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Calcium in decomposing foliar litter – A synthesis for boreal and temperate coniferous forests

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ABSTRACT

We have synthesized available data for calcium (Ca) dynamics in decomposing foliar litter of mainly pine (*Pinus*), spruce (*Picea*), and birch (*Betula*) species to determine patterns of Ca concentration with climate in newly shed litter and its dynamics in decomposing litter as well as a possible role for Ca as regards limit values.

Initial Ca concentration was negatively related to mean annual precipitation (MAP) with different relationships among genera. A limited data set showed a positive relationship across species ($p < 0.05$) to extractable Ca in soil. In paired stands, litter of both Norway spruce (*Picea abies*) and lodgepole pine (*Pinus contorta*) had higher Ca concentrations than Scots pine (*Pinus silvestris*), Norway spruce litter even twice as high. Relationships between initial concentrations of Ca and those of other nutrients appeared to be dominated by the positive ones to potassium (K) and magnesium (Mg) and specifically for deciduous litter there was a negative relationship to nitrogen (N).

In decomposing litter, Ca concentration followed a negative quadratic ($Ca = a + t - t^2$) function and had a maximum, which was variable. The Ca maximum concentration during decomposition was positively related to initial Ca concentration both within and among species. Separate linear relationships based on species were combined into one, in common for all investigated species and genera ($R^2 = 0.914$, $n = 63$, $p < 0.001$).

Limit values for decomposition were positively related to maximum Ca concentration at $p < 0.05$ with separate functions for pine and spruce litter.

Calcium net release started directly after the incubation and was linear to accumulated mass loss of litter, giving a slope coefficient for each study. The net release rates were linear to initial Ca concentration both within and across species/genera. All studies combined gave a negative linear relationship ($R^2 = 0.894$, $n = 67$, $p < 0.001$).

1. Introduction

Nutrient concentrations and dynamics in decomposing foliar litter often have been studied to investigate nutrient availability to plants. Some nutrients have been considered to limit the degradation of plant litter and studied for that reason.

For some time, there has been an awareness that several nutrients may be integrated parts of microbial enzyme systems or have an enzyme-regulating function. There is also an awareness that some nutrients may be limiting for metabolic reasons and even sodium (Na) and potassium (K) have been found to limit litter decomposition rate (Kaspari et al., 2008, 2009) at least in environments at distances from

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the sea and sea spray.

Calcium (Ca) is a main nutrient for the living plants and for decomposing microorganisms. For groups of boreal and temperate tree species it has the highest concentrations in foliar litter, normally higher than that of nitrogen (N). In two papers on litter from Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) we gave a range from 2.8 mg g^{-1} in newly shed Scots pine litter (Johansson et al., 1995) to 31.7 mg g^{-1} in needle litter of Norway spruce (Berg et al., 2000).

The Ca concentration in litter may be related to its availability in the soil (Staaf, 1982). Its concentration in litter may be negatively related to that of N in both foliage and foliar litter. This has been found when N was added as a fertilizer (Berg and Staaf, 1980; van Diepen et al., 2015) or naturally present in raised concentrations, e.g. through N_2 fixation (Perakis et al., 2013). A suggested mechanism is that high soil N would result in lower soil pH with the consequence that available Ca is removed by leaching and therefore given a lower concentration in foliage and foliar litter (Perakis et al., 2013).

The concentrations of several nutrients in newly shed foliar litter have been related to climate factors such as mean annual temperature (MAT) and annual actual evapotranspiration (AET) at the site for growth. For example – for Scots pine needle litter Berg et al. (1995) found positive relationships for N, phosphorus (P), sulfur (S), and K, to climate indices such as MAT or AET whereas concentrations of Ca showed a highly significant relationship to MAT but not to AET.

Nutrient concentrations may be positively related to a high mass-loss rate and/or to the limit value for decomposition. An experiment by Lovett et al. (2015) indicated that a high Ca supply may support a more far-going decomposition. Possibly, Lovett et al. (2015) have found a path to follow as they observed that newly added Ca (as $CaSiO_4$) to forest soil significantly decreased the resistant litter fraction. Their study indicated that Ca in soil was of higher importance than that in the shed litter, which may reflect a different availability of Ca from fertilizer as compared to that in litter. Davey et al. (2007) related limit values for leaf litter of common oak (*Quercus robur*) to the initial Ca concentration as did Berg (2000) for needle litter of Norway spruce. However, the relationship of Ca for limit values and extent of decomposition is so far empirical.

We have not found any larger compilation or synthesis of Ca dynamics in decomposing litter. Considering the potential importance of Ca, we have compiled available data from mainly northern Europe with focus on two coniferous systems, namely pine (*Pinus*) species and Norway spruce on acid mor soils. This study is part of a long-term investigation on litter decomposition and nutrient dynamics in two model systems, namely those of Scots pine and Norway spruce. We have compared our results to those of litter from birch (*Betula*) species and a few single studies on common beech (*Fagus sylvatica*) and alder (*Alnus*) species.

Although this study has the character of a descriptive one for Ca dynamics we have focused on three aims; (i) to determine any pattern in Ca concentration (newly shed litter) related to climate, soil, and substrate properties, (ii) to demonstrate that the patterns for Ca concentration and net release during decomposition are similar across litter from different plant species, and (iii) to determine any relationship between litter Ca concentration and limit value across dominant foliar plant litter species along a Scandinavian climate gradient. To this purpose, we have reviewed available decomposition studies from mainly boreal and temperate systems using mainly pine, spruce, and birch foliar litter with Ca dynamics described during the whole decomposition process. We define the term *'decomposition study'* for all values of accumulated mass loss and Ca for a given batch of litter that has been installed in a given stand at a given date. There is very few soil data available for these stands and we have thus a focus on Ca concentration and net amount in the decomposing litter.

2. Materials and methods

2.1. Sites and data used

We have used litter decomposition data from in all 48 sites (69 stands), some of which had paired stands, namely Norway spruce *vs* Scots pine (8 stands), lodgepole pine (*Pinus contorta* var contorta) *vs* Scots pine (3 stands), Norway spruce *vs* common beech (5 stands) and Norway spruce *vs* downy birch (*Betula pubescens*, 3 stands). There were in all 36 sites (36 stands) with monocultures of Scots pine, 5 sites (6 stands) had lodgepole pine (*Pinus contorta* var contorta and *Pinus contorta* Dougl ex Loud), and 24 sites (24 stands) had Norway spruce, and 4 stands Sitka spruce (*Picea sitchensis*). We also used data for 3 single stands with downy birch, one of them with some few oaks (common oak) and one stand with silver birch (*Betula pendula*), 5 stands with common beech, and one stand with Sitka alder (*Alnus viridis* Chaix.).

The Scots pine stands in a climatic gradient ranged from a site in northernmost Finland (69°45′N; 27°01′E), close to Barents Sea, *via* two sites close to the Arctic circle (65°47′N; 20°37′E) over Sweden, Finland, and Denmark to a site in Normandy (westernmost France) and one in central Germany. Three stands with lodgepole pine were located in central Sweden, one in central British Columbia, Canada (53°40′N; 135°39′W) and one in Normandy (48°28′N; 01°34′W). All pine stands have been described in published articles (Johansson et al., 1995; Berg et al., 1997; Berg and Lundmark, 1987; Sanborn and Brockley, 2009; Gloaguen and Touffet, 1976; Merila and Derome, 2008; Tamm, 1999). The Norway spruce stands range from close to the Arctic circle (66°22′N; 20°02′E) in Sweden via central Denmark to central Germany (51°31′N; 09°34′E). All spruce sites are described in Berg et al. (2000), Tamm et al. (1974), Vesterdal and Raulund-Rasmussen (1998), and Ellenberg et al. (1986). All 4 birch stands were located in Sweden. The common beech stands are located in Denmark and central Germany, mainly south of the birch stands within the range 56°28′N–51°31′N with locations and descriptions given by Vesterdal and Raulund-Rasmussen (1998) and Ellenberg et al. (1986). One stand of Sitka alder is located in central British Columbia at 53°40′N; 135°39′W (Sanborn and Brockley, 2009).

The pine, spruce, and birch sites were arranged in climatic gradients, with MAT ranging from −1.7 to 10.5 °C for pine and spruce and from 3.8 to 7.4 °C for birch. Mean annual precipitation (MAP) ranges from 396 to 1500 mm for pine, from 469 to 1067 mm for spruce and from 527 to 747 mm for birch species. Further site data is given in Supplement, Table S1.

The full data set encompassed 94 determinations of initial Ca concentration and 68 decomposition studies with Ca dynamics. For pine species we used 40 and for Norway spruce 17 decomposition studies. For deciduous litter we used 11 decomposition studies of which 8 covered birch species.

Of the *68 decomposition studies*, 58 were carried out using local litter and 10 using transplanted litter. The Scots pine litter sets were mainly incubated in the stand of sampling. Three sets of downy birch leaf litter were incubated in their own stands as was one set of common oak litter and one set of litter from Sitka alder. In 12 stands, locally collected litter of Norway spruce was incubated, in some of them repeatedly. One set of lodgepole pine litter was transplanted and incubated in a Scots pine stand. We also used data for transplanted litter for silver birch and grey alder (*Alnus incana*), incubated in a Scots pine stand.

For pine species we had in all 40 data sets (351 value pairs) for Ca dynamics and release, 16 sets for Norway spruce (160 value pairs), and 11 sets of deciduous litter of 5 species (118 value pairs), of which 8 sets with birch species encompassed 84 value pairs. In all there were 68 sets with 629 pairs of values.

We used decomposition data collected over a period from 1973 thru 2000. Samplings of incubated litter bags took place for between 3 and 5 years. Climate data for the sites covered the incubation period. At one site (Jädraås) 13 repeated (annual) incubations were made using Scots