Biol Fertil Soils (1990) 9:245–251

Biology and Fertility of Soils

Fungal communities associated with the decomposition of a common leaf litter (*Quercus leucotrichophora* A. Camus) along an elevational transect in the Central Himalaya

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Received July 3, 1989

Summary. We studied the fungal communities associated with decomposing common leaf litter (*Quercus leucotrichophora* A. Camus) placed in five forests of Central Himalaya between the elevations of 330 and 2150 m. During the initial period of decay, coinciding with the rainy season, a progressive increase in fungal counts and species diversity was observed in all forest sites. The sal forest site had a greater weight loss and supported the largest fungal densities, whereas the pine forest had a lower weight loss and the smallest fungal densities. Deuteromycetes were the dominant group in all the forest sites. Most of the species isolated during the annual cycle of the forest sites were of the "accidental type". Species diversity and fungal counts on the common leaf litter were markedly affected by the environmental changes brought about by the native leaf litter. This effect was most obvious in the chir pine forest site where the leaf litter of the native dominant species was distinctly more resistant to decay than those of the other sites, making the soil environment of the site markedly different from that of other sites. The pattern of fungal-species changes with progressive decay of the substrate was similar to that suggested by the tolerance model of Connel and Slatyer.

Key words: Litter decomposition – Fungal communities – *Quercus leucotrichophora* litter – Diversity – Central Himalayan forests – Substrate quality – Deuteromycetes

The present study is part of an attempt to describe the structure and functioning of the Central Himalayan forests located along an elevational gradient of 300–2200 m. The vegetation of this gradient consists of sal (*Shorea robusta* Gaertn F.) forest towards the lower elevations, chir pine (*Pinus roxburghii* Sarg.) in the middle elevations and oak (*Quercus* spp.) towards the higher elevations. Apart from these, in this transect, some mixed forest communities also occur.

In this investigation we described fungal communities that developed on the same decomposing substrate (leaf litter of *Q. leucotrichophora* A. Camus, the species with the widest elevational range within the transect) placed in different forest sites along the above elevation gradient. The absence of variation in substrate quality enabled us to focus on the influence of site-specific environmental factors on the rate of decomposition and associated fungal communities. The influence of major climatic factors, such as temperature and soil moisture, on litter decomposition has been well documented by several studies (Rochow 1974; Singh and Gupta 1977). However, the microbial biota that develop at a site can also be influenced by the litter of the dominant tree species of the site. For example, N is an essential nutrient for microbes, and its concentration in leaves influences the densities of decomposers (Anderson 1973; Melillo et al. 1982). Since the litter properties of dominant forest species such as chir pine, oak and other broadleaf species differ markedly, we expected that the differences in native litter would lead to the development of habitats with different fungal reservoirs. We assumed that these variations would also influence the development of fungal communities on a decomposing common leaf litter (*Q. leucotrichophora*) placed at different forest sites. The description of fungal communities was mainly focused on changes in species composition and diversity during the course of decomposition.

Material and methods

Study sites

The study sites are located between 29°7′ and 29°26′N and between 79°15′ and 79°38′E in the Indian Central Himalaya. The sal forest site, located at about 300 m, represented the warmest habitat. *Shorea robusta* was the dominant forest species. The pine-mixed broadleaf forest site was located at 1350 m elevation. The main associates of *P. roxburghii* Sarg. (chir pine) in this forest were *Q. leucotrichophora*, *Lyonia ovalifolia* (Wall) Drude, *Q. glauca* Thunb, and *Rhododendron ar-*

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boreum Smith. The third site, selected in the pine forest at an elevation of 1750 m, was dominated by *P. roxburghii*. The mixed oak-pine forest situated at an elevation of 1850 m was dominated by *Q. leucotrichophora* and *P. roxburghii*. The mixed oak forest site was located at an elevation of 2150 m. The dominant species were *Q. lanuginosa* D. Don, *Q. floribunda* Lindl, and *Q. leucotrichophora*.

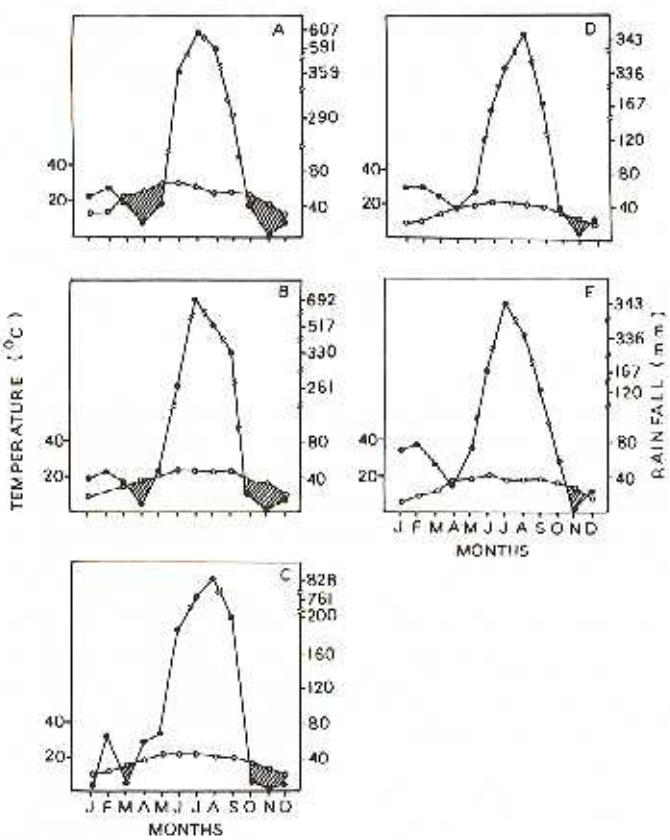

Fig. 1. Climatic diagrams for different forest sites; **A**, sal forest; **B**, pine-mixed broadleaf forest; **C**, pine forest; **D**, mixed oak-pine forest; **E**, mixed oak

The monsoon pattern of rainfall, in which three-quarters or more of the annual rainfall occurs during mid-June to mid-September, is the characteristic climatic feature throughout the elevational gradient. This period is preceded by a summer season and followed by a dry winter season. The sites tend to become increasingly mesic with increasing elevation (Fig. 1). The soil (Table 1) is sandy loam in all sites except for the sal forest site, where it is loamy sand. The pH is acidic (5.7–6.8) and the organic-C content is in the range 3.5%–4.2%, except at the sal forest site where it is markedly lower (1.1%).

Leaf litter decomposition

We selected the leaf of *Q. leucotrichophora* as the common material for the decomposition study, because it has the widest distribution within the elevational transect.

Weight loss

Nylon litter bags (10×10 cm) with a mesh size of 1 mm were filled with 5 g air-dried senesced leaves of *Q. leucotrichophora*, which were collected from the middle canopy of a single tree in July 1981. At the sal forest site, steel-wire netting mesh bags of the same size and mesh were used to prevent termite attacks. At each site 120 litter bags were placed randomly on the forest floor. Five litter bags were recovered each month from each site and were used to observe the percentage weight loss, litter moisture in the residual material, and the microbial population over a 1 year period (from the rainy season of 1981 to the summer season of 1982).

Microbial population

One gram of leaf litter was taken from each sample and a suspension was made with 100 ml sterilized distilled water. The suspension was further diluted by 10^4, in different sterile conical flasks, for the isolation of fungi. Potato dextrose agar (Riker and Riker 1936) media was used to isolate the fungi. Five milliliters of each dilution was poured on different sterilized agar plates, and eight agar plates were incubated at 28 °C (±1°). The colonies were counted on the 3rd and 15th days of incubation, and their average number per gram oven-dry weight of litter was calculated using the formula:

$$F = (C \times L_1 \times Z)/L_d ,$$

Table 1. Vegetation, soil, and litter parameters of the study sites

	Forest sites (elevation)				
	Sal (330 m)	Pine-mixed broadleaf	Pine (1700 m)	Mixed oak-pine (1850 m)	Mixed oak (2150 m)
Vegetation characteristics					
Dominant tree spp.	*Shorea robusta*	*Pinus roxburghii*, *Quercus leucotrichophora*, *Rhododendron arboreum*	*P. roxburghii*	*Q. leucotrichophora*, *P. roxburghii*	*Q. lanuginosa*; *Q. floribunda*
Tree spp. (no)	5	22	5	9	4
Tree spp. diversity (Shannon-Weiner index)	1.8	3.9	0.7	1.7	1.4
Soil (0–10 cm) characteristics					
Organic C (%)	1.1	3.5	3.7	3.5	4.2
C:N ratio	7.1	11.6	14.2	10.6	9.1
pH	6.8	6.6	5.7	6.1	6.0
Native fresh leaf litter characteristics					
N (%)	0.99	0.90	0.68	0.82	1.1
C:N ratio	48.32	62.3	70.67	62.8	42.7
Lignin (%)	9.3	15.0	23.4	17.0	16.9
Lignin:N ratio	9.4	16.6	35.0	20.8	15.3

where F is the average number of fungi, C is the average number of colonies on the culture plates, L_f is the fresh weight of litter, Z is the dilution factor and L_d is the oven-dry weight of litter.

The frequency of fungi appearing on the litter was calculated by dividing the number of petri dishes colonized by a fungus by the total number of dishes observed, expressed as a percentage. The relative abundance of each fungal species was calculated as the number of fungal colonies of a species divided by the total number of fungal colonies, expressed as a percentage. The relative importance of each species in the population for each forest site and sampling period was calculated as the importance index, the sum of relative frequency and average per cent relative density. Relative frequency was calculated as the number of colonies of a species divided by the total number of colonies, expressed as a percentage and the average relative density was defined as:

$$D = D_1 + D_2 - \ldots D_n/N \times 100 \ ,$$

where n is the number of replicated plates and D is the density of the species.

The values of the importance index so obtained may vary between 0 and 200 and were used to calculate the similarity index, obtained by the formula $2\ W\ (A + B) \times 100$, where W is the sum of the smaller number of the species common to two communities, A is the sum of all the species in one of the two communities, and B is the sum of all the species in the other community. The diversity of the fungal communities was calculated by using the Shannon-Weiner information function (Shannon and Weiner 1963). The temporal β diversity (or inter-sample diversity) of the fungal species was calculated following the expression given by Whittaker (1975) for spatial β diversity. This expresses the degree of difference in fungal species composition among the sample of decomposing leaf litter; the formula used was: β diversity $= S_c/S$, where S_c is the total number of species occurring in a decomposition cycle or decomposing samples, counting each species only once whether or not it occurs more than once, and S is the average number of species per individual in the decomposing leaf litter sample.

Table 2. Weight loss in common leaf litter (*Quercus leucotrichophora*) placed in different forest sites after varying periods of time

Forest site and altitude (m)	Weight loss (%)		
	After 1 month of summer	End of rainy season	End of the year
Sal (330)	29	62	99
Pine-mixed hoardleaf (1350)	17	40	88
Pine (1750)	16	17	75
Mixed oak-pine (1850)	9	34	77
Mixed oak (2150)	28	48	88

Results

Rate of decomposition

The rate of litter decomposition (*Q. leucotrichophora* leaves) was not correlated with elevation (Table 2). For example, in the most elevated forest site (2150 m) the rate of litter decomposition was about the same as in the pine-mixed broadleaf forest site, located in the middle of the transect (1350 m).

Fungal counts and qualitative nature of fungi

The total fungal counts in all sites increased during the initial months, and peaked 3–4 months after the placement of the litter bags, i.e., October – November (Fig. 2).

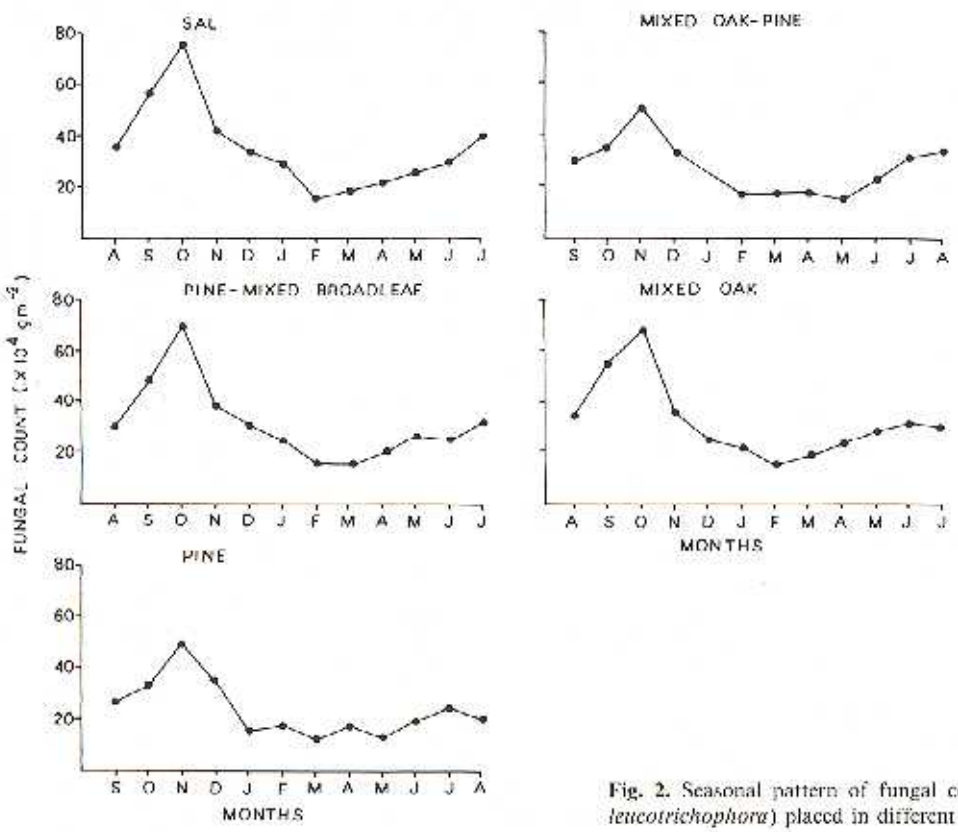

Fig. 2. Seasonal pattern of fungal counts of decomposing leaf litter (*Quercus leucotrichophora*) placed in different forest sites

Thereafter, with the commencement on the dry cold period, a sharp decline in the populations generally occurred from February to April. In all sites the fungal counts increased again with the continued drought as temperatures rose during the summer season, to attain a secondary but much smaller peak in the residual litter.

The peak fungal count varied across the sites, the largest being at the sal forest site and the smallest at the pine forest site. Thus, the fungal count, also was not correlated with elevation.

Deuteromycetes were the dominant group in each forest site, accounting for 83%–92% of the total species.

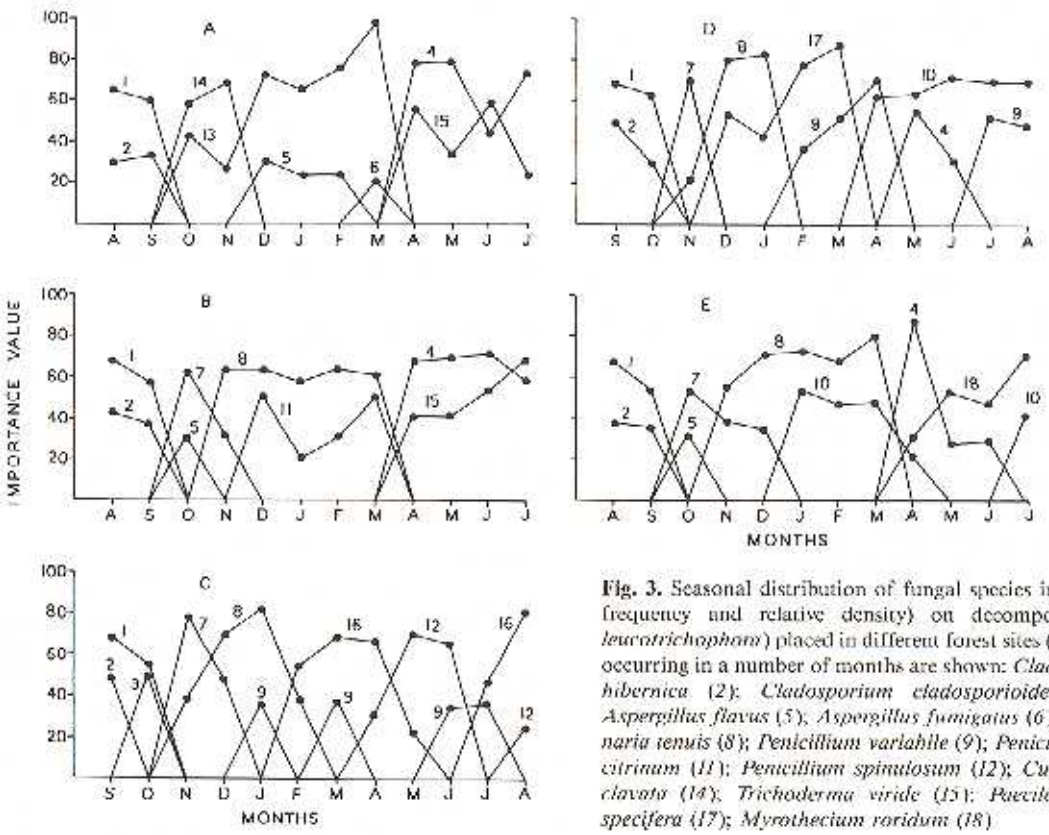

Fig. 3. Seasonal distribution of fungal species importance value (sum of relative frequency and relative density) on decomposing oak leaf litter (*Quercus leucotrichophora*) placed in different forest sites (see Fig. 2 for types). Only species occurring in a number of months are shown: *Cladosporium herbarum* (*1*); *Phoma hibernica* (*2*); *Cladosporium cladosporioides* (*3*); *Aspergillus niger* (*4*); *Aspergillus flavus* (*5*); *Aspergillus fumigatus* (*6*); *Alternaria alternata* (*7*); *Alternaria tenuis* (*8*); *Penicillium variabile* (*9*); *Penicillium negricans* (*10*); *Penicillium citrinum* (*11*); *Penicillium spinulosum* (*12*); *Curvularia lunata* (*13*); *Curvularia clavata* (*14*); *Trichoderma viride* (*15*); *Paecilomyces varioti* (*16*); *Drechslera specifera* (*17*); *Myrothecium roridum* (*18*)

Table 3. Fungi occurring on decomposing leaf litter (*Quercus leucotrichophora*) in different forest sites

Sal forest	Pine-mixed broadleaf forest	Pine forest	Mixed oak-pine forest	Mixed oak forest
Ubiquitous species				
Curvularia lunata	*Acremonium furcatum*	*Alternaria alternata*	*Aspergillus niger*	*Alternaria tenuis*
Aspergillus niger	*Aspergillus terreus*	*Cladosporium herbarum*	*Cladosporium herbarum*	*Cladosporium herbarum*
Mortierella subtilissima	*Aspergillus niger*	*Penicillium spinulosum*	*Drechslera specifera*	*Drechslera specifera*
Trichoderma viride	*Penicillium citrinum*			*Aspergillus flavus*
	Trichoderma viride			
Differential species				
Chaetomium globosum	*Alternaria alternata*	*Acremonium furcatum*	*Acremonium furcatum*	*Nigrospora sphaerica*
Cladosporium herbarum	*Aspergillus luchensis*	*Aspergillus niger*	*Alternaria alternata*	*Phoma hibernica*
Phoma glomerata	*Cladosporium herbarum*	*Trichoderma viride*	*Chaetomium globosum*	*Trichoderma viride*
Penicillium funiculosum	*Mortierella subtilissima*		*Myrothecium roridum*	*Mucor hemalis*
	Pestalotia macrotricha			
Accidental species				
Aspergillus sp.	*Aspergillus fumigatus*	*Aspergillus humicola*	*Fusarium* sp.	*Acremonium furcata*
Penicillium sp.	*Aspergillus flavus*	*Aspergillus luchuensis*	*Penicillium rubrum*	*Chaetomium indicum*
Mucor sp.	*Aspergillus terreus*	*Fusarium solani*	*Helminthosporium* sp.	*Aurobasidium pullulans*
	Alternaria humicola	*Mucor hemalis*	*Trichoderma viride*	
	Alternaria tenuis			
	Aurobasidium pullulans			
	Chaetomium globosum			

Ubiquitous, occurring in at least 6 months with an importance index of 5 or more; differential, occurring in 3–5 months with an importance index of at least 5; accidental, all other important species

Among the different orders of Deuteromycetes, Moniliales was by far the most important group, contributing 74%–86% species to the class Deuteromycetes. The four families of Moniliales were represented by: Moniliaceae (55%–65%); Dematiaceae (12%–19%); Tuberculaceae (7%–16%). Ascomycetes and Phycomycetes accounted for less than 9% of the total species. The species found on the decomposing leaf litter over an annual cycle were categorized as: ubiquitous, occurring in at least 6 months with an importance value index of 5 or more; differential, occurring in 3–5 months with an importance value index of at least 5; and accidental, all other important species (Table 3).

Across all the forest sites, 14% species were ubiquitous, 20% differential, and 66% accidental.

Successional pattern and community character

The dominant primary colonizers of the litter were the same for all sites because litter taken from one tree was colonized by a specific community in all forest sites (Fig. 3). The primary colonizers were *Cladosporium herbarum,* and *Phoma hibernica.* In the mid-course of decomposition the dominant species were *Curvularia lunata* and *Aspergillus flavus* in the sal forest site; *Alternaria tenuis, Alternaria alternata,* and *Penicillum citrinum* in the pine-mixed broadleaf forest site; *Alternaria alternata, Alternaria tenuis,* and *Drechslera specifera* in the mixed oak-pine forest site; and *Alternaria alternata, Alternaria tenuis,* and *Penicillium negricans* in the mixed oak forest site. Thus, with the exception of the sal forest site, *Alternaria tenuis* and *Alternaria alternata* were dominant in all sites. At the late-successional stage, *Aspergillus niger* and *Trichoderma viride* were dominant in both the sal and the pine-mixed broadleaf forest sites; *Penicillium spinulosum* and *Paecilomyces varioti* in the pine forest site; *Penicillium negricans, P. variabile,* and *Aspergillus niger* in the mixed oak-pine forest site; and *Myrothecium roridum* and *Aspergillus niger* in the mixed oak forest site.

Both the species richness and species diversity (Shannon-Wiener Index) showed a trend similar to that of fungal population at each site (Figs. 4 and 5). Regardless of the rate of decomposition, both the species richness and the diversity of fungal species peaked in the 3rd or 4th month of decomposition at each site, i.e., when the fungal populations were also at a maximum. During the dry winter season, as decomposition slowed down and possibly as labile compounds became scarcer, both species richness and species diversity declined.

The fungal species recorded over an annual cycle and also the peak species number recorded reached a maximum in the sal forest site and a minimum in the pine forest site. The maximum β diversity (index of the rate of change in species during the course of decomposition) occurred in the sal forest site and the minimum in the pine forest site. The per cent weight loss of litter at the end of the annual cycle was positively related both to the β diversity (Fig. 6a) and the total number (Fig. 6b) of the fungal species recorded during the annual cycle.

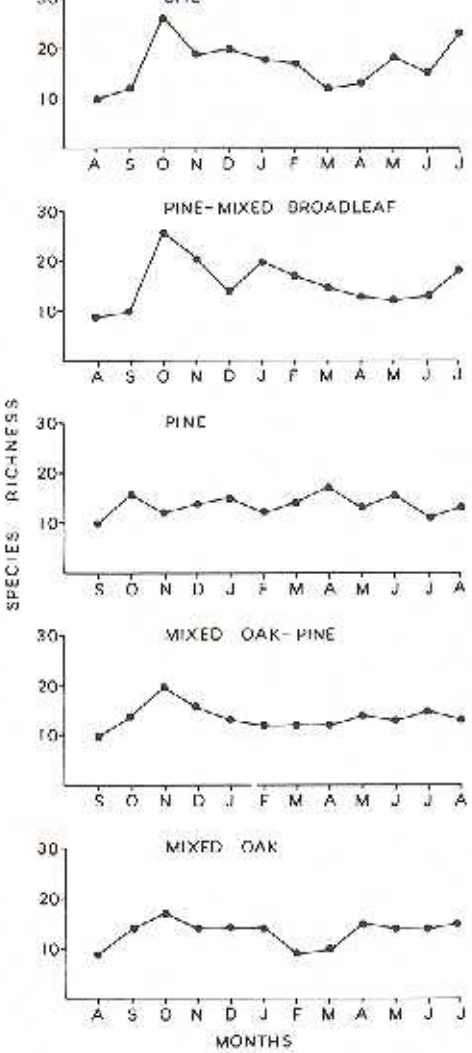

Fig. 4. Fungal species richness (number of species per sample of decomposing material) in different months on decomposing leaf litter (*Quercus leucotrichophora*) placed in different forest sites

It seems that the rate of change in the litter composition was initially rapid, compared with subsequent stages, for the temporal β diversity of fungal communities was distinctly higher during the initial period than during the later stages (Table 4).

Discussion

The lowest rate of decomposition for the pine forest site seems to be related to the adverse effects of the leaf litter of the dominant native species (*Pinus roxburghii*) and of frequent burning (Singh et al. 1984) on the development of fungal flora and fungal populations. The distinctly wider C:N ratio and the higher lignin content of pine-leaf litter, compared with the native dominant species of other forest sites (Upadhyay et al. 1989), seem to limit the decomposition of *Quercus leucotrichophora* leaf litter. In the mixed oak-pine forest site where decomposition is also slow, *P. roxburghii* is also one of the dominant spe-

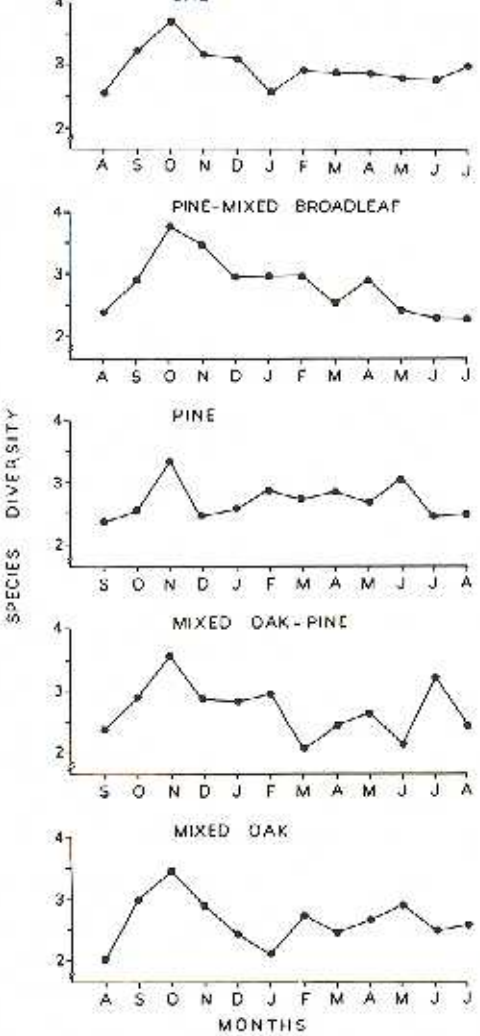

Fig. 5. Fungal species diversity (Shannon-Weiner index) in different months on decomposing leaf litter (*Quercus leucotrichophora*) placed in different forest sites

cies. In these forest sites both the fungal counts and the fungal species diversity were lower than in the other sites (Figs. 2 and 5). The resistant pine-leaf litter also appears to partly account for the lower populations of bacteria and actinomycetes (Upadhyay et al. 1985) and microarthropods (Upadhyay et al. 1985). Among the various

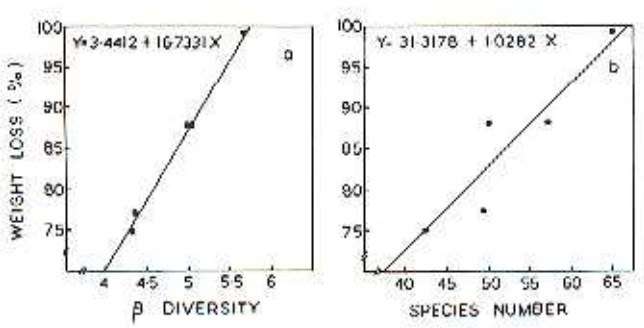

Fig. 6. Relationship between leaf-litter weight loss and (**a**) β diversity; (**b**) number of fungal species

Table 4. β Diversity of fungal species associated with decomposing oak leaf litter (*Quercus leucotrichophora*) at different forest sites in different seasons

Forest	Seasons		
	Rainy	Winter	Summer
Sal	2.09	1.35	2.03
Pine-mixed broadleaf	2.11	1.64	1.84
Pine	2.00	1.65	1.46
Mixed oak-pine	1.87	1.87	1.38
Mixed oak	1.77	1.61	1.68

sites, the most dissimilar fungal communities developed in the pine forest site. If climate were the sole determinant, the fungal community developing at this site should have been the most similar to those of other sites, for the climate of this site located in the mid-elevational part of the transect was of the intermediate type. To summarize, the fungal community developing on *Q. leucotrichophora* leaves is also dependent on the species reservoir of the habitat. If this is poor, the community on decomposing *Q. leucotrichophora* leaves will also be poor. The poor microflora at the pine forest site was due to the resistant nature of the surrounding leaf litter of native plant species which restricted decomposition.

The effect of native leaf litter on the development of fungal flora was also evident at the sal compared with the mixed oak forest sites. The climates of these two sites were the most dissimilar from each other (Fig. 1), but the similarity index between the fungal communities of decomposing litter at these two sites was the second highest among the values recorded (Table 5). The native litter that influenced the development of the fungal communities associated with decomposition was similar at both sites, the initial C : N ratio and the N content being 48.3 and 1%, respectively, for sal litter and 42.7 and 1.15% for oak litter; the soil C : N ratio was 7.5 for the sal forest site and 8.5 for the mixed oak forest site. This further indicates that the climatic variations within the present elevation transect are not wide enough to cause conspicuous differences in the fungal communities on the leaf litter, even at the extremes of elevation. Though the mean annual temperature declines with the elevational rise, temperatures in the highest sites, particularly during moist periods of the

Table 5. Similarity index (%) between fungal communities of decomposing oak leaf litter (*Quercus leucotrichophora*) placed at different forest sites

Sal × pine-mixed broadleaf	52.6
Sal × pine	18.4
Sal × mixed oak-pine	32.4
Sal × mixed oak	39.9
Pine-mixed broadleaf × pine	38.2
Pine-mixed boardleaf × mixed oak-pine	20.3
Pine-mixed broadleaf × mixed oak	23.8
Pine × mixed oak-pine	34.0
Pine × mixed oak	19.3
Mixed oak-pine × mixed oak	39.2

Average over all sampling dates

year, are not low enough to cause any drastic modification in the development of fungal communities compared with those developed at the lowest site.

The pattern of changes occurring in decomposing leaf litter is in contrast to the traditional succession described for green plants, in which resources such as nutrients and light do not decline either in quantity or quality. In fact, unless erosion is excessive, the nutrients, particularly N, may increase as a result of biofixation. At all the forest sites the overall pattern of fungal species richness and diversity on the decomposing material was broadly similar to that described by Hogg and Hudson (1966), Swift (1976), and Wicklow and Whittingham (1974), in which the species diversity declined continuously with the progressive decay of litter. This pattern of diversity is the reverse to that witnessed in the terrestrial succession of green plants where species diversity generally increases during the course of succession as a consequence of greater niche differentiation and widening of niche axes (Whittaker 1975).

The significant positive relation between the β diversity of species and the per cent annual weight loss of litter indicates that the rate of change in species composition over time has a marked influence on the rate of decomposition. This also emphasizes the fact that a particular group of fungi can bring about only a limited amount of decomposition and that the various decomposition steps are accomplished more efficiently when there are corresponding changes in the fungal species composition.

Mechanism of succession

The pattern of species change with progressive decay of the substrate was similar to that suggested by the tolerance model of Connel and Slatyer (1977). Of the species arriving on the bare litter substrate, only certain "early successional" species, possibly those adapted to occupy aerial leaf environments of the forest can establish themselves. The high β diversity indicates that the changes in species content occurred rapidly in the initial stage when a variety of physical and chemical changes occur in the litter (Swift 1976; Frankland 1981). As the litter environment is modified by the early colonizers, it becomes less suitable for them and more suitable for recruitment of late successional species, including the soil-borne taxa. In the present study the late successional species were those adapted to occupy the resistant substrate. Since our species descriptions were based on the spores, we can safely conclude that the species arriving in the later stages were not derived from the initial species pool, as suggested by the Initial Floristic Composition model (Egler 1954). We found broad overlaps between the fungal species populations that did not show parallel distribution (Fig. 2). This pattern is similar to that suggested by Gleason (1926) and Whittaker (1975) for the successional course of green plant communities.

Acknowledgment. The authors gratefully acknowledge financial support from the Department of Science and Technology, Government of India, New Delhi.

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