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Do ectomycorrhizas alter leaf-litter decomposition in monodominant tropical forests of Guyana?

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Summary

• This work tested the hypothesis that ectomycorrhizas (EM) of *Dicymbe corymbosa* alter leaf-litter decomposition and residual litter quality in tropical forests of Guyana.

• Mass loss of leaf litter in litter bags was determined on three occasions, in two experiments, during a 12-month period. Paired root-exclusion plots were located randomly within a *D. corymbosa* forest. Both *D. corymbosa* and mixed-species leaf litters were reciprocally transplanted into their respective forest types. Elemental analysis was performed on the residual *D. corymbosa* leaf litter after 1 yr.

• Leaf litter mass loss in the *D. corymbosa* forest was not influenced by EM, despite high EM colonization. Elemental analysis of *D. corymbosa* leaf litter residues demonstrated reduced calcium levels in the presence of EM, which were negatively correlated with EM rootlet-colonizing mass.

• The lack of EM effect on the litter decomposition rate, coupled with high EM colonization, suggests an important but indirect role in mineral nutrient acquisition. Lowered Ca concentration in leaf litter exposed to EM may suggest a high Ca demand by the ectotroph system.

Key words: calcium (Ca), *Dicymbe corymbosa* (Caesalpiniaceae), ectomycorrhizas (EM), fungal ecology, Gadgil effect, Guiana shield.

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Introduction

Tropical monodominant forests are a long-standing point of interest in tropical ecology because they contrast sharply with more typical, highly tree-diverse rain forests (Davis & Richards, 1933; Richards, 1952; Gérard, 1960; Connell & Lowman, 1989; Leigh *et al.*, 2004). In Guyana, *Dicymbe corymbosa* (Caesalpiniaceae) is a leguminous, ectomycorrhizal (EM) canopy tree species exhibiting one of the most striking examples of monospecific dominance in the Neotropics (Richards, 1996; Henkel *et al.*, 2002; Henkel, 2003). Throughout the central Pakaraima Mountains of Guyana, at the eastern extent of the Guayana Highlands, *D. corymbosa* occurs in a mosaic of stands ranging in size from one to many hectares immersed in a matrix of tree species-rich, arbuscular mycorrhizal (AM) mixed rain forest. In these stands, which occur on a wide variety of soils, *D. corymbosa* comprises 70–95% of the total basal area and maintains high densities of seedlings and saplings, indicative of self-replacement (Henkel, 2003). Mast fruiting, shoot reiteration, and closed nutrient cycling via EM have been suggested as contributing to *D. corymbosa* monodominance through the competitive exclusion of AM trees (Henkel, 2003; Henkel *et al.*, 2005).

Elsewhere in the tropics, the best known and most widespread monodominant rain forest tree species also form EM, suggesting that this mycorrhizal type may be necessary to maintain monodominance (Alexander, 1989; Connell & Lowman, 1989; Hart *et al.*, 1989; Newbery, 2005). Mechanisms proposed for EM-mediated monodominance have centred on the superior ability of EM in mineral nutrient acquisition, storage and translocation relative to the more common AM characterizing most tropical trees (Janos, 1983;

Leake & Read, 1997; Dighton, 2003). When both monodominant EM and tree-diverse AM tropical forests segregate into sharply demarcated, co-occurring stands, such as in Guyana, inherent differences in nutrient cycling resulting from their mycorrhizal type may contribute to the success of the monodominant species. Such differences might include EM control over mineral cycling (Newbery *et al.*, 1997; Chuyong *et al.*, 2000), which can be particularly important on highly weathered tropical soils where P is often the nutrient most limiting to plants (Vitousek, 1984; Richter & Markewitz, 2001; Cleveland *et al.*, 2002). Ectomycorrhizal acquisition of N and P from various organic molecules *in vitro* suggested that EM may also access N and P directly from litter (Leake & Read, 1997; Pérez-Moreno & Read, 2000, 2001a, 2001b). The uptake and mycelial transfer of various sources of Ca and magnesium may also contribute to host-plant fitness (Andersson *et al.*, 1996). The degree to which these processes occur in nature, however, remains unclear (Allen *et al.*, 2003; Dighton, 2003; Read & Pérez-Moreno, 2003; Cairney, 2005).

Ectomycorrhizas could affect *D. corymbosa* fitness directly or indirectly. For instance, seedling shade tolerance may be enhanced through carbon and mineral nutrient sharing via a common EM network (Arnebrant *et al.*, 1993; He *et al.*, 2004). Direct acquisition of organic nutrients by EM fungi may lead to a reduced mineral nutrient pool available for AM trees, precluding establishment of AM seedlings (Allen, 1991). Additionally, resulting alteration of the C:N/P ratio of leaf litter could lead to delayed decomposition rates (Abuzinadah *et al.*, 1986; Bending & Read, 1996; Cleveland *et al.*, 2002), deeper litter layers, and further reduction in AM establishment.

Inhibition of saprotrophic fungi is another mechanism by which EM may obtain greater access to mineral nutrients contained in litter, thereby facilitating host tree success (Gadgil & Gadgil, 1971, 1975; Leake *et al.*, 2002). Root-excluding trenched plots eliminated EM activity in a monospecific *Pinus radiata* plantation, which resulted in an increased decomposition rate of *P. radiata* needles, suggesting that saprotrophic fungi were released from EM suppression (the 'Gadgil effect'; Gadgil & Gadgil, 1971, 1975). Support for the Gadgil effect has subsequently been equivocal, but evidence for competitive interactions of EM with saprotrophic fungi is substantial (Chalot & Brun, 1998; Lindahl *et al.*, 1999, 2001; Cairney & Meharg, 2002; Leake *et al.*, 2002; Wu *et al.*, 2003; Cairney, 2005). The nature of EM/saprotroph interactions will affect mineral nutrient-cycling pathways and, ultimately, the EM tree's competitive success (Entry *et al.*, 1991; Northup *et al.*, 1995; Allen *et al.*, 2003; Langley & Hungate, 2003). In an ongoing effort to discern potential advantages gained by *D. corymbosa* through the EM symbiosis, this study is the first to address the role that EM may play in *D. corymbosa* litter decomposition and nutrient cycling.

The *D. corymbosa* forest is an ideal system in which to explore EM influences on decomposition and mineral nutrient cycling, for several reasons. (1) No study has examined EM interactions with saprotrophic fungi in an otherwise AM-dominated landscape (Leake *et al.*, 2002). (2) *Dicymbe corymbosa* stands have deeper leaf litter layers and greater humic accumulations relative to the surrounding AM-dominated forest (Henkel, 2003; this study) suggestive of altered litter decomposition processes (Read, 1991; Bending & Read, 1995a, 1995b). (3) The dense proliferation of EM rootlets and extramatrical hyphae in *D. corymbosa* litter layers, as well as the high mineral nutrient investment in mast fruiting by *D. corymbosa*, are suggestive of an EM-mediated nutrient cycling mechanism (Newbery *et al.*, 1997; Henkel *et al.*, 2005; Newbery, 2005). This study addressed two main questions: first, within a monodominant stand of *D. corymbosa*, does the elimination of viable EM alter leaf-litter decomposition? Second, will the presence of EM alter the net mineral nutrient content of residual leaf litter after 1 yr of decomposition? If such processes occur in *D. corymbosa* forests, they may indicate EM-mediated pathways which contribute to the host tree's competitive success through preferential nutrient acquisition, increased litter depth and AM–seedling inhibition.

Materials and Methods

Site characterization

The study site was located within a 5-km radius of a previously established base camp in the Pakaraima Mountains of west-central Guyana (5°18′04.8″ N, 59°54′40.4″ W, elevation 710 m; Henkel, 2003). The site occurred approx. 15 km east of Mount Ayanganna in a regional seasonal evergreen forest of the *Eschweilera–Licania* association (Fanshawe, 1952). Within the intermountain valleys of the region there is a mosaic of primary *Dicymbe corymbosa* Spruce ex Benth. single-dominant stands, one to many hectares, sharply juxtaposed with surrounding AM mixed-species forests lacking *Dicymbe* (Henkel, 2003). Soils of the *D. corymbosa* and mixed-species forests were variable in texture but uniformly acidic, low in extractable P and high in Al. Further details of geology, soils and vegetation of the site are given by Henkel (2003); Henkel *et al.* (2005).

Stand delimitation

Within a larger homogeneous area of monodominant *D. corymbosa* forest, a 100 × 30-m stand was delimited in June 2003 (DF). A second 100 × 30-m stand was delimited approx. 0.5 km to the east of DF in an exclusively AM mixed-species forest lacking *Dicymbe* (MF). These areas were selected to receive the decomposition plots based on the criteria of having no large canopy gaps, a slope < 10%, well drained soils, and being representative of a much larger area of forest. We can be confident that the 100 × 30-m stands were representative of their respective forest types at a much larger scale, based on

previous studies of both forest types (Henkel, 2003; Henkel *et al.*, 2005) and the perceived uniformity of the forest topographies and litter depths. For this reason the random locations of decomposition study plots within these representative stands (reduced interspersion) encompassed much of the variability in the forest-floor environment, and are therefore statistically valid localized experiments, the results of which, in the strict sense, should be tentatively valid at larger scales.

To characterize site variables that might covary with leaf-litter decomposition, tree communities were enumerated, canopy cover quantified, and leaf-litter depth measured. In both DF and MF, all trees = 10 cm were mapped and diameter at breast height (dbh, 1.37 m above the ground) was recorded. All trees were identified to morphospecies in the field and later assigned to genus and species when possible. Basal area was calculated for each species (Henkel, 2003). Canopy cover was estimated for both plots using a Model-A spherical densiometer (Forestry Suppliers Inc., Jackson, MI, USA). Canopy cover measurements were made at 20-m intervals along a 200-m transect in both DF and MF, and averaged for each. Leaf-litter depth in MF and DF was sampled systematically within a 2-d period during July 2004. A litter probe was inserted at 40 equally spaced points distributed throughout MF and DF until contact with the mineral soil was made, and the depth was recorded.

To complement stand-wide litter-depth measurements, litter accumulations were characterized around large *D. corymbosa* trees. Twenty-two trees > 100 cm dbh were selected randomly from within five previously established plots at the Potaro site (Henkel *et al.*, 2005) and basal root mounds were measured. Using a litter probe, root mound depth from surface of suspended litter horizon to mineral soil was recorded immediately adjacent to the tree trunk, in the middle of the mound, and again at the exterior edge of the mound where the slope flattened to 0°. The pH of mound humus was recorded from three of the 22 trees used for root mound measurements using colorpHast pH indicator strips (EMD Chemicals Inc., Gibbstown, NJ, USA).

Root-excluding trenching experiment (E1)

In experiment 1 (E1), 20 root-excluding trenched plots were constructed in DF to eliminate any influence of living EM on leaf-litter decomposition. Twenty random locations were generated within DF for placement of the trenched plots, each paired with a control plot. Plot coordinates that fell on obstructions such as trees, rock piles or local soil depressions were randomly reassigned 2 m away to assure litter-bag contact with an intact, well drained litter layer.

Trenched plots were constructed as follows: (1) surface and F-horizon litter contained within the plot area (1.37 × 1.37 m) was removed and set aside; (2) the plot perimeter was trenched with a shovel to a depth ≥ 30 cm and distinct soil layers, including roots, were removed separately and set aside to allow for insertion of the trench liner; (3) the trench was lined with 12-gauge, flexible PVC plastic, extending 5–10 cm above the surface root mat to prevent root and hyphal regrowth into the plots. Plot perimeters were backfilled with soil and roots in their order of removal, and litter was replaced evenly over the surface. Untrenched control plots were established in litter 2 m from each trenched plot in a paired design to minimize microsite variability. Trenching without insertion of a trench liner was not applied to the control plots because the severing of tree roots and EM would require an unknown regeneration period and thus negate the rationale for conducting the year-long experiment. Therefore the effects of trenching may be partially obscured by soil disturbance.

Reciprocal transplant experiment (E2)

Experiment 2 (E2) involved reciprocal transplantation of *D. corymbosa* and mixed-species leaf litter in 12 paired, randomly located plots within both DF and MF. Transferring both litter types and retention of 'parent' litter types to each forest type allowed for detection of litter and forest effects on decomposition, as well as any interactions between them. As the mixed-species forest lacks EM trees (Henkel, 2003; unpublished data), E2 allowed for an additional method to assess EM-mediated effects on the decomposition process, assuming an otherwise consistent decomposition environment.

Leaf-litter selection, processing, and litter-bag placement in E1 and E2

Leaf litter was collected during June 2003. Leaves for both E1 and E2 were collected from the forest floor directly adjacent to both DF and MF, based on the criteria of: (1) having no visible fungal hyphae or rhizomorphs attached to them; and (2) appearing to be in a state of decay similar to leaves caught in litterfall traps used in a concurrent study (Henkel *et al.*, 2005). The assemblage of mixed-species leaves used in E2 represented a cross-section of the most abundant species comprising the surface leaf-litter layer within the mixed forest at the time of this study, including, but not limited to, the common genera *Eschweilera*, *Licania*, *Protium* and *Swartzia*. Both the *D. corymbosa* and mixed-species leaves were air-dried for 24 h and bulked separately in large plastic bags for 24–32 h to standardize remaining moisture contents. Leaf litter bags consisted of 17 g wet weight of leaves placed within 30 cm^2 fibreglass windowscreen envelopes with a mesh size approx. 1 mm, arranged in a single layer to prevent compaction. Whole leaves were used to avoid prior fractionation which might have influenced subsequent decay rates (Swift *et al.*, 1979). Five *D. corymbosa* litter bags were placed beneath the loose leaf litter layer in each of the trench and control plots of E1. Five bags of *D. corymbosa* litter and five bags of mixed-species litter were similarly placed in each of the reciprocally transplanted litter plots of E2 in both DF and MF, totalling 10 litter bags per plot. Two bags in each plot remained unharvested after 12 months because of logistical problems.

To estimate initial percentage moisture of litter, three 100-g subsamples from each bulked leaf-litter type were taken over the course of litter-bag preparation (Swift *et al.*, 1979). These 100-g subsamples were weighed wet, air dried for 2 d, and placed in sealed containers with silica gel desiccant for ≥ 48 h before weighing on an Ohaus triple beam balance (Forestry Suppliers), accurate to 0.01 g. The mean percentage moisture content, calculated from these 100-g subsamples, was multiplied by the original leaf wet mass in each litter bag (17.0 g) to obtain actual dry masses at time = 0 of 4.8 g mixed-species litter per bag and 6.2 g *D. corymbosa* litter per bag. All litter bags used in E1 and E2 were placed in, and harvested from, each plot within 2 d of each other.

Litter-bag harvests

Harvests of the *D. corymbosa* and mixed-species leaf litter bags occurred at 1-, 6- and 12-month intervals. At each harvest a litter bag was chosen randomly and extracted from each E1 and E2 plot, visually assessed for EM hyphal proliferation, meticulously cleaned of exterior roots and organic material, and returned to base camp for processing. The 1- and 6-month samples were processed for leaf litter only, while the 12-month sample was processed for both leaf litter and root colonization of the litter bags. For the 12-month sample, roots were clipped at a distance from the exterior to ensure that no roots were removed from inside the litter bags. Harvested litter bags were rinsed in rain water to remove clay and mineral deposits, and air dried for a minimum of 3 d before being processed. Leaf litter fragments and fine roots from inside the bags were removed carefully and dried separately in plastic containers with silica gel desiccant for 36–48 h, and the dry mass of each fraction was recorded (±0.01 g). Leaf litter fragments for *D. corymbosa* were then packed in Whirl-Pak bags (Forestry Suppliers), placed in air-tight containers and returned to the laboratory for elemental analysis.

Ectomycorrhizal rootlet determination

In order to quantify the EM biomass within litter bags, and to determine any correlation between EM dry mass and residual leaf litter mineral nutrient concentration, ectomycorrhizal proliferation was assessed in both E1 and E2 litter bags within DF at the 12-month harvest. Entire fine root contents (< 1 mm diameter) of each litter bag were dried and weighed as noted above, clipped into 1-cm^2 sections, and suspended in water in a Petri dish. Using a dissecting microscope, the percentage of EM rootlets was quantified by scoring each rootlet that intersected the lines of a subtending 1-cm square grid and scoring it as EM (mantle evident) or not EM (mantle not evident). The presence of a Hartig net in putative EM rootlets was periodically confirmed by examining transverse root sections using a compound microscope. Ectomycorrhizal rootlet mass colonizing each litter bag was estimated by multiplying the percentage EM of the rootlet sample by total root mass (g per bag). Nearly 80% of the EM rootlets in all samples were of a single morphotype, characterized by dark brown, wefty extramatrical hyphae with frequent septal clamp connections, consistent with those formed by members of the Thelephoraceae (Agerer, 1995).

Elemental analysis

Nitrogen concentrations at the 12-month interval for *D. corymbosa* litter of both E1 and E2 were determined by flash combustion and gas chromatography (AOAC, 2003); P, K, Ca, and Mg concentrations were determined using an acid digest and emission spectrometry (Gavlak *et al.*, 2003). Values were reported as an elemental fraction of dry weight subsamples remaining at 12 months.

Data analyses

Leaf-litter decomposition data, represented as proportions of original dry mass, were normally distributed and tested for homogeneity of variances using the modified Levene's test (Hintze, 2001). A paired *t*-test was used in E1. A repeated-measures ANOVA was used in E2, where the proportion of mass remaining was the response variable; litter type and forest type were between-factor variables; plot number was the subject variable; and time (6 and 12 months only) was the within-factor variable (Ramsey & Schafer, 2002). Mauchley's test of sphericity and Tukey's test of covariance were calculated and found to be in agreement with the ANOVA requirements of sample independence and equal variance (Hintze, 2001). A Tukey–Kramer pairwise comparison of means was selected to determine actual variable differences in E2 (Ramsey & Schafer, 2002), and a *post hoc* MANOVA was performed on both the 6- and 12-month data. Fractions of original leaf litter mass in E1 and E2 were regressed using both linear and quadratic equations to determine the best-fitting models (Wieder & Lang, 1982).

Nutrient concentration data were normalized using the arcsine square-root transformation typically used for proportions (Ramsey & Schafer, 2002). In E1, an Aspen–Welch unequal variance *t*-test was used for N concentrations, and an equal variance *t*-test was used for P, K, Ca, and Mg concentrations, with treatment type as the fixed variable (Hintze, 2001). In E2, an equal variance *t*-test was used for N, P, K, Ca and Mg concentrations, with forest type as the fixed variable. In E1, plot 3 data were removed before analyses because of P and K statistical outliers (> 2 SD above the mean); this was probably caused by contamination from a termite nest found among litter bags collected from this plot. Regression analyses were performed on all transformed elemental concentrations with root mass (g), EM mass (g), and litter mass (g) remaining at 12 months. Only significant results are reported.

Results

Forest structure

DF and MF 0.3-ha study stands were in primary forests on upland sites with no indication of past fires or anthropogenic disturbances. Percent canopy coverage was similar between DF and MF (97 vs 94.4%). In DF, *D. corymbosa* was highly dominant, with 50 individual *D. corymbosa* trees comprising 89% of the basal area (21.2 m^2). There were 57 mixed-species trees ≥ 10 cm dbh in DF, comprising 21 species and contributing 11% of the total basal area. In MF, no *Dicymbe* trees were present, and 37 non-*Dicymbe* tree species comprised 96 stems ≥ 10 cm dbh with a combined basal area (6.6 m^2) much lower from that of *D. corymbosa* in DF. These results are within the range of previous studies (Henkel, 2003; Henkel *et al.*, 2005). In DF, 10 *D. corymbosa* trees were > 100 cm dbh; the maximum dbh of a *D. corymbosa* individual in DF was 234 cm^2; in MF, a single individual of *Macrolobium* sp. was 92 cm^2 dbh.

Litter depth and root-mound characteristics

Mean litter depth in DF was relatively high (6.5 cm), and even greater (10 cm) with inclusion of root-mound sample points, compared with a mean litter depth of 3 cm in MF. These values, recorded over two consecutive days during the rainy season of June 2004, probably varied from mean litter depth values if averaged over one to many years. Litterfall is presumably greater and decomposition slower during the two short intra-annual dry seasons recorded for the Guiana Shield (Scott *et al.*, 1992; Brouwer, 1996) and a similar tropical EM forest in Cameroon (Chuyong *et al.*, 2002).

In the basal root mounds of the 22 large *D. corymbosa* trees sampled forest-wide, humic accumulations ranged up to 57 cm in depth, with pH from 2.7 to 3.5. The mean root mound thickness (litter/root layer and underlying air space) at the outer edge was 21 cm (range 10–32 cm); at mid-mound, 37 cm (range 13.5–60.5 cm); and at the juncture with the trunk, 58 cm (range 22–98 cm). Mean mound length from outer mound edge to trunk was 236 cm (range 122.5–335 cm). In the upper 10 cm of litter on these mounds, and on the root mat occurring between *D. corymbosa* trees, an F horizon of decomposing litter was well developed and extensively permeated by EM rootlets and extramatrical hyphae of various morphotypes. The large amount of root-mound litter and humic accumulations on the *D. corymbosa* trees sampled forest-wide suggested that in DF, where 20% of *D. corymbosa* trees were > 100 cm dbh, significant stand-wide accumulation of litter and resulting acidic humus was occurring.

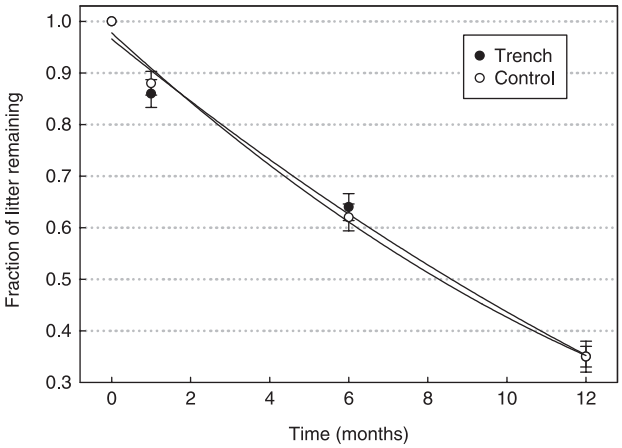

Fig. 1 Mean fraction of original mass remaining of *Dicymbe corymbosa* leaf litter following 12 months' decomposition in litter bags placed in 20 root-excluding trenched and control plots within a 0.33-ha, monodominant stand of *D. corymbosa*, Upper Potaro River, Guyana. Error bars, ±1 SEM. Data points are regressed using the best-fit quadratic equation: $y = y_0 + ax + bx^2$ (trench $r^2 = 0.986$; control $r^2 = 0.994$).

Leaf-litter decomposition in the trenching experiment (E1)

The leaf-litter decomposition rate in *D. corymbosa* litter bags was not significantly affected by the removal of EM over the course of the experiment (Fig. 1). For trenched and control litter bags the mean percentage dry mass of remaining leaf litter at the 1-month sample was *c.* 87%, at 6 months *c.* 63%, and at 12 months *c.* 35%. The consistency over time between the treatment and control plots indicated that similar decomposition rates were occurring regardless of EM presence or other effects of trenching.

Effects of trenching (E1) on mineral nutrient content of litter

Elimination of EM through trenching had no significant effect on N, P or Mg concentrations after 12 months' decomposition (Table 1). However, in the control litter Ca concentration was

Table 1 Mineral nutrients of *Dicymbe corymbosa* leaf litter remaining in trenched and control plots in root-excluding trenching experiment (E1) after 12 months' decomposition, Upper Potaro River, Guyana

	Mineral nutrient (mg g^{-1} dry mass)				
Treatment	N	P	K*	Ca*	Mg
Control	1.77 ± 0.034	0.031 ± 0.001	0.055 ± 0.002	0.321 ± 0.036	0.071 ± 0.004
Trenched	1.71 ± 0.034	0.034 ± 0.001	0.041 ± 0.002	0.602 ± 0.036	0.075 ± 0.004

Values are means ± SE.
*, Values significantly different at $P < 0.001$, df = 36, equal variance *t*-test of square-root arcsine-transformed values.

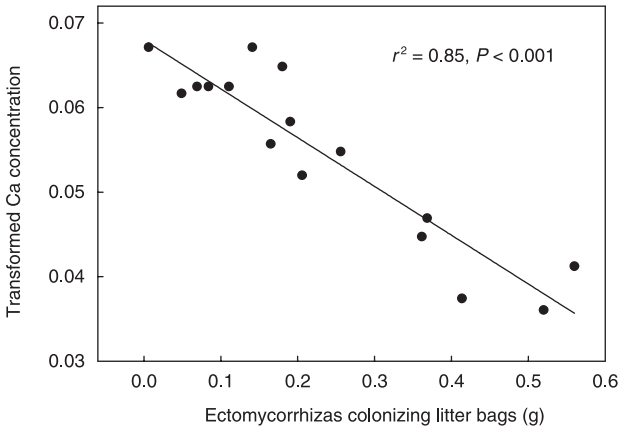

Fig. 2 Relationship between arcsine square-root transformed calcium concentration and mass of colonizing ectomycorrhizas in *Dicymbe corymbosa* litter bags from control plots of experiment 1 after 12 months' decomposition in a monodominant *D. corymbosa* forest, Upper Potaro River, Guyana.

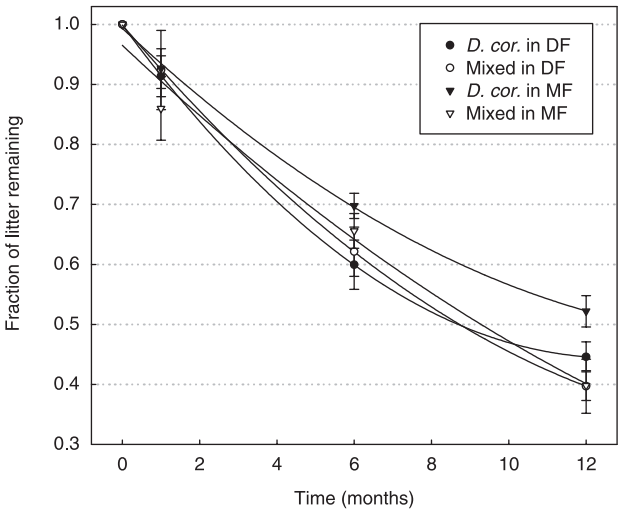

Fig. 3 Fraction of original mass of *Dicymbe corymbosa* and mixed-species leaf litter remaining in litter bags reciprocally transplanted into a 0.33-ha *D. corymbosa* forest (DF) and mixed-species forest (MF), Upper Potaro River, Guyana. Error bars, ±1 SEM. Data points are regressed using the best-fit quadratic equation: $y = y_0 + ax + bx^2$ (*D. corymbosa* in DF, mixed in DF and *D. corymbosa* in DF: $r^2 = 0.999$; mixed in MF: $r^2 = 0.983$).

significantly lower and K concentration significantly higher (Table 1). Both root ($r^2 = 0.58$, $P < 0.001$) and EM mass ($r^2 = 0.85$, $P < 0.001$) of the E1 control litter bags were negatively correlated with Ca concentration of litter after 12 months (Fig. 2).

Leaf-litter decomposition in the reciprocal transplant experiment (E2)

Litter and forest type did not significantly affect litter decomposition at the strict $P = 0.05$ level (litter, $P = 0.072$; forest, $P = 0.052$; time, $P < 0.001$; litter : time $P = 0.088$, repeated-measures ANOVA; Fig. 3). However, decomposition of *D. corymbosa* litter in MF differed from decomposition of mixed-species litter in DF ($P < 0.05$, Tukey–Kramer multiple comparison test). Additionally, an *a posteriori* test found a difference in litter-type mass remaining at 12 months ($P = 0.008$, MANOVA).

Mineral nutrient content of litter from the reciprocal transplant experiment (E2)

In E2, Ca concentration in *D. corymbosa* litter within DF was significantly lower than that of *D. corymbosa* litter in MF after 12 months (Table 2). Conversely, P concentration in *D. corymbosa* litter in DF was higher at 12 months (Table 2) and, unlike in E1, K was unaffected. Calcium reduction in the presence of EM was consistent with E1 results. This result was corroborated by the negative correlation between EM colonizing mass and litter Ca concentration seen in E1 (Fig. 2). No correlations were found between EM colonizing mass and other elemental concentrations of the leaf litter after 12 months' decomposition.

Table 2 Mineral nutrients of *Dicymbe corymbosa* leaf litter reciprocally transplanted in two forest types (E2) after 12 months' decomposition, Upper Potaro River, Guyana

	Mineral nutrient (mg g^{-1} dry mass)				
Forest	N	P**	K	Ca*	Mg
DF	1.83 ± 0.051	0.031 ± 0.002	0.060 ± 0.005	0.224 ± 0.039	0.062 ± 0.006
MF	1.79 ± 0.051	0.024 ± 0.002	0.050 ± 0.005	0.475 ± 0.039	0.065 ± 0.006

Values are mean ± SE.
*, Values significantly different at $P << 0.001$, df = 22, equal variance *t*-test on square-root arcsine-transformed values.
**, Values significantly different at $P = 0.05$, df = 22, equal variance *t*-test on square-root arcsine-transformed values.
DF, 0.33-ha *Dicymbe corymbosa* forest area; MF, 0.33-ha mixed-species forest area.

Rootlet colonization of litter bags

All litter bags in E1 trench plots, regardless of sample period, were devoid of rootlets, EM or otherwise. All control litter bags were permeated with roots: mean fine root weight was 0.54 g per bag, and on average 53% of rootlets were EM. Visual assessment of litter bags at 1, 6 and 12 months revealed that >80% of the control litter bags were heavily colonized by a dark thelephoroid EM morphotype with profuse brown, frequently clamped, extramatrical hyphae. In MF of the E2 reciprocal transplant, EM were absent from all litter bags; *D. corymbosa* leaf litter and mixed-species leaf litter contained a mean of 0.31 and 0.32 g of nonEM fine roots. In DF of E2, EM abundantly colonized both litter types: the *D. corymbosa* litter bags contained a mean of 0.53 g fine roots, 60% of which were EM; and mixed-species litter bags a mean of 0.54 g roots, 73% of which were EM. In E2 no significant differences in overall root colonization of litter bags were found, regardless of litter type or forest type.

Discussion

Ectomycorrhizas do not suppress decomposition

The lack of a significant EM effect on decomposition rates seen in this study argues against saprotrophic suppression (a Gadgil effect) as a contributing factor to any EM-mediated modifications to nutrient cycles. Rather, with the possible exception of Ca discussed below, the rate of nutrient release from leaf litter in the *D. corymbosa* forest is probably governed by saprotrophic activity and carbon quality of the leaves (*sensu* Chapin *et al.*, 2002). However, the great proliferation of EM in the litter layers of *D. corymbosa* forests suggests that EM involvement in mineral nutrient acquisition from the decomposing litter may be substantial and, by achieving an indirectly closed nutrient loop, could contribute to competitive superiority of *D. corymbosa*.

While some studies in temperate forests have demonstrated a Gadgil effect (Fisher & Gosz, 1986; Faber & Verhoef, 1991; Parmelee *et al.*, 1993; Koide & Wu, 2003), others found no such effect (Harmer & Alexander, 1985; Staaf, 1988). Additionally, EM presence has stimulated leaf-litter decomposition in some instances (Entry *et al.*, 1991; Zhu & Ehrenfeld, 1996). These contrasting results can be partially attributed to soil-quality differences (Parmelee *et al.*, 1993); disturbance history; trenching effects (Harmer & Alexander, 1985; Yamashita & Takeda, 2003); or differences in the enzymatic capacity of the specific EM and saprotrophic fungi involved (Entry *et al.*, 1991). It has been suggested that EM inhibition of saprotrophic decomposition in pine litter may have resulted from water removal by EM (Koide & Wu, 2003). A reduction in moisture content can slow decomposition rates because of inhibitory effects on decomposer organisms (Swift *et al.*, 1979; Cornejo *et al.*, 1994). Such a basis for a Gadgil effect may have been lacking in *D. corymbosa* forests where high rainfall (3866 mm yr^{-1}; Fanshawe, 1952) with a seasonal peak in May–July could have provided ample moisture for decomposition of leaf litter by saprotrophs despite any potential EM-mediated water removal.

As mentioned, the exclusion of EM in the trench plots is accompanied by a disturbance and aeration of the soil layers in the perimeter of the trench and, presumably, a pulse of nutrients resulting from the decomposition of tree roots and fungal hyphae – effects that the control plots were not exposed to. Therefore it remains possible that any effect caused by trenching *per se*, be it suppression or acceleration of decomposition, remained masked because of an equal but opposite response in the decomposer community.

Decomposition rates and leaf-litter depth

Both leaf-litter types followed a nonlinear quadratic decay pattern suggesting an increasing proportion of recalcitrant compounds in the residual litters. *Dicymbe corymbosa* litter appears to be more recalcitrant than the mixed-species litter, most apparent after 12 months' decomposition. Additionally, the apparent trend towards slower decomposition of *D. corymbosa* litter when transplanted to MF suggests a biological interaction, as mixed-species litter did not follow this trend. The increased decomposition rate of *D. corymbosa* leaf litter in DF may be caused by the action of specialized saprotrophic fungi. A survey of macrofungal communities between the *D. corymbosa* and mixed-species forests in permanent study plots at the Potaro site, spanning the 2000–04 wet seasons, has revealed a small guild of saprotrophic macrofungi with apparent specificity for recently fallen *D. corymbosa* leaves. In particular, a *Gymnopus* sp. (Tricholomataceae) was highly abundant, fruiting exclusively on recently fallen *D. corymbosa* leaves in > 80% of 525 wet-season subsampling plots (each 10×10 m) in *D. corymbosa* forest, and was absent from the mixed forest (T.W.H., M.C. Aime and S.L. Miller, unpublished data). The near ubiquity of this *Gymnopus* sp. and its strong substratum specificity for *D. corymbosa* leaves suggest that it may have contributed to the relatively faster rate of *D. corymbosa* litter decomposition in DF.

The basis for greater leaf-litter depths in DF relative to MF remains elusive. It could be caused by greater recalcitrance in later stages of decomposition of *D. corymbosa* leaves combined with high seasonal litterfall; ongoing studies are addressing this. Deep litter within the *D. corymbosa* stands could inhibit small-seeded non-*Dicymbe* seedling establishment, contributing to persistence of the dominant species through a reduced pool of potential seedling competitors (Molofsky & Augspurger, 1992; Christie & Armesto, 2003). Seedlings of non-*Dicymbe* tree species consistently occurred at densities much lower than those dominant in *D. corymbosa* stands throughout the Pakaraima Mountains (Henkel, 2003; Henkel *et al.*, 2005). Deep litter layers inhibited seedling establishment of AM tree species in a monodominant, ectotrophic *Gilbertiodendron dewevrei* (Caesalpiniaceae) forest in north-eastern Congo (Torti *et al.*, 2001). The deep litter layers in *D. corymbosa* forests

not only may reduce AM plant invasion success through inhibited germination, but also may promote a more suitable moisture and aeration environment for growth of EM fungi (Read, 1991), enabling *D. corymbosa* seedlings to form EM rapidly and establish in large numbers following mast fruiting events (Henkel *et al.*, 2005). In many ecosystems, litter of EM-forming tree species have intermediate to poor decomposability, which could promote EM success under conditions of deep and recalcitrant (high C : N) litter layers (Singer & Araujo, 1979; Northup *et al.*, 1995; Cornelissen *et al.*, 2001; Strack *et al.*, 2003). The large accumulations of moisture-holding humus in root mounds of large *D. corymbosa* trees could be beneficial to the growth of EM fungi and long-term nutrient storage of the system (Woolley & Henkel, 2005). Therefore deeper litter layers in *D. corymbosa* forests may contribute to monodominance of the species through reduced invasion of competitor trees, an increase in EM proliferation, and enhanced establishment of *D. corymbosa* seedlings.

Elemental concentrations of decomposed *D. corymbosa* leaf litter

The presence of EM had no consistent effect on N, P, K or Mg concentrations in *D. corymbosa* leaf litter after 12 months' decomposition. The disparity in P and K trends under EM influence between E1 and E2 were probably a result of inadequate sampling in E2 (df = 22 vs 36 in E1). However, the *D. corymbosa* leaf litter exhibited consistently lower Ca concentrations when EM were present in both experiments. For this reason, we treat the Ca data as tentative but worthy of hypothetical exploration. The consistent Ca depletion in leaf litter under EM influence implied some form of EM-mediated Ca release, further supported by the negative correlation of Ca concentration with EM rootlet mass (g) in control-plot litter bags. The congruence of these data suggests that the reduction of Ca in the presence of EM is more than a spurious corroboration. A larger-scale study incorporating greater interspersion and sample sizes seems warranted.

Ectomycorrhizas may have been directly or indirectly involved in the removal of Ca. Perhaps a stimulation of saprotrophic activity by EM hyphal or root exudates, as demonstrated elsewhere (Sun *et al.*, 1999; Dakora & Phillips, 2002), led to greater release of Ca from decomposing *D. corymbosa* leaves. The use of labelled Ca could aid in determining the fate of the released Ca. For now, we do not know whether the Ca was translocated to the trees or lost to the soil, nor how EM were involved in the process. Calcium uptake from limed soil, combined with translocation to a host tree, has been demonstrated by EM associated with *Picea* and ericaceous plants from temperate forests (Leake & Read, 1989; Finlay, 1992; Andersson *et al.*, 1996), but cation acquisition by EM from leaf litter has yet to be demonstrated in field or laboratory settings.

Could EM-mediated supply of Ca be vital to the growth of *D. corymbosa*? If unfavourable soil conditions (e.g. high Al and Fe) create a situation where Ca is limiting to tree growth in upland areas of Guyana, then an EM-mediated Ca release, with subsequent EM uptake, could reduce Ca losses to the ecosystem, an inevitable process in ageing soils (Chadwick *et al.*, 1999). Total Ca concentrations from ultisol/oxisol soils along the Upper Potaro River ranged from 78.3 to 250.5 mg kg^{-1} with a cation-exchange capacity (CEC) of 1.4–3.4 meq 100 g^{-1} (Henkel *et al.*, 2005). Low values were also found in Guyana for mixed-species forest soils near Mabura Hill (CEC = 3–4.1 meq 100 g^{-1}, total Ca = 27.5–40 mg kg^{-1}; Brouwer, 1996). The very low concentration of Ca in litterfall and throughflow at the Mabura site was believed to indicate high Ca-use efficiency by *Chlorocardium rodiaei*, *Dicymbe altsonii* and *Eschweilera sagotiana* (Brouwer, 1996). Highly weathered, acidic soils rich in Al, such as those of the Pakaraima Mountains, can limit Ca, Mg and P uptake by, and be toxic to, plant roots (Marschner, 1991; van Praag *et al.*, 1997; Rengel & Zhang, 2003; St Clair & Lynch, 2005).

Alternatively, if Ca release and subsequent uptake by EM is occurring, it may be beneficial to the fungi involved. Some saprotrophic and EM fungi are known to accumulate Ca-oxalate crystals both internally and externally, which may facilitate P uptake in acidic, Al/Fe-rich soils (Wallander *et al.*, 2002; Arvieu *et al.*, 2003; Hagerberg *et al.*, 2003) while also ameliorating Al toxicity (Ahonen-Jonnarth *et al.*, 2000; Ma, 2000; Cumming *et al.*, 2001). Through such mechanisms, enhanced uptake of Ca by the *D. corymbosa*–EM system could promote overall mineral nutrient acquisition, physical and temporal stability of the system and, ultimately, competitive superiority of *D. corymbosa* in its monodominant forests. However, the indirect methods used here merely demonstrated a reduction in Ca concentration in leaf litter exposed to EM after 1 yr. The mode of Ca release and how it is related to the nutrient-use efficiency of *D. corymbosa* trees remains to be demonstrated.

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