Available online at www.sciencedirect.com
SCIENCE DIRECT
Forest Ecology and Management 229 (2006) 285–293
Forest Ecology and Management
www.elsevier.com/locate/foreco

Effects of litter manipulation on early-stage decomposition and meso-arthropod abundance in a tropical moist forest

E.J. Sayer [a,*], E.V.J. Tanner [a], A.L. Lacey [b]

[a] Department of Plant Sciences, Downing Street, Cambridge CB2 3EA, UK
[b] Department of Zoology, Downing Street, Cambridge CB2 3EJ, UK

Received 22 April 2005; received in revised form 2 March 2006; accepted 3 April 2006

Abstract

Differences in forest productivity due to climate change may result in permanently altered levels of litterfall and litter on the forest floor. Using experimental litter removal and litter addition treatments, we investigated the effects of increased and decreased litterfall on early-stage litter decomposition and the abundance of meso-arthropods in a moist tropical forest. Litterbags containing freshly fallen leaves of *Cecropia insignis* (above and below the litter on the forest floor, and with and without fungicide) and *Simarouba amara*, or untreated birch wood (*Betula* sp.) were placed in either (1) plots where all litterfall was removed monthly (L−); (2) plots where litterfall was doubled monthly (L+), or (3) control plots (CT). Litter removal significantly slowed decomposition of both species and reduced the abundance of meso-arthropods on *Simarouba* litter. The fungicide treatment did not reduce apparent mass loss of *Cecropia* leaves. The litter addition treatment accelerated the decay of birch wood, probably because of increased nutrient availability from the extra litter; but there was no change in leaf-litter decomposition or meso-arthropod abundance in the L+ treatment. After 68 days, the concentrations of nitrogen, phosphorus, potassium, and magnesium in partially decomposed *Cecropia* litter were higher in the L+ treatment and lower in the L− treatment. The accumulation of phosphorus and nitrogen was greater in the litter in L+ plots and lower in the L− plots while the release of potassium and magnesium from decomposing litter was lower in the L+ treatment and greater in the L− plots. Thus, differences in the quantity of litterfall affect decomposition with consequences for carbon and nutrient storage and cycling.

Keywords: Decomposition; Leaf-litter; Litterbag method; Mesofauna; Nutrient dynamics; Tropical forest

1. Introduction

In many tropical forests litterfall and decomposition represent the major pathway for the transfer of nutrients between the plants and the soil (Swift et al., 1979; Vitousek and Sanford, 1986) and it is widely believed that the release of nutrients from decaying plant matter is critical for the maintenance of ecosystem production (Jordan, 1985; Cuevas and Medina, 1986). Climatic conditions in the lowland wet tropics are generally highly favourable to decomposition (Couteaux et al., 1995) and although seasonal drought in many tropical forests leads to the inhibition of decomposition processes and a transient build-up of leaf-litter (e.g. Madge, 1965; Wieder and Wright, 1995), most of the litter in lowland moist and wet tropical forests decays within a year (Sampaio et al., 1993), ensuring rapid nutrient cycling in these systems.

The litter layer helps to maintain favourable conditions for decomposition by regulating the microclimate (e.g. Anderson and Swift, 1983; Vasconcelos and Lawrence, 2005; Sayer, 2006) and creating habitats for arthropods (Pearse, 1943; David et al., 1991; Arpin et al., 1995). Litter removal and litter addition treatments in temperate forests not only caused substantial changes to the microclimate on the forest floor, but also affected the number of decomposer organisms, such as arthropods (Pearse, 1943; Poser, 1990; David et al., 1991; Ponge et al., 1993; Arpin et al., 1995) and fungi (Tyler, 1991; Cullings et al., 2003). Furthermore, changes in litterfall modify the amounts of available nutrients in the soil (Sayer, 2006), which may also affect decomposition rates (Ostertag and Hobbie, 1999; Hobbie and Vitousek, 2000; Rothstein et al., 2004). Thus, the amount of leaf litter on the forest floor influences factors affecting its decomposition. For example, pulses of litter following hurricanes have been shown to

* Corresponding author at: Smithsonian Tropical Research Institute-BCI, Unit 948, APO AA 34002, USA. Tel.: +1 507 212 8929; fax: +1 507 212 8975.
E-mail address: sayere@si.edu (E.J. Sayer).

0378-1127/$ – see front matter © 2006 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2006.04.007

increase the forest floor by 20–150%. This large single input of mostly green litter caused an acceleration of decomposition resulting in the return to prehurricane forest floor levels within five months (Ostertag et al., 2003).

Litterfall has been shown to increase with rising atmospheric CO_2 levels (DeLucia et al., 1999; Allen et al., 2000; Schlesinger and Lichter, 2001; Finzi et al., 2001; Zak et al., 2003), but decreases are also conceivable if changes in rainfall patterns affect tree phenology. Although litter quality is one of the most important factors in determining decomposition rates in the tropics (Bloomfield et al., 1993; Anderson and Swift, 1983), changes in the *quantity* of litter on the forest floor may also affect decomposition rates.

In a model of litterfall and decomposition in a tropical forest, Sampaio et al. (1993) calculated the rates of mass transfer between fresh litter and older organic matter layers and the turnover times of the Oi (litter), Oe (fermentation), and Oa (humus) horizons. They then simulated the effects of increased or decreased litterfall over time and found that after a permanent 50% increase in litterfall, a new equilibrium of the transfers and turnover times of organic matter would only be reached after 4, 14, and 40 years for the Oa, Oe, and Oi horizons, respectively. However, the decomposition rates used in the model were kept constant; if changes in the amount of litterfall alter decomposition rates, the turnover time of organic matter in the forest floor may differ greatly from the values calculated. Longer or shorter turnover times for litter in the forest floor may have wide-reaching consequences for tropical forest carbon and nutrient cycling.

Despite the substantial number of studies on decomposition in a wide range of ecosystems, the influence of a sustained change in litter quantity on decay rates has thus far been largely neglected. In the humid tropics, micro- and mesoarthropods and fungi are considered to be among the most important decomposers (e.g. Zhang and Zak, 1998; Heneghan et al., 1999; Gonzalez and Seastedt, 2001). Thus, we collected mesofauna from decomposing litter within large-scale litter addition and litter removal treatments in a tropical moist forest to investigate whether increased or decreased litterfall affects early-stage decomposition of litter and whether this was correlated with changes in meso-arthropod abundance. In addition, we treated a subset of litterbags with fungicide to determine whether reduced fungal infection affects decomposition.

2. Materials and methods

2.1. Study site

The study site is in old-growth lowland moist tropical forest located on the Gigante Peninsula of the Barro Colorado Nature Monument in Panama, Central America. The soil is an oxisol with pH ca. 5.0, a low 'available' phosphorus concentration, but relatively high total nitrogen and exchangeable potassium, magnesium, and calcium (Cavalier, 1992; Sayer et al., 2006). Nearby Barro Colorado Island (ca. 5 km from the study site) has a mean annual rainfall of 2600 mm with a strong dry season, typically for four months from January to April, and an average temperature of 27 °C (Leigh, 1999).

Fifteen 45 m × 45 m plots were set up in 2000. The plots were trenched to a depth of 0.5 m to minimize nutrient- and water import via the root/mycorrhizal network, the trenches were double-lined with plastic and backfilled; a 7.5-m buffer was left around the inside of the trenches to eliminate trenching effects, resulting in a measurement plot size of 30 m × 30 m. Starting in January 2003, the litter (including branches with a diameter <100 mm) in five plots was raked up and removed once a month, resulting in low, but not entirely absent, litter standing crop (L− plots). The removed litter was immediately added to five further plots, where it was spread out as evenly as possible, effectively doubling the litterfall (L+ plots); five plots were left undisturbed as controls (CT plots).

2.2. Decomposition

To investigate how changes in litterfall affect decomposition rates, a litterbag experiment was set up in the 15 litter manipulation plots. Leaves of the common forest species *Cecropia insignis* Liebm. (henceforth referred to as *Cecropia*) were used as the trees grow abundantly in the study area and the nitrogen concentration of freshly fallen leaves is similar to the average concentration in mixed litter collected from litter traps in this forest (1.5%; Sayer and Tanner, unpublished data). Freshly fallen *Cecropia* leaves were collected from the study area in March and April 2003 and oven-dried at 60 °C. Litterbags were made of 1.2-mm fiber-glass mesh and measured 200 mm × 250 mm; 160 bags received 12 g (±0.05 g; 10 g of leaf and 2 g of petiole) of *Cecropia* leaf-litter and 60 bags received 10 g (±0.05 g) of oven-dried craft sticks made from untreated birch wood (henceforth referred to as 'wood'). Craft sticks were used instead of native wood because the samples were homogeneous in size, shape, and composition. To determine the importance of fungal decomposition in the litter manipulation treatments 60 *Cecropia* litterbags were treated with the common broad-spectrum fungicide chlorothalonil. Fungicide was reapplied to the treated bags every 2 weeks. In order to avoid contaminating untreated bags with fungicide, the treated bags were placed 3–5 m from all other decomposition bags. The fungicide was applied to each bag separately by lifting the bags onto a large plastic bag (1000 mm × 800 mm) and spraying the fungicide at a close range (200–300 mm); lifting the bags reinforced the fungicide treatment by severing any existing hyphal connections (Cuevas and Medina, 1988).

In May 2004, four bags of wood, four untreated bags of *Cecropia* leaf-litter, and four bags treated with fungicide were placed in each of the 15 litter manipulation plots. The bags were placed on the surface of the litter layer in the CT and L+ plots and on the soil surface in the L− plots. To determine whether the position of leaf-litter in the forest floor influences decomposition rates, four additional untreated *Cecropia* bags were placed on the surface of the mineral soil in each of the the CT and L+ plots and covered with litter. All litterbags, except fungicide treated bags, were anchored to the soil surface to

avoid movement that could sever roots and fungal hyphae. Litterbags in the CT plots were covered with natural litterfall, and litterbags in the L+ plots by natural litterfall and by additional litter during each raking cycle; in the L− plots fallen litter was carefully removed from the surface of the bags twice a month. One bag of each subtreatment (untreated control, fungicide treated, beneath the forest floor, and wood) was collected at random from each plot every 21–26 days for 68 days. The collected litterbags were washed to remove soil particles. As the bags in the litter removal plots tended to accumulate more soil particles due to rain splashing, the washing time for each bag was standardised by first washing the bag with the most soil particles and timing the washing required to remove the soil; all other bags were then washed for the same length of time. After the third collection (68 days) the bags in the litter removal plots contained so much soil that it was not possible to wash the contents without losing a large proportion of the remaining biomass. The contents of the bags were dried to constant weight at 60 °C and weighed. Decomposition rates were calculated as percent mass loss per day (% day^{-1}).

The dried contents of the untreated litterbags of *Cecropia* were finely ground and composite samples (one per treatment and time) were made from the litterbags after 21 and 42 days; these composite samples and all the bags (one per plot) from the final litter collection (after 68 days) were analysed for nutrient concentrations. The analyses were carried out by Waite Analytical Services, Adelaide, Australia. Phosphorus and cations were determined by nitric acid digestion, finished with hydrochloric acid, and radial view inductively coupled plasma-optical emission spectrometry (ICP-OES); total nitrogen was determined using a Carlo Erba elemental analyser (NA1500, series 2, Carlo Erba, Milan, Italy). Nutrient accumulation or release was calculated as the increase or decrease in the absolute amount of a given nutrient in the leaf-litter after 68 days.

2.3. Meso-arthropod abundance

A second litterbag experiment was set-up to assess whether changes in litterfall affect meso-arthropod abundance on decomposing litter. Freshly fallen leaves of *Simarouba amara* Aubl., (henceforth referred to as *Simarouba*) were collected in January 2003. Litterbags were made of 1.2-mm fibre-glass mesh and measured 250 mm × 250 mm; thirty bags received 10 (±0.05) g of oven-dried (60 °C) *Simarouba* leaves. In May 2003, two bags were placed randomly on the soil surface in each plot beneath the crown of an adult *Simarouba* tree and anchored to the soil surface; the bags in the litter addition plots were immediately covered with litter. Litterbags in the CT plots were covered with natural litterfall and litterbags in the L+ plots by natural litterfall and by additional litter during each raking cycle; in the L− plots fallen litter was carefully removed from the surface of the bags twice a month. One bag was collected at random from each plot after 30 and 59 days and placed in a cloth bag to allow oxygen diffusion to the samples. Immediately upon returning from the field the contents of the litterbags were placed in Berlese funnels for 48 hours, after which the leaf litter was desiccated and any remaining arthropods were likely to be dead. Extracted fauna was stored in 70% alcohol and the litter was washed, oven-dried at 60 °C, and weighed to determine mass loss due to decomposition. In each sample the total number of meso-arthropods (body size 0.1–2 mm; Swift et al., 1979) and the abundances of mites and springtails were determined under a dissecting microscope. Voucher specimens were deposited in the insect collection at the University Museum of Zoology, Cambridge, UK.

2.4. Data analysis

The comparison of litter decomposition in the treatments was based on the values of dry mass remaining at each collection. Repeated measures ANOVAs were performed to assess differences between litter manipulation treatments (CT, L+, L−) in decomposition for each experiment separately: (i) untreated *Cecropia* leaves placed above the forest floor, (ii) untreated *Cecropia* leaves placed below the forest floor, (iii) fungicide-treated *Cecropia* leaves, (iv) wood, (v) *Simarouba* leaf litter, (vi) total meso-faunal abundance on *Simarouba* leaf litter. In addition, separate paired *t*-tests were performed to assess differences in decomposition between untreated *Cecropia* leaf-litter and either fungicide-treated leaf-litter or leaf-litter beneath the forest floor within a given litter manipulation treatment.

Differences between treatments in the final nutrient concentrations and the accumulation or release of nutrients from *Cecropia* litter and the abundance of springtails and mites at each collection time were compared between treatments using separate one-way ANOVAs. Post hoc comparisons were made using Fisher's LSD test. Relationships between mass loss of *Simarouba* leaf-litter and the total number of arthropods, mites, and springtails were investigated using Pearson's correlations.

All analyses were carried out using Genstat 7.0.2 (VSN International Ltd., Hemel Hempstead, UK).

3. Results

3.1. Decomposition

Litter removal slowed the decomposition of untreated *Cecropia* leaf-litter relative to the control and litter addition treatments ($P < 0.001$, rep. measures ANOVA; Fig. 1a). The rate of decay was more than twice as high in the CT (0.22% day^{-1}) and the L+ plots (0.25% day^{-1}) than in the L− plots (0.09% day^{-1}). Mass-loss from the litter after 68 days was 7% in the L− plots, but 17% and 20% in the CT and L+ plots, respectively. *Cecropia* leaf-litter treated with fungicide also decomposed more slowly in the L− plots compared to the other two treatments ($P < 0.001$, rep. measures ANOVA; Fig. 1b); mass-loss after 68 days was 12% in the L− plots, 23% in the CT plots, and 20% in the L+ plots. In all litter manipulation treatments there was a trend towards faster decay of leaf-litter in fungicide-treated litterbags compared to untreated litterbags, which was marginally significant ($P = 0.06$, rep. measures

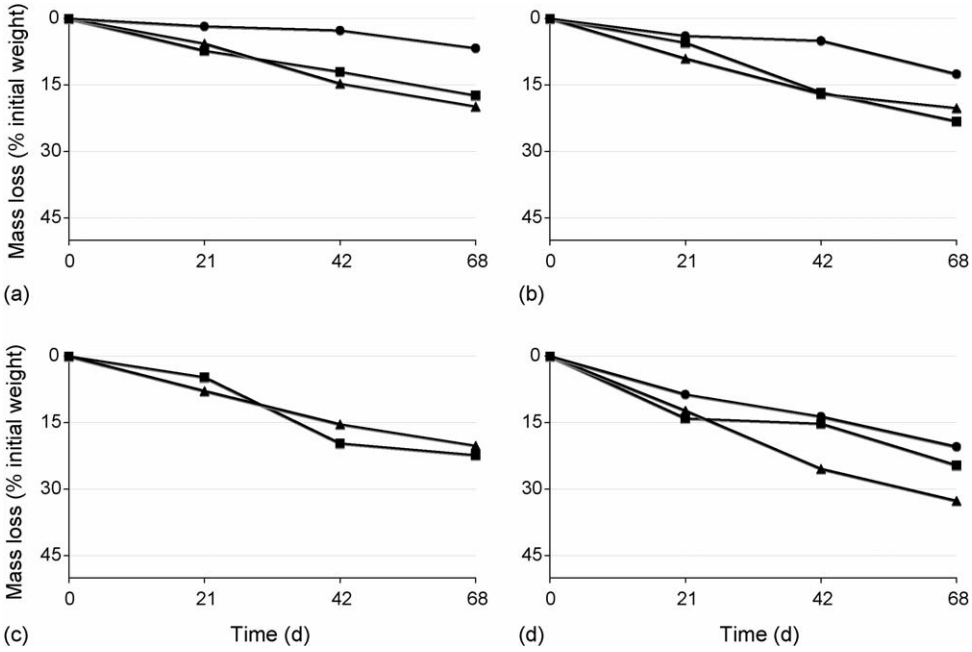

Fig. 1. Mass loss during 68 days of decomposition of (a) untreated *Cecropia insignis* leaves placed on the litter surface, (b) *C. insignis* leaves treated with fungicide, (c) untreated *C. insignis* leaves placed beneath the litter layer, and (d) birch wood sticks in litter manipulation plots in moist tropical forest, Panama, Central America; squares: control, triangles: litter addition, and circles: litter removal.

ANOVA). The position of the litter in the CT and L+ plots (whether on the surface or beneath the forest floor) had no effect on decomposition rates (Fig. 1c).

Wood decomposed faster in the L+ treatment than in the L− or the CT plots, which did not differ ($P < 0.001$, rep. measures ANOVA; Fig. 1d). The decay rate was 0.48% day^{-1} in the L+ plots, 0.36% day^{-1} in the CT plots, and 0.30% day^{-1} in the L− plots. The mass-loss of wood after 68 days was 33% in the L+ plots, compared to 25% and 20% in the CT and L− plots, respectively.

Simarouba leaf-litter decomposed more slowly in the L− treatment than the CT or L+ plots ($P = 0.01$, rep. measures ANOVA; Fig. 2). The rate of *Simarouba* leaf-litter decay was 0.90% day^{-1} in the CT and L+ plots but only 0.60% day^{-1} in the L− treatment. There was a strong time × treatment interaction, with no difference between treatments in mass loss of *Simarouba* leaf-litter after 30 days, but after 59 days the percentage of mass lost in the L− treatment (36%) was less than in the CT or L+ plots (both 53%).

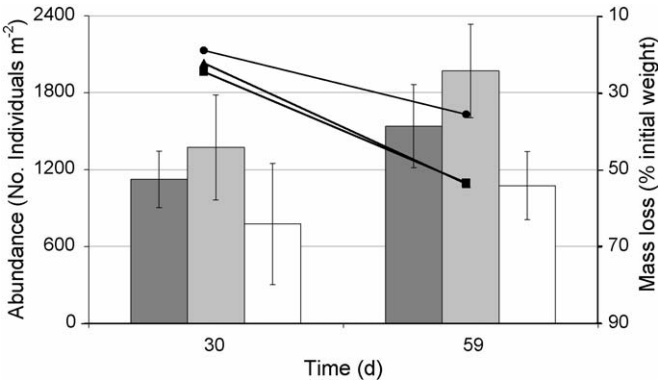

Fig. 2. Total abundance of arthropods extracted from litterbags of *Simarouba amara* after 30 and 59 days (bars) and mass loss during 68 days of decomposition of *S. amara* leaves (lines) in litter manipulation plots in moist tropical forest, Panama, Central America; dark grey bars and squares: control, light grey bars and triangles: litter addition, and white bars and circles: litter removal.

3.2. Meso-arthropods

The total number of meso-arthropods on *Simarouba* leaf-litter was lower in the L− plots than in the other two treatments ($P = 0.02$, rep. measures ANOVA; Table 1). The abundance of springtails was marginally lower in the L− treatment than in the CT or L+ plots after 30 days ($P = 0.058$, one-way ANOVA; Table 1) and the abundance of mites was lower in the L− plots after 59 days ($P = 0.019$, one-way ANOVA; Table 1). The abundance of mites in June and the abundance of springtails in July were significantly greater in the L+ plots than in the CT plots ($P = 0.41$ and $P = 0.42$, respectively, LSDs; Table 1).

Mass loss of *Simarouba* leaf-litter over 59 days was related to both the total number of arthropods and the number of mites in the litterbags ($P = 0.003$, $R = 0.48$ and $P = 0.016$, $R = 0.39$, respectively, Pearson correlation; Fig. 2).

3.3. Nutrient concentrations in decomposing Cecropia leaf-litter

The concentrations of nitrogen, phosphorus, potassium, and magnesium in decomposing *Cecropia* litter at 68 days were higher in L+ and lower in L− plots and the net accumulation or release of these nutrients were altered by litter addition and

Table 1
Total abundance of mesofauna, mites, and springtails extracted from decomposing *Simarouba amara* leaf-litter in litter manipulation treatments in Panama, Central America, given as the number of individuals per m^{-2}

	Mites (Acari)		Springtails (Collembola)		Total mesofauna	
	June	July	June	July	June	July
CT	422 ± 67 b	886 ± 177 b	365 ± 109	154 ± 28 b	1123 ± 221 b	1539 ± 325 b
L+	752 ± 239 a	598 ± 81 b	291 ± 90	666 ± 10 a	1372 ± 410 b	1971 ± 365 b
L−	346 ± 147 b	314 ± 73 a	115 ± 37*	198 ± 86 b	774 ± 475 a	1075 ± 266 a

CT: control, L+: litter addition, L−: litter removal. Standard errors for $N = 5$ plots per treatment are given. Different letters in a column denote significant differences between treatments at $P < 0.05$.
* Denotes a marginally significant difference ($P = 0.058$) to the other two treatments.

litter removal (Table 2). Nitrogen accumulated in decomposing *Cecropia* litter in all three treatments (Fig. 3a), but litter addition significantly increased the net accumulation of nitrogen relative to the L− treatments ($P = 0.036$; Table 2) and nitrogen concentrations were 10% higher in the L+ plots compared to the L− plots ($P = 0.017$; Table 2) at the end of the experiment. Net accumulation of phosphorus occurred in all three treatments over the 68 days of decomposition (Fig. 3b), but the net accumulation of phosphorus in the L+ treatment was three times as high as in the L− treatment ($P = 0.019$) and almost twice as high as in the controls (Table 2). The final concentration of phosphorus was 40% greater in the L+ plots compared to the L− plots ($P = 0.019$; Table 2). Less potassium was released in the L+ treatment than in the controls ($P = 0.055$) or L− treatments ($P = 0.008$; Fig. 3c) and the concentration of potassium in *Cecropia* litter in the L+ plots after 68 days was almost twice as high as in the controls ($P = 0.049$), and three times greater than in the L− plots ($P = 0.005$; Table 2). The release of magnesium from decomposing litter (Fig. 3d) was also reduced in the L+ plots compared to the controls ($P = 0.009$) or L− plots ($P < 0.001$; Table 2); the concentration of magnesium was 25% higher in the L+ plots and 21% lower in the L− compared to the controls ($P = 0.002$ and 0.008, respectively; Table 2). Calcium accumulated equally in the decomposing litter in all three treatments (Fig. 3e) and the final concentrations of calcium did not differ between treatments (Table 2). Sodium and sulphur were released from decomposing *Cecropia* litter in all three treatments (Fig. 3f and g, respectively) but at the end of the experiment, the concentration of sodium was 38% higher and the concentration of sulphur was 33% higher in the L+ plots than in the L− plots ($P = 0.013$ and 0.005, respectively; Table 2).

4. Discussion

4.1. Decomposition of litter and abundance of mesofauna

Litter removal treatments slowed the decomposition of leaf-litter. Although litterbags in the CT and L+ plots were covered by litter during the experiment while the litterbags in the L− plots remained exposed, it is unlikely that the decreased decomposition rates in litterbags in the L− plots were due to greater exposure. Frequent rainfall during the study period (rainy season) prevented drying-out, especially as litterbags usually keep litter wetter than under natural conditions (Tanner, 1981); the litterbags were generally very wet at each collection time. Furthermore, the initial position of the *Cecropia* litterbags (above or beneath the forest floor) in the CT and L+ plots had no effect on decomposition rates. Lower abundance of decomposer organisms and decreased nutrient availability following litter removal are the most likely causes for slower decomposition in the L− plots.

Litter removal reduces the amount of substrate for microorganisms and the habitat space for arthropods (Sayer, 2006). Litter arthropods are important for the comminution of leaf-litter, which exposes a greater surface for attack by microbial decomposers (Singh and Gupta, 1977; Petersen and Luxton, 1982; Bradford et al., 2002), and meso- and microarthropods, in particular mites and springtails, are thought

Table 2
Concentrations and net accumulation or release of nutrients in *Cecropia insignis* leaves after 68 days of decomposition in litter manipulation plots in old-growth forest in Panama, Central America

	Initial concentration (mg g^{-1})	Final concentration (mg g^{-1})			Net accumulation/release (mg g^{-1})		
		CT	L+	L−	CT	L+	L−
N	15.0	17.7 ab	18.2 b	16.4 a	2.67 ab	3.22 a	1.39 b
P	0.25	0.37 ab	0.46 b	0.31 a	0.12 ab	0.21 a	0.06 b
K	2.50	0.51 a	0.97 b	0.37 a	−1.99 a	−1.53 b	−2.13 a
Ca	11.6	17.1	17.8	15.6	5.53	6.16	4.04
Mg	4.50	2.67 a	3.28 b	2.42 a	−1.83 a	−1.22 b	−2.08 a
Na	1.21	0.10	0.12	0.10	−1.11	−1.09	−1.11
S	1.88	1.55	1.65	1.51	−0.33	−0.23	−0.37

CT: control, L+: litter addition, L−: litter removal. Different letters denote differences between treatments in the final concentration or the net accumulation/release for a given nutrient at $P < 0.05$. Where a row has no letters, there were no significant treatment differences for that nutrient.

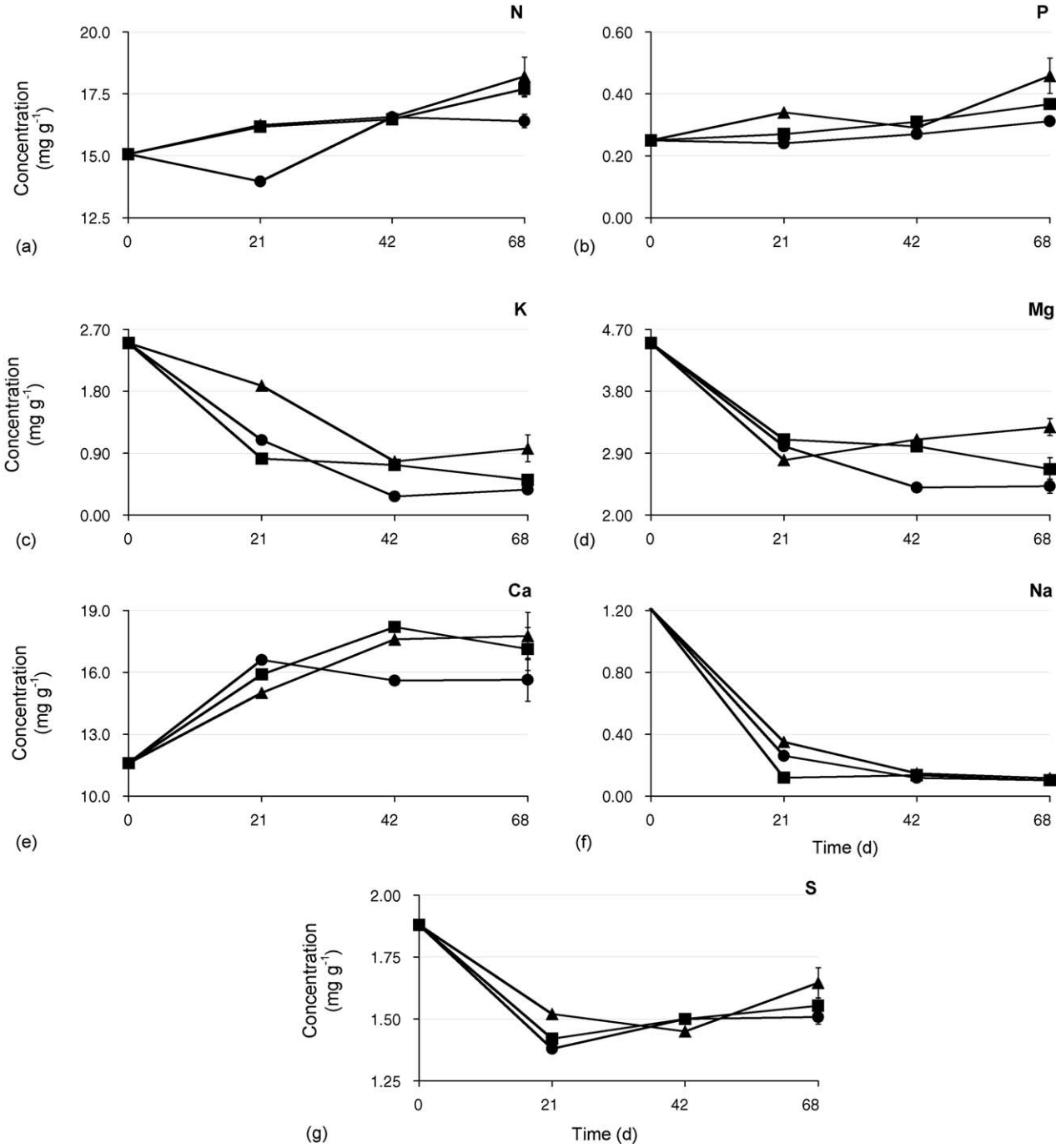

Fig. 3. Changes in the concentrations of (a) nitrogen, (b) potassium, (c) phosphorus, (d) magnesium, (e) calcium, (f) sodium, and (g) sulphur during 68 days of decomposition of *C. insignis* leaves in litter manipulation plots in moist tropical forest, Panama, Central America; squares: control, triangles: litter addition, and circles: litter removal. Standard errors are given for the values at 68 days; values given for 21 and 42 days are composite samples made by combining samples from each of the five plots per treatment.

to play an important role in decomposition in the tropics (Madge, 1965; Heneghan et al., 1999; Gonzalez and Seastedt, 2001). In our study, mites and springtails made up between 64% and 76% of the total fauna in the litterbags in the CT and L+ plots and between 47% and 60% of the total in the L− plots. Lower abundances of meso-arthropods, especially mites, were found in litterbags in the L− plots; the significant relationship between the decrease in mass of *Simarouba* leaf-litter with the decreased abundance of meso-arthropods suggests that the lower numbers of decomposers in the L− plots contributed greatly to the reduced decomposition rates of the leaf-litter.

Surprisingly, the total abundance of meso-arthropods in the litterbags did not differ greatly between the CT and L+ treatment, despite the increase in substrate and habitat space with the addition of litter, and we observed only transient increases in mite and springtail abundance in the L+ plots. Similar results have been reported for temperate forests, where changes in both abundance and community composition in

litter addition treatments were generally less than expected (Poser, 1990; David et al., 1991; Ponge et al., 1993; Arpin et al., 1995; Sayer, 2006). The lack of expected increase in litter addition treatments may be due to possible adverse effects of litter addition treatments on soil and litter fauna such as reduced diffusion of oxygen in the denser forest floor (Judas, 1990), increases in the numbers of predators (Uetz, 1979), and greater amounts of phytochemicals (Sayer, 2006).

Although the initial nutrient concentration of the litter is important in determining decay rates, nutrient availability in the surface soil may also have some influence (Prescott et al., 1993; Hobbie and Vitousek, 2000). The increase of nutrient concentrations in decomposing litter generally indicates which nutrients are limiting the activity of decomposer organisms (Anderson et al., 1983; McGroddy et al., 2004). In our study, the concentrations of nitrogen and phosphorus increased in *Cecropia* leaf-litter during the early stages of decomposition (Fig. 3a and b, respectively). An analysis of surface soil samples (0–20 mm) showed that the availability of these nutrients was lower in the L− plots than the controls (Sayer and Tanner, unpublished data). Thus, the lower decay rates are related to the lower soil nutrient content in the L− treatment.

In contrast to the patterns of decomposition for leaf-litter, wood decomposed faster in the L+ treatment than in the CT or L− plots, which did not differ. As our litterbags excluded larger saprophagous insects such as termites and beetles, fungi were the main decomposers of woody debris in this experiment; this result therefore suggests that fungal activity in the forest floor is greater in the L+ plots than the other treatments. Higher nutrient availability in the forest floor in the L+ plots appears to have reduced the nutrient limitation of decomposition for nutrient-poor, high-lignin substrate such as wood.

Although it has been suggested that fungi are more critical for decomposition processes in the dry season than the rainy season (Cornejo et al., 1994; Lodge et al., 1994), Yavitt et al. (2004) found greater abundance of fungi on decomposing litter during the rainy season in the same forest type on Barro Colorado Island, 5 km away from our study site. This indicates that fungi are important decomposers during the rainy season in this forest. Nevertheless, contrary to expectations, the leaf-litter in bags treated with fungicide decomposed at the same rate as, or slightly faster than, untreated litter. It is unlikely that wetting the leaf-litter by fungicide application had an effect on their decomposition during the rainy season, as the litter on the ground was generally very wet and did not dry out between rainfall events. It is also improbable that lifting the bags resulted in a noticeable loss of fine material from the treated bags, as fine mesh was used for the litterbags; furthermore, the greater losses during washing render any small losses due to lifting and/or transportation negligible.

There remain two possible explanations for the similarity in mass loss between treated and untreated litterbags:

(i) Untreated leaf-litter decomposed faster than fungicide-treated litter, but fungal biomass in the untreated litterbags compensated for the lost weight. Casual observation of the samples supports this suggestion, as there was no visible evidence of fungal mycelium in the treated litterbags, while untreated bags often had a high proportion of mycelium on the litter.
(ii) The application of fungicide reduced the competition between fungi and bacteria and bacterial decomposition increased (Møller et al., 1999).

It is probable that a combination of these two factors contributed to the lack of differences in decomposition between fungicide-treated and untreated *Cecropia* litter. Similarly, the differences in mass loss between CT and L+ plots in wood, but not in leaf-litter, may be a consequence of greater fungal biomass in the L+ plots. In early stages of decomposition, fungal hyphae and mycelium can be removed from the surface of wood samples during washing, but leaf fragments and fungal biomass cannot be separated. In this study, an increase in fungal biomass in the L+ plots would therefore contribute to the measured weight remaining in leaf-litter, but not in wood.

We could find no studies on the effects of chlorothalonil on soil fauna and did not measure meso-arthropods in the fungicide experiment, so there is a small possibility that chlorothalonil affected decomposition via an effect on litter fauna.

4.2. Nutrient dynamics in decomposing litter

Litter manipulation modified the timing and degree of nutrient release or accumulation during early-stage decay in this experiment, and resulted in differences between treatments in the concentrations of nitrogen, phosphorus, potassium, and magnesium in *Cecropia* litter after 68 days of decomposition. There are generally three phases of nutrient dynamics during decomposition: (i) initial release caused by leaching, (ii) net accumulation (immobilization), and (iii) net release with mineralization (Gosz et al., 1973; Swift et al., 1979; Chuyong et al., 2002). When a nutrient is limiting to the metabolic processes of decomposer microorganisms the initial release does not take place and accumulation occurs until the nutrient concentration approaches that of microbial tissue (Anderson et al., 1983), in tropical forests this pattern is typical for phosphorus and nitrogen (Vitousek and Sanford, 1986; Rogers, 2002). Decomposition processes are often primarily nitrogen-limited, but other nutrients can become limiting when nitrogen is in sufficient supply (Swift et al., 1979) and although nitrogen concentrations in the *Cecropia* litter increased during the study period, net accumulation was relatively low (Fig. 3a; Table 2). Phosphorus is thought to be the main limiting nutrient in the study area, as concentrations in the soil are low (Cavalier, 1992; Sayer et al., 2006), and the net accumulation of phosphorus in the decomposing litter supports this assumption (Fig. 3b; Table 2). Greater accumulation of phosphorus in the L+ plots compared to the controls suggests higher phosphorus availability in the forest floor (Rothstein et al., 2004), as the import of phosphorus into fresh litter is facilitated by the release of phosphorus from the greater mass of older decomposing organic matter.

Despite the lack of effects of the fungicide treatments, the differences in the concentrations of potassium are suggestive of greater fungal activity in the L+ plots. Potassium is selectively

taken up by fungi during the decomposition process (Cromack et al., 1975; Tyler, 2005) and the net release of potassium was 23% less in the L+ treatment than in the controls and 28% less than in the L− plots. As potassium is normally readily leached from litter (Lousier and Parkinson, 1978), the greater concentration and amount of potassium in the litter in the L+ plots may be indicative of increased fungal biomass. Although it is possible that litter addition reduced leaching, there were no differences between treatments in release of sodium (Fig. 3f), which was the element most readily leached from the litter. Washing the litterbags likely caused leaching in particular of water-soluble nutrients from the litter, especially potassium and sodium, therefore comparisons of the concentrations of these nutrients with other datasets should be treated with caution. However, in this study, between-treatment comparisons are valid as all the bags were washed for the same length of time.

5. Conclusions

Decreased litter standing crop slowed the decomposition of leaf-litter by decreasing the population of decomposers and by reducing the supply of available nutrients in the soil. Increased litterfall appeared to have little effect on early-stage leaf-litter decomposition, but the accelerated decomposition of wood suggests greater availability of nutrients to decomposer organisms in the L+ treatment. It is possible that greater fungal biomass in litter in the L+ plots obscured increased mass loss due to decomposition compared to the controls; this merits further study.

Litterfall in forests may be affected by climate change through changes in precipitation and increased primary production. Thus, although many studies have found that differences in litter quality under elevated CO_2 levels had little effect on the decay rates of litter in forests (Hirschel et al., 1997; Gahrooee, 1998; Finzi et al., 2001), the effects of climate change on litter quantity may influence the decomposition of litter and woody debris and greatly modify the transfer of organic matter through the forest floor in tropical forests, with consequences for the carbon and nutrient cycle.

Acknowledgments

We thank Jesus Valdez and Ruscena Wiederholt for help with fieldwork, Dr. M. Kaspari and Mary Johnston for helpful comments and the use of the Berlese funnels, and two anonymous reviewers for critical comments that improved this manuscript. This study was funded by the Mellon Foundation, the Gates Cambridge Trust, the Smithsonian Tropical Research Institute, a Worts' Travelling Scholarship, and a Cambridge Philosophical Society Travel Grant. The entire study was carried out at the Smithsonian Tropical Research Institute, to whom we are very grateful.

References

Allen, A.S., Andrews, J.A., Finzi, A.C., Matamala, R., Richter, D.D., Schlesinger, W.H., 2000. Effects of free-air CO_2 enrichment (FACE) on belowground processes in a *Pinus taeda* forest. Ecol. Appl. 10, 437–448.

Anderson, J.M., Proctor, J., Vallack, H.W., 1983. Ecological studies in four contrasting lowland rain forests in Gunung-Mulu National Park Sarawak. 3. Decomposition processes and nutrient losses from leaf litter. J. Ecol. 71, 503–527.

Anderson, J.M., Swift, M.J., 1983. Decomposition in tropical forests. In: Sutton, S.L., Whitmore, T.C., Chadwick, A.C. (Eds.), Tropical Rain Forest: Ecology and Management. Blackwell Scientific, Oxford, pp. 287–309.

Arpin, P., Ponge, J.F., Vannier, G., 1995. Experimental modifications of litter supplies in a forest mull and reaction of the nematode fauna. Fund. Appl. Nematol. 18, 371–389.

Bloomfield, J., Vogt, K.A., Vogt, D.J., 1993. Decay-rate and substrate quality of fine roots and foliage of 2 tropical tree species in the Luquillo experimental forest. Puerto-Rico. Plant Soil 150, 233–245.

Bradford, M.A., Tordof, G.M., Eggers, T., Jones, H., Newington, J.E., 2002. Microbiota, fauna, and mesh size interaction in litter decomposition. Oikos 99, 317–323.

Cavalier, J., 1992. Fine-root biomass and soil properties in a semi-deciduous and a lower montane rain forest in Panama. Plant Soil 142, 187–201.

Chuyong, G.B., Newbery, D.M., Songwe, N.C., 2002. Litter breakdown and mineralization in a central African rain forest dominated by ectomycorrhizal trees. Biogeochemistry 61, 73–94.

Cornejo, F.H., Varela, A., Wright, S.J., 1994. Tropical forest litter decomposition under seasonal drought: nutrient release, fungi and bacteria. Oikos 70, 183–190.

Couteaux, M.-M., Bottner, P., Berg, B., 1995. Litter decomposition, climate and litter quality. Trends Ecol. Evol. 10, 63–66.

Cromack, K., Todd, R.L., Monk, C.D., 1975. Patterns of basidiomycete nutrient accumulation in conifer and deciduous forest litter. Soil Biol. Biochem. 7, 265–268.

Cuevas, E., Medina, E., 1986. Nutrient dynamics within Amazonian forests. I. Nutrient flux in fine litter fall and efficiency of nutrient utilization. Oecologia 68, 466–472.

Cuevas, E., Medina, E., 1988. Nutrient dynamics within Amazonian forests. II. Fine root growth, nutrient availability and leaf litter decomposition. Oecologia 76, 222–235.

Cullings, K.W., New, M.H., Makhija, S., Parker, V.T., 2003. Effects of litter addition on ectomycorrhizal associates of a lodgepole pine (*Pinus contorta*) stand in Yellowstone National Park. Appl. Environ. Microb. 69, 3772–3776.

David, J.-F., Ponge, J.F., Arpin, P., Vannier, G., 1991. Reactions of the macrofauna of a forest mull to experimental perturbations of litter supply. Oikos 61, 316–326.

DeLucia, E.H., Hamilton, J.G., Naidu, S.L., Thomas, R.B., Andrews, J.A., Finzi, A.C., Lavine, M., Matamala, R., Mohan, J.E., Hendrey, G.R., Schlesinger, W.H., 1999. Net primary production of a forest ecosystem with experimental CO_2 enrichment. Science 284, 1177–1179.

Finzi, A.C., Allen, A.S., DeLucia, E.H., Ellsworth, D.S., Schlesinger, W.H., 2001. Forest litter production, chemistry, and decomposition following 2 years of free-air CO_2 enrichment. Ecology 82, 470–484.

Gahrooee, F.R., 1998. Impacts of elevated CO_2 on litter quality litter decomposability and nitrogen turnover rate of two oak species in a Mediterranean forest ecosystem. Glob. Change Biol. 4, 667–677.

Gonzalez, G., Seastedt, T.R., 2001. Soil fauna and plant litter decomposition in tropical and subalpine forests. Ecology 82, 955–964.

Gosz, J.R., Likens, G.E., Bormann, F.H., 1973. Nutrient release from decomposing leaf and branch litter in the Hubbard Brook Forest New Hampshire. Ecol. Monogr. 43, 173–191.

Heneghan, L., Coleman, D.C., Zou, X., Crossley, D.A., Haines, B.L., 1999. Soil microarthropod contributions to decomposition dynamics: tropical-temperate comparisons of a single substrate. Ecology 80, 1873–1882.

Hirschel, G., Korner, C., Arnone, J.A., 1997. Will rising atmospheric CO_2 affect leaf litter quality and in situ decomposition rates in native plant communities? Oecologia 110, 387–392.

Hobbie, S.E., Vitousek, P.M., 2000. Nutrient limitation of decomposition in Hawaiian forests. Ecology 81, 1867–1877.

Jordan, C.F., 1985. Nutrient Cycling in Tropical Forest Ecosystems. John Wiley and Sons Ltd., Chichester.

Judas, M., 1990. The development of earthworm populations following manipulation of the canopy leaf litter in a beechwood on limestone. Pedobiologia 34, 247–255.

Leigh Jr., E.G., 1999. Tropical Forest Ecology. Oxford University Press, Oxford.

Lodge, D.J., McDowell, W.H., McSwiney, C.P., 1994. The importance of nutrient pulses in tropical forests. Trends Ecol. Evol. 9, 384–387.

Lousier, J.D., Parkinson, D., 1978. Chemical element dynamics in decomposing leaf litter. Can. J. Bot. 56, 2795–2812.

Madge, D.S., 1965. Leaf fall and litter disappearance in a tropical forest. Pedobiologia 5, 273–288.

McGroddy, M., Silver, W.L., Cosme de Olveira Jr., R., 2004. The effect of phosphorus availability on decomposition dynamics in a seasonal lowland Amazonian forest. Ecosystems 7, 172–179.

Møller, J., Miller, M., Kjøller, A., 1999. Fungal-bacterial interaction on beech leaves: influence on decomposition and dissolved organic carbon quality. Soil Biol. Biochem. 31, 367–374.

Ostertag, R., Scatena, F.N., Silver, W.L., 2003. Forest floor decomposition following hurricane litter inputs in several Puerto Rican forests. Ecosystems 6, 261–273.

Ostertag, R., Hobbie, S.E., 1999. Early stages of root and leaf decomposition in Hawaiian forests: effects of nutrient availability. Oecologia 121, 564–573.

Pearse, A.S., 1943. Effects of burning-over and raking-off litter on certain animals in the Duke Forest. Am. Midl. Nat. 406–424.

Petersen, H., Luxton, M., 1982. A comparative analysis of soil fauna populations and their role in decomposition processes. Oikos 39, 287–388.

Ponge, J.F., Arpin, P., Vannier, G., 1993. Collembolan response to experimental perturbations of litter supply in a temperate forest ecosystem Eur. J. Soil Sci. 29, 141–153.

Poser, T., 1990. The Influence of litter manipulation on the centipedes of a beech wood. In: Minelli, A. (Ed.), Proceedings of the Seventh International Congress on Myriapods. Brill, Leiden, pp. 235–245.

Prescott, C.E., Taylor, B.R., Parsons, W.F.J., Durall, D.M., Parkinson, D., 1993. Nutrient release from decomposing litter in Rocky Mountain coniferous forests: influence of nutrient availability. Can. J. For. Res. 23, 1576–1586.

Rogers, H.M., 2002. Litterfall decomposition and nutrient release in a lowland rain forest, Morobe Province Papua New Guinea. J. Trop. Ecol. 18, 449–456.

Rothstein, D.E., Vitousek, P.M., Simmons, B.L., 2004. An exotic tree alters decomposition and nutrient cycling in a Hawaiian montane forest. Ecosystems 7, 805–814.

Sampaio, E.V.D.B., Dall'Olio, A., Nunes, K.S., Delemos, E.E.P., 1993. A model of litterfall, litter layer losses and mass-transfer in a humid tropical forest at Pernambuco Brazil. J. Trop. Ecol. 9, 291–301.

Sayer, E.J., 2006. Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. Biol. Rev. 81, 1–31.

Sayer, E.J., Tanner, E.V.J., Cheesman, A.W, 2006. Increased litterfall changes fine root distribution in a moist tropical forest. Plant Soil 281, in press.

Schlesinger, W.H., Lichter, J., 2001. Limited carbon storage in soil and litter of experimental forest plots under increased atmospheric CO_2. Nature 411, 466–469.

Singh, J.S., Gupta, S.R., 1977. Plant decomposition and soil respiration in terrestrial ecosystems. Bot. Rev. 43, 449–528.

Swift, M.J., Heal, O.W., Anderson, J.M., 1979. Decomposition in Terrestrial Ecosystems. University of California Press, Berkley.

Tanner, E.V.J., 1981. The decomposition of leaf litter in Jamaican montane rain forests. J. Ecol. 69, 263–275.

Tyler, G., 1991. Effects of litter treatments on the sporophore production of beech forest macrofungi. Mycol. Res. 95, 1137–1139.

Tyler, G., 2005. Changes in the concentrations of major, minor and rare-earth elements during leaf senescence and decomposition in a *Fagus sylvatica* forest. Forest Ecol. Manage. 206, 167–177.

Uetz, G.W., 1979. The influence of variation in litter habitats on spider communities. Oecologia 40, 29–42.

Vasconcelos, H.L., Lawrence, W.F., 2005. Influence of habitat, litter type, and soil invertebrates on leaf-litter decomposition in a fragmented Amazonian landscape. Oecologia 144, 456–462.

Vitousek, P., Sanford Jr., L., 1986. Nutrient cycling in moist tropical forest. Ann. Rev. Ecol. Syst. 17, 137–167.

Wieder, R.K., Wright, J.S., 1995. Tropical forest litter dynamics and dry season irrigation on Barro Colorado Island, Panama. Ecolology 76, 1971–1979.

Yavitt, J.B., Wright, S.J., Wieder, R.K., 2004. Seasonal drought and dry-season irrigation influence leaf- litter nutrients and soil enzymes in a moist, lowland forest in Panama. Austral. Ecology 29, 177–188.

Zak, D.R., Holmes, W.E., Finzi, A.C., Norby, R.J., Schlesinger, W.H., 2003. Soil nitrogen cycling under elevated CO_2: a synthesis of forest FACE experiments. Ecol. Appl. 13, 1508–1514.

Zhang, Q., Zak, J.C., 1998. Potential physiological activities of fungi and bacteria in relation to plant litter decomposition along a gap size gradient in a natural subtropical forest. Microb. Ecol. 35, 172–179.