Cetraria islandica*
Amanita muscaria	X	X	+.05	X
A. rubescens	.01	+.01	+.05	X
Cenococcum graniforme	X	X	X	X
Collybia botyracea	+.05	X	X	X
C. dryophylla	.01	.01	.05	.01
Corticium bicolor	X	X	X	.05
Laccaria laccata	X	X	.01	.01
Lepiota procera	X	X	.01	.01
Marasmius androsaceus	.05	.05	.01	.01
Paxillus involutus	.001	.001	.001	.001
Suillus bovinus	.05	X	X	X
S. luteus	X	+.05	X	X
S. variegatus	X	X	X	X
Tricholoma flavobrunneum	X	.05	X	X
T. imbricatum	X	.05	X	.001

*Revised from Brown and Mikola, 1974.

TABLE 7. Pinus sylvestris ^{32}P activity and mycorrhizal association with different lichen extracts. P activity is measured in area of radioautographs of seedlings.*

Treatment	^{32}P Activity		% Mycorrhizae
	+**	-	
Inoculated control - average of all fungi	162 mm^2	171 mm^2	55
Inoculated + *Cladina stellaris* extract	116	101	46
Inoculated + *Cladina rangiferina* extract	201	77	62
Inoculated + *Cetraria islandica* extract	227	66	68
Control nutrient solution		228	

* Revised from Brown & Mikola 1974.

** + indicates mycorrhizae on seedlings, - indicates non-mycorrhizal seedlings.

TABLE 8. Mycorrhizal development and ^{32}P absorption efficiency of ten fungi when treated with different lichen extracts.*

Mycorrhizal fungus	Lichen extracts					
	Cladina stellaris		C. rangiferina		Cetraria islandica	
	Percentage of mycorrhizal seedlings	^{32}P activity, mm^2	Percentage of mycorrhizal seedlings	^{32}P activity, mm^2	Percentage of mycorrhizal seedlings	^{32}P activity, mm^2
Lactarius repraesentaneus	88	76	57	72	13	54
Tricholoma flavobrunneum	22	92	63	116	44	118
Tricholoma imbricatum	100	130	17	54	71	139
Boletus variegatus	20	44	88	259	67	164
Amanita muscaria	29	154	38	95	57	115
E-57	25	177	50	165	33	76
Corticium bicolor	50	109	57	181	75	91
Amanita rubescens	63	50	91	192	75	167
Boletus luteus	78	147	60	120	88	251
Paxillus involutus	0	136	80	232	71	458

*Revised from Brown and Mikola, 1974.

TABLE 9. The growth of *Pinus silvestris* seedlings and mycorrhizal development with and without *Cladina stellaris* at border zone (Raja-Jooseppi).*

Site	Average age, yrs	Average basal area, mm^2	Average basal area growth, mm^2/year	Average number mycorrhizal
Cladina stellaris	21.3	10.3	0.51	27
Denuded roadside	6.4	18.6	2.91	195

*Revised from Brown and Mikola 1974.

Figure 1. Growth of Pinus silvestris seedlings with different densities of three associated ground cover plants.