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Review

From Litter to Humus in a Norwegian Spruce Forest: Long-Term Studies on the Decomposition of Needles and Cones

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Abstract: The aim of this review and synthesis is to illustrate the gradual transformation of needles and cones from litter to humus. Individual needles may follow quite different decomposition pathways, which contributes to a diverse humus structure. In the litter layer (Oi), about 40% of the needles were excavated by special mites that produced slowly decomposable excrements. In the fermentation layer (Oe), needles which happened to be in close contact with fine roots decomposed more rapidly. Cones decomposed slower than needles during the first 3–5 years, so the role of cones in carbon (C) storage may be greater than indicated by their fraction of fresh litter. Over a 13 years period, potassium (K), magnesium (Mg) and phosphorus (P) in cones was released, while the total amount of calcium (Ca), manganese (Mn), iron (Fe) and aluminium (Al) increased strongly. Nitrogen concentration increased but the total nitrogen content remained rather constant. After 13 years, the cones had sunk about 6 cm into the soil and lost 60% of their dry weight but were morphologically intact. A cone monitored for 28 years was fully recognizable and had not yet reached the stable Oa layer. The most inert decomposition products in the Oa layer were fragments of needles and cone scales, microarthropod excrements and chitinous insect remains.

Keywords: decomposition; spruce needles; cones; long-term; soil profile; microarthropods

1. Introduction

Northern taiga forests represent an important global carbon (C) sink. They produce slowly decomposable litter and can develop deep humus layers with stabilized organic matter. This is possible because at a certain decomposition stage, further degradation of humus elements comes to a halt, which is termed "the limit value approach" [1]. Humus layers deeper than 20 cm are common in boreal Scandinavia and 6% of 15,000 Swedish plots had humus layers deeper than 60 cm [1]. If not interrupted by fire or massive storm felling, net accumulation of humus can go on for millennia [2]. As an extreme case, a 1.4 m thick humus layer was reported on a small island in northern Sweden, with a bottom age of nearly 3000 years [3]. Climate change motivates letting taiga forests build up and maintain as much organic material in soils as possible. This aim calls for a rethinking about harvesting methods and the need for protection measures. But it also calls for a better understanding of long-term decomposition processes.

In Norway and Sweden, representing the western part of the taiga, Norway spruce (*Picea abies* (L.) H. Karst.) is the most common tree species. The litter fall in spruce stands is dominated by needles [4–6] but in certain sites and years, cones can represent a considerable fraction of the litter fall [4,7].

From Sweden, there are several rather short-term studies on the decomposition of spruce needles [8–13] but none on cone decomposition. In Norway, the large project "Effects of acid rain on forest and fish" during the 1970s initiated long-term decomposition studies of needles and cones in

a spruce forest near Oslo. Four experiments, each of 4–13 years duration [14–17] represent the most detailed and long-lasting case study of decomposition in a spruce forest.

The present paper is a review and synthesis of these four experiments. The aim is to illustrate the gradual transformation of needles and cones from litter to humus. This is a story about dry weight loss and the immobilisation and release of nutrients, of vertical transport through the soil profile and the successive influence of soil animals and fine roots. As such, it can be regarded as a journey down through the soil layers. Alternative decomposition routes for individual needles are discussed. An attempt is made to explain the mixed structure of deep humus in the light of a decomposition process which includes phases and options.

2. Material and Methods

2.1. Study Site and Habitats

The study site was a spruce forest on a flat plain of glacifluvial sandy deposits in the Nordmoen forest area, about 40 km north of Oslo, Norway and 4 km south of the village Råholt. In 1986, when two of the experiments commenced, the trees were about 50 years old and 10–20 m high. Most studies were made within a radius of 50 m. An adjacent clearcut area with newly planted trees was also used. The soil profile was a stone-free podzol, with a raw humus pH of approximately 3.9. In these acid conditions, earthworms were rare and the species were epigeal and had little effect on the soil profile [18]. Therefore, the vertical transport of a newly shed needle or cone would be the result of two simultaneous processes: The gradual accumulation of new litter above and the continuous decomposition of the organic layers below. Also, some nylon strips left for a long time on the forest floor were assumed to move vertically at a natural rate.

In moss vegetation, the litter surface was defined as the bottom of green moss. Beneath green vegetation, the organic material was divided into litter layer (Oi) with non-fragmented plant residue, the fermentation layer (Oe) with different stages of decomposition and the humus layer (Oa) with decomposed material. The total thickness of these three organic layers in the experimental area was 6–9 cm, of which Oi made up 1–1.5 cm, Oa only about 0.5 cm and Oe the rest. There was a sharp border to the spodic horizon (E) below Oa.

Four different ground habitats were chosen:

A. *Moss vegetation*. The forest floor had a several cm thick cover of mosses, mainly *Pleurozium schreberi* (Brid.) Mitt., but also *Hylocomium splendens* (Hedw.) Schimp. There were two experimental sites, named Moss I and II, each about 50 m^2.

B. *Bilberry vegetation*. In addition to mosses, there was field layer of bilberry (*Vaccinium myrtillus* L.). There were two experimental sites, named Bilberry I and II, each about 50 m^2.

C. *No vegetation*. Below certain trees, there existed a vegetation-free "needle mat" of 1–2 m^2. Within approximately 100 m^2, eight such patches were chosen for experiments.

D. *Clearcut area*. A clearcut area nearby had about 0.5 m high planted spruce trees when decomposition studies started there in 1977. Mosses and bilberry were to a large degree substituted by *Deschampsia flexuosa* (L.).

2.2. Experiments

Between 1977 and 2008, four different experiments of 4–13 years' duration were performed [14–17] and key information of each is presented in Table 1. Naturally shed needles and cones sampled on the snow surface were used.

Experiment 1. Cylindrical litter bags, 3.4 cm in diameter and 3 cm high, were filled with 4.2 g of dry needles. In September 1977, they were inserted into holes made in the organic layer on the clearcut area. With a mesh size of 0.6 mm, microarthropods like springtails (Collembola) and mites (Acari) could migrate freely in and out. Between 20 and 60 bags were harvested at each of six samplings: After 7 weeks, 8 months, 1 year, 2 years, 5 years and 10 years. Trees grew up to 2–3 m height during this

period. Dry weight loss was measured and microarthropods extracted. The litter bags did not represent the natural position of fresh litter, as they were in contact with both Oi and Oe. However, since both litter-living and deeper-living species had continuously access to the bags, the experiment was suitable for studying the preference among microarthropod species for the various decomposition phases.

Table 1. Key information on four long-term experiments on the decomposition and vertical transport of spruce needles and cones in a podzol soil profile.

Experiment No.	Litter Type	Method	Habitat	Purpose	Duration	Period	Reference
1	Spruce needles	Cylindrical litter bags	Clearcut area	Decomposition rate Microarthropod succession	10 years	1977–1987	[14]
2	Spruce needles	Needles fastened to nylon strips	No vegetation Moss vegetation Bilberry and moss	Decomposition rate Effect of mites inside needles Vertical transport	4 years Strips 28 years	1986–1990 Strips to 2014	[15,16]
3	Spruce needles	Marked needles dropped on the ground	No vegetation Moss vegetation Bilberry and moss	Vertical transport	9 years	1986–1995	[17]
4	Spruce cones	Marked cones placed on the ground	No vegetation Moss vegetation	Vertical transport Decomposition rate Chemistry	13 years	1995–2008	[16]

Experiment 2. The experiment was designed to follow the decomposition of needles in a natural and controlled way, where needles with a known age could be recollected, weighed and dissected for excavating mites inside. Nylon strips, 80–100 cm long and 4 cm wide, with needles fastened as shown in Figure 1, were placed at the litter surface in three different habitats. In vegetated sites, the strips were placed in furrows gently made in the moss cover. Strips with needles were sampled after 4, 12, 16, 24, 35, 38, 40 and 52 months. They were frozen in the field by solid CO_2 to ensure that mites inside the needles remained in position before dissection. Dry weight loss of needles with or without mites was measured and mite excrements were included. Also the developmental stages and life cycle of three mite species living inside needles were studied. The biology of one of the mite species was further studied in cultures on moistened plaster of Paris, partly at natural temperatures and partly at room temperature. They were fed newly shed spruce needles. Some strips were left in the profile for 22 and 28 years, at which time their vertical position was noted.

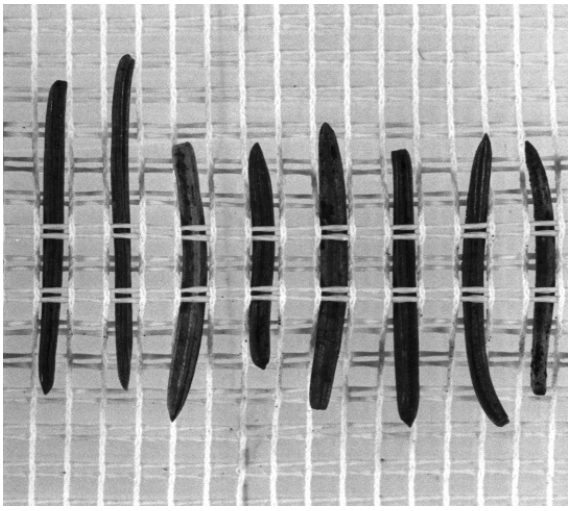

Figure 1. Naturally shed spruce needles were fastened to strips of nylon mesh before being placed in the field. In this way, needles of known age could be sampled and studied. From [15].

Experiment 3. The vertical transport of single needles was studied for nine years, as naturally as possible. Two thousand five hundred needles were each marked with a narrow belt of white paint

(ordinary correction fluid) for recognition. Ten small patches, each 10 cm × 10 cm, were marked off in each of the following habitats: No vegetation, Moss I, Moss II, Bilberry I and Bilberry II. Fifty marked needles were dropped from half a meter height over each patch in order to simulate a natural drop. In the vegetated sites the needles came to rest at various depths of the green moss layer. Samplings were done after 4, 12, 16, 24, 35, 52 and 108 months by digging up soil cores and bringing them to the laboratory. Under a stereomicroscope, marked needles were recorded at various depths by digging downwards with forceps. Even more or less fragmented needles could be recognized because of the white ring of paint. More than 80% of the marked needles were usually recollected.

Experiment 4. Decomposition and vertical transport of cones was studied in two habitats: No vegetation and Moss I. One hundred cones, which were individually weighed and marked with sticks, were placed in each habitat. Sampling was done after 1, 3, 5, 7, 9, 11 and 13 years. In addition to dry weight loss and depth in the soil profile, several chemical parameters were measured.

3. Results

3.1. Dry Weight Loss

Dry weight loss of cones (Experiment 4) was nearly linear throughout the thirteen years, with a total loss of about 60% in both habitats (Figure 2). Differences between habitats were significant after 3, 5, 7 and 9 years ($p < 0.05$) [16]. Decomposition was slower on the vegetation-free needle mat but speeded up when cones became buried by new litter.

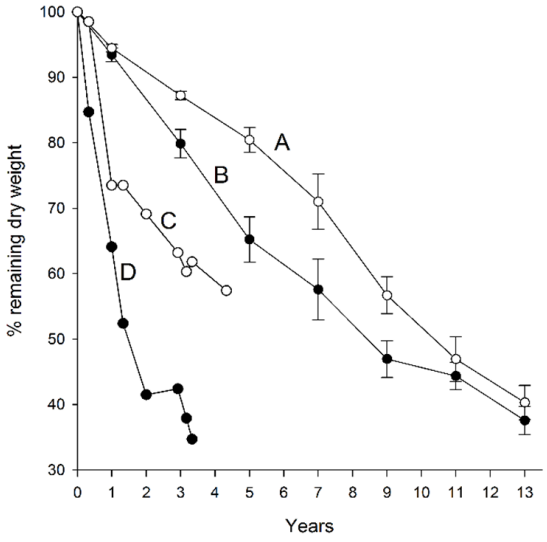

Figure 2. Dry weight loss of spruce cones during 13 years (A–B) and spruce needles during 3–5 years (C–D). It is distinguished between moss-covered forest floor (filled circles) and vegetation-free needle mats below trees (open circles). Vertical bars show standard error (SE). Modified from [16].

Needles fastened to strips in experiment 2 could be weighed as long as they remained unfragmented, which meant 3–5 years. During this period, needles decomposed more rapid than cones in both habitats (Figure 2) [15,16]. In the moss habitat, 60% dry weight loss of needles was reached already after about three years and the curves for both habitats showed a tendency to flatten out. Curves for needles in Figure 2 illustrate mean values without taking into consideration the retarding effect of mites living within some of the needles (see below). The weight loss curve for the vegetation-free needle mat is without replications but the curve for moss habitat is a mean of four replications (Moss I-II and Bilberry I-II). Also needles in the litter bag experiment (Experiment 1), although not quite representative, decomposed faster than cones (Experiment 4), as needles lost half of their dry weight after four years [14].

The decomposition rate of both cones and needles was well described by the single exponential according to [19], in all cases at $p < 0.001$. Calculations were made in SigmaPlot: $Y = a \cdot e^{-bx}$. The rate constants (b) and half times for curves A–D in Figure 2 have been listed in Table 2.

Table 2. Decomposition Rates and Half Times for Cones and Needles in Moss Vegetation and in Vegetation-Free Needle Mats.

Curve in Figure 2	Habitat	Litter Type	Rate Constant	Half Time (Years)
A	Needle mat	Cones	0.0703	9.9
B	Moss	Cones	0.0777	8.9
C	Needle mat	Needles	0.0119	4.9
D	Moss	Needles	0.0274	2.1

3.2. Chemistry

In fresh litter, the chemical composition of cones differed from that of needles (Table 3). Cones had a much lower concentration of calcium (Ca), manganese (Mn), iron (Fe) and aluminium (Al). During thirteen years of decomposition, with a final dry weight loss of about 60%, the total amount of these elements in a given cone increased, up to a certain level (Figure 3). Contrary, the total amount of phosphorus (P), potassium (K) and magnesium (Mg) decreased gradually, indicating a release of these elements (Figure 4). The total amount of nitrogen (N) and sulphur (S) was rather stable throughout the years in vegetation-free plots, but was somewhat reduced in the moss habitat (Figure 5). If we look at concentrations instead of at total amounts, only K showed a clear reduction and P and Mg were rather stable. Even the concentration of N and S increased markedly during the experiment in both habitats (Figures 6–8). A common trait for both total amount and concentrations was that values were generally higher in vegetation-free plots than in moss vegetation (Figures 3–8). Table 3 summarizes the main trends in concentration and total amount of each element during cone decomposition. For exact values, see [16].

Table 3. Start concentrations of some elements in newly shed spruce needles (mean of two values) [6] and cones (±SD). For cones, main changes in concentration and total amount during 13 years of decomposition are indicated. Modified from [16].

Element	Needles	Cones		
	Concentration at Start ($mg \cdot g^{-1}$)	Concentration at Start ($mg \cdot g^{-1}$)	Change in Concentration	Change in Total Amount
N	8.5	4.80 ± 0.81	Increase	Rather stable
P	1.05	0.51 ± 0.17	Stable	Decrease
K	1.73	3.03 ± 0.95	Decrease	Decrease
Ca	7.00	0.16 ± 0.05	Increase	Increase to stable
Mg	0.60	0.62 ± 0.13	Decrease or stable	Decrease
S	0.73	0.43 ± 0.10	Increase	Rather stable
Mn	1.98	0.083 ± 0.017	Increase	Increase to stable
Fe	0.116	0.031 ± 0.009	Increase	Increase to stable
Cu	0.0034	0.0037 ± 0.0008	Increase	Decrease
Zn	0.050	0.025 ± 0.007	Increase	Varying
Al	0.322	0.06 ± 0.01	Increase	Increase to stable

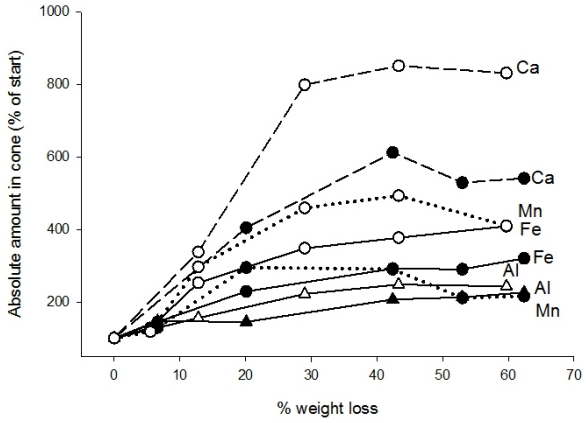

Figure 3. Changes in the absolute amount of iron (solid lines and round symbols), aluminium (solid lines and triangles), calcium (stippled lines) and manganese (dotted lines) during decomposition of cones. Filled symbols: moss habitat. Open symbols: needle mat habitat. All lines start at 100% for newly shed cones. From [16].

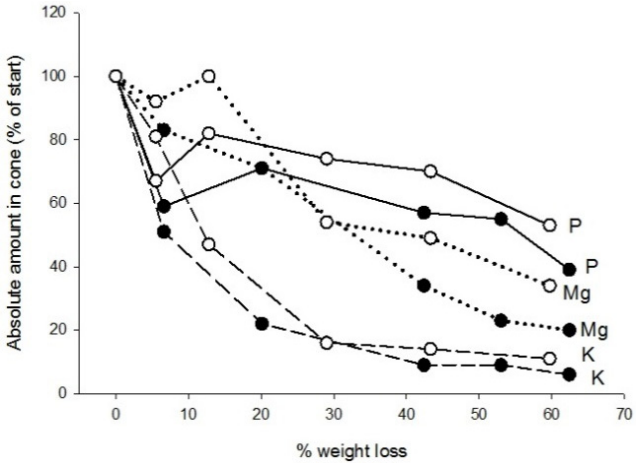

Figure 4. Changes in the absolute amount of phosphorus (solid lines), potassium (stippled lines) and magnesium (dotted lines) during decomposition of cones. Filled circles: moss habitat. Open circles: needle mat habitat. All lines start at 100% for newly shed cones. From [16].

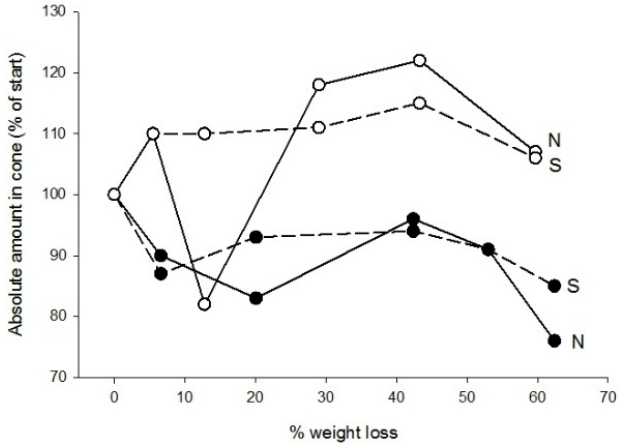

Figure 5. Changes in the absolute amount of nitrogen (solid lines) and sulphur (stippled lines) during decomposition of cones. Filled circles: moss habitat. Open circles: needle mat habitat. All lines start at 100% for newly shed cones. From [16].

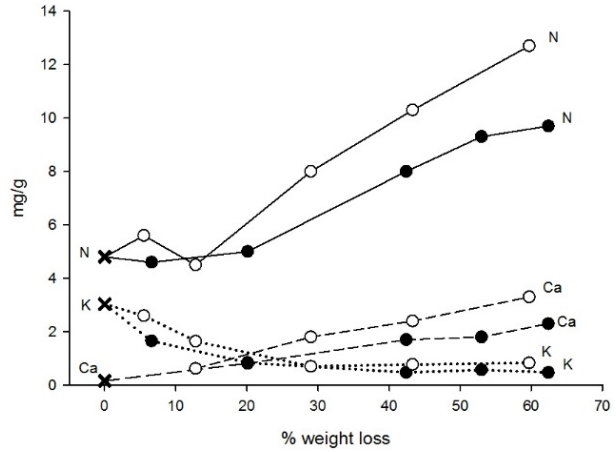

Figure 6. Changes in the concentration of nitrogen (solid lines), calcium (stippled lines) and potassium (dotted lines) during decomposition of cones. Filled circles: moss habitat. Open circles: needle mat habitat.

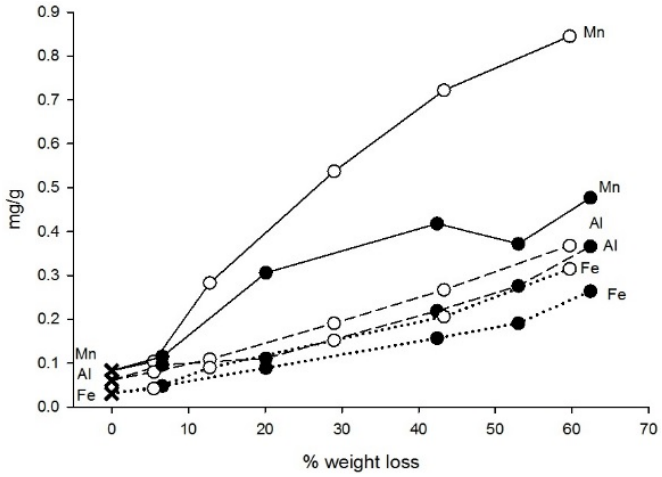

Figure 7. Changes in the concentration of manganese (solid lines), aluminium (stippled lines) and iron (dotted lines) during decomposition of cones. Filled circles: moss habitat. Open circles: needle mat habitat.

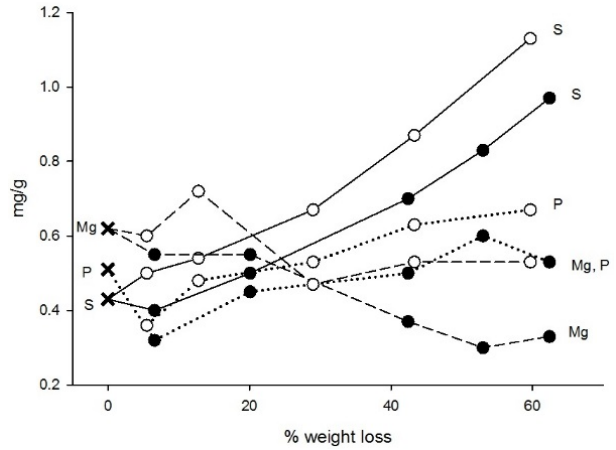

Figure 8. Changes in the concentration of sulphur (solid lines), magnesium (stippled lines) and phosphorus (dotted lines) during decomposition of cones. Filled circles: moss habitat. Open circles: needle mat habitat.

3.3. Vertical Transport

Figure 9 illustrates the gradual vertical transport of needles in a moss-covered soil profile. During the first year, needles were situated at different depths in the moss vegetation but most of them reached the upper litter layer after one year. Two years later, the 1 cm thick litter layer (Oi) had been passed. Then, the vertical transport rate slowed markedly down. It took two more years to sink through the upper cm of the Oe layer and another four years to pass to the next cm. It should be noted that five year old needles had entered the fine root zone. Nine years after being shed from the tree, a typical needle was situated 7.2 cm below the top of green moss and 3.1 cm below the bottom of green moss. Ten of the nylon strips used in experiment No. 2 remained in soil. Five of them were recovered 22 years after they were laid out and the remaining five after 28 years (each time, three strips from moss habitats and two from needle mats were found). Their mean depth was not very different at these two samplings and they had sunk through about 80% of the organic layers but not yet reached the Oa layer. Since strips in moss vegetation were placed at a depth typical for one year old needles, ages of these strips have been corrected to 23 and 29 years. Figure 9 shows the position of these nylon strips in the moss habitat, assuming that their vertical transport rate was similar to needles. The Oa layer was still not reached after three decades.

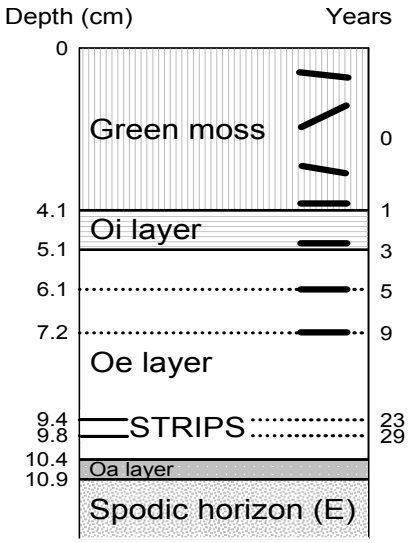

Figure 9. Vertical position of spruce needles in the moss-covered soil profile after different number of years. It took about one year to be transported through the 4 cm thick layer of living, green moss and two additional years to pass the 1 cm thick litter layer (Oi). Five year old needles had sunk 1 cm into the fermentation layer (Oe) and nine year old needles only one more cm. Nylon strips, recovered after 23 and 29 years still had not reached the humus layer (Oa). Modified from [16].

The depth of the cones was measured after 9, 11 and 13 years. After 9 years in the moss-covered forest floor, the upper cone surface was 2.5 cm below the bottom of green moss and 3.3 cm below after 11 and 13 years. Since cones were 2.5 cm thick, the latter position means that the underside was 5.8 cm below the bottom of green moss. The actual site had a 2 cm thicker Oe layer than in Figure 9, so the centre of the cone was situated in the middle of the Oe layer. Fine roots surrounded the cone [16].

In Figure 10, data on the vertical transport has been combined for needles, cones and strips in experiments 2, 3 and 4 to illustrate the gradual sinking over nearly 30 years. Since the thickness of the Oe layer could vary within the study area, the depth is given as a percentage of the total organic layer. Figure 10 illustrates how the vertical transport rate slows down over time.

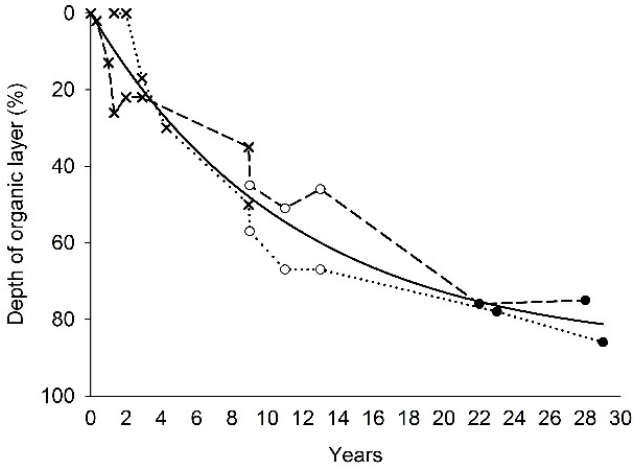

Figure 10. Vertical transport of needles, cones and strips in the moss habitat (dotted line) and the needle mat habitat (stippled line) over time. Crosses are needles, open circles represent underside of cones and filled circles are nylon strips. The degree of vertical transport is shown by how many % of the organic layer (Oi + Oe + Oa) that had been passed. Hundred % would indicate that the spodic horizon had been reached. The adapted, dark curve indicates a gradual reduction in the rate of vertical transport with time. From [16].

3.4. How Deep Can Fragments of Needles and Cones Be Recognized?

Needles situated just beneath 28 year old nylon strips showed large variation in the degree of decomposition. Most of them were strongly disintegrated or not recognizable but there were also needle fragments that had retained their three-dimensional shape. A cone, found by chance below a 28 years old strip in a vegetation-free plot, had its underside about 1 cm above the spodic horizon. There was, in other words, still 0.5 cm left until the Oa layer was reached. As shown in Figure 11, the actual cone had retained its shape, illustrating the slow decomposition rate in the lowest part of Oe.



Figure 11. A spruce cone with intact shape was found just beneath a 28 years old nylon strip. By chance it was cut longitudinally during sampling. The underside of the cone was situated about 1 cm above the spodic horizon. From [16].

The structure of the deepest organic layer (Oa), which was only about 0.5 cm thick, was studied under steromicroscope. By inverting soil cores and carefully removing the spodic horizon, the Oa layer could be studied intact. Most of the organic material was too strongly decomposed to be identified but certain resistible elements were recognized: Several needle fragments, often with microarthropod excrements inside; a few remains of cone scales; and various chitinous parts of beetles (Figures 12 and 13).



Figure 12. Recognizable needle fragments in the Oa layer. A fine root had penetrated the three upper needles and only the resistable cuticula was left. The three lower fragments however, had to a large degree retained their three-dimentional shape. Dark faecal pellets of microarthropods can be seen on and outside the needle remains, especially the lower right and the middle upper one.



Figure 13. Remnants of cone scales and a chitinous head capsule of a weevil beetle in the Oa layer.

3.5. Soil Animals Associated with Needle Decomposition

Litter bags with spruce needles were colonized by a total of 12 springtail species and 19 mite taxa (including species groups) during a ten year period. Most of these were fungal feeders living between needles [14]. However in experiment 2, three species of mites were found to develop inside needles [15]: *Steganacarus* cf. *striculus* (C. L. Koch), which may be an undescribed species; *Rhysotritia ardua* (C. L. Koch); and *Adoristes ovatus* (C. L. Koch) (Figure 14). While all three species were present in needles from the moss-covered forest floor, *R. ardua* was absent from the drier, vegetation-free ground. Often, two species occurred in the same needle and up to three individuals of *S.* cf. *striculus* could develop within one needle. Eggs were probably laid in tiny cracks in the needle epidermis, created by the fungus *Lophodermium piceae* (Fuckel) Höhnel. During a two-year period, while the needle moved through the 1 cm thick litter layer (Figure 9), juvenile stages developed safely within the needle and appeared as adults about three years after the needle was shed [15]. Laboratory cultures with simulated field temperatures indicated a life cycle of a minimum two years [15].

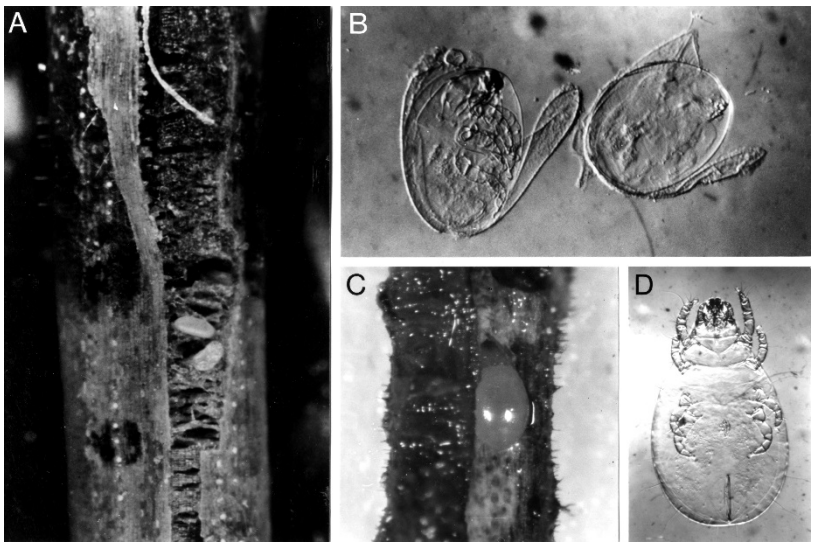

Figure 14. Developmental stages of the mite *Adoristes ovatus*: (**A**) Two newly laid eggs in a partly opened needle; (**B**) Eggs under hatching; (**C**) Deuteronymph (second last juvenile stage) within its cavity in an opened needle; (**D**) Tritonymph (last juvenile stage). From [15].

Approximately 40% of the needles in each habitat became colonized by mites. Needle cavities excavated by mites were filled up with their faecal pellets, which seemed very resistant to decomposition. In all five habitats, needles which were inhabited by mites decomposed slower than needles without mites. The difference was significant at least during one sampling in each site [15]. After 40 months in the four vegetated sites, decomposition was on average 28% slower in needles with mites, than in needles without mites. In the vegetation-free patches, the effect was less (15%). These retarding effects were due to the activity of juveniles developing within needles.

Laboratory cultures revealed that also adult mites, after escaping from their hidden juvenile life, could consume and fragment needles. Adults of *Steganacarus* cf. *striculus* were kept in cultures at 20 °C for two weeks, given moistened, naturally shed needles. As shown in Figures 15 and 16, they bored into the needles, fragmented them and produced faecal pellets.

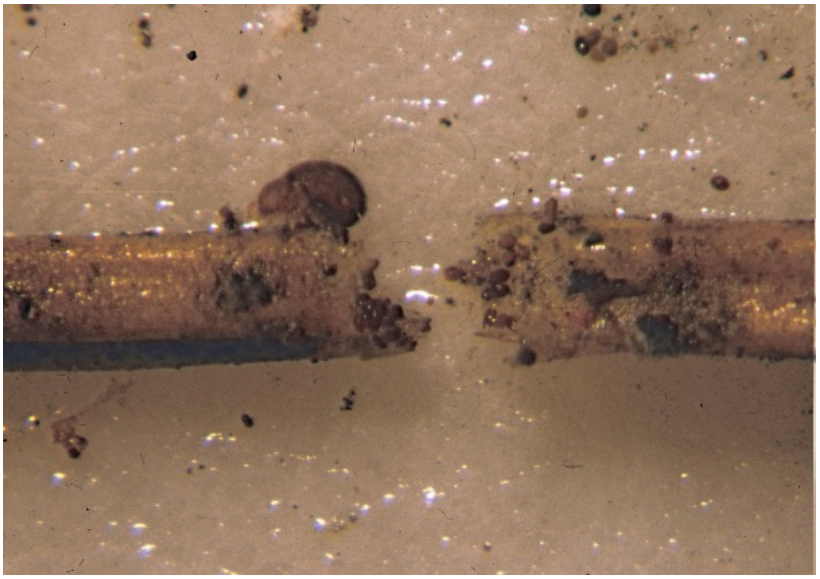

Figure 15. The mite species *Steganacarus* cf. *striculus* is seen walking on a fragmented needle. Its faecal pellets are easily seen where the needle is broken.



Figure 16. Adults of the mite *Steganacarus* cf. *striculus* have bored into these two needles and left many faecal pellets.

4. Discussion

4.1. Vertical Transport in the Soil Profile

The transformation of litter to humus is very much a story of vertical transport. In moss-covered forest floor, newly shed needles were hanging at different depths in the moss vegetation (Figure 9). They could be washed further down by rain water but the growth rate of the moss is also likely to be an important factor. In a Swedish study, newly shed pine (*Pinus silvestris* L.) needles were overgrown and in this way brought downward in the profile [20].

The further vertical transport slowed down with time (Figure 10). It took for instance, five years until needles and cones came into contact with the upper fine roots, about 1 cm into the Oe layer. After 28 years, nylon strips had passed about 80% of the organic layer but there was still 1–2 cm left until the spodic horizon was reached. Deep organic layers in northern forest soils typically contain stabilized organic matter with a very slow decomposition rate [1], so the remaining 1–2 cm might take a long time to pass through. The deepest layer (Oa) of 0.5 cm thickness will probably grow in thickness. Radiocarbon dating of this layer indicated "modern age", indicating less than 60 years [16]. However, the actual samples were not suitable for exact radiocarbon dating, being contaminated by more recent carbon, either by fine roots or fungal hyphae.

4.2. Chemistry and Decomposition Rate

Microflora is able to import elements into the litter-microbe complex from the surroundings [1]. This explains the marked increase in the total amount of Ca, Mn, Fe and Al in decomposing cones. Consequently, these elements were immobilized for a long time. The total amount of N was retained rather well, at the same time as dry weight of cones was reduced. That means that the concentration of N increased, which is a typical phenomenon for decomposing litter. A high N level is correlated with slower decomposition rate, which may result in a stable humus phase [1].

The all-over higher values of all the elements in cones from vegetation-free plots, both regarding total amount and concentrations, is difficult to explain. It might in some way be related to drier conditions and a slower decomposition rate. Maybe microflora had a higher need for minerals here, or it was easier for fungi and bacteria to extract minerals from the compact needle mat than from the less compact humus in the moss-covered forest floor.

The chemical changes in decomposing spruce cones until 60% dry weight loss can be compared with a Swedish long-term case study on decomposing Scots pine needles until 60%–80% dry weight loss [1]. Several chemical trends were in common, for instance an increased concentration of N, S, Fe, Cu, Zn and Al; and a reduced concentration of K. However, Ca and Mn increased in cones and decreased in pine needles. Calcium concentration ended up at similar levels in both types of litter at about 60% dry weight loss, around 3 $mg \cdot g^{-1}$. One may wonder whether this level was created by the microflora as a favourable value at that stage of decomposition.

The weight loss curve for cones had still not reached the phase of flattening out after 13 years. The record of a cone with intact shape beneath a 28 years old nylon strip indicated that transformation to stable humus may go on for a few more decades. With a half time of around 10 years for cones, about 12.5% of the dry weight should be left after 30 years. It is an open question as to whether there is a limit value for cones, where the decomposition comes to a halt.

In the needle mat, the half time of cones was twice that of needles and in moss vegetation, about four times as high. The slow decomposition of cones compared to needles, at least during the first 3–5 years, indicates that their role in humus composition and C storage may be greater than their fraction of fresh litter. Climate change may affect cone production of coniferous trees [21]. If the fraction of cones in the total litter increases, more cone material may be included in humus layers.

4.3. Alternative Pathways from Litter to Humus

The present studies illustrate that the decomposition rate of individual cones or needles depends on several factors. Both cones and needles decomposed slower in vegetation-free patches than in moss-covered forest floor, probably due to drier conditions [15,16]. Needles which happened to be colonised by excavating juvenile mites in the litter layer decomposed slower than non-colonized needles. In culture, even the adults of *S.* cf. *striculus* were observed to excavate and fragment needles [15]. The total retarding effect of mites is therefore probably higher than measured only for juveniles, which was 28% for colonised needles in moss habitat, see [15]. Since the type of feeding marks left by adults were not regularly seen during the first years of the field study, newly hatched adults probably start to feed in the lower litter layer where they emerge and then migrate upwards to the litter surface to deposit eggs. Eggs should be laid in freshly deposited needles because these contain the most food and have an intact cuticula to protect the juveniles from predators during their 2–3 years of development.

When needles reached the fine root layer after five years, those that came in touch with a root decomposed much faster than needles without root contact [17]. This was probably due to root volatiles and exudates which stimulate microbial activity [22,23].

The decomposition of spruce needles cannot be described in a 'standard' way but rather as a mix of optional pathways. Table 4 illustrates alternative pathways that single needles may follow during decomposition. Many combinations of factors are possible and each pathway produces a certain end product. Some needles followed pathways that made them recognizable as three-dimensional fragments even in the Oa layer. Other needles became more or less dissolved due to close root contact. Needles situated very close to each other in the soil could follow quite different decomposition routes from litter to humus. The final composition of deep humus was therefore a mix of individual decomposition products. A high percentage of mite-excavated needles could for instance, result in a larger fraction of slowly decomposable excrements in deeper layers.

According to literature, the activity of microarthropods generally increases the decomposition rate, probably by stimulating fungal activity through moderate grazing [24]. The decomposition rate of those needles which were not inhabited by mites may thus have been speeded up by microarthropod grazing. The majority of microarthropod species which colonized litter bags with spruce needles were fungal feeders and showed a clear succession from litter-living to deeper-living species during the ten years [14]. Another litter bag experiment with birch leaves (*Betula pubescens* Ehrh.) demonstrated how fungus-feeding microarthropod species colonized and grazed hyphae and spores during a period of rapid leaching of nutrients, especially K and P [25,26].

Table 4. Alternative decomposition pathways for individual spruce needles. Options are many, since each alternative may have two new alternatives in the following box.

Age of Needle (Years)	**0**	**0**	**1–3**	**3–4**	**5 Years or More**	**Several Decades**
Soil layer	Surface	Green moss	Litter (Oi)	Upper Oe	Oe	Oa
Alternatives for a single needle	Forest floor: No vegetation or moss cover?	If moss, how deep into the moss did the falling needle penetrate?	Is the needle inhabited by juvenile mites?	Is the needle fed upon by adult mites?	Is the needle close to a fine root?	Results in Oa
Slower decomposition	No vegetation	Needle landed in upper moss	Yes	Yes	No	Resistable faecal pellets. Recognizable, three-dimentional fragments of needles.
Faster decomposition	Moss cover	Needle penetrated through moss at landing	No	No	Yes	No faecal pellets. No recognizable fragments of needles.

The present case study shows that the influence of microarthropods is complicated. Certain specialized mites are not fungal grazers but attack and transform the inner structure of needles, retard their decomposition and influence the structure of humus. The actual species are few and cryptic-living and their activity can easily be overlooked.

Cryptic-living mites may use litter of different kind. Regarding *A. ovatus*, French studies have described their ability to excavate needles of *Abies alba* Mill. [27–29]. *R. ardua* can make cavities in bark pieces of yellow birch (*Betula alleghaniensis* Britton) and hemlock (*Tsuga* sp.) and even heart wood of twigs of yellow birch [30]. *Steganacarus magnus* can develop both in beech (*Fagus* sp.) cupules [31] and within pine cone scales [32]. In the present site, the old cone in Figure 11 had cavities which could have been excavated by mites, and spruce twigs and other woody litter can probably also be more or less transformed to faecal pellets.

In a Swedish study, the presence of adult "box mites" (*Phthiracarus* spp. and *Rhysotritia ardua*) reduced the decomposition rate of pine needles [33] and the authors suggested that the adult mites in some way interacted with the microflora. One might wonder whether excavating juvenile mites in the present study produced antiseptics in order to outcompete microflora, which otherwise could consume resources which the mite needs during its long development. The inertness of their excrements could be a combination of compactness and antiseptics. A study of 2 mm thick soil sections in a black pine (*Pinus nigra* Arnold) plantation concluded that faecal pellets of oribatid mites decomposed very slowly and that pellet congregations were usually not colonized by fungi [34]. Microarthropod excrements were assumed to contribute significantly to humus production, to reduce the leaching process and to ensure a slow but steady supply of nutrients to plants. Also other studies have pointed to the importance of microarthropod excrements in humus formation [35,36].

5. Conclusions

A productive supplement to data on dry weight loss and chemical changes is to consider the decomposition process as a gradual transport downwards through the soil layers. The present case study showed that certain factors were triggered in specific layers but without affecting all needles. Examples are the colonisation of excavating mites in 40% of the needles while passing through the litter layer and the rapid decomposition of certain needles in the fermentation layer because they happened to come into close contact with fine roots. Therefore, individual needles even if situated near each other in the soil, could follow quite different decomposition routes and produce different types of humus elements. This may explain the heterogenic structure of the deepest humus, where fine-grained dark material was mixed with fully recognizable needle fragments and microarthropod faecal pellets.

6. Suggestions for Future Research

Northern coniferous forests with an acid podzol profile lacking soil-mixing earthworms are well suited for studies on decomposition, vertical transport and the gradual accumulation of carbon-binding

humus elements. However, instead of starting with fresh litter and waiting many decades for the later phases, humus samples taken from different depths might be placed back in litter bags and resampled for analysis, for instance after 10 years. Of special interest would be the depth at which the degradation stops or is strongly reduced.

Three candidates for stable humus may deserve special attention: moss litter, microarthropod excrements and dead fungal hyphae. The first is a much neglected litter type, while the other two are products of soil organisms.

(1) Moss litter. Nordic coniferous forests often have a several cm thick moss cover on the ground. Moss plants produce considerable amounts of litter and the moss litter of boreal forest floors decomposes slowly [37,38]. At the present study site, moss litter was easily defined in layers which were at least six years old [17]. In a Swedish Scots pine forest, identifiable moss remnants constituted 10% of dead organic matter in the litter layer [39]. In the same forest type, moss litter was found to decompose slowly and contributed more than twice as much to the organic layer as the same amount of needle litter did [40]. In general, bryophytes may significantly affect soil structure and chemistry. Besides increasing soil moisture and changing the density of soil organic matter, they fix C and N from atmospheric pools, release dissolved compounds that are immobilized by soil microbes and transform C and N into recalcitrant organic matter [41].

(2) Microarthropod excrements. These are good candidates for remaining stable over a very long time but systematic studies on their decomposition are lacking. Microarthropods occur throughout the organic layers and even in the mineral soil but excrements produced by mites within needles have a well-defined origin. Their possible resistance to fungal colonisation and microbial decomposition could be studied in fine-meshed litterbags, as well as in the laboratory. Excavating mites should also be looked for in other litter elements than needles, for instance within cones and twigs. Such cryptic-living mites that feed directly on the substrate and produce compact faecal pellets may be humus producers but they are often overlooked in decomposition studies.

(3) Dead fungal hyphae. Recent studies on symbiontic ectomycorrhiza fungi show that dead hyphae can be very difficult to decompose and may represent a considerable carbon sink in humus-rich soils [42]. While the role of living fungi has been much studied, the value of dead hyphae now deserves attention.

Questions of interest for forestry practices could be: Will selective cutting, that does not allow for an increase in the forest floor temperature, better preserve humus layers from decomposition and release of CO_2? Will certain management practices better conserve the diversity and vitality of mycorrhiza fungi? Should we encourage a deep moss cover to develop in the forest floor, since mosses produce slowly decomposable litter that contributes to carbon sequestration? Should we avoid disturbing the soil profile during and after cutting, in order to preserve natural humus layers from being exposed and to maintain good living conditions for the rich soil fauna, that may be important humus producers through their durable faecal pellets?

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