Chapter 3

Nutrient cycling by fungi in wet tropical forests

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Introduction

Fungi are primarily responsible for the recycling of mineral nutrients through decomposition of organic matter (Swift, Heal & Anderson, 1979) and the uptake and transfer of these nutrients into plants via mycorrhizal fungi (Janos, 1983). In addition, fungi and other soil microorganisms serve alternately as sources and sinks of labile nutrients that are necessary for plant growth (Marumoto, Anderson & Domsch 1983 Yang & Insam 1991). Thus, fungal and microbial biomass can control significant fractions of the labile nutrient pools in some humid and wet tropical forests (Marumoto et al., 1982; Lodge, 1985; Yang & Insam, 1991), and regulate the availability of nutrients that may limit plant growth (Jordan 1985; Hilton, 1987; Singh et al., 1989 Lee, Han & Jordan 1990 Behera Pati & Basu, 1991; Yang & Insam, 1991). The term biomass normally refers only to living organisms, but it is used more broadly in this chapter to refer to dead as well as living microorganisms as both contain nutrients.

Although humid tropical forests often have large stature and an abundance of vegetation, their growth and productivity is frequently limited by the availability of mineral nutrients. A diversity of soils occurs in the wet tropics so it is difficult to generalise about nutrient limitation. However, the availability of phosphorus to higher plants is generally limited because phosphorus combines with aluminium and iron oxides in the highly weathered soils to form insoluble complexes (Sanchez 1976). Elements such as nitrogen and potassium can be leached from ecosystems if the soil has little cation and anion exchange capacity (e.g. sands and highly weathered clay soils with low cation exchange capacity), and their availability may thus be quite low in a few tropical forests with high rainfall. Among wet tropical forests, limited availability of nitrogen appears to be most frequent in high elevation montane sites (Vitousek, 1984), but the causes are unknown. Other elements such as calcium and magnesium can be limiting in wet tropical forests (Cuevas & Medina...
1988), depending on the characteristics of the soil parent material and
degree of weathering. Cuevas & Medina (1988) found greater root 
production in response to small scale applications of nitrogen in Tall 
Caatinga and Low Bana forests, to phosphorus in Bana forest, and to both 
phosphorus and calcium in Tierra Firme Amazonian forests of Venezuela. 
Vitousek (1984) hypothesised that phosphorus availability limited 
litterfall in some wet tropical forests based on the ratio of litterfall mass 
to litterfall phosphorus content. The few experimental plot fertilisation 
studies made in wet tropical forests have shown increased leaf litter mass 
and sometimes wood production with nutrient addition in Venezuela 
(Tanner, Kapos & France, 1992; N and P), Hawaii (P.M. Vitousek, pers. 
comm.), and Puerto Rico (Zimmerman et al., 1992 complete nutrients), 
supporting the hypothesis that tree productivity is often limited by 
nutrient availability in these forests. The degree to which fungi and other 
microorganisms regulate the availability of limiting nutrients depends on 
the size of the labile nutrient pool, the quantity of fungal and microbial 
biomass, the fluctuations in fungal and other microbial biomass and its 
nutrient content through time (Hunt, Elliott & Walter, 1989).

In this Chapter, data on fungal and microbial biomass and nutrient 
contents, mostly from wet tropical forests, are compared. The tightness 
of nutrient cycling in wet and seasonally wet tropical forests is also 
discussed but with the emphasis on the role of saprotrophic rather than 
mycorrhizal fungi.

**Fungal biomass and nutrient stores**

Fungal biomass and total biomass of all microorganisms contain 
significant fractions of the labile nutrients in the forest floors of some 
tropical ecosystems (Marumoto et al., 1982; Srivastava & Singh, 1988; 
1984) and soil microbial biomass (Srivastava & Singh, 1988) to 
concentrate and store nutrients such as phosphorus when they are in short 
supply can accentuate the role of fungi and other microorganisms in 
regulating nutrient availability in nutrient depauperate sites. 
Furthermore, nutrients tend to be immobilised and thereby conserved by 
fungi and other microorganisms in their biomass during periods of high 
rainfall that cause leaching (Jordan, 1985 Hilton, 1987 Singh et al., 1989; 
Behera et al., 1991; Yang & Insam, 1991). Growth of higher plants in such 
systems may be dependent on nutrients released upon death and 
mineralisation of microbial biomass. Again, microorganisms can have 
relatively large effects relative to their biomass because microbial
activities and products can maintain phosphorus in plant-available forms in highly weathered ultisols with phosphorus-fixing clays (Lee et al., 1990).

**Fungal and total microbial biomass**

Relatively few publications contain estimates of fungal or total microbial biomass in wet tropical forests, and a variety of methods has been employed to make these estimations, none of them perfect under all conditions (see West, Ross & Cowling, 1986; Frankland, Dighton & Boddy, 1990). In addition, estimates made using different methods are often not directly comparable. For example, estimates obtained by fumigation followed by incubation (for measurement of carbon mineralised from the dead microorganisms; Jenkinson & Powlson, 1976) or extraction and measurement of microbial nitrogen (Brookes et al. 1985) are thought to reflect both active and dormant microbial biomass whereas estimates obtained through the substrate-induced respiration method (SIR, Anderson & Domsch 1978) are thought to reflect only the active microbial biomass. Again, the selective inhibition method (Anderson & Domsch 1973) is thought to measure biomass of only the active fungi or bacteria, whereas the most commonly employed direct observation methods detect active, dormant and dead fungi and bacteria. However, the various means of obtaining estimates of fungal and bacterial biomass are often within a factor of ten, and are useful in giving an indication of where the true value lies.

In this study, total (live plus dead) fungal volume was measured in litter and surface soil at two week intervals in subtropical wet forest located at El Verde in the Luquillo Experimental Forest of Puerto Rico (alt. 350 m) by direct observation using an agar film method (Lodge & Ingham, 1991; modified from Jones & Mollison, 1948). Soil samples were collected using a 12 cm diam. steel cylinder driven to 9 cm depth. Five samples were taken at preselected random coordinates on each date within a 1 ha plot. Initial samples were collected on 26 November 1984, and further samples were taken every two weeks from 11 February to 3 June 1985, with an additional sampling on 18 September. Measurements of hyphal lengths and frequency distributions of hyphal diameters among 7 classes were used to estimate fungal volumes per g of dry litter or soil, assuming that fungal hyphae are perfect cylinders. Hyphal diameter distributions were determined before drying the agar films to ensure that the hyphae were not collapsed. Conversion factors of 0.26 and 0.20 g cm⁻³ fungus were used to convert fungal volume into fungal biomass in litter and soil respectively (Lodge, 1987).
Fig. 1. Box plots showing cumulative weekly rainfall during the 7 days preceding sampling (a), number of days in the previous week with rainfall sufficient to reach the forest floor >3 mm (b), and fluctuations in fungal volume in the litter layer (c) and upper 9 cm of soil (d) in a subtropical wet forest in El Verde, Puerto Rico. Fungal data are expressed per gram oven dry litter or soil. Median values are shown by horizontal bars, the boxes contain the 25% of the variation on either side of the median, the bars extending from the boxes indicate variation (see McNeil, 1977), and extreme values are shown with an asterisk. Data for soil on date 112 and for litter on date 126 are missing (m). Data represent five samples on each date except for soil samples on dates 42, 152 and 261 (s, where \(n = 3\), 2, and 1 respectively).
Median fungal biovolume estimates for litter and soil on each date are shown by the bars within the box plots in Figs 1c and 1d respectively. Mean fungal biomass estimates for each sampling date were used to obtain overall mean fungal biomass estimates ± S.E.M. of 5.2 ± 2.4 mg fungus g⁻¹ leaf litter and 2.7 ± 2.7 mg fungus g⁻¹ soil in the upper 0-9 cm (Table 1). Fungal biomass was sometimes much higher in individual samples: up to 15.2 mg g⁻¹ litter and 9.7 mg g⁻¹ soil. All these extreme high values were from samples containing cords of decompose basidiomycetes and all but two were collected near decomposing wood.

Data on fungal and total microbial biomass in soil and litter from El Verde, Puerto Rico (described above) as well as from various other tropical and subtropical sites are compared in Table 1. The data cited from other sources are: Guzman, Puerto Rico, microbial N (L. M. Babilonia, pers. comm., 0-10 cm depth); El Verde, Puerto Rico, substrate-induced respiration (unpublished data of D. J. Lodge, C. E. Asbury, A. Masso & R. Pollit, 0-10 cm depth); Manãús, Brazil (Luizão, Bonde & Rosswall, 1992,0-5 and 5-20 cm depths); Hainan Island China (Chang & Insam 1991,0-12.5 cm depth); Orissa, India (Behera et al., 1991,0-3,3-8,8-13 and 13-18 cm depths, winter dry and summer monsoon seasons); pastures and grasslands in New Zealand, direct observations and fumigation incubation (from West et al., 1986, 0-7.5 cm depth, low number from dry season and high from wet season, no direct observations in wet season), while the substrate-induced respiration data for New Zealand are from Sparling et al. (1985, 0-5 cm depth). Ranges given in Table 1 include variation among seasons and soil depths. Calculations were performed to convert microbial carbon into microbial biomass for data from Puerto Rico, Brazil and China by assuming that microbial C is 0.4 x microbial biomass.

The estimates of total fungal biomass in soil at El Verde (means for each date ranging from 0.2 to 9.7 mg g⁻¹ soil) were high when compared with other tropical forests and grasslands (0.2 to 1 mg g⁻¹; Table 1). One comparable study of fungal biomass in tropical forest using direct observation was carried out in a seasonally dry monsoon forest in Orissa India where total fungal biomass varied from 0.2 to 0.4 mg g⁻¹ dry soil in the upper 0-7.5 cm horizon (Behera et al., 1991). Yang & Insam (1991) studied soil fungal biomass in another tropical monsoon forest in China using the selective inhibition method and obtained values for active fungal biomass (0.2 to 0.5 mg g⁻¹) that were comparable with the total fungal biomass estimates for monsoon forest in India (Behera et al., 1991). The only other published study of fungal biomass or volume in tropical forest known was that on a 22 year old native second growth forest in Puerto Rico (Lodge & Ingham, 1991) at ca 350 m altitude in Guzman near El Verde (Luquillo Experimental Forest Tropical Soil Biology and Fertility.
<table>
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<tr>
<th>Ecosystem</th>
<th>Fungal biomass</th>
<th>Biomass of all microorganisms</th>
<th>Microbial N</th>
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<td></td>
<td>Live &amp; dead</td>
<td>Active</td>
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<td><strong>Upper soil horizon</strong></td>
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<td>El Verde, Puerto Rico</td>
<td>(0.2-4.8)</td>
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Entries are mean values ± S.E. mg g⁻¹ oven dried litter or soil. ND = not done. SIR = substrate induced respiration. Figures in parentheses indicate range of values.
Programme plots). In this study using direct observation, Ingham examined soils from 0-5 cm depth and found hyphal lengths ten-fold greater than in temperate Douglas fir forest (Lodge & Ingham, 1991). These hyphal lengths were converted into hyphal volumes using mean hyphal diameter distributions for September and then to fungal mass, as above, to obtain an estimated 5·2 mg fungus cm\(^{-3}\) (6·1 mg g\(^{-1}\)) soil in the upper 5 cm (Table 1). These data suggest that fungal biomass is generally high in the subtropical wet forest life zone of Puerto Rico, and that the fungal biomass estimates for El Verde are probably not excessive.

Fungi comprise only a fraction of the soil microbial biomass. For example, fungi represented 21 to 41% of the active microbial biomass carbon in the monsoon tropical forest soils studied by Yang & Insam (1991). Thus, some check on the validity of fungal biomass estimates can be done by determining whether or not they are within an order of magnitude or less than the estimated biomass of all microorganisms. Data presented in Table 1 from an unpublished in situ substrate-induced respiration (SIR) experiment suggested that there were relatively large quantities of active microbial biomass in the upper 10 cm of soil at El Verde, which is consistent with the high values for fungal biomass. This experiment (D. J. Lodge, C. E. Asbury, R. Pollit & A. Masso, unpublished) was carried out using intact soil cores 25·4 cm diam. and 10 cm deep, rather than sieved soils, for two reasons. Firstly, previous attempts to use the SIR method on sieved soils resulted in declining levels of carbon dioxide evolution at all levels of glucose addition. This result occurred because of very high initial respiration induced as an artifact of sieving possibly because of exposure of new substrate surfaces or by disruption of fungal hyphae whose contents then fuelled respiration. Secondly, intact soil cores containing severed roots were used to mimic the conditions in soil nitrification tubes as well as in the forest following hurricane Hugo (after Hugo, mortality of fine roots was near 100% in the top 0 to 10 cm; Parrotta & Lodge, 1991). Each core was placed on a plastic funnel containing washed silica sand and replaced in its original hole. Respiration at 23°C was measured for 1 h before and 1 h after the addition of sugar by enclosing a trap of sodium hydroxide solution on the soil surface and then sealing the top of each tube with Mylar. The quantity of CO\(_2\) evolved was determined by titration of the NaOH in the CO\(_2\) traps. Weight of soil in the cores was estimated using a 5067 cm\(^3\) volume and a mean bulk density for ridge tabonuco forest sites of 0·77 g cm\(^{-3}\). Glucose (3·76 g) was added to each tube in 50 ml of water (1·51 mg C g\(^{-1}\) soil), and an equal volume of distilled water was added to the control cores (4 replicates per treatment).

Respiration rates of the soil microbial biomass of intact soil cores using the SIR method increased from 84·1 ± 33·9 to 610·0 ± 28·6 mg CO\(_2\)-C
m\textsuperscript{2}\textsuperscript{h}\textsuperscript{-1} in response to the addition of glucose solution whereas respiration in control tubes increased from 82.9 ± 19.8 to only 119.7 mg CO\textsubscript{2}\textsuperscript{-C} m\textsuperscript{2}\textsuperscript{h}\textsuperscript{-1} in response to addition of water. Active microbial biomass was estimated to be 25.6 ± 1.3 mg g\textsuperscript{-1} soil using the formula from Ocio & Brookes (1990), who added 1.6 mg glucose-C g\textsuperscript{-1} soil. This value is 10 times higher than soil microbial biomass estimated using the SIR method in temperate and subtropical pastures and grasslands in New Zealand (Sparling, West & Whale, 1985; Table 1) and 100 times higher than estimates from China in humid tropical forest on the island of Hainan (Yang & Insam, 1991; Table 1). The high soil organic carbon (3.9%) and the presence of dead roots and surface litter in the Puerto Rican study probably contributed to the high rates of microbial respiration, since microbial biomass and soil carbon are closely related (H. Insam, pers. comm.). The use of unsieved soils in Puerto Rico also differed from the other studies. However, Domsch \textit{et al.} (1979) have also reported that the SIR method gave high values for active fungal biomass compared with direct observation of total fungal biomass.

The flush of CO\textsubscript{2} evolution following reinoculation of fumigated soils (fumigation-incubation; FI) has been the most widely used method to determine live (active plus dormant) soil microbial biomass in tropical soils. Estimates of live soil microbial biomass obtained using FI have ranged from 0.8 to 4.2 mg microbial biomass g\textsuperscript{-1} surface soil (assuming 0.45 g C g\textsuperscript{-1} microbial biomass Table 1). The highest estimates of live microbial biomass were found in native second growth subtropical wet forest (2.8 to 3.4 mg g\textsuperscript{-1} soil) in Puerto Rico (personal observations using direct observation methods in Anderson & Ingram, 1989). Soil of a pine plantation in Puerto Rico (personal observations) and of a tropical humid forest in Manaus, Brazil (Luizão, Bonde & Rosswall, 1992) contained a similar or slightly lower amount of soil microbial biomass (1.9 to 2.4 and 1.6 to 4.2 mg g\textsuperscript{-1} soil). These data are consistent with the high estimates for total fungal biomass and active microbial biomass obtained for subtropical wet forest soils in Puerto Rico.

Total soil fungal biomass per square metre in wet and seasonally wet tropical forests was equal to or greater than fungal biomass in temperate forests. Among the tropical forest sites, Behera \textit{et al.} (1991) found 116 g m\textsuperscript{-2} total soil fungal biomass from 0 to 23 cm depth in India; Yang & Insam (1991) found 8 to 80 g m\textsuperscript{-2} active fungal biomass from 0 to 12.5 cm depth in China and this study found total fungal biomass of 14 to 333 g m\textsuperscript{-2} (mean 207 g m\textsuperscript{-2}) from 0 to 9 cm depth at El Verde and 260 g m\textsuperscript{-2} from 0 to 5 cm depth at Guzman in Puerto Rico. Among the studies summarized by Kjøller & Struwe (1982), estimates of total fungal biomass for temperate woodlands ranged from 16 to 51 g m\textsuperscript{-2} in the 0 to 10 cm horizon and 20 to 112 g m\textsuperscript{-2} in the 0 to 20 cm horizon. There are few studies of fungal biomass
in litter, but this study found 1 to 5 g fungus m$^{-2}$ at El verde in Puerto Rico (9 yr mean litter mass of 525 g m$^{-2}$; Lugo, 1992) which was comparable to the values of 1.3 and 8.0 g m$^{-2}$ determined for litter of deciduous woodlands in the U.K. (Meathop Wood; J. C. Frankland, cited in Kjøller & Struwe, 1982) and the U.S.A. (Liriodendron forest; Witkamp, 1974), respectively.
**Fungi and nutrient availability**

Data from the study of a subtropical wet forest at El Verde in Puerto Rico suggest that fungi can ‘control’ a substantial proportion of the phosphorus in the litter layer. Total fungal biomass in litter was relatively large in this forest (mean, 0.2 to 1% of the litter dry weight, some samples up to 3.6%; Fig. 1c, Table 1). Based on litter and basidiomycete nutrient concentrations (Lodge, 1987) and on the biomass data above, a mean of 22.2% of the litter P and 3.7% of the litter K could have been immobilized in fungal biomass (Fig. 2c). Phosphorus immobilization by fungi in the Luquillo Experimental Forest was considerable because leaf decompose fungi maintained P concentrations (4.99 to 35.66 mg g\(^{-1}\); Lodge, 1987) that were much greater than P concentrations in fresh leaf litter (0.25 to 0.42 mg g\(^{-1}\); Lodge et al., 1991). Phosphorus concentrations in litter fungi can increase by 10-fold (Lodge, 1987) and the biomass can vary greatly with time (Fig. 1c), so the proportion of forest floor P in fungal biomass may vary from 3% to 85%. The variation in both fungal biomass and fungal P concentrations therefore may have regulated P availability and the timing of nutrient mineralization from leaf litter in this forest.

Fungi may also have controlled a significant fraction of labile nutrient pools in the upper 0 to 9 cm of mineral soil at El Verde in Puerto Rico. Estimates of soil fungal biomass per g of soil (Table 1) and mean nutrient concentrations in field-collected fungal mycelia (Lodge, 1987) were used to calculate the quantities of nutrients stored in the upper 9 cm at El Verde. Mean fungal biomass was 2.7 mg g\(^{-1}\) in the upper 9 cm of soil (range 0.2 to 4.8 mg g\(^{-1}\)). Assuming that the appropriate specific fungal density (0.2 g cm\(^{-3}\)) and nutrient concentrations were applied, fungal nutrient stores in the upper 9 cm of soil at El Verde were 7 to 178 \(\mu g\) N g\(^{-1}\), 2 to 40 \(\mu g\) P g\(^{-1}\), 1 to 24 \(\mu g\) K g\(^{-1}\), 1 to 17 \(\mu g\) Mg g\(^{-1}\), and 8 to 189 \(\mu g\) Ca g\(^{-1}\). These fungal nutrient stores represent 0.8 to 20% of the Olson-extractable phosphorus from dried soils, and 24%. of the total soil calcium but only 0.5% of the nitrogen, 3.5% of the extractable soil potassium, and 3% of the magnesium in the upper 10 cm of soil (soil nutrient data from Odum, 1970; Fig. 2). The percent extractable soil P held in fungal biomass at the Puerto Rican site (0.8 to 20%) was similar to the percent of soil organic P in all microbial biomass of a monsoon forest woodland and a teak plantation in India (9 to 12%; Srivastava & Singh, 1988). Fungal control of the labile pools of soil phosphorus is probably significant in regulating soil fertility in the Puerto Rican forest. Fluctuations in fungal and microbial biomass may well determine whether such biomass acts as a net sink for nutrients or as a potential source of nutrients for plants.
Fluctuations in fungal and microbial biomass with moisture conditions are common even in non-seasonal and slightly seasonal wet tropical forests. Fungal biomass was found to change significantly between sampling dates both in the litter and in the soil at El Verde in Puerto Rico (Fig. 1; $P = 0.001$, and $P = 0.008$ for litter and soil respectively Kruskal-Wallis one-way non-parametric ANOVA). Similar fluctuations were observed in monsoon tropical forests by Yang & Isham (1991) in China and by Behera et al. (1991) in India. At El Verde in Puerto Rico, fungal biomass in both litter and soil were significantly correlated with percent moisture in the substratum ($P = 0.038$ and $0.001$, respectively Fig. 1). Fungal biomass in litter was also strongly related to the number of days in the preceding week in which rainfall was sufficient to reach the forest floor (3 mm; Wilcoxon Signed Ranks test, $P < 0.001$) but not with the cumulative amount of rainfall in the preceding week (linear regression; $P = 0.27$). These fluctuations in fungal and microbial biomass can be very rapid, especially in the litter layer, and can result in pulses of nutrient mineralisation.

Raghubanshi et al. (1990) and Singh et al. (1989) showed that the pulsed release of nutrients by death and mineralisation of the microbial biomass during the first 4 weeks of the rainy season closely synchronised with rapid plant uptake and growth in Indian monsoon forest. Similarly, a study of fungal biomass in another Indian monsoon forest (Behera et al., 1991) and in a slightly seasonal humid forest on Hainan Island in China (Yang & Insam, 1991) both showed that fungal biomass was directly related to soil moisture. In both studies cited above, the authors attributed the conservation of nutrients against losses during the rainy season to immobilisation of nutrients in fungal and other microbial biomass. Yang & Insam (1991) found that soil microbial biomass was related to the abundance of decomposable organic matter as well as soil moisture. Root activity, as measured by $^{32}$P uptake, also reached an annual maximum soon after the first rain at the end of the dry season in a seasonal African forest (FAO/IAEA 1975). Root production was frequently greatest at the beginning of the rainy season at La Selva (R. Sanford, pers. comm.), and at Barrow Colorado Island in Panama there were two peaks in root production which corresponded with peaks in nutrient leaching from litter during both transitions between wet and dry seasons (J. Wright, pers. comm.).

The proportion of nutrients available for plant growth may differ, depending upon timing and whether the nutrients are released in large
bursts or gradually at low concentrations. The studies cited above suggest that massive bursts can occur, especially in transitions between wet and dry periods. According to the current paradigm, plants cannot compete effectively with saprotrophic microbes for limiting nutrients (Elliott et al., 1989). When nutrients are released in large pulses, they may saturate the immobilisation capacity of the existing soil microbial biomass. Therefore, proportionately more nutrients may be available to higher plants when mineralisation is a pulsed rather than being a gradual process of release. Alternatively, such pulsed nutrient release might also increase the susceptibility of nitrogen to leaching losses or the completing of phosphorus with iron and aluminium in highly weathered soils.

Asynchrony of nutrient mineralisation with plant uptake may lead to net nutrient export from the ecosystem via leaching (Frankland, 1982) or loss from the biotic system via chemical fixation into aluminium and iron oxides (Sanchez, 1976). Consequently, both the INTECOL Tropical Biology Workshop (Hayes & Cooley 1987) and the Tropical Soil Biology and Fertility Programme (Anderson & Ingram, 1989) have emphasised the importance of the timing of nutrient release. Lack of synchrony between nitrogen mineralisation and root uptake in mountain forests of northeastern Puerto Rico following hurricane Hugo may have resulted in significant nitrogen losses from these ecosystems (Lodge & McDowell, 1991). The virtual absence of shallow fine roots for three months following the hurricane (Parrotta & Lodge, 1991) at the time when nitrogen was mineralised from large quantities of hurricane litter may have accelerated export of stream nitrogen and denitrification (Steudler et al., 1991). After a temporary disappearance of nitrate from stream waters (probably by microbial immobilisation) nitrate concentrations increased 10-fold in streams draining the subtropical wet forest (C. Asbury, pers. comm.).

**Nutrient conservation by fungi in wet tropical forests**

Since fungi can physically translocate nutrients among resources that are separated in space (Thompson & Rayner, 1983 Thompson, 1984), they tend to conserve limiting nutrients more tightly than other microorganisms. Temperate wood-decomposing fungi have been found to incorporate most of the nitrogen and phosphorus of one food base and then translocate up to 81% of the original nitrogen and phosphorus into a new food base via hyphal cords (Watkinson, 1971; 1984), rather than releasing these nutrients upon death when the availability of carbon in their resource base becomes limiting. The translocation of limiting nutrients causes a short circuit in the nutrient cycle whereby nutrients are
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re-immobilised by fungi rather than being mineralised in a form available to plants. Thus, wood-decomposing fungi can influence the availability of nutrients to higher plants. Wells, Hughes & Boddy (1991) found that phosphorus was translocated from soil to wood by temperate wood decomposer fungi and the same phenomenon apparently occurs in wet subtropical forest of Puerto Rico. Zimmerman et al. (1992) recorded significantly lower forest productivity as measured by rates of leaf litterfall 1·5 to 2 years after hurricane Hugo in control plots compared to plots in which all the fine and woody hurricane litter had been removed. Simulation modeling using the Century model (Partow 1988; Sanford et al., 1991) for tropical forests indicated that immobilisation of phosphorus by fungi in the ‘hurricane-downed’ wood (and presumably translocation of phosphorus from soil to wood) was responsible for less productivity in the control plots (W. Parton & R. Sanford, pers. comm.). It is probably not coincidental that in this study all but two of the extremely high values for fungal biomass were in samples of both litter and soil (Table 1) taken close to decomposing wood, and that cords and mycelia of wood-decomposing basidiomycetes were observed in these samples. Nutrient recycling between resource bases also occurs among fungi that decompose leaf litter in the tropics where the phosphorus content of the leaf litter is extremely low. The generally low availability of phosphorus in many wet tropical soils is associated with lower phosphorus concentrations in foliage and greater nutrient retranslocation during senescence (Vitousek & Sanford, 1986). For example, retranslocation of leaf phosphorus before abscission in subtropical wet forest of Puerto Rico was estimated as 72%. This was calculated from nutrient concentration data of Odum (1970) and Medina, Cuevas & Weaver (1981), using the formula of Vitousek & Sanford (1986) which includes ratios of phosphorus to calcium to control for declines in leaf specific gravity during leaf senescence, because calcium is not retranslocated and thus remains constant. As a consequence of differences in nutrient retention by plants, concentrations of phosphorus in the leaf litterfall of many wet tropical forests are ten times lower than concentrations in leaf litter of temperate forests (Vitousek, 1984). For example, mean concentrations of phosphorus in leaf litterfall are 0-24 to 0-42 mg g⁻¹ in subtropical wet and lower montane rain forest of Puerto Rico (Lodge et al., 1991; Lugo, 1992), while concentrations of phosphorus in individual litter species can be even lower: 0-16 mg g⁻¹ in Dacryodes excelsa Vahl. leaves, the dominant tree of subtropical wet forest in Puerto Rico (Odum, 1970), and 0-27 mg g⁻¹ in Ficus fistulosa Reinw.: Blume leaves in Hong Kong (Lam & Dudgeon 1985).

Several species of agaric decomposers from Puerto Rico were found to translocate ³²P from partially decomposed leaf litter into freshly fallen
Fig. 3. Percentage of the original mass of nitrogen (a & b) and phosphorus remaining (c & d) in decomposing leaf litter enclosed in 1 mm-mesh bags placed in two plots (3 & 3x, shown with closed circles and open squares, respectively) at El Verde, Puerto Rico. Fresh litter from a 1 ha plot (plot 3) was placed in bags and was distributed in the same plot (3), as well as in a small, 10 x 10 m uniform plot nearby (plot 3x) during October (a & c) and March (b & d). (Carol P. Zucca, unpublished data). Arrows point to important accumulations of nitrogen or phosphorus in litter during the early stages of decomposition (a, c & d), although some nutrient accumulations are preceded by a leaching phase (c & d).

unlabeled leaves through rhizomorphs and hyphal cords across a 4 mm gap (personal observations). Translocation rates varied among species, and in some cases were quite high. The translocating structures of these litter fungi also contribute to nutrient conservation in mountainous wet tropical forests when they bind the thin litter layer into a mat, thereby protecting the forest floor and surface soil from loss of nutrients by erosion during heavy rains (Lodge & Asbury, 1988). Rainfall in these forests is typically 2500-3000 mm yr⁻¹.

Nutrient translocation by decompose fungi probably accounts for much of the increase in nutrient content (% of initial nutrient mass remaining) observed during the first 3 to 8 weeks of leaf litter
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decomposition in wet tropical forests, although depositions from the canopy and N-fixation could be partly responsible. C.P. Zucca (pers. comm.; Fig. 3) found increases in phosphorus content of freshly fallen mixed leaf litter of 120 to 140% at El Verde in the Luquillo Experimental Forest of Puerto Rico during the first 6 weeks of decomposition. Similarly, a litterbag study of *F. fistulosa* leaves in Hong Kong indicated that phosphorus content increased 135% to 150% above the initial content after 12 to 18 days of decomposition (Lam & Dudgeon 1985; data reanalyses by Lodge (1989) to obtain % initial content remaining).

Nitrogen is apparently translocated by leaf-decomposing fungi in some wet tropical forests but not in others. For example, C. P. Zucca (pers. comm.; Fig. 3) found increases in nitrogen content of leaf litter up to 128% of initial nitrogen during decomposition in Puerto Rico, when freshly fallen mixed litter was placed in one area (plot 3x; Fig. 3) but not when the same litter was placed in another area (plot 3; Fig. 3). Cuevas & Medina (1988) showed an increase in nitrogen content of decomposing leaves of 110% to 160% during the first 10 weeks of decomposition in three types of Amazonian forest in the Rio Negro area of Venezuela (Tierra Firme, Caatinga, and especially in Low Bana forest types) but little change in phosphorus (probably a small net loss). Lam & Dudgeon’s data (1985; Lodge, 1989) showed an initial leaching loss followed by a 150% increase in nitrogen content of *Ficus* leaves between the 8th and 18th day of decomposition.

That mycorrhizas associated with the litter layer in tropical forests take up phosphorus and other nutrients released from leaf litter has been well documented, but whether mycorrhizal fungi in association with plant roots are capable of decomposing leaf litter to obtain nutrients (i.e. direct nutrient cycling, Went & Stark, 1968a, b) is highly controversial (Janos 1987). In subtropical wet forest of Puerto Rico, the appearance of mycorrhizas inside leaf litter bags after about 6-8 weeks of decomposition coincides with increased rates of nutrient loss from the litter (C. Zucca, pers. comm.). Cuevas & Medina (1988) showed in Venezuela that permanent or intermittent separation of leaf litter decomposition bags from the soil substratum to prevent root penetration or attachment greatly reduced the rate of disappearance of phosphorus, calcium and magnesium in Tierra Firme forest. This treatment lowered the mass loss rate only slightly in the Tall Caatinga forest type, an effect that may be unrelated to the activity of mycorrhizal fungi. Elliott et al. (1989) applied *P* tracer to leaf litter in a vesicular-arbuscular mycorrhizal (VAM) coastal rainforest in northeastern Brazil, and found that 20% to 70% was apparently initially absorbed by saprotrophic microorganisms in humus, 0·1 to 57% was found in the upper 0 to 5 cm of mineral soil, and only 5% was removed by the mycorrhizas. They suggested that VAM fungi do not
compete effectively for nutrients against saprotrophic microbes in the litter layer. In contrast, the Amazonian white sands vegetation studied by Went & Stark (1968a, b) was dominated by ectotrophic rather than VAM plants, but as yet there are no definitive studies of direct nutrient cycling by this very different group of fungi in tropical forests. Evidence from laboratory experiments shows that some of the basidiomycetes that form ectomycorrhizas with temperate forest trees obtain organic forms of nitrogen directly from organic matter (Read, Lake & Langdale, 1989), lending credence to the Went & Stark (1968a, b) hypothesis of direct nutrient cycling in ectotrophic tropical forests. However, most wet tropical forests are dominated by VAM plants (Janos, 1989). Nutrient cycling is nevertheless tight in these VAM forests where any superficial root mats are the first to take up nutrients mineralised upon death of saprotrophic microbes. For example, at El Verde in Puerto Rico, eventual uptake by mycorrhizas of radioactive phosphorus applied to the litter layer was 10 to 20 times greater than the amount transferred to soil (Luse, 1970).

Conclusions

From these studies it can be concluded that fungi are important in controlling the availability of nutrients to plants in wet and seasonally wet tropical forests. VAM root mats were very efficient in absorbing nutrients mineralized from the litter mat (Luse, 1970; Cuevas & Medina, 1988; Elliott et al., 1989), but mineralisation of nutrients from litter was apparently due to the activity of saprotrophic rather than VAM fungi (Elliott et al., 1989). Both litter- and wood-decomposer fungi in tropical forests translocated nutrients among resource bases, thereby accentuating their ability to immobilise nutrients important for plant growth. Fungi comprised 0.03 to 1.7% (mean 5.2 mg g⁻¹) of the mass of the litter layer of a wet forest in Puerto Rico, accounting for up to one third to two thirds of the phosphorus on the forest floor. Soil fungal biomass ranged from 0.02 to 1.3% of the surface soil dry weight (mean 2.7 mg g⁻¹) accounting for 24% of the extractable soil Ca and up to 20% of the labile soil phosphorus in Puerto Rico. Biomass of fungi in wet tropical forests in China (Yang & Insam, 1991), India (Behera et al., 1991), and Puerto Rico was similar or greater than fungal biomass in temperate forests (Witkamp, 1974; Kjøller & Struwe, 1982). Fungal and other microbial biomass fluctuated rapidly in response to wetting and drying cycles even in non-seasonal tropical forests. Such fluctuations in fungal biomass may have resulted in net nutrient immobilisation followed by pulses of
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mineralisation. Thus, fungi may influence nutrient uptake by plants or losses from the ecosystem by the timing of nutrient immobilization and mineralization. Immobilisation of nutrients by fungi was highest in the rain season, which may have helped to conserve nutrients against leaching (Behera et al., 1991; Yang & Insam, 1991), whereas mineralization of nutrients from microbial biomass synchronized with fine root production in seasonally wet forests contributed to tight nutrient cycling.

Fungi were found to play other important roles in nutrient cycles of tropical forests in addition to immobilizing and mineralizing nutrients from organic matter and aided uptake of plant nutrients. For example, Lee & Jordan (1990) found that the activities and products of fungi and other microorganisms kept phosphorus in labile forms, thus conserving it against leaching and fixation onto weathered clay. In addition, Lodge & Asbury (1988) showed that rhizomorphs and cords of litter decomposers helped to retain litter and soil organic matter on steep slopes during heavy rains thereby reducing erosion. Thus, the importance of fungi in nutrient cycling in wet and seasonally wet tropical forests far exceeds that due to the quantity of nutrients held in fungal biomass.

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References


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