Effects of base cation fertilization on litter decomposition

in a sugar maple forest.

by

T.K. Lukumbuzya

Department of Natural Resource Sciences, McGill University, Macdonald Campus, Ste. Anne de Bellevue QC H9X 3V9

A thesis submitted to the faculty of Graduate Studies and Research

in partial fulfilment of the requirements for the

degree of Master of Science

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Short Title

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Effects of Cation Fertilization on Decomposition in a Maple Forest.

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ABSTRACT

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Renewable Resources

Subset is take foliage litters from fertilized and unfertilized plots on a base-poor site and $\frac{1}{2} \cos \frac{1}{2}$ - usually base such site were incubated in litterbags of 1 and 3 mm mesh on fertilized and $\frac{1}{2}$ - critized plots at the base-poor site. Mass loss of unfertilized litter was slower in fertilized plots at the base-poor site. Mass loss of unfertilized litter was slower in fertilized plots, suggesting a negative effect of fertilization on decomposers. $\frac{1}{2} \cos \frac{1}{2}$ of fertilized biter was faster than unfertilized litter in the same plots, indice $\frac{1}{2} \sin \frac{1}{2} \cos \frac{1}{2}$ in litter quality due to fertilization enhanced microbial decomposition. $\frac{1}{2} \sin \frac{1}{2} \cos \frac{1}{2}$ higher in large mesh than in small mesh size bags, suggesting that $\frac{1}{2} \sin \frac{1}{2} \cos \frac{1}{2}$ and played a significant role in litter decomposition.

Potassium appeared to be rapidly leached, whereas Ca and Mg were released at rates more closely related to litter mass loss. Nitrogen was mineralized from N-rich Arboretum litter only ; all other litters immobilized N. Release of Ca and Mg was reduced significantly on fertilized plots. Large soil fauna enhanced Ca release, while they delayed N-mineralization in Arboretum litter.

RESUME

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Resources Renouvelables

Les litières foliaires de l'érable à sucre des parcelles fertilisées et non-fertilisées d'un site pauvre en bases et d'un site naturellement riche en bases ont été incubées dans des sacs à litière dont la taille des mailles variait de 1 à 3 mm. La perte de masse de la litière non-fertilisée était plus lente dans les parcelles fertilisées que dans celles nonfertilisées, suggérant un effet négatif de la fertilisation sur les décomposeurs. La perte de masse de la litière fertilisée était plus rapide que pour la litière non-fertilisée incubée dans les mêmes parcelles, indiquant que des changements dans la qualité de la litière, créés suite à la fertilisation en cations basiques, accélèreraient la décomposition microbienne. La perte de masse était plus élevée dans les sacs à grandes mailles que dans ceux à mailles plus petites, suggérant que la macrofaune du sol joue un rôle important dans la décomposition de la litière.

Le K semblait rapidement lessivé de toutes les litières, tandis que le Ca et le Mg montraient un taux de minéralisation plus proche du taux de perte de masse de la litière. L'azote était sculement minéralisé dans les litières de l'Arboretum riche en N; toutes les autres litières immobilisaient le N. La minéralisation du Ca et du Mg était significativement réduite dans les parcelles fertilisées. La macrofaune du sol a augmenté la mineralisation du Ca de toutes les litières alors qu'elle augmentait l'immobilisation de N dans la litière de l'Arboretum.

Preface

The purpose of this study was to evaluate the effects of base cation fertilization on litter decomposition and nutrient release in a sugar maple forest. The first chapter is a review of the current literature. Factors which affect litter decomposition are discussed, in particular those factors that are mediated by soil fauna. The second chapter examines the process of litter decomposition. The effects of increased litter chemical content; changes in site properties due to fertilization; and the exclusion of large soil fauna from decomposing litters, are assessed. The third chapter evaluates the effects of litter quality, site fertility and soil fauna on patterns of nutrient mineralization from decaying litter. The second and third chapters are presented in a format suitable for submission to journals for publication.

The following statements concerning the authorship of papers is excerpted from <u>Guidelines Concerning Thesis Preparation</u> published by the Faculty of Graduate Studies and Research:

"The inclusions of manuscripts co-authored by the candidate and others is acceptable but the candidate is required to make an explicit statement on who contributed to such work and to what extent, and supervisors must attest to the accuracy of the claims before the oral committee. Since the task of the examiners is made more difficult in these cases, it is in the candidate's interest to make the responsibilities of authors perfectly clear. Candidates following this option must inform the department before it submits

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the thesis for review."

Chapter II was prepared for submission to the Canadian Journal of Forest Research and was co-authored by the candidate, his supervisor, Dr. J.W. Fyles, and Dr. B. Côté. Chapter III will be co-authored by the candidate and his supervisor, Dr. J.W. Fyles. The candidate has been responsible for both conducting the studies and preparing the two manuscripts. Supervision was provided by Dr. J.W. Fyles through guidance and editorial advice during manuscript preparation.

Acknowledgements

I would like to express my sincere gratitude to my supervisor, Professor J. W. Fyles, for his support, guidance, patience and in particular his constant words of encouragement. I wish to thank Yuan Hua Wen and Terry Valladarez for their technical assistance. I thank Khosro Mousavi, Eric Aubin, Hélène Lalande, Wendy Jones, Matgaret Hope-Simpson and Elizabeth Russell for all the assistance received in the laboratory.

I would like to thank E. Johns for her statistical advice, and Peter Kirby for his patience and good counsel in statistical processing of data. This research project was supported financially by NSERC, FCAR and the Ministry of Forestry of Quebec.

Special thanks to my family, without whom this thesis would not have been attempted let alone completed. I would especially like to thank my wife Judy, my brother Heri and my sister Tunu for all the "unofficial" hours invested in this work.

This work is dedicated to the memories of my father Mwinamila and my brother Lukumbuzya. Ningependa kuchukua hii nafasi kuwakumbusha waafrika wote kwamba sasa ndio wakati wa kuchangamuka.

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CHAPTER I

REVIEW OF LITERATURE

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Review of Literature

Introduction

Soil acidification and associated loss of base cations (Na, K, Ca, Mg) from forest ecosystems by leaching is a natural consequence of the long term actions of organic acid release during organic matter decomposition (Reuss and Johnson 1986). Deposition of acid pollutants has accelerated the processes of soil acidification and base cation leaching in many areas of North America and Europe, these changes in soil properties may have led to nutrient deficiencies due to changes in nutrient cycling rates and patterns in forest ecosystems. Nutrient cycling is a condition for the existence of a forest ecosystem: decomposition of dead plant material results in nutrient release and the subsequent reutilization of these nutrients by the ecosystem through a number of complex pathways (Berg, 1986).

Decomposition is the process by which dead organic matter undergoes a decline in mass due to the biologically-mediated breakdown of this substrate, the elements released are used to support microbial respiration and the synthesis of microbial tissue (Carlyle, 1986). Although fungi and bacteria are directly responsible for most of the organic matter breakdown, a diverse assemblage of protozoans, nematodes, annelids and arthropods greatly influences the functioning of the decomposer flora as a result of their direct and indirect feeding activities (Schaefer 1990). Decomposition of organic matter has been considered a synergistic relationship between invertebrate fauna and microflora despite the fact that soil metabolism (CO₂ production) that can be attributed to all soil animals is 10% or less of the total amount (Seastedt, 1984). Soil fauna are more prominent in deciduous than in coniferous systems, but decomposition in all systems is accelerated by conditions that enhance microbial growth or activity (McClaugherty et al. 1985). Litter decomposition rates have been related to climate, organic chemical quality of the litter and exogenous nutrient availability, whereas mineralization and immobilization of nutrients from organic matter is governed primarily by soil heterotroph requirements. Mineralization is the biologically-mediated release of organically bound elements from a substrate and their conversion into inorganic forms, whereas immobilization is the conversion of inorganic forms of elements into microbial tissue (Carlyle 1986).

A general model for litter decomposition has been suggested by Berg (1986) which can be divided into two phases. The first phase of decomposition is dominated by rapid rates of mass loss and leaching of nutrients. Leaching may be highly significant in litter with high nutrient contents. A certain net uptake into the litter of some elements (N, P, S, and Ca) has been noted during this first phase (Gosz et al., 1973), attributable to incorporation of these nutrients into microbial biomass. The second stage of litter decomposition occurs when litter mass loss is controlled by the rate of mass loss of lignin. Most of the initial amounts of nitrogen remain stored in the litter until this phase shift occurs (Berg 1986). When net release of nutrients starts, it will be proportional to the mass loss of litter and consequently also to the mass loss of lignin. This type of relationship has been found for the nutrients N, P, S, Ca, K, Mg, and Mn (Berg and Staaf, 1981).

Factors affecting Litter Decomposition and Nutrient release.

Litter Quality

Litter quality refers to the physical and chemical characteristics which influence breakdown of dead plant material. These include the nature of the carbon source, nutrient availability, modifying compounds and recalcitrant properties. Litter quality varies between and within species, depending also on site conditions (Berg and Ekbohm, 1983).

Water-soluble and acetone-soluble components of litter have been shown to decompose first, disappearing within the first year after leaf fall. This group of compounds includes sugars, amino-acids, steryl esters and triglycerides. These are followed by cellulose and hemicelluloses and then lignin. All of these compounds can act as carbon and energy sources for microbes (Carlyle, 1986). Deciduous leaf litter contains a higher proportion of labile C relative to coniferous litter, and, as a result, deciduous litter decomposition is more rapid in the first phase than coniferous litter. Among deciduous species, decay rates have been positively correlated with labile C content of litter (Harris and Riha 1991).

Comparisons of species with generally similar amounts of labile products indicate that nutrient availability plays an important role in determining decomposition rates and nutrient release. Decay rates were reported to have been faster for fertilized pine needles than unfertilized Scots pine needles, but only until the onset of lignin degradation, after which the decay rates of fertilized and unfertilized needles converged (Berg et al. 1987). After measuring a number of variables during the incubation of beech litter Staaf (1987) concluded that litter pH and the concentrations of Ca and Mg were much more important than lignin content in regulating litter decomposition. Similarly Nicolai (1988) found that beech litter collected from limestone sites with higher levels of Ca, Mg, Na, and K and lower levels of phenolics decomposed faster than beech litter collected from sandstone sites and therefore with lower levels of these nutrients. Thirty-nine years after fertilization with potassium fertilizer, Shepard and Mitchell (1990) found that elemental contents of N, K, Ca, Mg, Na, and S in treated plots of red pine were substantially higher than the unfertilized plots. In this study maintenance of the elevated potassium in the fertilized plots. Approximately 80% of the difference in total ecosystem K between the fertilized and unfertilized treatments was accounted for by the above ground vegetation indicating efficient nutrient cycling had been a consequence of enhanced litter nutrient content.

Many studies have implicated initial N content of litter as a major determinant of litter decay rates. Decomposition rates, as well as N and Ca release were highly correlated with initial N content in 12 different leguminous plant materials (Tian et al. 1992). Prescott et al. (1992) found that forb leaves from N fertilized plots decayed significantly faster than leaves from control plots although nutrient mineralization was not enhanced. On the other hand decomposition rates were unaffected whereas N mineralization was accelerated by high initial N of pine litter (Berg and Ekbohm, 1983; Theodoru and Bowen, 1990).

In a study in which mass loss was measured for red maple, red spruce, and white pine individually and mixed together in litterbags, it was observed that mass loss in the first year was correlated with carbon loss but that after this mixed species decomposition was most rapid, indicating that a chemically heterogenous substrate can provide a more favourable microenvironment for decomposer heterotrophs (Rustad and Cronan, 1988).

Recalcitrant products

Lignin degradation has long been implicated as being a key factor in litter decay, but the effects of factors which influence lignin turnover and the interaction of these factors with other variables in forest ecosystems is poorly understood. It is well known that fungal species able to degrade lignin cannot utilize the energy stored within this molecule and therefore require other carbon sources for their growth and for lignin breakdown. It follows therefore, that a higher proportion of sugars and celluloses to lignin in litter favours more rapid litter turnover. In addition, the addition of carbohydrates to decomposing litter systems can increase the rate of lignin degradation (Connors et al. 1976; McClaugherty and Berg, 1987). It has also been reported that lignin or partly degraded lignin is able to chemically react with ammonium and phenolic groups to give rise to recalcitrant products which are able to repress fungal enzyme systems (Nommik and Vahtras, 1982; Stevenson, 1982).

A number of studies have demonstrated that once the process of lignin degradation has started that nitrogen has the effect of retarding lignin decomposition. Recent work has shown that lignin decomposition is actually depressed in litter that had high initial N concentration (Berg et al. 1982). Furthermore the same workers found that Scots pine and Norway spruce litter had higher lignin concentrations after nitrogen fertilization and the concentration of lignin was proportional to the concentration of nitrogen in the litter (Berg, 1986). It appears that there is an inhibitory effect of certain forms of nitrogen on the lignolytic enzyme systems of microbes (Keyser et al. 1978).

A high polyphenol content in leaves has been shown to slow down the decomposition of leaves by lowering the activity of microbes and enzymes due to their bacteriocidal properties (Tian et al. 1992; Staaf, 1987; Nicolai, 1988). Sivalpan et al. (1985) reported that a high plant N content resulted in increased N-mineralization, but the effect was lowered in the presence of high concentrations of polyphenols. Palm and Sanchez (1991) reported a similar effect of polyphenols on N-mineralization. Polyphenols are stored in cell vacuoles and are released at leaf senescence. They have a tanning effect on plant proteins and microbial enzymes resulting in complexes that are very resistant to microbial attack (Carlyle, 1986). The quantity and diversity of polyphenols in leaves is inversely proportional to site fertility. Calcium causes polyphenols to polymerize which renders them inactive and consequently the degree of tanning caused by a given concentration of polyphenols is greater on an acid than on a base-rich site (Davies, 1971).

Site Effects

A number of factors associated with a particular site may interact with biologically mediated litter decomposition processes, resulting in decay and mineralization patterns that are specific to that particular site. Soil physical and chemical characteristics such as bulk density, cation exchange capacity, acid/base buffering capacity and C/N ratio have been demonstrated to have a variety of effects on soil based microbial and faunal activities (Wolters and Joergensen 1991).

Douglas fir needle decomposition rates were significantly higher in litterbags placed on mat soils of the ectomycorrhizal fungi *Hysterangium setchellii* with more N, P, K, Mg, and B released and more Ca and Zn retained in litters decomposing on these soils than from adjacent non-mat soils. Furthermore microbial biomass was four times higher than in non-mat soils (Entry et al. 1991). Although a link between site characteristics and mycorrhiza was not demonstrated in this study, Björkman (1942) found that mycorrhizal frequency was negatively correlated with soil fertility of beech forests in southern Sweden. Numerous other studies have reported that fungal hyphae and other soil microbes concentrated in mat soils stimulate organic matter decomposition through saprophytic action and by providing a favourable environment for soil arthropods resulting in accelerated nutrient turnover (Ingham et al. 1985; Cromack et al. 1988).

Red maple litter incubated on an aspen dominated site disappeared at twice the rate at which the maple litter decomposed on its own native site. This difference in mass loss rate was found to be due to the presence of white-rot fungus only in the aspen stand, demonstrating that microorganisms can produce dramatically different rates of mass loss under similar environmental conditions (McClaugherty et al. 1985).

Microbial carbon turnover was investigated in six beech forest soils ranging in soil pH from 4.8 to 8.3. The results demonstrated that the edaphic microflota was strongly related to bulk density, exchangeable Ca, CEC and soil pH (Wolters and Joergensen 1991). It was evident from this study that increased soil acidity acted to shift the population structure of the microbial community so that the relatively small microflota in the more acidified soils had a less efficient level of carbon use. Consequently increased C availability in acid soils did not lead to increased production of microbial products.

The impact of earthworms on litter decomposition was studied in three beech forest stands that differed in soil pH, base saturation and clay content. Mass loss was found to be most rapid on the most base rich site even in 1mm mesh bags which excluded earthworms. The conditions on this site were more favourable for microbial and microfaunal decomposition than the other two less fertile sites (Staaf, 1987). Nutrient rich soils were shown to produce beech leaf litter with half the level of phenolics that sandstone sites produced, resulting in a quicker turnover of the leaves on these soils (Nicolai, 1988).

The level of decomposition of previously fallen litter can also have an impact on decay rates of freshly fallen litter (McClaugherty et al. 1985). Sugar maple and red maple litters were incubated along with indigenous litters in stands dominated by white oak, bigtooth aspen, white pine and hemlock. Overall decomposition of litter was not strongly affected by the soil environment (with the exception of red maple in aspen stands). In contrast, net nitrogen mineralization was significantly correlated with decomposition rates of the dominant native litter. Nitrogen mineralization in freshly fallen litter was negatively correlated with the amount of acid-insoluble substances remaining in native litter.

Soil C/N ratios have been implicated in the regulation of nitrogen release from decomposing litter. Sugar maple, ash and black locust litter incubated on both locust and hardwood sites showed no difference in rates of decomposition, but litters on the locust site all showed a significant increase in total nitrogen (Hirschfeld et al., 1984). The dates on which total N started decreasing was earlier for treatments on the hardwood sites, with locust leaves 'beginning N-loss first, but only locust leaves decomposing on the locust site displayed both immobilization and mineralization. It would appear that the more N available in the locust system resulted in more N being immobilized, whereas the lower C/N ratio of the locust litter resulted in accelerated N-mineralization.

The critical C/N ratio at which Scots pine needle litter released nitrogen was higher in a 120 year old pine forest stand relative to a recently clearcut site (Berg and Ekbohm, 1983), the authors of this study speculated that a higher limit for release of nitrogen acted to protect and regulate against too heavy losses of nitrogen from the clear cut area, indicating differences in the nitrogen statuses of the soil systems.

Soil Fauna

Although soil animals make only a small direct contribution towards litter decomposition and nutrient mineralization, they play an important role in affecting the quantity, community composition and activity of the soil microflora (Ineson et al. 1982). The effects of grazing by the soil fauna on microbial metabolism gives different results depending on the interaction studied, the population density of soil animals on the substrate and the particular manipulation that the experimental system undergoes. It is generally concluded that soil animals by their feeding activity are able to expose more surfaces on decomposing litter to the soil microflora.

A microcosm study demonstrated that fungal standing crop incubated on oak litter was greater in the presence of small numbers of collembola relative to litter lacking collembola, yet at higher grazing intensities, the fungal standing crop fell markedly. Significant increases in the leaching of ammonium, nitrate and Ca occurred as a result of animal grazing, but K and Na losses from the litter were unaffected (Incson et al. 1982) Similar results were found when birch leaf litter and raw humus was incubated in the presence of a community of soil animals, total-N, ammonium-N liberation and mass loss of litter and humus was greatly enhanced in the presence of the soil fauna (Huhta et al. 1988). Oak and beech leaves incubated with and without a mix of soil animals showed significant increases in ammonium, calcium, potassium and sodium leaching (Anderson et al. 1983), these authors suggested that animal grazing not only reduced fungal biomass, but it also enhanced bacterial growth due to passage through the gut of the soil animals resulting in a higher proportion of ammonifiers. In a series of experiments using mixed desert shrubs it was demonstrated that the particular assemblage of soil animals could have very different end results on litter decomposition (Santos et al. 1981; Santos and Whitford, 1981). In one case it was shown that microarthropods inoculated litter with fungal spores, grazed on the fungi and preyed on free-living microbivorous nematodes.

Many studies have shown that the presence of soil animals on litter can result in retention of some elements in the decomposing litter. The presence of the collembola *Onchyiurus subtenuis* on sterile aspen leaf litter led to a decrease in the leachability of nitrate (Visser et al. 1981). In this study it appeared that the collembola introduced microorganisms onto the otherwise sterile leaves. All the collembola that were tested were shown to be carrying at least one type of microorganism. Similar cases of N immobilization in the presence of soil animals have been demonstrated for Scots pine needles (Verhoef and Brussaard, 1990).

In a study of the effects of simulated acid rain on litter decomposition in a calcareous soil the presence of mesofauna significantly reduced the ability of the acid rain to inhibit C mineralization from beech litter. The ash content of the litterbags indicated that this was due to the transport of base rich mineral soil into the litter (Wolters, 1991a).

In another study, the effects of simulated acid rain on soil biotic processes was studied in a beech forest on moder soil (Wolters, 1991b). In limed soils, the negative effects c. acid rain were less pronounced than in natural soil, but in limed soil the litter colonizing microflora were not able to respond rapidly after termination of the acid rain regime in contrast to natural soil. In contrast to it's effect in natural soils the collembolan *Isotoma tigrina* did not accelerate the recovery of the microflora in limed soils. It was concluded that the reduction in the bacterial biomass in the limed soil was due to a modification of microbial growth rather than suppression by grazing.

Effect of Fertilization on Litter Decomposition

and Nutrient release

Loss of base cations from forest ecosystems has been shown to be an important consequence of soil acidification, and, at the same time, cation deficiency has been implicated as a contributor to forest decline. The general perception that forest systems are nitrogen limited combined with nutrient deficiencies associated with cation depletion have led to increased interest in the impact of inorganic fertilizer on forest ecosystems.

Fertilization studies have been difficult to interpret because of contradictory results, with N-fertilizers increasing or decreasing rates of litter decay depending on the form of N applied. Excessive addition of one nutrient has been implicated in inducing shortage of others, whereas other forms of fertilizer are thought to result in toxicity to the soil microflora (Titus and Malcolm 1987).

Shepard and Mitchell (1990) found that red pine consistently responded to K fertilization on a sandy, K-deficient, outwash soil, even 40 years after fertilization. The same plots did not respond to fertilization with N, P, Ca, or Mg. Elemental contents of N, K, Ca, Mg, Na and S were substantially higher in treated plots than unfertilized plots. Maintenance of increased K resulted from increased K associated with the foliage in fertilized plots, with foliage alone accounting for 53% of additional K relative to the control plot. Furthermore, fluxes of K in litterfall were greater in treated plots than in the control.

Application, over a period of three years, of an N:P:K fertilizer to a 12-year old pine plantation increased litterfall and nutrient concentration in litter, but litter decomposition was unaffected by fertilization (Theodorou and Bowen, 1990). Both treatments exhibited initial N retention in the litter, but after 72 months fertilized litter began to mineralize N. It was concluded that a critical N concentration was reached earlier in fertilized than unfertilized litter. In addition, increased N in litter, resulting from increased N availability to the tree, decreases the polyphenol and organic-acid content of litter and thus facilitates N mineralization (Vitousek et al., 1982; Gosz, 1984).

The influence of N:P:K fertilizer on decomposition of litter on a clearfelled Sitka spruce stand was followed for two years (Titus and Malcolm, 1987). Fertilization of litter significantly reduced decay rates for the first year. Nitrogen concentration increased for the two year period indicating that nitrogen was limiting for microbial activity in this system. Calcium concentration of litter increased with fertilization and remained constant, the Ca content on both plots decreasing at the same rate as weight loss indicating that this element was bound to needles so that it required litter breakdown by decomposers for release.

Application of ammonium nitrate fertilizer to different coniferous forest systems resulted in decreased microbial biomass and reduced soil respiration rates. The decrease observed three months after fertilization was still evident after three years (Söderström et al., 1983). These authors suggested that inorganic N may have repressed microbial lignolytic enzymes. Gill and Lavender (1983) found that urea and gypsum-coated urea greatly stimulated rates of western hemlock litter decomposition. In contrast, calcium nitrate retarded decomposition rates during the first 6 months, but after 12 months it had little impact relative to control plots. Although it was not demonstrated, the authors speculated that the sudden addition of nitrate may have adversely affected the indigenous microorgansims which, because of low amounts of naturally occurring nitrate, probably lacked nitrate reductase

Nutrient cycling in mature stands of lodgepole pine, white spruce and Engelmann spruce-subalpine fir was monitored for four years after fertilization with ammonium phosphate sulphate (Prescott et al. 1992). Decomposition and nutrient release from the leaves of the forb *Epilobium angustifolium*, was more rapid in leaves harvested from, or incubated on, fertilized plots. The increase in decomposition and N mineralization due to fertilization was observed for only the first year after fertilizer application. After 4 years mineralizable N in the forest floor was higher on fertilized plots at the most N-rich sites only. These results suggest that long term improvements in nutrient availability through cycling of added nutrients may be possible, but the amount added should be sufficient to overcome the immobilization capacity of the site

Conclusions

Fertilization of forest ecosystems as a method of alleviating nutrient deficiencies has produced contradictory results. Release of nutrients from litter appears to be governed by two mechanisms. The first is the physico-chemical nature of the litter. The lignin content of litter determines to a large extent the degree to which chemically bound elements will be released from decomposing litter. The second mechanism is the nutrient demands of soil heterotrophs. Microbes, which are responsible for litter decay may mineralize or immobilize a particular element depending on their own metabolic requirements.

In general, those factors that favour microbial activity should enhance the cycling of nutrients in soil systems. Inorganic fertilizers must therefore interact with factors such as soil bulk density, cation exchange capacity, acid buffering abilities and soil C/element ratios, as well as biotic factors such as soil faunal activity and mycorrhizal distribution. Soil fauna in particular appear to be sensitive to nutrient supplies in decaying litter. Although their direct contribution to mass loss is small, they can have a profound effect on microbial population structure and activity.

The effects of mixed nutrient and single nutrient fertilization have proved to be long lasting, with effects detected 40 years after application in one case. The addition of nutrients has led to complex interactions with both biotic and abiotic systems in forest soils. Fertilization has been shown to improve litter quality in many cases, increasing nutrient content and reducing the effect of recalcitrant products, but, enhanced litter quality has not always led to long term increases in rates of litter decomposition. Nitrogen fertilization has, in some cases, been associated with reductions in litter decay rates, and repression of microbial activity has usually been implicated in this effect. Results of fertilization of forest ecosysytems are difficult to interpret because of the many pathways and processes that take place in the soil.

References

- Anderson, J.M., Ineson, P., and Huish, S.A. 1983. Nitrogen and cation mobilization by soil fauna feeding on leaf litter and soil organic matter from deciduous woodlands. Soil Biology and Biochemistry 15:463-467.
- Berg, B., Wessen, B. and Ekbohm, G. 1982. Nitrogen level and lignin decomposition in Scots pine needle litter. Oikos 38:291-296.
- Berg, B. and Ekbohm, G. 1983. Nitrogen immobilization in decomposing needle litter at variable carbon:nitrogen ratios. Ecology 64:63-67.
- Berg, B., Staaf, H. and Wessen, B. 1987. Decomposition and nutrient release in needle litter from from nitrogen fertilized scots pine stands. Scandinavian Journal of Forest Research 2:399-415.
- Berg, B. and Staaf, H. 1981. Leaching, accumulation and release of nitrogen in decomposing forest litter. In: F.E. Clarl: and T. Rosswall (Editors), Terrestrial nitrogen cycles. Processes, ecosystem strategies and management impacts. Ecological Bulletin Stockholm 33:373-390.

- Berg, B. 1986. Nutrient release from litter and humus in coniferous forest soils-a mini review. Scandinavian Journal of Forestry Research 1:359-369.
- Bjorkman, E. 1942. Uber die bedingungen der mykorrhizabildung bei kiefer und fichte Symb. Bot. Upsalla 6: 191pp
- Carlyle, J.C. 1986. Nitrogen cycling in forested ecosystems. Forestry Abstracts 47:307-336.
- Connors, W.L., Kirk, K., and Zeikus, J. 1976. Requirement for growth substrate during lignin decomposition. Applied and Environmental Microbiology 32:192-194.
- Cromack, K., Fichter, B., Moldenke, A.M. and Entry, J.A. 1988. Interactions between soil animals and fungal mats. Agriculture, Ecosystems and Environment 24:161-168.
- Davies, R.I. 1971. Relation of polyphenols to decomposition of organic matter and pedogenic process. Soil Science 111:80-85.

- Entry, J.A., Rose, C.L. and Cromack, K. 1991. Litter decomposition and nutrient release in Ectomycorrhizal mat soils of a Douglas fir ecosystem. Soil Biology and Biochemistry 23:285-290.
- Gill, R.S. and Lavender, D.P. 1983. Litter decomposition in coastal hemlock stands: impact of nitrogen fertilizers on decay rates. Canadian Journal of Forest Research 13:116-121.
- Gosz, J.R. 1984. Biological factors influencing nutrient supply in forest soils. In: G.D. Bowen and E.K.S. Nambiar (Editors), Nutrition of Plantation forests. Academic Press London. pp119-146
- Gosz, J.R., Likens, G.E., and Bormann, F.H. 1973. Nutrient release from decomposing leaf and branch litter in the Hubbard brook forest., New-Hampshire. Ecological Monographs 43:173-191.
- Harris, M.M. and Riha, S.J. 1991. Carbon and nitrogen dynamics in forest floor during short term laboratory incubations. Soil Biology and Biochemistry 23:1035-1041.

- Hirschfeld, J.R., Finn, T.J. and Patterson, W.A. 1984. Effects of *Robinia pseudoacacia* on leaf litter decomposition and nitrogen mineralization in a northern hardwood stand. Canadian Journal of Forest Research 14:201-205.
- Huhta, V., Setälä, H., and Haimi, J. 1988. Leaching of N and C from birch leaf litter and raw humus with special emphasis on the influence of soil fauna. Soil Biology and Biochemistry 20:875-878.
- Ineson, P., Leonard, M.A., and Anderson, J.M. 1982. Effect of collembolan grazing upon nitrogen and cation leaching from decomposing leaf litter. Soil Biology and Biochemistry. 14:601-605.
- Ingham, R.E., Trofymow, J.A., Ingham, E.R. and Coleman, D.C. 1985. Interactions of bacteria, fungi and their nematode grazers: effects on nutrient cycling and plant growth. Ecological monographs 55:119-140.
- Keyser, P., Kirk, T.K., and Zeikus, I.G. 1978. Lignolytic enzyme of *P. chrysosporium*. Journal of Bactericiogy 135:790-797.
- McClaugherty, C.A., Pastor, J., Aber, J.D., and Melillo, J.M. 1985. Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. Ecology 66:266-275.



- McClaugherty, C. and Berg, B. 1987. Cellulose, lignin and nitrogen levels as rate regulating factors in forest litter decomposition. Pedobiologia 30:101-112.
- Nicolai, V. 1988. Phenolic and mineral contents of leaves influence decomposition in European forest ecosystems. Oecologia 75:575-579.
- Nommik, H. and Vahtras, K. 1982. Retention and fixation of ammonium and ammonia in soils. Agronomy 22:123-166.
- Palm, C.A. and Sanchez, P.A. 1991. Nitrogen release from the leaves of some tropical legumes as affected by their lignin and polyphenolic contents. Soil Biology and Biochemistry 23:83-88.
- Prescott, C.E., Corbin, J.P. and Parkinson, D. 1992. Immobilization and availability of N and P in the forest floors of fertilized Rocky Mountain coniferous forests. Plant and Soil 143:1-10.
- Reuss, J.O. and Johnson, D.W. 1986. Acid deposition and the acidification of soils and waters. Springer-Verlag. New York.
- Rustad, L.E., and Cronan, C.S. 1988. Element loss and retention during litter decay in a red spruce stand in Maine. Canadian Journal of Forestry Research 18:947-953.
- Santos, P.F., Phillips, J., and Whitford, W.G. 1981. The role of mites and nematodes in early stages of buried litter decomposition in a desert. Ecology 62:664-669.
- Santos, P.E. and Whitford, W.G. 1981. The effects of microarthropods on litter decomposition in a Chihuahuan desert ecosystem. Ecology 62:654-663.
- Schaefer, M. 1990. The soil fauna of a beech forest on limestone. Oecologia 82:128-136.
- Seastedt, T.R. 1984. The role of microarthropods in decomposition and mineralization processes. Annual Review of Entomology 29:25-46.
- Shepard, J.P. and Mitchell, J.M. 1990. Nutrient cycling in a red pine plantation: Thirtynine years after potassium fertilization. Soil Science Society of America Journal 54:1433-1440.
- Sivapalan, K., Fernando, V. and Thenabadu, M. 1985. N-mineralization in polyphenolrich residues and their effects on nitrification of applied ammonium sulphate. Soil Biology and Biochemistry 17:547-551.

Söderström, B., Bååth, E. and Lundgren, B. 1983. Decrease in soil microbial activity and biomass owing to nitrogen amendments. Canadian Journal of Microbiology 29:1500-1506.

Stevens, F.J. 1982. Organic forms of soil nitrogen. Agronomy 22:67-114.

- Staaf, H. 1987. Foliage litter turnover and earthworm populations in three beech forests. Oecologia 72:58-64.
- Theodoru, C. and Bowen, G.D. 1990. Effects of fertilizer on litterfall and N and P release from decomposing litter in a *Pinus radiata* plantation. Forest Ecology and Management 32:87-102.
- Tian, G., Kang, B.T. and Brussaard, L. 1992. Effects of chemical composition on N, Ca and Mg release during incubation of leaves from selected agroforestry and fallow plant species. Biogeochemistry 16:103-119.
- Titus, B.D. and Malcolm, D.C. 1987. The effect of fertilization on litter decomposition in clearfelled spruce stands. Plant and Soil 100:297-322.
- Verhoef, H.A. and Brussaard, L. 1990. Decomposition and N-mineralization in natural and agroecosystems: The contribution of soil animals. Biogeochemistry 11:175-211.



- Vitousek, P., Gosz, J.R., Grier, C.C. Melillo, J,M. and Reiners, W.A. 1982. A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems 52:155-177.
- Visser, S., Whittaker, J.B., and Parkinson, D. 1981. Effects of collembolan grazing on nutrient release and respiration of a leaf litter inhabiting fungus. Soil Biology and Biochemistry 13:215-218.
- Wolters, V. 1991 a. Effects of acid rain on leaf litter decomposition in a beech forest on calcareous soil. Biology and Fertility of Soils 11:151-156.
- Wolters, V. 1991 b. Biological processes in two beech forest soils treated with simulated acid rain. Soil Biology and Biochemistry 23:381-390.
- Wolters, V., and Joergensen, R.G. 1991. Microbial carbon turnover in beech forest soils at different stages of acidification. Soil Biology and Biochemistry 23:897-902.

CHAPTER II

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EFFECTS OF BASE CATION FERTILIZATION ON LITTER DECOMPOSITION IN A SUGAR MAPLE FOREST

Abstract

Application of base cation fertilizers has been shown to increase tree growth and vigour in declining sugar maple stands in southern Quebec but little is known about the effects of such fertilizers on litter quality or decomposition. Sugar maple foliage litters from fertilized and unfertilized plots on a base-poor site and from a naturally base-rich site were incubated in litterbags of 1 and 3 mm mesh sizes on fertilized and unfertilized plots at the base-poor site. Mass loss of unfertilized litter was slower in fertilized than in unfertilized plots, suggesting a negative effect of fertilization on the decomposer community. Faster mass loss of fertilized than unfertilized litter incubated in the same plot indicated that changes in litter quality brought about by fertilization enhanced decomposition. Mass loss of fertilized litter on fertilized plots did not differ from that of unfertilized litter on control plots, indicating that although decomposition processes are affected by fertilization the overall effect on decomposition is negligible. Mass loss was significantly, but only slightly, higher in large mesh than in small mesh bags indicating that larger soil fauna play a limited role in litter decomposition in this forest.



Introduction

Symptoms of forest decline have been observed in Quebec sugar maple forests for more than a decade (Gagnon and Roy 1989). Various causes have been suggested for the decline but none have been definitively demonstrated (Hendershot and Jones 1989). Much of the research into the causes of decline has concluded that disruption of tree nutrition is involved with declining stands showing nutrient deficiencies, mainly in K and Mg (Bernier and Brazeau 1988 a,b). Management of declining stands has focused on fertilization with base cations. Applications of K have been shown to improve foliar nutrient status and growth rates (Ouimet and Fortin 1992), and fertilization with Ca and Mg has improved tree vigour (Hendershot 1991).

Although several studies have examined the effects of base cation fertilization on foliar nutrient concentrations and tree growth (Hendershot 1991, Ouimet and Fortin 1992, Côté et al. 1993), none has examined the effects of these fertilizers on litter decomposition. Numerous studies, however, comparing naturally base-rich and base-peor ecosystems, have indicated that cation availability plays an important role in controlling nutrient dynamics in the litterfall/decomposition/mineralization pathway of forest ecosystems (Boerner 1984). Site acidification and loss of base cations have been implicated in shifting decomposition from efficient bacteria- dominated pathways to less efficient pathways dominated by fungi (Wolters and Joergensen 1991). High contents of polyphenols in litter in base-poor sites increase complexing of proteins, thereby reducing palatability of litter to decomposers (Carlyle 1986, Nicolai 1988). Low populations of large soil fauna (millipedes, isopods, earthworms) on base-poor sites have been attributed to low cation availability and poor acid/base buffering (Nicolai 1988, Staaf 1987).

On the basis of these studies we hypothesized that base cation enrichment of sugar maple stands on base-poor sites would increase rates of foliar litter decomposition in two ways; by increasing cation concentrations and thus improving litter quality and palatability, and by altering forest floor nutrient or buffering conditions thereby increasing populations or activities of soil fauna. The specific objectives of this study were 1) to determine the effect of base cation fertilization on the chemical quality of sugar maple foliage litter and resultant effects on decomposition rate; 2) to determine the effects of base cation fertilization on decomposition that are mediated by soil conditions (eg. soil fertility, decomposer community) and independent of litter quality; and 3) to determine how the presence of large soil fauna affects the response of decomposition rate to fertilizer-induced changes in litter quality and site fertility.

Materials and Methods

Study site

The study site was located at the Station de Biologie de l'Université de Montréal near Saint-Hippolyte, in the Laurentian Highlands 80 km north of Montreal. The soils were acidic Orthic Humo-Ferric podzols developed on bouldery glacial till of sandy loam texture derived from local andositic bedrock. Soils were generally well to imperfectly drained. The LF-horizon was 3-7cm deep and developed as a moder.



The forest was dominated by sugar maple (Acer saccharum Marsh.) with some red maple (Acer rubrum L.) paper birch (Betula papyrifera Marsh.), large toothed and trembling aspen (Populus grandidentata Michx. and P. tremuloides Michx.) and American beech (Fagus grandifolia Ehrh.), and was initiated by fire about 70 years previous.

Six plots (40x40m) were established on the site. In early spring 1989, three randomly selected plots were fertilized with 500 kg/ha K_2SO_4 , 250 kg/ha calcite, 250 kg/ha dolomitic limestone. These levels of fertilization have been shown to increase foliar concentrations of K, Ca and Mg on sugar maple sites (Hendershot and Jones 1989).

A second site, located at the Morgan Arboretum on the island of Montreal in the upper St. Lawrence region, was used for bulk collection of litter. This site was dominated by sugar maple with scattered white ash (*Fraxinus americana* L.). Soils were moderately acid with a thin litter layer and well developed mull humus. Foliage litter from this mull site was expected to have higher levels of nutrients and therefore to be of higher quality than Saint-Hippolyte litter. Base rich Morgan Arboretum litter was included in the study for comparison with fertilized Saint-Hippolyte that was expected to be more base rich than the unfertilized Saint-Hippolyte litter.

Field Methods

Sugar maple foliar litter was collected using large polyurethane net traps during the autumn of 1989 from fertilized and unfertilized plots at Saint-Hippolyte and from the Morgan Arboretum site. Air dried litter (2.00g of original tissue) was sewn into nylon bags of 1 and 3 mm mesh sizes. Subsamples of litter were retained for correction to oven dry weights. Litterbags were laid out in the litter layer of each plot at Saint-Hippolyte in sets of 6 bags in each of 7 locations per plot to allow for the collection of 7 replicates of each mesh size on 6 sampling dates throughout the following growing season. Our intent was to install the bags in the field in the autumn of 1989 but early snowfall made it necessary to delay installation of bags in the field until late April of 1990. Sampling took place on May 29, June 12, July 22, August 21, September 20, and November 2 1990, respectively 30, 44, 84, 114, 144 and 187 days after placement.

Laboratory Analysis

Collected litterbags were opened and litter was sorted, removing any contaminants such as soil, insects and non-litter plant parts. Sorted litter was oven dried for 24 hours at 65°C and then weighed. Ground samples of each initial litter were digested in H_2O_2/H_2SO_4 (Allen 1989) and digests were analyzed for N and P using a Technicon autoanalyser, and K, Ca and Mg by atomic absorption spectophotometry.

Statistical analysis

The data was analyzed as a completely randomized block design on Statistical Analysis Systems (SAS) (SAS Institute Inc. 1984). Tests for homogeneity of variance by Bartlett's test indicated heterogeneity and a logarithmic transformation of all mass loss data was performed which improved homogeneity but did not eliminate the problem. However the analysis of variance used to determine significant treatment effects is robust with respect to the assumption of homogeneity of variance when sample size is large, as in this case (Winer 1971). The data were analyzed as a four way analysis of variance with date, mesh, litter and plot fertilizer treatment as main effects. Least significant difference was used to determine differences between means. Litter nutrient concentration data were analysed by onc-way ANOVA followed by calculation of Least Significant Difference (LSD).

Results and Discussion

The three sugar maple foliage litters used in this study differed significantly in nutrient concentrations (Table 1). Fertilization at the Saint-Hippolyte site resulted in litter with significantly higher concentrations of K and Ca but unchanged levels of the other nutrients. Relative to the Saint-Hippolyte litters, the Arboretum litter had significantly higher N, Ca and Mg but lower K concentrations. On the basis of these chemical characteristics, we expected to find significant differences in decomposition between the litters, and in particular between the Saint-Hippolyte and Arboretum litters because of the large difference in nutrient concentration between them.

Fertilization was expected to result in a litter with chemical quality similar to that of litter from the base-rich site but, although the fertilized litter was higher in K and Ca than unfertilized litter, it remained chemically distinct from the Arboretum litter.

A weakness of this study, which introduces uncertainty as to how well our results reflect field conditions, is that litter samples were not exposed in the field during the late fall and winter. Biological decomposition is likely to have been reduced by low temperature during this period but weathering due to freeze/thaw cycles and leaching may have been higher than during the period following bag placement in the early spring. We have no data on over-winter decomposition in this system and consequently it is an assumption of this study that, although absolute mass loss was probably altered, treatment effects were unaffected by the timing of bag placement.

In presenting and discussing the results, it should be noted that there are two separate fertilizer effects. Fertilizer application to plots is designated as the fertilizer treatment or site fertility effect whereas differences between litter collected in fertilized and unfertilized plots and Morgan Arboretum is designated as the litter effect or litter quality. The analysis of variance (Table 2) demonstrated significant (p<0.05) interactions involving date, specifically a three-way fertilizer*date*mesh interaction and two-way date*litter and date*mesh interactions. Date as a main effect was highly significant. The strong date effect was expected since all litters lost a large proportion of their mass over time. The date*litter interaction indicated that the pattern of mass loss differed among the three litters through the growing season whereas date*mesh size interaction indicated that mass loss patterns among mesh sizes did not differ consistently over time.

The analysis also indicated a significant three-way fertilizer*mesh*litter and two-way fertilizer*mesh interactions, demonstrating complex behaviour of litter with respect to these factors. Interpretation of these results requires examination of the effects of the different factors in simple combinations, as presented below.

Site Fertilization - Mesh Size - Date Interactions

Mass loss of unfertilized Saint-Hippolyte litter incubated in small mesh bags was significantly higher in unfertilized than fertilized plots on dates 114 and 144 (Figure 1a)

but prior to day 84 there was no difference in decomposition rates between the two fertilization treatments. These site fertility differences apparently disappeared by the end of the growing season (187 days). A similar pattern of site fertilization effects was observed for Arboretum litter in small mesh bags with mass loss significantly greater in unfertilized plots on dates 114 and 144 (data not shown). In contrast, however, there was no consistent fertilization effect on fertilized litter in small mesh bags (Figure 1b). Site fertilization also reduced decomposition rates of unfertilized litter in large mesh bags (Figure 2a). There was no effect of site fertilization on mass loss of fertilized litter in large mesh bags (Figure 2b).

Site fertilization affected the litters in both mesh sizes in the same way, that is, site fertilization reduced decomposition rates of unfertilized and Arboretum litters late in the season yet did not affect fertilized litter. A comparison of Figures 1a and 2a, however, suggests that the site fertilization effect was more pronounced in small mesh than in large mesh bags.

This was also observed with Arboretum litter where the site fertility effect was significant on dates 114 and 144 for small mesh bags, but was not significant on any date for large mesh bags (data not shown). These results suggest that site fertilization has the potential to reduce litter decomposition processes mediated by both small and large organisms. The negative fertilization effect is, however, more pronounced in the absence of larger decomposer organisms (small-mesh bags) than when they are present. The negative site fertilization effect was more evident on unfertilized and Arboretum litter than fertilized litter.

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Our data are insufficient to determine the mechanisms that caused the observed negative effect of site fertilization on litter decomposition but at least two are possible. Fertilizer application may have increased soil fauna populations, thereby increasing microbial grazing (Seastedt 1984, Elkins and Whitford 1982, Santos et al. 1981) and decreasing the activity of the primary microbial decomposers. Alternatively, fertilization may have directly affected the population structure of the soil microbial community in a way that reduced normal decomposition. Results from nitrogen fertilization studies have shown that microbial decomposition of litter can be either increased or decreased depending on the the form of N-fertilizer added (Gill and Lavender 1983, Titus and Malcolm 1987, Prescott et al. 1992), and that these site fertilization effects can persist for as long as 3 years after fertilizer addition (Söderström et al. 1983).

Litter Quality - Date Interactions

Mass loss of fertilized litter in large mesh bags was significantly greater than that of unfertilized litter on days 44, 84 and 187 (Fig. 3a). Mass loss of Arboretum litter initially was not significantly different from that of fertilized litter but it resembled unfertilized litter more closely from date 44 onwards. This litter effect in large mesh bags was also observed for litters incubated on unfertilized plots, where mass loss of fertilized litter was significantly greater than that of unfertilized and Arboretum litters on days 30 and 44 (data not shown). The pattern of litter decomposition was different in small mesh bags (Fig. 3b), with all litters showing similar mass loss early in the season but differing significantly on dates 114 and 144. Fertilized litter again had higher mass loss than



unfertilized litter, while Arboretum litter closely resembled unfertilized litter. The decomposition rate of the fertilized litter appeared to be relatively constant from day 30 to 144, but for both Arboretum and unfertilized litters the rate decreased after day 84 implying that cation enrichment of litter delays the reduction in late season decomposition.

These results indicate that litter quality had a similar effect on decomposition in the presence and absence of larger decomposer organisms but that the presence of larger organisms changed the temporal pattern of decomposition. When only smaller organisms participated in decomposition, all litters decomposed at the same rate until mid-season after which fertilized litter decomposed faster than unfertilized litters, although these litter quality differences apparently disappeared by the end of the season. When larger organisms were present, however, fertilized litter decomposed faster at the beginning of the growing season, this mesh size - litter interaction implies that soil macrofauna perceived, or allowed the smaller organisms alone the litters were qualitatively similar until day 84 when 35% of the initial litter mass had been lost. This contention is supported by mass loss data of fertilized litter incubated in bags of different mesh sizes (Figs. 1b, 2b broken lines), mass loss was significantly greater in large mesh bags on dates 30, 44, and 84.

One mechanism that may have caused this effect is that the activity of larger soil fauna in tragmenting litter allowed microbes access to litter components, such as internal tissues, that differed in quantity or susceptibility to decomposition or leaching among the litters. Various studies have shown that the activity of soil microbes and mineralization of organic matter is enhanced by the presence of a diverse soil animal community (Setälä et al. 1988, Anderson 1983). This is also consistent with the relatively high content of potassium, a highly leachable component in fertilized litter. Several studies have shown that elements such as potassium, magnesium and sulphur may be rapidly leached or mineralized from decomposing litter, while calcium, nitrogen, and phosphorus exhibit slower rates of release that are closely related to litter mass loss (Gosz et al. 1973, Berg and Staaf 1987, Rustad and Cronan 1988, Boerner 1984). Potassium content represents a very small proportion of total mass litter so that degradation or leaching of other components must have been involved to account for the observed differences in mass loss.

Main Effects

Litter type as a main effect was highly significant (Table 2). This strong litter effect was expected since fertilization at the Saint-Hippolyte site resulted in a significant increase in concentrations of some nutrients, while Arboretum litter had levels of most nutrients, including N, significantly higher than those of the Sainte-Hippolyte litters (Table 1). The high degree of similarity in decomposition rates between the Morgan Arboretum and unfertilized Saint-Hippolyte litters was, however, unexpected given the differences in chemistry between these litters. Physically, the Arboretum litter could be easily distinguished from the others by its thinner blade and softer consistence wherea., chemically it had higher concentrations of all nutrients except K and P (Table 1). The similarity in mass loss among litters despite apparently large qualitative differences raises



questions about magnitude of quality difference required to result in differences in mass loss between litters from the same species, and whether litters from the same species always decompose at similar rates in the same environment.

Mesh size as a main effect was also highly significant (Table 2). Litters incubated in large mesh bags had significantly, but only slightly, higher rates of decomposition than litters in small mesh bags (Table 2). The results indicate that the contribution of soil fauna to decomposition at the site was small. This minor effect of large soil fauna on decomposition was, however, clearly influenced by fertilization.

The lack of a significant main effect of fertilization on decomposition (Table 2) is described by the comparison of mass loss of fertilized litter on fertilized plots with that of unfertilized litter on unfertilized plots (Fig. 4a,b). The data for both large and small mesh bags shows that there was no difference in mass loss rates between the two litters on their natural site. This implies that although cation enrichment enhanced litter quality, the effect was offset by the negative impact of fertilization on late season decomposition. Comparable studies of base cation fertilization have not been reported but numerous studies on the effects of N fertilization on decomposition have shown contradictory results concerning mass loss rates, microbial activity and nutrient mineralization (Prescott et al. 1992, Gill and Lavender 1983, Titus and Malcom 1987, Söderström et al. 1983). Furthermore, the results of studies on the effects of various soil animals on litter decomposition have shown that soil animals can both enhance and inhibit microbial activity while the feeding activity of soil animals can greatly alter the characteristics of soil microbiology, for instance by changing the ratio of bacteria to fungi (Anderson 1983).

In light of these studies it is perhaps not surprising that both negative and positive interactions were observed in the current study.

In conclusion, this study has shown that base cation fertilization of a sugar maple foresty may affect decomposition in several respects. Fertilization effects on the site lead to a short term reduction in decomposition whereas cation enrichment of litter can increase decomposition. The effects appear to be more pronounced in the absence of larger fauna than when these organisms are present. The combined result of these effects, however, is that base cation fertilization does not change litter mass loss rate. Had we taken a logistically simpler approach to this study and measured only mass loss of litter decomposing in the plot in which it was produced, we would have concluded that fertilization had no effect on decomposition. This study has demonstrated, however, that fertilization had a complex influence on decomposition involving an interaction of both positive and negative effects.

References

- Allen, S.E. 1989. Analysis of vegetation and other organic constituents. In: S.E. Allen (Editor), Chemical Analysis of Ecological Materials. Blackwell Scientific, Oxford. pp.160-200.
- Anderson, J. 1983. Life in the soil is a ferment of littler rotters. New Scientist 100:29-34.
- Berg, B., and Staaf, H. 1987. Release of nutrients from decomposing white birch leaves and Scots pine needle litter. Pedobiologia 30:55-63.
- Bernier, B., and Brazeau, M. 1988. Foliar nutrient status in relation to sugar maple dieback and decline in the Quebec Appalachians. Canadian Journal of Forestry Research 18:754-761.
- Bernier, B., and Brazeau, M. 1988. Nutrient deficiency symptoms associated with sugar maple dieback and decline in the Quebec Appalachians. Canadian Journal of Forestry Research 18:762-767.
- Boerner, R.E.J. 1984. Foliar nutrient dynamics and nutrient use efficiency of four deciduous tree species in relation to site fertility. Journal of Applied Ecology 21:1029-1040.

- Carlyle, J.C. 1986. Nitrogen cycling in forested ecosystems. Forestry Abstracts 47:307-336.
- Côté, B., Hendershot, W.H. and O'Halloran, I.P. 1993. Response of declining sugar maple to seven types of fertilization in southern Quebec: growth and nutrient status. In: Huettl and Dombois (Editors), Proceedings of the Symposium on Forest Decline in the Atlantic and Pacific Region. Hilo, Hawaii.pp.162-174.
- Elkins, N.Z., and Whitford, W.G. 1982. The role of microarthropods and nematodes in decomposition in semi-arid ecosystems. Occologia 55:303-310.
- Gagnon, G. and Roy, G. 1989. Etat du dépérissement dans les forets au Québec. In Atelier sur le dépérissement des érablieres. Ministère de l'Agriculture, des Pêcheries et de l'Alimentation du Québec. pp. 14-17.
- Gill, R.S. and Lavender, D.P. 1983. Litter decomposition in coastal hemlock stands: impact of nitrogen fertilizers on decay rates. Canadian Journal of Forest Research 13:116-121.

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- Gosz, J.R., Likens, G.E., and Bormann, F.H. 1973. Nutrient release from decomposing leaf and branch litter in the Hubbard brook forest., New-Hampshire. Ecological Monographs 43:173-191.
- Hendershot, W.H. 1991. Fertilization of sugar maple showing dieback symptoms in the Quebcc Appalachians, Canadaian Fertilizer Research 27:63-70.
- Hendershot, W.H., and Jones, A.R. 1989. Maple decline in Quebec: A discussion of possible causes and the use of fertilizers to limit damage. The Forestry Chronicle 65:280-287.
- Nicolai, V. 1988. Phenolic and mineral contents of leaves influence decomposition in European forest ecosystems. Oecologia 75:575-579.
- Ouimet, R. and Fortin, J.-M. 1992. Growth and foliar nutrient status of sugar maple: incidence of forest decline and reaction to fertilization. Canadian Journal of forest Research 22:699-706.
- Prescott, C.E., Corbin, J.P. and Parkinson, D. 1992. Immobilization and availability of N and P in the forest floors of fertilized Rocky Mountain coniferous forests. Plant and Soil 143:1-10.

Rystad, L.E., and Cronan, C.S. 1988. Element loss and retention during litter decay in a red spruce stand in Maine. Canadian Journal of Forestry Research 18:947-953.

SAS. 1984. SAS/ETS Users Guide 5th ed. SAS Institute Inc. Cary, North Carolina.

- Santos, P.F., Phillips, J., and Whitford, W.G. 1981. The role of mites and nematodes in early stages of buried litter decomposition in a desert. Ecology 62:664-669.
- Seastedt, T.R. 1984. The role of microarthropods in decomposition and mineralization processes. Annual Review of Entomology 29:25-46.
- Setälä, H., Haimi, J. and Hunta, V. 1988. A microcosm study on the respiration and weight loss in birch litter and raw humus as influenced by soil fauna. Biology and Fertility of Soils 5:282-287.
- Söderström, B., Bååth, E. and Lundgren, B. 1983. Decrease in soil microbial activity and biomass owing to nitrogen amendments. Canadian Journal of Microbiology 29:1500-1506.
- Staaf, H. 1987. Foliage litter turnover and earthworm populations in three beech forests. Oecologia 72:58-64.

- Titus, B.D. and Malcolm, D.C. 1987. The effect of fertilization on litter decomposition in clearfelled spruce stands. Plant and Soil 100:297-322.
- Winer, B.J. 1971. Statistical Principles in Experimental Design. 2nd ed. McGraw-Hill. New York.
- Wolters, V., and Joergensen, R.G. 1991. Microbial carbon turnover in beech forest soils at different stages of acidification. Soil Biology and Biochemistry 23:897-902.

Table 1. Nutrient concentrations of sugar maple litter from Saint-Hippolyte fertilized and unfertilized plots and the Morgan Arboretum site. Values are means of 15 sub-samples of each litter from the bulk collection used to make the litterbags. For each nutrient, values followed by the same letter do not differ significantly (LSD; P<0.05).

	N	Р	K	Ca	Mg
			mg g ^t		
Saint-Hippolyte Fertilized	5.8b	0.7a	5.2a	15b	1.4b
Saint-Hippolyte Unfertilized	5.9b	0.9a	2.5b	11c	1.3b
Morgan Arboretum	8.4a	0.9a	2.0c	23a	2. 5a

Table 2. Analysis of variance table for mass loss of sugar maple litter with two fertilizer treatments (F) on three replicate plots within each treatment (R(F)), two mesh sizes (M), three litters (L). Bags representing each treatment combination were laid out in seven quadrats within each plot (Q(F*R*M*L)). Bags were collected on six dates (D). For the purposes of hypothesis testing the following error terms were used: R(F) as error for F; Q(F*R*M*L) as error for M,L, and interactions;Error for D and interactions involving D.

Source	DF	SS	MS	F	P>F
F	1	0.8659	0.8659	0.2514	0.64
R(F)	4	13.7754	3.4438		
М	1	2.9789	2.9789	13.3989	<0.001
L	2	2.8453	1.4226	6.3988	0.002
M*L	2	0.9593	0.4796	2.1574	0.12
F*M	1	1.5064	1.5064	6.7755	0.01
F*L	2	0.0394	0.0197	0.0886	0.95
F*M*L	2	1.5502	(.7751	3.4863	0.03
Q(F*R*M*L)	236	52.469	0.2223		
D	5	1012.36	202.4738	1570.8333	<<0.001
F*D	6	1.5272	0.2545	1.9747	0.1
D*M	6	4.6290	0.7715	5.9855	<0.001
D*L	12	5.0603	0.4216	3.2715	<0.001
D*M*L	12	2.4986	0.2082	1.6154	0.1
F*D*L	12	2.0477	0.1706	1.3238	0.25
F*D*M	6	2.2027	0.3671	2.8482	0.01
F*D*M*L	12	2.3863	0.1988	1.5428	0.25

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Figure 1. Mass loss of unfertilized (1a) and fertilized (1b) Saint-Hyppolyte litter incubated in small mesh bags on fertilized and unfertilized sites. For dates on which values differ significantly (LSD P<0.05), values designated by the same letter are not significantly different.



Figure 2. Mass loss of unfertilized (2a) and fertilized (2b) Saint-Hyppolyte litter incubated in large mesh bags on fertilized and unfertilized sites. For dates on which values differ significantly (LSD P<0.05), values designated by the same letter are not significantly different.



Figure 3. Mass loss of fertilized and unfertilized Saint-Hyppolyte and Morgan Arboretum litters incubated in large (3a) and small (3b) mesh bags on fertilized plots. For dates on which values differ significantly (LSD P<0.05), values designated by the same letter are not significantly different.



Figure 4. Mass loss of fertilized Saint-Hyppolyte litter on fertilized plots and unfertilized Saint-Hyppolyte litter on unfertilized plots; litters incubated in large (4a) and small (4b) mesh bags. For dates on which values differ significantly (LSD P<0.05), values designated by the same letter are not significantly different.



Connecting Paragraph

In the previous chapter base cation fertilization of a maple stand was shown to have reduced the rate of decay of unfertilized litters in fertilized plots. Fertilization of litters increased the rate of decomposition of these litters. Reduction of decay rates due to site fertilization was more pronounced in the absence of large soil fauna. Exclusion of large soil fauna reduced the decomposition of fertilized litter. The combination of these effects resulted in mass loss of unfertilized litter in control plots declining at the same rate as fertilized litters in treated plots.

In chapter III, the effects of base cation fertilization on nutrient release from decomposing litter will be examined. The elements that were measured are Ca, Mg, K and N. The role of litter quality, site fertility and soil fauna will be assessed.

CHAPTER III

EFFECTS OF BASE CATION FERTILIZATION ON NUTRIENT RELEASE IN A SUGAR MAPLE FOREST

Abstract

Application of base cation fertilizers has been shown to increase tree growth and vigour in declining sugar maple stands in southern Quebec but little is known about the effects of such fertilizers on litter quality or decomposition. Sugar maple foliage litters from fertilized and unfertilized plots on a base-poor site and from a naturally base-rich site were incubated in litterbags of 1 and 3 mm mesh sizes on fertilized and unfertilized plots at the base-poor site. Fertilization of litter significantly increased levels of potassium and calcium in sugar maple litter, but nitrogen levels were unaffected by cation fertilization. Potassium appeared rapidly leached from all litters, whereas Ca and Mg exhibited patterns of mineralization more closely related to microbial decomposition of litter. Nitrogen was mineralized only from N-rich Arboretum litter after 40% mass loss; all other litters immobilized N through out the study period. Site fertilization reduced Ca and Mg mineralization and this effect was more pronounced for Ca release in the absence of large soil fauna. Large soil fauna delayed N mineralization from Arboretum litter.

Introduction

Symptoms of forest decline have been observed in North American sugar maple forests for more than a decade (Gagnon and Roy, 1989). Research into the causes of decline have focussed on the disruption of tree nutrition which led to stands showing nutrient deficiencies, mainly in K and Mg (Bernier and Brazeau, 1988 a,b). Application of K has been shown to improve foliar nutrient status, growth rates and improve nutrient cycling efficiency (Ouimet and Fortin, 1992; Shepard and Mitchell, 1990). Fertilization with Ca and Mg has improved tree vigour and soil fauna mediated litter decomposition, whereas nutrient cycling is enhanced in litters with high Ca levels (Staaf, 1987; Wolters and Jorgensen, 1991; Hendershot, 1991).

The release of nutrients from litter is a fundamental process in nutrient cycling within an ecosystem. The dynamics of nutrients in litter can be complicated, especially for those nutrients that are subject to many types of transformations (Berg and Ekbohm, 1983). An element may be either rapidly leached, immobilized (absolute increase), mineralized (net release), or a combination of all or some of these processes (Berg and Staaf, 1981). Studies suggest the existence of a critical C:element ratio for many nutrients which seperate the processes of mineralization and immobilization (Gosz et al., 1973).

Although a general fixed initial C/N ratio in litter as a limit for release or accumulation of nitrogen has been proposed, there appears to be little experimental data to support this hypothesis (Berg and Ekbohm, 1983).
It has been found, for example, that decomposition rate affects the C/N ratio at which release takes place (Berg and Staaf, 1981). These findings are evidence of strong biological control of nutrient release in natural systems.

It is apparent that, as leaf litter decomposes, a succession of soil fauna is involved in the process of litter breakdown. A method used in sampling leaf litter has been successful in revealing the structure of fauna species involved in litter fragmentation (Crossley and Hoglund, 1962). Enclosure of selected litter in mesh bags has resulted in the physical seperation of leaf litter from the forest floor, while allowing soil fauna and microbes access to the litter. Selecting litterbags of different mesh sizes allows the determination of the relative contribution of different size soil animals to litter decay (Edward and Heath, 1963; Staaf, 1987; Verhoef and Brussaard, 1990).

On the basis of these studies we hypothesized that base cation enrichment of sugar maple stands on base poor sites would increase rates of foliar litter decomposition and enhance the release of nutrients from this litter. The specific objectives of this study were to determine the effect of base cation fertilization on the chemical quality of sugar maple litter and resultant effects on nutrient release; and to determine how the presence of large soil fauna affects the response of decomposition rate and nutrient release to changes in litter quality and site fertility.

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Materials and Methods

Study site

The study site was located at the Station de Biologie de l'Université de Montréal near Saint-Hippolyte, in the Laurentian Highlands 80 km north of Montreal. The soils were acidic Orthic Humo-Ferric podzols developed on bouldery glacial till of sandy loam texture derived from local andositic bedrock. Soils were generally well to imperfectly drained. The LF-horizon was 3-7cm deep and developed as a moder.

The forest was dominated by sugar maple (Acer saccharum Marsh.) with some red maple (Acer rubrum L.) paper birch (Betula papyrifera Marsh.), large toothed and trembling aspen (Populus grandidentata Michx. and P. tremuloides Michx.) and American beech (Fagus grandifolia Ehrh.), and was initiated by fire about 70 years previous.

Six plots (40x40m) were established on the site. In early spring 1989, three randomly selected plots were fertilized with 500 kg/ha K_2SO_4 , 250 kg/ha calcite, 250 kg/ha dolomitic limestone. These levels of fertilization have been shown to increase foliar concentrations of K, Ca and Mg on sugar maple sites (Hendershot and Jones 1989).

A second site, located at the Morgan Arboretum, on the island of Montreal in the upper St. Lawrence region was used for bulk collection of litter. This site was dominated by sugar maple with scattered white ash (*Fraxinus americana* L.). Soils were moderately acid with a thin litter layer and well developed mull humus. Foliage litter from this mull site was expected to have higher levels of nutrients and therefore to be of higher quality than Saint-Hippolyte litter. Base rich Morgan Arboretum litter was included in the study for comparison with fertilized Saint-Hippolyte litter that was expected to be more base rich than the unfertilized Saint-Hippolyte litter.

Field Methods

Sugar maple foliar litter was collected using large polyurethane net traps during the autumn of 1989 from fertilized and unfertilized plots at Saint-Hippolyte and from the Morgan Arboretum site. Air dried litter (2.00g of original tissue) was sewn into nylon bags of 1 and 3 mm mesh sizes. Subsamples of litter were retained for correction to oven dry weights. Litterbags were laid out in the litter layer of each plot at Saint-Hippolyte in sets of 6 bags in each of 7 locations per plot to allow for the collection of 7 replicates of each mesh size on 6 sampling dates throughout the following growing season. Our intent was to install the bags in the field in the autumn of 1989 but early snowfall made it necessary to delay installation of bags in the field until late April of 1990. Sampling took place on May 29, June 12, July 22, August 21, September 20, and November 2 1990, respectively 30, 44, 84, 114, 144 and 187 days after placement.

Laboratory Analysis

Collected litterbags were opened and litter was sorted, removing any contaminants such as soil, insects and non-litter plant parts. Sorted litter was oven dried for 24 hours at 65°C and then weighed. Ground samples of each litter were pooled across subplots resulting in each litter treatment being replicated 6 times corresponding to the six main plots.

Pooled ground samples of each litter were digested in H_2O_2/H_2SO_4 (Allen 1989) and digests were analyzed for N using a Technicon autoanalyser, and K, Ca and Mg by atomic absorption spectophotometry.

Statistical analysis

The data was analyzed as a completely randomized block design on Statistical Analysis Systems (SAS) (SAS Institute Inc. 1984). . For each element, the data was analyzed as a four way analysis of variance with date, mesh, litter and plot fertilizer treatment as main effects. Least significant difference was used to determine differences between means.

Results and Discussion

A weakness of this study, which introduces uncertainty as to how well our results reflect field conditions, is that litter samples were not exposed in the field during the late fall and winter. Biological decomposition is likely to have been reduced by low temperature during this period but weathering due to freeze/thaw cycles and leaching may have been higher than during the period following bag placement in the early spring. We have no data on over-winter decomposition in this system and consequently it is an assumption of this study that, although absolute mass loss may have altered, treatment effects were unaffected by the timing of bag placement. In presenting and discussing the results, it should be noted that there are two separate fertilizer effects. Fertilizer application to plots is designated as the fertilizer treatment or site fertility effect whereas differences between litter collected in fertilized and unfertilized plots and Morgan Arboretum is designated as the litter effect or litter quality. The analysis of variance (Table 1) demonstrated that Date as a main effect was highly significant for all 4 elements studied. The strong date effect was expected since all litters lost a large proportion of their mass with time, releasing or retaining nutrients as a result.

Patterns of nutrient release

The three sugar maple foliage litters used in this study differed significantly in nutrient content (Chapter II). Fertilization at the Saint-Hippolyte site resulted in litter with significantly higher concentrations of K, Ca and Mg than unfertilized litter from the same site. Relative to the Saint-Hippolyte litters, the Arboretum litter had significantly higher N, Ca and Mg but lower K concentrations. These large chemical differences between the litters explain the significant effect of litter on nutrient content observed for all 4 elements (Table 1). The significant date*litter interaction for all 4 elements (Table 1) indicates that the pattern of nutrient release differed among the three litters through the growing season. The exact manner in which the litters mineralized nutrients is presented and interpreted below.

Initially fertilized litter had more than twice the amount of K that either unfertilized or Arboretum litter had (Figure 1), whereas the minimum K contents for all litters were very similar (days 114, 144 and 187). Loss of K was rapid from all litters during the first month of incubation, by day 44 the litters had released 57%, 45% and 40% of their initial K content for fertilized, unfertilized and Arboretum litters respectively. There was only 10% difference between fertilized and unfertilized litter K content by day 114 and K content of all litters had converged to the same level of about 1.5 mg K/bag by day 187. The rapid loss of K from all litters can be explained by the high mobility of K⁺ which promotes rapid leaching. Similar patterns of potassium release have been reported in various studies with a variety of different litter species (Gosz et. al. 1973; Titus and Malcolm 1987; Berg and Staaf 1987). The fact that the K content in all litters remained constant after day 114 indicates that a quantity of K was fixed or immobilized in the litter. This is probably related to heterotroph demand since K is not a structural component of tissue and would not be held against leaching and decomposition loss (Gosz et. al. 1973).

Release from litter of Ca and Mg followed similar patterns. Base cation fertilization increased the levels of both elements in fertilized Saint-Hippolyte litter relative to unfertilized litter, but, Arboretum litter had much higher contents of both Ca (Fig. 2) and Mg than either litter from Saint-Hippolyte (Fig. 2). All litters continuously released both Ca and Mg as mass loss progressed, however, loss of Ca was less than Mg (mass loss of Mg was 53%, 49% and 59% during the season, compared to, 46%, 29% and 47% Ca loss for fertilized, unfertilized and Arboretum litters respectively), suggesting that Ca was less susceptible to leaching. All litters appeared to be converging towards a minimum Mg concentration of around 1.3 mg Mg/bag.

Although Arboretum litter maintained significantly greater concentrations of Mg than either Saint-Hippolyte litter, Mg levels declined from an initial value 65% higher than that in Saint-Hippolyte litters to a level only 35% higher on day 187. The fact that all litters appeared to converge towards a constant Mg level suggests a small amount of this element is fixed or immobilized.

The pattern of Ca release was different from Mg release in a few important ways. Unlike both Mg and K, significant differences in Ca levels between litters were maintained until late in the season (day 144), in other words, it did not appear that Ca levels were converging as rapidly as they did for K and Mg. Fertilized, unfertilized and Arboretum litters released 26%, 14% and 24% of their initial Ca content respectively, in the first month (Figure 2), followed by continued mineralization of Ca at much slower rates through the remainder of the season. The rapid initial Ca release in all litters combined with the fact that less than 50% of Ca content was released by day 187 for all litters, unlike K and Mg release, suggests that after an initial leaching period further release of Ca was slower and more dependant upon microbial decomposition of leaf litter. Similar patterns of Ca mineralization have been reported in other studies, but, Ca mineralization showed great variation in release pattern relative to other cations, because it is less mobile due to the role it plays in plant structure and because mineralization of this element is highly dependant on heterotroph demand (Gosz et. al. 1973; Titus and Malcolm 1987; Berg and Staaf 1987; Rustad and Cronan 1988).

There was no significant effect of base cation fertilization on N content of fertilized litter, and fertilized and unfertilized litters behaved similarly throughout the



study period, Arboretum litter had significantly greater levels of N than both Saint-Hippolyte litters (Fig. 3). Patterns of N release differed between Arboretum and Saint-Hippolyte litters, with both Saint-Hippolyte litters accumulating N during mid season decomposition (days 84 and 114) and then retaining N through the rest of the season. Arboretum litter did not accumulate N, but N was retained until late in the season when it was mineralized (day 187). These results suggest that N-mineralization in this system was dependent upon a combination of litter N content and litter mass loss so that a critical C:N ratio had to be achieved before N could be mineralized from decomposing litter.

Other studies have demonstrated a similar, site specific, critical litter C/N ratio that is required for N-mineralization from decaying litter (Berg and Ekbohm, 1983; Berg and Staaf, 1987). N was immobilized for much of the study period in all the litters, suggesting the microbial decomposers were N limited. Numerous studies have demonstrated a relationship between litter N concentration, substrate C:N ratio and N mineralization from decomposing litter (Titus and Malcolm 1987; Theodorou and Bowen 1990; and Berendse et. al. 1989).

In summary, the three litters studied showed great variation in the manner and pattern in which different elements were released. Potassium was rapidly leached from all litters, whereas Mg and Ca showed a rapid initial leaching followed by a more gradual nutrient release related to microbial decomposition. Nitrogen was accumulated in the Npoor Saint-Hippolyte litters, while it was retained in Arboretum litter apparently until a critical C:N ratio corresponding to 40% litter mass loss was attained. Results similar to these were observed in decomposing white birch leaf litter for N, Ca, Mg and K (Berg and Staaf 1987).

Site fertilization effects

The analysis of variance indicated significant effects of site fertilization and site fertilization*date interactions on Ca and Mg release (Table 1). These effects indicate that nutrient release was affected by site fertilization and that this site effect on nutrient release changed with time. The effect of site fertilization was similar for both elements in that site fertilization significantly reduced the rate of both Mg and Ca released from decomposing litter. The site fertilization effect was more pronouced for Mg release, where the rate of mineralization was significantly greater on unfertilized plots relative to fertilized plots on all sampling dates after day 30 (Fig. 4), whereas significant differences in Ca mineralization occurred on days 84, 114 and 187. The significance of this effect on Ca and Mg can be explained by the fact that release of both these elements was more closely related to litter mass loss than was either K or N release. The site fertility*date interaction was significant for mass loss (Chapter II), suggesting that Ca and Mg mineralization are closely tied to the microbial decomposition of sugar maple litter.

The data are insufficient to identify specific mechanisms that caused the observed negative site fertilization effect on litter decomposition and related Ca and Mg mineralization. Other studies that have observed a negative effect of fertilization or site fertility on microbially mediated decomposition and nutrient mineralization have suggested, however, that altering site fertility may directly affect the population structure



of the soil microbial community, including mycorrhiza, in a manner that reduces decomposition and mineralization (Staaf 1980; Titus and Malcolm 1987; Entry et. al. 1991).

Mesh size effects

The analysis of variance demonstrated a significant mesh-size main effect for N release as well as interactions involving mesh-size, specifically a two way litter*mesh-size interaction for nitrogen content and three way site fertilization*litter*mesh-size and litter*mesh-size*date interactions for Ca and Mg respectively (Table 1). The complex interactions of these factors on nutrient release are interpreted in simple combinations and presented in the following section. The interaction of site fertilization*litter and mesh size had a significant effect on Ca mineralization. Fertilized litter in large mesh bags released significantly more Ca on unfertilized plots than on fertilized plots on days 30, 84 and 114, (Fig.5), whereas the same litter in small mesh bags released significantly more Ca on unfertilized plots that on fertilization effects were significant only on two dates (days 144 and 187) for unfertilized litter and one date (day 114) for Arboretum litter, in large mesh bags, whereas no date showed significant site effects for either unfertilized or Arboretum litter in small mesh bags.

Increased Ca release in large mesh bags suggests that microbial Ca release from litter is enhanced in the presence of large soil fauna, while the more pronounced effect in fertilized litter implies that these larger soil animals perceive or allow microbes to perceive litter quality differences.

It is interesting to note that Ca mineralization reflects the same interactions as litter mass loss where fertilized litter in large mesh bags was shown to decompose faster in the middle of the season on unfertilized plots, whereas the same litter in small mesh bags decomposed faster at the end of the season (Chapter II). These results further link litter mass loss and Ca mineralization. Although patterns of Ca mineralization show great variation in the literature many studies have demonstrated an enhanced rate of Ca mineralization from leaf litter due to the presence of soil animals (Huhta et. al. 1988; Anderson et. al. 1983; Incson et. al. 1982)

There was a significant mesh size main effect (Prob.>F 0.05) and significant mesh size*litter interaction for nitrogen content (Table1). Litters decomposing in large mesh bags retained nitrogen longer into the season than did litters in small mesh bags (Fig. 7). This effect was most pronounced for Arboretum litter where end of season N release occurred later for large mesh litter (Fig. 8). Arboretum litter in large mesh bags in fact showed some N accumulation on day 144 before releasing N on day 187, whereas small mesh litter retained but did not accumulate N until day 144 when mineralization started. It would appear from these results that somehow microbial immobilization of N in decomposing leaf litter was prolonged by the presence of large soil fauna, perhaps because faunal activity increased exposure of N immobilizing tissues. Many studies have shown that just the opposite is true in that N mineralization is enhanced in the presence of soil fauna (Ineson et al. 1982; Anderson et al. 1983), however, Visser et al. (1981) were able to demonstrate that soil fauna by "tracking-in" bacteria and fungi enhanced N retention in leaf litter, while Bååth et el. (1978) observed microbial N immobilization from pine litter in the presence of high numbers of microbivorous animals.

In conclusion, this study has shown that cation fertilization of a sugar maple forest affected nutrient release from decomposing leaf litter in a number of ways. Fertilization significantly increased K and Ca levels in fertilized litters so that significantly more of these elements were released from fertilized litter than unfertilized litter. Site fertilization, by temporarily reducing microbial decomposition of litter significantly reduced the amount of Ca and Mg mineralized from fertilized plots. Excluding large soil fauna enhanced the soil fertilization effect, whereas soil fauna delayed N release from Arboretum litter.

References

- Allen, S.E. 1989. Analysis of vegetation and other organic constituents. In: S.E. Allen (Editor), Chemical Analysis of Ecological Materials. Blackwell Scientific, Oxford. pp.160-200.
- Anderson, J.M., Ineson, P., and Huish, S.A. 1983. Nitrogen and cation mobilization by soil fauna feeding on leaf litter and soil organic matter from deciduous woodlands. Soil Biology and Biochemistry 15:463-467.
- Bååth, E., Lohm, U., Lundgren., B., Rosswall, T., Söderström, B., Sohlenius, B. and Wiren, A. 1978. The effect of N and C on the development of soil organism populations and pine seedlings : a microcosm experiment. Oikos 31:153-156.
- Berendse, F., Bobbink, R. and Rouwenhorst, G. 1989. A comparative study on nutrient cycling in wet heathland ecosystems. II. Litter decomposition and nutrient mineralization. Oecologia 78:338-348.
- Berg, B. and Ekbohm, G. 1983. Nitrogen immobilization in decomposing needle litter at variable carbon:nitrogen ratios. Ecology 64:63-67.



- Berg, B. and Staaf, H. 1981. Leaching, accumulation and release of nitrogen in decomposing forest litter. In: F.E. Clark and T. Rosswall (Editors), Terrestrial nitrogen cycles. Processes, ecosystem strategies and management impacts. Ecological Bulletin Stockholm 33:373-390.
- Berg, B., and Staaf, H. 1987. Release of nutrients from decomposing white birch leaves and Scots pine needle litter. Pedobiologia 30:55-63.
- Bernier, B., and Brazeau, M. 1988 b. Nutrient deficiency symptoms associated with sugar maple dieback and decline in the Quebec Appalachians. Canadian Journal of Forestry Research. 18:762-767.
- Bernier, B., and Brazeau, M. 1988 a. Foliar nutrient status in relation to sugar maple dieback and decline in the Quebec Appalachians. Canadian Journal of Forestry Research 18:754-761.
- Boerner, R.E.J. 1984. Foliar nutrient dynamics and nutrient use efficiency of four deciduous tree species in relation to site fertility. Journal of Applied Ecology 21:1029-1040.

- Carlyle, J.C. 1986. Nitrogen cycling in forested ecosystems. Forestry Abstracts 47:307-336.
- Côté, B., Hendershot, W.H. and O'Halloran, I.P. 1993. Response of declining sugar maple to seven types of fertilization in southern Quebec: growth and nutrient status. In: Huettl and Dombois (Editors), Proceedings of the Symposium on Forest Decline in the Atlantic and Pacific Region. Hilo, Hawaii.pp.162-174.
- Crossley, D.A. and Hoglund, M.P. 1962. A litterbag method for the study of microarthropods inhabiting leaf litter. Ecology 43:571-573.
- Edwards, C.A. and Heath, G.W. 1963. The role of soil animals in breakdown of leaf material. In: J. Doeksen and J. Van der Drift (Editors), Soil Organisms. North Holland Amsterdam. pp. 76-84.
- Entry, J.A., Rose, C.L. and Cromack, K. 1991. Litter decomposition and nutrient release in Ectomycorrhizal mat soils of a Douglas fir ecosystem. Soil Biology and Biochemistry 23:285-290.
- Gagnon, G. and Roy, G. 1989. Etat du dépérissement dans les forets au Québec. In Atelier sur le dépérissement des érablieres. Ministère de l'Agriculture, des Pêcheries et de l'Alimentation du Québec. pp. 14-17.

- Gosz, J.R., Likens, G.E., and Bormann, F.H. 1973. Nutrient release from decomposing leaf and branch litter in the Hubbard Brook forest., New-Hampshire. Ecological Monographs 43:173-191.
- Hendershot, W.H. 1991. Fertilization of sugar maple showing dieback symptoms in the Quebec Appalachians, Canadaian Fertilizer Research 27:63-70.
- Hendershot, W.H., and Jones, A.R. 1989. Maple decline in Quebec: A discussion of possible causes and the use of fertilizers to limit damage. The Forestry Chronicle 65:280-287.
- Huhta, H., Setala, H. and Haimi, H. 1988. Leaching of N and C from birch leaf litter and humus with special emphasis on the influence of soil fauna. Soil Biology and Biochemistry 20:875-878.
- Ineson, P., Leonard, M.A., and Anderson, J.M. 1982. Effect of collembolan grazing upon nitrogen and cation leaching from decomposing leaf litter. Soil Biology and Biochemistry 14:601-605.
- Ouimet, R. and Fortin, J.-M. 1992. Growth and foliar nutrient status of sugar maple: incidence of forest decline and reaction to fertilization. Canadian Journal of forestry Research 22:699-706.

Rustad, L.E., and Cronan, C.S. 1988. Element loss and retention during litter decay in a red spruce stand in Maine. Canadian Journal of Forestry Research 18:947-953.

SAS. 1984. SAS/ETS Users Guide 5th ed. SAS Institute Inc. Cary, North Carolina.

- Shepard, J.P. and Mitchell, J.M. 1990. Nutrient cycling in a red pine plantation: Thirtynine years after potassium fertilization. Soil Science Society of America Journal 54:1433-1440.
- Staaf, H. 1980. Influence of chemical composition, addition of raspberry leaves, and nitrogen supply on decompositon rate and dynamics of nitrogen and phosphorus. Oikos 35:55-62.
- Staaf, H. 1987. Foliage litter turnover and earthworm populations in three beech forests. Oecologia 72:58-64.
- Theodoru, C. and Bowen, G.D. 1990. Effects of fertilizer on litterfall and N and P release from decomposing litter in a *Pinus radiata* plantation. Forest Ecology and Management 32:87-102.
- Titus, B.D. and Malcolm, D.C. 1987. The effect of fertilization on litter decomposition in clearfelled spruce stands. Plant and Soil 100:297-322.

- Verhoef, H.A. and Brussaard, L. 1990. Decomposition and N-mineralization in natural and agroecosystems: The contribution of soil animals. Biogeochemistry 11:175-211.
- Visser, S., Whittaker, J.B., and Parkinson, D. 1981. Effects of collembolan grazing on nutrient release and respiration of a leaf litter inhabiting fungus. Soil Biology and Biochemistry 13:215-218.
- Wolters, V., and Joergensen, R.G. 1991. Microbial carbon turnover in beech forest soils at different stages of acidification. Soil Biology and Biochemistry 23:897-902.

Table 1. Significance of the F-value of the analysis of variance table for nutrient content of sugar maple litter with two fertilizer treatments (F) on three replicate plots within each treatment (R(F)), two mesh sizes (M), three litters (L). Bags representing each treatment combination were laid out in each of six plots (R(F*M*L)). Bags were collected on six dates (D). For the purposes of hypothesis testing the following error terms were used: R(F) as error for F; R(F*M*L) as error for M,L, and interactions; Error for D and Interactions involving D.

----P>F-----

Source	DF	Ca	Мсј	К	N
F	1	0.0239	0.0421	0.8388	0.4668
R(F)	4	0.0036	0.0001	0.0001	0.0011
М	1	0.2213	0.1691	0.2811	0.0530
L	2	0.0001	0.0001	0.0001	0.0001
M*L	2	0.2030	0.6152	0.1341	0.0461
F*M	1	0.9648	0.8003	0.8221	0.8855
F*L	2	0.2048	0.2079	0.7841	0.8387
F*M*L	2	0.0173	0.7752	0.6097	0.6136
R(F*M*L)	20	0.9828	0.0001	0.0291	0.3027
D	6	0.0001	0.0001	0.000L	0.0001
F*D	6	0.0207	0.0001	0.2969	0.2138
D*M	6	0.8515	0.3631	0.8641	0.3078
D*L	12	0.0001	0.0001	0.0001	0.0049
D*M*L	12	0.5919	0.0262	0.5154	0.1997
F*D*L	12	0.4304	0.2624	0.8507	0.3751
F*D*M	6	0.8055	0.3828	0.6888	0.9839
F*D*M*L	12	0.3831	0.6977	0.4882	0.4083



Figure 1. Potassium content of fertilized and unfertilized Saint-Hyppolyte and Morgan Arboretum litters incubated in mesh bags. For dates on which values differ significantly (LSD P<0.05), values designated by the same letter are not significantly different.

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Figure 2. Calcium content of fertilized and unfertilized Saint-Hyppolyte and Morgan Arboretum litters incubated in mesh bags. For dates on which values differ significantly (LSD P<0.05), values designated by the same letter are not significantly different.



Figure 3. Nitrogen content of fertilized and unfertilized Saint-Hyppolyte and Morgan Arboretum litters incubated in mesh bags. For dates on which values differ significantly (LSD P<0.05), values designated by the same letter are not significantly different. For each litter, bars indicate least significant difference.



Figure 4. Magnesium content of sugar maple leaf litter incubated in mesh bags on fertilized and unfertilized sites. For dates on which values differ significantly (LSD P<0.05), values designated by the same letter are not significantly different.



Figure 5. Calcium content of sugar maple leaf litter incubated in large mesh bags on fertilized and unfertilized sites. For dates on which values differ significantly (LSD P<0.05), values designated by the same letter are not significantly different.

Figure 6. Calcium content of sugar maple leaf litter incubated in small mesh bags on fertilized and unfertilized sites. For dates on which values differ significantly (LSD P<0.05), values designated by the same letter are not significantly different.





Figure 7. Nitrogen $C = A^{-1} D^{-1} D^{-1$

Figure 8. Nitrogen content of Arboretum litter incubated in large and small mesh bags. For dates on which values differ significantly (LSD P<0.05), values designated by the same letter are not significantly different. For each litter treatment, bars indicate least significant difference.



CHAPTER IV

SUMMARY OF RESULTS AND GENERAL CONCLUSIONS

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Summary of results and General Conclusions

Results presented in this thesis indicate that base cation fertilization of sugar maple forests may affect decomposition in several respects. Site fertilization resulted in a short term reduction in microbial decomposition of litters, suggesting that base cation fertilization had a negative effect on the decomposer community even though one year had passed since fertilizer application. Cation enrichment of litter increased litter decay rates indicating that potassium, which was the only element that occurred in higher levels in fertilized than in Arboretum litter, was effective in improving litter quality. The exclusion of large soil fauna from litterbags increased the site fertilization effect, whereas fertilized litter decomposition was accelerated in their presence. The combined result of the negative site fertilization effect and the beneficial effects of litter fertilization, was that base cation fertilization did not change overall litter mass loss rate.

Potassium was rapidly leached from decaying litters, K content of all litters appeared to converge to a minimum level by mid-season. Fertilized litter released significantly more K than unfertilized or Arboretum litters, because of it's high initial K-content. Calcium and magnesium mineralization closely followed patterns of litter mass loss, in that, site fertilization and soil fauna affected Ca and Mg release in the same way that mass loss was affected.

Fertilization of litter did not affect nitrogen levels of litter. N was immobilized throughout the study period, except in N-rich Arboretum litter, where it was mineralized at the end of the season. This result suggests that the microbial population was N-deficient in this maple stand and that a critical litter C/N ratio was required before N could be released.

Suggestions for Future Research

Had a simpler experimental approach been taken, with only mass loss of litter decomposing in the plot in which it was collected being monitored, the conclusions reached at the end of the study would have been that fertilization had no effect on decomposition. In light of these results, future research should evaluate the impact of inorganic fertilizers on the different levels of the soil decomposer community. In particular an attempt should be made to characterize the soil fauna that inhabit acidified sugar maple forests. Fauna to fauna, as well as, fauna to microflora relationships need to be determined.

Other studies have determined that potassium fertilization of forest stands results in increased and more efficient nutrient cycling. More work needs to be done to assess the beneficial affects of potassium on the litterfall/decomposition/mineralization pathway of K-deficient forests.