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THE EFFECT OF ARTHROPOD GRAZING ON FUNGAL SUCCESSION ON NEEDLES OF PICEA ABIES L. KARST.

Sarah Sandra Lynn Levy

A Thesis

in

The Department

of

Biology

Presented in Partial Fulfilment of the Requirements
for the degree of Master of Science at
Concordia University
Montreal, Quebec, Canada

April 1995

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ABSTRACT

THE EFFECT OF ARTHROPOD GRAZING ON FUNGAL SUCCESSION ON NEEDLES OF PICEA ABIES L. KARST.

Sarah Sandra Lynn Levy

Dark-pigmented fungi, primary saprophytes, on above-ground senescent and dead leaves are replaced by non-pigmented fungi, secondary saprophytes, in the litter layer, even though primary saprophytes are capable of surviving in the soil. Dark pigmented fungi are good competitors, and possess a wide range of enzymes. Laboratory and field experiments were used to test the hypothesis that soil arthropods, by preferentially feeding on primary saprophytes, removed them from the litter layer, allowing for their replacement by non-pigmented fungi, thus affecting both the structure of the microfungal community and its function in decomposition.

Naphthalene was used for defaunation since laboratory experiments indicated that it successfully reduced the number of soil animals more efficiently than the non-chemical use of heat, without significantly affecting the fungal community structure.

The hypothesis was confirmed as a general trend. Both laboratory and field experiments showed the numbers of primary saprophytes to be lower in the presence of soil animals, particularly in the field experiment in July, when microfauna were most abundant in the litter layer. This occurred without an increase in the number of secondary saprophytes.

Laboratory experiments indicated that needles inoculated with primary saprophytes lost more weight than those inoculated with secondary saprophytes. Although primary saprophytes were more abundant in the defaunated enclosures, litterbags of needles in control enclosures lost significantly more weight, after a period of one year, than those in naphthalene treated enclosures. This suggested that soil animals affect the decomposition process in other ways than by reducing the number of primary saprophytes.

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INTRODUCTION

Although successional changes in communities of plants had been adequately described, little research on fungal species replacement on naturally occurring plant debris took place before 1950. This was due to the minuteness of the fungi, difficulties in recognizing species in their vegetative state, and general taxonomic problems (Hudson, 1968). The pattern of succession of saprophytic fungi was first described by Webster (1956,1957) on decaying cocksfoot culms (Dactylis glomerata), followed by Hogg and Hudson (1966) on leaves of beech (Fagus sylvatica), by Kendrick and Burges (1962), and Richards (1974), on the needles of Scots pine (Pinus sylvestris), and by Gourbière (1981), on white pine (Picea alba Mill.). These studies and others have shown that succession on the above-ground decaying remains of many different plants, begins with dark-pigmented or dematiacious fungi, the primary saprophytes. These fungi, which include Alternaria, Cladosporium and Epicoccuum attack the plant at the onset of senescence. These are replaced by non-pigmented or hyaline, secondary saprophytic fungi in the litter layer and in the soil, with Trichoderma and Penicillia highly represented here.

Although the initial stages of succession seem to be the result of random, opportunistic events, environmental conditions exert selective pressure on those species which survive (Drury and Nisbet, 1973). The phylloplane, or surface of leaves, is a site of high stress due to severe fluctuations in temperature and moisture,

particularly in trees (Pugh and Boddy, 1988). On above-ground substrates, dark-pigmented primary saprophytes have a definite advantage as colonizers, due to the presence of melanin, which is thought to confer protection from ultraviolet radiation (Pugh, 1974) and increase toleration for low moisture levels (Park, 1955). Webster and Dix (1960) showed that dark-pigmented saprophytes on cocksfoot culms had a shorter latent time before germination and their growth rate was faster than that of non-pigmented secondary saprophytes under conditions of low humidity. Diem (1971) determined that dark-pigmented fungal germ tubes were more resistant to desiccation than those of hyaline species.

Lysis, arising from the destruction of fungal surface structures by bacteria, is an important mechanism by which fungi are destroyed in nature. However, dark-pigmented species are not readily susceptible to enzymatic digestion. Lockwood (1960) noted that the darker hyphae of Helminthosporium sativum and Alternaria solani were more resistant to microbial lysis than the hyaline hyphae. In lab experiments, Lockwood (1960) was able to show that melanin-producing Aspergillus nidulans was resistant to solubilization by beta(1-3)glucanase and chitinase, whereas a non-pigmented mutant was not. He hypothesized that melanin could inhibit the enzymes that participate in lysis, or act as a barrier to enzymatic hydrolysis of surface localized polymers. Bloomfield and Alexander (1967) found that Aspergillus phoenicus QM 1005 conidia, that had their dark spicules removed by abrasion with glass beads, in a mixer, were readily degraded by the soil

microorganisms Bacillus and Streptomyces while the spicule-containing hyphal walls resisted hydrolysis.

Interactions among different fungal species influence the organization of microbial communities, particularly when they have the same requirement for resources. Possible outcomes of fungal interactions are neutral intermingling, deadlock, where one species does not enter the territory held by another species, and species replacement. Using in vitro interactions of seven common soil fungi, Stahl and Christensen (1992) stated that on low resource media, most interactions resulted in neutral intermingling. In oligotrophic soil, the cost to benefits ratio of allocating resources to attack another species may be less than developing neutral, exploratory hyphae. Territorial or competitive behaviour would be more logical when one species was already established on a resource.

Succession is believed to occur when one fungal species on a resource is replaced by another possessing greater "competitive saprophytic ability", which Garrett (1956) defined as the ability to colonize a substrate in the presence of competitors. Thus fungi possessing inhibitory compounds, which could inhibit or interfere with other fungi (Wicklow, 1981), could influence the species composition of the microfungal community. Non-pigmented Trichoderma and Penicillia may become more important in the humus and A1 profiles of forest soils, due to their ability to produce antifungal toxins (Widden and Parkinson, 1973). However, pigmented fungi have been shown to be competent competitors in the soil, and

some, such as Epicoccum, possess antifungal compounds (Brown et al., 1987). Thus their disappearance in the litter layer may be due to other factors than their displacement by other fungi.

A species can be more competitive if it possesses a wider range of depolymerizing enzymes than other species. Garrett's "substrate utilization theory" (1963) maintained that species with limited enzyme systems were replaced by others whose enzyme system was more complex. He suggested that "Sugar fungi", that first appeared on the senescent plant tissues, were only able to use the simple sugars found on leaves in the canopy, and were replaced by cellulose decomposers, the secondary saprophytes, when the plant tissue reached the ground. However Frankland (1976) stated that simple sugars were always available in the soil. On bracken litter, Pteridium aquilinium, the non-cellulolytic Mucor hiemalis replaced the cellulolytic Mycena galopus at the stage when the initial sugar content of the substrate was used up, suggesting that M. galopus could generate sugar for fungi at later stages of succession. These "secondary sugar fungi" might stimulate the rate of cellulose breakdown by their interaction with the cellulolytic fungi.

Pugh et al. (1972) indicated that the majority of primary saprophytes are cellulolytic, and have other depolymerizing enzymes. Phylloplane fungi, which arrive at the leaf surface as airborne conidia, can persist on leaves for long periods of time, suggesting that primary saprophytes are not confined to simple soluble carbohydrates, such as hexoses or pentoses (Cooke and Rayner, 1984). Hogg and Hudson (1966) recorded the presence of

Cladosporium herbarum on leaves of *Fagus sylvatica* for a period of sixteen months.

The "inhibition" theory applies to situations where all species present are equally fit to occupy a site or a resource. A secondary species can replace the first only when the primary invader has been removed by local disturbances, pathogens or predators. Widden (1986a) determined that abiotic factors, such as soil temperature, depth and particle type, accounted for only part of the variation in the fungal communities from four types of soils in southern Quebec. He suggested that if soil fungi respond independently of soil properties, then interactions with other microorganisms may be influential in shaping the fungal species composition.

Filamentous fungi are among the most nitrogen-rich natural foods commonly used by invertebrates. When ecosystems are nutrient limited, particularly by nitrogen, phosphorus and/or potassium, translocation of these elements take place in plants before litter enters the decomposer system. Fungi are highly efficient at penetrating plant remains, extracting nutrients and incorporating them into microbial tissues. Fungal tissue is a good source of choline, sodium, B vitamins, which are dietary requirements for insects, ergosterol, which insects need for growth and reproduction (Cromack et al., 1977), calcium, in the form of calcium-oxalate, necessary for oribatid cuticles (Norton and Behan-Pelletier, 1990), and secondary metabolites, such as melanins, which may serve as stimulants to invertebrate feeding and oviposition (Martin, 1979).

Since few invertebrates have cellulase, to break down cellulose, the major part of dead plant matter, they must depend on internal microbial symbionts, such as the gut bacteria of termites (Collins, 1989), enter into mutualistic relationships with microorganisms, such as the fungus gardens of Attine ants (Cherrett, 1989), or obtain nutrients indirectly, by eating the microorganisms that first attack the litter (Engelmann, 1961). Luxton (1972) studied the enzyme components of various cryptostigmatid mites and concluded that while many of the species that fed mainly on fungi did not possess cellulase, they could digest amylose and chitin. This ability allows them to break down fungal cell walls and obtain trehalose, a fungal sugar. In addition, Usher et al. (1978) noted that in Scots pine litter, collembolans and cryptostigmatid mites were located in the top 2cm of the litter, where most of the fungi are located. Thus invertebrates have the potential for interacting with the fungal community through grazing. Light grazing acts as pruning, and can stimulate growth by relieving density-dependent inhibitory situations, such as the accumulation of waste products, and rejuvenating the colony by removing senescent structures. Heavy grazing can destroy a fungus when the intensity of the grazing exceeds its capacity to regenerate (Hanlon, 1981).

Invertebrates are sensitive to differences in quality of their food, and will alter their feeding habits in response to nutritional changes over time (Waldbauer and Friedman, 1991).
By selective feeding, soil animals can reduce the competitive ability or inoculum potential of one species, giving a normally

weak competitor an advantage, or weakening a strong one. Newell (1984a) showed that the presence of the basidiomycete Marasmius androsaceus (L. ex Fr.) Fr., caused the basidiomycete Mycena galopus (Pers. ex Fr.) Kummer to originate its fruiting body 10mm below the litter. When M. androsaceus was removed, by preferential feeding of the collembolan Onychiurus latus Gisin., M. galopus had a mean depth of fruiting of about 6mm. Thus it spent less energy on vertical growth and more on reproduction, and in the process, replaced M. androsaceus in the fungal community. Newell (1984b) indicated that when both fungi were inoculated on sterile needles of Sitka spruce (Picea sitchensis Carr), in flasks, M. androsaceus colonized the needles almost twice as quickly as M. galopus. When the collembolan O. latus was introduced into the flasks containing both fungi the colonizing ability of M. galopus was greater than that of M. androsaceus.

Researchers (Hartenstein, 1962; Luxton, 1972; Mitchell and Parkinson, 1976; Klironomos et al., 1992), using laboratory experiments, have shown that while soil animals do not feed exclusively on dark-pigmented fungi, these fungi are always high on the list of preferred fungi. Mills and Sinha (1970) indicated that the springtail, Hypogastrura tullgergi, a springtail, most readily consumed dark-pigmented fungi that allowed for the greatest rate of reproduction, and had a low hyphal mat, allowing free movement of the insects. Visser (1985) suggested that feeding selectivity of soil animals could contribute to fungal succession.

When Klironomos et al. (1992) added collembolans to

microcosms, containing needles of Norway spruce, inoculated with primary and secondary saprophytes, the primary saprophytes were greatly reduced within two weeks, while little change in the fungal composition was noted in the absence of animals. Although this laboratory experiment indicated that preferential feeding by soil animals could drive fungal succession, this has never been tested in the field. Therefore I set up field experiments, using control and defaunated sample plots, to compare the effect of grazing of soil animals on the structure of microfungal communities.

Naphthalene, which has been used by researchers such as Witkamp and Crossley (1966) and Kurcheva (1960) in deciduous forests, was chosen as the defaunation agent, since, unlike other pesticides, such as aldrin, it is non-persistent in soil, and non-toxic to the environment. Before using naphthalene in the field, it was necessary to know how this product would affect the soil microfauna. Therefore laboratory microcosms were used to determine the effectiveness of naphthalene in driving the microfauna out of the litter layer, and to compare naphthalene to the non-chemical use of heat for defaunation.

It was also necessary to know if naphthalene would have any effect on the species composition of the fungi. Witkamp and Crossley (1966) compared the effects of the insecticides dieldrin, para-dichlorobenzene, chlordane and naphthalene on fungal density, mycelial growth and respiration. Naphthalene was found to have the least effect on fungal counts and mycelium lengths, while it reduced the arthropod population to 20% of the controls. Ghilarov

(1983) found that the reduction of soil animals from oak forest litter by naphthalene did not affect the activity of bacteria and fungi. However, Torstensson and Wessen, (1984), Wardle and Parkinson, (1990), and Suyama et al., (1993), reported changes in the composition of the fungal flora as the result of the application of various pesticides. Therefore the effect of naphthalene on the fungal community composition was also examined in laboratory microcosms.

Decomposition of plant litter is a series of steps whereby the energy and nutrients stored in this material are released in a form accessible to plants, the primary producers (Crossley, 1977). This is due to interacting activities of various components of the soil biota (Armson, 1977). Coniferous litter is characterized by a paucity of nutrient elements, such as nitrogen, the presence of waxes, resins, tannins, and high levels of lignin, cellulose (sclerophyll), phenolics, terpenoids and non-nitrogen based allelochemicals (Mattson, 1980). The acidity of the litter favours fungi as the dominant decomposer organisms, responsible for nutrient release from needles. In order to interpret the results of the field experiment, a laboratory experiment was set up to determine whether or not primary and secondary saprophytes were equally capable of causing needles to decompose.

Because of the recalcitrant nature of coniferous litter, and the presence of toxins such as phenolics and tannins, which are capable of precipitating proteins as well as digestive enzymes (Robbins et al., 1987), saprophagous soil animals can only consume

litter after it has been partially broken down and detoxified by fungi. Soil arthropods participate in decomposition either directly, by feeding on litter, or indirectly, through their effect on the microbial community. Since fungi and bacteria contribute most to litter breakdown in the coniferous ecosystem, some researchers, such as Crossley (1977), consider that the indirect effect may exceed the direct one.

Mitchell and Parkinson (1976) suggested that selective feeding that contributed to the structure of the microbial community also affected the decomposition process. Since fungi are the principal agents of decomposition in coniferous systems, and if fungi differ in their enzyme components, and decomposing ability, any change in the composition of the microfungal population, caused by the removal of soil animals, could have significant effects on decomposition. To test this hypothesis, nylon bags containing a fixed amount of litter were placed in control and defaunated enclosures. After a period of one year the weight of litter in the control plots was compared to that of the defaunated enclosures. The implications of these findings were discussed with reference to the coniferous ecosystem as a whole.

The hypotheses tested in this thesis were:

(1)- soil animals change the pattern of fungal succession on the needles of Norway spruce by preferentially feeding on primary saprophytes, and by removing them, allow for their replacement by secondary saprophytes

(2)- by changing the structure of the microfungal community,

microfaunal grazing changes the contribution of the fungi to decomposition, and alters the rate of decomposition.

MATERIALS AND METHODS

Study site

The study site was a mature Norway spruce plantation (*Picea abies* *L.* *Karst*.) on the Concordia University property, the Lacolle Center, located 60km south of Montreal. This plantation, and one of white pine (*Pinus strobus* *L.*) were established approximately sixty-five years ago, after the original vegetation was destroyed by fire. The Norway Spruce plantation is bordered, on the eastern side, by a white pine plantation and by naturally regenerated deciduous trees on the other three sides. Little interference occurs with regard to litter input and decomposition of organic matter since the different soil layers have not been disturbed by forest management practices for at least twenty years.

Preparation of the microcosms

On May 20, 1993, a soil corer was used to remove intact cores of soil, approximately 450 cubic cm, 7cm in diameter, from the top 12cm of the litter and soil layer, from random points in the study area, outside of the plots set up for the field experiment. Preliminary investigation showed that the litter, humic and fermentation layers comprised the top 4cm of the soil. The rest was the mineral layer. Each soil core was placed in a microcosm, maintaining the same vertical orientation as in the field.

The microcosms consisted of 15cm polyvinyl chloride cylinders with a layer of 1 mm nylon mesh glued to the bottom. A 2.5cm layer of gravel was placed at the bottom of each cylinder, to prevent the fine soil of the mineral layer from escaping. The microcosms were kept in a shaded area on the roof of the Hall building, Concordia University for the duration of the experiments.

Preparation of the field plots

In May, 1993, an area 20 m X 25m, in the Norway spruce plantation, at Lacolle, was subdivided into twenty $5m^2$ plots. In the center of 10 of the plots, chosen at random, a $1m^2$ area was blocked off, using pieces of untreated plywood, 30cm high by 1m wide, to form a square enclosure, extending into the mineral layer to a depth of at least 5cm. A sheet of nylon mesh was stapled to the top of each enclosure to prevent the entry of additional needles once the experiment had begun. This sheet was removed for the sampling of needles, soil and the application of naphthalene, and then restapled in place.

Five enclosures, chosen at random, were used as controls, and five were defaunated by use of 100g naphthalene, applied approximately every ten days (Witkamp and Crossley, 1966). The naphthalene was evenly sprinkled over the entire surface of the enclosures. The naphthalene application began after the first sampling of needles, October 10,1993, and continued through the fall until the ground froze. Treatment recommenced when the snow

disappeared in April 1994.

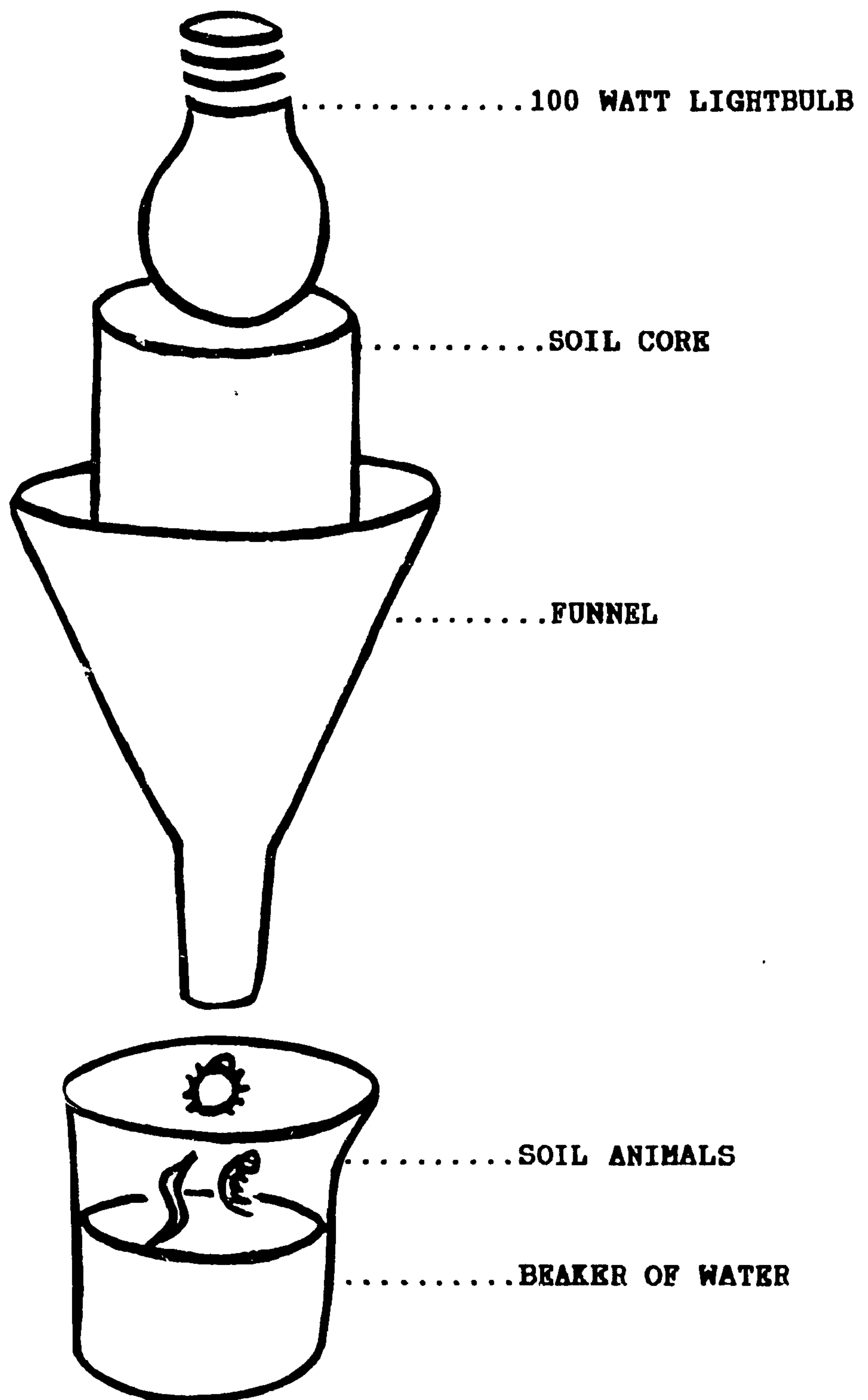
Enumeration of the soil animals

Soil cores, from laboratory or field experiments, used to monitor the microfauna, were placed in Tullgren funnels. A 100 watt light bulb, placed 2.5cm above the top of each microcosm or soil core, heated and dehydrated them. Soil animals escape the heat and drought by migrating downward, through the soil core. They fall through the nylon mesh, down the funnel, into a beaker of water placed under each funnel (Fig. 1). This treatment was carried out for one week. The number of soil animals that fell into the beakers was recorded.

Enumeration of the fungi

Five needles, selected at random, from each microcosm and flask, for the different laboratory experiments, and thirty needles from each enclosure, were first washed, for ten cycles, in an automatic soil washing apparatus (Bisset and Widden, 1972), to remove all fungi not actually growing on the needles. The needles were then dried on filter paper for 24h and cut into 1mm fragments. Fragments of each needle were plated, four fragments to a plate, on Czapek Dox Agar plates, which was acidified to pH 4.5. The plates were incubated at 20°C, in light conditions, to encourage sporulation. The fungi growing out of fragments were identified,

Fig. 1. Tullgren funnel


100 WATT LIGHTBULB
SOIL CORE
FUNNEL
SOIL ANIMALS
BEAKER OF WATER

some to the genus, some to the species level, according to Barron (1968), Pitt (1979) and Domsch et al. (1980).

Laboratory experiments

Microcosms

The microcosms were used in a laboratory experiment designed: (1)- to investigate the effectiveness of naphthalene as a defaunation agent and to compare its effectiveness to that of heat. (2)- to examine the effect of defaunation on the species composition of the microfungi. The microcosms were divided into three groups, for (A) controls, (B) heat treatment, and (C) naphthalene treatment. Each group was further divided into those microcosms for examining the fungal population, and those that would be used to monitor any change in the number of soil animals.

Heat is effective in driving soil animals away from the source of heat. The heat treatments, set up May 20, 1993, consisted of positioning the microcosms in Tullgren funnels for a week to extract the soil animals, after which time the microcosms were rehydrated with distilled water. The number of animals found in the beakers were counted and identified as "mites", "collembolans", "others" and "total". The naphthalene treated microcosms had 0.5 grams of naphthalene applied to the surface of the soil cores weekly.

Approximately every two weeks, one microcosm from each

treatment group for monitoring the microfaunal population was placed in a Tullgren funnel, as described above. The soil cores were discarded after the number of extracted animals were counted. The numbers of soil animals extracted from the "control", "heat treatment" and "naphthalene treatment" microcosms were compared.

The experimental design consisted of one microcosm for each treatment, and was replicated five times. To examine any change in the species composition of the microfungi on Norway Spruce needles over time, samplings of fungi on the needles took place May 20, 1993, before any treatments were initiated, and after treatments had begun, June 23 and July 27, 1993. At each sampling the fungi growing out of fifty fragments, cut from five needles randomly chosen from each microcosm were identified.

Effect of naphthalene on the species composition of the microfungi

To determine whether the presence of naphthalene had any effect on the species composition of the microfungi, on September 20, 1993, 2g needles, that had been washed in a soil washing apparatus (Bisset and Widden, 1972), were placed in a 125ml flask that was sealed with a foam plug, (A) the control. The weight of flask, needles and plug was carefully noted. A second flask (B), contained washed needles, plus 0.5g naphthalene. The amount of water loss, through evaporation, was determined by weighing the first flask, every third day. The lost water was replaced in flasks A and B. A third flask (C), contained 2g of washed needles, that

were allowed to dry out, and 0.5g of naphthalene. Naphthalene loss, through vaporization, was determined by weighing the flask, every third day. The naphthalene loss was replaced in flasks B and C. This experiment was replicated five times. On January 11, 1994, approximately three months after the experiment was set up, five needles, selected at random from (A) control and (B) naphthalene-treated flasks were prepared for sampling as described previously. The fungi growing out of fifty needle fragments from each flask were then identified.

Decomposition abilities of primary and secondary saprophytes

To compare the weight loss of needles inoculated with primary saprophytes to needles inoculated with secondary saprophytes, the most frequently observed primary and secondary saprophytes were isolated and grown in pure culture on 2% malt extract agar plates. The primary saprophytes were Alternaria, Cladosporium, Epicoccum, and two unidentified sterile dark fungi, "Sterbrown" and "Sterdark". The secondary saprophytes were Trichoderma koningii, Trichoderma polysporum and two variants of Penicillium spinulosum.

On June 20, 1994, 2g of Norway spruce needles were placed in 125ml Erlenmeyer flasks with 10ml water, sealed with a foam plug and sterilized by autoclaving for 20min. Two grams of a) fresh needles and b) those that had been autoclaved were oven-dried for 24h, at 90°C, to act as the reference dry weight of the needles before treatment. This was replicated five times. On July 1, 1994,

two agar discs, 0.5mm in diameter, cut from the edge of the growing fungal colony of each primary and secondary saprophyte were placed, separately, in flasks with the sterile needles. The same procedure was followed with a combination of all primary saprophytes and all secondary saprophytes, to determine whether primary or secondary saprophytes decompose at different rates when acting separately or together. Controls were set up for each sample and the experiment was replicated five times. On October 1, 1994, after three months, the needles in each flask were oven-dried, and their weights compared to that of the reference autoclaved sample.

Field experiments

Effect of naphthalene defaunation on the species composition of the microfungi and the numbers of the microfauna

Picea abies have a heavy needle fall in late autumn. Sampling began after the bulk of needle loss had taken place. To determine when this occurred, in September 1993, ten cotton cloth bags, approximately 30 X 90cm, with openings of 30cm diam were suspended from branches of randomly chosen trees in the study site. The needles that fell in each bag were collected and weighed weekly. The weight of needles collected October 1 and October 7, 1993, was almost ten times that recorded during the last weeks of September, suggesting that the autumn needle fall had taken place and needle sampling could begin.

On the first day of sampling, October 11, 1993, before the first application of naphthalene, 30 needles and a soil core, were taken, at random, from each enclosure to determine the soil microfungal and faunal population in the enclosures. Naphthalene was then applied to the five treatment plots, and all the plots were covered with nylon mosquito netting, to prevent the entrance of additional litter. The needles were prepared for sampling, as previously described. The fungi growing from 100 needle fragments, from each enclosure were identified. Further sampling of needles took place November 11, 1993, December 4, 1993, May 11, 1994, June 3, 1994, July 2, 1994 and July 22 1994. The soil microfauna was monitored approximately every 14 days, beginning before naphthalene was applied to the end of September 1994.

Weight of needles in litterbags

Two nylon litter-bags, $15cm^2$, of mesh size 1mm, each containing 10g fresh needles, were placed in each enclosure, on October 3, 1993. A further five 10g samples of needles were oven dried before the treatment began, to act as the reference dry weight of needles before the treatment began. In October 7, 1994, the litter-bags were retrieved, the needles in the litter-bags oven-dried and the dry weight of needles for each treatment compared.

Statistical analysis

Multivariate analysis of variance (MANOVA) was used to compare the number of occurrences of different fungal species, and fungal groups, (primary saprophytes, secondary saprophytes, other fungi), growing on the needles of Norway spruce, in the different treatment microcosms and in the control and naphthalene-treated flasks. MANOVA was also used to compare the fungal species compositions and number of soil animals in the control and treatment enclosures at each sampling date in the field experiment. Matched pair design tests were used to compare the overall numbers of fungal groups, and soil animals over time, after treatment had begun. The Pearson Product Moment Correlation Coefficient (r) was determined for primary saprophytes and mites, and primary saprophytes and collembolans for each sampling date. The different weights of needles in litterbags, taken from control and treatment enclosures, after a period of one year, in the field decomposition experiment, were compared using a one-way ANOVA. While data were being collected it was noted that some of the enclosures were submerged in water in spring. To control for flooding as a possible confounding variable, statistical analysis for the field experiment and the litterbag experiment was carried out twice, using data from (a) 'Total", all enclosures, and (b) "Dry", all enclosures except numbers 1, 6 and 8, the ones that were flooded.

These analyses were done using log(X+1) transformed data since this transformation was the most successful at correcting the

variations from a normal distribution of the variables. The software package "Systat" was used (Wilkinson, 1990).

RESULTS

Laboratory experiments

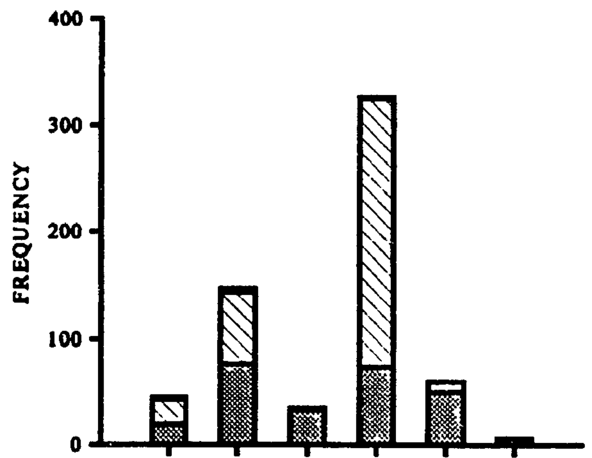
Microcosms

The naphthalene-treated microcosms had between 41.2% and 94.2% fewer animals extracted than the control on the different sampling dates after treatment began (the first sampling date was before treatment), and between 40% to 92% fewer animals than heat-treated microcosms (Fig. 2). The greatest treatment effects occurred after 6 weeks, which corresponded to the second needle sampling from the microcosms, with 325 animals extracted from the control microcosm, 194 from the one with animals added, 117 from the heat-treated microcosm and 18 from the naphthalene-treated one. There were consistently more soil animals in the control microcosms than in the treatment microcosms for the first six weeks. After that time, the numbers of soil animals decreased in all microcosms.

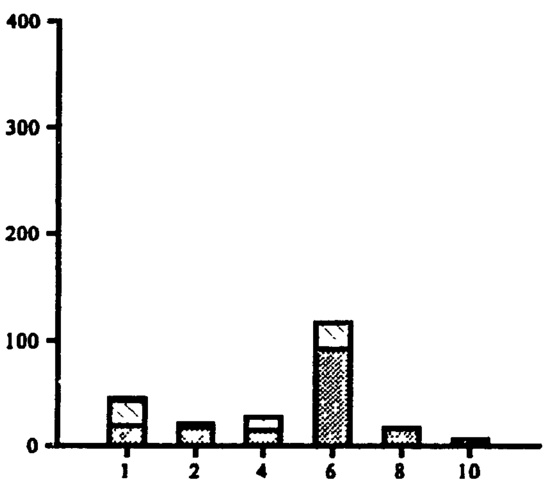
There was no significant difference in the numbers of fungi in the different microcosms (MANOVA: $F=0.338$; $df=6,22$; $p=0.909$) on the first sampling date, before treatment (Appendix Table 1).

Although the effect of treatment on soil animals was greatest after 6 weeks, with the highest number of animals extracted from the "control" microcosms, this did not occur with any significant change in the composition of the fungal populations (MANOVA:

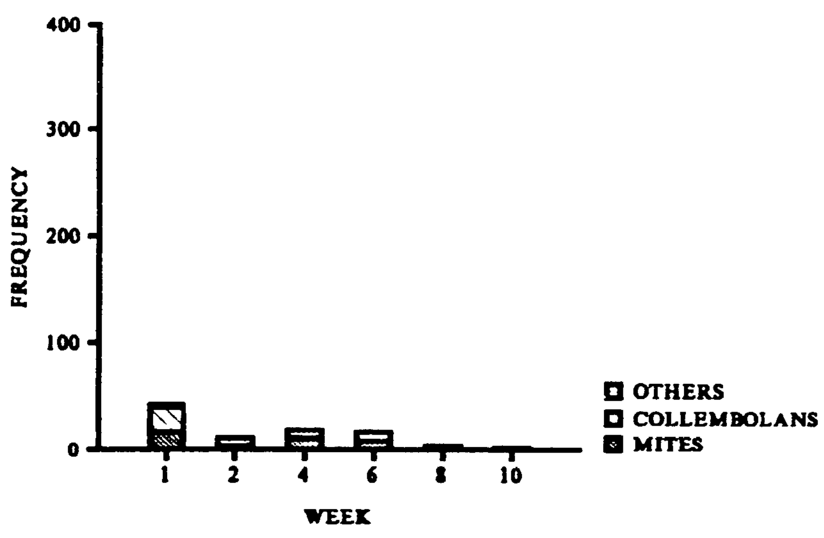
Fig. 2. Number of soil animals extracted from microcosms at different weeks



(A) CONTROL
FREQUENCY
400
300
200
100
0
1
2
4
6
8
10



(B) HEAT TREATED
400
300
200
100
0
1
2
4
6
8
10



(C)NAPHTHALENE TREATED
FREQUENCY
400
300
200
100
0
1
2
4
6
8
10
WEEK
OTHERS
COLLEMBOLANS
MITES

F=1.222; df=6,22; p=0.333) (Fig. 3) (Appendix Table 2). The numbers of all primary saprophytes, except Ulocladium, were higher in the naphthalene-treated microcosms, but not significantly so.

Similarly, after 10 weeks, when only low numbers of soil animals were extracted from the microcosms, no significant effect of treatment on the microfungi was noted (MANOVA: F=1.331; df=6,22; p=0.285), although the group "other fungi" was highest in the naphthalene treated microcosms (ANOVA: F=3.969; df=2,12; p=0.048) (Fig. 3) (Appendix Table 3).

Effect of naphthalene on the species composition of microfungi

Naphthalene had an effect on the fungal population (MANOVA: F=7.651; df=3,6; p=0.018), with numbers of primary saprophytes higher (ANOVA: f=5.398; df=1,8; p=0. 049) in the naphthalene-treated flasks (Fig.4). Closer examination of the fungi that comprised that group indicated that only "Sterbrown", an unidentified, sterile dark fungus, was significantly higher in the naphthalene treated flasks (Fig. 4)(Appendix Table 4). The number of secondary saprophytes was higher in the control flasks, with Trichoderma koningii being highly inhibited by naphthalene. Of the group of sterile, unidentified fungi and "sugar" fungi, known as "other fungi" (ANOVA: F=13.858; df=1,8; p=0.006), three unidentified species, "Sterbuff" (ANOVA: F=15.743; df=1,8; p=0.004), "Sterile 1" (ANOVA: F=5.443; df=1,8; p=0.048) and "Sterile 4" (ANOVA: F=8.420; df=1,8; p=0.020) occurred

Fig. 3. (A) Number of fungi from microcosms one month after treatment began. Error bars represent 95% confidence limits

(B) Number of fungi from microcosms two months after treatment began. Error bars represent 95% confidence limits

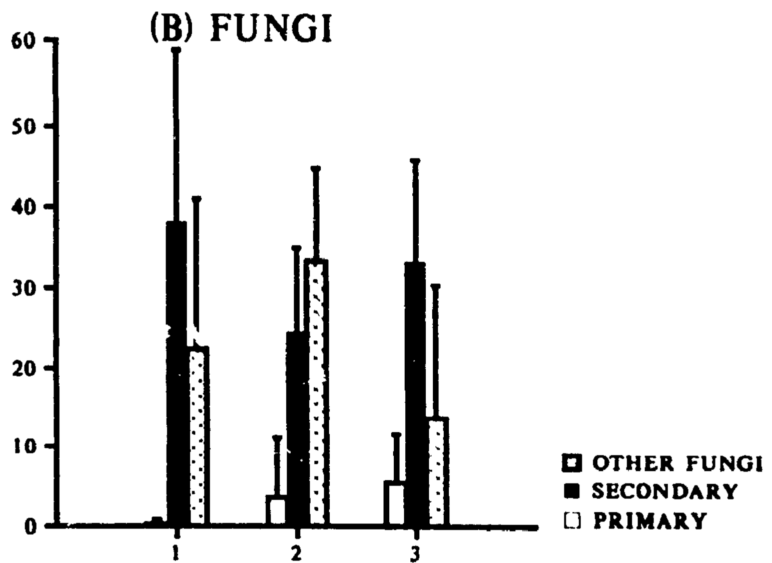
(C) Number of soil animals from microcosms one month after treatment began

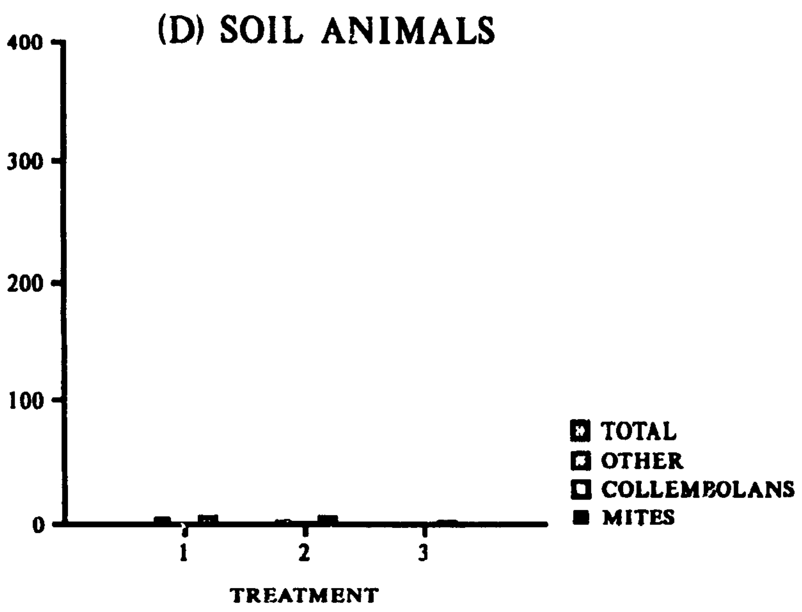
(D) Number of soil animals from microcosms two months after treatment began

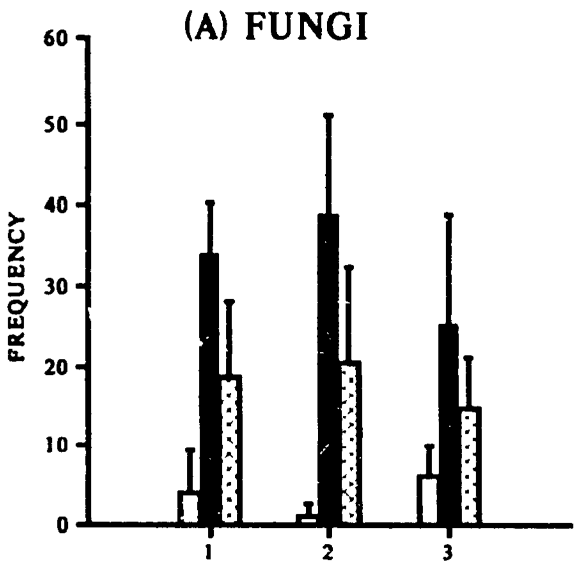
1) CONTROL

2) HEAT-TREATMENT

3) NAPHTHALENE TREATMENT


(A) FUNGI
FREQUENCY
60
50
40
30
20
10
0
1
2
3


(B) FUNGI
60
50
40
30
20
10
0
1
2
3
OTHER FUNGI
SECONDARY
PRIMARY


(C) SOIL ANIMALS
FREQUENCY
400
300
200
100
0
1
2
3
TREATMENT

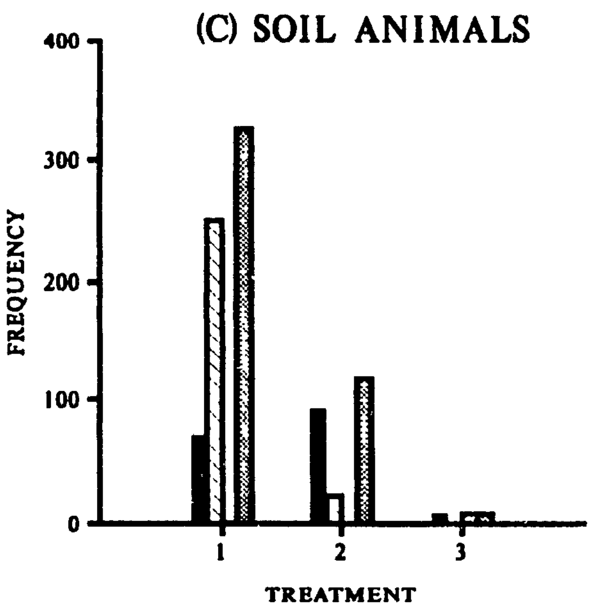
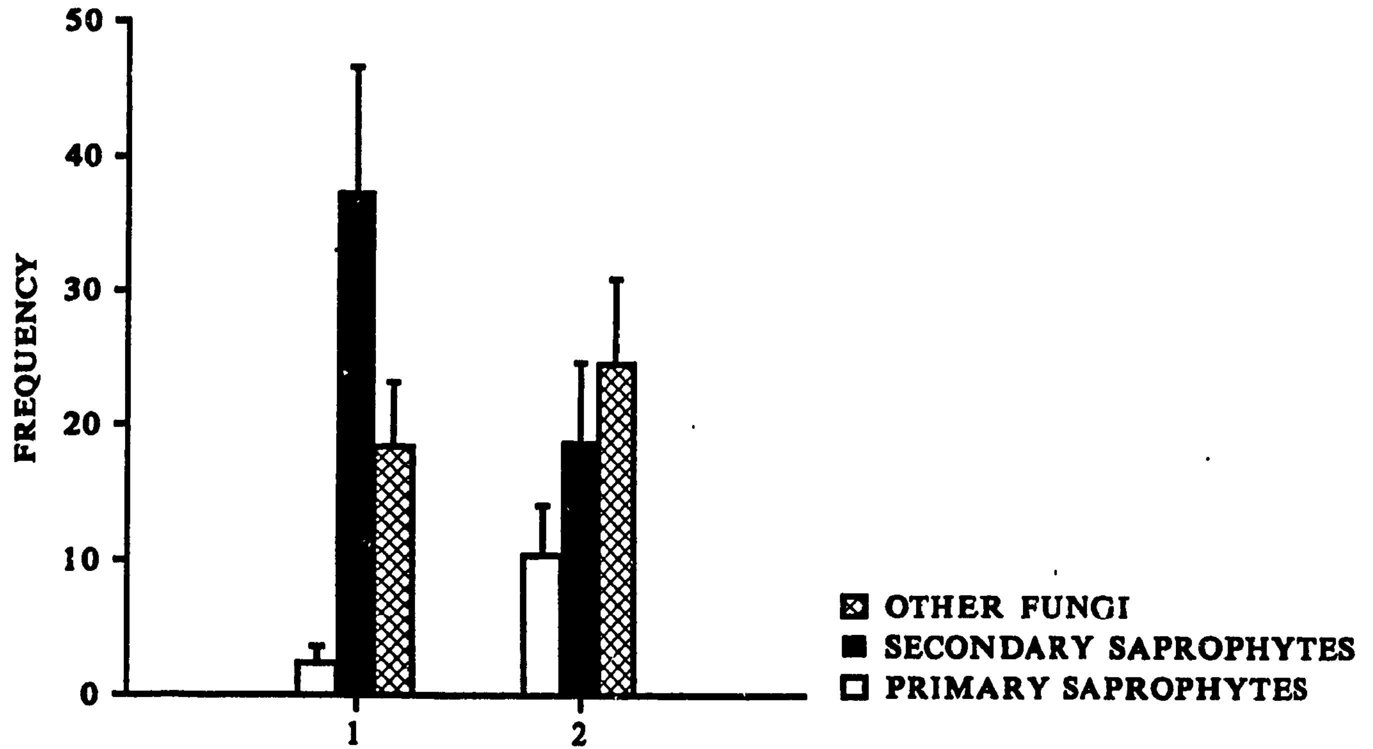
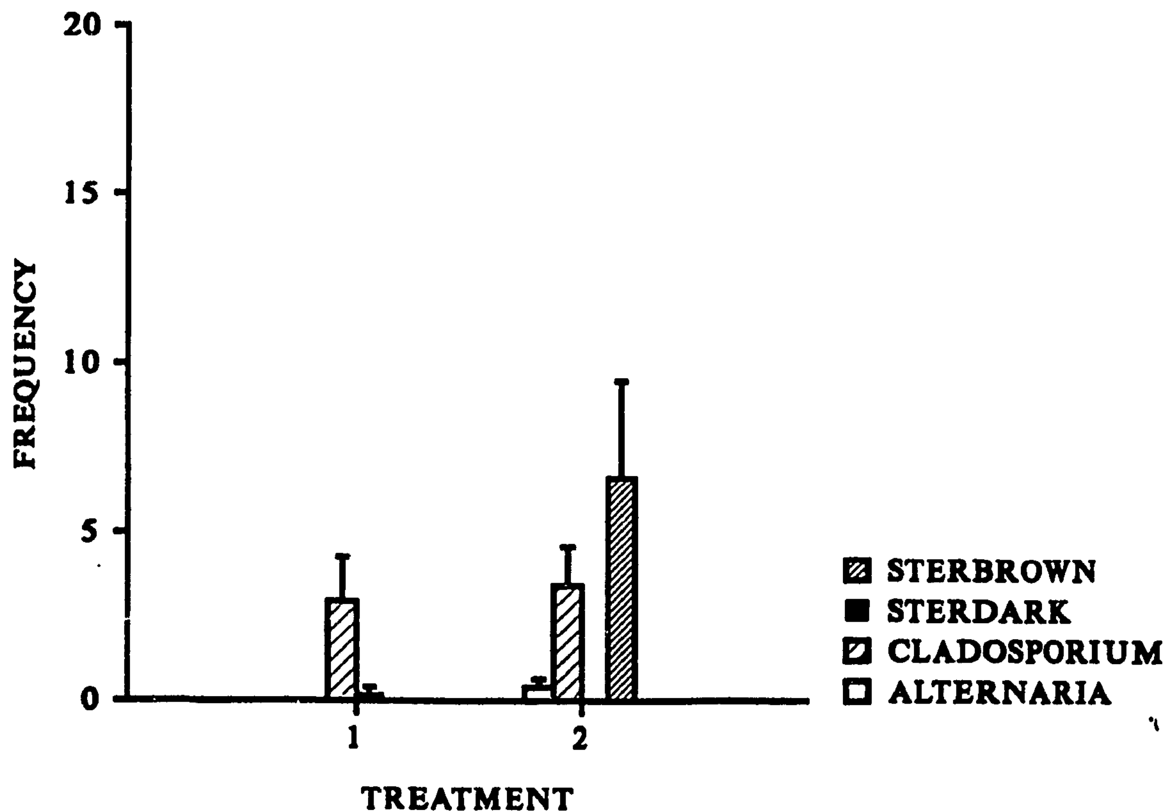

(D) SOIL ANIMALS
400
300
200
100
0
1
2
3
TREATMENT
TOTAL
OTHER
COLLEMBOLANS
MITES

Fig. 4. (A) Number of fungi in (1) CONTROL and (2) NAPHTHALENE TREATED flasks. Error bars represent standard errors. (B) Number of primary saprophytes in (1) CONTROL and (2) NAPHTHALENE TREATED flasks. Error bars represent standard errors.


(A) ALL FUNGI
50
40
30
20
10
0
FREQUENCY
1
2
OTHER FUNGI
SECONDARY SAPROPHYTES
PRIMARY SAPROPHYTES


(B) PRIMARY SAPROPHYTES
20
15
10
5
0
FREQUENCY
1
2
TREATMENT
STERBROWN
STERDARK
CLADOSPORIUM
ALTERNARIA

significantly more often in the naphthalene-treated flasks.

Decomposition abilities of primary and secondary saprophytes

At the end of three months, only needles in flasks inoculated with primary saprophytes showed any weight loss, ranging from 0.146g lost from needles inoculated with Alternaria to 0.197g lost from needles inoculated with "Sterbrown" (Fig. 5).

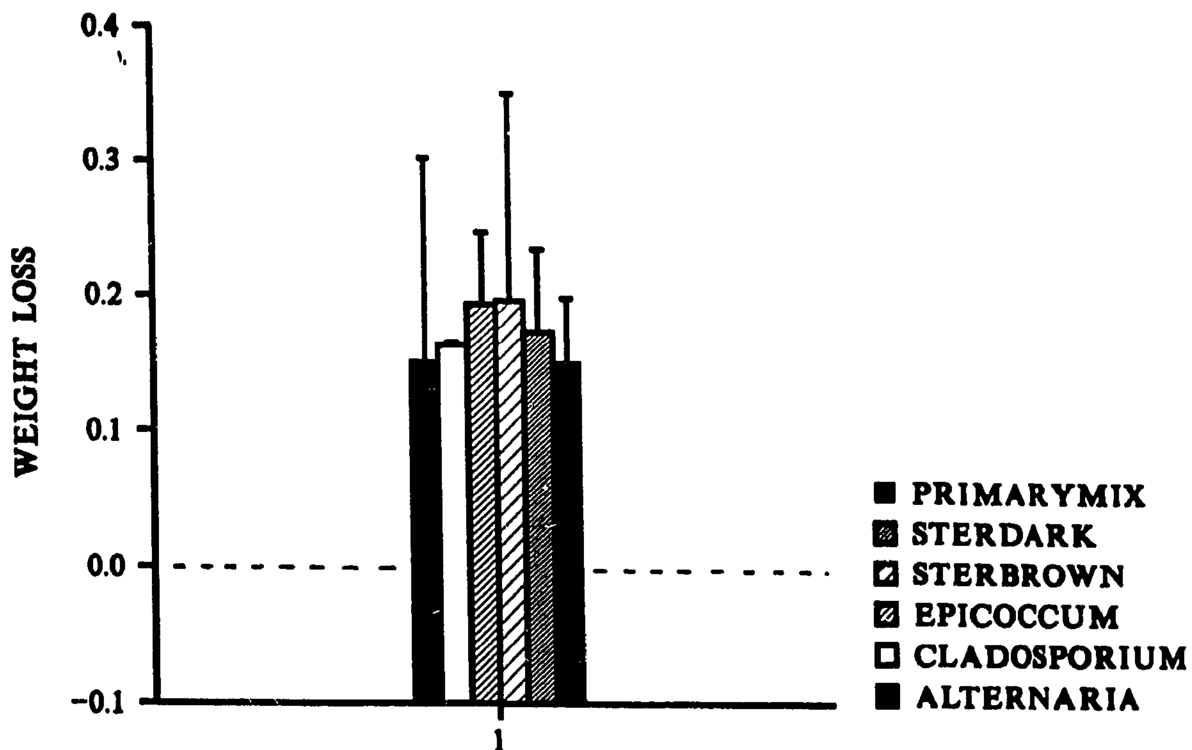
Field experiments

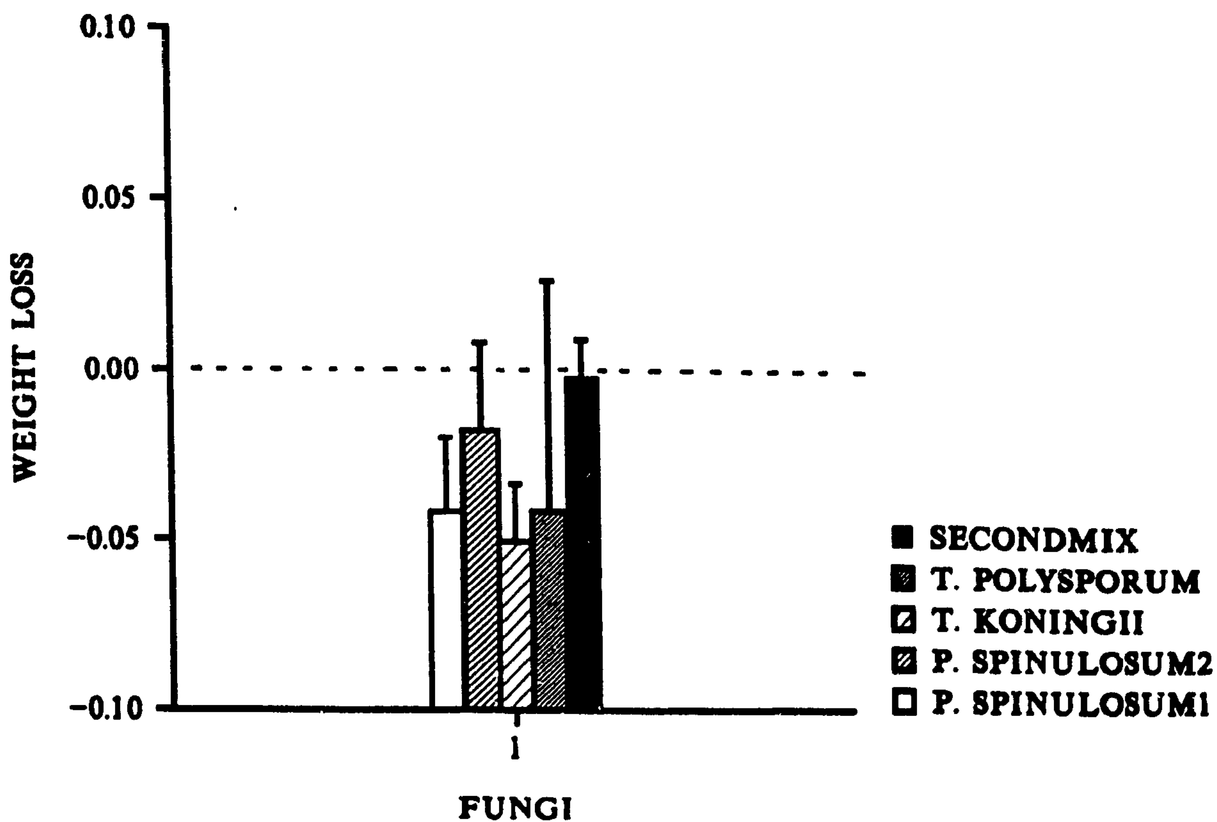
Effect of naphthalene defaunation on the species composition of microfungi and numbers of microfauna

Since it was observed that spring flooding was greater in some enclosures than in others, and since excess moisture might have acted as a confounding variable, data from (A) the total number of enclosures and (B) the total number without the "wet" enclosures were analyzed separately. Little difference in the overall results was noted.

There was no significant negative correlation between mites and primary saprophytes and collembolans and primary saprophytes at any sampling date for the "total" number of enclosures. Before the application of naphthalene, October 11, 1993, there was no significant difference in the fungal populations (MANOVA: $F=0.468$; $df=3,6$; $p=0.715$) or in the population of the soil animals in the

Fig. 5. Weight loss (grams) of needles in flasks inoculated with (A) primary saprophytes, single species and in combination, and (B) secondary saprophytes, single species and in combination after three months incubation at 25° C. Error bars represent 95% confidence limits
The reference dry weight of needles, before treatment was 0.878 g.


(A) PRIMARY SAPROPHYTES
WEIGHT LOSS
0.4
0.3
0.2
0.1
0.0
-0.1
1
PRIMARYMIX
STERDARK
STERBROWN
EPICOCCUM
CLADOSPORIUM
ALTERNARIA


(B) SECONDARY SAPROPHYTES
WEIGHT LOSS
0.10
0.05
0.00
-0.05
-0.10
1
FUNGI
SECONDMIX
T. POLYSPORUM
T. KONINGII
P. SPINULOSUM2
P. SPINULOSUM1

enclosures (MANOVA: F=0.202; df=2,7; p=0.821) (Fig. 6) (Appendix Table 5).

The application of naphthalene reduced the number of soil animals at all times. The difference in numbers between control and treated enclosures was significant November 11, 1993 (MANOVA: F=9.813; df=2,7; p=0.009) (Appendix Table 6), December 4, 1993 (MANOVA; F=7.646; df=2,7; p=0.017) (Appendix Table 7), July 2, 1994 (MANOVA; F=5.767; df=2,7; p=0.033) (Appendix Table 10) and July 22, 1994 (MANOVA; F=5.044; df=2,7; p=0.044) (Appendix Table 11) (Fig. 6), but not in May 11, 1993 (MANOVA; F=4.194; df=2,7; p=0.063) (Appendix Table 8) and June 3, 1993 (MANOVA; F=3.555; df=2,7; p=0.086)(Appendix Table 9)(Fig. 6).

The decrease in the numbers of the microfauna in the treated enclosures was not reflected in a significant difference in the microfungal population until July 2, 1994 (MANOVA; F=0.046; df=3,6; p=0.046) (Appendix Table 10), when higher numbers of primary saprophytes were recorded in the naphthalene treated enclosures (ANOVA; F=0.033; p= 0.033) (Appendix Table 10). The numbers of primary saprophytes remained higher in the treated enclosures July 22, 1994 (ANOVA; F= 6.065; df=1,8; p=0.039) (Appendix Table 11).

The results of the Matched-pair Design tests indicated that, over all sampling dates, the numbers of soil animals were much lower in the treated enclosures (mites, t=7.61; df=5; $p>0.001$)(collembolans, t=8.17; df=5, $p>0.001$). As a general, but not significant trend, the number of primary saprophytes (t=-1.807; df=5; $0.20<p<0.10$) was higher in the treated enclosures (Fig. 7).

Fig. 6.(A) fungi from CONTROL and

(B) fungi from NAPHTHALENE TREATED

enclosures at different sampling dates

(C) soil animals from CONTROL and

(D) soil animals from NAPHTHALENE TREATED

enclosures at different sampling dates

Date 1- October 11, 1993

Date 2- November 11, 1993

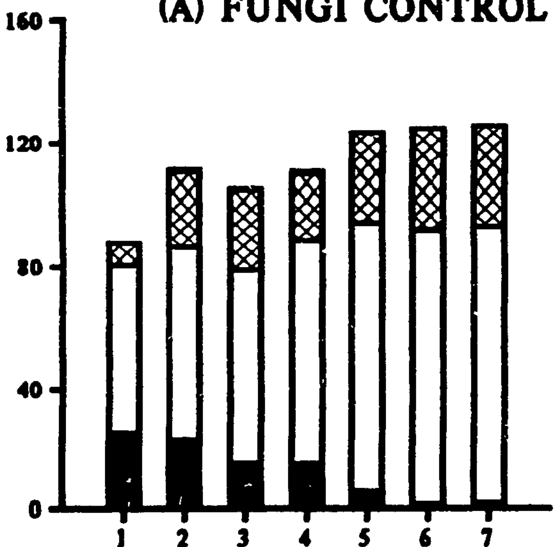
Date 3- December 4, 1993

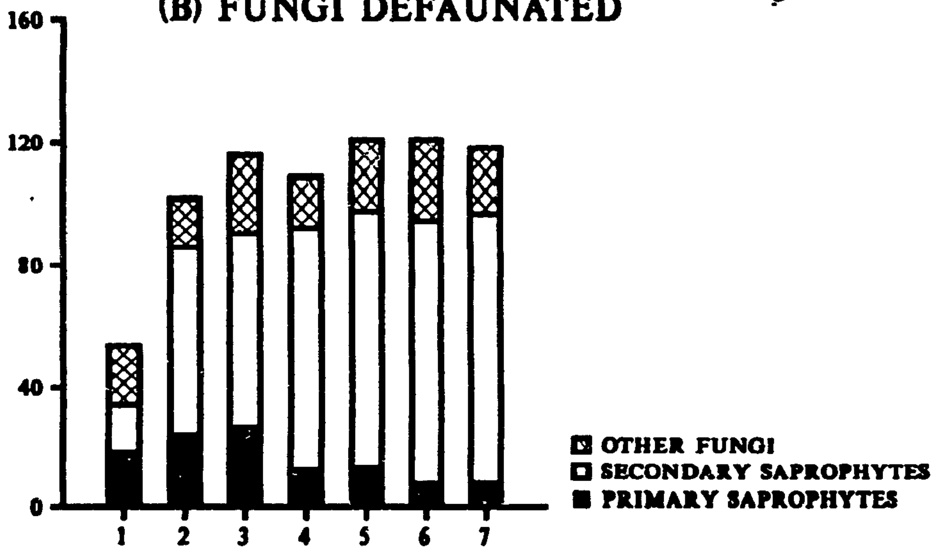
Date 4- May 11, 1994

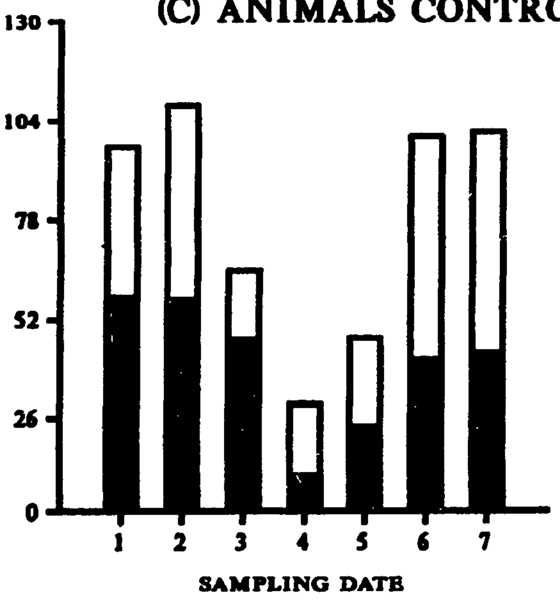
Date 5- June 3, 1994

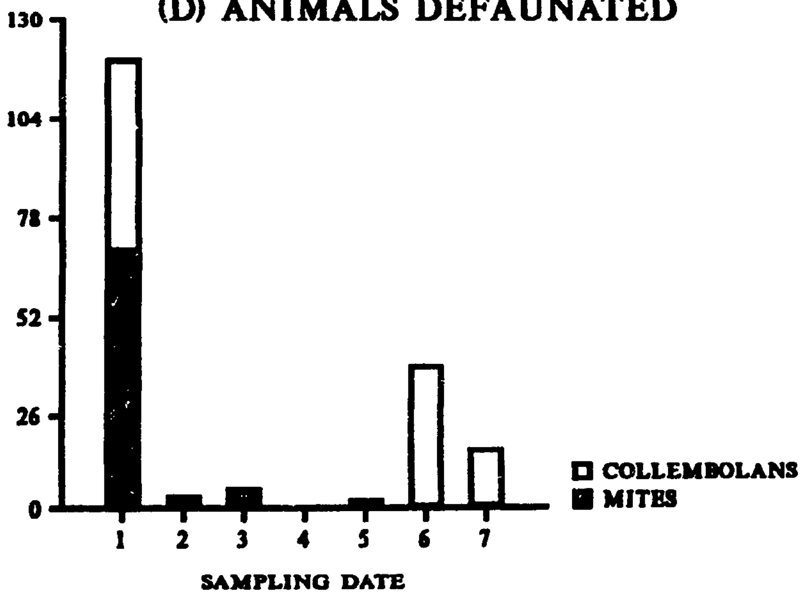
Date 6- July 2, 1994

Date 7- July 22, 1994


(A) FUNGI CONTROL
160
120
80
40
0
1 2 3 4 5 6 7


(B) FUNGI DEFAUNATED
160
120
80
40
0
1 2 3 4 5 6 7
OTHER FUNGI
SECONDARY SAPROPHYTES
PRIMARY SAPROPHYTES


(C) ANIMALS CONTROL
130
104
78
52
26
0
1 2 3 4 5 6 7
SAMPLING DATE


(D) ANIMALS DEFAUNATED
130
104
78
52
26
0
1 2 3 4 5 6 7
SAMPLING DATE
COLLEMBOLANS
MITES

Little difference in the number of secondary saprophytes in control and treated enclosures was noted ($t=-0.143$; $df=5$; $p<0.50$).

Weight of needles in litterbags

After one year, the needles in litterbags, in the control enclosures, weighed significantly less (ANOVA; $F=5.686$; $df=1,8$; $p=0.044$) than those in litterbags in the defaunated enclosures.

Fig. 7. Numbers of (A) PRIMARY SAPROPHYTES and (B) SOIL ANIMALS in CONTROL and NAPHTHALENE TREATED enclosures at different sampling dates. Error bars represent standard errors.

Date 1- October 11, 1993

Date 2- November 11, 1993

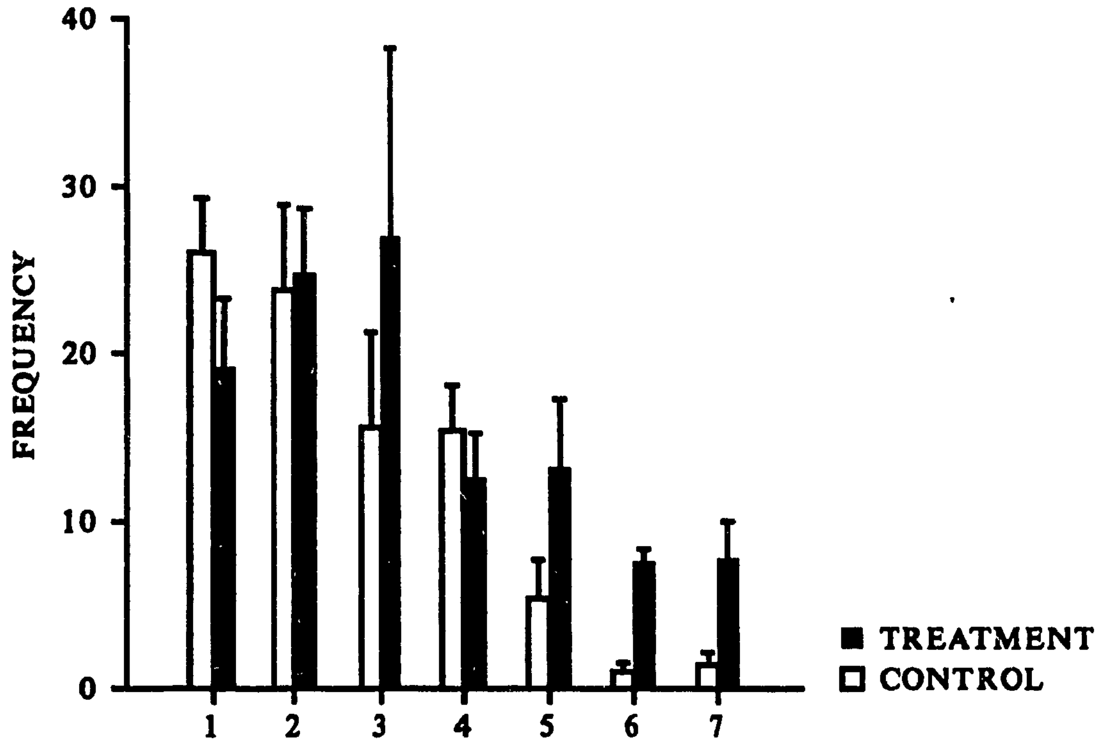
Date 3- December 4, 1993

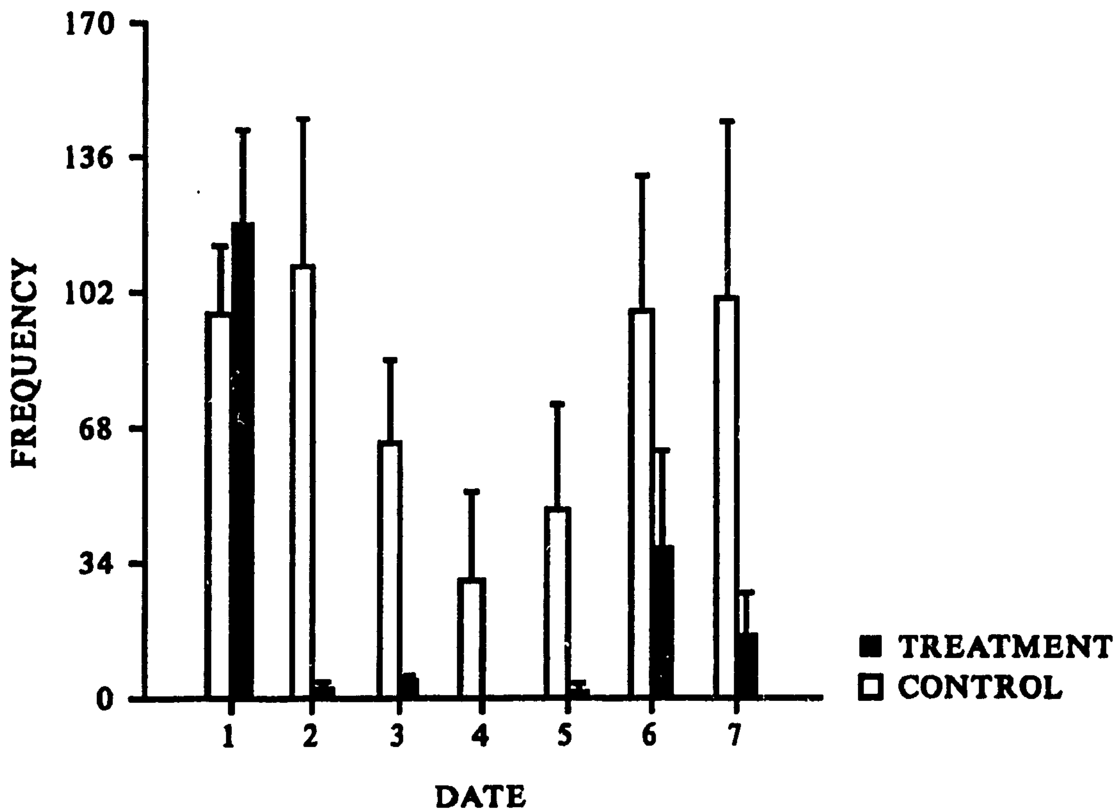
Date 4- May 11, 1994

Date 5- June 3, 1994

Date 6- July 2, 1994

Date 7- July 22, 1994


(A) PRIMARY SAPROPHYTES
FREQUENCY
40
30
20
10
0
1 2 3 4 5 6 7
TREATMENT
CONTROL


(B) SOIL ANIMALS
FREQUENCY
170
136
102
68
34
0
1 2 3 4 5 6 7
DATE
TREATMENT
CONTROL

DISCUSSION

Laboratory experiments

Microcosms

Naphthalene proved to be effective at reducing the numbers of soil animals.

Kurcheva (1960), Witkamp and Crossley (1966), and Ghilarov (1983), who used this hydrocarbon in field experiments, found that although the soil animal population was greatly reduced, it was not totally eliminated from the site. The heterogeneity that exists in the soil includes small pockets of air, which allow some animals to survive. Animals may vary in their susceptibility to naphthalene. Eggs and animals in diapause are less affected by cold and drought than active animals (Danielevskii, 1965; Slansky, 1982). They may also be less affected by naphthalene fumes.

The application of heat has been known to be effective at repelling soil animals since many are highly sensitive to changes in temperature and humidity, requiring a moisture level in the air that is close to saturation. However, this method is difficult to apply in a forest situation. Naphthalene proved to be a more efficient defaunation agent. There were always fewer animals extracted from naphthalene treated microcosms than those defaunated by means of heat. In addition, the numbers of soil

animals in the naphthalene treated microcosms remained low, suggesting that larvae were killed upon hatching.

It was thought that due to the large difference in the number of microarthropods between the control and the defaunated enclosures, there would be an effect of selective grazing by these animals on the species composition of the microfungi. However no significant effect of defaunation on the structure of the fungal populations was noted at any sampling date. At the second sampling, when the range of the numbers of animals extracted from the different treatment microcosms was greatest, there was a higher number of primary saprophytes in the naphthalene-treated flasks, where numbers of soil animals was lowest, but this was not significant.

Field and laboratory experiments have determined that the distribution of mites and collembolans is affected by temperature and moisture (Poole, 1966; Hale, 1966; Usher, 1970; Mitchell, 1977; Takeda, 1978). The temperature and moisture fluctuations at the surface of the litter in the microcosms were greater than they would have been in the more stable environment of a spruce forest, where the closed canopy of trees restricts air movement, and reduces temperature change and evaporation (Cabàrt, 1970; Cole and Rapp, 1981).

In a natural setting, water is moved by means of evaporation, gravity, and the capillary action of dry regions, that is, the water is drawn from wetter to drier areas, and much water is taken up by the roots of plants. The waterproof polyvinyl chloride walls

of the microcosms prevented lateral translocation of water. Water could only be removed through evaporation, from the surface of the cores, or by gravity, through the bottom. This process, which was slower than in nature, may have resulted in water accumulation within each microcosm. In addition, each new rainfall contributed to an increased moisture level in the interior of the microcosms. This may, in turn, have affected the behaviour of the soil animals.

Many soil animals respond to increases in moisture in the spring and the fall by egg-laying (Usher, 1970). This may explain the rise in numbers of soil animals up to week six regardless of the treatment. However, after that time, the interior of the microcosms may have become waterlogged, and anaerobic. It was noted that the level of soil in the microcosms decreased over the duration of this experiment. As the soil becomes waterlogged, it also becomes compacted, reducing the size of the soil pores. Mites and collembolans, the dominant microfauna in coniferous forests, do not burrow through the soil as do earthworms (Satchell, 19?7). They require aerated soil pores for movement (Wallwork, 1976). These two factors may explain the decrease in numbers of animals after week 6. Problems of an increase in the numbers of some soil animals and the difficulty in controlling moisture levels in microcosms have been reported by Taylor and Parkinson (1987). Any effect that the microfauna might have had on the species composition of the microfungi may have been diminished by the microcosm environment. Larger microcosms (mesocosms), made of a more porous material, might have solved the problem of water movement.

Effects of naphthalene on the species composition of microfungi

Although statistical results indicated that naphthalene significantly influenced the fungal populations, with numbers of primary saprophytes higher in the naphthalene treated flasks, of the fungi that made up the group of primary saprophytes, only "Sterbrown", an unidentified sterile dark fungus appeared significantly more often in the naphthalene treated flasks. Sewell (1959) attributed the higher numbers of sterile dark fungi at low temperatures to the absence of the antagonistic fungus *Trichoderma viride*. The presence of "Sterbrown" in the naphthalene treated flasks may be the result of the release of competitive pressure from other fungi and by the conditions in the flasks because "Sterbrown" was never significantly more numerous in the naphthalene treated field enclosures than in the controls. This fungus only appeared infrequently in the field fungal community.

Fungi exhibit high biochemical diversity, from "generalists" that can degrade all substrates to "specialists" with an extremely limited capacity (Swift, 1976). Of the group "other fungi", three fungi appeared significantly more often in the naphthalene treated flasks. These were "Sterbuff", a sterile fungus which appeared in microcosm and field experiments, and two unidentified sterile fungi. The unidentified sterile fungi did not appear in any other experiment, suggesting that either they were able to use naphthalene as a substrate or they were stimulated by conditions in the flasks. Although *Trichoderma koningii*, a secondary saprophyte,

was significantly more numerous in the control flasks, this fungus also appeared in the naphthalene treated field enclosures. This suggests that T. koningii may have been responding to the concentration of naphthalene used in the flask, which was effectively higher than in the field because of the reduced circulation of air in the flasks. Although it cannot be stated with absolute certainty that the fungi were totally unaffected by the presence of naphthalene, the results suggest that the effect of this hydrocarbon on the fungal community structure was small.

Decomposition abilities of primary and secondary saprophytes

If fungi differ in their complements of depolymerizing enzymes, even a small change in the microfungal species composition may have an effect on the function of the microfungal community and rate of litter breakdown. Although some rare fungi may make an important contribution to decomposition, only the most frequently appearing fungi were chosen as representatives of primary and secondary saprophytes. Bissett and Parkinson (1979) suggested that the dominant members of the fungal community may influence the development and the functioning of the other fungi.

Since pure culture studies do not allow for synergistic interactions between decomposers of differing biochemical potential, they may not reflect the true contribution of particular fungi. For this reason, flasks containing a combination of primary or secondary saprophytes may give a more realistic picture of the

activities of these fungi.

Ideally, decomposition experiments should be conducted at temperatures as close to those in the environment from which the fungi were isolated as possible (Parkinson, 1977). The flasks were incubated at 25°C, which may have been higher than the summer temperature at Lacolle, Quebec when this experiment was set up, June 30, 1993.

After three months incubation at 25°C, weight loss only occurred for needles in flasks inoculated with primary saprophytes. The catabolism of cellulose involves at least four enzymes, C1(hydrocellulase), endo and exo-beta-glucanase, and CX components, beta-glucosidase, each catalysing a different step in the depolymerizing of cellulose. Since not every fungus has this complete range of enzymes, fungi may act synergistically in attacking cellulose, the endoglucanase of one fungus acting with the exoglucanase of another, to result in a complete cellulase complex (Flanagan and Scarborough, 1974, Ljungdahl and Erikson, 1977). Since primary saprophytes in the phylloplane encounter less fungal species than secondary saprophytes in the soil they may have had to evolve a complete enzyme system to break down plant material. Secondary saprophytes coexist with a much larger number of fungi and actinomyces. While individual secondary saprophytes may lack all the enzymes necessary to break down the needles, they have more opportunities to interact with other microorganisms for effective decomposition.

The cellulolytic activity of any particular fungus is related

to various abiotic conditions, such as temperature, and pH, with temperature imposing physiological limits on growth, reproduction, spore germination and fungal competitive abilities by stimulating or inhibiting the production of extracellular enzymes, and antibiotics (Widden, 1984, 1986b). The temperature in the flasks, which seemed to favour the activities of primary saprophytes, occurs in spring and early summer. This corresponds to the time of the year when the numbers of soil animals are highest in the litter layer, and their effect in reducing the number of primary saprophytes in the control enclosures is potentially greatest. A clearer picture of the decomposing abilities of the fungi could be obtained if the temperature at which the flasks were incubated was regularly adjusted to mimic the external temperature of the site from which the fungi were isolated, or if this experiment was to be repeated, incubating groups of flasks at different temperatures (Carreiro and Koske, 1992a,b).

The results of the laboratory experiments indicated that naphthalene could significantly reduce the number of soil animals, with only a small effect on the species composition of the microfungi. The primary saprophytes used in the decomposition experiment were able to cause weight loss in the needles in the flasks, while the secondary saprophytes were unable to do so.

Field experiments

Effect of naphthalene defaunation on the species composition of the microfungi and numbers of the microfauna

No significant differences were noted in either fungal or soil animal populations in the enclosures in October, 1993, before naphthalene was applied.

Although naphthalene greatly reduced the microfaunal populations in the treated enclosures in November and December 1993, and the effect on the fungal population was not significant, the numbers of primary saprophytes actually rose in November and December where the soil animals had been removed. This suggests a response of the primary saprophytes to release from grazing pressure.

Although food may be one of the most important influences in the physiology, behaviour, ecology and evolution of soil animals, affecting the timing and extent of reproduction of the adult, and growth rate, developmental time and probability of survival of the offspring (Slansky, 1982), the food choices of soil animals are determined not only by the nutritional quality of the substrate, but by factors such as temperature. Soil animals are poikilotherms, and cannot compensate for temperature change, they must escape excessive heat and cold or die (Slansky, 1982).

While many researchers (Poole, 1959; McMillan and Healy, 1971;

McMillan, 1975; Takeda and Ishimura, 1983; Slansky and Rodriques, 1987; Walter, 1987) consider soil animals to be omnivorous, since fungi are numerous in the litter layer, selective feeding is possible. However the cold temperatures can affect feeding behaviour. Although the snow cover in the forest provides some portection against the cold, allowing for microfaunal activity in the litter layer (Aitchison, 1979), the numbers of soil animals generally decrease in winter (Usher et al., 1978). This was noted in the December sampling. Some animals may migrate deeper into the soil profile and use food sources other than fungi (Warcup, 1951; Bodvarson, 1970; Gilmore and Raffensperger, 1970). Some collembolans may go into diapause (Danielivskii, 1965), although mites remain active all winter in this area (Behan-Pelletier, personal communication). Winter active collembolans feed less as the temperature gets colder (Aitchison, 1983). Thus any effect of selective feeding by soil animals on primary saprophytes may have been reduced by cold temperatures in November and December.

The soil was still very wet in May and June 1994, and few animals were extracted from the soil cores at that time. Little difference was noted between the fungal populations. The presence of excess water is as detrimental to the survival of soil animals as drought since they cannot survive in a waterlogged, anaerobic environment. Addison (1977) indicated that the distribution of collembolans is related to the water content of the soil. The soil animals in May and June, may not have been sufficiently numerous for any feeding preferences to affect the structure of the

microfungal population.

On July 2, the numbers of primary saprophytes were significantly higher in the naphthalene-treated enclosures, and remained higher in the July 22 sampling (Tables 10, 11). At this time of the year the numbers of soil animals in the control enclosures, particularly collembolans, were high. The population of both mites and collembolans increase in the spring (Usher et al., 1978; Vegter, 1987), with many heavily feeding juveniles (Pande and Berthet, 1973). Luxton (1991) stated that in a Danish beech wood soil, mites that are omnivorous as adults, begin life as microvores. If this occurs in soils of coniferous ecosystems, then the numbers of fungivores would be highest at this time of the year. This period of high numbers of soil animals, egg maturation and larval development also corresponds to the periods of high microbial biomass (Widden 1986b).

Primary saprophytes may be a more valuable food than secondary saprophytes for soil animals, particularly for the newly-hatched, that need nitrogen for growth. Because primary saprophytes attack needles upon the onset of senescence, before nitrogen is totally redirected into the tree, they may be able to sequester more of this nutrient. Albert and Bauce (1994) indicated that the fourth instar of the Spruce budworm Choristoneura fumeriferana Clem. preferred extracts from terminal shoots of young and old balsam fir (Abies balsamea (L.) Mill.) with the higher nitrogen content, while the sixth instar preferred extracts from lateral shoots of young trees with the higher sugar content. Spores of

primary saprophytes, which are highly nutritious (Dowding, 1975), are generally larger than those of secondary saprophytes. Since laboratory experiments showed that feeding on primary saprophytes resulted in higher fecundity for the collembolan Folsomia candida (Klironomos et al, 1992) it suggests that either these fungi are not toxic or that soil animals are adapted to them (Kukor and Martin, 1987).

Water from melting snow submerged three enclosures in spring and kept them wetter than the other enclosures during the early summer. Because populations of both fungi and soil animals are affected by moisture, this suggested the hypothesis that the moisture level in the soil affects the microfloral/fungal interactions, but lack of sufficient sampling units prevented the testing of this hypothesis. There were no significant differences in the fungal populations in the July 2, and July 22 samplings for the "Dry" enclosures (Appendix Tables 12, 13).

The results of matched-pair design tests indicated that, over the year, although the numbers of mites and collembolans were reduced by the application of naphthalene, no significant treatment effect was recorded for primary saprophytes. Because the number of primary saprophytes decreased in both the control and the defaunated enclosures through the period of this experiment, selective feeding cannot be considered to be the only factor determining the disappearance of the primary saprophytes. However, since the numbers of primary saprophytes were not only lower in the control enclosures, but significantly so when the soil animals

presence in the litter layer was highest, the hypothesis that selective grazing by microfauna reduces the number of primary saprophytes, as a trend, is not negated.

Thorpe (1986), after examining eighteen different freshwater assemblages, concluded that predation must be ranked with other biotic and abiotic factors in maintaining the community structure since relatively few predators are principally responsible for diversity within the communities. The numbers of primary saprophytes may decrease over the year because phylloplane fungi in old leaf litter and soil may consist of resting spores, those that allow the fungus to survive adverse conditions, rather than the reproductive propagules, the conidia (Pugh and Buckley, 1971). The fungi may simply have reached the end of their life cycle when they reach the ground.

While the numbers of primary saprophytes decreased faster in the presence of soil animals, the numbers of secondary saprophytes were similar in the control and treated enclosures. Thus the removal of primary saprophytes did not facilitate their replacement by secondary saprophytes.

Weight of needles in litterbags

Studies conducted in the last three decades have indicated that arthropods have a variable, but generally significant effect on litter disappearance (Crossley and Hogland, 1962; Drift van der, 1963; Edwards and Heath, 1963; MacLean, 1974; Santos and Whitford,

1981). While soil invertebrates, as a group, are responsible for 5% or less of the total decomposer respiration in most ecosystems (Peterson and Luxton, 1982), when considered as an integral functional group, in close association with microorganisms, such as bacteria and fungi, their influence may be greater than that suggested by respiration. If soil animals graze selectively on specific fungi, and fungi differ in their enzymatic properties and decomposing abilities, then, even a small change in the distribution of fungi may affect the rate of decomposition.

Since microfaunal grazing reduced the number of primary saprophytes in the control enclosures, and primary saprophytes were shown to be more capable of causing needles to lose weight in the flasks, it was expected that the needles in litterbags in the defaunated enclosures, those with the higher number of primary saprophytes, would weigh less than needles in litterbags in the control enclosures. However, the needles in the litterbags in the control enclosures, the ones with low numbers of primary saprophytes and higher numbers of soil animals, weighed significantly less than those in the defaunated enclosures. This suggests that the contribution of the microfauna to decomposition is more complex than their effect on the species composition of the microfungi through selective grazing.

Some researchers consider that the important role of the soil animals in decomposition is indirect, through their effect on the fungi, by enriching the substrate through the addition of faeces (Teuben and Verhoef, 1992) and by transporting spores to new

substrates on their bodies (Behan and Pelletier, 1978; Lussenhop, 1992). They may also provoke greater fungal activity through removal of senescent hyphae, leading to increased mass loss of litter through microfungal compensatory growth and respiration (Seastedt, 1984; Newell, 1984b). However, further research may show that the direct effect of soil animals on decomposition, by consumption of litter, and fragmentation of the needles to render them more susceptible to further microbial activity (Berthet, 1967), is more important than the indirect effect. The techniques used in my research did not permit the identification of the basidiomycetes, which are prominant members of the microfungal community. Further research on the effect of the interaction of the basidiomycetes and the microfauna in decomposition may yield valuable informantion.

My research has indicated that, over the year, microfaunal grazing contributes to reducing the numbers of the effective decomposers, the primary saprophytes but not to facilitating their replacement by secondary saprophytes. Needles in litterbags in the control enclosures weighed less than those in the defaunated ones, suggesting that, in Norway spruce litter, the contribution of soil animals to decomposition consists of more than changing the structure of the microfungal community.

The rate of conversion of carbohydrates, the product of photosynthesis, into new plant tissues, is controlled by the amount and availability of nitrogen (Ericsson and Persson, 1980), which is, in turn, regulated by the microfauna (Harrison et al., 1990).

Microfauna contribute to the cycling of important nutrient elements, such as nitrogen, from the tissues of microfungi, where they are first immobilized, towards mineralization and timely release to plants, through microfaunal feeding and excretion (Heal,1979). This underlies the complexity of microfungal/faunal relationships. More research is needed to understand the interactions of the organisms involved with underground energy and nutrient transfer, since these ultimately affect plants, the primary producers.

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APPENDIX

Table 1. (A) MANOVA table with probability values for the microfungal community, before treatment began.

(B) ANOVA table with probability values for primary and secondary saprophytes and other fungi, before treatment began.

Ho: The means of the number of microfungi in the different treatment microcosms are equal

(A) MULTIVARIATE TEST STATISTICS

VARIABLE	PILLAI TRACE	F	DF	PROB
microfungi	0.169	0.338	6, 22	0.909

(B) UNIVARIATE F TESTS

VARIABLE	SOURCE OF VARIATION	SS	DF	MS	F	PROB
primary saprophytes	groups	0.071	2	0.035	0.229	0.645
	error	0.807	12	0.067	0.525	0.605
secondary saprophytes	groups	0.000	2	0.000	0.006	0.994
	error	0.196	12	0.016		
other fungi	groups	0.096	2	0.048	0.533	0.600
	error	1.080	12	0.090		

Table 2. (A) MANOVA table with probability values for the microfungal community, one month after treatment began
(B) ANOVA table with probability values for primary and secondary saprophytes and other fungi, one month after treatment began
Ho: The means of the number of microfungi in the different treatment microcosms are equal.

(A) MULTIVARIATE TEST STATISTICS

VARIABLE	PILLAI TRACE	F	DF	PROB
microfungi	0.500	1.222	6, 22	0.333

(B) UNIVARIATE F TESTS

VARIABLE	SOURCE OF VARIATION	SS	DF	MS	F	PROB
primary saprophytes	groups	2.380	2	1.190	2.595	0.116
	error	5.502	12	0.459		
secondary saprophytes	groups	2.581	2	1.291	1.154	0.348
	error	13.418	12	1.118		
other fungi	groups	1.569	2	0.785	2.341	0.139
	error	4.022	12	0.335		

Table 3. (A) MANOVA table with probability values for the microfungal community, two months after treatment began
(B) ANOVA table with probability values for primary and secondary saprophytes and other fungi, two months after treatment began
Ho: The means of the number of microfungi in the different treatment microcosms are equal.

(A) MULTIVARIATE TEST STATISTICS

VARIABLE	PILLAI TRACE	F	DF	PROB
microfungi	0.533	1.331	6, 22	0.285

(B) UNIVARIATE F TESTS

VARIABLE	SOURCE OF VARIATION	SS	DF	MS	F	PROB
primary saprophytes	groups	1.339	2	0.669	2.117	0.163
	error	3.394	12	0.316		
secondary saprophytes	groups	1.945	2	0.972	0.325	0.729
	error	35.897	12	2.991		
other fungi	groups	7.776	2	3.888	3.969	0.048
	error	11.754	12	0.980		

Table 4. (A) MANOVA table with probability values for the effect of naphthalene on the microfungal community

(B) ANOVA table with probability values for the effect of naphthalene on primary and secondary saprophytes and other fungi

Ho: The means of the number of microfungi in control and naphthalene treated flasks are equal.

(C) MANOVA table with probability values for the effect of naphthalene on primary saprophytes

(D) ANOVA table with probability values for the effect of naphthalene on individual primary saprophytes

Ho: The means of the number of primary saprophytes in control and naphthalene treated flasks are equal.

(A) MULTIVARIATE TEST STATISTICS

VARIABLE	PILLAI TRACE	F	DF	PROB
microfungi	0.793	7.651	3, 6	0.018

(B) UNIVARIATE F TESTS

VARIABLE	SOURCE OF VARIATION	SS	DF	MS	F	PROB
primary saprophyte	groups	2.382	1	2.382	5.398	0.049
	error	3.530	8	0.441		
secondary saprophyte	groups	1.228	1	1.228	0.694	0.429
	error	14.163	8	1.770		
other fungi	groups	9.794	1	9.794	13.838	0.006
	error	5.654	8	0.707		

(C) MULTIVARIATE TEST STATISTICS

VARIABLE	PILLAI TRACE	F	DF	PROB
primary saprophytes	0.672	2.565	4, 5	0.165

(D) UNIVARIATE F TESTS

VARIABLE	SOURCE OF VARIATION	SS	DF	MS	F	PROB
Alternaria	groups	0.036	1	0.036	2.667	0.141
	error	0.109	8	0.014		
Cladosporium	groups	0.094	1	0.094	0.692	0.430
	error	1.093	8	0.137		
Sterdark	groups	0.009	1	0.009	1.000	0.347
	error	0.072	8	0.009		
Sterbrown	groups	1.301	1	1.301	12.097	0.008
	error	0.861	8	0.108		

Table 5. (A) MANOVA table with probability values for the microfungal community October 11, 1993, before treatment began

(B) ANOVA table with probability values for the primary and secondary saprophytes and other fungi October 11, 1993, before treatment began

Ho: The means of the number of microfungi in control and naphthalene treated enclosures are equal.

(C) MANOVA table with probability values for the microfauna October 11, 1993, before treatment began

(D) ANOVA table with probability values for mites and collembolans October 11, 1993, before treatment began

Ho: The means of the number of microfauna in control and naphthalene treated enclosures are equal.

(A) MULTIVARIATE TEST STATISTICS

VARIABLE	PILLAI TRACE	F	DF	PROB
microfungi	0.190	0.468	3, 6	0.715

(B) UNIVARIATE F TESTS

VARIABLE	SOURCE OF VARIATION	SS	DF	MS	F	PROB
primary saprophytes	groups	0.257	1	0.257	0.661	0.440
	error	3.940	16	0.246		
secondary saprophytes	groups	0.240	1	0.240	0.240	0.637
	error	7.984	8	0.998		
other fungi	groups	0.024	1	0.024	0.086	0.777
	error	2.248	8	0.281		

(C) MULTIVARIATE TEST STATISTICS

VARIABLE	PILLAI TRACE	F	DF	PROB
microfauna	0.055	0.202	2, 7	0.821

(D) UNIVARIATE F TESTS

VARIABLE	SOURCE OF VARIATION	SS	DF	MS	F	PROB
mites	groups	0.002	1	0.002	0.029	0.869
	error	0.677	8	0.085		
collembolans	groups	0.034	1	0.034	0.034	0.516
	error	0.593	8	0.074		

Table 6. (A) MANOVA table with probability values for the microfungal community November 11, 1993

(B) ANOVA table with probability values for the primary and secondary saprophytes and other fungi November 11, 1993

Ho: The means of the number of microfungi in control and naphthalene treated enclosures are equal.

(C) MANOVA table with probability values for the microfauna November 11, 1993

(D) ANOVA table with probability values for mites and collembolans November 11, 1993

Ho: The means of the number of microfauna in control and naphthalene treated enclosures are equal.

(A) MULTIVARIATE TEST STATISTICS

VARIABLE	PILLAI TRACE	F	DF	PROB
microfungi	0.060	0.127	3, 6	0.940

(B) UNIVARIATE F TESTS

VARIABLE	SOURCE OF VARIATION	SS	DF	MS	F	PROB
primary saprophytes	groups	0.000	1	0.000	0.000	0.993
	error	3.088	8	0.386		
secondary saprophytes	groups	0.442	1	0.442	0.486	0.506
	error	7.284	8	0.911		
other fungi	groups	0.018	1	0.018	0.078	0.787
	error	1.899	8	0.237		

(C) MULTIVARIATE TEST STATISTICS

VARIABLE	PILLAI TRACE	F	DF	PROB
microfauna	0.737	9.813	2, 7	0.009

(D) UNIVARIATE F TESTS

VARIABLE	SOURCE OF VARIATION	SS	DF	MS	F	PROB
mites	groups	3.828	1	3.828	22.333	0.001
	error	1.371	8	0.171		
collembolans	groups	3.777	1	3.777	10.194	0.013
	error	2.964	8	0.371		

Table 7. (A) MANOVA table with probability values for the microfungal community December 4, 1993

(B) ANOVA table with probability values for the primary and secondary saprophytes and other fungi December 4, 1993

Ho: The means of the number of microfungi in control and naphthalene treated enclosures are equal.

(C) MANOVA table with probability values for the microfauna December 4, 1993

(D) ANOVA table with probability values for mites and collembolans December 4, 1993

Ho: The means of the number of microfauna in control and naphthalene treated enclosures are equal.

(A) MULTIVARIATE TEST STATISTICS

VARIABLE	PILLAI TRACE	F	DF	PROB
microfungi	0.199	0.497	3, 6	0.698

(B) UNIVARIATE F TESTS

VARIABLE	SOURCE OF VARIATION	SS	DF	MS	F	PROB
primary saprophytes	groups	0.476	1	0.476	0.210	0.698
	error	18.135	8	2.267		
secondary saprophytes	groups	0.017	1	0.017	0.006	0.945
	error	24.185	8	3.023		
other fungi	groups	0.131	1	0.131	0.817	0.945
	error	1.285	8	0.161		

(C) MULTIVARIATE TEST STATISTICS

VARIABLE	PILLAI TRACE	F	DF	PROB
microfauna	0.686	7.643	2, 7	0.017

(D) UNIVARIATE F TESTS

VARIABLE	SOURCE OF VARIATION	SS	DF	MS	F	PROB
mites	groups	1.613	1	1.613	8.645	0.019
	error	1.492	8	0.187		
collembolans	groups	2.267	1	2.267	17.376	0.003
	error	1.044	8	0.130		

Table 8. (A) MANOVA table with probability values for the microfungal community May 11, 1994

(B) ANOVA table with probability values for the primary and secondary saprophytes and other fungi May 11, 1994

Ho: The means of the number of microfungi in control and naphthalene treated enclosures are equal.

(C) MANOVA table with probability values for the microfauna May 11, 1994

(D) ANOVA table with probability values for mites and collembolans May 11, 1994

Ho: The means of the number of microfauna in control and naphthalene treated enclosures are equal.

(A) MULTIVARIATE TEST STATISTICS

VARIABLE	PILLAI TRACE	F	DF	PROB
microfungi	0.156	0.369	3, 6	0.779

(B) UNIVARIATE F TESTS

VARIABLE	SOURCE OF VARIATION	SS	DF	MS	F	PROB
primary saprophytes	groups	0.144	1	0.144	0.229	0.645
	error	5.0322	8	0.629		
secondary saprophytes	groups	0.245	1	0.245	0.108	0.751
	error	18.114	8	2.264		
other fungi	groups	0.720	1	0.720	1.361	0.277
	error	4.235	8	0.529		

(C) MULTIVARIATE TEST STATISTICS

VARIABLE	PILLAI TRACE	F	DF	PROB
microfauna	0.545	4.194	2, 7	0.063

(D) UNIVARIATE F TESTS

VARIABLE	SOURCE OF VARIATION	SS	DF	MS	F	PROB
mites	groups	0.983	1	0.983	4.446	0.068
	error	1.768	8	0.221		
collembolans	groups	1.709	1	1.709	6.118	0.038
	error	2.234	8	0.279		

Table 9. (A) MANOVA table with probability values for the microfungal community June 3, 1994

(B) ANOVA table with probability values for the primary and secondary saprophytes and other fungi June 3, 1994

Ho: The means of the number of microfungi in control and naphthalene treated enclosures are equal.

(C) MANOVA table with probability values for the microfauna June 3, 1994

(D) ANOVA table with probability values for mites and collembolans June 3, 1994

Ho: The means of the number of microfauna in control and naphthalene treated enclosures are equal.

(A) MULTIVARIATE TEST STATISTICS

VARIABLE	PILLAI TRACE	F	DF	PROB
microfungi	0.539	2.340	3, 6	0.173

(B) UNIVARIATE *F* TESTS

VARIABLE	SOURCE OF VARIATION	SS	DF	MS	F	PROB
primary saprophytes	groups	6.295	1	6.295	2.692	0.139
	error	18.709	8	2.339		
secondary saprophytes	groups	0.712	1	0.712	0.932	0.362
	error	6.110	8	0.764		
other fungi	groups	0.040	1	0.040	0.476	0.510
	error	0.667	8	0.083		

(C) MULTIVARIATE TEST STATISTICS

VARIABLE	PILLAI TRACE	F	DF	PROB
microfauna	0.504	3.555	2, 7	0.086

(D) UNIVARIATE *F* TESTS

VARIABLE	SOURCE OF VARIATION	SS	DF	MS	F	PROB
mites	groups	1.831	1	1.831	5.649	0.045
	error	2.593	8	0.324		
collembolans	groups	2.137	1	2.137	7.962	0.022
	error	2.148	8	0.268		

Table 10. (A) MANOVA table with probability values for the microfungal community July 2, 1994

(B) ANOVA table with probability values for the primary and secondary saprophytes and other fungi July 2, 1994

Ho: The means of the number of microfungi in control and naphthalene treated enclosures are equal.

(C) MANOVA table with probability values for the microfauna July 2, 1994

(D) ANOVA table with probability values for mites and collembolans July 2, 1994

Ho: The means of the number of microfauna in control and naphthalene treated enclosures are equal.

(A) MULTIVARIATE TEST STATISTICS

VARIABLE	PILLAI TRACE	F	DF	PROB
microfungi	0.713	4.976	3, 6	0.046

(B) UNIVARIATE F TESTS

VARIABLE	SOURCE OF VARIATION	SS	DF	MS	F	PROB
primary saprophytes	groups	2.223	1	2.223	6.584	0.033
	error	2.701	8	0.338		
secondary saprophytes	groups	0.798	1	0.798	0.261	0.623
	error	24.460	8	3.057		
other fungi	groups	0.620	1	0.620	0.956	0.357
	error	5.186	8	0.648		

(C) MULTIVARIATE TEST STATISTICS

VARIABLE	PILLAI TRACE	F	DF	PROB
microfauna	0.622	5.767	2, 7	0.033

(D) UNIVARIATE F TESTS

VARIABLE	SOURCE OF VARIATION	SS	DF	MS	F	PROB
mites	groups	3.421	1	3.421	11.033	0.011
	error	2.481	8	0.310		
collembolans	groups	0.502	1	0.502	0.632	0.450
	error	6.358	8	0.795		

Table 11. (A) MANOVA table with probability values for the microfungal community July 22, 1994

(B) ANOVA table with probability values for the primary and secondary saprophytes and other fungi July 22, 1994

Ho: The means of the number of microfungi in control and naphthalene treated enclosures are equal.

C) MANOVA table with probability values for the microfauna July 22, 1994

(D) ANOVA table with probability values for mites and collembolans July 22, 1994

Ho: The means of the number of microfauna in control and naphthalene treated enclosures are equal.

(A) MULTIVARIATE TEST STATISTICS

VARIABLE	PILLAI TRACE	F	DF	PROB
microfungi	0.597	2.969	3, 6	0.119

(B) UNIVARIATE F TESTS

VARIABLE	SOURCE OF VARIATION	SS	DF	MS	F	PROB
primary saprophytes	groups	5.641	1	5.641	6.065	0.039
	error	7.452	8	0.931		
secondary saprophytes	groups	0.000	1	0.000	0.012	0.915
	error	0.065	8	0.008		
other fungi	groups	0.684	1	0.684	1.499	0.256
	error	3.653	8	0.457		

(C) MULTIVARIATE TEST STATISTICS

VARIABLE	PILLAI TRACE	F	DF	PROB
microfauna	0.549	5.044	2, 7	0.044

(D) UNIVARIATE F TESTS

VARIABLE	SOURCE OF VARIATION	SS	DF	MS	F	PROB
mites	groups	3.043	1	3.043	11.512	0.009
	error	2.115	8	0.264		
collembolans	groups	1.478	1	1.478	3.539	0.097
	error	3.342	8	0.418		

Table 12. (A) MANOVA table with probability values for the microfungal community in "dry" enclosures, July 2, 1994
(B) ANOVA table with probability values for the primary and secondary saprophytes and other fungi in "dry" enclosures, July 2, 1994
Ho: The means of the number of microfungi in control and naphthalene treated enclosures are equal.
(C) MANOVA table with probability values for the microfauna in "dry" enclosures, July 2, 1994
(D) ANOVA table with probability values for mites and collembolans in "dry" enclosures, July 2, 1994
Ho: The means of the number of microfauna in control and naphthalene treated enclosures are equal.

(A) MULTIVARIATE TEST STATISTICS

VARIABLE	PILLAI TRACE	F	DF	PROB
microfungi	0.875	6.995	3, 3	0.072

(B) UNIVARIATE F TESTS

VARIABLE	SOURCE OF VARIATION	SS	DF	MS	F	PROB
primary saprophytes	groups	0.748	1	0.748	1.930	0.223
	error	1.939	5	0.388		
secondary saprophytes	groups	0.303	1	0.303	0.070	0.802
	error	21.597	5	4.319		
other fungi	groups	0.009	1	0.009	0.020	0.891
	error	2.065	5	0.413		

(C) MULTIVARIATE TEST STATISTICS

VARIABLE	PILLAI TRACE	F	DF	PROB
microfauna	0.965	55.851	2, 4	0.001

(D) UNIVARIATE F TESTS

VARIABLE	SOURCE OF VARIATION	SS	DF	MS	F	PROB
mites	groups	3.793	1	3.793	124.160	0.000
	error	0.153	5	0.031		
collembolans	groups	3.627	1	3.627	29.072	0.003
	error	0.624	5	0.125		

Table 13. (A) MANOVA table with probability values for the microfungal community in "dry" enclosures, July 22, 1994
(B) ANOVA table with probability values for the primary and secondary saprophytes and other fungi in "dry" enclosures, July 22, 1994
Ho: The means of the number of microfungi in control and naphthalene treated enclosures are equal.
(C) MANOVA table with probability values for the microfauna in "dry" enclosures, July 22, 1994
(D) ANOVA table with probability values for mites and collembolans in "dry" enclosures, July 22, 1994
Ho: The means of the number of microfauna in control and naphthalene treated enclosures are equal.

(A) MULTIVARIATE TEST STATISTICS

VARIABLE	PILLAI TRACE	F	DF	PROB
microfungi	0.769	3.337	3, 3	0.174

(B) UNIVARIATE F TESTS

VARIABLE	SOURCE OF VARIATION	SS	DF	MS	F	PROB
primary saprophytes	groups	1.315	1	1.315	5.732	0.062
	error	1.147	5	0.229		
secondary saprophytes	groups	0.000	1	0.000	0.012	0.985
	error	0.028	5	0.006		
other fungi	groups	0.263	1	0.263	0.740	0.429
	error	1.775	5	0.355		

(C) MULTIVARIATE TEST STATISTICS

VARIABLE	PILLAI TRACE	F	DF	PROB
microfauna	0.549	5.044	2, 7	0.044

(D) UNIVARIATE F TESTS

VARIABLE	SOURCE OF VARIATION	SS	DF	MS	F	PROB
mites	groups	3.043	1	3.043	11.512	0.009
	error	2.115	8	0.264		
collembolans	groups	1.478	1	1.478	3.539	0.097
	error	3.342	8	0.418		