Distribution and Role of Mat-Forming Saprobic Basidiomycetes in a Tropical Forest* † ‡

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Abstract

This chapter provides a brief synopsis of previous studies on the ecology of agaric decomposers that form litter 'mats' in tropical forests, augmented by data from temperate forest studies. Description of several experiments in tropical forests of the Luquillo Mountains in Puerto Rico is included. These studies showed higher rates of mass loss in leaves that were decomposed on basidiomycete mycelia (i.e., white-rot) than in the absence of

basidiomycetes. The density of litter mats that were bound by basidiomycetes decreased with elevation and increased with slope. Addition of nitrogen inhibited mycelial growth. Capture of new litter by basidiomycetes was inhibited by nitrogen at high elevation. Litter-binding basidiomycetes exhibited differential responses to moisture, associated with full and partial shades. *Micromphale bevipes* was the only species that grew better in partial than in full shade. *Marasmius crinis-equi* had the highest rates of new attachments to litter in both full and partial shade, and was considered most suitable for use in restoration of steep road cuts and landslides to reduce erosion.

1. INTRODUCTION

Colonies of saprobic basidiomycetes in the Agaricales commonly bind leaf litter together in both tropical and temperate forests. These fungi regulate nutrient cycling and rates of decomposition, and their litter-binding activity reduces erosion on steep slopes in forests where they are abundant. Published research on the ecology of basidiomycete litter mats is summarized here. While most of the previous work on decomposer basidiomycete ecology has been conducted in temperate zones, the principles are essentially the same in the tropics—it is primarily the relative strengths of various ecosystem drivers and flux rates that differ between temperate and tropical forests.

A series of experiments that examined the ecology of basidiomycete litter decomposers in a montane forest on the Caribbean island of Puerto Rico are described: (1) comparison of early leaf decomposition rates with different levels of basidiomycete-induced white-rot; (2) a survey of basidiomycete litter mat abundance along an elevation gradient in the Luquillo Mountains; (3) mycelial mat movements in relation to slope; (4) basidiomycete mat growth and litter trapping rate in response to nitrogen addition; and (5) effects of shading and associated moisture on four litter-binding basidiomycetes, that was part of an experiment testing use of fungal mats to control erosion.

2. THE ROLE OF BASIDIOMYCETE LITTER DECOMPOSERS IN NUTRIENT CYCLING

In temperate and boreal forests, fungi play an important role in ecosystems by decomposing organic matter, thereby releasing nutrients that then become available to plants (Swift *et al.*, 1979; Beare *et al.*, 1992). Unlike most other fungi, basidiomycetes have enzymes that enable them to delignify 'low-quality' litter with high lignin and low nutrient content (Hintikka, 1970; Carreiro *et al.*, 2000; see Chapters 3 and 10). Non-unit-restricted basidiomycetes (i.e., those that grow from one resource in search of others; Chapter 1) have the potential to colonize and degrade low-quality resources more rapidly than unit-restricted fungi, by translocating nutrients from partly decomposed resources, enabling them to build biomass in new resources that are deficient in nutrients (Swift, 1977;

Frankland, 1982; Watkinson, 1984; Chapters 2, 10 and 11). This is equally the case in tropical systems (Lodge, 1993; Lodge *et al.*, 1994).

3. BASIDIOMYCETE EFFECTS ON DECOMPOSITION RATES

Most studies on effects of basidiomycetes on leaf decomposition have been from temperate zones, specifically in relation to the inhibitory effects of exogenous nitrogen inputs on rates of decomposition of high lignin resources (Magill and Aber, 1988; Berg and Matzner, 1997; Carreiro *et al.*, 2000; Hobbie and Vitousek, 2000) or on enzymes involved in delignification (Fenn and Kirk, 1981; Kirk and Farrell, 1987; Carreiro *et al.*, 2000; Waldrop *et al.*, 2004; Chapter 2 and 10). Several temperate zone studies examined effects of fungal enzyme systems on rates of leaf decomposition (Cromack and Caldwell, 1992; Osono and Takeda, 2002; Chapter 10), but there have been few studies on tropical basidiomycete (Urairuj *et al.*, 2003; Chapter 2). Santana *et al.* (2005) found that basidiomycetes significantly increased rates of decomposition in low-quality leaf litter by 22% beyond that caused by microfungi alone in a microcosm experiment in Puerto Rico.

Similarly, white-rot basidiomycetes significantly increased the rate of mass loss during a field experiment in a secondary wet subtropical forest at Sabana in the Luquillo Mountains of Puerto Rico (D.J. Lodge *et al.*, unpublished). A natural mixture of freshly fallen leaves (10 g fresh mass = 4.0 g oven dry mass) was allowed to decompose for 3 months beginning in mid-June 2004 (rainy season). In paired comparisons, after 3 months, decay of litter placed on white-rot litter basidiomycete mats was 8.4% greater than on adjacent (<50 cm away) forest floor lacking mats (12 pairs; Figure 1).

The acceleration of early leaf decomposition by some basidiomycetes may be partly attributed to their capacity to colonize rapidly and translocate nutrients, via rhizomorphs and cords, which allows them to build biomass quickly in new
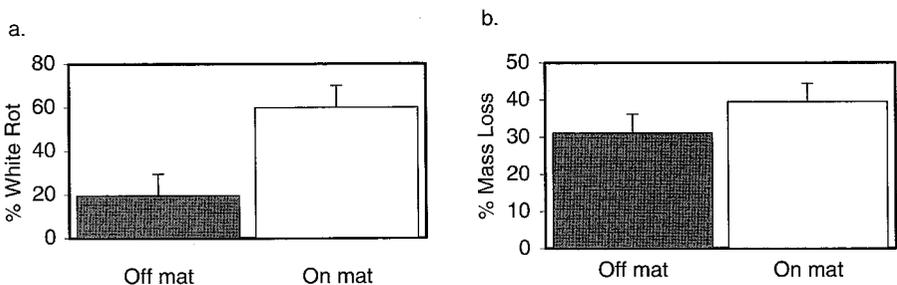
Figure 1 Percent white-rot and mass loss in freshly fallen leaves that were decomposed in wet subtropical forest in Puerto Rico for 3 months situated on or off (<50 cm away) litter mats formed by white-rot basidiomycetes. Percent of leaf area with white-rot was estimated visually twice using calibrated leaf models. (a) Percent of leaf area affected by white-rot on and off of basidiomycete litter mats. (b) Percent mass loss on and off of basidiomycete litter mats. The difference in rate of mass loss between treatments was significant (paired *t*-test, *P* = 0.0028).

resources where nutrients are in short supply (Hintikka, 1970; Lodge, 1993; Carreiro *et al.*, 2000; Chapters 1, 3 and 10). Nutrient translocation by basidiomycetes may be largely responsible for early increases in nutrient content beyond 100% of the initial content in some tropical studies (Lodge, 1993; Lodge *et al.*, 1994). In temperate leaf litter nitrogen is generally in short supply, whereas phosphorus is more limiting in low elevation tropical forests, and both N and P may be cycled tightly in tropical montane forests (Vitousek, 1984).

At least part of the increased rate of decomposition we observed when litter was placed on basidiomycete mats could be attributed to the greater ligninolytic capacities of basidiomycetes compared to microfungi (Cromack and Caldwell, 1992; Chapter 2). Santana *et al.* (2005) found a similar increase in leaf mass loss beyond that caused by microfungi alone in microcosms that contained ligninolytic basidiomycetes. Similarly, fungi with ligninolytic capabilities caused the greatest mass loss in a comparison of litter fungi from a temperate deciduous forest in Japan (Osono and Takeda, 2002), and in a comparison of tropical endophytic fungi (Urairuj *et al.*, 2003). Most microfungi present in litter are anamorphic states of ascomycetes that lack ligninolytic enzymes, but species of Xylariaceae do have the ability to decompose lignocellulose (Osono and Takeda, 2002; Urairuj *et al.*, 2003).

4. LITTER MAT ABUNDANCE ALONG AN ELEVATION GRADIENT

Percent of ground covered by basidiomycete litter mats, and extent of individual mats, was assessed along an elevation gradient in the Luquillo Experimental Forest (from 8 June to 4 July 1994; rainy season), by examining leaves along transects to determine if they were attached to surrounding litter by hyphal strands, cords, rhizomorphs or holdfasts (D.J. Lodge *et al.*, unpublished). The percentage of ground covered by litter mats generally increased with slope and decreased with elevation (Figure 2).

The decrease in mat cover with elevation was not constant, however, and there was a strong dip associated with the cloud condensation level at ca. 600 m above sea level (asl) in the Palo Colorado forest type, independent of slope (Figure 2).

Inputs from leaf litter fall decreased sharply in elfin forest at high elevation in the Luquillo Mountains (Weaver *et al.*, 1986; Lodge *et al.*, 1991). The litter layer in high-elevation forests is discontinuous and thin (Weaver *et al.*, 1986) — a condition unfavorable to basidiomycetes that require a nearly continuous layer of litter on the forest floor to maintain their mycelia and incorporate new resources rapidly. Most of the basidiomycetes that formed litter mats in Palo Colorado and elfin forest bound litter that was in direct contact, and lacked rhizomorphs and cords. Adding litter to the forest floor significantly increased the number of rhizomorphs and cords in a forest at lower elevation in the Luquillo Mountains (D.J. Lodge, unpublished data), indicating that litter depth and supply rate influence mat-forming basidiomycetes. It is not known why a dip in litter mat cover occurred ~600 m asl, but there are corresponding boundaries in plant
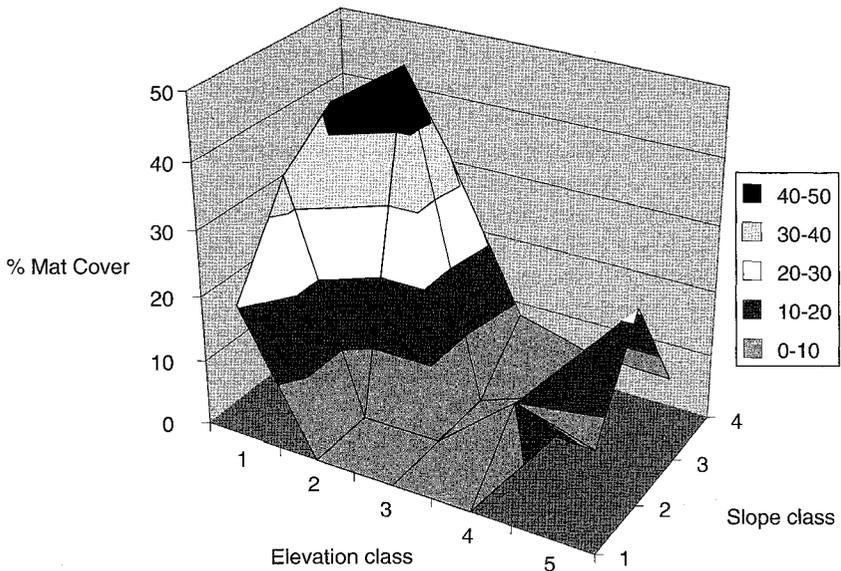
Figure 2 Percent of land area covered by decomposer basidiomycete litter mats as a function of slope (percent) and elevation along three 5–30 m transects, in the Luquillo Mountains of Puerto Rico, laid from ridge crest to stream bank at 50 m intervals along an elevation gradient from 150 to 1,000 m asl. Samples were divided into the following classes, with sample sizes (n) in parentheses. Elevation classes were: (1) 150–300 m (n = 5); (2) 301–450 m (n = 8); (3) 451–600 (n = 3); (4) 601–750 m (n = 8); (5) 751–1,000 m (n = 10). Slope classes were: (1) 0–10%; (2) 11–20%; (3) 21–30%; (4) 31–40%; (5) 41–50%.

species ranges at this elevation (J. Barone, J.K. Zimmermann, J. Thomlinson, N.L. Brokaw and P. Anglada, unpublished data).

The increase in litter mat cover with increasing slope (Figure 2) was probably influenced by two factors. First, many of the shallower slopes were near stream channels that overflowed during storms, disrupting the mats. Second, litter accumulated on the upslope sides of mats located on steep slopes, providing a concentration of new resources (see below).

## 5. EFFECTS OF NITROGEN ADDITION ON LITTER BASIDIOMYCETES

Forests are increasingly affected by nitrogen inputs from air pollutants. Several studies have focused on the effects of nitrogen additions from fertilizer or actual or simulated air pollutants on litter decomposition in tropical (Hobbie and Vitousek, 2000) as well as temperate forests (Magill and Aber, 1988; Berg and Matzner, 1997; Carreiro et al., 2000; Schröter et al., 2003; Gallo et al., 2004; Waldrop et al., 2004; Chapter 10). High nitrogen concentrations can have paradoxical effects on litter decomposition rates, accelerating decay of labile components while inhibiting decay of recalcitrant highly lignified components in both temperate (Fog, 1988; Carreiro et al., 2000; Wardle, 2000) and tropical forests (Hobbie

and Vitousek, 2000). Nitrogen additions often inhibit basidiomycete production or activity of ligninolytic enzymes during decomposition of refractory organic material (Kirk and Farrell, 1987; Cromack and Caldwell, 1992; Carreiro et al., 2000; Gallo et al., 2004; Waldrop et al., 2004). Shifts in the composition of a basidiomycete decomposer community in response to nitrogen additions may reflect reduced competitive advantage of fungi that produce hyphal cords and rhizomorphs able to translocate nutrients into nutrient-depauperate food bases (Cromack and Caldwell, 1992; Boddy, 1993; Lodge, 1993). Cords and rhizomorphs of basidiomycete decomposers disappeared from the litter layer of plots receiving complete fertilization (macro- and micronutrients) in Puerto Rico (Lodge, 1993). Such losses of cord and rhizomorph systems may accelerate losses of soil organic matter and nutrients on steep slopes (Lodge and Asbury, 1988; Lodge, 1993; Miller and Lodge, 1997).

The effects of nitrogen addition on basidiomycete litter decomposers were studied at two sites in the Luquillo Experimental Forest in Puerto Rico (D.J. Lodge et al., unpublished). The Bisley watershed (18°18'58"N, 65°44'10"W) was a low-elevation (250–300 m asl) subtropical wet forest that received ~3,500 mm of rain per year. This was a late secondary forest in which the native forest was characterized by tabonuco trees (Dacryodes excelsa), but there was an abundance of nitrogen-fixing trees in the Fabaceae (Inga vera) that had been planted as overstorey for a coffee plantation. The Icacos site (18°16'32"N, 65°47'4"W) was a high-elevation (620 m asl) lower montane rainforest characterized by Palo Colorado trees (Cyrilla antillana) that received 4,000–4,500 mm of rain per year.

At each location, three pairs of plots (nitrogen addition and control) were matched for slope, dominant vegetation, elevation and watershed type. The nitrogen plots had received 50 kg N ha^{-1} year^{-1} since January 2002 (25 kg N ha^{-1} in two applications per year) as ammonium nitrate pellets (as in Hall and Matson, 1999; Magill et al., 2004). The control plots did not receive fertilizer. The location and maximum extent of three to five discrete basidiomycete litter mats was marked with flags in each of the plots at Icacos and Bisley before the first fertilization in January 2002, and again in June 2003. Mean fungal mat sizes increased over the 18-month study because they were originally marked during the dry season and remeasured during the rainy season. However, mat sizes increased more in control than in nitrogen treatment plots, though not quite significantly (one-sided test, $P = 0.062$), and were more marked for plots at higher elevation in Icacos than those at lower elevation in Bisley (Figure 3).

Changes in leaf attachment rates in response to nitrogen addition at Bisley and Icacos plots were determined by tethering numbered, freshly fallen leaves to marker flags with 1 m lengths of nylon line and placing them on basidiomycete mats (Table 1). The marker flags were placed downslope of the attached leaves, so the leaves were free to move. The leaves were checked at 8 days for the presence or absence of fungal attachments to the litter mat. At Icacos there was suggestion of correlation between nitrogen addition and decreased leaf attachment rate, after 8 days ($P = 0.0625$). Rate of leaf attachment decreased after fertilization but increased in control plots (Figure 4). In contrast, there was no relationship between nitrogen fertilization and leaf attachment at Bisley (Figure 4).
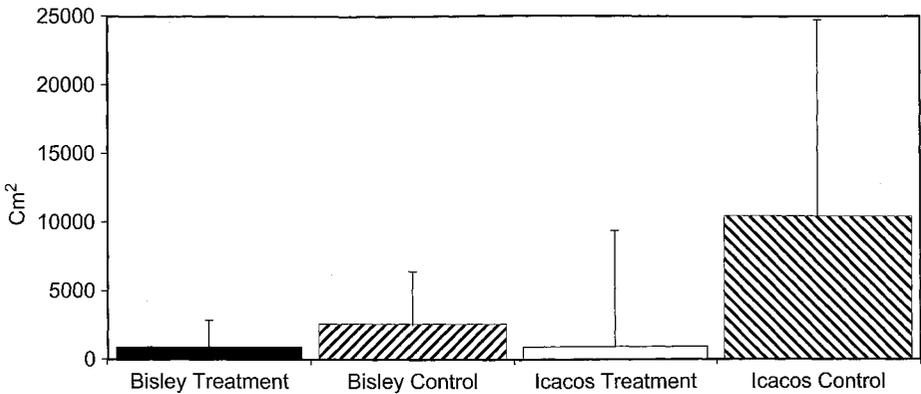
Figure 3 Mean increases in decomposer basidiomycete litter mat size from the early dry season (January 2002, just prior to nitrogen additions to treatment plots) to the early wet season (July) 18 months later. Treatment plots received 25 kg N ha^{-1} each January and June in the form of ammonium nitrate pellets; paired control plots had no nitrogen additions. Forests were located at Bisley (250–300 m asl) and Icacos (620 m asl) in the Luquillo Mountains of Puerto Rico (three pairs of replicate plots at high and low elevations). Data on mean mycelial mat area for the five pairs of plots were pooled among sites. Pair-wise differences in mat area were analyzed using a one-sided Wilcoxon Signed Ranks Test ($P = 0.0625$; Hollander and Wolfe, 1973).

Table 1 Numbers of tethered, freshly fallen leaves of *Dacryodes excelsa* and *Clusia krugiana* placed on litter mats in paired nitrogen loading and control plots before and after nitrogen fertilization in June 2003

	Bisley	Icacos
Plots	3 pairs, +N and control	3 pairs, +N and control
2 weeks before fertilization	10 *D. excelsa* leaves per plot (1 per mat)	6 *C. krugiana* leaves per plot (1 per mat)
1 week after fertilization	20 *D. excelsa* leaves per plot (1 per mat)	20 *C. krugiana* and 20 *D. excelsa* (2 each per mat)

Note: Rate of leaf attachment to the mats by basidiomycetes was determined at 8 days. Paired comparisons between treatments within forest type were made using Wilcoxon Signed Ranks tests (Hollander and Wolfe, 1973).

The decreased growth and inhibition of new resource capture by white-rot basidiomycetes following nitrogen addition at Icacos fits with previous studies that showed nitrogen inhibition of ligninolytic enzyme production by white-rot fungi (Kirk and Farrell, 1987; Cromack and Caldwell, 1992; Carreiro *et al.*, 2000; Gallo *et al.*, 2004; Waldrop *et al.*, 2004), which probably affects their competitive abilities (Carreiro *et al.*, 2000). The lack of response to nitrogen addition in the lower elevation forest at Bisley may have been related to the natural abundance of nitrogen there. Lowland tropical forests are often saturated with nitrogen (Silver *et al.*, 2005). The low-elevation forest at Bisley had more nitrogen cycling via fine litter than forests at higher elevation in the Luquillo Mountains (Lodge *et al.*, 1991).
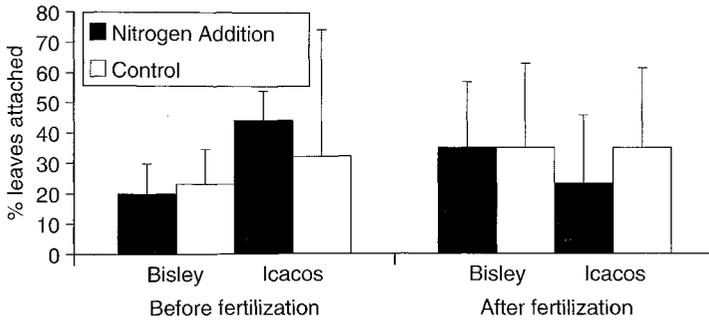
Figure 4 Percent of marked leaves attached to litter mats by decomposer basidiomycete fungi after 8 days in subtropical forest at low and high elevations (Bisley and Icacos, respectively) in the Luquillo Mountains of Puerto Rico, immediately before and after a nitrogen addition. Suppression of basidiomycete leaf attachment rates was suggestive in the high-elevation forest at Icacos ($P = 0.0625$) but not at low elevation in bisley.

Slope in Degrees
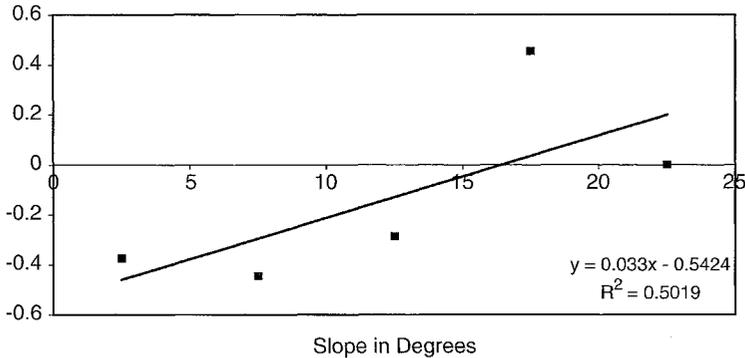
Figure 5 Mean frequency of decomposer basidiomycete litter mats moving up- or downslope as a function of degree of slope. Movements of mats over 18 months were recorded as +1 for upslope, −1 for downslope and 0 for no movement relative to slope axis. The slopes were determined using a level and plumb line. Data were pooled from two forests at low and high elevations in the Luquillo Mountains of Puerto Rico (Bisley and Icacos, respectively) and divided among five slope classes at 5° intervals: 0–5, >5–10, >10–15, >15–20 and >20–25°. The effect of slope on the mean frequency of mat movement was analyzed using regression analysis in excel (Version 9.0.3821, Microsoft Corp.).

6. MOVEMENT OF BASIDIOMYCETE LITTER MATS

There was a trend (though not significant, $R^2 = 0.5019$, $P = 0.18$) of movement of mats proportional to slope, over the 18-month study at Bisley and Icacos, mats on shallow slopes more frequently moving downslope while those on steeper slopes more frequently moving uphill (Figure 5). Two factors probably contributed to this pattern. First, as noted above, many of the shallower slopes in Bisley were in valleys subjected to overland flow during torrential storms (Weaver *et al.*, 1987). Thus, litter and soil organic matter that has been exported from slopes is

probably exported in streams during high rainfall events (Weaver *et al.*, 1986; Lodge and Asbury, 1988), resulting in the highest soil organic matter contents being located on ridges and slopes (Weaver *et al.*, 1986) rather than in bottom-lands, as occurs in the Appalachian Mountains of the USA (Orndorff and Lang, 1984). Mortality and damage to basidiomycete mycelia from overland flow was higher in valleys than on slopes in the Bisley plots during this study. Second, litter mats acted as terrestrial debris dams, and the basidiomycetes then grew into litter that had tumbled downslopes and accumulated on their upslope side.

7. BASIDIOMYCETE RESPONSES TO MOISTURE

Opening of a forest canopy by natural or anthropogenic disturbance causes dramatic environmental changes on the forest floor. Following canopy damage in Puerto Rico caused by Hurricane Hugo, the litter layer experienced more rapid drying as a result of greater exposure to solar irradiation and wind (Lodge *et al.*, 1991, 1994), resulting on ridges in higher mortality of *Collybia johnstonii* — a species that forms superficial mycelial fans on leaf surfaces, and was the dominant litter fungus in tabonuco forest prior to the hurricane (Lodge and Cantrell, 1995; Lodge, 1996). Higher stress tolerance of some marasmioid species allowed them to replace *C. johnstonii* on ridges (Lodge and Cantrell, 1995).

Effect of moisture on attachment rate of litter by mycelial mats of *Micromphale brevipes*, *Marasmius guyanensis* (both terrestrial species), *Marasmius crinis-equi* and *Micromphale* sp. (both aerial species), from Luquillo Experimental Forest, was studied by dividing mats and placing them in separate baskets (18 cm × 25 cm, with mesh bottoms) and placing in either shade or partial shade, moistened with 2 l of stream water on alternate days (except on rainy days), and resupplied with litter weekly. Evaporation potential was measured in the mat source environments, and the shade and partial shade propagation areas (using 3 ml vials of distilled water into which a 2 mm diameter cotton wick was inserted with 5 mm of the wick exposed to the air). Mean evaporation potentials were higher in partial (2.5 mm week^{-1}) than in full shade (0.75 mm week^{-1}). There were significant ($P = 0.009$) differences in attachment rates among species; *M. crinis-equi* formed significantly more attachments than the other species (Figure 6). Differences between attachment rates were not significant between light environments ($P = 0.548$), though two of the four species had better attachment rates in full shade, but *M. brevipes* had better development in partial shade (Figure 5). *M. brevipes* also had the driest source environment.

8. EFFECTS OF BASIDIOMYCETE LITTER MATS ON EROSION

Litter mat formation by basidiomycete decomposers benefits tropical forest ecosystems as a whole, both by conserving nutrients against leaching losses (Lodge, 1993; Lodge *et al.*, 1994) and by reducing erosion (Lodge and Asbury, 1988; Lodge *et al.*, 1994). The presence of basidiomycetes reduced downhill litter
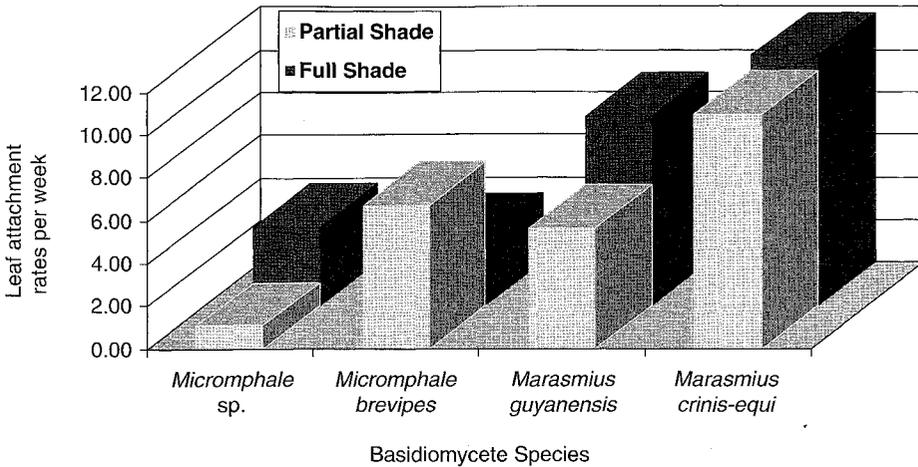
Figure 6 Mean weekly rates of leaf attachment by mycelia of four decomposer basidiomycetes in full and partial shades at El Verde in the Luquillo Mountains of Puerto Rico. Mycelia were grown in baskets (18 cm × 25 cm) filled with a thin layer of old fallen leaves or twigs lacking basidiomycetes, then the mats followed by freshly fallen leaves or more twigs on the top. Control treatments were constructed similarly, but without the mats (these remained free of fungal attachments). Every week during June 2006, the number of attached and unattached leaves or twigs in each basket were counted, followed by addition of freshly fallen leaves and twigs. Mean weekly attachment rates were compared using one-way ANOVA followed by Tukey's adjusted LSD comparisons. The overall two-way ANOVA for attachment rates was significant ($P = 0.0025$) and differences were found among species ($P = 0.009$), but not light environments ($P = 0.548$).

loss on steep slopes of a subtropical wet forest in Puerto Rico by up to 41% (Lodge and Asbury, 1988). Furthermore, the fungal litter mats protected soil surfaces from erosion losses of soil organic matter and nutrients, thereby maintaining soil fertility (Lodge and Asbury, 1988).

9. SUMMARY AND FUTURE WORK

White-rot basidiomycetes that formed litter mats significantly increased rates of mass loss during the first 3 months of decomposition in field experiments in a Puerto Rican tropical wet forest. Litter mats generally decreased in density with increasing elevation and decreasing slope. The decrease in mat density with increasing elevation was correlated with reduced litter fall rates at high elevation, but more studies are needed to confirm this relationship. While abundance of white-rot litter decomposers is expected to decrease with increasing litter nutrient concentrations, this aspect has not been explored in tropical forests.

Litter mats tended to move upslope on steep inclines, probably because they grew into the litter that accumulated on their upslope side, but downslope on more gentle gradients associated with overland flows in valleys. The mobile basidiomycete mats in tropical montane forests are thus less likely to leave

distinctive signatures in soils, such as the patchwork of mull and mor soils observed in Finland in association with decomposer basidiomycete mats (Hintikka, 1970). Studies of the abundance of litter mats formed by decomposer basidiomycetes are needed from tropical forests with less topographic relief and from non-insular areas in order to determine their general importance in the tropics.

Nitrogen additions had a significant negative effect on litter mat size and leaf trapping rates in high-elevation forest that had limited nitrogen cycling, but little or no effect on basidiomycete mats in a lower elevation forest where nitrogen in litter fall was more abundant. This raises the possibility of partial resilience among decomposer basidiomycetes to nitrogen loading. Studies of ligninolytic enzyme production in response to nitrogen addition are needed to explore this possibility. As nutrient cycling in lowland tropical forests is more often limited by phosphorus than nitrogen, and decomposer basidiomycetes play a key role in recycling of phosphorus in the litter layer (Lodge, 1993, 1996), negative effects of nitrogen from air pollutants on decomposer basidiomycetes could significantly slow leaf decomposition in tropical forests.

Basidiomycetes that formed litter mats and subcanopy nets were tested for moisture preferences. The fungi tested indicated differential responses to shading and associated moisture. *M. crinis-equi* (a subcanopy species) produced most attachments, and has potential for reclamation of steep eroding slopes. Further applied studies are needed to develop protocols for using litter-binding basidiomycetes in reclamation of road cuts and landslides, and to determine their effectiveness.

ACKNOWLEDGMENTS

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