Soil Biol. Biochem. Vol. 6, pp. 73 to 78. Pergamon Press 1974. Printed in Great Britain.

COMPARISON OF SOIL MICROFUNGI IN 40-YEAR-OLD STANDS OF PURE ALDER, PURE CONIFER, AND ALDER–CONIFER MIXTURES

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(*Accepted 5 November* 1973)

Summary—The species composition of soil microfungal populations in adjacent stands of red alder *Alnus rubra*, conifers *Pseudotsuga menziesii*, *Tsuga heterophylla*, and *Picea sitchensis*, and mixed alder–conifer correlated strongly with the dominant vascular vegetation. A total of 92 species were isolated: 55 from the alder stand; 45 from the conifers; and 46 from the mixed alder–conifer, with few species (16, 7, and 5 in the three plots, respectively) reaching average frequencies of 50 per cent or higher. *Penicillium nigricans*, *Aureobasidium pullulans*, *Cephalosporium curtipes*, and *Cladosporium herbarium* were present with high frequency at all sites. *Penicillium daleae*, which occurred with a frequency of 83 per cent in alder soil, appears to be a rare fungus elsewhere. There was little difference in species composition among soil horizons within a stand.

INTRODUCTION

This study compares populations of soil microfungi in adjacent stands of red alder, conifers, and mixed alder–conifers, and is a contribution to a long study of these 40-year-old forest stands. The stands are located in the Cascade Head Experimental Forest, 6·4 km from the Pacific Ocean, near Otis, Oregon. The study plots slope gently to the southwest from 198 to 183 m in elevation. The stands are in the coastal fog belt, and characterized by equatable temperatures, cloudiness, frequent rains, and summer fog. Precipitation is approximately 220 cm/year (Madison, 1957) and is heaviest during November and lighest in July (Bollen *et al.*, 1967). Mean annual temperature is approximately 10°C. Temperatures below freezing or above 27°C are rare. Seasonal and diurnal fluctuations of temperature are slight (Ruth, 1954).

Description of study area.

Three adjacent plots, one of pure red alder (*Alnus rubra* Bong.), one of pure conifers and one of a mixture of alder and conifers were established by removing unwanted species when the conifers were 8 years old in 1938 and the alder 11 years old in 1941. The conifers consisted of Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and sitka spruce (*Picea sitchensis* (Bong.) Carr.). Each plot was square; the alder plot contained 0·4 ha; the other two 0·6 ha.

Franklin and Pechanec (1968) found the understory vegetation much better developed under pure alder than under conifer, with the mixed stand intermediate. Most of the differences were attributed to variation in canopy density and soil nutrients, especially nitrogen fixed by alder nodules. A shrub layer found only in the pure alder stand, contained black elderberry (*Sambucus racemosa* var. *melanocarpa* (Gray) McMinn.) and salmonberry (*Rubus spectabilis* Pursh). The herb layer was similar in the alder and mixed stands, but lacking in the conifer stand. Coverage by terrestrial cryptogams was considerably higher in the conifer and mixed stands than in the pure alder stand. The moss *Eurhynchium oreganum* (Sull.) Jaeg. was the most abundant cryptogam (Pechanec and Franklin, 1968).

The soil is Astoria-like Sols Bruns Acides, a reddish-brown latosol. It is moderately fine textured and moderately well drained. Soils on the three plots were similar in horizon sequence and morphology. Water content of the soils is directly related to precipitation; highest in winter and early spring. Due to its higher organic matter content the F layer contains more moisture than the A horizons. Soil pH in the alder stand is about one unit lower than in the soil from the conifer stand. In March, the average pH values of the F and A_{11} layers were, respectively 3·6 and 3·9 in alder and 5·1 and 5·3 in conifer. The alder soils have a higher acidity in both the F layer and the A_{11} layer (3·9–4·4) throughout the seasons. The mixed alder–conifer soils are more acid than conifer soils, presumably because of the alder (Bollen Chen, Lu and Tarrant, 1967). The organic matter content of the F and A_{11} layers varies considerably with season within each forest type, and from one forest type to the next. Organic matter in the alder soil is highest in fall and lowest in spring. The organic matter content of conifer soil varies only slightly with seasons (Franklin, Dyrness, Moore and

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Tarrant, 1968). Nitrogen content of surface soils under alder is consistently higher than in those under conifers. In the F layer and the A_{11} layer, alder soil maintains a higher nitrogen content than the conifer soil, with the largest percentage differences in the F layer (Bollen *et al.*, 1967; Franklin *et al.*, 1968).

This paper reports the influences of the soil conditions and higher vegetation in the three plots on soil fungi, notably Ascomycetes, Zygomycetes, and Fungi Imperfecti. Higher vegetation can influence the microbial activity of a soil in several ways. These include: effects on soil moisture and temperature as a consequence of shading; effects due to differences in litter fall; and effects due to root exudates or leachates. Hence differences in the higher vegetation would be expected to have a primary influence on the microfungal populations. In an attempt to determine the flora most characteristic of the soils three isolating techniques have been used. Each technique facilitates the isolation of a diverse flora which will enable the investigators to more accurately define the dominant fungi of each forest stand.

MATERIALS AND METHODS

At seasonal intervals, from February, 1968 to September, 1969 on randomly selected sites within each stand, samples of litter (L), fermentation layer (F) and the mineral soil (A_{11}) were taken with precautions against contamination and placed in sterile vials. Initially, three sampling areas were chosen within each site and samples collected at each of the three visible horizons. Thereafter, samples were collected at only one site within each area. Seven sites within each stand were sampled over two seasons. A total of 63 samples were examined. These were frozen the same day, following the procedure of Christensen, Whittingham and Novak (1962), and all samples were processed within 72 h. The samples from the immersion tubes were processed immediately without freezing.

Isolations were made by three methods: dilution plates (James and Sutherland, 1939), soil plates (Warcup, 1951), and immersion tubes (Gochenaur, 1964). Rose bengal streptomycin medium (Martin, 1950) was used in the dilution plates and soil plates. Glucose–ammonium nitrate medium (Gochenaur, 1964) was used in the immersion tube method. The litter was prepared for the Warcup soil plates by cutting it up into small pieces. Similarly, small cut up pieces of litter were used in preparing the immersion tubes for incubation.

After incubation for 5 days, hyphal tips from colonies on the plates were transferred to potato dextrose agar slants. Any colonies which appeared later and were morphologically different from the original isolates, were also isolated. After 14 days, the slant cultures were sorted into presumptive species groups. Each culture was then examined microscopically, identified if possible, and cross-matched with isolates from the other populations.

The frequency each fungus in each stand was computed by the formula of Christensen *et al.* (1962).

RESULTS

Table 1 is a nearly complete list of the microfungi identified in this survey (excluding unidentified species isolated only once) with their frequencies for each of the three stands.

A total of 92 species were isolated by the three different isolation techniques from beneath the three stands (Table 1): 55 from alder, 45 from conifer, and 46 from the mixed alder–conifer. Of these, 18 occurred at frequencies of 50 per cent or more and are considered dominants. Many of these are dominants in other soil types and ubiquitous in their distribution; others have not been reported commonly from soils.

Species isolated from a single sample within a stand were as a group, of low frequency, accounting for 59 per cent of the total species, but only 22 per cent of the total isolates. This is in agreement with Christensen *et al.* (1962), and Christensen and Whittingham (1965).

A large majority of the isolates were representatives of the family Moniliaceae (Moniliales) due to the high percentage of *Penicillium* species present in all three stands. In total, 16 genera were isolated representing the family Moniliaceae.

The family Dematiaceae and the order Mucorales were equally represented in percentages of total isolates. Although most isolates in the Mucorales were members of the Mucoraceae, species of *Mortierella* (Mortierellaceae) were isolated frequently from alder soil. Neither the family Dematiaceae nor the order Mucorales were represented by many genera.

Not only did the alder soil support a greater variety of species, but 30 per cent of these species occurred with a frequency of 50 per cent or greater. This is compared with 15 per cent of the species from conifer occurring with a frequency of 50 per cent or greater, and only 11 per cent of the mixed alder–conifer species occurring with a frequency of 50 per cent or greater. Although the mixed alder–conifer supported a variety of species (46) comparable to either the alder or the conifer, only one of these species (M11–5) occurred only in the mixed stand soil with a frequency of 50 per cent or greater. The mixed alder–conifer soil had few species unique to it or with frequencies higher than in pure alder or conifers.

Populations characteristic of certain soil horizons were anticipated at the outset of the study. However, species differed but little between the various layers. Nearly equal numbers of species were isolated from the litter layer of all three stands. Half of these species were present in two or all three of the stands. In the F horizon, there are fewer species in the conifer and mixed alder–conifer stands, whereas under alder the number remained nearly constant. The number of species increased in the A_{11}, especially in the alder sites. The number of isolates from a horizon does not correspond directly with the number of species, because some species produce large numbers of propagules; others, few.

Table 1. Frequencies of microfungi isolated*†

	Alder				Conifer				Mixed			
	L	F	A11	Stand‡	L	F	A11	Stand	L	F	A11	Stand
Asperillus chevalieri (Mangin) Thom and Church	0	0	14	17	0	0	0	0	0	0	0	0
Aspergillus flavipes (Bain. and Sart.) Thom and Church	17	0	0	17	0	0	0	0	0	0	0	0
Aspergillus sp. (A22-4)	0	33	0	33	0	0	0	0	0	0	0	0
Candida sp.	17	0	0	17	0	0	0	0	0	0	0	0
Cephalosporium humicola Oudemans	0	0	14	17	0	0	0	0	0	0	0	0
Cephalosporium sp. (A1-5)	17	0	0	17	0	0	0	0	0	0	0	0
Cephalosporium sp. (A3-14)	0	0	14	17	0	0	0	0	0	0	0	0
Cordana pauciseptata Preuss	0	17	0	17	0	0	0	0	0	0	0	0
Fusidium viride Grove	17	33	28	50	0	0	0	0	0	0	0	0
Monilia geophila Oudemans	0	0	14	17	0	0	0	0	0	0	0	0
Paecilomyces farinosus (Fr.) Brown and G. Smith	0	0	14	17	0	0	0	0	0	0	0	0
Paecilomyces marquandii (Massee) Hughes	0	0	14	17	0	0	0	0	0	0	0	0
Penicillium italicum Wehmer	0	17	14	33	0	0	0	0	0	0	0	0
Penicillium piscarium Westling	0	0	14	17	0	0	0	0	0	0	0	0
Penicillium raistrickii Smith	17	0	0	17	0	0	0	0	0	0	0	0
Penicillium thomii Maire	17	33	0	50	0	0	0	0	0	0	0	0
Sporotrichum carnis Brooks and Hansford	0	0	14	17	0	0	0	0	0	0	0	0
Torula herbarum Pers.	0	0	14	17	0	0	0	0	0	0	0	0
Unidentified A11-1	17	17	14	50	0	0	0	0	0	0	0	0
Unidentified A11-2	17	17	14	50	0	0	0	0	0	0	0	0
Unidentified A12-8	0	17	14	33	0	0	0	0	0	0	0	0
Unidentified A4EP5	0	0	14	17	0	0	0	0	0	0	0	0
Mycelia sterila	0	0	28	17	0	0	0	0	0	0	0	0
Aspergillus brunneo-uniseriatus Singh and Bakshi	0	0	14	17	17	0	0	17	0	0	0	0
Cephalosporium sp. (A3-9)	0	0	14	17	17	0	17	17	0	0	0	0
Hyalodendron sp.	0	17	28	17	0	17	0	17	0	0	0	0
Penicillium rugulosum Thom	0	33	0	33	0	0	17	17	0	0	0	0
Trichocladium sp.	33	17	28	50	17	17	33	17	0	0	0	0
Verticillium terrestre (Link) Lindau	17	0	0	17	17	0	0	17	0	0	0	0
Unidentified A11-4	43	0	0	50	17	0	0	33	0	0	0	0
Aspergillus sydowi (Bain. and Sart.) Thom and Church	0	0	0	0	17	0	0	17	0	0	0	0
Cylindrocarpon radicicola Wollenweber	0	0	0	0	17	0	0	17	0	0	0	0
Eupenicillium pinetorium Stolk	0	0	0	0	0	0	17	17	0	0	0	0
Eupenicillium stolkiae Scott	0	0	0	0	0	17	17	17	0	0	0	0
Monocillium sp.	0	0	0	0	0	0	17	17	0	0	0	0
Monodictys sp.	0	0	0	0	0	0	17	17	0	0	0	0
Penicillium funiculosum Thom	0	0	0	0	0	0	17	17	0	0	0	0
Penicillium soppi Zaleski	0	0	0	0	0	17	17	33	0	0	0	0
Penicillium spinulosum Thom	0	0	0	0	33	0	17	33	0	0	0	0
Pestulotia sp.	0	0	0	0	17	0	0	17	0	0	0	0
Sporotrichum pruinosum Gilman and Abbott	0	0	0	0	33	0	0	33	0	0	0	0
Stemphylium botryosum Wallroth	0	0	0	0	0	17	0	17	0	0	0	0
Trichoderma sp. (variant No. 2)	0	0	0	0	0	0	33	33	0	0	0	0
Unidentified C32-1	0	0	0	0	0	17	0	17	0	0	0	0
Unidentified C12-1	0	0	0	0	0	17	0	50	0	0	0	0
Unidentified C31-3	0	0	0	0	17	0	0	33	0	0	0	0
Absidia glauca Hagem	17	0	0	17	17	0	17	33	17	0	0	17
Aspergillus niger V. Tieghem	0	17	0	17	0	0	17	17	33	17	0	33
Aspergillus subsessilis Raper and Fennell	33	17	14	50	0	17	0	17	17	17	0	17
Aureobasidium pullulans (de Bary) Arnaud	33	33	43	83	33	50	66	66	33	33	66	83

Table 1.—*continued*

	Alder				Conifer				Mixed			
	L	F	A11	Stand‡	L	F	A11	Stand	L	F	A11	Stand
Cephalosporium curtipes Saccardo	66	66	14	66	33	0	66	83	33	0	33	50
Cladosporium herbarum (Pers.) Link	50	33	14	66	33	17	17	33	50	33	33	50
Gliocladium penicilloides Corda	0	17	14	17	0	17	17	33	17	0	0	17
Gliocladium salmonicolor Raillo.	66	17	14	83	0	33	33	50	0	17	33	33
Gliomastix murorum var. *felina* (March) Hughes	17	17	28	50	0	0	17	17	0	17	17	33
Mortierella pusilla Oudemans	33	33	0	33	17	17	17	33	0	33	17	33
Mortierella ramanniana var. *angulispora* (Naumov) Linnemann	0	0	14	17	17	0	0	17	0	0	17	17
Penicillium daleae Zaleski	66	50	28	83	17	17	0	17	17	17	33	33
Penicillium janthinellum Biourge	0	17	28	50	83	60	50	83	0	0	33	33
Penicillium nigricans (Bain.) Thom	83	100	57	100	83	50	66	66	66	50	83	100
Trichoderma viride Pers. ex. Fr.	66	83	57	100	50	50	66	100	33	33	17	33
Botrytis cinerea Pers. ex. Fr.	17	17	14	33	0	0	0	0	17	0	0	17
Mortierella isabellina (Oudemans) Zycha	33	17	14	33	0	0	0	0	33	0	0	33
Penicillium jenseni Zaleski	17	0	14	17	0	0	0	0	17	17	0	17
Penicillium lanoso-coeruleum Thom	0	0	14	17	0	0	0	0	0	0	17	17
Penicillium purpurogenum Stoll	17	0	14	17	0	0	0	0	0	17	0	17
Penicillium simplicissimum (Oudemans) Thom	17	0	14	33	0	0	0	0	0	0	17	17
Penicillium steckii Zaleski	17	0	0	17	0	0	0	0	17	17	17	17
Umbelopsis versiformis Amos and Barnett	0	17	14	17	0	0	0	0	0	0	17	17
Unidentified A23-1	0	0	14	17	0	0	0	0	0	0	17	17
Unidentified M3EP1	17	0	0	17	0	0	0	0	0	0	17	17
Paecilomyces variotii Bain.	0	0	0	0	0	17	17	17	17	0	0	17
Penicillium frequentans Westling	0	0	0	0	17	0	17	17	0	17	33	33
Pencillium lividum Westling	0	0	0	0	17	0	0	17	0	33	0	33
Penicillium oxalicum Currie and Thom	0	0	0	0	17	0	0	17	17	0	0	17
Penicillium variabile Sopp.	0	0	0	0	17	0	0	17	0	0	17	17
Rhizopus rhizopodiformis Hesseltine	0	0	0	0	0	0	17	17	0	17	0	17
Unidentified M21-2	0	0	0	0	17	0	0	17	17	0	0	33
Absidia capillita van Tieghem	0	0	0	0	0	0	0	0	17	0	0	17
Cephalosporium acremonium Corda.	0	0	0	0	0	0	0	0	0	0	17	17
Gelasinospora tetrasperma Dowding	0	0	0	0	0	0	0	0	17	0	0	17
Mycogone nigra (Morgan) Jensen	0	0	0	0	0	0	0	0	0	0	17	17
Myrothecium verrucaria (Albertini and Schweinitz) Ditmar	0	0	0	0	0	0	0	0	17	0	0	17
Penicillium aceleatum Raper and Fennell	0	0	0	0	0	0	0	0	17	0	0	17
Penicillium canescens Sopp.	0	0	0	0	0	0	0	0	17	0	0	17
Penicillium miczynskii Zaleski	0	0	0	0	0	0	0	0	0	17	0	17
Penicillium ochoro-chloron Biourge	0	0	0	0	0	0	0	0	17	17	17	17
Sporotrichum epigaeum var. *terrestre* Daszewska	0	0	0	0	0	0	0	0	0	0	17	17
Trichoderma album Preuss	0	0	0	0	0	0	0	0	0	17	0	17
Unidentified M11-12	0	0	0	0	0	0	0	0	17	0	0	33
Unidentified M11-5	0	0	0	0	0	0	0	0	17	17	17	50
Unidentified M22-6	0	0	0	0	0	0	0	0	0	17	0	33
Total species:	29	27	40	55	26	18	26	45	25	21	24	46

* Unidentified species with a single isolation are omitted.
† Frequencies computed by the formula of Christensen *et al.* (1962).
‡ Stand frequencies based on 21 samples per stand.

Table 2. Similarity coefficients for the alder, conifer, and mixed stand

Paired stands	No. of shared species	Similarity coefficients
Alder stand–conifer stand	22	44·00
Alder stand–mixed stand	25	49·50
Conifer stand–mixed stand	22	48·35

In general with dilution plates the number of isolates increased between the L and F horizons (292–351 isolates) and decreased between the F and A_{11} horizons (351–298 isolates).

Three different isolation techniques were used in the expectation that they would reduce the bias introduced by any single technique. Although there were both quantitative and qualitative differences in the populations isolated by the three techniques, these differences were small when compared to the overall sample. Species with high frequencies were commonly isolated by all three methods. *Penicillium nigricans*, *Gliocladium salmonicolor*, *Trichoderma viride*, and *Mortierella pusilla* were isolated with equal frequency by all three methods. The dilution plate method produced the greatest number of isolates from a given sample. Common species which were isolated only on dilution plates include: *Cephalosporium curtipes*, *Gliomastix murorum* var. *felina*, *Cladosporium herbarum*, and *Mortierella ramanniana* var. *angulispora*. *Penicillium janthinellum* and *Penicillium daleae*, both common, were most often isolated by immersion tube or soil plate. *Penicillium purpurogenum* was isolated only by immersion tube, and *Trichocladium* sp. and *Hyalodendron* sp. only by soil plate.

Coefficients of similarity were calculated for the three stands using species presence in the formula $2w/a + b$, where a is the number of species in one population, b is the number of species in the other population, and w is the number of species found in both populations (Bray and Curtis, 1957; Christensen *et al.*, 1962). This permitted a comparison of the three stands by species composition of their microfungal populations. Table 2 shows these coefficients of similarity, multiplied by 100, for each pair of populations. All isolates regarded as separate species were included, including unidentified ones. The least similar populations, i.e. those having the lowest coefficient, are the alder population and the conifer population. Based solely upon similarities in microfungal populations, the arrangement of stands corresponds exactly to an arrangement by dominant tree species.

DISCUSSION

The alder–conifer study plots at Cascade Head Experimental Forest consist of stands of pure red alder, pure conifer, and mixed alder–conifer which have grown side by side in plots equivalent with respect to soil type and climate. Since differences in the soil are a product of the vascular vegetation, the effects of the dominant vegetation on the soil microfungal populations can be studied directly and in this respect these plots provide a unique opportunity for this type of study.

Tresner *et al.* (1954), Christensen (1960), Christensen *et al.* (1962), and Christensen and Whittingham (1965) have shown that the microfungal population of soil reflects the species composition of higher vegetation. Our study confirms this, revealing dominance of relatively few but diverse fungal species under the different stands. A greater diversity of dominant species was found on the alder plot which also had a greater diversity of higher vegetation (Franklin and Pechanec, 1968).

The soil microfungi of the three stands can be characterized as follows: the alder plot supports a large number (16) of codominant species. Those most characteristic of this plot were: *Penicillium nigricans*, *Trichoderma viride*, *Penicillium daleae*, *Aspergillus subsessilis*, *Gliomastix murorum* var. *felina*, *Penicillium thomii*, and *Trichocladium* sp. *Penicillium daleae*, which occurred with a frequency of 83 per cent in alder soil, appears to be a rare fungus elsewhere. Since its original isolation by Zaleski (1927), it has been reported only twice (Al-Doory, Tolba and Al-Ari, 1959; Christensen and Backus, 1961).

In relation to dominant tree species and understory vegetation, the mixed stand is intermediate in species composition between pure red alder and pure conifer (Franklin and Pechanec, 1968). Similarly, the mixed stand is intermediate between the alder and the pure conifer in species composition of microfungal populations. Because soil minerals, climate, and moisture are nearly equal throughout the stands, the differences in soil microfungal populations among the trees stands is probably related to differences in the species composition of the higher vegetation as they affect soil properties.

Some of the greatest influences of higher vegetation on a soil are those that effect soil moisture and temperature, deposition of litter, and production of root exudates or leachates. At the experimental stands, roots are abundant in all A_{11} horizons (Franklin *et al.*, 1968). Differences in species between the L and A_{11} horizons are probably due to the effect of root exudates and leachates in this horizon. In alder soil, the increase in numbers of fungal species in the A_{11} could be related to this reported abundance of roots as well as the lower C:N ratio (Bollen *et al.*, 1967; Franklin *et al.*, 1968).

Although the total number of fungi isolated by dilution plates is highest in the F horizon (Lu *et al.*, 1968), the number of species reported in our study was the same or less than in the L horizon. Possibly the composition of the organic material restricts fungal activity to a few species or the differences may be due to differences in sporulation by the fungi present. Bollen *et al.*

(1967) found a decrease in the number of molds in the A_{11} horizon in all three soils. In our study, although the number of isolates was less in the A_{11}, the number of species was not. The A_{11} horizon supported a large number of species, especially in the alder soil. In addition to the discussion above, the increase in species numbers in the A_{11} horizon could also be attributed to fall through of spores from species found in the L or F horizon which are isolated in the A_{11} horizon. These additional spores would enhance species numbers as indicated for the A_{11} horizon.

The species composition of the soil microfungal populations in the adjacent stands correlates well with the dominant vascular vegetation. The microfungal population of the mixed alder–conifer plot is intermediate between those of the pure alder and the pure conifer. This correlation is presumably due either to direct or to indirect influences of the dominant tree species on the soil, since other factors such as soil type, soil moisture, climate, etc. are consistent throughout the plots.

Acknowledgements—This research was aided in part by National Science Foundation Grant No. GB-6191. The authors are grateful to Mrs. Margaret Tulloch for her help in identification of many *Penicillium* species.

REFERENCES

AL-DOORY U., TOLBA M. K. and AL-ARI H. (1959) On the fungal flora of Iraqui soils. II. Central Iraq. *Mycologia* **51,** 429–439.

BOLLEN W. B., CHEN C. S., LU K. C. and TARRANT R. F. (1967) Influence of red alder on fertility of a forest soil. Microbial and chemical effects. *Research Bull.* **12,** Oregon State University, Corvallis.

BRAY J. R. and CURTIS J. T. (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* **27,** 325–349.

CHRISTENSEN M. (1960) *The Soil Microfungi of Conifer–Hardwood Forests in Wisconsin.* Ph.D. Thesis. University of Wisconsin, Madison.

CHRISTENSEN M. and BACKUS M. P. (1961) New or noteworthy *Penicillia* from Wisconsin soils. *Mycologia* **53,** 451–463.

CHRISTENSEN M. and WHITTINGHAM W. F. (1965) The soil microfungi of open bogs and conifer swamps in Wisconsin. *Mycologia* **57,** 882–896.

CHRISTENSEN M., WHITTINGHAM W. F. and NOVAK R. O. (1962) The soil microfungi of wet-mesic forests in southern Wisconsin. *Mycologia* **54,** 374–388.

COBB H. J. (1932) A quantitative study of the micro-organic population of a hemlock and a deciduous forest soil. *Soil Sci.* **33,** 325–345.

FRANKLIN J. F., DYRNESS C. T., MOORE D. G. and TARRANT R. F. (1968). Chemical soil properties under coastal Oregon stands of alder and conifers. In *Biology of Alder* (J. M. Trappe, Ed.) pp. 157–172. Pacific Northwest For. Range Exp. Sta. Portland, Oregon.

FRANKLIN J. F. and PECHANEC, ANNA A. (1968) Comparison of vegetation in adjacent alder, conifer, and mixed alder–conifer communities. I. Understory vegetation and stand structure. In *Biology of Alder* (J. M. Trappe, Ed.) pp. 37–43. Pacific Northwest For. and Range Exp. Sta. Portland, Oregon.

GOCHENAUR S. E. (1964) A modification of the immersion tube method for isolating soil fungi. *Mycologia* **56,** 921–923.

JAMES N. and SUTHERLAND M. (1939) The accuracy of the plating method for estimating the numbers of bacteria and fungi from one dilution and one aliquot of a laboratory sample of soil. *Can. J. Res.* **17,** 97–108.

JENSEN H. L. (1934) Contribution to the microbiology of Australian soils. I. Numbers of micro-organisms in soil and their relation to external factors. *Proc. Linnean Soc. New South Wales* **59,** 101–117.

LU K. C., CHEN C. S. and BOLLEN W. B. (1968) Comparison of microbial populations between red alder and conifer soils. In *Biology of Alder* (J. M. Trappe, Ed.) pp. 37–43. Pacific Northwest For. and Range Exp. Sta. Portland, Oregon.

MADISON R. W. (1957) *A Guide to the Cascade Head Experimental Forest.* Pacific Northwest For. Range Exp. Sta. Portland, Oregon.

MARTIN J. P. (1950) Use of acid, rose bengal and streptomycin in the plate method of estimating soil fungi. *Soil Sci.* **69,** 215–233.

PECHANEC, ANNA A. and FRANKLIN J. F. (1968) A vegetational comparison of adjacent alder, conifer, and mixed alder–conifer communities. II. Epiphytic, epixylic, and epilithic cryptogams. In *Biology of Alder* (J. M. Trappe, Ed.) pp. 85–98. Pacific Northwest For. and Range Exp. Sta. Portland, Oregon.

RUTH R. H. (1954) *Cascade Head Climatological Data* 1936–1952. Pacific Northwest For. Range Exp. Sta. Portland, Oregon.

THORNTON R. H. (1956) Fungi occurring in mixed oakwood and heath soil profiles. *Trans. Br. Mycol. Soc.* **39,** 485–494.

TRESNER H. D., BACKUS M. P. and CURTIS J. T. (1954) Soil microfungi in relation to the hardwood forest continuum in southern Wisconsin. *Mycologia* **46,** 314–333.

WARCUP J. H. (1951) The ecology of soil fungi. *Trans. Br. Mycol. Soc.* **34,** 376–399.

WILLIAMS S. T. and PARKINSON D. (1964) Studies of fungi in a podsol. I. Nature and fluctuation of the fungus flora of the mineral horizons. *J. Soil Sci.* **15,** 331–341.