

Biogeography of litter depth in tropical forests: evaluating the phosphorus growth rate hypothesis

M. Kaspari^{1,2} and S. P. Yanoviak^{3,4}

¹Department of Zoology, Ecology and Evolutionary Biology Program, University of Oklahoma, Norman OK, 73019-0235, USA; ²Smithsonian Tropical Research Institute, Balboa, Republic of Panama; ³Department of Pathology, University of Texas Medical Branch, Galveston, TX 77555-0609, USA; and ⁴Department of Biology, University of Arkansas at Little Rock, 2801 S. University Avenue, Little Rock, AR 72204-1099, USA

Summary

1. The leaf litter of tropical forests serves as a carbon sink, slows soil erosion and leaching, and is home to a large fraction of the forest's biodiversity. Standing leaf litter reflects the balance of litterfall and decomposition; both rates may be limited by element availability. We propose a mechanism for this regulation that assumes phosphorus limits metabolism in tropical soils, and that phosphorus limitation is more pronounced in faster growing organisms.

2. Leaf litter depth varied 16-fold (1.4–22.4 cm) across 28 forest stands in Panama and Peru and was deeper on sand vs. clay soils. Of five elements tested (N, P, K, Mg and Ca), the concentration of P in decomposing litter best predicted litter depth ($r^2 = 0.76$, $C : P^{1.90}$). This relationship broke down in the most impoverished sandy soils.

3. These data are consistent with the hypothesis that the weathering of tropical soils limits the metabolism of microbes first and trees second, with decomposition and litterfall co-limiting litter depth in ecosystems with the least available phosphorus. This has implications for the dynamics of weathering: nutrient leaching may be regulated through negative feedback if deeper litter buffers soil from rainfall.

Key-words: growth rate hypothesis, K, litter depth, Mg, N, P, Panama, Peru, resource gradients, soils, tropical forest, tropics

Introduction

Leaf litter is a conspicuous part of any tropical forest. As leaf litter accumulates, so does habitat space for the brown food web (microbial decomposers and their consumers). This biota can account for a large fraction of ecosystem biodiversity (Longino & Colwell 1997; Lawrence & Wise 2000; Moore *et al.* 2003) and contribute in a variety of ways to ecosystem fluxes (Heneghan *et al.* 1998; Wardle *et al.* 2004a; Fitter *et al.* 2005). Deep litter represents more stored carbon and a more effective buffer against soil erosion and nutrient loss (Baar & ter Braak 1996; Sayer 2005). Yet we know of no geographic study of how and why litter depth varies across tropical forests.

Litter depth reflects the balance of litterfall and decomposition. At the global scale, both rates increase with the co-availability of water and solar energy (Rosenzweig 1968; Gholz *et al.* 2000; Allen, Gillooly & Brown 2005). Within biomes of similar precipitation and temperature, nutrient limitation of litterfall and decomposition can map onto

gradients of biogeochemistry (Vitousek 1984; Sterner & Elser 2002). Two such gradients include soil age and type. Younger soils are relatively rich in rock-born P, K, Mg, but can be poor in biologically fixed N. Weathering, in turn, depletes rock-born elements even as N-fixing symbioses accumulate (Walker & Syers 1976; Wardle, Walker, & Bardgett 2004b). Likewise, soil of different origins can also vary in nutrient availability. Much of northern Amazonia is a mosaic of red clay oxisols and ultisols and oligotrophic white sands (Cuevas & Medina 1988). These sands may have one-tenth of the soil nutrients (Anderson 1981) and understorey (Gentry & Emmons 1987) of clay soils.

Phosphorus, given its dearth in old tropical soils and relative abundance in the cells of plants and consumers (Sterner & Elser 2002) is a strong candidate to constrain rates of litterfall and decomposition. If it constrains both equally, then the effect of phosphorus gradients on litter depth should be nil. Elser *et al.* (1996), however, suggest this may not be the case if taxa with higher growth rates (and thus higher titers of P-rich ribosomes) generate a higher per-capita demand for phosphorus. Bacteria and fungal decomposers generally grow

*Correspondence author. E-mail: mkaspari@ou.edu

faster than trees (Peters 1983). In the Growth Rate Hypothesis (Elser *et al.* 1996) microbial decomposition should thus be limited by P at higher levels of availability, all else being equal, than arboreal litterfall.

There is some evidence for a discrepancy in phosphorus effects on decomposition and litterfall. In montane Hawai'i forests, decomposition was frequently enhanced on +P plots after 3 years (Hobbie & Vitousek 2000; Vitousek 2004) as it was after 6 years in a lowland Panama moist forest (Kaspari *et al.* 2008). A third experiment in a Costa Rican wet forest found no effect of P on leaf mass loss when the site was pre-fertilized for 1 year (Cleveland, Reed & Townsend 2006).

There is less evidence for P limitation of litterfall. In Vitousek's (1984) comparative study of 55 sites, a small positive correlation between litter P and litterfall rate arose only in the most P-impooverished litters (0.02–0.04%, see his Fig. 2). When P was used to fertilize tropical forests, litterfall failed to increase after 6 years in a relatively P-rich Panama forest (Kaspari *et al.* 2008). Similarly, it failed to increase after 4 years (Tanner, Kapos & Franco 1992), and 2 years (Vitousek *et al.* 1995) in two montane tropical forests.

Here we combine the hypotheses of Walker & Syers (1976: P limitation is widespread in old tropical forests) and Elser *et al.* (1996: P limitation expresses itself in decomposer microbes at higher levels of availability than trees). This produces the working hypothesis that as forest ecosystems lose phosphorus, standing crops of litter should increase. Furthermore, the rate of this increase should decline when P becomes sufficiently scarce to also limit litterfall. Here we evaluate this prediction with a geographical survey of litter chemistry and depth. We sample younger and older red clay soils (10 from the isthmus of Panama and 9 from Amazonian Peru) and 9 from Amazonian white sands of Peru. We compare C : P's ability to predict litter depth compared with C : X ratios of four other elements (N, K, Ca, Mg) that have been linked in other studies to decomposition and litterfall (Tanner *et al.* 1992; Vitousek *et al.* 1995; Hobbie & Vitousek 2000; Berg & Laskowski 2006; Hobbie *et al.* 2006). We show that gradients in the C : P of decomposing litter account for 76% of the variance in standing litter depth, and that this effect diminishes in high C : P sandy soils.

Materials and methods

Litter depth and chemistry were sampled from 28 lowland forest stands in Panama and Peru. We sampled three types of lowland forest. The Panama clays came from 10 stands on Barro Colorado nature monument (BCNM) in the Republic of Panama (9°06'N, 79°50'W). The species composition and stature of these forests are characteristic of a high canopy seasonal forest with c. 2400 mm annual rainfall (Leigh, Rand & Windsor 1996). A previous survey of BCNM (Knight 1975) was used to guide selection of most stands on eight clay and two gley soils suggested by Knight (1975) to show a range of soil fertility. Stands were sampled June and July 2004 near the beginning of the wet season. The minimum distance between stands was c. 0.5 km.

The other two forests types were from 9 clay oxisols and ultisols (Vitousek & Sanford 1986) and 9 sandy soils ('varillal alto', Anderson 1981; Villacorta, Reátegui & Zumaeta 2002) in a mosaic around the

city of Iquitos in Loreto Province, northeastern Peru (4°00'S, 73°50'W, Madigosky & Vatnick 2000; Mäki, Kalliola & Vuorinen 2001). These forests have grossly similar vegetation structure but differ in species composition (Fine, Mesones & Coley 2004). The region is roughly aseasonal, receiving 2400–2800 mm annual rainfall (Madigosky & Vatnick 2000). All stands were located between highway kilo-meter markers 10 and 60 (km 0 is in Iquitos) and within 3 km due E or due W of the road. The minimum distance between stands within a soil type was c. 150 m.

At each of the 28 forest stands we collected leaf litter from five sampling quadrats spaced 5 m apart on a 25 m transect. This was part of a larger project studying the trophic ecology of brown food webs (Kaspari and Yanoviak, unpublished data). The starting point for each transect was selected haphazardly, and all sampling points were > 50 m from a forest edge. Litter depth was measured in each corner of a PVC frame by inserting a surveyor's flag marked in 1-cm increments down to mineral soil. Leaf litter (excluding woody material > 4 cm diameter) inside the frame was collected by hand down to mineral soil. This litter was shaken over a 1 cm mesh for 30 s, generating a fine litter siftate (Agosti *et al.* 2000). Since litter was deeper in Peru, and to standardize siftate quantity, Peru quadrats were smaller (0.125 m² vs. 0.25 m² in Panama). Tullgren funnels (40 W incandescent bulb, 48 h) were used to separate arthropods from the siftate (Agosti *et al.* 2000). Once arthropods had been extracted, a 10 g subsample of the dried litter was analyzed for chemical composition at the Oklahoma State Soil, Water, and Forage Analytical Laboratory (OSU 2006). Briefly, nitrogen (as NO₃) was extracted with calcium sulfate and measured on a Lachat™ flow injection autoanalyzer. Potassium, phosphorus, calcium and magnesium were all first extracted using Mehlich 3 (Mehlich 1984) and quantified with a Spectro CirOs™ ICP spectrometer (for P, the solution was additionally mixed with ascorbic acid colour complex and analyzed at 880 nm). Neutral detergent fibre (the percentage of lignin, cellulose and hemicellulose) was measured using an Ankom™ fibre analyzer. See (OSU 2006) for further details. C : X ratios were calculated based on mass. One Peru sand and clay forest sample was lost before analysis.

We first quantified the effects of geography and soil type comparing Panama with Peru, and clay and sandy soils within Peru using an ANOVA. We tested for the predicted increase in litter depth by regressing log₁₀ litter depth against log₁₀ C : P (power law models accounted for 11% more variation than arithmetic models). We evaluated C : P as the best predictor using multiple regression ($P < 0.05$ for variable entry or exclusion Draper & Smith 1981), in which C : N, C : P, C : K, C : Ca and C : Mg were available for model selection. Finally, as sandy soils are more impooverished than clay soils (Coleman & Crossley 1996) we used ANCOVA (on log₁₀-transformed variables) to compare the predictive ability of C : P for litter of clay vs. sandy soils. We used SAS 9.1 (SAS 2006) in all cases to perform these analyses.

Results

Litter chemistry and depth differed across soils and regions (Fig. 1). Among the 140 individual sample plots, litter depth ranged from 0 to 25.5 cm. Among the 28 forest stands, litter depth varied 16-fold (1.37–22.4 cm), increased significantly from Panama to Peru ($F_{1,26} = 77$, $P < 0.0001$, Fig. 1), and was twice as deep on sandy vs. clay soils within Peru ($F_{1,16} = 36$, $P < 0.0001$, Fig. 1). The deeper litter on sandy soils had higher concentrations of celluloses and lignin (neutral detergent fibre: 72% on sand vs. 65% and 64% on Peru and Panama clay, $F_{2,23} = 9.0$, $P = 0.0013$).

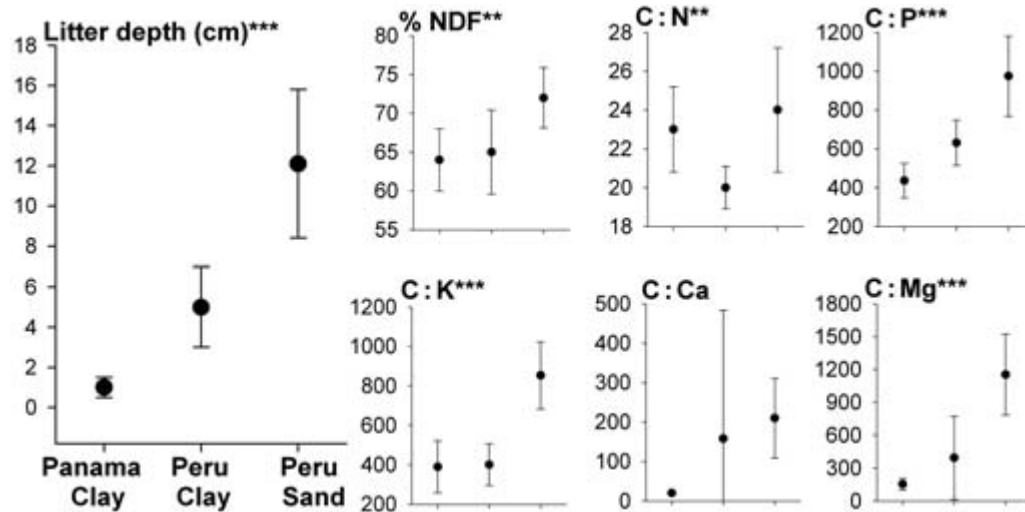


Fig. 1. Litter depth and chemistry (of leaf litter + microbes) for three groups of forest stands—Panama clay soils ($n = 10$), Peru Clay soils, and Peru sandy soils ($n = 8$ for chemistry, $n = 9$ for litter depth). Means are given with standard deviations. ANOVA significance: * $P > F < 0.05$, ** $P > F < 0.01$, *** $P > F < 0.001$. NDF (neutral detergent fibre) is a measure of the celluloses, hemicelluloses, and lignins in the decomposing litter.

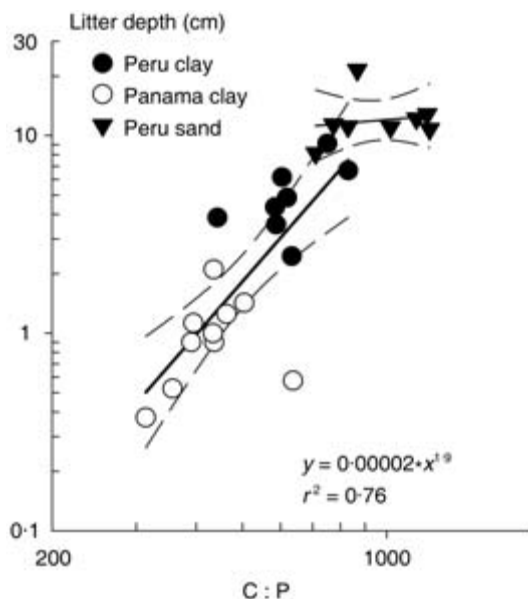


Fig. 2. Standing litter depth covaries with the ratio of carbon to phosphorus in decomposing litter across 26 forest sites in Panama and Peru. The overall regression equation is given; regressions for clay and sandy soils (with 95% CI) drawn separately.

The nutrient makeup of decomposing litter differed regionally (Fig. 1). C : P varied in a manner similar to litter depth ($F_{2,23} = 32$, $P < 0.0001$) with Peru clays 50% higher in C : P than Panama clays, and Peru sands 50% higher than Peru clays. C : K, in contrast, was twice as high in Peru sands than in either clay site ($F_{2,23} = 31$, $P < 0.0001$), as was C : Mg ($F_{2,23} = 27$, $P < 0.0001$). C : N ratios were highest on Panama clay and Peru sands ($F_{2,23} = 7.4$, $P = 0.0033$). C : Ca failed to vary significantly across the region-soil combinations ($F_{2,23} = 2.5$, $P = 0.11$).

Stepwise multiple regression selected C : P as the best predictor of litter depth across the 26 forest stands ($x = 0.00002y^{1.90}$, $r^2 = 0.76$, $F_{1,24} = 77.2$). An additional 5% of

variation in litter depth was accounted for by the positive effect of C : Ca. This produced a model that accounted for 81% of the variation in litter depth ($y = 0.00052E^{-4}$ ($C : P^{1.27} + C : Ca^{0.25}$), $C : P$ $F_{1,23} = 77.2$, $P < 0.0001$; $C : Ca$ $F_{1,23} = 5.73$, $P = 0.025$).

The exponent of the relationship between C : P and litter depth differed between clay and sandy soils, however (Fig. 2). Litter depth increased with C : P ($F_{1,22} = 7.19$, $P = 0.014$) and was higher on sandy soils ($F_{1,22} = 5.17$, $P = 0.033$) although the litter-phosphorus relationship varied with soil type $F_{1,22} = 4.76$, $P = 0.040$). Clay soils, where C : P ranged from 313 to 830 yielded an exponent of 1.8 ($F_{1,16} = 23.7$, $P = 0.0002$) with C : P accounting for 60% of the variation in litter depth. Sandy soils, in contrast, where C : P ranged from 710–1228, failed to show a significant increase in litter depth along this gradient ($F_{1,7} = 0.15$, $P = 0.71$).

Discussion

Understanding the factors underlying rates of production and decomposition remains a key goal of ecology. Litter depth is an easily measured variable that integrates across both processes. Here we combine theory and data to provide a simple hypothesis on the role of phosphorus in shaping the distribution of litter depth across tropical forests. The survey of 26 forest stands supports a key prediction: along a gradient of decreasing phosphorus on tropical soils, the rate of microbial decomposition is constrained before the rate of arboreal litterfall. This results in a biphasic curve linking litter depth to C : P of decomposing litter (see also Koide & Shumway 2000 for a similar increase phase across four temperate pine plantations). These data reinforce the hypothesis that P regulates the carbon cycle at a regional scale (McGroddy *et al.* 2004; Reich & Oleksyn 2004).

Any geographical analysis comes with caveats. First, these forest stands are not a random sample from the Neotropics, but are centred in two regions. However, nutrient availability

varies at mesoscales in tropical forests (John *et al.* 2007). The forest stands sampled here represent *c.* twofold gradients of C : P for Panama clay (313–637), Peru clay (442–830) and Peru sand (710–1228). Litter depth also varied commensurately (5.6-, 3.7- and 2.6-fold respectively). Second, BCNM is more seasonal than Iquitos in climate, and likely, litterfall (Leigh *et al.* 1996). We sampled BCNM 1–2 months after the onset of the wet season (when litter is at its deepest, Leigh *et al.* 1996), and 4 months before the end of the wet season (when litter is most shallow). None-the-less, we do not interpret the exponent of the regression in Fig. 2 beyond the fact that it was positive, as predicted. Note, however, that the Peru forest stands of similar seasonality still generate an increase in litter depth with C : P ($y = 0.0016 * C : P^{1.3}$, $F_{1,14} = 18.6$, $P = 0.0007$, $r^2 = 0.57$). Finally, low nutrient environments are predicted to favour plants with C-based defences (Coley, Bryant & Chapin 1985; Orians & Milewski 2007). White sand forests are characterized by sclerophyll leaves resistant to herbivory (Fine *et al.* 2004), and presumably, decomposition. We find higher levels of fibre in the litter of white sand forest stands, and average litter fibre content correlates with C : P ($r = 0.63$, $P = 0.0004$). This suggests that decreases in leaf quality may also contribute to the accumulation of litter shown here. Fertilization experiments in white sand forests (testing for the predicted increase in decomposition and litterfall rates) and common garden decomposition experiments (e.g. Hobbie & Vitousek 2002) are logical next steps toward evaluating these hypotheses.

The 16-fold variation in litter depth across forests of similar rainfall, and the role of P in generating this variation, has two implications for the dynamics of tropical forests. First, decomposition reflects the rate at which litter is converted into microbial biomass. This biomass, in turn, feeds the microbivores, predators, and top predators of the brown food web (Heneghan *et al.* 1998; Moore *et al.* 2003; Wardle *et al.* 2004a; Fitter *et al.* 2005). At the same time, decomposition destroys the physical habitat in which these organisms live. This 'more food, less habitat' dynamic of brown food webs (Koide & Shumway 2000; Scheu & Setälä 2002) differs fundamentally from that of green food webs, where high productivity is associated with more food, more habitat, and higher abundance of consumers (e.g. Kaspari, Alonso & O'Donnell 2000). If food and habitat co-limit the populations of the brown food web, then abundance should show a nonlinear, and perhaps unimodal, relationship with litter depth.

Second, our results suggest a process by which mineral leaching in tropical forests is progressively slowed. Leaf litter slows soil erosion and mineral leaching (see review in Sayer 2005), particularly in tropical ecosystems where rainfall is measured in meters. As these warm wet ecosystems lose phosphorus and other mineral nutrients, a built-in negative feedback mechanism may slow further leaching: a thicker blanket of leaf litter.

Acknowledgments

This project was funded by the National Science Foundation under Grant No. 0212386 to M.K. Special thanks to S Bagwell, and J Morrison for assistance in

the laboratory, to Y. Milton, W. Sanchez, E. Requena, and C. Valderrama for assistance in the field, and to the numerous private landowners who provided access to forest stands in Peru. Discussions with Brad Stevenson, Sarah Hobbie, Jennifer Powers and Peter Tiffin provided many insights and greatly increased the clarity of our thinking. The Smithsonian Tropical Research Institute, the Panamanian Autoridad Nacional del Ambiente (ANAM), and the Peruvian Instituto Nacional de Recursos Naturales (INRENA) provided permits.

References

- Agosti, D., Majer, J.D., Alonso, L.E. & Schultz, T.R. (2000) *Measuring and Monitoring Biological Diversity: Standard Methods for Ground-living ants*. Smithsonian Press, Washington, DC.
- Allen, A.P., Gillooly, J.F. & Brown, J.H. (2005) Linking the global carbon cycle to individual metabolism. *Functional Ecology*, **19**, 202–213.
- Anderson, A.B. (1981) White-sand vegetation of Brazilian Amazonia. *Biotropica*, **13**, 199–210.
- Baar, J. & ter Braak, C.J.F. (1996) Ectomycorrhizal sporocarp occurrence as affected by manipulation of litter and humus layers in Scots pine stands of different age. *Applied Soil Ecology*, **4**, 61–73.
- Berg, B. & Laskowski, R. (2006) Litter decomposition: a guide to carbon and nutrient turnover. *Advances in Ecological Research*, **38**, 0–428.
- Cleveland, C.C., Reed, S.C. & Townsend, A.R. (2006) Nutrient regulation of organic matter decomposition in a tropical rain forest. *Ecology*, **87**, 492–503.
- Coleman, D.C. & Crossley, D.A. (1996) *Fundamentals of Soil Ecology*. Academic Press, New York.
- Coley, P., Bryant, J. & Chapin, F. (1985) Resource availability and plant antiherbivore defense. *Science*, **230**, 895–899.
- Cuevas, E. & Medina, E. (1988) Nutrient dynamics within Amazonian forests. II. Fine root growth, nutrient availability and leaf litter decomposition. *Oecologia*, **76**, 222–235.
- Draper, N.R. & Smith, H. (1981) *Applied Regression Analysis*. John Wiley & Sons, New York.
- Elser, J., Dobberfuhl, D., MacKay, N. & Schampel, J. (1996) Organism size, life history, and N : P stoichiometry. *Bioscience*, **46**, 674–684.
- Fine, P.V.A., Mesones, I. & Coley, P.D. (2004) Herbivores promote habitat specialization by trees in Amazonian forests. *Science*, **305**, 663–665.
- Fitter, A.H., Gilligan, C.A., Hollingworth, K., Kleczkowski, A., Twyman, R.M. & Pitchford, J.W. (2005) Biodiversity and ecosystem function in soil. *Functional Ecology*, **19**, 369–377.
- Gentry, A. & Emmons, L. (1987) Geographical variation in fertility, phenology, and composition of the understory of neotropical forests. *Biotropica*, **19**, 216–227.
- Gholz, H.L., Wedin, D.A., Smitherman, S.M., Harmon, M.E. & Parton, W.J. (2000) Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. *Global Change Biology*, **6**, 751–765.
- Heneghan, L., Coleman, D.C., Zou, X., Crossley, D.A.J. & Haines, B.L. (1998) Soil microarthropod community structure and litter decomposition dynamics: a study of tropical and temperate sites. *Applied Soil Ecology*, **9**, 33–38.
- Hobbie, S.E. & Vitousek, P.M. (2000) Nutrient limitation of decomposition in Hawaiian forests. *Ecology*, **81**, 1867–1877.
- Hobbie, S.E., Reich, P.B., Oleksyn, J., Ogdahl, M., Zykowiak, R., Hale, C. & Karolewski, P. (2006) Tree species effects on decomposition and forest floor dynamics in a common garden. *Ecology*, **87**, 2288–2297.
- John, R., Dalling, J.W., Harms, K.E., Yavitt, J.B., Stallard, R.F., Mirabello, M., Hubbell, S.P., Valencia, R., Navarrete, H., Vallejo, M. & Foster, R.B. (2007) Soil nutrients influence spatial distributions of tropical tree species. *PNAS*, **104**, 864–869.
- Kaspari, M., Alonso, L. & O'Donnell, S. (2000) Three energy variables predict ant abundance at a geographic scale. *Proceedings of the Royal Society London B*, **267**, 485–490.
- Kaspari, M., Wright, J., Yavitt, J., Harms, K., Garcia, M. & Santana, M. (2008) Multiple nutrients regulate litterfall and decomposition in a tropical forest. *Ecology Letters*, **11**, 35–43.
- Knight, D.H. (1975) A phytosociological analysis of species-rich tropical forest on Barro Colorado Island, Panama. *Ecological Monographs*, **45**, 259–284.
- Koide, R.T. & Shumway, D.L. (2000) On variation in forest floor thickness across four red pine plantations in Pennsylvania, USA. *Plant and Soil*, **219**, 57–69.
- Lawrence, K.L. & Wise, D.H. (2000) Spider predation on forest-floor Collembola and evidence for indirect effects on decomposition. *Pedobiologia*, **44**, 33–39.
- Leigh, E.G. Jr., Rand, A.S. & Windsor, D.W. (1996) *The Ecology of a Tropical Forest*, 2nd edn. Smithsonian Press, Washington, DC.

- Longino, J.T. & Colwell, R.K. (1997) Biodiversity assessment using structured inventory: capturing the ant fauna of a tropical rain forest. *Ecological Applications*, **7**, 1263–1277.
- Madigosky, S.R. & Vatnick, I. (2000) Microclimatic characteristics of a primary tropical Amazonian rain forest, ACEER, Iquitos, Peru. *Selbyana*, **21**, 165–172.
- Mäki, S., Kalliola, R. & Vuorinen, K. (2001) Road construction in the Peruvian Amazon: causes and consequences. *Environmental Conservation*, **28**, 199–214.
- McGroddy, M.E., Daufresne, T. & Hedin, L.O. (2004) Scaling of C:N:P stoichiometry in forests worldwide: implications of terrestrial redfield-type ratios. *Ecology*, **85**, 2390–2403.
- Mehlich, A. (1984) Mehlich 3 soil test extractant: a modification of Mehlich 2 extractant. *Soil chemistry and physics*, **15**, 1409–1416.
- Moore, J.C., McCann, K., Setälä, H. & Ruiterd, P.C.D. (2003) Top-down is bottom-up: does predation in the rhizosphere regulate aboveground dynamics? *Ecology*, **84**, 846–857.
- Orians, G.H. & Milewski, A.V. (2007) Ecology of Australia: the effects of nutrient-poor soils and intense fires. *Biological Reviews*, **82**, 393–423.
- OSU (2006) Soil, water and forage analytical laboratory. Available at <http://www.soiltesting.okstate.edu/>.
- Peters, R. (1983) *The Ecological Implications of Body Size*. Cambridge University Press, Cambridge, UK.
- Reich, P.B. & Oleksyn, J. (2004) Global patterns of plant leaf N and P in relation to temperature and latitude. *PNAS*, **101**, 11001–11006.
- Rosenzweig, M. (1968) Net primary productivity of terrestrial environments: predictions from climatological data. *American Naturalist*, **102**, 67–74.
- SAS (2006) *SAS/STAT User's guide, Version 9-1*. Sas Institute Inc., Cary, NC.
- Sayer, E.J. (2005) Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. *Biological Reviews*, **80**, 1–31.
- Scheu, S. & Setälä, H. (2002) Multitrophic interactions in decomposer food-webs. *Multitrophic Level Interactions* (eds T. Tscharrntke & B.A. Hawkins), pp. 223–264. Cambridge University Press, Cambridge.
- Sterner, R.W. & Elser, J.J. (2002) *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*. Princeton University Press, Princeton, NJ.
- Tanner, E.V.J., Kapos, V. & Franco, W. (1992) Nitrogen and phosphorus fertilization effects on Venezuelan montane forest trunk growth and litterfall. *Ecology*, **73**, 78–86.
- Villacorta, R.G., Reátegui, M.A. & Zumaeta, M.O. (2002) Clasificación de bosques sobre arena blanca de la Zona Reservada Allpahuayo Mishana. *Folia Amazonica*, **14**, 1–22.
- Vitousek, P.M. (1984) Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology*, **65**, 285–298.
- Vitousek, P.M. (2004) *Nutrient Cycling and Limitation: Hawai'i as a Model System*. Princeton University Press, Princeton, NJ.
- Vitousek, P.M. & Sanford, Jr. R.L. (1986) Nutrient cycling in moist tropical forest. *Annual Review of Ecology and Systematics*, **17**, 137–167.
- Vitousek, P.M., Gerrish, G., Turner, D.R., Walker, L.R. & Mueller-Dombois, D. (1995) Litterfall and nutrient cycling in four Hawaiian montane rainforests. *Journal of Tropical Ecology*, **11**, 189–203.
- Walker, T.W. & Syers J.K. (1976) The fate of phosphorus during pedogenesis. *Geoderma*, **15**, 1–19.
- Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., van der Putten, W.H. & Wall, D.H. (2004a) Ecological linkages between aboveground and belowground biota. *Science*, **304**, 1629–1633.
- Wardle, D.A., Walker, L.R. & Bardgett, R.D. (2004b) Ecosystem properties and forest decline in contrasting long-term chronosequences. *Science*, **305**, 509–513.

Received 14 March 2008; accepted 5 June 2008

Handling Editor: James Cresswell