Nutrient piracy: evidence for the role of litter-trapping fungi in forest nutrient cycling in Sabah, Malaysia

Abstract: Litter-trapping fungi are abundant in forest canopies across the tropics. By intercepting litter fall, these fungal systems have been shown to be important in supporting the diverse arthropod community in lowland forest. These fungal litter-trapping systems are also likely to influence the nutrient cycling. This study, carried at the Danum Valley field Centre, Sabah, Malaysia, compares the decomposition of litter within these fungal systems with litter on the forest floor. Results show that while decomposition was lower in the canopy there was a significant increase in mass loss with fungal attachment to the litter.

Keywords: Danum Valley; decomposition; forest canopy; fungi; leaf litter; rainforest,

Authors [1]

[1]Jake L. Snaddon[1,2]*, Chey Vun Khen[3], and William A. Foster[2]

[1]Centre for Biological Sciences, Faculty of Natural & Environmental Sciences, University of Southampton, Southampton SO17 1BJ, UK.
[2] Insect Ecology Group, University Museum of Zoology, Downing Street, Cambridge CB2 3EJ, UK.
[3] Forest Research Centre, Forestry Department, P. O. Box 1407, 90715 Sandakan, Sabah, Malaysia

*Corresponding author (jlsnaddon@gmail.com)

INTRODUCTION

The accumulation of leaf-litter within forest canopies is usually associated with litter-trapping systems such as epiphytes (Authors 2004), junctions of large branches, specialised palms (Rickson and Rickson 1986, Alvarez-Sanchez and Guevara 1999) and trees e.g. *Barringtonia corneri* trees (Kiew and Wong 1988). Litter not held by these prominent litter-trapping systems was thought to be intermittent and transient, being easily dislodged by disturbances such as strong winds, rain and animal movements (Nadkarni and Matelson 1991). However, a recent study has shown that a considerable amount of leaf-litter is held in place by rhizomorph-forming fungi (Authors et al. 2013). This study showed that the fungi trap over 250 kg of leaf litter per hectare of lowland Dipterocarp forest in Sabah, Malaysia and are a vital resource for canopy arthropods. Though the taxonomy of the litter-trapping fungi is not well known, it is thought that a suite of marasmioid fungal species of similar taxa to that found in the leaf litter of the forest floor, are involved in this process: with the dominant genera being *Marasmius*, *Marasmiellus* and *Mycena* (Hedger et al. 1993).

The fungal systems are supported in the lower canopy on the understory vegetation forming networks of dark thread-like rhizomorphs (dense masses of hyphae), which trap falling leaf litter (Fig. 1). This litter is then attached to the fungal network through adhesive zones wherever contact is made with the vegetation or litter surface (Hedger 1990). Visual inspection of the trapped leaf-litter shows pale discolouration around these adhesion zones, and microscopy of these areas has revealed that the hyphae penetrate the litter, indicating that saprotrophic exploitation and litter decomposition is occurring Hedger et al. (1993).

With optimal microclimatic conditions for decomposition, the forest floor of moist tropical forests has highly active and diverse terrestrial decomposer communities (Anderson and Swift 1983). By inhabiting an aerial habitat, litter-trapping fungi maybe getting one step ahead of the competition, obtaining nutrients from litterfall before it reaches the forest floor. The aim of this study is to compare leaf litter decomposition within the litter-trapping fungal systems and on the forest floor.

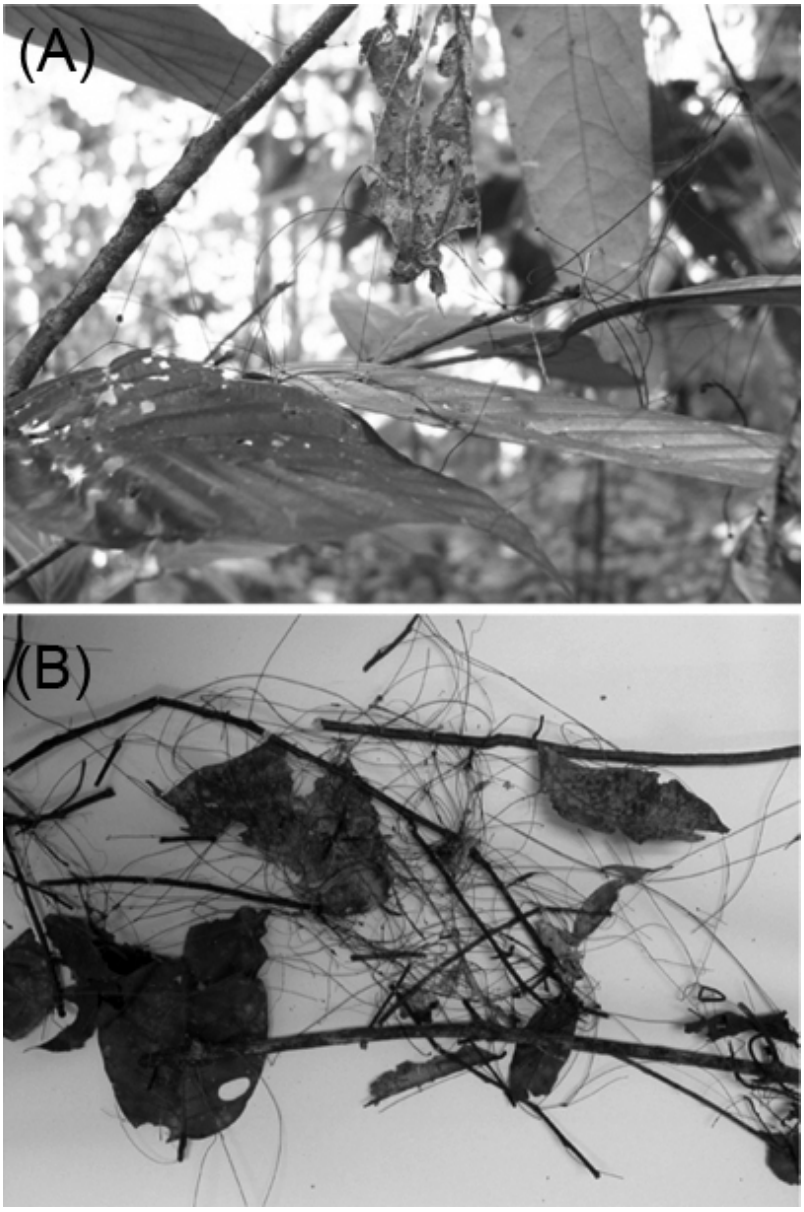

Figure 1: Canopy rhizomorph-forming fungi: (A) fungal growth in the understory and (B) mass of litter attached to rhizomorphs.

MATERIALS AND METHODS

The study was conducted in primary dipterocarp forest in the Danum Valley Conservation Area, Sabah, Malaysia (5°01′ N, 117°40′ E, altitude *ca* 170m). Decomposition was assessed as percentage mass loss from tethered whole leaves (Witkamp and Olson 1963). Recently senesced (>24h) *Shorea johorensis* leaves were collected in litter traps and sterilised in a dry oven at 75°C for 24 h before being placed in the forest in four sites, (>100m between sites). In each site, 15 leaves were tied with nylon fishing line to litter suspended by rhizomorph systems in the understorey and 15 leaves were secured on the forest floor. After 21 days the leaves were collected and attachment of the leaves to the fungal networks leaves was recorded. The leaves were then oven-dried to a constant weight.

The data were assessed using non-parametric analyses, as the data did not conform to normal distributions. The differences in leaf mass loss were tested using Mann-Whitney tests and Chi-square test were used to assess fungal attachment to the leaves placed on the ground and suspended in the rhizomorph systems.

RESULTS

After three weeks the percentage mass loss from the leaves suspended in fungal systems was 10.7%, significantly lower than on the forest floor 17.1% (Mann-Whitney test: $W_{60,60} = 2720$, $P < 0.001$; Fig 2a). The percentage of leaves that were attached to fungal networks was also significantly greater on the forest floor (88%) than in the rhizomorph systems (65%) ($X^2 = 7.87$, df = 1, P = 0.005). Where leaves were attached to the canopy fungal systems the mass loss was significantly higher (Mann-Whitney test $W_{21,39} = 479$, P = 0.013; Fig 2b). However, on the forest floor there was no significant effect of fungal attachment (Mann-Whitney test $W_{7,53} = 209$, P = 0.923; Fig 2c).

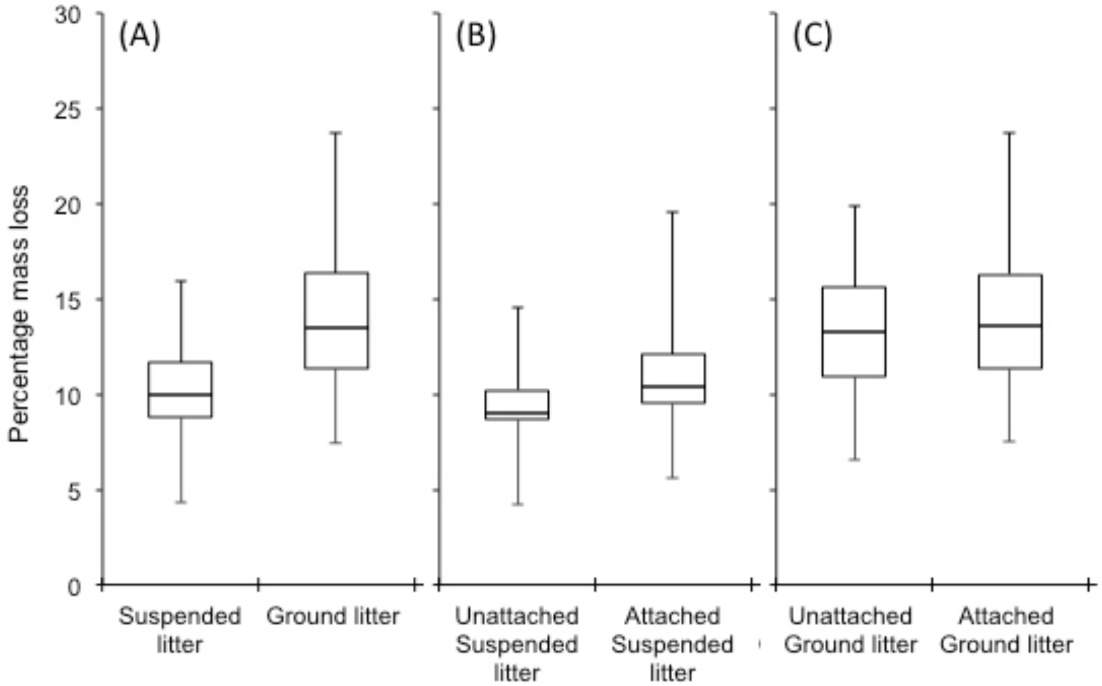

Figure 2: Differences in percentage mass loss from *Shorea johorensis* leaves after 21 days. (A) Percentage mass loss from leaves placed on the ground was significantly greater than from the leaves suspended in the rhizomorph systems ($P = <0.001$). (B) The leaves suspended in the fungal litter-trapping systems had a significantly higher mass loss when they were attached to the fungal rhizomorphs ($P = 0.013$). (C) On the ground there was no difference in the mass loss of litter attached or unattached to fungal networks. Horizontal line = median, boxes = the inter-quartile range, vertical line = the range of values.

DISCUSSION

As expected, the mass loss from the tethered leaves was greater on the forest floor than in the rhizomorph systems. This finding is consistent with previous studies that have compared litter decomposition on the forest floor with canopy sites (Nadkarni and Matelson 1991, Cardelus 2010, Li et al. 2014); where the decomposition in canopy epiphytes has been reported to be 15-30% slower (Li et al. 2014). Microclimatic differences between the forest floor and canopy (Bohlman et al. 1995) are thought to be the main driver of this difference, which is further impacted by an inferior decomposer community in the canopy (Li et al. 2014). The similarity in mass loss between litter attached or unattached to fungal networks on the forest floor is probably due to the activity of the complex community of other decomposer microorganisms and invertebrates.

The difference in mass loss between the attached and unattached litter in the canopy fungal systems confirms the fungi are actively exploiting the trapped litter as a source of nutrients. The litter-trapping fungi are well adapted to the canopy environment, being less susceptible to desiccation, and rhizomorph growth has been shown to respond rapidly to suitable humid conditions after rain (Hedger et al. 1993). Fungi are more efficient than other micro-organisms at conserving immobilised nutrients and rhizomorph-forming fungi are known to physically translocate nutrients, reallocating them for further exploitation (Lodge et. al. 1994, Lodge and Cantrell 1995). Therefore, as well as interrupting the litterfall pathway, litter-trapping fungi can arrest the return of mineral nutrients to the forest floor.

These rhizomorph-forming fungi have been shown to be abundant and efficient litter-trapping systems in tropical forest canopies across the globe (Hedger et al. 1993, Authors et al. 2012). Through trapping litterfall and actively decomposing the trapped organic matter, these systems can have important consequences for nutrient cycling and spatial heterogeneity of the forest ecosystem.

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