

Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems

Emma J. Sayer

Department of Plant Sciences, Downing Street, Cambridge CB2 3EA, UK

(Received 1 December 2004; revised 26 May 2005; accepted 8 June 2005)

ABSTRACT

The widespread use of forest litter as animal bedding in central Europe for many centuries gave rise to the first litter manipulation studies, and their results demonstrated that litter and its decomposition are a vital part of ecosystem function. Litter plays two major roles in forest ecosystems: firstly, litterfall is an inherent part of nutrient and carbon cycling, and secondly, litter forms a protective layer on the soil surface that also regulates microclimatic conditions. By reviewing 152 years of litter manipulation experiments, I show that the effects of manipulating litter stem from changes in one, or both, of these two functions, and interactions between the variables influenced by the accumulation of litter can result in feedback mechanisms that may intensify treatment effects or mask responses, making the interpretation of results difficult.

Long-term litter removal increased soil bulk density, overland flow, erosion, and temperature fluctuations and upset the soil water balance, causing lower soil water content during dry periods. Soil pH increased or decreased in response to manipulation treatments depending on forest type and initial soil pH, but it is unclear why there was no uniform response. Long-term litter harvesting severely depleted the forests of nutrients. Decreases in the concentrations of available P, Ca, Mg, and K in the soil occurred after only three to five years. The decline in soil N occurred over longer periods of time, and the relative loss was greater in soils with high initial nitrogen concentration. Tree growth declined with long-term litter removal, probably due to lower nutrient availability. Litter manipulation also added or removed large amounts of carbon thereby affecting microbial communities and altering soil respiration rates.

Litter manipulation experiments have shown that litter cover acts as a physical barrier to the shoot emergence of small-seeded species; further, the microclimate maintained by the litter layer may be favourable to herbivores and pathogens and is important in determining later seedling survival and performance. Litter manipulation altered the competitive outcomes between tree seedlings and forbs, thereby influencing species composition and diversity; changes in the species composition of understorey vegetation following treatments occurred fairly rapidly. By decreasing substrate availability and altering the microclimate, litter removal changed fungal species composition and diversity and led to a decline in populations of soil fauna. However, litter addition did not provoke a corresponding increase in the abundance or diversity of fungi or soil fauna.

Large-scale long-term studies are still needed in order to investigate the interactions between the many variables affected by litter, especially in tropical and boreal forests, which have received little attention. Litter manipulation treatments present an opportunity to assess the effects of increasing primary production in forest ecosystems; specific research aims include assessing the effects of changes in litter inputs on the carbon and nutrient cycles, decomposition processes, and the turnover of organic matter.

Key words: leaf litter, litter manipulation, forests, nutrient cycle, carbon cycle, microclimate, plant growth, soil fauna, seedling emergence, mycorrhizal fungi.

CONTENTS

I. Introduction	000
(1) Definition of terms	000
II. Historical aspects	000
III. The forest floor environment	000
(1) Compaction, runoff, erosion, and leaching	000
(2) Soil water content and temperature	000
(3) Soil pH	000
IV. The carbon cycle	000
(1) Humus, soil organic matter, and soil C/N ratios	000
(2) Soil respiration and microbial biomass	000
V. The nutrient cycle	000
(1) Nutrients in the soil	000
(a) Nitrogen	000
(b) Phosphorus and other mineral nutrients	000
(2) Nutrients in foliage, litter, and wood	000
VI. Direct and indirect effects on vegetation	000
(1) Tree growth	000
(2) Seed germination, seedling emergence, establishment, and survival	000
(a) Early life stages – seed germination and seedling emergence	000
(b) Seedling survival and performance	000
(c) Competition	000
(3) Plant community structure and diversity	000
(a) Forest biodiversity	000
(b) Understorey vegetation	000
VII. Soil and litter fauna	000
(1) Microarthropods, macroarthropods, and nematodes	000
(2) Earthworms	000
VIII. Fungi and mycorrhizae	000
IX. Conclusions	000
X. Acknowledgements	000
XI. References	000
XII. Appendix	000

I. INTRODUCTION

Litter plays an important role in forest ecosystems; this is clear from many observational studies and also from litter manipulation experiments. Not only is it an essential part of nutrient cycling, but litter cover also acts as a protective layer by buffering changes in soil water content (Ginter, McLeod & Sherrod, 1979) and temperature (Ramann, 1883; MacKinney, 1929; Pearse, 1943; Judas, 1990; Poser, 1990; Ponge, Arpin & Vannier, 1993) and hindering erosion (Lowdermilk, 1930; Walsh & Voigt, 1977; Coelho Netto, 1987), leaching (Němec, 1929; Lunt, 1951; Mo *et al.*, 2003) and soil compaction (Benkobi, Trlica & Smith, 1993; Geddes & Dunkerley, 1999). Litter provides habitats and substrate for earthworms (Gonzalez & Zou, 1999), arthropods (Arpin, Ponge & Vannier, 1995), fungi (Tyler, 1991), and micro-organisms (Jordan, Ponder & Hubbard, 2003). Plant diversity is influenced by litter depth (Grime, 1979); the heterogeneous nature of litter cover promotes species coexistence (Facelli & Pickett, 1991 *b*) by facilitating or suppressing seed germination and seedling emergence,

and influencing seedling survival at a small scale in patches throughout the forest. The litter layer exercises direct and indirect influences on soil physical and chemical properties, nutrient availability, and the diversity of fungi and soil organisms. As litter affects so many different variables simultaneously, it is difficult to quantify the consequences of changes to litter inputs at the ecosystem level. Experimental removal and addition of litter is needed to provide a sound basis for assessing the importance of the litter layer.

The quantity of litterfall varies greatly over a range of spatial and temporal scales and is determined mainly by climate, seasonality, topography, soil parent materials, and species distribution. Management practices can cause drastic changes in litter production by modifying species composition and productivity; climate change may affect litterfall as changes in rainfall patterns and mean annual temperatures can affect tree phenology and tree species distribution (Condit, Hubbell & Foster, 1996) and increases in productivity and litterfall have been observed as a consequence of elevated atmospheric CO₂ levels (DeLucia *et al.*, 1999; Allen *et al.*, 2000; Finzi *et al.*, 2001; Schlesinger & Lichter, 2001; Zak *et al.*, 2003). Experiments involving

litter removal and litter addition treatments amplify these changes in litter quantity, thus invoking stronger effects over shorter time periods, which are more easily detectable than the effects of natural variation. The drawbacks to these litter manipulation studies include intensive labour (raking and moving the litter), few short-term results (e.g. tree growth and nutrient dynamics often take years to respond), and the fact that in manipulating the litter layer, many variables are affected simultaneously, making results difficult to interpret. Nevertheless, carefully planned experiments can provide important insights into the role of the litter layer in forest ecosystems, information which is required in order to make accurate predictions of changes to forest and soil dynamics in years to come.

I review the results of 152 years of litter manipulation experiments and observational studies in order to show how quantitative studies of litter have contributed to our understanding of forest ecosystems and to identify future research objectives. The majority of the reviewed studies, and all the long-term experiments, were conducted in temperate forests; there exist only few observational and short-term studies in the taiga and tropical forests. There also exist more than twice as many studies on the effects of litter removal than of litter addition (see the Appendix for details of the reviewed studies). As experimental manipulations of litter in this review usually involve only a change in litter quantity, I shall discuss the effects of litter quality only where they are particularly relevant. The findings from experiments on litter manipulation in non-forest ecosystems are beyond the scope of this review, although I have included studies on tree seedlings in old fields and in glasshouse experiments. Facelli & Pickett (1991*b*) have reviewed experiments on litter in grasslands, and the effects of litter on the structure and dynamics of grassland communities.

(1) Definition of terms

One of the great difficulties in reviewing a large number of studies dating from different centuries and focussing on a variety of variables is the lack of consistent methodology and terminology. In the interests of clarity, I shall use the definitions and expressions given below throughout the text; the designations of soil horizons follow the classification of the United States Department of Agriculture (USDA, 2003). As the profiles and prevalent layers differ between soil types, I use two general terms in order to make comparisons: 'soil' refers to the mineral soil (mineral matter plus incorporated organic matter), unless otherwise stated, and does not include the 'forest floor', which encompasses litter and unincorporated humus on the surface of the 'mineral soil'; the forest floor usually comprises at least two of the three organic sub-horizons, Oi, Oe, and Oa. The litter layer (Oi) refers to the surface layer of the forest floor, which is not in an advanced stage of decomposition and consists of fallen leaves, needles, fruits, flowers, and twigs. The fermentation layer (Oe) occurs below the litter layer on many forest soils, where the litter is not mixed with the mineral soil by soil animals. It is composed of partially decomposed organic material, in which some plant structures are still recognisable. Mor humus, moder, and peat have an Oa subhorizon,

which consists of well-decomposed organic matter of unrecognisable origin. It should be noted at this point that most of the studies in this review were conducted in beech or coniferous forests and therefore in many cases the organic horizon is mor humus with Oe and Oa subhorizons. Soil organic matter (SOM) or humus refers to the organic matter incorporated into the mineral soil, exclusive of undecayed plant and animal residues, and soil water content refers to the gravimetric or volumetric water content of the soil.

The duration of 'long-term' litter-raking ranges from a decade to over a century and in most cases was not determined exactly. I have defined those studies as long-term when litter removal was carried out for more than 10–12 years (and therefore short-term is less than 10 years). In general, the effects of long-term litter raking were studied by comparing a traditionally raked forest to a nearby stand of the same tree species on similar soil where litter harvesting had not been permitted. By using this approach, no account can be made of initial differences between sites or stands that may influence the results. Notable exceptions were Krutzsch (1869), von Schröder (1876), Ramann (1883), and Schwappach (1887), who did take pretreatment measurements and conducted the first experimental litter manipulations over a period of 20, 13, 16, and 21 years, respectively. Litter removal in all of the large-scale studies was carried out by raking, but in some of the small-scale studies, litter was excluded by nets above the plots, or collected by hand to avoid damage to seedlings or disturbance to soil animals. There is a great lack of consistency in data collection in almost all of the studies with a duration of more than a year. In many studies only the final results are presented, with little information on the intermediate findings. Most of the studies before the 1960s did not replicate treatment plots, fail to describe a large part of the methodology used, or, in the case of the 19th Century studies, use antiquated units and methods that cannot be directly compared to modern-day techniques. I have therefore attempted to separate the older, long-term studies from the more recent shorter ones. I have also converted almost all results into percentages in order to make direct comparison possible.

II. HISTORICAL ASPECTS

Forest litter was an indispensable resource for cattle small-holdings in central Europe for many centuries, and its use in agriculture has provided us with the first detailed insights into its importance in forest ecosystems. From around the 12th Century onwards the removal of litter from the forest floor was one of the most common forest management practices in central Europe, alongside pollarding and pastoral use of forest land (Mitscherlich, 1955; Ellenberg, 1988; Glatzel, 1991). The raked-up litter was used as bedding for farm animals (Mitscherlich, 1955; Ellenberg, 1988; Glatzel, 1991; Farrell *et al.*, 2000; Jandl *et al.*, 2002), and subsequently, when it was saturated with animal dung and urine, it was applied to crops as fertilizer (Glatzel, 1991; Farrell *et al.*, 2000). The increase in cultivation of potatoes, tobacco, and hops in the 18th Century led to a decrease in

Table 1. Nutrient export with litter removal and whole-tree harvesting in different forest types.

Litter production t ha ⁻¹ year ⁻¹	Litter removal					Forest type	Source
	N	P	K	Ca	Mg		
	kg ha ⁻¹ year ⁻¹						
4.0–4.2	33	10.5	10	82	12	<i>Fagus sylvatica</i>	Ebermayer (1876)
—	37–55	9–13	8–12	77–116	11–17	<i>Fagus sylvatica</i>	Ganter (1927)
5.8	60	4	18	151	29	<i>Fagus sylvatica</i>	Ellenberg (1988)
2.7–5.7	—	—	—	—	—	<i>Fagus sylvatica</i>	Tschermak (1926)
1.9–4.4	—	—	—	—	—	<i>Fagus sylvatica</i>	Feinstumantel (1876)
—	32–63	8–15	7–14	68–134	10–19	<i>Carpinus betulus</i>	Ganter (1927)
3.9–4.4	39	6.5	5	61	7	<i>Picea abies</i>	Ebermayer (1876)
2.7–3.8	38	3.5	5	19	5	<i>Pinus sylvestris</i>	Ebermayer (1876)
—	17	2.7	1.3	6.7	1	<i>Pinus sylvestris</i>	Ramann (1883)
1.4–1.8	—	—	—	—	—	<i>Pinus sylvestris</i>	Schwappach (1887)
—	32	4	5	19	5	<i>Pinus sylvestris</i>	Ganter (1927)
—	11–18	—	—	—	—	<i>Pinus sylvestris</i>	Kreutzer (1972)
8.7	—	—	—	—	—	<i>Pinus elliottii</i>	Lopez-Zamora <i>et al.</i> (2001)
2.3	14.4	0.6	2.7	5.6	1	<i>Pinus massoniana</i>	Brown <i>et al.</i> (1995)
3.8	—	—	—	—	—	<i>Pinus palustris</i>	Haywood <i>et al.</i> (1998)
3.5–4.1	—	—	—	—	—	<i>Pinus palustris</i>	McLeod <i>et al.</i> (1979)
4.0	40.5	3.1	22.6	25.9	9.4	various	Krapfenbauer (1983)
—	33–70	5–11	—	13–27	—	various	Mitscherlich (1955)
—	8.5–20	0.5–1.5	0.5–1.5	1.5–4.5	2.5–10	various	Kilian (1998)
—	20–50	2–4	12–25	14–40	3–10	various	Glatzel (1991)
3.6–7.4	30–71	4–15	9–34	98–174	13–36	various	Ellenberg (1988)
Whole tree harvest (<i>c.</i> 100-year-old stand)							
	N	P	K	Ca	Mg	Forest type	Source
	kg ha ⁻¹						
—	248–379	19–54	135–253	374–558	50–65	various	Hornbeck <i>et al.</i> (1990)
—	1120	114	650	1040	140	<i>Picea abies</i>	Kilian (1998)
—	1200	139	634	1334	159	<i>Picea abies</i>	Krapfenbauer (1983)
—	1070	107	142	680	885	<i>Pinus sylvestris</i>	Kilian (1998)

the area of available forest pasture as forested areas were converted to crop land and more and more animals were kept in stables (Mitscherlich, 1955). By the early 1800s litter harvesting had become indispensable to small farms (Mitscherlich, 1955) and litter use peaked (Kilian, 1998). The amount of litter removed from the forest with the first raking ranged from 6–15.6 t ha⁻¹ (Ebermayer, 1876; Tschermak, 1926; Kreutzer, 1972) with the lower values from *Pinus sylvestris*, intermediate values from *Picea abies*, and higher values from *Fagus sylvatica* forests. Subsequent harvests removed 1.4–8.7 t ha⁻¹ year⁻¹ (Table 1) and litter production declined further as forest productivity was reduced. This practice continued until after World War II in some areas, even though its detrimental effects on soil and forest productivity had been well documented by the end of the 19th Century.

The first extensive studies on the importance of litter were conducted as early as the 1850s, and showed that long-term litter removal destabilises forests not only by depleting them

of nutrients, but also by damaging the physical and chemical properties of the soil and disrupting the formation of humus (Kruttsch, 1850, 1852, 1863, 1869; Ebermayer, 1876; von Schröder, 1876). Long-term litter removal from forests was shown to deplete nitrogen to a severe degree (Table 2), while grazing or timber use alone usually had a less severe impact (Ellenberg, 1988; Glatzel, 1991). In terms of nutrient losses, a few decades of litter harvesting are comparable with the whole tree harvest of a 100-year old stand (Kilian, 1998; Table 1). Peak litter removal by raking destroyed the acid-neutralizing capacity more quickly than acid rain (Glatzel, 1991) and the combined effect of soil acidification and nutrient depletion was the principal cause of destabilization in forest ecosystems in central Europe, which led to mixed deciduous forests being replaced by, or areas replanted with, less nutrient-demanding conifer stands (Ebermayer, 1876; Wittich, 1954; Ellenberg, 1988; Jandl *et al.*, 2002). Productivity in litter-harvested forests sank drastically in the 1800s; the average decline in wood production of raked

Table 2. Percentage losses of nutrients from different forest soils with litter removal, ordered by treatment duration. T = change in total concentration; A = change in available concentration. Ranges are given for studies at multiple sites.

Treatment duration (years)	N		P		K	Mg	Ca	Mn	S	Fe	Sampling depth (cm)	Source
	T	A	T	A	T	T	T	T	T	T		
>50	43	—	—	30	30	73	32	—	—	—	0–47	Ebermayer (1876)
>50	47	44	41	48	37	—	45	—	—	16	0–10	Němec (1929)
>50	6–44	7–62	—	—	—	—	—	—	—	—	0–10 & 0–15	Němec (1931)
>50	—	5–78	—	47	—	—	69	—	—	—	0–10 & 0–15	Wittich (1951)
34	40	—	37	—	—	—	—	—	—	—	?	Peng <i>et al.</i> (2003)
25	33	—	—	—	—	—	—	—	—	—	0–5	Lindholm & Nummelin (1983)
20	No effect	—	21	—	—	—	75	—	—	—	0–3	Lunt (1951)
16	13	—	—	53	64	22	—	28	73	19	0–15	Ramann (1883)
16	No effect	—	—	No effect	—	—	65	—	—	—	0–13	Dzwonko & Gawronski (2002a)
15	18	—	—	—	—	—	—	—	—	—	0–10	Ganter (1914)
12	41	—	17	—	32	60	—	—	41	—	0–15	Hanamann (1881) cited in Ramann (1883)
4	—	—	—	67	—	—	—	—	—	—	0–5	Lopez-Zamora <i>et al.</i> (2001)
3	No effect	—	—	No effect	24	—	No effect	—	—	—	0–20	McLeod <i>et al.</i> (1979)
—*	—	8	—	52	26	—	—	—	—	—	0–5	Baar & Ter Braak (1996)

* Entire forest floor removed.

stands is thought to have been around 50% (Jandl *et al.*, 2002). The effects of long-term litter use persist for many decades after cessation of the harvesting practice and are still reflected in forest soils today in Austria (Glatzel, 1991; Jandl *et al.*, 2002), Switzerland (Perruchoud *et al.*, 1999), and Germany (Wittich, 1954; Kreutzer, 1972; Prietzel, Kolb & Rehfuss, 1997). Litter raking was banned from most forests in Europe by the 1950s (Mitscherlich, 1955), but it remains a common management practice in pine stands in the USA, where ‘pine straw’ has an important commercial value as garden mulch (McLeod, Sherrod & Porch, 1979; Ross, McKee & Mims, 1994; Haywood *et al.*, 1998; Lopez-Zamora *et al.*, 2001), and in China, where litter and understorey harvesting provides an important fuel source to peasants (Brown, Lenart & Mo, 1995; Mo, Brown & Lenart, 1995; Mo *et al.*, 2003; Peng *et al.*, 2003).

III. THE FOREST FLOOR ENVIRONMENT

The litter layer acts as an interface between the soil surface and the atmosphere, and provides a degree of protection to the soil surface by intercepting rain (Benkobi *et al.*, 1993) and solar radiation (Pearse, 1943; Wilke, Bogenrieder & Wilmanns, 1993; Ogee & Brunet, 2002), and buffering the soil surface against fluctuations in temperature (Ramann, 1883; MacKinney, 1929; Pearse, 1943; Judas, 1990; Poser, 1990; Ponge *et al.*, 1993) and water content (Ginter *et al.*, 1979). Litter is also a major source of soil organic matter, which strongly influences the structure of the soil and increases its stability (Marshall, Holmes & Rose, 1996). Soil organic matter often plays a role in determining the pH of

the soil surface horizons, as pH is regulated by humic acids to a large extent in some soils (Wilke *et al.*, 1993). Litter and soil organic matter affect soil porosity and aeration indirectly, as they constitute the major food supply to earthworms and soil arthropods (Arpin *et al.*, 1995; Marshall *et al.*, 1996; Gonzalez & Zou, 1999). Any changes to the supply of organic matter through litterfall will therefore have wide-reaching effects on soil chemistry and soil physical properties.

(1) Compaction, runoff, erosion, and leaching

A covering of freshly fallen and partially decomposed leaves, in combination with living vegetation, protects the soil surface from the direct impact of raindrops and throughfall (Benkobi *et al.*, 1993; Geddes & Dunkerley, 1999). Litter cover decreases or prevents the destruction of aggregates and separation of fine particles by raindrop impact, prevents soil surface compaction and sealing and consequently helps to prevent run-off and subsequent erosion during rainfall events (Walsh & Voight, 1977; Morgan, 1995; Marshall *et al.*, 1996).

Although few studies have quantified changes to soil physical properties such as bulk density or pore volume following litter removal or litter addition, the few studies that exist show an increase in soil bulk density in the absence of a litter layer. Bulk density of surface soil layers in litter-raked forests can be up to twice that of undisturbed stands (Mitscherlich, 1955) and the effects are greater deeper down in the soil profile (Wiedemann, 1935; Mo *et al.*, 2003). Lower pore densities measured in long-term litter-raked plots relative to undisturbed controls also indicate soil compaction (Tschermak, 1926; Ganter, 1927). Changes in bulk

density in litter-raked forests are most likely to be a combination of higher raindrop and throughfall impact, trampling, and reduced soil organic matter content.

Erosion and overland flow are greater when litter cover is absent. Litter provides direct protection against erosion by retaining water (Walsh & Voigt, 1977; Marshall *et al.*, 1996), thereby reducing run-off and overland flow (Lowdermilk, 1930; Coelho Netto, 1987; Benkobi *et al.*, 1993; Kimoto *et al.*, 2002) and suppressing rill formation, which in turn reduces the sediment produced by overland flow (Marshall *et al.*, 1996). Simulated rainfall events on a clay-loam soil showed that a 60% surface cover of litter reduced soil loss by 60% compared to bare soil (Benkobi *et al.*, 1993). Earlier litter removal studies demonstrated greater surface run-off and erosion in soils without litter cover (Ganter, 1927; Lowdermilk, 1930).

(2) Soil water content and temperature

The high water retention capacity of litter and soil organic matter helps to maintain maximum infiltration rates (Lowdermilk, 1930; Walsh & Voigt, 1977), which allow the penetration of water to greater depths in the soil profile, thereby slowing soil desiccation due to evaporation (Lowdermilk, 1930; Walsh & Voigt, 1977). Early litter manipulation studies show a reduction in water retention capacity in the soil of 13–14% in the upper soil layers and 4–7% in the lower soil layers in long-term raked forests compared to undisturbed stands (Ebermayer, 1876; Ramann, 1883).

Litter removal may increase or decrease water content depending on the season and the interval between rainfall events, which leads to inconsistent results between studies. Although Ramann (1883) measured greater soil water content in raked plots during the spring, he found no differences during the rest of the year and most other studies have shown that litter removal decreases soil water content. Lower soil water content in raked plots has been shown: throughout the year (Ganter, 1927), during the spring and autumn, but not in summer or winter (Gill, 1969), only in spring (Ponge *et al.*, 1993), or even during only one month of the year (Judas, 1990). Studies involving more frequent measurements of soil water content demonstrated that the response of soils to changes in water content are generally more buffered and gradual when a litter layer is present. Litter removal was found to increase water content shortly after rainfall events and to decrease it during dry periods (Lunt, 1951; Ginter *et al.*, 1979). These opposing effects, combined with differences between sites and between years explain the contradictory results found in less intensive studies.

Litter addition appears to have little effect on soil water content (Gill, 1969; Uetz, 1979; Poser, 1990), although increased soil water content in litter addition treatments has been shown in one study (Judas, 1990).

Litter buffers fluctuations in soil temperature by reducing evaporation from the soil surface and by intercepting radiation (Pearse, 1943; Wilke *et al.*, 1993; Ogee & Brunet, 2002), thus delaying freezing in temperate sites in winter (MacKinney, 1929; Walsh & Voigt, 1977); and increasing

the length of the growth period (Krutzsch, 1863). Litter removal caused greater fluctuations in soil temperature (Ramann, 1883; MacKinney, 1929; Pearse, 1943; Judas, 1990; Poser, 1990; Ponge *et al.*, 1993) and higher soil temperatures during warm periods (Ramann, 1883; Ganter, 1927; Gill, 1969; Uetz, 1979; Judas, 1990), whereas soil temperatures in plots with litter cover, whether litter addition treatments or controls, are less variable throughout the year (Pearse, 1943; Gill, 1969; Judas, 1990; Poser, 1990; Ponge *et al.*, 1993; Facelli *et al.*, 1999).

The general lack of changes in soil water content and temperature with litter addition treatments suggests that natural litter cover is adequate protection for the soil. However, changes to soil water content and temperature following litter removal can be quite drastic and may affect the forest carbon balance, as soil water content and surface temperature are driving factors of soil respiration (Singh & Gupta, 1977; Ogee & Brunet, 2002) and strongly influence decomposition rates (Krutzsch, 1863; Facelli & Pickett, 1991*b*).

(3) Soil pH

Soil organic matter, or humus, plays a dual role in determining soil pH. Soil pH is determined by the concentration of cations, mainly hydrogen and aluminium, in soil water (Brady, 1974). Clay particles and soil organic matter complexes provide negative binding sites for cations and in soils with near-neutral or alkaline pH, cations such as calcium, ammonium, potassium, and magnesium replace hydrogen and aluminium ions on these exchange sites (Killham, 1994). These cations are not tightly bound, but can be exchanged with other cations in the soil solution; the cation exchange capacity (c.e.c.) of the soil acts as a buffer controlling the input and release of nutrients (Davis *et al.*, 1992). Soil organic matter may provide the bulk of exchange sites in soils with low clay content, and therefore strongly influence c.e.c. and nutrient availability. However, the negative charges on complexes of soil organic matter are not permanent, but susceptible to changes in pH. Microbial decomposition of organic matter can increase soil acidity through the production of organic acids (Killham, 1994). Litter removal can potentially either decrease soil pH by diminishing the supply of exchangeable base cations (Wittich, 1951), or increase soil pH by reducing the amount of organic acids produced (Mitscherlich, 1955).

Soil pH decreased with litter removal on various soil types (Ellenberg, 1988; Glatzel, 1991; Ponge *et al.*, 1993), many of which were sandy (Wittich, 1951) or nutrient-poor (Wittich, 1951; Dzwonko & Gawronski, 2002*a*). Soil pH increased with litter removal on nutrient-poor oxisols (Mo *et al.*, 2003), where c.e.c. is determined by the generally high clay content, and on a highly acidic sandy soil under mor humus (Němec, 1929). The removal of the entire forest floor in *Pinus sylvestris* stands on mor humus also increased pH by reducing the amounts of humic acids leaching into the mineral soil (Fiedler *et al.*, 1962; Baar & Ter Braak, 1996).

An increase in soil pH with litter addition has only been shown in one study (Ponge *et al.*, 1993), but natural accumulation of litter and organic matter has also been

associated with an increase in pH of up to half a unit (Beatty & Sholes, 1988; Wilke *et al.*, 1993).

Interestingly, the studies showing a decrease in pH with litter removal were in mixed deciduous or mixed pine-deciduous forests on soils with initial pH values of 5–5.5 (Ponge *et al.*, 1993; Dzwonko & Gawronski, 2002a); the studies showing no difference in pH with litter removal were conducted in pine forests on soils with a pH of around 5 (Lunt, 1951; McLeod *et al.*, 1979; Fisk & Fahey, 2001), while those showing an increase were in *Pinus* species stands on acidic soils with a pH of around 3–3.5 (Němec, 1929; Baar & Ter Braak, 1996; Mo *et al.*, 2003). The direction and magnitude of changes to soil pH following litter manipulation appear to be driven by initial pH, soil-, and vegetation type and result in soil pH values that are similar to the pH of rainfall, which suggests that litter removal reduces the buffering capacity of the soil for changes in pH.

IV. THE CARBON CYCLE

Litter manipulation also adds carbon to or removes it from the system, which affects the organic matter content of the soil and the build-up of the forest floor; these influence decomposition and soil respiration rates. The amount of carbon removed from central European forests with the first litter harvest has been estimated as 3.0–7.8 t ha⁻¹ (Tschermak, 1926), depending on forest type and site fertility; subsequent harvests removed 1.4–2.8 t ha⁻¹ year⁻¹ (Feinstmantel, 1876; Tschermak, 1926; Krapfenbauer 1983; Ellenberg, 1988). These estimates agree with Ebermayer's (1876) measurements of average annual carbon loss by litter raking of 1.5 t ha⁻¹ year⁻¹ in *Fagus sylvatica* stands, and 1.4 t ha⁻¹ year⁻¹ in stands of *Picea abies* and *Pinus silvestris*.

(1) Humus, soil organic matter, and soil C/N ratios

The thickness of the organic layers (Oe and Oa horizons) that form on some soils is diminished by litter removal. Long-term litter raking reduced the depth of the Oe and Oa horizons in forests dominated by *Pinus sylvestris* and *Fagus sylvatica* by around 50% (von Schröder, 1876; Ramann, 1883; Němec, 1929, 1931; Wiedemann, 1935) although an extensive study in 17 different forests showed very high variation (0–89% decrease in depth) between stands of *Pinus sylvestris* on different soil types; the relative reduction depended largely on the duration of litter removal (Wittich, 1951). Significant reductions in the depth of the organic horizons only occur after about a decade of litter removal (Dzwonko & Gawronski, 2002a). Few short-term studies have measured soil organic matter (SOM) or organic horizon thickness and no differences between treatments had occurred after five (Ponge *et al.*, 1993) and seven years of raking (Ross *et al.*, 1994). However, treatments in the latter study were only carried out every three years.

One or more decades may be necessary for the recovery of SOM content after the cessation of litter removal (Fiedler *et al.*, 1962; Baar & Ter Braak, 1996; Mo *et al.*, 2003);

increasing levels of soil carbon content have been detected after 10–15 years (Mao *et al.*, 1992).

Data from litter addition treatments are scarce. However, increased C/N ratios in mor humus (Lunt, 1951; Park & Matzner, 2003), and a twofold increase in soil carbon in the mineral soil surface layers (Ponge *et al.*, 1993) have been measured after only a few years (2–5) of litter addition. Soil fertility and species composition determine the quality of litter, strongly affecting decomposition rates (Vesterdal, 1999; Sariyildiz & Anderson, 2003) and carbon accumulation (Cote *et al.*, 2000; Giardina *et al.*, 2001; Franklin *et al.*, 2003), and therefore influence the effects of increased litter inputs on SOM and forest floor thickness.

(2) Soil respiration and microbial biomass

Litter removal leads to a decline in fresh decaying organic matter in the soil surface layers, which affects microbial communities and generally causes a decrease in soil respiration (Bowden *et al.*, 1993; Jandl & Sollins, 1997; Nadelhoffer *et al.*, 2004; Li *et al.*, 2004; Vasconcelos *et al.*, 2004). In a mixed deciduous forest, litterfall data and the measurements of carbon content and decay rates from the litter horizon showed that fresh organic matter contributed about 11% to total soil respiration (respiration from the mineral soil and the forest floor including root respiration; Edwards & Harris, 1977). Data from root- and litter-exclusion treatments provided a similar value of 12% from decomposing recent litter and show that 26% of the total respiration derives from the decay of older organic matter (Bowden *et al.*, 1993; Nadelhoffer *et al.*, 2004). Long-term litter harvesting in China decreased soil respiration by 40–63% (Mao *et al.*, 1992), and litter removal experiments in tropical forests measured a decrease in soil respiration of 28% after one year (Vasconcelos *et al.*, 2004) and 54% after seven years (Li *et al.*, 2004). Long-term changes in litter inputs may also influence soil respiration rates by modifying soil temperature and soil water content (Schlentner & Van Cleve, 1985), pH (Kowalenko, Ivarson & Cameron, 1978), nutrient availability (Singh & Gupta, 1977), soil carbon content, and cation exchange capacity (La Scala *et al.*, 2000). These secondary effects of litter on soil respiration rates complicate predictions and estimates of the long-term consequences of changes to litter inputs.

Litter addition treatments in a temperate deciduous forest had no effect on total soil respiration after one year of treatment, but respiration in laboratory incubations of soil from litter addition plots was 40% higher than controls after five years (Bowden *et al.*, 1993; Nadelhoffer *et al.*, 2004).

The addition or removal of litter alters soil microbial biomass and activity by changing the amount of available substrate. Total microbial biomass in the upper 25 cm of the mineral soil declined by an average of 67% after seven years of litter removal treatments in a young secondary montane tropical rainforest (Li *et al.*, 2004). Substrate-induced respiration (SIR) is commonly used as a measure of active microbial biomass (Anderson & Domsch, 1978); long-term litter harvesting in *Eucalyptus* forests in tropical China decreased SIR in the upper 25 cm of the soil by 40% on average and by 61% during the rainy season (Peng *et al.*,

2003). In a temperate deciduous forest, SIR in the organic horizon declined by 17% over nine years when litter was removed every other year (Fisk & Fahey, 2001). Removing leaf litter from pots of forest floor material taken from boreal *Pinus sylvestris* and *Betula alba* stands decreased SIR by 7% and 30%, respectively, after two growing seasons (Nilsson, Wardle & Dahlberg, 1999). One study showed no decrease in microbial biomass with litter removal, but there was a strong decrease in the active microbial biomass in the soil in treatments in which the O and A horizons had been removed (Nadelhoffer *et al.*, 2004). This result suggests that organic matter in some soils may be sufficient substrate for microbial growth over long periods of time without fresh litter inputs (Park & Matzner, 2003). The measure of total microbial biomass allows no conclusions to be drawn about microbial community structure, but shifts in dominance towards microbes feeding on older organic matter (Fontaine, Mariotti & Abbadie, 2003) can be expected following litter removal.

In a temperate deciduous forest, litter addition had little effect on microbial biomass in the forest floor after two years (Park & Matzner, 2003), but another study showed increased total fungal biomass in the forest floor, as well as decreased total fungal biomass and active bacterial biomass in the mineral soil after five years of litter addition (Nadelhoffer *et al.*, 2004).

V. THE NUTRIENT CYCLE

Fine litter forms an inherent part of the nutrient cycle. In terms of nitrogen loss, a single litter harvest was equivalent to harvesting half to a full crop of rye (Ehwald, 1957). It is therefore hardly surprising that the most dramatic results relating to soil nutrients have been obtained in forests where litter harvesting was a common management practice over many decades. No recent experimental studies have quantified nutrient removal with litter harvesting, but estimates for central European forests range from 8.5 to 71 kg ha⁻¹ yr⁻¹ for nitrogen (Ebermayer, 1876; Ramann, 1883; Ganter, 1927; Mitscherlich, 1955; Kreutzer, 1972; Krapfenbauer, 1983; Killian, 1998) and from 0.5 to 15 kg ha⁻¹ yr⁻¹ for phosphorus (Ramann, 1883; Ganter, 1927; Mitscherlich, 1955; Krapfenbauer, 1983; Killian, 1998) (Table 1). The high variation between the values given in different studies can be attributed to differences in soil fertility, vegetation, and their combined effect on litter quality, with higher litter quality and therefore higher nutrient export for mixed deciduous forests on nutrient-rich soils, and the poorest litter quality and lowest nutrient export for conifer forests on nutrient-poor soils (Ebermayer, 1876). The nutrient export from long-term raked forests will have decreased over time with the decline in litter production (Tschermak, 1926; Mitscherlich, 1955; Kreutzer, 1972; Krapfenbauer, 1983), and litter quality (Mo *et al.*, 1995). Deciduous forests on nutrient-rich soils lost greater amounts of nutrients through litter removal, as angiosperm deciduous leaves tend to have higher nutrient concentrations than pine needles (Ebermayer, 1876; Krapfenbauer, 1983). Furthermore,

deciduous trees are usually badly adapted to low nutrient conditions (Small, 1972; Goldberg, 1982; Givnish, 2002) and productive mixed deciduous forests are usually found on relatively fertile soils where nutrient use (*sensu* Vitousek, 1982) is less efficient (Goldberg, 1982).

Changes in soil water content, soil temperature and pH with differing litter quantity have an indirect influence on nutrient availability. The environmental conditions in the litter layer and the quality of the litter affect decomposition rates and microbial activity, and thus regulate the rate of nutrient release from organic matter (Facelli & Pickett, 1991*b*; Blair, Crossley & Callahan, 1992; Stump & Binkley, 1993; Scott & Binkley, 1997). The cation exchange capacity and base saturation of the soil depend largely on organic matter content (Wittich, 1951; Mitscherlich, 1955; Marshall *et al.*, 1996). Therefore, litter removal will affect the amounts of nutrients available for growth in two ways: directly, by exporting nutrients with fine litter, and indirectly by reducing the availability of nutrients in the soil. With time a positive feedback ensues as nutrient concentrations in the leaves decrease and litter quality deteriorates, so that effects persist even after the cessation of litter removal.

(1) Nutrients in the soil

Litter removal decreases the concentrations of nutrients in the soil, especially on nutrient-poor soils such as sand. Nutrient availability can also be influenced by changes in cation exchange capacity, which was shown to decrease after litter removal (Dzwonko & Gawronski, 2002*a*). Leaching also increases in the absence of litter cover; lower nutrient concentrations in the surface soil and higher concentrations in the lower layers of the soil profile in raked stands compared to controls indicate leaching downwards through the soil profile by rainwater (Němec, 1929; Lunt, 1951). High leaching losses in particular of nitrogen can occur in long-term litter raked forests (Mo *et al.*, 1995), and they may even be greater than those caused by the removal of nitrogen in fine litter (Ramann, 1883).

(a) Nitrogen

The great majority of long-term studies showed that litter harvesting diminished the amount of total and available nitrogen in the soil (Table 2). The first study of the effects of long-term litter raking on soil nitrogen concentration showed a 43% overall decrease in total nitrogen and a reduction of almost 90% in the upper 0.5 m of the soil (Ebermayer, 1876). Later studies in different forests showed a strong but less dramatic mean decrease of 18% of total nitrogen in the upper 10 cm of the mineral soil (Němec, 1929), but decreases of up to 78% in available nitrogen (Wittich, 1951). Although the depletion of nitrogen over many decades of litter removal is hardly surprising, decreases of 41 and 18% total nitrogen concentration have been measured in the upper 15 cm of the soil after raking for only 12 and 15 years by Hanamann (*in* Ramann, 1883) and Ganter (1914), respectively. There is high variation (5–78%) in the loss of nitrogen caused by long-term litter removal

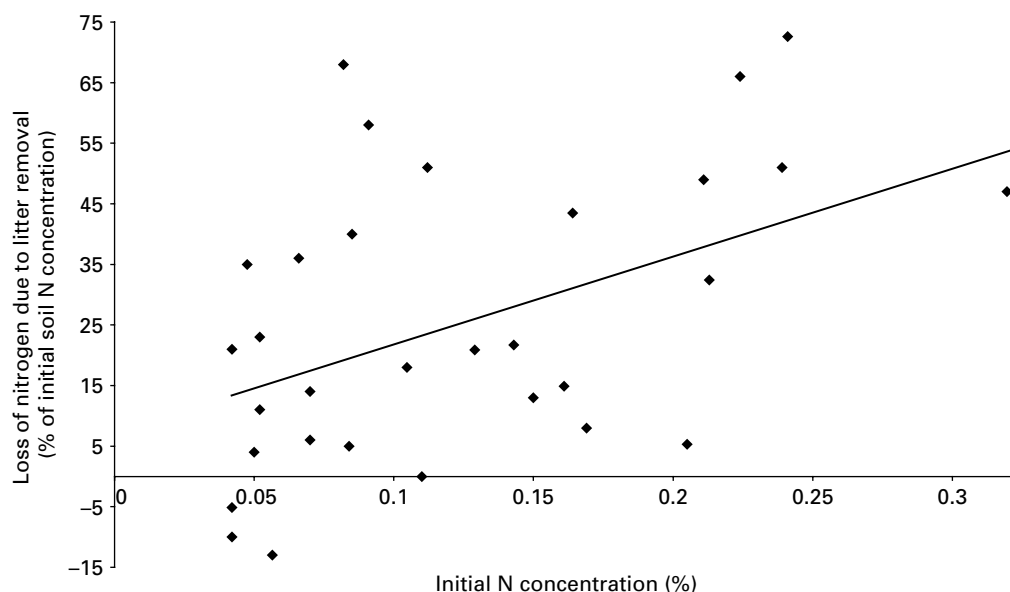


Fig. 1. The proportion of total nitrogen lost from the soil with litter removal as a function of the initial nitrogen concentration. Data are taken from the studies listed in Table 2.

between sites (Table 2) depending on soil type and in particular soil fertility (Fig. 1). Regression analysis of 30 litter removal studies in forests showed that the relative soil nitrogen loss from the top 10 cm of mineral soil generally increased with increasing initial nitrogen concentration in the soil (linear regression analysis: d.f. = 30; $R^2 = 0.216$, $P = 0.005$), especially in sandy soils (linear regression analysis: d.f. = 24; $R^2 = 0.23$, $P = 0.009$). However, many of the available data are from sandy soils and general conclusions will be biased towards the responses in forests on that soil type.

Studies of long-term harvesting of litter in China have also shown a decrease in total soil nitrogen of up to 40% (Peng *et al.*, 2003). Concentrations of ammonium and nitrate in the soil of the raked plots in another study fluctuated much more strongly than in undisturbed forest (Mo *et al.*, 2003), which may be attributed to greater seasonal changes in soil temperature and soil water content in the absence of the litter layer and low rates of uptake and immobilization by microbes (Mo *et al.*, 2003).

By contrast, most short-term manipulation experiments have shown no significant decreases in soil nitrogen concentration (McLeod *et al.*, 1979; Ross *et al.*, 1994; Fahey, Battles & Wilson, 1998), although nitrogen mineralization rates can decrease fairly rapidly after a single forest floor removal treatment (Gomez *et al.*, 2002). It is possible that the duration of most of the more recent studies has not been sufficient to detect differences in the nitrogen balance of forests, but methodology may also have had a strong influence on results as total Kjeldahl organic nitrogen was determined and changes to inorganic nitrogen concentrations would not have been detected.

In recent studies atmospheric nitrogen deposition may have masked nitrogen depletion with litter removal, but nitrogen levels may eventually decline if treatments

are continued (Fahey *et al.*, 1998). Mean chronic nitrogen deposition in Europe amounts to approximately $17 \text{ kg ha}^{-1} \text{ yr}^{-1}$ and in the USA to around $7.7 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (Stevens *et al.*, 2004) and would therefore 'replace' much of the nitrogen being removed with the litter, or even exceed annual nitrogen export (Table 1). Litter removal has been proposed as a forest management practice for the amelioration of eutrophicated forests in the Netherlands on the basis of similar calculations (Baar & Kuyper, 1998). Nitrogen deposition was initially thought to reverse the most important effects of long-term litter removal (Prietz *et al.*, 1997), but other effects of litter removal and soil acidification with atmospheric nitrogen deposition remain a problem.

Treatments in which the entire forest floor is removed constitute a greater disturbance to the forest nutrient balance than litter removal, as the organic horizons have developed over decades or even centuries and losses caused by their removal cannot be rapidly replenished. A single removal of the forest floor in *Pinus sylvestris* stands on mor humus in the Netherlands caused an 8% decrease in available nitrogen in the soil and a reduction of ammonium and nitrate concentrations by 56 and 31%, respectively, within a period of only three years (Baar & Ter Braak, 1996). In a similar stand in Germany, measurements taken 47 years after the removal of the forest floor still showed a thinner organic horizon with lower nitrogen concentrations than in the control plots (Fiedler *et al.*, 1962), demonstrating that several decades are necessary for the ecosystem to recover when large amounts of organic matter and nutrients have been removed.

Little is known about the changes in nitrogen concentrations with increased litter supply, but a 38% increase in dissolved organic nitrogen in forest floor leachates (Park & Matzner, 2003) was observed after two years of litter addition in a temperate mixed deciduous forest.

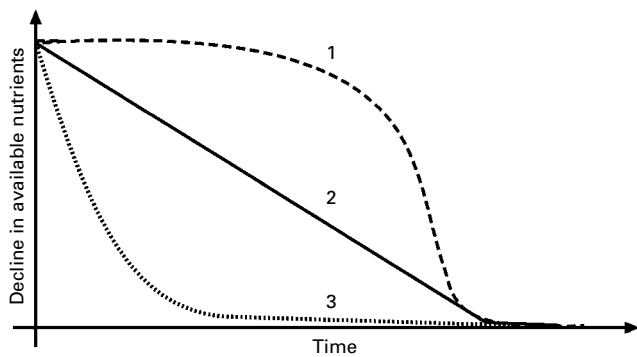


Fig. 2. The three theoretical patterns of available nutrient loss caused by litter removal over time. See text for further explanation.

(b) *Phosphorus and other mineral nutrients*

Long-term litter removal in central Europe caused a large decline in soil nutrient concentrations. Total phosphorus decreased on average by 26% and available phosphorus by 45% (Table 2). One study of long-term litter raking calculated decreases of between 65 and 85% in exchangeable base cations (Wittich, 1951); averaged over all long-term studies, potassium concentrations decreased by 42%, calcium by 57% and magnesium by 52% but variation between sites was high for all nutrients (Table 2). Large decreases in available phosphorus, potassium, and magnesium concentrations have been detected after only 12 and 15 years of treatments (Ramann, 1883), indicating that changes in these nutrients may occur relatively rapidly. Litter removal also appears to decrease sulphur, iron, and manganese concentrations in the soil (Ramann, 1883; Nĕmec, 1929), but very few data are available on these nutrients. Although all of the above values were measured in the soil surface layers (0–15 cm), where the effect is expected to be strongest, lower availability of nutrients in soils of raked stands relative to controls generally persisted to a depth of 30 cm.

Long-term use of litter as garden mulch in the USA or for fuel in China has similar negative effects on total phosphorus and calcium availability in the soil. Significant decreases of 21% in total phosphorus and 75% in exchangeable calcium concentrations have been found after 20 years of 'pine straw' harvesting (Lunt, 1951), and litter harvesting for fuel use depleted total soil phosphorus concentration by 37% after 34 years (Peng *et al.*, 2003).

There are three possible patterns of 'available' nutrient loss over time (Fig. 2), depending on the buffering capacity of the system for a given nutrient. The first pattern is that of no apparent change for a number of years and then a sudden decrease in nutrient concentrations once a critical level is reached, indicating that the system is buffered against losses of these nutrients (line 1 in Fig. 2). The second pattern (line 2) is a steady, more or less linear decline in nutrient concentrations with litter raking over time, which occurs when the system has an intermediate buffering capacity for the nutrients in question. The third pattern (line 3) is that of a strong decrease after a relatively short period of litter

removal, indicating that the system is not well buffered against losses of these nutrients, or that a large proportion is recycled in fine litter. Most nutrients seem to follow the first pattern of a sudden decline in nutrient concentrations after a number of years; short-term studies did not show a difference in nutrient concentrations, but large decreases were found in long-term studies. The loss of available phosphorus and potassium appear to follow the third pattern, as a 67% decrease in available phosphorus in the soil was measured after four years of litter removal in one study (Lopez-Zamora *et al.*, 2001), and a 24% decrease in potassium after only three years in another (McLeod *et al.*, 1979). The buffering capacity of some forests may be at least partly determined by the nutrient reserves in decomposed organic matter; Baar & Ter Braak (1996) removed the entire forest floor in a *Pinus sylvestris* stand, and although this treatment was carried out only once, available nitrogen in the upper 5 cm of mineral soil sank by 8%, available phosphorus by 52%, and potassium by 26%.

Litter addition has not been shown to increase nutrient concentrations in the mineral soil (Lunt, 1951), but higher tree growth rates were found in litter addition plots, probably due to extra nutrients (see section VI.1).

(2) **Nutrients in foliage, litter, and wood**

Litter removal reduced foliar nitrogen concentrations by 15% and 13% in long-term studies (Nĕmec, 1929; Mo *et al.*, 1995), but short-term studies have found no differences between litter treatments (McLeod *et al.*, 1979; Baar & Ter Braak, 1996; Fahey *et al.*, 1998). However, a 20% decrease in the nitrogen concentration of the litter in one of the short-term studies, despite the lack of changes in foliar nitrogen concentration, demonstrated greater retranslocation of nitrogen after three years of litter removal (McLeod *et al.*, 1979).

By contrast, reductions in foliar concentrations of phosphorus, calcium, and magnesium after litter removal have been observed in both long- and short-term studies. Foliar phosphorus was lower at four out of ten sites (Nĕmec, 1929; Wittich, 1951; McLeod *et al.*, 1979; Haywood *et al.*, 1998; Lopez-Zamora *et al.*, 2001), magnesium at three out of eight sites, and calcium at four out of eight sites (Nĕmec, 1929; Wittich, 1951; McLeod *et al.*, 1979). The timing of foliage sampling is crucial, as nutrient concentrations differ through the year (e.g. Bockheim & Leide, 1991). The importance of timing when sampling foliage for nutrient analyses becomes clear when samples are taken several times a year. Differences in foliar nitrogen concentrations between treatments in *Pinus elliottii* needles during a five-year litter removal study varied from 14 to 2% depending on the period in which the needles were sampled; the only significant reduction in foliar nutrients in the litter removal plots occurred during the main growth period (Lopez-Zamora *et al.*, 2001).

Wood ash from trees in litter removal treatments contained less phosphorus and potassium than in undisturbed forest; *Fagus sylvatica* and *Pinus sylvestris* showed a 61–76% decrease in phosphorus concentration and a 10–49% decrease in potassium concentration in long-term litter

removal plots (von Schröder, 1876; Němec, 1929). Although reductions in the concentrations of sulphur (62%), magnesium (17%), and calcium (12%) were also apparent in *F. sylvatica* (von Schröder, 1876) the concentrations of these nutrients increased in the wood ash of *P. sylvestris* by 23, 72, and 22%, respectively (Němec, 1929). Litter addition treatments increased the concentrations of calcium (29%), magnesium (66%), sulphur (32%), and manganese (35%) in the wood ash of *F. sylvatica* but had no effect on magnesium and even reduced phosphorus concentrations by 36% (von Schröder, 1876). As these studies were conducted at different locations, the apparent differences between the two species will be strongly influenced by site characteristics.

Many factors can influence the nutrient concentrations measured in plant material and there exist discrepancies between studies and even within studies in multiple sites. This is hardly surprising when one considers that the soil fertility of a site influences leaf and litter quality and therefore the nutrient loss to the system with litter removal. Furthermore, water stress, competition for nutrients, and the degree of retranslocation of scarce nutrients will determine foliar nutrient concentrations, and therefore litter nutrient concentrations, to some extent; all of these factors are also site-specific and species-specific. Differences in leaf production and tree growth may mask increases or decreases in foliar nutrient concentrations, especially nitrogen (Tanner, Vitousek & Cuevas, 1998), a phenomenon that is known from fertilization experiments (Waring & Schlesinger, 1985; Tanner *et al.*, 1998). Nitrogen fertilization has been shown to have little effect on foliar nutrient concentrations, even though the additional nitrogen caused increased plant growth (Healey, 1989; Tanner *et al.*, 1998); decreased tree growth in litter removal treatments may therefore explain the modest changes – or lack of change – in foliar nitrogen concentrations. Evidence for this is provided by litter manipulation studies where an increase or decrease in soil nutrients or tree growth was not accompanied by a corresponding change in foliar nutrient concentrations (Wittich, 1951; Němec, 1929; Baar & Ter Braak, 1996; Lopez-Zamora *et al.*, 2001).

VI. DIRECT AND INDIRECT EFFECTS ON VEGETATION

Changes to soil properties and disturbances to the nutrient supply of the forest following litter manipulation will directly or indirectly influence plant growth and survival. Changes to the soil water balance and the nutrient cycle constitute direct influences on plant growth as they modify the availability of resources. Soil compaction and other changes to the soil structure will indirectly affect tree growth by diminishing the available pore space, thus inhibiting root expansion (Ebermayer, 1876). Increases or decreases in organic matter content can cause changes in pH (Wilke *et al.*, 1993), base saturation (Wittich, 1951; Mitscherlich, 1955; Marshall *et al.*, 1996), and the water retention capacity of the soil (Lowdermilk, 1930; Walsh & Voigt, 1977), all of which may influence nutrient uptake, and therefore potentially

growth and survival, of the vegetation. Furthermore, litter cover can influence seed germination and seedling establishment and survival both positively and negatively, changing competitive outcomes between tree seedlings and forbs (Sydes & Grime, 1981; Facelli & Pickett, 1991 *a, c*; Wilson & Zammit, 1992; Barritt & Facelli, 2001) and thus contributing to the species composition and structure of the forest understorey (Sydes & Grime, 1981; Facelli & Pickett, 1991 *b*).

(1) Tree growth

Long-term litter raking drastically decreased wood production in the forests of central Europe (Ebermayer, 1876; Mitscherlich, 1955). Indeed, declines in timber production of forests of one-third (Schwappach, 1887; Klietsch, 1950; Wittich, 1954) and even almost two-thirds (Wiedemann, 1935) have been reported. Calculations from tree ring widths show a 15–20% lower diameter increment after two to three decades of litter raking (Mitscherlich, 1955) and stands replanted on formerly raked soil grew only half as fast as stands planted on unraked ground (Wiedemann, 1935). While long-term studies of the effects of litter-harvesting unequivocally show decreases in tree growth of around 30–60% (Schwappach, 1887; Němec, 1931; Wiedemann, 1935), these reductions in growth rates generally only become apparent after about 15 years (Table 3).

Concerns that 'pine straw' harvesting for garden mulch would affect timber production in plantations in the USA appear to have been unfounded. Although most studies demonstrated a negative effect of pine straw raking on diameter at breast height or basal area increment of *Pinus echinata* (Jemison, 1943), *P. resinosa* (Lunt, 1951), *P. palustris* (McLeod *et al.*, 1979; Haywood *et al.*, 1998), and *P. eliottii* (Lopez-Zamora *et al.*, 2001), the reductions in growth were small and not considered commercially important (Lunt, 1951; Jemison, 1943). Recent studies have shown a decrease in growth of only a few per cent in annually raked plots after four years (Lopez-Zamora *et al.*, 2001) and no differences in growth in plots where pine straw was removed only every two, three, or four years (Ross *et al.*, 1994; Lopez-Zamora *et al.*, 2001).

Inconsistent short-term reductions in growth in some study years but not in others (McLeod *et al.*, 1979; Haywood *et al.*, 1998) may stem from changes in soil water content (Ginter *et al.*, 1979). Measurements of the pressure potential in the xylem of needles have shown a decrease in trees in raked plots only 14 days after treatment. Although the trees responded rapidly to rainfall, they did not fully recover their pressure potential to the level of the controls, and the differences existed throughout the entire experiment thereafter, with trees in the litter-removal plots always showing significantly lower water potential following dry periods (Ginter *et al.*, 1979). The nature and the magnitude of the effects of litter removal on tree growth through changes in the water balance vary between wetter and drier years, with reduced tree growth in dry periods (Mitscherlich, 1955) and even increased growth in wetter years, possibly due to greater root-soil contact with soil compaction (Gomez *et al.*, 2002), as long as nutrient supply is sufficient.

Table 3. Effects of litter removal on tree growth sorted by treatment duration. Values shown are the percentage reductions in growth in diameter at breast height, height, basal area, and total timber volume or mass, as compared to control stands/plots. ‘+’ indicates an increase in growth. ‘n/a – reduction’ indicates that a reduction in growth was apparent, but no values were given by the source.

Diameter	Height	Basal area	Total volume/ mass	Forest type	Treatment duration (years)	Source
—	—	—	42	<i>Pinus sylvestris</i>	>50	Némec (1931)
—	39–60	—	—	<i>Pinus sylvestris</i>	>50	Wiedemann (1935)
—	—	—	15–20	<i>Pinus sylvestris</i>	23 & 33	Mitscherlich (1955)
2–33	7–36	—	20–30	<i>Pinus sylvestris</i>	21	Schwappach (1887)
4	1	—	No effect	<i>Pinus resinosa</i>	20	Lunt (1951)
—	—	6	—	<i>Fagus sylvatica</i>	18	Krutzsch (1869)
—	—	+4	—	<i>Picea abies</i>	18	Krutzsch (1869)
—	—	31.5	—	<i>Pinus sylvestris</i>	18	Krutzsch (1869)
20	+8	27	30	<i>Carpinus betulus</i>	15	Ganter (1927)
32	20	51	63	<i>Fagus sylvatica</i>	15	Ganter (1927)
13	16	16	25	<i>Pinus sylvestris</i>	15	Ganter (1927)
—	No effect	—	—	<i>Fagus sylvatica</i>	13	von Schröder (1876)
—	—	n/a – reduction	—	<i>Pinus echinata</i>	12	Jemison (1943)
—	—	No effect	—	<i>Pinus palustris</i>	7	Ross <i>et al.</i> (1994)
—	—	No effect	—	<i>Pinus taeda</i>	7	Ross <i>et al.</i> (1994)
No effect	—	—	—	northern hardwood	6	Fahey <i>et al.</i> (1998)
1	0.5	3	3.5	<i>Pinus palustris</i>	5	Haywood <i>et al.</i> (1998)
0.5–2	—	No effect	No effect	<i>Pinus elliottii</i>	4	Lopez-Zamora <i>et al.</i> (2001)
c. 5	—	—	—	<i>Pinus palustris</i>	3	McLeod <i>et al.</i> (1979)
n/a – reduction	n/a – reduction	n/a – reduction	—	<i>Pinus sylvestris</i>	1*	Fiedler <i>et al.</i> (1962)

* Entire forest floor removed.

Thus, rapid declines in tree growth rates following the beginning of treatments (McLeod *et al.*, 1979; Haywood *et al.*, 1998) are most likely a consequence of changes to the water balance, but long-term litter removal affects tree growth mainly as a consequence of reduced nutrient availability; lasting negative effects on tree growth will occur once a critical level of nutrients is reached (von Schröder, 1876).

Only two studies have investigated the effects of litter addition on tree growth, both were in stands of *Fagus sylvatica*, and neither showed a treatment effect (Krutzsch, 1863; von Schröder, 1876).

(2) Seed germination, seedling emergence, establishment, and survival

The most frequent application of experimental litter manipulation is to investigate the effects of patches of differing litter quantity on seeds and seedlings. Small-scale variation in litter distribution can be very high and is influenced by factors such as species distribution, wind redistribution (e.g. Wilke *et al.*, 1993), water flow from tree trunks (Wilke *et al.*, 1993) and differences in topography (Beatty & Sholes, 1988); the resulting patches of differing depths of litter cover affect seedling emergence, establishment and survival in a variety of ways.

(a) Early life stages – seed germination and seedling emergence

Litter removal can induce germination in small seeds. Shifts in light levels to lower red/far-red ratios beneath the canopy

increase further beneath litter cover and strongly inhibit the germination of photoblastic seeds, especially during the dry season in tropical forests (Vazquez-Yanes *et al.*, 1990). By inducing seed dormancy, the litter layer may be an important factor in maintaining the soil seed bank in lowland rain forest (Vazquez-Yanes *et al.*, 1990; Metcalfe & Turner, 1998). A combination of litter removal, litter addition and soil scarification treatments in an experimental study of seed germination from the soil seed bank (Metcalfe & Turner, 1998) showed that the combined treatment of soil scarification and litter removal promoted the germination of very small-seeded species (<100 mg), but that scarifying the soil and replacing the litter had no effect on germination. While soil scarification brought buried seeds to the surface, it was the removal of the litter layer that exposed them to stimulatory wavelengths, even without simultaneous opening of the canopy (Metcalfe & Turner, 1998). Such ‘litter gap demanders’ can survive at least six months in the soil seed bank (Metcalfe & Turner, 1998), and may survive even longer, until disturbance provides litter-free sites for germination (Putz, 1983; Vazquez-Yanes & Orozco-Segovia, 1992). A similar study in tropical montane rainforest showed that soil scarification greatly enhanced germination of large seeds (1.2–7.3 mm diameter) from the soil seed bank regardless of whether litter was present or absent, and litter removal alone had no effect (Dalling, 1995).

Litter represents a physical barrier to shoot emergence. Multiple-species studies using varying litter cover depths have shown a clear relationship between seed size and the

ability to germinate under and emerge from litter cover: the general rule is that the smaller-seeded the species, the greater the inhibition with increasing litter layer thickness (Tao, Xu & Li, 1987; Molofsky & Augspurger, 1992; Cintra, 1997; Vazquez-Yanes & Orozco-Segovia, 1992; Metcalfe & Turner, 1998; Dzwonko & Gawronski, 2002*b*), as small seeds do not possess sufficient reserves to penetrate the litter and reach the light needed for further growth (Facelli & Pickett, 1991*b*; Guzman-Grajales & Walker, 1991; Vazquez-Yanes & Orozco-Segovia, 1992; Dzwonko & Gawronski, 2002*b*). The responses of seedlings of small-seeded species to the presence of litter are species-specific, ranging from strongly inhibited to mildly negatively affected (Molofsky & Augspurger, 1992) and vary greatly with litter cover thickness (Vazquez-Yanes & Orozco-Segovia, 1992).

There is often an interaction between litter thickness and canopy openness. A moderate cover of litter may protect some species, in particular shade-tolerant species, from intense radiation and resulting desiccation (Guzman-Grajales & Walker, 1991; Molofsky & Augspurger, 1992) and thus promote emergence of these seedlings in open habitats such as gaps. Litter addition treatments enhanced the emergence of late-successional, large-seeded tree seedlings in a tropical old field, where light levels are high (Ganade & Brown, 2002) and facilitated the germination and seedling emergence of shade-tolerant species after opening of the canopy following hurricane disturbance, while removal of the litter layer resulted in massive recruitment of pioneers and shade-intolerant species (Guzman-Grajales & Walker, 1991). The sensitivity of shade-intolerant species to the depth of litter in high-light conditions varies, but emergence is generally strongly reduced, and litter cover may result in the failure of some species to colonize newly formed gaps (Molofsky & Augspurger, 1992), while the emergence of shade-tolerant species in high-light environments is either unaffected or significantly increased by litter cover but is not affected by litter cover in the understorey (Molofsky & Augspurger, 1992; Ganade & Brown, 2002). Litter has been discussed as a strong evolutionary selective pressure on seed size in trees (Vazquez-Yanes & Orozco-Segovia, 1992), as the ability of large-seeded species to germinate beneath the litter confers the advantage of protection from seed predators (Reader, 1993; Cintra, 1997; Ganade & Brown, 2002). However, although there exists empirical evidence to back this theory, there are many examples where no relationships between seed size and shade-tolerance or predation were found and the support for this theory in general is therefore not very strong (Coomes & Grubb, 2003).

Interactions between litter cover, water availability, and the desiccation tolerance of seeds and seedlings also affect seedling emergence. Litter cover may maintain a sufficiently humid microenvironment for imbibition of seeds (Facelli *et al.*, 1999) and the water retention capacity of the litter layer may prevent desiccation (Lopez-Barrera & Gonzalez-Espinosa, 2001). Evidence for this is provided by a study in which litter addition increased emergence of *Eucalyptus* species from humid habitats but had no effect on the emergence of species from more xeric environments (Facelli & Ladd, 1996).

The physical structure of the litter layer (e.g. pine needles or leaves of deciduous species), and whether it is matted (e.g. by fungal hyphae) or loose, can further influence the emergence of shoots (Barrett, 1931; Facelli & Pickett, 1991*b*). Just as a thick layer of litter may obstruct emerging shoots when seeds germinate on the soil surface, the radicle of seeds germinating on the surface of a dense litter mat can be prevented from reaching the soil and is more prone to desiccation, whereas seeds on loose litter can be displaced downwards and remain covered until seedling emergence (Lopez-Barrera & Gonzalez-Espinosa, 2001).

(b) Seedling survival and performance

Litter creates growth conditions that are more, or less, suitable for seedlings of different species. Thicker litter cover may favour some species (Barrett, 1931; Cintra, 1997), while having no effect on others (Cintra, 1997), and the presence of litter cover of different depths may change the ranking of the species' survival (Molofsky & Augspurger, 1992). The input of nutrients from decomposing litter may also increase seedling growth (Brearley, Press & Scholes, 2003) and therefore increase survival. Litter cover also influences seedling survival and performance at later life stages through interactions with biotic factors such as herbivores and pathogens. Litter can provide microhabitats for arthropods and create a shady and wet environment that favours fungal pathogens (Hermann & Chilcote, 1965; Sydes & Grime, 1981; Fowler, 1988; Facelli & Pickett, 1991*b*). In general leaf damage by herbivores in tropical lowland rainforest was increased in litter addition treatments and decreased in litter removal treatments (Benitez-Malvido & Kossmann-Ferraz, 1999; Garcia-Guzman & Benitez-Malvido, 2003), and thicker litter cover increased the likelihood of damage by pathogens (Benitez-Malvido & Kossmann-Ferraz, 1999). Higher mortality of seedlings in some studies has been attributed to pathogen damage (Facelli *et al.*, 1999; Hastwell & Facelli, 2000), and this finding was supported by decreased mortality following fungicide application (Facelli *et al.*, 1999). However, increased litter depth may also positively affect the survival of some seedlings by reducing the likelihood of discovery by herbivores (Cintra, 1997).

(c) Competition

Naturally occurring patchiness of litter and the species-specific responses to litter during various life stages can alter the outcome of competition (Facelli & Pickett, 1991*a, b*; Molofsky & Augspurger, 1992; Ganade & Brown, 2002).

In old fields, litter addition favours the emergence and survival of tree seedlings by suppressing the growth of forbs (Monk & Gabrielson, 1985; Facelli & Pickett, 1991*a, c*; Facelli, 1994), while litter removal favours herbaceous species (Monk & Gabrielson, 1985), many of which are very small-seeded and cannot penetrate litter cover. Tree seedlings may fare better than herbaceous plants in the presence of litter cover, even if seed size is alike, as lignified shoots can facilitate penetration of the litter layer (Cintra, 1997), although there are also examples of forbs and grasses with

robust shoots, which can easily penetrate a thick layer of litter (Grime, 1979). Litter addition in old fields was shown to have as great an effect on tree seedling growth and survival as the experimental removal of above-ground competition (Facelli & Pickett, 1991*a*; Facelli, 1994); and combining the removal of below-ground competition (trenching to remove roots) with litter addition enhanced seedling densities of perennials by 84% (Monk & Gabrielson, 1985).

Various litter manipulation experiments have shown that the effects of litter cover on the germination and survival of seedlings is particularly important in the invasion of trees in old fields (Facelli & Pickett, 1991*a, b, c*; Myster & Pickett, 1993; Facelli, 1994; Xiong & Nilsson, 1999; Ganade & Brown, 2002). Such differences in competitive outcomes between forbs and tree seedlings caused by litter can persist in closed canopy forest (Sydes & Grime, 1981; Wilson & Zammit, 1992; Barritt & Facelli, 2001), and tree litter may be the major determining factor of the species composition of the herbaceous layer in some woodlands (Sydes & Grime, 1981). The addition of tree litter to understorey plots with herbaceous seedlings strongly reduced the total biomass of many forb species (Sydes & Grime, 1981; Wilson & Zammit, 1992; Eriksson, 1995; Shelton, 1995; Barritt & Facelli, 2001).

Litter cover may also influence competition between seedlings of tree species with differing seed sizes. Moreover, the immobilization of nutrients during litter decomposition and the resulting decrease in nutrient availability may cause an increase in competition intensity between established tree seedlings (Nilsson *et al.*, 1999).

(3) Plant community structure and diversity

The effects of litter cover on seedling establishment and competitive interactions will ultimately influence species diversity and community structure (Sydes & Grime, 1981; Facelli & Pickett, 1991*a, b, c*; Guzman-Grajales & Walker, 1991; Molofsky & Augspurger, 1992; Peterson & Facelli, 1992; Benitez-Malvido & Kossmann-Ferraz, 1999; Berendse, 1999; Xiong & Nilsson, 1999; Dzwonko & Gawronski, 2002*a, b*). Naturally occurring patchiness of litter and differing litter depths and structure facilitate the establishment of seedlings of some species while inhibiting others and thus contribute to small-scale heterogeneity of the vegetation and coexistence of species. Although many litter manipulation studies focussing on seedling establishment have addressed the possible role of litter in structuring the forest plant community at the seedling level, few have attempted to quantify changes to plant diversity and above-ground biomass.

(a) Forest biodiversity.

It is widely accepted that centuries of litter removal in central Europe destabilised forest ecosystems and caused a complete change in forest type and dominant species (Ellenberg, 1988). In many areas where litter removal was practiced over long periods of time, deciduous forests were felled and replanted with coniferous species that could grow

better on the impoverished soils (Ebermayer, 1876; Klietsch, 1950; Wittich, 1954; Ellenberg, 1988; Jandl *et al.*, 2002). Two long-term studies show a decrease in biodiversity with litter harvesting in China. Diversity in a *Eucalyptus* plantation was lowest in a stand that had been raked for 34 years; no other tree species had been able to establish in the plantation, and the herb and shrub layer was entirely absent. A stand that had been raked for 28 years showed a slight improvement after six years of recovery, while the stand in which litter harvesting had not taken place was relatively diverse with a fully developed herb and shrub layer (Peng *et al.*, 2003). In a different area of China, Brown *et al.* (1995) suggested that long-term litter raking had arrested natural succession; unraked stands in the area were composed of mixed broadleaf forest, the buffer zone between unraked and raked stands was in the transitional stage of pine-broadleaf forest, while the raked stand was pine forest of low structural complexity.

(b) Understorey vegetation

Changes to the forest floor vegetation following litter manipulation treatments manifest themselves primarily as changes in species composition. Species composition of the forest floor in the Wiener Wald, Austria, differed between plots after only one year of litter removal and addition treatments (Onno, 1969) and the species composition of a mixed deciduous forest in southern Poland changed significantly after only three years of treatment and by 66% over a period of 16 years (Dzwonko & Gawronski, 2002*a, b*). Surface-attached species, such as lichens and mosses (Fiedler *et al.*, 1962; Lindholm & Nummelin, 1983), and resilient grasses (Onno, 1969) have been found more frequently in litter removal treatments, probably because they can better withstand raking treatments. Raking damage also accounts for lower ground cover in raked plots relative to controls despite the more frequent colonisation of raked plots by small-seeded species (Dzwonko & Gawronski, 2002*a, b*).

Litter tends to gather in treefall pits, contributing to lower plant species richness and ground cover than on mounds (Beatty & Sholes, 1988). The soil in old pits tends to have higher contents of nutrients, soil water, and organic matter (Beatty & Sholes, 1988). When litter was removed from pits, species number increased and the species composition became more similar to that normally found on mounds. Species composition differed significantly between pits with and without litter after only one year of treatment and this change persisted over the three years of study, although the most profound effects took place in the first year (Beatty & Sholes, 1988).

Litter manipulation has a much greater effect on species richness than on total above-ground biomass (Dzwonko & Gawronski, 2002*a, b*), a finding that is supported by a meta-analysis of studies of the effects of plant litter on a wide variety of vegetation (Xiong & Nilsson, 1999). This may be attributed to the facilitated establishment of some species in the absence of litter cover and increased competitive ability with litter cover in others. While the invasion or disappearance of species with litter manipulation changes overall diversity, changes in the degree of cover and therefore in the

relative importance of those species already present may be even more important. Several studies have shown shifts in species ranking due to litter manipulation (Onno, 1969; Lindholm & Nummelin, 1983; Beatty & Shoels, 1988). However, in many cases, damage to existing seedlings and forbs by raking and trampling may have had a greater effect on species diversity than the change in the amount of litter itself.

VII. SOIL AND LITTER FAUNA

Litter is important in maintaining populations of animals in the soil. Besides being an important food source (Judas, 1990; Poser, 1990; David *et al.*, 1991; Arpin *et al.*, 1995; Gonzalez & Zou, 1999), the litter layer helps to maintain a stable and favourable microclimate at the soil surface (Pearse, 1943; David *et al.*, 1991; Arpin *et al.*, 1995) and its three-dimensional structure provides habitats (Pearse, 1943; David *et al.*, 1991; Ponge *et al.*, 1993; Arpin *et al.*, 1995) and protection from predators (Pearse, 1943). Furthermore, organic matter incorporated into the soil makes it more favourable to soil fauna by increasing porosity and therefore aeration (Pearse, 1943). Although litter quality is often a strong determinant of soil fauna communities (Wardle, 2002), quantitative changes to the litter layer also affect the population dynamics and community structure of soil animals that in turn affect the breakdown of organic matter and its incorporation into the soil.

(1) Microarthropods, macroarthropods, and nematodes

Litter removal generally leads to a decline in populations of micro- and macroarthropods, while litter addition does not always have a clear effect. Reductions in populations of soil fauna with litter removal were often due to factors other than a decrease in substrate, as the relatively small responses to litter addition treatments (Poser, 1990; David *et al.*, 1991) suggest that litter is not a limiting food source (David *et al.*, 1991). Furthermore, litter manipulation treatments provoked changes in the abundance of species that were not directly dependent on fine litter for food; all trophic groups were affected by litter removal as the availability of food sources such as fungi, bacteria, and the faeces of litter-consuming animals, were also decreased (Ponge *et al.*, 1993), and decreasing numbers of prey species led to a decline in populations of predators (Uetz, 1979; David *et al.*, 1991). For example, Arpin *et al.* (1995) showed that the decline in nematode populations in the upper 10 cm of the soil in litter removal treatments over five years was particularly strong in bacteria-feeding species (40%), fungal-feeding species (20%), and predators (24%). In a different study, litter removal resulted in a significant decline in the number of individuals and total biomass of saprophagous diplopods and isopods, and this was followed by a decrease in the number of zoophagous chilopods (David *et al.*, 1991).

Disturbances to the litter layer affect the soil fauna by changing temperature and moisture regimes (David *et al.*,

1991; Reynolds, Crossley & Hunter, 2003); declines in populations in litter removal plots in spring but increases relative to the controls in autumn may well be a consequence of such changes (Arpin *et al.*, 1995). Litter manipulation treatments affect soil and litter-dwelling fauna differently in wetter or drier, warmer or colder years and the greatest decreases in soil fauna abundance following litter removal seem to occur in disturbed or unfavourable sites (Jahn, 1981). An experiment using artificial (polyester) litter simulated the microclimatological conditions of the litter without its nutritional value (Gill, 1969). The population densities of four groups of Acari in the surface soil layers (0–9 cm) declined in litter removal plots in an old field, while abundance in plots with artificial polyester litter did not differ from controls; Collembola had disappeared entirely from the top 4.5 cm of the soil in the litter removal plots, but were still present at low densities in the artificial litter treatments. This study demonstrated that Collembola and Acari are primarily affected by the changes in the microclimate at the soil surface caused by decreased litter inputs (Gill, 1969). Seasonal differences in spider species abundance in litter removal and addition treatments have been attributed to changes in soil water content, soil temperature, or the effect of litter thickness on prey densities (Uetz, 1979). In spring, the main season for spider growth and development, prey density was the driving force for spider species richness; during the driest summer months the presence of moist and shady microhabitats was the most important criterion, while reduced variation in temperature became relatively more important in autumn. The structural complexity of an intact litter layer may play an important role in arthropod densities by providing habitat space (Uetz, 1979; Poser, 1990), while a thin litter layer with decreased structural complexity may be unattractive to many species simply because of the lack of refuges from predators (Gill, 1969; Uetz, 1979). Periodic burning was found to be less detrimental to soil and litter fauna than litter raking, as patches of ash and charred logs still provided habitat space and some degree of protection (Pearse, 1943).

Changes in species abundance and species richness with litter removal are often accompanied by shifts in dominance and vertical distribution, as strictly litter-dwelling taxa disappear (Poser, 1990) and others migrate into the upper soil layers (Pearse, 1943; Poser, 1990). Such shifts will have implications for population dynamics as species ranking is changed and niche space becomes more limiting (Poser, 1990).

Slight increases in soil fauna abundance and diversity have been shown in litter addition treatments (Poser, 1990; David *et al.*, 1991; Ponge *et al.*, 1993; Arpin *et al.*, 1995), but they were generally not as pronounced as would be expected given the magnitude of the response to litter removal treatments; litter addition also caused a decline of populations in some species (Uetz, 1979; Poser, 1990). Nevertheless, fungal-feeding nematodes increased in numbers in litter addition treatments (Arpin *et al.*, 1995) and spider species richness has been shown to be strongly correlated with litter depth in both naturally occurring patches of litter and artificially manipulated plots (Uetz, 1979), probably as a consequence of greater numbers of prey species in high-litter

patches. Migration and changes in species ranking also occurred in litter addition treatments as litter-dwelling taxa increased in abundance and importance (Uetz, 1979; Poser, 1990).

(2) Earthworms

Earthworms play a major role in many forest soils. By turning over the soil and mixing organic matter with mineral soil (pedoturbation), they are very important in creating and maintaining soil fertility and soil aeration. A well-developed earthworm population can bury the annual litter-fall of a mature forest in a matter of months (Killham, 1994), and this breakdown and mixing of organic matter accelerates decomposition. Earthworms can be classified into three major groups according to their habitat preferences; acecic earthworms, such as *Lumbricus terrestris* build vertical burrows from the soil surface into the mineral soil layers, but they feed mainly on decaying surface litter, while epigeic worms live in loose soil surface layers and in the litter and feed on organic debris. The third group, the endogeic earthworms, build lateral burrows in the upper layers of the mineral soil and rarely come to the surface. Acecic and epigeic earthworms are strongly dependent on fine litter. Endogeic species are not directly influenced by litter as they feed on older soil organic matter and on mineral soil fragments.

The number of acecic and epigeic earthworms in a given area of soil declines rapidly with litter removal, as fine litter constitutes a major food source for these two groups. Reductions of 40% in the abundance and 43% in total biomass of epigeic species in litter-raked plots compared to controls has been observed after only one year of treatment (Judas, 1989, 1990) and decreases of 83% and 76% were shown over a five-year period (Pearse, 1943). The number of acecic lumbricids present in litter removal plots declined by at least 50% in all experiments in which they were studied (Nielsen & Hole, 1964; Judas, 1989, 1990; David *et al.*, 1991). There was a positive relationship between the amount of litter on the soil surface and the number of casts produced by *Lumbricus terrestris* in a temperate mixed deciduous forest (Nielsen & Hole, 1964). Litter removal over a period of five years reduced the number of casts by 65% while doubling the litter supply for the same period of time increased cast abundance by 49%. A third treatment involving the removal of the upper 15 cm of the A horizon and replacing the litter did not influence earthworm activity (Nielsen & Hole, 1964), indicating that litter is a more important resource for this species than older soil organic matter.

Litter addition treatments seem to have no general effect on acecic or epigeic earthworms (Judas, 1989, 1990; David *et al.*, 1991). Out of four epigeic species studied, one increased in numbers while the populations of another species decreased and two remained unchanged (Judas, 1989, 1990; David *et al.*, 1991). Although cast formation by the acecic species *L. terrestris* was positively correlated with litter amount (Nielsen & Hole, 1964), the populations of other acecic species were found to decline strongly with litter addition (Judas, 1989, 1990). This lack of a positive response

to increased litter inputs indicates that it is not a limiting resource in most situations. Litter quality is more important than litter quantity (Zou, 1993) and negative effects of litter addition treatments could result from changes in resource quality (Judas, 1989). The total biomass of endogeic and acecic earthworms in a subtropical wet forest was positively related to nitrogen and phosphorus concentrations in fine litter and negatively related to concentrations of tannin (Gonzalez & Zou, 1999). Changes in decomposition and subsequent accumulation of leaf chemicals may make sites with high litter inputs less favourable, and fine litter as a resource less palatable, to earthworms and many other taxa of soil fauna. This would ultimately lead to the steady accumulation of litter observed in high-input treatments (David *et al.*, 1991).

Litter may also be important in maintaining the moisture and temperature conditions favourable to all three groups of earthworms, as the greatest observed decrease in earthworm abundance in the litter removal plots occurred during a very dry summer, while worms in the controls and litter addition plots remained little affected (Judas, 1989). Although endogeic earthworms rarely come to the surface and are not direct consumers of litter, their numbers generally decreased in litter removal plots (Judas, 1989, 1990), which may be a result of greater temperature and moisture fluctuations near the soil surface. Litter manipulation may increasingly affect endogeic species over greater time scales as soil organic matter content changes.

VIII. FUNGI AND MYCORRHIZAE

A change in the quantity of litter on the forest floor can affect fungal growth and diversity by modifying the amount or quality of available substrate for decomposers (Tyler, 1991), by changing the microclimate at the soil surface (Tyler, 1991; Cullings *et al.*, 2003), by release of chemical compounds during leaching and decomposition (Baar & Kuyper, 1993; Baar *et al.*, 1994*b*), by influencing the number of diaspores present (Cullings *et al.*, 2003) and by supplying nutrients. Considering the importance of many fungi in decomposition processes in forest ecosystems, it follows that changes to the fungal community of the forest will affect the residence time of coarse organic matter, woody debris, and the formation of humus. Few litter manipulation studies have focussed on fungal growth and diversity, although litter removal has been recommended as a management practice to restore ectomycorrhizal diversity in forests suffering from eutrophication through atmospheric nitrogen deposition (Baar & Kuyper, 1998). As with tree seedlings and herbaceous plants the responses to litter removal or addition are species-specific, but unlike seedlings the individual responses are not consistent and the reasons for them are not always clear.

In a stand of *Pinus sylvestris* the removal of the forest floor (Oi, Oe, and Oa horizons) increased the diversity and the abundance of fruiting bodies of ectomycorrhizal fungi (Baar & Kuyper, 1993, 1998; Baar & Ter Braak, 1996) and the rates of mycorrhizal infection of seedlings (Baar & De Vries,

1995). Experiments with *Laccaria bicolor* showed that the removal of the organic layers stimulated the formation of fruiting bodies from mycelia present in the soil (Baar, Ozinga & Kuyper, 1994a). The abundance and diversity of fungal species characteristic of early succession increased most, indicating that the removal of the forest floor returns the soil to an earlier successional stage (De Vries *et al.*, 1995). Nitrogen depletion with organic matter removal was probably one of the driving factors for increased ectomycorrhizal infection and fruiting-body production (Baar & Ter Braak, 1996), although doubling the thickness of the forest floor had little effect on fruiting body production (Baar & Kuyper, 1993, 1998; De Vries *et al.*, 1995; Baar & Ter Braak, 1996). However, forest floor removal and addition treatments constitute a much greater disturbance than does litter manipulation.

Litter removal also causes substantial changes to the fruiting body production of mycorrhizal species, but whether the response is negative or positive appears to be species-specific. In a beech forest, the number of ectomycorrhizal fruiting bodies of *Russula* species was 79% higher in raked plots compared to controls after two years of litter removal, while the abundance of another mycorrhizal species was 90% lower in the raked plots (Tyler, 1991). Decomposer fungi are likely to be at a disadvantage in litter removal treatments because of the lack of substrate; five out of seven decomposer species had fewer fruiting bodies in the litter removal plots in one study (Tyler, 1991). Surprisingly, litter addition also had a negative effect on the abundance of four decomposer species, and only one species increased fruiting body production (by 64%) in litter addition plots (Tyler, 1991).

The microclimatic conditions determined by the litter layer play a decisive role in fungal fruiting body production; fungi whose fruiting bodies originate from deeper in the soil, such as *Russula* species, may not be as strongly affected by unfavourable changes to soil water content and temperature induced by litter manipulation as other species (Tyler, 1991). The addition of perlite as a litter substitute demonstrated that some mycorrhizal fungi are more sensitive to changes in microclimatic factors, as they showed the same response regardless of whether litter or perlite was added to the plots. Other species were influenced by resource availability or litter leachates, as they were affected only by the presence or absence of litter itself (Cullings *et al.*, 2003). Although changes in soil water content or soil temperature may cause a negative reaction of some fungi to litter addition treatments, laboratory experiments have shown that high concentrations of leachates from a thick litter layer may also have inhibitory effects on fungal growth (Baar *et al.*, 1994b).

Increased ectomycorrhizal abundance or infection with litter addition cannot be explained by the transfer of spores. Even when litter was solarized to kill extant spores, ectomycorrhizal infection in the surface soil layer increased by 10% and diversity decreased by 31% following litter addition, while perlite application had no effect (Cullings *et al.*, 2003). Although no effect of litter addition on mycorrhizal colonisation rates was found in a glasshouse study with seedlings of three dipterocarp species, ectomycorrhizal

diversity and species evenness was lower in treatments with litter relative to no-litter controls (Brearley *et al.*, 2003). The main cause of these changes appeared to be a reduction in the colonisation of roots by one of the common ectomycorrhizal species, possibly because of the loss of its competitive ability with the higher soil water content associated with litter cover (Brearley *et al.*, 2003).

IX. CONCLUSIONS

(1) Litter plays two principal roles in forest ecosystems: firstly, it forms an inherent part of the nutrient cycle of the forest and is a major source of soil organic matter; secondly, its physical presence on the forest floor acts as protection against microclimatic fluctuations, erosion, and soil compaction. Litter manipulation changes the effectiveness of these two functions simultaneously and a complex web of interactions results (Fig. 3), which complicates the interpretation of data. Negative effects of litter removal are often exacerbated by positive feedbacks between the variables altered by it; this can lead to stronger responses than were expected. Moreover, changes to variables other than those measured can weaken or mask responses. Large-scale, long-term experiments are necessary to investigate these interactions. Once a good baseline understanding has been established, the stepwise elimination of confounding factors can help to elucidate results; artificial litter substitutes, for example, have been used to quantify the relative importance of changes to microclimate and changes to nutrient availability, while irrigation treatments could be used to eliminate differences in water supply.

(2) The same methodological issues exist for litter manipulation experiments as for studies on the forest nutrient cycle. Sampling periods for leaf nutrients, for example, need to be predetermined and adhered to, as nutrient concentrations change through the year (e.g. Bockheim & Leide, 1991). Changes in nutrient concentrations may also be masked by the choice of method. Resin bags to measure soil nutrient availability, for instance, may detect leaching losses from the soil surface and the humus, fermentation, and litter layers as well as nutrients in the soil (Mo *et al.*, 2003). Sampling at greater depths may also result in no detectable changes or even an apparent increase in soil nitrogen concentration as it is leached downwards in the soil profile. Tree density between plots or stands should also be taken into account, as it may obscure results of tree growth measurements by increasing or decreasing the importance of competition for available nutrients. Buffers around plots are essential to avoid an 'effect gradient' towards plot edges, and trenching plots will greatly reduce nutrient and water import *via* the roots and/or mycorrhizal network, which could otherwise weaken treatment effects.

(3) Despite having to compare litter manipulation studies in different forest types, on different soils, and that used different methodology, this review presents some general findings on the role of fine litter in the nutrient cycle that merit further attention. (i) Nitrogen-rich soils appear to lose a greater relative proportion of nitrogen following litter removal than nitrogen-poor soils. This is in agreement with

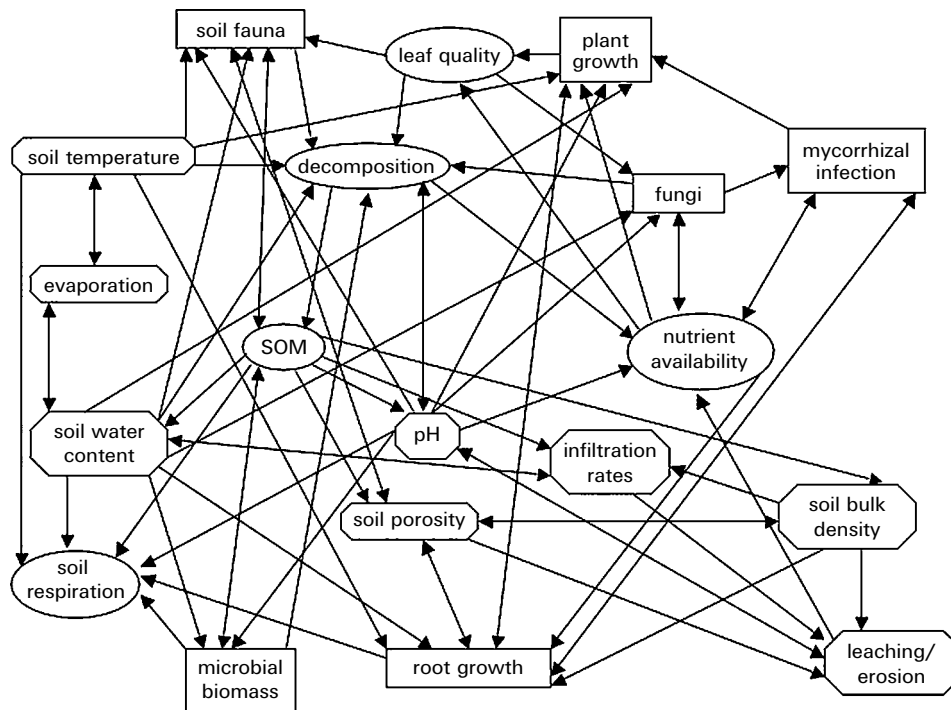


Fig. 3. Simplified conceptual diagram showing the parameters affected by litter manipulation and their most important interactions. Octagons show variables influenced by leaf litter as a protective layer; ovals show variables influenced by leaf litter that form part of the nutrient and carbon cycle; rectangles show variables affected by leaf litter either through its protective function or through its role in the carbon and nutrient cycle; SOM is soil organic matter.

the theory of nutrient-use efficiency *sensu* Vitousek (1982), which states that nutrient-cycling is more efficient in low-fertility sites, and the lower relative loss on nitrogen-poor soils may be a result of low litterfall nutrient inputs. (ii) The concentrations of P, K, Mg, and Ca in the soil and the foliage in litter removal treatments decrease more rapidly than do nitrogen concentrations. The difference in the decrease of nutrients in the soil may simply be a methodological artefact, as short-term studies measured available phosphorus and exchangeable bases but total organic nitrogen, which may respond more slowly to treatments. (iii) Although there is no clear effect of soil nutrient status on leaf nutrient retranslocation when trees at different sites are compared (Aerts, 1996), the withdrawal of nutrients from the soil may result in greater retranslocation of nutrients over time. Decreased tree growth and greater retranslocation may mask differences in foliar nitrogen concentrations, especially in forests where nitrogen is thought to be the primary limiting nutrient; it remains to be seen if similar patterns emerge in forests where other nutrients are limiting.

(4) The great majority of litter manipulation studies have been conducted in temperate forests. However, in the light of global climate change and the present discussion on carbon sequestration, there will be ever more demand for information on the effects of changes in primary production in boreal and tropical forests. Tropical forests in particular should receive more attention as many lowland tropical forest soils lack a thick organic horizon and are generally

nutrient-poor; litter may therefore play a relatively more important role in carbon and nutrient cycling in the tropics.

(5) Few data are available on changes in soil respiration, soil carbon content, and carbon fractions with differing litter inputs. However, in the light of rising atmospheric CO₂ levels and increased primary productivity, studies on the role of litter in the forest carbon cycle will be essential in making predictions on carbon sequestration and in calculating future carbon budgets. Although there is a paucity of data from litter addition treatments, results from the few existing studies suggest that increasing litter inputs will lead to an accumulation of organic matter on the forest floor, as artificial increases in litter supply are not accompanied by the corresponding increases in soil fauna, microbial, or fungal populations needed to decompose the additional organic matter. A build-up of partially decomposed litter may initially only affect seedling emergence but in time this would alter the community structure and diversity of the understorey. Greater Oi and Oe horizons could increase the incorporation of dissolved and particulate organic matter into the mineral soil. Increased litter inputs may also cause the 'priming effect' (*sensu* Fontaine *et al.*, 2004), the increased decomposition of older organic matter with increasing fresh organic matter inputs. Litter addition studies also provide an excellent opportunity to assess some of the effects of increasing primary production in forests and therefore improve predictions of the effects of elevated CO₂ levels in forest ecosystems.

X. ACKNOWLEDGEMENTS

I wish to acknowledge J. S. Powers (University of Minnesota), D. A. Wardle (Swedish University of Agricultural Sciences/Landcare Research New Zealand), E. G. Leigh Jr. (STRI), D. Molbo (STRI), and in particular E. V. J. Tanner (University of Cambridge) and P. J. Grubb (University of Cambridge), for their comments on earlier drafts of this manuscript. My thanks also go to C. Mullins (University of Aberdeen) for additional information on soil physics, and to the STRI library in Panama, who managed to obtain most of the 19th century publications.

XI. REFERENCES

- AERTS, R. (1996). Nutrient resorption from senescing leaves of perennials: are there general patterns? *Journal of Ecology* **84**, 597–608.
- ALLEN, A. S., ANDREWS, J. A., FINZI, A. C., MATAMALA, R., RICHTER, D. D. & SCHLESINGER, W. H. (2000). Effects of free-air CO₂ enrichment (FACE) on belowground processes in a *Pinus taeda* forest. *Ecological Applications* **10**, 437–448.
- ANDERSON, J. P. E. & DOMSCH, K. H. (1978). A physiological method for quantitative measurement of microbial biomass in soils. *Soil Biology and Biochemistry* **29**, 1133–1142.
- ARPIN, P., PONGE, J. F. & VANNIER, G. (1995). Experimental modifications of litter supplies in a forest mull and reaction of the nematode fauna. *Fundamental and Applied Nematology* **18**, 371–389.
- BAAR, J. & DE VRIES, B. W. L. (1995). Effects of manipulation of litter and humus layers on ectomycorrhizal colonization potential of Scots pine stands of different age. *Mycorrhiza* **5**, 267–272.
- BAAR, J. & KUYPER, T. W. (1993). Litter removal in forests and effect on mycorrhizal fungi. In *Fungi of Europe: Investigation, Recording and Conservation* (eds D. N. Pegler, L. Boddy, B. Ing and P. M. Kirk), pp. 275–286. Royal Botanic Gardens, Kew.
- BAAR, J. & KUYPER, T. W. (1998). Restoration of aboveground ectomycorrhizal flora in stands of *Pinus sylvestris* (Scots pine) in the Netherlands by removal of litter and humus. *Restoration Ecology* **6**, 227–237.
- BAAR, J., OZINGA, W. A. & KUYPER, T. W. (1994a). Spatial distribution of *Laccaria bicolor* genets reflected by sporocarps after removal of litter and humus layers in a *Pinus sylvestris* forest. *Mycological Research* **98**, 726–728.
- BAAR, J., OZINGA, W. A., SWEERS, I. L. & KUYPER, T. W. (1994b). Stimulatory and inhibitory effects of needle litter and grass extracts on the growth of some ectomycorrhizal fungi. *Soil Biology and Biochemistry* **26**, 1073–1079.
- 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.
- BARRETT, L. I. (1931). Influence of forest litter on the germination and early survival of chestnut oak, *Quercus montana*, Willd. *Ecology* **12**, 476–484.
- BARRITT, A. R. & FACELLI, J. M. (2001). Effects of *Casuarina pauper* litter and grove soil on emergence and growth of understorey species in arid lands of South Australia. *Journal of Arid Environments* **49**, 569–579.
- BEATTY, S. W. & SHOLES, O. D. V. (1988). Leaf litter effect on plant species composition of deciduous forest treefall pits. *Canadian Journal of Forest Research* **18**, 553–559.
- BENITEZ-MALVIDO, J. & KOSSMANN-FERRAZ, I. D. (1999). Litter cover variability affects seedling performance and herbivory. *Biotropica* **4**, 598–606.
- BENKOBI, L., TRLICA, M. J. & SMITH, J. L. (1993). Soil loss as affected by different combinations of surface litter and rock. *Journal of Environmental Quality* **22**, 657–661.
- BERENDESE, F. (1999). Implications of increased litter production for plant biodiversity. *Trends in Ecology and Evolution* **14**, 4–5.
- BLAIR, J. M., CROSSLEY, D. A. & CALLAHAM, L. C. (1992). Effects of litter quality and microarthropods on N-dynamics and retention of exogenous N-15 in decomposing litter. *Biology and Fertility of Soils* **12**, 241–252.
- BOCKHEIM, J. G. & LEIDE, J. E. (1991). Foliar nutrient dynamics and nutrient-use efficiency of oak and pine on a low-fertility soil in Wisconsin. *Canadian Journal of Forest Research* **21**, 925–934.
- BOWDEN, R. D., NADELHOFFER, K. J., BOONE, R. D., MELILLO, J. M. & GARRISON, J. B. (1993). Contributions of aboveground litter, belowground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest. *Canadian Journal of Forest Research* **23**, 1402–1407.
- BRADY, N. C. (1974). *The Nature and Properties of Soils*, 8th edn. Macmillan, New York.
- BREARLEY, F. Q., PRESS, M. C. & SCHOLES, J. D. (2003). Nutrients obtained from leaf litter can improve the growth of dipterocarp seedlings. *New Phytologist* **160**, 101–110.
- BROWN, S., LENART, M. & MO, J. (1995). Structure and organic matter dynamics of a human-impacted pine forest in a MAB reserve of subtropical China. *Biotropica* **27**, 276–289.
- CINTRA, R. (1997). Leaf litter effects on seed and seedling predation of the palm *Astrocaryum murumuru* and the legume tree *Diptryx micrantha* in Amazonian forest. *Journal of Tropical Ecology* **13**, 709–725.
- COELHO NETTO, A. L. (1987). Overlandflow production in a tropical rainforest catchment: the role of litter cover. *Catena* **14**, 213–231.
- CONDIT, R., HUBBELL, S. P. & FOSTER, R. B. (1996). Assessing the response of plant functional types to climatic change in tropical forests. *Journal of Vegetation Science* **7**, 405–416.
- COOMES, D. A. & GRUBB, P. J. (2003). Colonization, tolerance, competition and seed-size variation within functional groups. *Trends in Ecology and Evolution* **18**, 283–291.
- COTE, L., BROWN, S., PARE, D., FYLES, J. & BAUHUS, J. (2000). Dynamics of carbon and acid nitrogen mineralization in relation to stand type, stand age, and soil texture in the boreal mixed-wood. *Soil Biology and Biochemistry* **32**, 1079–1090.
- CULLINGS, K. W., NEW, M. H., MAKHJA, S. & PARKER, V. T. (2003). Effects of litter addition on ectomycorrhizal associates of a lodgepole pine (*Pinus contorta*) stand in Yellowstone National Park. *Applied and Environmental Microbiology* **69**, 3772–3776.
- DALLING, J. W. (1995). The effect of litter and soil disturbance on seed germination in upper montane rain forest, Jamaica. *Caribbean Journal of Science*, **31**, 223–229.
- 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.
- DAVIS, B., WALKER, N., BALL, D. & FITTER, A. (1992). *The Soil*. Harper Collins, London.
- DE VRIES, B. W. L., JANSEN, E., VAN DOBBEN, H. F. & KUYPER, T. W. (1995). Partial restoration of fungal and plant species diversity by removal of litter and humus layers in stands of Scots pine in the Netherlands. *Biodiversity and Conservation* **4**, 156–164.

- 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 CO₂ enrichment. *Science* **284**, 1177–1179.
- DZWONKO, Z. & GAWRONSKI, S. (2002*a*). Effect of litter removal on species richness and acidification of a mixed oak-pine woodland. *Biological Conservation* **106**, 389–398.
- DZWONKO, Z. & GAWRONSKI, S. (2002*b*). Influence of litter and weather on seedling recruitment in a mixed oak-pine woodland. *Annals of Botany* **90**, 245–251.
- EBERMAYER, E. (1876). *Die Gesamte Lehre der Waldstreu mit Rücksicht auf die Chemische Statik des Waldbaues*. Julius Springer Verlag, Berlin.
- EDWARDS, N. T. & HARRIS, W. F. (1977). Carbon cycling in a mixed deciduous forest floor. *Ecology* **58**, 431–437.
- EHWALD, E. (1957). *Über den Nährstoffkreislauf des Waldes*. Hirzel Verlag, Leipzig.
- ELLENBERG, H. (1988). *Vegetation Ecology of Central Europe*, 4th edn. Cambridge University Press, Cambridge.
- ERIKSSON, O. (1995). Seedling recruitment in deciduous forest herbs: the effects of litter, soil chemistry and seed bank. *Flora* **190**, 65–70.
- FACELLI, J. M. (1994). Multiple indirect effects of plant litter affect the establishment of woody seedlings in old fields. *Ecology* **75**, 1727–1735.
- FACELLI, J. M. & LADD, B. (1996). Germination requirements and responses to leaf litter of four species of eucalypt. *Oecologia* **107**, 441–445.
- FACELLI, J. M. & PICKETT, S. T. A. (1991*a*). Indirect effects of litter on woody seedlings subject to herb competition. *Oikos* **62**, 129–138.
- FACELLI, J. M. & PICKETT, S. T. A. (1991*b*). Plant litter: it's dynamics and effects on plant community structure. *The Botanical Review* **57**, 1–32.
- FACELLI, J. M. & PICKETT, S. T. A. (1991*c*). Plant litter: light interception and effects on an old-field plant community. *Ecology* **72**, 1024–1031.
- FACELLI, J. M., WILLIAMS, R., FRICKER, S. & LADD, B. (1999). Establishment and growth of seedlings of *Eucalyptus obliqua*: interactive effects of litter, water and pathogens. *Australian Journal of Ecology* **24**, 484–494.
- FAHEY, T. J., BATTLES, J. J. & WILSON, G. F. (1998). Responses of early successional northern hardwood forests to changes in nutrient availability. *Ecological Monographs* **68**, 183–212.
- FARRELL, E. P., FUEHRER, E., RYAN, D., ANDERSSON, F., HUETTL, R. & PIUSSI, P. (2000). European forest ecosystems: building the future on the legacy of the past. *Forest Ecology and Management* **132**, 5–20.
- FEINSTMANTEL, R. (1876). *Allgemeine Waldbestandsstafeln*, 2nd edn. Braumüller Verlag, Vienna.
- FIEDLER, H. J., FIEDLER, E., HOFFMANN, F., HÖHNE, H., SAUER, G. & THOMAS, H. (1962). Auswertung eines Streunutzungsversuches von H. Vater aus dem Jahre 1912. *Archiv für Forstwesen* **11**, 70–128.
- FINZI, A. C., ALLEN, A. S., DELUCIA, E. H., ELLSWORTH, D. S. & SCHLESINGER, W. H. (2001). Forest litter production, chemistry, and decomposition following two years of free-air CO₂ enrichment. *Ecology* **82**, 470–484.
- FISK, M. C. & FAHEY, T. J. (2001). Microbial biomass and nitrogen cycling responses to fertilization and litter removal in young northern hardwood forests. *Biogeochemistry* **53**, 201–223.
- FONTAINE, S., MARIOTTI, A. & ABBADIE, L. (2003). The priming effect of organic matter: a question of microbial competition? *Soil Biology and Biochemistry* **35**, 837–843.
- FONTAINE, S., BARDOUX, G., ABBADIE, L. & MARIOTTI, A. (2004). Carbon input to soil may decrease soil carbon content. *Ecology Letters* **7**, 314–320.
- FOWLER, N. L. (1988). What is a safe site?: neighbor, litter, germination date, and patch effects. *Ecology* **69**, 947–961.
- FRANKLIN, O., HOGBERG, P., EKBLAD, A. & ÅGREN, G. I. (2003). Pine forest floor carbon accumulation in response to N and PK additions: bomb C-14 modelling and respiration studies. *Ecosystems* **6**, 644–658.
- GANADE, G. & BROWN, V. K. (2002). Succession in old pastures of Central Amazonia: role of soil fertility and plant litter. *Ecology* **83**, 743–754.
- GANTER, K. (1914). *Bodenuntersuchungen über die Rotbuchen-Streulflächen im Forstbezirk Philippsburg in Baden*. Dissertation, Technische Hochschule Karlsruhe.
- GANTER, K. (1927). Streuversuchsflächen der badischen forstlichen Versuchsanstalt an der Universität Freiburg i. Br. *Allgemeine Forst und Jagdzeitung* **103**, 353–358.
- GARCIA-GUZMAN, G. & BENITEZ-MALVIDO, J. (2003). Effect of litter on the incidence of leaf-fungal pathogens and herbivory in seedlings of the tropical tree *Nectandra ambigens*. *Journal of Tropical Ecology* **19**, 171–177.
- GEDDES, N. & DUNKERLEY, D. (1999). The influence of organic litter on the erosive effects of raindrops and of gravity drops released from desert shrubs. *Catena* **36**, 303–313.
- GIARDINA, C. P., RYAN, M. G., HUBBARD, R. M. & BINKLEY, D. (2001). Tree species and soil textural controls on carbon and nitrogen mineralization rates. *Soil Science Society of America Journal* **65**, 1272–1279.
- GILL, R. W. (1969). Soil microarthropod abundance following old-field litter manipulation. *Ecology* **50**, 805–816.
- GINTER, D. L., MCLEOD, K. W. & SHERROD, C. (1979). Water stress in longleaf pine induced by litter removal. *Forest Ecology and Management* **2**, 13–20.
- GIVNISH, T. J. (2002). Adaptive significance of evergreen vs. deciduous leaves: solving the triple paradox. *Silva Fennica* **36**, 703–743.
- GLATZEL, G. (1991). The impact of historic land-use and modern forestry on nutrient relations of Central European forest Ecosystems. *Fertilizer Research* **27**, 1–8.
- GOLDBERG, D. E. (1982). The distribution of evergreen and deciduous trees relative to soil type: an example from the Sierra Madre, Mexico, and a general model. *Ecology* **63**, 942–951.
- GOMEZ, A. G., POWERS, R. F., SINGER, M. J. & HORWATH, W. R. (2002). N uptake and N status in ponderosa pine as affected by soil compaction and forest floor removal. *Plant and Soil* **242**, 263–275.
- GONZALEZ, G. & ZOU, X. (1999). Plant and litter influences on earthworm abundance and community structure in a tropical wet forest. *Biotropica* **31**, 486–493.
- GRIME, J. P. (1979). *Plant Strategies and Vegetation Processes*. John Wiley & Sons, Chichester.
- GUZMAN-GRAJALES, S. M. & WALKER, L. R. (1991). Differential seedling response to litter after Hurricane Hugo in the Luquillo Experimental Forest, Puerto Rico. *Biotropica* **23**, 407–413.
- HASTWELL, G. T. & FACELLI, J. M. (2000). Effects of leaf litter on woody seedlings in xeric successional communities. *Plant Ecology* **148**, 225–231.

- HAYWOOD, J. D., TIARKS, A. E., ELLIOTT-SMITH, M. L. & PEARSON, H. A. (1998). Response of direct seeded *Pinus palustris* and herbaceous vegetation to fertilization, burning and pine straw harvesting. *Biomass and Bioenergy* **14**, 157–167.
- HEALEY, J. R. (1989). A bioassay of soils in the Blue Mountains of Jamaica. In *Mineral Nutrients in Tropical Forests and Savanna Ecosystems* (ed. J. Proctor), pp. 273–287. Blackwell Scientific, Oxford.
- HERMANN, R. K. & CHILCOTE, W. W. (1965). *Effect of seedbeds on germination and survival of Douglas-fir*. Forest Management Research, Forest Research Laboratory, Oregon State University, Corvallis.
- HORNBECK, J. W., SMITH, C. T., MARTIN, Q. W., TRITTON, L. M. & PIERCE, R. S. (1990). Effects of intensive harvesting on nutrient capitals of three forest types in New England. *Forest Ecology and Management* **30**, 55–64.
- JAHN, E. (1981). Auswirkungen von mehrjährigem Streurechen in reinen Laubholz- und Nadel-Laubwald-Mischbeständen auf die Kleintierfauna im Wienerwald. *Mitteilungen der Deutschen Gesellschaft für Angewandte Entomologie* **3**, 44–48.
- JANDL, R. & SOLLINS, P. (1997). Water-extractable soil carbon in relation to the belowground carbon cycle. *Biology and Fertility of Soils* **25**, 196–201.
- JANDL, R., STARLINGER, F., ENGLISCH, M., HERZBERGER, E. & JOHANN, E. (2002). Long-term effects of a forest amelioration experiment. *Canadian Journal of Forest Research* **32**, 120–128.
- JEMISON, G. M. (1943). Effect of litter removal on diameter growth of shortleaf pine. *Journal of Forestry* **41**, 213–214.
- JORDAN, D., PONDER, F. JR. & HUBBARD, V. C. (2003). Effects of soil compaction, forest leaf litter and nitrogen fertilizer on two oak species and microbial activity. *Applied Soil Ecology* **23**, 33–41.
- JUDAS, M. (1989). Die Reaktion der Lumbriciden-Zönose eines Kalkbuchenwaldes auf experimentell veränderte Streumengen (Zur Funktion der Fauna in einem Mullbuchenwald 7). In *Verhandlungen der Gesellschaft für Ökologie*, Vol. XVII, pp. 251–256. Gesellschaft für Ökologie, Göttingen.
- JUDAS, M. (1990). The development of earthworm populations following manipulation of the canopy leaf litter in a beech wood on limestone. *Pedobiologia* **34**, 247–255.
- KILIAN, W. (1998). Forest site degradation-temporary deviation from the natural site potential. *Ecological Engineering* **10**, 5–18.
- KILLHAM, K. (1994). *Soil Ecology*. Cambridge University Press, Cambridge.
- KIMOTO, A., UCHIDA, T., MIZUYAMA, T. & CHANGHUA, L. (2002). Influences of human activities on sediment discharge from devastated weathered granite hills of southern China: effects of 4-year elimination of human activities. *Catena* **48**, 217–233.
- KLIETSCH, W. (1950). Bedeutung und Schaden der Waldstreunutzung unter besonderer Betonung der Verhältnisse im Spessart. *Allgemeine Forstzeitschrift* **5**, 513–517.
- KOWALENKO, C. G., IVARSON, K. C. & CAMERON, D. R. (1978). Effect of moisture content, temperature, and nitrogen fertilization on carbon dioxide evolution from field soils. *Soil Biology and Biochemistry* **10**, 417–423.
- KRAPFENBAUER, A. (1983). Von der Streunutzung zur Ganzbaumnutzung. *Centralblatt für das Gesamte Forstwesen* **100**, 143–174.
- KREUTZER, K. (1972). Über den Einfluss der Streunutzung auf den Stickstoffhaushalt von Kiefernbeständen (*Pinus silvestris* L.). *Forstwissenschaftliches Centralblatt* **91**, 263–270.
- KRUTZSCH, H. (1850). Untersuchungen über die Waldstreu. *Forstlichwirtschafliches Jahrbuch* **6**, 88–270.
- KRUTZSCH, H. (1852). Untersuchungen über die Waldstreu. *Jahrbuch der Königlichen Akademie für Forst- und Landwirthe zu Tharand* **8**, 263–270.
- KRUTZSCH, H. (1863). Untersuchungen über die Waldstreu. *Jahrbuch der Königlichen Akademie für Forst- und Landwirthe zu Tharand* **15**, 32–71.
- KRUTZSCH, H. (1869). Untersuchungen über die Waldstreu. *Tharandter Forstliches Jahrbuch* **19**, 193–227.
- LA SCALA, N. JR., MARQUES, J. JR., PEREIRA, G. T. & CORÁ, J. E. (2000). Carbon dioxide emission related to chemical properties of a tropical bare soil. *Soil Biology and Biochemistry* **32**, 1469–1473.
- LI, Y., XU, M., SUN, O. J. & CUI, W. (2004). Effects of root and litter exclusion on soil CO₂ efflux and microbial biomass in wet tropical forests. *Soil Biology and Biochemistry* **36**, 2111–2114.
- LINDHOLM, T. & NUMMELIN, M. (1983). Changes in the community structure of forest floor vegetation after repeated litter disturbance by raking. *Silva Fennica* **17**, 289–300.
- LOPEZ-BARRERA, F. & GONZALEZ-ESPINOSA, M. (2001). Influence of litter on emergence and early growth of *Quercus rugosa*: a laboratory study. *New Forests* **21**, 59–70.
- LOPEZ-ZAMORA, I., DURYEA, M. L., MCCORMACK WILD, C., COMERFORD, N. B. & NEARY, D. G. (2001). Effect of pine needle removal and fertilization on tree growth and soil P availability in a *Pinus elliotii* Englem. var. *elliotii* stand. *Forest Ecology and Management* **148**, 125–134.
- LOWDERMILK, W. C. (1930). Influence of forest litter on run-off, percolation, and erosion. *Journal of Forestry* **28**, 474–491.
- LUNT, H. A. (1951). Liming and twenty years of litter raking and burning under red (and white) pine. *Soil Science Society of America Proceedings* **15**, 381–390.
- MACKINNEY, A. L. (1929). Effects of forest litter on soil temperature and soil freezing in autumn and winter. *Ecology* **10**, 312–321.
- MAO, D. M., MIN, Y. W., YU, L. L., MARTENS, R. & INSAM, H. (1992). Effect of afforestation on microbial biomass and activity in soils of tropical China. *Soil Biology and Biochemistry* **24**, 865–872.
- MARSHALL, T. J., HOLMES, J. W. & ROSE, C. W. (1996). *Soil Physics*, 3rd edn. Cambridge University Press, Cambridge.
- MCLEOD, K. W., SHERRROD, C. JR. & PORCH, T. E. (1979). Response of longleaf pine plantations to litter removal. *Forest Ecology and Management* **2**, 1–12.
- METCALFE, D. J. & TURNER, I. M. (1998). Soil seed bank from lowland rain forest in Singapore: canopy-gap and litter-gap demanders. *Journal of Tropical Ecology* **14**, 103–108.
- MITSCHERLICH, G. (1955). Untersuchungen über das Wachstum der Kiefer in Baden. 2. Teil: Die Streunutzungs- und Düngungsversuche. *Allgemeine Forst und Jagdzeitung* **126**, 193–204.
- MO, J., BROWN, S. & LENART, M. (1995). Nutrient dynamics of a human-impacted pine forest in a MAB reserve of subtropical China. *Biotropica* **27**, 290–304.
- MO, J., BROWN, S., PENG, S. & KONG, G. (2003). Nitrogen availability in disturbed, rehabilitated and mature forests of tropical China. *Forest Ecology and Management* **175**, 573–583.
- MOLOFSKY, J. & AUGSPURGER, C. K. (1992). The effect of leaf litter on early seedling establishment in a tropical forest. *Ecology* **73**, 68–77.
- MONK, C. D. & GABRIELSON, F. C. G. (1985). Effects of shade, litter and root competition on old-field vegetation in South Carolina. *Bulletin of the Torrey Botanical Club* **112**, 383–392.
- MORGAN, R. P. C. (1995). *Soil Erosion and Conservation*, 2nd edn. Longmans, Harlow.
- MYSTER, R. W. (1994). Contrasting litter effects on old field tree germination and emergence. *Vegetatio* **114**, 169–174.

- MYSTER, R. W. & PICKETT, S. T. A. (1993). Effects of litter, distance, density and vegetation patch type on postdispersal tree seed predation in old fields. *Oikos* **66**, 381–388.
- NADELHOFFER, K. J., BOONE, R. D., BOWDEN, R. D., CANARY, J., KAYE, J., MICKS, P., RICCA, A., MCDOWELL, W. & AITKENHEAD, J. (2004). The DIRT experiment. Litter and root influences on forest soil organic matter stocks and function. In *Forests in Time* (eds D. R. Foster and J. D. Aber), pp. 300–315. Yale University Press, New Haven.
- NĚMEC, A. (1929). Der Einfluss des Streurechens auf die chemische Zusammensetzung des Bodens, der Nadeln und des Holzes eines Kiefernbestandes. *Allgemeine Forst und Jagdzeitung* **109**, 214–219.
- NĚMEC, A. (1931). Zur Kenntnis des Stickstoffhaushaltes streubrechter Waldböden. *Forstwissenschaftliches Centralblatt* **53**, 49–67 & 147–156.
- NIELSEN, G. A. & HOLE, F. D. (1964). Earthworms and the development of coprogenous A1 horizons in forest soils of Wisconsin. *Soil Science Society of America Proceedings* **28**, 426–430.
- NILSSON, M.-C., WARDLE, D. A. & DAHLBERG, A. (1999). Effects of plant litter species composition and diversity on the boreal forest plant-soil system. *Oikos* **86**, 16–26.
- OGEE, J. & BRUNET, Y. (2002). A forest floor model for heat and moisture including a litter layer. *Journal of Hydrology* **255**, 212–233.
- ONNO, M. (1969). Laubstreunutzungsversuche in Waldgesellschaften des Wienerwaldes. In *Experimentelle Pflanzensoziologie* (ed. R. Tüxen), pp. 206–212. Junk, Den Haag.
- PARK, J.-H. & MATZNER, E. (2003). Controls on the release of dissolved organic carbon and nitrogen from a deciduous forest floor investigated by manipulations of aboveground litter inputs and water flux. *Biogeochemistry* **66**, 265–286.
- PEARSE, A. S. (1943). Effects of burning-over and raking-off litter on certain animals in the Duke Forest. *American Midland Naturalist* **29**, 406–424.
- PENG, S., REN, H., WU, J. & LU, H. (2003). Effects of litter removal on plant species diversity: a case study in tropical *Eucalyptus* forest ecosystems in South China. *Journal of Environmental Sciences* **15**, 367–371.
- PERRUCHOUD, D., KIENAST, F., KAUFMANN, E. & BRAEKER, O. U. (1999). 20th Century carbon budget of forest soils in the alps. *Ecosystems* **2**, 320–337.
- PETERSON, C. J. & FACELLI, J. M. (1992). Contrasting germination and seedling growth of *Betula alleghaniensis* and *Rhus typhina* subjected to various amounts and types of plant litter. *American Journal of Botany* **79**, 1209–1216.
- PONGE, J. F., ARPIN, P. & VANNIER, G. (1993). Collembolan response to experimental perturbations of litter supply in a temperate forest ecosystem. *European Journal of Soil Science* **29**, 141–153.
- POSER, T. (1990). The influence of litter manipulation on the centipedes of a beech wood. In *7th International Congress on Myriapods* (ed. A. Minelli), pp. 235–245. Brill, Leiden.
- PRIETZEL, J., KOLB, E. & REHFUESS, K. E. (1997). Langzeituntersuchung ehemals streugennutzter Kiefernökosysteme in der Oberpfalz: Veränderungen von bodenchemischen Eigenschaften und der Nährelementversorgung der Bestände. *Forstwissenschaftliches Centralblatt* **116**, 269–290.
- PUTZ, F. E. (1983). Treefall pits and mounds, buried seeds, and the importance of soil disturbance to pioneer trees on Barro Colorado Island, Panama. *Ecology* **64**, 1069–1074.
- RAMANN, G. (1883). Die Einwirkung der Streuentnahme auf Sandboden. *Zeitschrift für Forst- und Jagdwesen* **12**, 577–663.
- READER, R. J. (1993). Control of seedling emergence by ground cover and seed predation in relation to seed size for some old-field species. *Journal of Ecology* **81**, 169–175.
- REYNOLDS, B. C., CROSSLEY, D. A. & HUNTER, M. D. (2003). Response of soil invertebrates to forest canopy inputs along a productivity gradient. *Pedobiologia* **47**, 127–139.
- ROSS, S., MCKEE, W. H. & MIMS, M. (1994). Loblolly and longleaf pine responses to litter raking, prescribe burning and nitrogen fertilization. In *The Eighth Biennial Southern Silvicultural Research Conference* (ed. M. B. Edwards), pp. 220–224. USDA Forest Service, Asheville.
- SARIYILDIZ, T. & ANDERSON, J. M. (2003). Interactions between litter quality, decomposition and soil fertility: a laboratory study. *Soil Biology and Biochemistry* **35**, 391–399.
- SCHLENTNER, R. E. & VAN CLEVE, K. (1985). Relationships between CO₂ evolution from soil, substrate temperature, and substrate moisture in four mature forest types in interior Alaska. *Canadian Journal of Forest Research* **15**, 97–106.
- SCHLESINGER, W. H. & LICHTER, J. (2001). Limited carbon storage in soil and litter of experimental forest plots under increased atmospheric CO₂. *Nature* **411**, 466–469.
- SCHWAPPACH, A. F. (1887). Über den Einfluss des Streurechens auf den Holzbestand. *Zeitschrift für Forst- und Jagdwesen* **19**, 401–406 & 698–700.
- SCOTT, N. A. & BINKLEY, D. (1997). Foliage litter quality and annual net N mineralization: comparison across North American forest sites. *Oecologia* **111**, 151–159.
- SHELTON, M. G. (1995). Effects of the amount and composition of the forest floor on emergence and early establishment of loblolly pine seedlings. *Canadian Journal of Forest Research* **25**, 480–486.
- SINGH, J. S. & GUPTA, S. R. (1977). Plant decomposition and soil respiration in terrestrial ecosystems. *The Botanical Review* **43**, 449–528.
- SMALL, E. (1972). Photosynthetic rates in relation to nitrogen recycling as an adaptation to nutrient deficiency in peat bog plants. *Canadian Journal of Botany* **50**, 2227–2233.
- STEVENS, C. J., DISE, N. B., MOUNTFORD, J. O. & GOWING, D. J. (2004). Impact of nitrogen deposition on the species richness of grasslands. *Science* **303**, 1876–1879.
- STUMP, L. M. & BINKLEY, D. (1993). Relationships between litter quality and nitrogen availability in Rocky Mountain forests. *Canadian Journal of Forest Research* **23**, 492–502.
- SYDES, C. & GRIME, J. P. (1981). Effects of tree leaf litter on herbaceous vegetation in deciduous woodland. *Journal of Ecology* **69**, 237–248.
- TANNER, E. V. J., VITOUSEK, P. M. & CUEVAS, E. (1998). Experimental investigation of nutrient limitation of forest growth on wet tropical mountains. *Ecology* **79**, 10–22.
- TAO, D. L., XU, Z. B. & LI, X. (1987). Effect of litter layer on natural regeneration of companion tree species in the Korean pine forest. *Environmental and Experimental Botany* **27**, 53–65.
- TSCHERMAK, L. (1926). Buchenlaubstreunutzung im Lande Salzburg. *Centralblatt für das Gesamte Forstwesen* **52**, 336–349 & 577–663.
- TYLER, G. (1991). Effects of litter treatments on the sporophore production of beech forest macrofungi. *Mycological Research* **95**, 1137–1139.
- UETZ, G. W. (1979). The influence of variation in litter habitats on spider communities. *Oecologia* **40**, 29–42.
- United States Department of Agriculture (2003). *Keys to Soil Taxonomy*, 9th edn. USDA-NRSC, Ankeny.

- VASCONCELOS, S. S., ZARIN, D. J., CAPANU, M., LITTELL, R., DAVIDSON, E. A., ISHIDA, F. Y., SANTOS, E. B., ARAUJO, M. M., ARAGAO, D. V., RANGEL-VASCONCELOS, L. G. T., OLIVEIRA, F. D., McDOWELL, W. H. & DE CARVALHO, C. J. R. (2004). Moisture and substrate availability constrain soil trace gas fluxes in an eastern Amazonian regrowth forest. *Global Biogeochemical Cycles* **18**, GB2009.
- VAZQUEZ-YANES, C., OROZCO-SEGOVIA, A., RINCON, E., SANCHEZ-CORONADO, M. E., HUANTE, P., TOLEDO, J. R. & BARRADAS, V. L. (1990). Light beneath the litter in a tropical forest: effect on seed germination. *Ecology* **71**, 1952–1958.
- VAZQUEZ-YANES, C. & OROZCO-SEGOVIA, A. (1992). Effects of litter from a tropical rainforest on tree seed germination and establishment under controlled conditions. *Tree Physiology* **11**, 391–400.
- VESTERDAL, L. (1999). Influence of soil type on mass loss and nutrient release from decomposing foliage litter of beech and Norway spruce. *Canadian Journal of Forest Research* **29**, 95–105.
- VITOUSEK, P. M. (1982). Nutrient cycling and nutrient use efficiency. *American Naturalist* **119**, 553–572.
- VON SCHRÖDER, J. (1876). Über den Einfluss des Streurechens auf den Mineralstoffgehalt und den Zuwachs des Buchenholzes. *Tharander Forstliches Jahrbuch* **26**, 310–330.
- WALSH, R. P. D. & VOIGT, P. J. (1977). Vegetation litter: an underestimated variable in hydrology and geomorphology. *Journal of Biogeography* **4**, 253–274.
- WARDLE, D. A. (2002). *Communities and Ecosystems: Linking the Aboveground and Belowground Components*. Princeton University Press, Princeton.
- WARING, R. H. & SCHLESINGER, W. H. (1985). *Forest Ecosystems – Concepts and Management*. Academic Press, London.
- WIEDEMANN, E. (1935). Über die Schäden der Streunutzung im Deutschen Osten. *Forstarchiv* **11**, 386–392.
- WILKE, B., BOGENRIEDER, A. & WILMANN, O. (1993). Differenzierte Streuerverteilung im Walde, ihre Ursachen und Folgen. *Phytocoenologia* **23**, 129–155.
- WILSON, S. D. & ZAMMIT, C. A. (1992). Tree litter and the lower limits of subalpine herbs and grasses in the Brindabella Range, ACT. *Australian Journal of Ecology* **17**, 321–327.
- WITTICH, W. (1951). Der Einfluss der Streunutzung auf den Boden. *Forstwissenschaftliches Centralblatt* **70**, 65–92.
- WITTICH, W. (1954). Die melioration streugenutzter Böden. *Forstwissenschaftliches Centralblatt* **73**, 211–232.
- XIONG, S. & NILSSON, C. (1999). The effects of plant litter on vegetation: a meta-analysis. *Journal of Ecology* **87**, 984–994.
- ZAK, D. R., HOLMES, W. E., FINZI, A. C., NORBY, R. J. & SCHLESINGER, W. H. (2003). Soil nitrogen cycling under elevated CO₂: a synthesis of forest FACE experiments. *Ecological Applications* **13**, 1508–1514.
- ZOU, X. M. (1993). Species effects on earthworm density in tropical tree plantations in Hawaii. *Biology and Fertility of Soils* **15**, 35–38.

XII. APPENDIX

Summary of litter experiments included in the review, ordered by author. The soil types given were taken from the original publications and do not adhere to a particular classification system. ‘?’ is information not given in the original publication; In ‘Focus’, DOM is dissolved organic matter; in ‘Other variables’, OM is organic matter, CEC is cation exchange capacity; in ‘Treatments’; LM is litter manipulation and the exact treatment is given in ‘Notes’, CT is control, LA is litter addition, LR is litter removal. In ‘Treatment duration’: ‘once’ refers to a litter treatment carried out at the beginning of the experiment and not repeated for the duration of the study; ‘long-term’ refers to litter removal as a management practice for more than 50 years.

Reference	Focus	Other variables	Vegetation type	Soil type	Treatment frequency	Treatment duration	Study duration	Treatments	No. replicates	Plot size	Notes
Arpin, Ponge & Vannier (1995)	Abundance & community structure of nematodes		Temperate <i>Quercus petraea</i> , <i>Fagus sylvatica</i> , <i>Carpinus betulus</i>	Brown earth	Every 2 weeks	5 years	5 years	LR/LA	2 LR, CT; 1LA	6 m × 3 m	Litter intercepted with baskets
Baar & De Vries (1995)	Colonisation of ectomycorrhizal fungi		Temperate <i>Pinus sylvestris</i>	Podzols	Once	Once	1 year	LR/LA	4 per stand	15 m × 15 m	Sod-cutting & sod-addition/2 stands of different age
Baar & Kuyper (1993)	Species richness & carpophore abundance of ectomycorrhizal fungi		Laboratory study/ temperate <i>Pinus sylvestris</i>	?	Once	Once	5 years	LR	2 per stand	100 m ²	Sod cutting/3 stands
Baar & Kuyper (1998)	Species richness & sporocarp density of ectomycorrhizal fungi		Temperate <i>Pinus sylvestris</i>	Sandy	Once	Once	3 years	LR	4 per stand	15 m × 15 m/ 20 m × 20 m	Sod-cutting & -addition/3 stands of different ages
Baar & Ter Braak (1996)	Sporocarp occurrence of ectomycorrhizal fungi	Soil N & P/ soil pH/foliar nutrients	Temperate <i>Pinus sylvestris</i>	Haplic-arenosol/ haplic podzol	Once	Once	3 years	LR/LA	4 per stand	15 m × 15 m/ 20 m × 20 m	Sod-cutting & -addition/6 stands of different ages
Baar <i>et al.</i> (1994a)	Spatial distribution of <i>Laccaria bicolor</i> genets		Temperate <i>Pinus sylvestris</i>	Sandy	Once	Once	1 year	LR	4	15 m × 15 m	Sod-cutting
Barritt & Facelli (2001)	Seedling emergence of understorey species	Seedling biomass	Temperate <i>Casuarina pauper</i>	Clay-loam	Once	Once	6 weeks	LM	16	2.5 cm × 2.5 cm	Litter added & no-litter controls
Beatty & Sholes (1988)	Plant species composition	Soil temperature & moisture	Temperate deciduous	?	Continuous	3 years	3 years	LR	10	0.65 m ² circular	Litter intercepted with wire mesh
Benitez-Malvido & Kossmann-Ferraz (1999)	Seedling performance & herbivory		Tropical rainforest	Alfic oxisols	Every 2 months	1 year	1 year	LR/LA	5	1 m ²	
Bowden <i>et al.</i> (1993)	Soil respiration		Northern mixed hardwood	Stony loam	Annually	?	3 months	LR/LA	3	3 m × 3 m	

Brearley, Press & Scholes (2003)	Ectomycorrhizal colonisation & abundance/seedling growth	Nutrient uptake/litter content	Dipterocarp seedlings in nursery	Alluvial	Once	Once	10 months	LM	12	1.2 l pots	Litter added & no-litter controls
Brown, Lenart & Mo (1995)	Tree growth/biomass/forest structure/organic matter	Litter biomass	Monsoon pine/pine-broadleaf/evergreen broadleaf	Lateritic red earth	1–2 × annually	45 years	c. 3 years	LR	20	10 m × 10 m	10 m buffer around plots
Cintra (1997)	Seed & seedling predation		Tropical rainforest	Silty alluvial	Weekly	1 year	1 year	LR/LA	10	30 cm × 30 cm/ 1 m × 1 m	LA treatments with different degrees of litter cover
Cullings <i>et al.</i> (2003)	Community structure of ectomycorrhizal fungi	Soil nutrients, pH, temperature, OM & moisture	Temperate <i>Pinus contorta</i>	Rhyolite	Once	Once	2 growing seasons	LA	3	5 m × 5 m	
Dalling (1995)	Seed germination		Tropical upper montane forest	Lithosol	Once a week/once a month	18 weeks	18 weeks	LR/LA	4	1 m × 1 m	
David <i>et al.</i> (1991)	Soil macrofauna abundance	Litter biomass	Temperate <i>Quercus petraea</i> , <i>Fagus sylvatica</i> , <i>Carpinus betulus</i>	Brown earth	Every 2 weeks	5 years	5 years	LR/LA	2 LR, CT; 1 LA	6 m × 3 m	Litter intercepted with baskets
De Vries <i>et al.</i> (1995)	Fruit body abundance & species richness of ectomycorrhizal fungi		Temperate <i>Pinus sylvestris</i>	Sand	Once	Once	4 years	LR	2 per stand	50 m ²	Sod-cutting & sod-addition/5 different stands
Dzwonko & Gawronski (2002 <i>a, b</i>)	Seedling recruitment/species richness	Soil pH, CEC & nutrients	Temperate <i>Quercus robur</i> , <i>Pinus sylvestris</i> , <i>Fagus sylvatica</i>	Podzolised	Annually	16 years	16 years	LR	3	5 m × 5 m	
Ebermayer (1876)	Soil nutrients		Temperate <i>Pinus sylvestris</i>	Sandy	Annually	Long-term	?	LR	1	Whole stand	
Eriksson (1995)	Seedling recruitment of forbs		Boreo-nemoral deciduous	?	Once	Once	6 months	LR	4	0.16 m ²	
Facelli (1994)	Seedling emergence, competition & herbivory	Arthropod abundance	Temperate old field	Silty loam	Once	Once	1 growing season	LM	10/4	1 m × 0.6 m/ 1 m × 0.8 m	Litter added & no-litter controls
Facelli & Ladd (1996)	Germination		Greenhouse using <i>Eucalyptus</i> species	Commercial potting mix	Once	Once	2 months	LM	10	0.9 l pots	Litter added & no-litter controls
Facelli & Pickett (1991 <i>a, c</i>)	Seedling emergence/competition		Temperate old field	Silty loam	Once	Once	1 growing season	LM	10	1 m × 0.6 m	Different amounts of litter added & no-litter controls

Reference	Focus	Other variables	Vegetation type	Soil type	Treatment frequency	Treatment duration	Study duration	Treatments	No. replicates	Plot size	Notes
Facelli <i>et al.</i> (1999)	Establishment & growth of seedlings	Water potential/soil temperature & water/seedling mortality	Greenhouse/mediterranean <i>Eucalyptus obliqua</i>	Soil medium mix	Once	Once	75 days	LM	10/5	0.9 l pots/ 1 m × 1 m plots	Litter added & no-litter controls
Fahey <i>et al.</i> (1998)	Tree growth/foiar nutrients/litterfall/soil respiration/root biomass		Northern hardwood	?	Every 2 years	6 years	6 years	LR	1 per stand	15 m × 15 m	2 m buffer around plots/3 different stands
Fiedler <i>et al.</i> (1962)	Tree growth/soil properties	Microbial biomass/spp. diversity of micro-fungi/pH	Temperate <i>Pinus sylvestris</i>	Sand	?	?	?	LR	3	0.2 ha	
Fisk & Fahey (2001)	Microbial biomass/soil nitrogen	pH/soil organic matter	Northern hardwood	?	Every 2 years	9 years	9 years	LR	1 per stand	15 m × 15 m	2 m buffer around plots/3 different stands
Ganade & Brown (2002)	Seed germination & seedling establishment	Soil N, P, K	Tropical old field	?	Every 2 weeks	10 months	10 months	LR	8	2.5 m × 0.5 m subplots	
Ganter (1914)	Soil nitrogen concentration		Temperate <i>Fagus sylvatica</i>	?	Annually/every 5 years	Long-term	?	LR	?	?	
Ganter (1927)	Tree growth/soil moisture & temperature/soil nutrient contents	Litter biomass/leaching/forb diversity	Temperate <i>Fagus sylvatica</i> / <i>Carpinus betulus</i> / <i>Pinus sylvatica</i>	Sandy	Annually/every 5 years	15 years	15 years	LR	1	0.1 ha	6 different stands
Garcia-Guzman & Benitez-Malvido (2003)	Leaf pathogens/herbivory		Tropical rainforest	?	Every month	1 year	1 year	LR/LA	5	1 m ²	30 cm buffer around plots
Gill (1969)	Soil arthropods	Soil temperature & moisture	Temperate old field	?	?	20 months?	20 months	LR/LA	2	3.7 m × 5.3 m	Included an artificial litter treatment
Ginter <i>et al.</i> (1979)	Soil moisture/tree water status	Tree growth	Temperate <i>Pinus palustris</i>	Loamy sand	Once	Once	52 days	LR	1	0.16–0.18 m ²	7.5 m buffer around plots
Gomez <i>et al.</i> (2002)	N uptake and N status of trees		Temperate <i>Pinus ponderosa</i>	Loam/fine-loam/sandy loam	Once	Once	4 growing seasons	LR	1 per site?	?	Forest floor removal

Gonzalez & Zou (1999)	Earthworm abundance & community structure	Litter nutrients & C/soil nutrients	Tropical wet forest	Ultisols/oxisols	Every 2 weeks	1 year	1 year	LR/LA	16	0.5 m ²	Litter intercepted with baskets
Guzman-Grajales & Walker (1991)	Seedling establishment & survival		Tropical rainforest	?	LR every 2 months, LA every 6 months	1 year	1 year	LR/LA	4	10 m × 10 m	
Hanamman (1881) in Ramann (1883)	Soil nutrients		Temperate <i>Pinus sylvestris</i> , <i>Fagus sylvatica</i>	Sand	Annually	12 years	?	LR	1	Whole stand?	
Hastwell & Facelli (2000)	Seedling emergence, growth & survival		Mediterranean <i>Eucalyptus incrassata</i>	Sand	Once	Once	3 months	LM	4 per site	50 cm × 50 cm	Litter added & no-litter controls/3 different sites
Haywood <i>et al.</i> (1998)	Foliar nutrients/tree growth/diversity of forbs	Litter biomass	Temperate <i>Pinus palustris</i>	Sandy loam	Annually	5 years	7 years	LR	4	0.16 ha	Plantation
Jahn (1981)	Soil fauna abundance & community structure		Temperate mixed deciduous	Clay	Annually	5 years	5 years	LR	1	300–400 m ²	5 different stands
Jandl & Sollins (1997)	Water-extractable C/soil respiration	C fractions	Temperate <i>Pseudotsuga menziesii</i>	?	Every 2 weeks	1 year	1 year	LR	1	4 m ²	
Jemison (1943)	Tree growth		Temperate <i>Pinus echinata</i>	?	Annually	12 years	12 years	LR	1	2023 m ²	
Jordan <i>et al.</i> (2003)	Soil nutrients/soil microbes/seedling biomass	15N uptake	Laboratory study using <i>Quercus coccinea</i> & <i>Q. rubra</i>	Ultisol	Once	Once	6 months	LM	3	15.2 cm diameter pots	Litter added & no-litter controls
Judas (1989, 1990)	Earthworm abundance & species composition	Soil temperature	Temperate <i>Fagus sylvatica</i>	?	Annually	5 years	5 years	LR/LA	8CT, 4LR, 2LA	100 m ²	
Kimoto <i>et al.</i> (2002)	Sediment discharge		Subtropical <i>Pinus massoniana</i>	?	?	4 years	6 years	LR	1	c. 1 ha	
Krutzsch (1850, 1852, 1863 & 1869)	Tree growth	Litter biomass	Temperate <i>Pinus sylvestris</i> / <i>Picea abies</i> / <i>Fagus sylvatica</i>	Sand/clay	Annually?	Up to 20 years	Up to 20 years	LR/LA	1	400 m ² ?	5 stands of different ages/4 m? buffer around plots
Li <i>et al.</i> (2004)	Soil respiration/microbial biomass		Secondary tropical rainforest/ <i>Pinus caribae</i> plantation	?	Continuous	9 months?	9 months	LR	3	3 m × 3 m	
Lindholm & Nummelin (1983)	Community structure of forest floor vegetation	Soil N & C	Subalpine conifer	?	Annually	25 years	1 growing season	LR	10	1 m × 1 m	

Appendix (cont.)

Reference	Focus	Other variables	Vegetation type	Soil type	Treatment frequency	Treatment duration	Study duration	Treatments	No. replicates	Plot size	Notes
Lopez-Barrera & Gonzalez-Espinosa (2001)	Emergence and early growth of seedlings		Laboratory study of <i>Quercus rugosa</i>	?	Once	Once	145 days	LM	3	24 cm diameter trays	Litter added & no-litter controls
Lopez-Zamora <i>et al.</i> (2001)	Tree growth/soil phosphorus	Litterfall/ foliar nutrients	Temperate <i>Pinus elliottii</i>	Sandy	Annually/ every 2 & 4 years	4 years	4 years	LR	2	25 m × 25 m	Plantation; 5 m buffer
Lowdermilk (1930)	Run-off/percolation/erosion		Laboratory study	?	Once	Once	c. 1 year	LR	4	2 × 5 ft	
Lunt (1951)	Soil moisture/soil temperature/soil nutrients/tree growth		Temperate <i>Pinus resinosa</i>	Loamy sand	Annually	20 years	20 years	LR/LA	1	102 m ²	Plantation
MacKinney (1929)	Soil temperature/soil freezing		Temperate <i>Pinus strobus</i> , <i>Pinus resinosa</i>	Loam	Once	Once	6 months	LR	1	12 ft × 17 ft	Plantation
Mao <i>et al.</i> (1992)	Microbial biomass and activity/soil respiration	Soil N, P, C, pH	Tropical monsoon forest	Lateritic	Continuous	Long-term	5 months	LR	1	Whole stand	
McLeod <i>et al.</i> (1979)	Litter nutrients/soil pH/foliar nutrients/tree growth		Temperate <i>Pinus palustris</i>	Loamy sand	Annually	3 years	3 years	LR	1CT, 2LR	0.32–0.41 ha	3 stands on different soil types
Metcalf & Turner (1998)	Seedling emergence		Tropical rainforest	?	Once	Once	6 months	LR/LA	25	50 cm × 50 cm	
Mitscherlich (1955)	Tree growth	Litter biomass/soil compaction/soil N	Temperate <i>Pinus sylvestris</i>	Sand	Annually/ every 5–7 years	23 & 33 years	23 & 33 years	LR	1	0.1 ha	2 different stands
Mo <i>et al.</i> (1995)	Nutrient contents of leaves, wood, roots, litter & soil	SOM	Monsoon pine/pine-broadleaf/evergreen broadleaf	Lateritic red earth	1–2 × annually	45 years	c. 3 years	LR	20	10 m × 10 m	10 m buffer around plots
Mo <i>et al.</i> (2003)	Nitrogen availability	Soil pH & bulk density	Monsoon pine/pine-broadleaf/evergreen broadleaf	Lateritic red earth	1–2 × annually	Long-term	9 months	LR	5	10 m × 10 m	10 m buffer around plots
Molofsky & Augspurger (1992)	Seedling establishment		Laboratory study/tropical semideciduous	?	Once	Once	4 months	LM	5/2	0.5 m × 0.25 m/ 0.25 m ²	Different amounts of litter added & no-litter controls

Monk & Gabrielson (1985)	Biomass & density of old-field forbs		Temperate old field	Loamy sand	Once	Once	2 growing seasons	LM	2	3 m ²	Different types of litter added & no-litter controls
Myster (1994)	Seedling emergence of old-field tree spp.		Greenhouse	?	Once	Once	10 weeks	LM	6	126.7 cm ² pots	Different amounts and types of litter added & no-litter controls
Myster & Pickett (1993)	Seed predation		Temperate old field	?	Once	Once	2 months	LM	20	13 cm × 13 cm	Litter added & no-litter controls/2 different litter types
Nadelhoffer <i>et al.</i> (2004)	Soil respiration/ microbial biomass		Northern mixed hardwood	Stony loam	Annually	7 years	5 years	LR/LA	3	3 m × 3 m	
Němec (1929, 1931)	Soil nutrients/leaf nitrogen/wood nutrients		Temperate <i>Pinus sylvestris</i>	Sandy	?	Long-term	?	LR	1 per stand	Whole stand?	1931: 8 different stands
Nielsen & Hole (1964)	Earthworm abundance		Temperate <i>Quercus alba</i> , <i>Quercus velutina</i> , <i>Prunus serotina</i>	?	Annually	5 years	6 months?	LR/LA	1	13.4 m ²	
Nilsson <i>et al.</i> (1999)	Microbial biomass and activity/ decomposition/ seedling growth		Boreal <i>Picea abies</i> - <i>Pinus sylvestris</i> / <i>Betula pendula</i> - <i>B. pubescens</i>	?	Once	Once	2 growing seasons	LM	8	100 mm diameter tubes	Litter added & no-litter controls
Onno (1969)	Diversity of forbs	Litter biomass & nutrient content	Temperate mixed deciduous	Clay	Annually	2 years	2 years	LR	1	300–400 m ²	5 different stands
Park & Matzner (2003)	DOM as vehicle for C and N transport	Microbial biomass	Temperate hardwood	Dystric cambiosol	Continuous	2 years	2 years	LR/LA	4	2 m × 2 m	
Pearse (1943)	Soil fauna	Soil temperature	Temperate <i>Pinus taeda</i>	Loam	Annually/ every 2 years	6 years	5 years	LR	1	405 m ²	Annually raked for first two years, then raked every 2 years
Peng <i>et al.</i> (2003)	Plant species diversity	Soil microbes/soil nutrients, pH & OM	Tropical <i>Eucalyptus exserta</i>	Laterite	?	34 & 28 years	34 years	LR	1	20 m × 20 m	Plantation
Peterson & Facelli (1992)	Germination & seedling growth		Greenhouse	?	Once	Once	5 months	LM	6	126.7 cm ² pots	Different amounts of litter added & no-litter controls

Appendix (cont.)

Reference	Focus	Other variables	Vegetation type	Soil type	Treatment frequency	Treatment duration	Study duration	Treatments	No. replicates	Plot size	Notes
Ponge <i>et al.</i> (1993)	Collembola abundance & species richness	Soil temperature/ soil C/soil pH	Temperate <i>Quercus petraea</i> , <i>Fagus sylvatica</i> , <i>Carpinus betulus</i>	Brown earth	Every 2 weeks	5 years	5 years	LR/LA	2 LR, CT; 1LA	6 m × 3 m	
Poser (1990)	Centipede abundance & species richness	Soil temperature/ soil moisture	Temperate <i>Fagus sylvatica</i>	Mull rendzina	Continually	5 years	5 years	LR/LA	4CT, LR; 2LA	10 m ²	Litter intercepted
Ramann (1883)	Soil properties/soil moisture/soil nutrients	Leaching	Temperate <i>Pinus sylvestris</i>	Sandy	Annually	16 years	?	LR	1	?	3 different stands
Reynolds <i>et al.</i> (2003)	Soil fauna		Temperate deciduous	Hapludults/ dystrochrepts/ haplubrepts	Once a week	22 months	22 months	LR	5	1 m ²	Litter intercepted with wire mesh
Ross <i>et al.</i> (1994)	Tree growth	Soil nutrients & soil OM	Temperate <i>Pinus taeda</i> / <i>P. palustris</i>	Sandy loam	Once every 3 years	7 years	7 years	LR	3/2	0.19 ha	Plantations
Schwappach (1887)	Tree growth and wood production		Temperate <i>Pinus sylvestris</i>	Infertile soil	Annually	21 years	21 years	LR	1	Whole stand	
Shelton (1995)	Emergence and establishment of seedlings	Biomass of seedlings and forbs	Temperate <i>Pinus taeda</i>	Silt loam	Once	Once	9 months	LM	4	26 cm × 55 cm	Different amounts of litter added & no-litter controls
Stoeckhardt (1861) <i>in</i> Ebermayer (1876)	Soil nutrients/ water retention capacity		Temperate <i>Pinus sylvestris</i>	Sand	Periodically	Long-term	?	LR	1	Whole stand	
Sydes & Grime (1981)	Germination & survival of forbs		Temperate deciduous	?	Periodically	Once	6 months	LM	5	44 cm × 44 cm	Different amounts of litter added & no-litter controls
Tao <i>et al.</i> (1987)	Seedling establishment & survival		Subarctic <i>Pinus koraiensis</i>	?	Once?	Once?	3 years	LA	10?	1 m × 1 m	
Tyler (1991)	Sporophore production of macrofungi		Temperate <i>Fagus sylvatica</i>	Cambiosol	Annually	2 years	2 years	LR/LA	10	5 m ² circular	
Uetz (1979)	Spider species richness and abundance	Soil moisture/soil temperature	Temperate deciduous	?	Once	Once	6 months	LR/LA	3	10 m × 10 m	LR and LA as 0, 0.5, 1, 1.5 & 2 × mean litter depth
Vasconcelos <i>et al.</i> (2004)	Soil respiration	Nitrification rates	Tropical montane regrowth forest	Sombriustox	Every 2 weeks	2 years	1 years	LR	4	20 m × 20 m	

Vazquez-Yanes & Orozco-Segovia (1992)	Seed germination & seedling establishment	Laboratory study using tropical rainforest species	?	Once	Once	6 weeks/4 months	LM	3/4	45 cm × 35 cm boxes	Different amounts of litter & paper added & no-litter controls
von Schröder (1876)	Nutrient contents of wood/tree growth	Temperate <i>Fagus sylvatica</i>	Clay	Annually	13 years	13 years	LR/LA	1	0.1845 ha	
Wiedemann (1935)	Tree growth, humus content, soil compaction	Temperate <i>Pinus sylvestris</i>	Sandy	?	Long-term	?	LR	1	Whole stand	3–8 different stands
Wilson & Zammit (1992)	Understorey biomass/seedling emergence	Subalpine <i>Eucalyptus dives</i> / <i>Eucalyptus pauciflora</i>	?	?	20 months	20 months	LR/LA	5	2 m × 2 m	Addition of own litter and of <i>E. dives</i> litter to <i>E. pauciflora</i> plots
Wittich (1951, 1954)	Soil properties/humus content/tree growth/leaf nutrients	Temperate <i>Pinus sylvestris</i>	Sand	?	Long-term	?	LR	1	Whole stand	17 forests sampled