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Effect of litter on the incidence of leaf-fungal pathogens and herbivory in seedlings of the tropical tree *Nectandra ambigens*

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Abstract: Effects of litter cover on insect herbivory, leaf-fungal damage, and seedling performance (survival, growth in height and leaf number), were assessed on established *Nectandra ambigens* seedlings in three sites of a Mexican tropical rain forest. Naturally occurring seedlings were measured for height, leaf number and standing levels of leaf damage by herbivores and pathogens. Thereafter, seedlings were exposed for 1 y to three litter treatments: (1) litter addition, (2) control and (3) continuous litter removal. There was a significant effect of site on the proportion of surviving seedlings and on the relative growth rates in terms of leaf number. Overall, seedlings with higher initial leaf number showed higher survival and produced more leaves after 12 mo than seedlings with lower initial leaf number. Litter addition resulted in seedlings with lower relative growth rates in height and higher levels of damage by herbivores and pathogens. On average, leaf area damaged by pathogens was < 6% and herbivory was < 27%. Seedlings with higher levels of herbivory showed higher levels of pathogen attack. Herbivory and pathogen attack had no effect on seedling performance. This study reveals the importance of litter-cover on the interactions between seedlings, herbivores and pathogens, as well as on the performance of tropical seedlings.

Key Words: disease, leaf damage, Los Tuxtlas, seedling performance, tropical rain forest

INTRODUCTION

Environmental variability in the understorey of tropical rain forests influences distribution, abundance and composition of the seedling community. In these systems, light is known to be a limiting factor for seedling emergence, survival and growth (Alvarez-Buylla & Martínez-Ramos 1992, Chazdon 1988). However, other factors, such as litter quantity and quality, have been shown to affect seedling regeneration (Benítez-Malvido & Kossmann-Ferraz 1999, Molofsky & Augspurger 1992, Vázquez-Yanes *et al.* 1990). Litter accumulation is highly variable across the forest understorey (Brandani *et al.* 1988, Facelli & Picket 1991, Guariguata 1990), ranging from areas where litter is completely absent (e.g. landslides, root zone of tree-fall gaps), to areas with high litter accumulation (e.g. crown zone of a tree-fall gap, slope bases, beneath acaulesent palms). Seedling species show contrasting responses to litter amount. Some species appear to regenerate in exposed mineral soils, as *Clethra occidentalis* and *Vaccinium meridionale* (Dalling & Tanner 1995, Newton & Healey 1989), while others grow and survive better in the presence of high amounts of litter as in *Sloanea berteriana* and *Micropholis venulosa* (Benítez-Malvido & Kossmann-Ferraz 1999, Guzmán-Grajales & Walker 1991). Besides its effect on seedling establishment and performance, litter amount affects the interaction of seedlings with other plants and animals, reduces herb competition, and also affects the levels of seedling damage by animals in temperate and tropical systems (Benítez-Malvido & Kossmann-Ferraz 1999, Facelli 1994). However, to our knowledge, there is no information on the effects of litter on seedling–pathogen interactions in the tropics. In tropical forests, many plant species are affected by herbivorous insects and fungal pathogens (Coley & Barone 1996, García-Guzmán & Dirzo 2001, Gilbert *et al.* 1994). Both types of predators can affect growth (Burdon 1987, Gange *et al.* 1989), competitive ability (García-Guzmán *et al.* 1996, Louda *et al.* 1990), and survival (Augspurger & Kelly 1984, Harper 1977), of different plant species in tropical and temperate systems.

Nectandra ambigens (S. F. Blake) C. K. Allen (Lauraceae), is a tropical rain-forest tree that produces large amounts of litter (Alvarez-Sánchez & Guevara-Sada 1985), and has abundant carpets of seedlings under conspecific canopies. Adults and seedlings are commonly attacked by fungal leaf pathogens (García-Guzmán & Dirzo 2001, unpubl. data) and herbivorous insects (Dirzo

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et al. 1997*b*). We selected this plant species to investigate experimentally the effects of litter amount on the incidence and levels of damage by leaf pathogens and herbivores, as well as on the performance of seedlings (survival and growth) for 1 y, in a Mexican tropical rain forest.

METHODS

Study site and study species

This study was carried out at the Los Tuxtlas Biological Station, located in Southern Mexico (between 95° 04′ and 95°09′W, 18°34′ and 18°36′N; Ibarra & Sinaca 1987). Mean monthly temperature ranges from 17 °C (January) to 29 °C (June). Annual rainfall averages 4725 mm with a dry season (April–May), a summer wet season (June–October) and a winter wet season (November–February) (Soto & Gama 1997). The vegetation of the area is classified as high evergreen rain forest (Pennington & Sarukhán 1998), characterized by trees exceeding 35 m in height. The forest understorey is dominated by *Astrocaryum mexicanum* palms, shrubs, lianas, herbs and epiphytic plants (Dirzo *et al*. 1997*a*). At Los Tuxtlas, as in many tropical rain forests, there is high heterogeneity in the production of litter fall across the forest, ranging from 450 to 1300 g m^{-2} y^{-1} (Martínez-Ramos 1991).

Nectandra ambigens is a tree species 20–35 m tall at maturity, found in the tropical rain forests of Mexico, Honduras and Guatemala (Dirzo *et al*. 1997*b*). Trees of *N. ambigens* are very abundant in the Los Tuxtlas region, reaching densities of up to 42 trees ha^{-1}, ≥ 10 cm dbh in some areas (Bongers *et al*. 1988). This plant species produces large amounts of litter (128 g m^{-2} y^{-1}), mainly during May when up to 31% of the leaves of adult trees fall (Alvarez-Sánchez & Guevara-Sada 1985). Seedlings form dense carpets under the parent tree (up to 135 seedlings m^{-2}), however survival of seedlings of the same cohort after 3 y is low (< 15%), and few survive to the sapling stage, probably due to the attack by orthopteran and lepidopteran larvae, which are mainly chewers and miners (Dirzo *et al*. 1997*b*). The fungi *Colletotrichum* sp. and *Phomopsis* sp. affect leaves of trees and seedlings, causing necrotic leaf spots (García-Guzmán & Dirzo 2001, unpubl. data). Preliminary studies have shown that up to 96% of *N. ambigens* seedlings may be affected by these fungal species (García-Guzmán 1990). However, their effect on seedling performance is not yet known.

Experimental design

In three sites of the biological reserve we selected three adult *N. ambigens* trees located on relatively flat areas. In each site we positioned fifteen 1-m^2 plots, at random distances in a radius of 10 m around the parent tree. In each site, five plots were randomly assigned to each of the following litter treatments: (1) litter addition, (2) control and (3) continuous litter removal; giving a total of five plots per treatment per site (n = 45). Initially, we removed by hand the litter (small branches, leaves, fruits, etc.) from five plots. To reduce border effects we also removed the litter from the surrounding 30 cm of each plot. Approximately 3 kg of fresh litter obtained from the removal-treatment plots and the surrounding area was added to the addition-treatment plots. Seedlings growing in the addition treatment were almost covered by litter. Litter was not manipulated in the control treatment. The experiment was established in November 1996. The litter accumulated on the removal-treatment plots was removed monthly for 1 y. In each plot we randomly selected ten 1-y-old *N. ambigens* seedlings and all the other individuals within the plot were removed to control for density-dependent effects on seedling performance. This gave a total of 50 seedlings per treatment and 150 seedlings per site. Mean density (± SD) of seedlings per site before removal was 35.3 ± 2.9 seedlings m^{-2}. To know if there were initial differences in seedling characteristics among sites, we measured their height and number of leaves, and their standing levels of damage by pathogens and herbivores. Before litter manipulation, we found no relationship between seedling density and damage by pathogens and herbivores on the study plots. After 1 y, we recorded seedling survival, relative growth rates in height (RGR_H) and number of leaves (RGR_L). RGR_H was obtained as:

$$RGR_H = (\log H_{t2} - \log H_{t1}) \,/\, (t_2 - t_1)$$

where: H_{t1} = height at t_1; H_{t2} = height at t_2; t_1 = time of the first height measurement and t_2 = time of the second height measurement (1 y). RGR_L was calculated as: $RGR_L = (L_2 - L_1) \,/\, L_1 \, (t_2 - t_1)$; where L_1 = number of leaves at t_1; L_2 = number of leaves at t_2; t_1 = time of first leaf measurement and t_2 = time of second leaf measurement (1 y). Estimates of the standing levels of herbivory and pathogen damage were determined by assigning leaves of all seedlings to one of the following categories of damage: 0 = intact; 1 = 1–6%; 2 = 6–12%; 3 = 12–25%; 4 = 25–50% and 5 = 50–100% of leaf area damaged. The percentage of leaf area damaged was assessed visually and an index of damage (*ID*) (Dirzo & Domínguez 1995) obtained with the following formula:

$$ID = \sum_{i=1}^{5} n_i \, (C_i) \,/\, N$$

where n_i is the number of leaves in *i*th category of damage, C_i is the midpoint of each category (i.e. C_1 = 3.5%, C_2 = 9%, C_3 = 18.5%, C_4 = 37.5% and C_5 = 75% respectively) and N is the total number of leaves per plant. The index of damage was modified after Dirzo & Domínguez (1995), and the values are given in percentage of leaf area damaged per plant (Benítez-Malvido & Kossmann-Ferraz 1999).

Data analysis

To test the effects of site and litter treatment and the influence of initial seedling condition (in terms of height, leaf number and damage by pathogens and herbivory) on seedling performance and leaf biotic (herbivory/pathogenic infection) damage, we used an analysis of covariance (ANCOVA), with two factors, site and litter treatment. To assess the effects on seedling performance, we used survival and relative growth rates (RGR_H, RGR_L) as response variables, initial seedling height, initial number of leaves and the average of initial and final levels of herbivore and pathogen damage as covariables). To assess the effects on final leaf biotic damage, we performed a second ANCOVA with initial height, number of leaves and initial levels of herbivore and pathogen damage as covariables.

The data were analysed by generalized linear models using the GLIM statistical package (Green & Payne 1994). The deviance of a GLIM measures the discrepancy between the data and the fitted values. The change in deviance when a new term is fitted is a measure of the adequacy of that term. In those cases in which a term was found to be insignificant it was removed from the model. In cases of significant terms, the individual levels of the term (i.e. site and treatment) were compared through t-tests following Crawley (1993). For binomial or Poisson data the deviance will be approximately distributed as a chi-square and can be used to test the validity of the new term (Crawley 1993). The percentage of leaf area damaged by pathogens and herbivory was arcsine-transformed, and leaf numbers were log (x+1)-transformed prior to analysis. To eliminate pseudoreplication (*sensu* Hurlbert 1984), we treated each 1-m^2 plot as a replicate by averaging height, number of leaves and the levels of seedling damage in the plot (Crawley 1993). Means and error terms reported in the figures are calculated on the basis of untransformed data.

RESULTS

Effects of litter cover on seedling performance

There was a significant effect of site on the proportion of surviving seedlings ($\chi^2 = 20.3$, df = 2, $P < 0.05$) and on RGR_L ($F_{2,42} = 17.3$, $P < 0.05$). Average survivorship (± SE) of seedlings growing in site 2 was significantly higher (0.8 ± 0.12) than seedlings growing in site 3 (0.6 ± 0.13) and 1 (0.7 ± 0.10), whereas average RGR_L (± SE) was significantly higher in site 2 (4.3 ± 0.35) than in sites 1 (2.3 ± 0.23) and 3 (2.5 ± 0.22). Litter treatment had no effect on survivorship and or RGR_L. However, there was a significant effect of litter treatment on RGR_H ($F_{2,42} = 10.8$, $P < 0.05$). Seedlings growing in the litter-addition treatment had significantly lower RGR_H than those from control and removal treatments (Table 1). Average seedling height (± SE) ranged from 29.9 ± 0.64 cm (addition treatment) to 33.1 ± 0.79 cm (control treatment) to 33.2 ± 0.70 cm (removal treatment). Initial seedling condition affected their performance after litter manipulation. Overall, after 1 y, seedlings with higher initial number of leaves showed significantly higher survival ($\chi^2 = 27.4$, df = 1) and produced more leaves (RGR_L) ($F_{1,43} = 72.9$, $P < 0.05$) than seedlings with lower initial leaf numbers (Figures 1a, b). Seedling damage by herbivores and pathogens had no effect on seedling survival and growth (RGR_H and RGR_L). Furthermore, initial seedling condition did not affect damage by pathogens and herbivores.

Effects of litter cover on seedling damage

Herbivory and pathogen infection ranged between 12.4–33.4% and 1.3–15.8% of leaf area damaged per seedling, respectively. On average, leaf area damaged by pathogens was < 6% and herbivory was < 27%. Litter treatment affected the levels of seedling damage. Litter addition produced higher levels of damage by herbivores ($F_{2,42} = 7.5$, $P < 0.05$) and by pathogens ($F_{2,42} = 11.9$, $P < 0.05$), than control and removal treatments. The levels of seedling biotic damage declined significantly from the addition, to

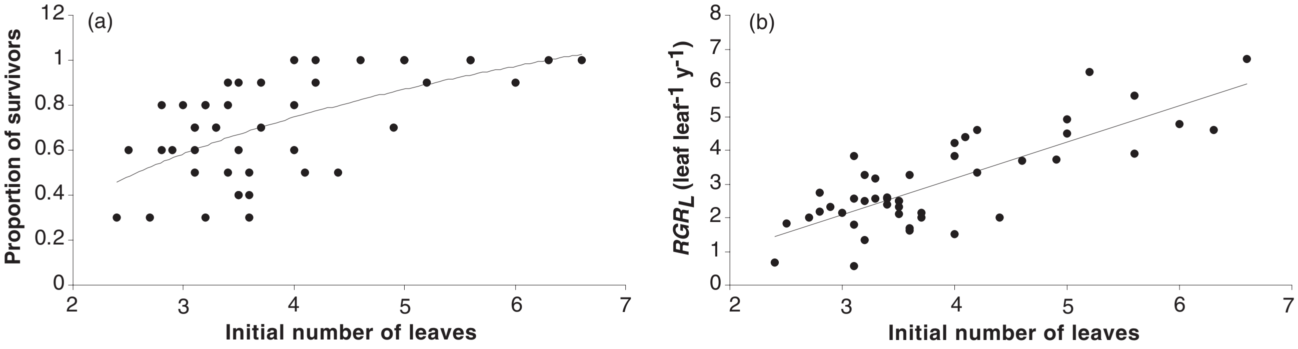

Figure 1. Best fit linear regression for the effect of initial number of leaves on (a) proportion of survivors ($y = 0.56 \ln(x) - 0.03$, $r = 0.38$, df = 43, $P < 0.05$) and (b) relative growth rate in leaf numbers after 1 y, in *N. ambigens* seedlings ($y = 1.08x - 1.15$, $r = 0.79$, df = 43, $P < 0.05$).

Table 1. Comparisons (mean ± SE) of relative growth rate in height (RGR_H) and the percentage of leaf area damaged by pathogens and herbivores in *N. ambigens* seedlings after 1 y growing across three different litter treatments. Means within a row that share the same superscript letter are not significantly different among litter treatments ($t \geq 2$, $P < 0.05$).

Variable	Litter treatment		
	Addition	Removal	Control
RGR_H (cm cm^{-1} y^{-1})	0.13 ± 0.08^a	0.96 ± 0.15^b	1.17 ± 0.08^b
Leaf area damaged by herbivores (%)	23.3 ± 1.31^a	17.0 ± 0.80^b	20.7 ± 1.25^c
Leaf area damaged by pathogens (%)	9.14 ± 1.07^a	4.10 ± 0.42^b	6.54 ± 0.69^c

the control, to the removal treatments (Table 1). There was a significant positive relationship between levels of damage by herbivores and by pathogens ($F_{2, 42} = 7.7$, $P < 0.05$). Seedlings with higher levels of herbivory showed higher levels of fungal attack (Figure 2).

DISCUSSION

Litter cover and seedling performance

Most of the effects of litter cover variability on seedling performance have been described for seedlings at early establishment, and little is known about the effects of litter cover variability for established seedlings (> 4 mo old; Benítez-Malvido & Kossmann-Ferraz 1999). At early establishment large-seeded seedling species can cope better with litter depth than do small-seeded species (< 0.005 g dry mass) (Grubb 1996, Kohyama & Grubb 1994). However, the information available for established seedlings shows that responses of seedlings to litter amount in terms of performance, are species specific and independent of seedling size and species seed size (Benítez-Malvido & Kossmann-Ferraz 1999, Cintra 1997). In our study, established (≥ 1 y old), large-seeded (> 0.005 g dry mass), seedlings of *N. ambigens* had lower growth rates in height when grown in the litter-addition treatment. This effect may have resulted from growth suppression due to a lower light availability in the addition treatment. Although *N. ambigens* can survive at low light intensities, growth is much more rapid in open sites (del Amo 1985).

The present study shows that the initial number of leaves in *N. ambigens* seedlings determined plant survival and leaf number after 1 y. This indicates that early events in the life of an individual may be very important in determining the later fate of that individual. Studies in naturally occurring populations, show that size plays an important role in differential survivorship from very early in the life cycle of plants. For example, average survival probability of the tropical palm *Astrocaryum mexicanum* (Arecaceae) is higher in juveniles with higher number of leaves (Sarukhán *et al.* 1984). Indeed, in a temperate system, survival of *Plantago lanceolata* is higher in individuals with higher number of leaves (Fowler & Antonovics 1981). According to Dickson & Isebrands (1991), leaves are major regulators of shoot development and carbon allocation within the whole plant. Furthermore, the meta-

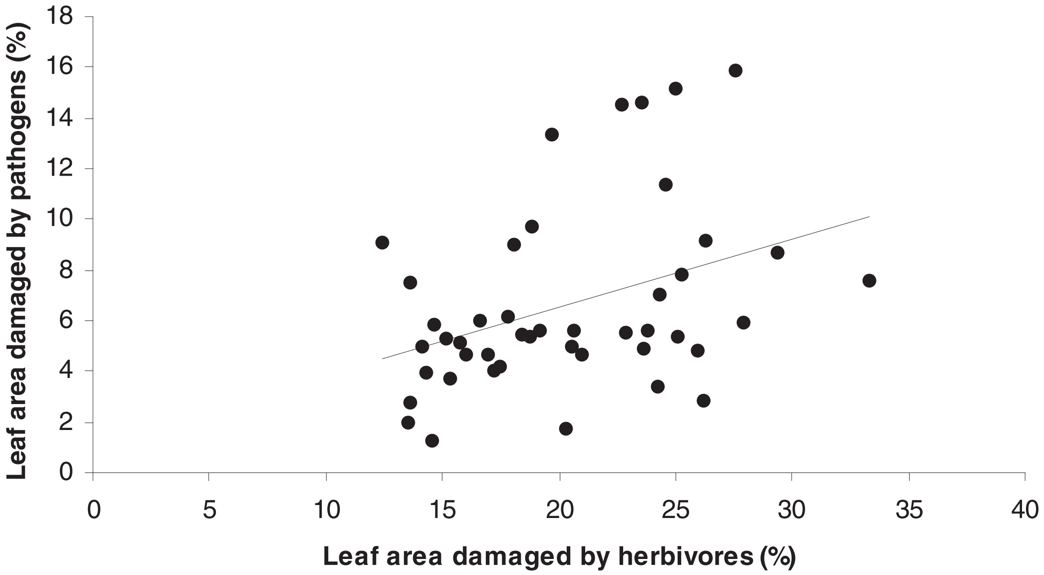

Figure 2. Best-fit linear regression for the effect of herbivory levels on leaf area damaged by pathogens in *N. ambigens* seedlings ($y = 0.27x + 1.14$; $r = 0.38$, $df = 43$, $P < 0.05$).

bolic responses of leaves to different environmental stresses largely regulate the growth and development of both shoots and roots, and as a result the performance of the whole plant.

However, performance of *N. ambigens* seedlings, was not affected by leaf damage. A possible explanation for this could be that the amount of leaf area damaged by herbivores and/or pathogens was not large enough to have a significant effect on seedling performance. The pathogens attacking *N. ambigens* caused discrete lesions, that individually, could have little noticeable effect on host fitness. Moreover, the leaf area damaged per seedling was low (< 7%). Burdon (1993) suggests that this kind of pathogen (local pathogens causing leaf spots) debilitates the host plants throughout the accumulation of lesions. It could be possible that the effects of disease in *N. ambigens* performance could be evident only after a larger period of time. Similarly, a number of observations suggest that plants respond slowly to herbivory by leaf-feeding insects, with significant effects observable only after several years (Brown 1990, Gange 1990). Moreover, the influence on plant performance of leaf-feeding insects is less marked than that of other types of herbivores (Brown & Gange 1989, Hulme 1996, Rees & Brown 1992). Therefore, our study probably provides a fair representation of the relative impacts of herbivores and pathogens on the performance of *N. ambigens* but was too short term to quantify the precise influence of these predators.

Litter cover and seedling damage

Litter accumulation may affect plants in three ways: (1) physically, by burying them, (2) chemically, by adding nutrients and phytotoxins and (3) biologically, by adding diaspores (Xiong & Nilsson 1997) and microfauna (Vasconcelos 1990). In this study we have shown that litter amount affects biotic interactions. The micro-environment created by the addition of litter, could have had benefit on the establishment and growth of leaf pathogens in two ways: (1) by creating a shady and wet environment favourable for establishment and growth of fungal pathogens (Achar 1998, Wu *et al.* 2000) and (2) by favouring infection when adding litter composed of leaves from *N. ambigens* adult trees, that might have been infected by pathogens. Furthermore, the seedlings in our experiments were growing very close to the parent trees and, therefore, exposed to fungal inocula from pathogens affecting the leaves above (Gilbert 1995). Preliminary studies have shown that up to 90% of the leaves of adult *N. ambigens* trees may be affected by pathogens (García-Guzmán 1990).

Several studies have shown the importance of inoculum-harbouring leaf litter as source of infection in crop systems (Aylor 1998, Sutton *et al.* 2000), but to our knowledge, ours is the first study revealing litter as a possible source of leaf-fungal infection in a natural tropical system. On the other hand, litter removal also results in micro-environmental changes at the soil surface (Vázquez-Yanes *et al.* 1990, Xiong 1999). Therefore, in the removal plots, the levels of moisture and nutrients provided by litter decomposition are likely to decrease, probably affecting the establishment and growth of pathogens.

In our study, leaf area damaged by herbivory was also higher in the litter-addition treatment. Some studies have shown that the shady and wet environment created by litter addition can also benefit phytophagous insects (Facelli 1994). For example, seedlings of *Pouteria peruviensis* and *Chrysophyllum pomiferum* in Central Amazonia were highly damaged by herbivores when seedlings grew in litter-addition plots (Benítez-Malvido & Kossmann-Ferraz 1999). In contrast, seedlings of the tropical tree *Micropholis venulosa* showed reduced herbivory in the presence of litter (Benítez-Malvido & Kossmann-Ferraz 1999); whereas at Los Tuxtlas, the palm *Astrocaryum mexicanum* has shown lower predation of its seeds in the presence of litter (J. Rodríguez-Velázquez and M. Martínez-Ramos, unpubl. data), probably because seeds/seedlings were less apparent to herbivores.

The apparency of a food plant is related to its number of predators (Soberón *et al.* 1988). Factors such as height, conspicuousness and density of conspecifics growing nearby affect the probability of being predated (Janzen 1970, Soberón *et al.* 1988). Seedlings of *N. ambigens* experienced micro-environmental changes depending on litter treatment, and the number of seedlings that died within treatment plots after 1 y. Changes in the neighbourhood, resource availability (light, moisture), and growth rates produced by the litter amount, could have influenced the chances of a seedling being located and predated. Spatial heterogeneity of the physical environment can account for the great variation in herbivory rates found among conspecific individuals in tropical rain forests (Coley 1983).

Our study shows that seedlings with higher levels of herbivory had higher levels of fungal attack. Studies in *N. ambigens* seedlings have shown that a high proportion of leaves are damaged by both herbivores and fungal pathogens (71%), while only a very small proportion of the leaves are affected by pathogens (5%) or herbivores (19%) alone (G. García-Guzmán & J. Benítez-Malvido, unpubl. data). Studies at the Los Tuxtlas forest, as well as in the Amazon, have shown that leaf spots caused by fungi are commonly associated with insect herbivory (Benítez-Malvido *et al.* 1999, García-Guzmán & Dirzo 2001). Therefore, the positive relationship between pathogen damage and herbivory levels found in our study could be attributed to this fact. However, it is also possible that infected leaves could be more attractive to herbivores. Whittaker & Warrington (1990) suggest that grazing by invertebrates may be stimulated in infected plants, due to an accumulation of soluble organic nitrogen compounds (White 1984), and other chemicals which accumulate at infection sites (Farrar & Lewis 1987).

Our findings show that litter cover variability in the forest understorey affects the performance of tropical seedlings and their complex interactions with herbivores and pathogens. However, full understanding of the role of litter in the establishment of plant pathogen–herbivore interactions, and their dynamics in natural systems, requires a proper analysis of the interactions between different ecological variables and litter accumulation.

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