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**Academic Dissertation**

*To be presented, with the permission of the Faculty of Mathematics and Natural Sciences of the University of Jyväskylä, for public criticism in Auditorium S212, on February 27, 1993, at 12 o'clock noon.*

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# ABSTRACT

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The effects of four earthworm species on decomposition, nutrient cycling and plant growth in coniferous forest soil were studied with microcosm experiments. The species were the epigeics *Dendrobaena octaedra* (Savigny) and *Lumbricus rubellus* (Hoffmeister), the endogeic *Aporrectodea caliginosa tuberculata* (Eisen), and an introduced anecic species *A. velox* (Bouché). Simulated forest soil was constructed into the microcosms, which were incubated in climate chambers for several months, including both summer and winter conditions. In two experiments, birch seedlings were also planted in the microcosms. In the experiments with *A.c. tuberculata* and *A. velox* the pH of the soil was manipulated by liming. In order to study the possibilities to introduce new deep burrowing species to northern latitudes, *A. velox* was also introduced to two different kinds of habitats in the field.

In each experiment, the soil processes in the control microcosms (without earthworms) were compared to processes in identically prepared microcosms with earthworms. Evolution of $CO_2$ was monitored throughout the experiments, and concentrations of nitrogen and phosphorus were analysed from the leached water. At destructive samplings, numbers of animals, mass loss, pH, and KCl-extractable nutrients, as well as growth of the seedlings were determined.

Generally, the earthworms increased the microbial activity in the soil, and they also enhanced the rate of nitrogen mineralization. Nitrification was also increased when nitrifying activity was present in the soil (in the presence of mineral soil layer, or after liming). The influence of earthworms on phosphorus mineralization was inconsistent being significant in some cases only.

Earthworms clearly raised the soil pH when only the humus layer was included in the microcosms. The influence was opposite when mineral soil was under the organic horizon. The effect of earthworms on pH seemed to be related to the increased amounts of mineral nitrogen and changes in the ratio of ammonium to nitrate. In the presence of living plants, when concentrations of mineral nitrogen were very low, there were no differences in the pH between soils with or without earthworms.

Both *L. rubellus* and *A.c. tuberculata* increased the growth of birch seedlings significantly. The nitrogen concentration of leaves was doubled and the shoot to root ratio increased in the presence of *L. rubellus*. Neither nitrogen fertilization, mechanical mixing with "artificial worms" nor the preworked soil by earthworms increased the growth of the seedlings.

The capacity of earthworms for improving the structure and fertility of soils, which has previously been shown in temperate and tropical habitats by several authors, became herein confirmed for northern coniferous forest soil. The results clearly showed that plants can derive benefit from enchanced decomposition and nutrient release from dead organic matter due to the activities of earthworms. Plants produced more biomass, and this biomass contained a higher concentration of nitrogen in the presence of earthworms. The results also encourage to study the possibilities to manipulate the earthworms in the field in order to increase the productivity of coniferous forests.

Key words: Earthworms; decomposition; nutrient dynamics; forest soil; plant growth.

## List of original publications

This thesis is based on the following articles, which will be referred to by their Roman numerals:

I Haimi, J. & Huhta, V. 1990: Effects of earthworms on decomposition processes in raw humus forest soil: A microcosm study. - Biol. Fertil. Soils 10: 178-183.

II Haimi, J. & Boucelham, M. 1991: Influence of a litter feeding earthworm, *Lumbricus rubellus*, on soil processes in a simulated coniferous forest floor. - Pedobiologia 35: 247-256.

III Haimi, J., Huhta, V. & Boucelham, M. 1992: Growth increase of birch seedlings under the influence of earthworms - a laboratory study. - Soil Biol. Biochem. 24: 1525-1528.

IV Haimi, J. & Einbork, M. 1992: Effects of endogeic earthworms on soil processes and plant growth in coniferous forest soil. - Biol. Fertil. Soils 13: 6-10.

V Haimi, J. 1993: Effect of an introduced earthworm *Aporrectodea velox* on nutrient dynamics of forest soil - Manuscript (submitted).

# Contents

# 1 INTRODUCTION

During the decomposition of organic matter, carbon and nutrient immobilization and mineralization are mainly carried out by the soil microflora. However, the function of microbes is strongly influenced by the activities of soil fauna (Coleman et al. 1983, Anderson & Ineson 1984). Soil animals fragmentate leaf litter and other organic residues, incorporate these into the soil, increase soil aeration, redistribute and graze microbes, etc. It has been calculated that in ecosystems where faunal biomass exceeds 5-10 g (dry mass) m$^{-2}$ the annual flow of elements through the soil fauna can reach the magnitude of the elements input via litterfall (Anderson & Ineson 1984).

On the other hand, it has been found that soil animals have only a small direct contribution to the energy flow in terrestrial ecosystems (e.g. Crossley 1977, Schaefer 1990). Persson et al. (1980) estimated that the soil fauna consume 30-60% of the production of microbes in the litter and humus layer of a pine forest. Thus, it can be argued that soil animals are most important in the decomposition processes through their indirect regulatory effects on microbial communities (Visser 1985, Coleman 1986, Anderson 1988).

Among saprophagous soil fauna, earthworms are one of the most important groups, partly because of their large size and often high biomass as compared with other soil animals. In many habitats, earthworms may easily consume all the litter produced by plants (Satchell 1983). Earthworms also strongly modify their biotic and abiotic environment through their burrowing and mixing activity. For these reasons considerable attention has been paid to the role of earthworms in decomposition and nutrient cycling, these processes determining the soil fertility and the overall productivity of the whole ecosystem.

A lot of knowledge has been accumulated on the role of earthworms in decomposition processes and soil fertility. Almost without exceptions the effects of earthworms have been observed to be positive: they have improved the structure of the soil, and increased the rate of decomposition and the amounts of mineral nutrients in the soil. The direct flux of nitrogen through earthworm biomass has been found to be substantial in many ecosystems (e.g. Lee 1983, Parmelee & Crossley 1988). Undoubtedly it can be said that earthworms are the most important component of the decomposer community in many natural and managed terrestrial ecosystems (Lee 1985). However, most of the studies have been conducted in temperate and tropical soils where the environmental conditions are usually favourable both for decomposition and for earthworms.

In northern coniferous forests, the rate of decomposition is slow causing accumulation of considerable amounts of carbon and nutrients in the uppermost layers of soil. Although humus layer contains large amounts of nitrogen, most of it is present in an organic form with often a very low rate of mineralization. Deficiency of plant available nitrogen is therefore usually the factor limiting the tree growth in coniferous forests (Kukkola & Saramäki 1983). For many groups of soil animals, including earthworms, boreal coniferous forests are marginal environments mostly because of low temperatures and high acidity of the soil. For example in Finland, coniferous forests are usually inhabited by only low densities of a few species of earthworms (Huhta et al. 1986a, Terhivuo 1989).

Much research has been focused on the introductions of earthworms, either to support the native populations or to introduce entirely new species to a certain area. Many research projects all over the world have been started within last few years (e.g. Blair et al. 1993, Brown et al. 1993). Dispersal capacity of earthworms is generally regarded as poor, and it is possible that they have not reached all potential habitats. Dispersal may have been prevented by different kinds of geographical barriers (seas, deserts, bogs, mountains) or, as is the case in northern latitudes, lack of time after the last glaciation.

Liming of soils has been reported to benefit earthworm populations by increasing immigration and reproduction, together with lower mortality (Persson 1988, Kratz et al. 1991). Huhta (1979) and Huhta & Kulmala (1987) have shown that coniferous forest soil could be rendered more favourable for earthworms by liming and/or adding leaf litter.

According to their vertical distribution, earthworms can be grouped into three main ecological categories (Bouché 1977), each having a unigue influence on the decomposition. Epigeic species live in organic layers near the soil surface. They comminute litter and rework relatively undecomposed organic matter with a high biological activity. Endogeic earthworms that live in the upper layers of mineral soil consume large amounts of soil and influence porosity and aggregate structure of the soil. Anecic species have large burrow systems in the soil, and they feed on plant residues which they take from the soil surface. Thus, they actively transport materials between the soil horizons.

In this work my objectives were to study the effects of both native and introduced earthworms on decomposition and nutrient cycling using soil taken from fresh coniferous forest. Species from each ecological category were taken for the studies. The soil processes in the presence of earthworms were compared to the processes in the soil where other soil fauna except earthworms were present. Disturbances in the soil were aimed to keep as small, but in order to reach high level of repeatability (to reduce high heterogeneity of the soil environment), mixing of the organic layer by sieving was found to be necessary. Experiments were carried out in the laboratory in microcosms in which fluxes of carbon and nutrients could be accurately determined. Finally, because plant productivity offers a good criterion to evaluate the outcome of invertebrate activities in soil (Wolters 1991), the microcosms with living birch seedlings were designed to study the importance of earthworms in primary production.

# 2 MATERIAL AND METHODS

## 2.1 The earthworms

Following species of earthworms were used in the experiments:

*Dendrobaena octaedra* (Savigny) (I, II) is a small, epigeic species, which is abundant in all types of forests in Finland (Terhivuo 1989). Its food consists of humus and plant material which has already been partly decomposed by other soil organisms.

*Lumbricus rubellus* (Hoffmeister) (I, II, III) feeds on leaf litter, and is common in coniferous forests, but abundant only in somewhat more fertile soils than the previous species. It is an epigeic species but can, to a some extent, mix the upper layers of soil.

*Aporrectodea caliginosa tuberculata* (Eisen) (IV) is an endogeic species which is most abundant in agricultural and garden soils, but it is also found in fertile forests (Bouché et al. 1988, Terhivuo 1989). This species burrows in deeper soil layers than the previous ones, taking its nutrition from soil organic matter.

*Aporrectodea velox* (Bouché) (V) is a large anecic species which is endemic in north-eastern France. It inhabits quite poor (low pH and low organic matter content) soils in a restricted area, but when occurring, it is an important species in the transformation of leaf litter (Rafidison 1982).

The earthworms, excluding *A. velox*, were sampled by hand near Jyväskylä and kept in laboratory cultures before their use for the experiments. Specimens of *A. velox* were taken by Dr. M. B. Bouché from Vosges, France. Before each experiment, the earthworms were introduced into the same soil and the same temperature in which the experiment will be done so that they could acclimatize.

Ten specimens of *A. velox* were introduced to a forest of moderate fertility, and ten to an abandoned field with low macrofaunal activity (V).

## 2.2 Soils used in the experiments

The soil materials used in the experiments were taken from moist coniferous forests near the town of Jyväskylä (Central Finland, 62°N and 25°E). The humus was sieved through a mesh (5-20 mm) and mixed thoroughly. Its initial pH was 4.0-4.2, and the organic matter content varied between 64 and 76%. The mineral soil was sand (II, III, V) or moraine (IV); it was sieved through a 4-mm mesh. The pH of the mineral soil was initially 5.0-5.9, and the organic matter content 0.5-1.4%. Litter layer consisted of fallen birch leaves (*Betula pendula* Roth) and spruce needles (*Picea abies* (L.) Karsten). In the experiments IV and V, the humus was slightly limed with $CaCO_3$ or $Ca(OH)_2$ before its use.

## 2.3 Experimental design

The experiments were carried out as microcosm experiments in the laboratory. The microcosms without plants were plastic vessels covered with air-tight lids. They contained either **1)** humus and litter layers (alcathene beads under the humus; I, V); or **2)** mineral soil, humus and litter layers (II, IV). The experiments with plants were carried out in acrylic cylinders with all three soil layers on the bottom. One seedling of silver birch (*Betula pendula*) was planted in each microcosm (III, IV). In the first experiment with plants, the microcosms were closed systems, through which a constant air flow was maintained (III). In the second experiment, open-top microcosms were used (IV).

In each experiment, there were basically two different kinds of treatments: the control with microbes and some soil animals that were initially present in the soil, and the identical system with additionally a certain number of earthworms. In the experiment IV, there were also treatments of inorganic N-fertilization (the level of nitrogen added corresponded to the increase due to earthworms), "artificial worms" (mechanical mixing), and soil preworked by earthworms (worms had been living in the soil but removed before the experiment). In addition, smaller scale experiments were carried out in order to study the effects of *A. c. tuberculata* on decomposition activity, and to find out a suitable pH-range for this species (IV). The detailed designs of each experiments (e.g. volumes of the microcosms) are described in the original papers.

All the experiment, excluding some preliminary tests (IV), were long lasting, at least four months and usually more than one year. The microcosms without plants were incubated in a climate chamber in the darkness at a constant temperature of 16±1°C, except during simulated winter conditions (I, II). To create the "winter", the temperature was lowered stepwise to 2±1°C, and raised again accordingly after 1-2 months (I-III). The microcosms with plants were incubated with varying temperature and illumination regimes in order to simulate the natural diurnal and seasonal cycles (III, IV).

## 2.4 Measurements during the experiments

Evolution of $CO_2$ in the microcosms was measured usually weekly using an infra-red carbon analyzer (URAS 7N). The air current was conducted from a compressor through the microcosms into the analyzer (I, II, V), or air samples were taken with a syringe and an injection needle from the air space of the microcosms and injected into the analyzer (III, IV). In the microcosms with plants, respiration was measured both in daylight and in darkness (III, not measured in the experiment IV). Cumulative respiration was calculated assuming linear change between measurements. The contribution of the earthworms to the total respiration was estimated by measuring the respiration from a known biomass of worms introduced into sterile, moistened sand (I).

The microcosms were irrigated at intervals (of 3-10 weeks excluding the winters) with distilled water to replace evaporated water and to analyze nutrient contents in leachates (I-V). In the experiment IV, the microcosms with plants were weighted once or twice a week, and evaporated water was replaced (no leachates were collected in this experiment). Concentrations of ammonium-N, nitrate-N, total N (including soluble organic, inorganic, and particulate N) and ortophosphate-P were measured photometrically according to standard methods used in water analyses (see I). The carbon in the leachates was determined with carbon analyzer after subsamples had been burned at +950°C (I, V). The pH of the leachates was measured, too (I-V).

Potential rate of denitrification was determined with the method based on the inhibition of nitrous oxide to gaseous nitrogen by acetylene gas (Kaspar & Tiedje 1980, Lumme & Laiho 1989).

## 2.5 Destructive samplings

After certain periods and the end of each experiment (part of the replicates) a destructive sampling was performed, and mass loss, pH (soil-distilled water suspension), KCl-extractable (2M) ammonium-N, nitrate-N, total-N, and ortophosphate-P were analyzed. Total carbon and nitrogen in the dry matter were analyzed with a Carlo Erba 1106 Elemental Analyzer (I, II, V). Total N in the plants was determined with the Kjehldal method separately from leaves, stems and roots (III, IV). The numbers of earthworms, their hatchlings and cocoons, as well as the numbers of other soil animals were counted. The adult earthworms were collected by hand from the soil, while the other fauna were extracted from the subsamples: enchytraeids and hatchlings of earthworms using the wet funnel method (O'Connor 1962), nematodes with modified wet funnels (Sohlenius 1979), and microarthropods with an extractor modified from the high gradient cylinder apparatus of Macfadyen (1961).

## 2.6 Statistical analyses

Differences between treatments were tested by Student's t-test (I-V) or by analyses of variance, followed by comparison in pairs by Tukey's test (IV). Square root transformation was used to normalize the distribution if necessary. Differences between treatments when the same replicates were measured several times during the long time period were tested by multivariate analysis of variance for repeated measurements (I, II).

# 3 RESULTS

## 3.1 Earthworms and other soil animals

The initial numbers and biomasses of the earthworms in the experiments (excluding *A. velox*) were within the natural ranges found in Finnish soils (Terhivuo 1989). In some experiments the biomasses decreased, particularly during the first half of the experiment (I-III). The earthworms, however, reproduced well, and new generations were present later (I, II). In every case, the adult (parent) earthworms were active for some periods of time (burrowing and mixing activity was observed), and they did not try to escape from the microcosms. In the experiments IV and V, when pH of the humus was raised by liming, the biomass of the earthworms increased.

The community of other soil animals was most diverse in the experiment II. Enchytraeids, nematodes and microarthropods from different taxa were included in the fauna. In the other experiments, the control fauna consisted mainly of nematodes (as well as protozoas and rotifers whose numbers were not estimated).

*A. velox* became established in the forest site, but not in the abandoned field. In the forest the earthworms survived some very cold winters, and reproduced, but dispersed only a few meters from the point of introduction (V).

## 3.2 pH of the soils

In the microcosms including only humus and litter layers, the earthworms significantly raised the pH of the soil and leaching water (I). In the presence of *L. rubellus* the increase was 0.2-0.6 pH units, and in the presence of *D. octaedra* 0.1-0.4 units (I).

When there was a mineral soil layer under the humus, the influence of earthworms was the opposite: during the first year of the experiment the pH was even 0.5 units lower in the presence of *L. rubellus* than without them. In this case, the difference levelled out later (II). When the humus was limed, earthworms either had no influence (*A.c. tuberculata*, with mineral soil; IV), or the pH was lower in the presence of earthworms (*A. velox*, without mineral soil; V).

In the experiments with birch seedlings, no significant differences were found in the pH of the soil with and without earthworms (III, IV).

## 3.3 Carbon losses through respiration and leaching

The litter feeding species *L. rubellus* and *A. velox* effectively consumed the leaf litter from the soil surface and incorporated it into the soil. Consumption of litter by the small epigeic species *D. octaedra* was also surprisingly high (I, II, V). *L. rubellus* and *A.c. tuberculata* also mixed organic matter into the mineral soil layer (II, IV).

In most cases the earthworms increased the soil respiration (I, II, IV, V). In addition to its own metabolism, *L. rubellus* stimulated the microbial respiration by 15-18%, and *A. c. tuberculata* by 16% (I, IV). The positive influence of *D. octaedra* was less marked (I). There were, however, variations in the differences of the respiration between worm worked soil and the controls during the time course. There were also periods when the respiration was lower in the presence of earthworms (see Fig. 1 in II). In the microcosms with birch seedlings, the plants assimilated almost all $CO_2$ from the air in both treatments (with and without earthworms). In darkness, the rate of respiration was higher in the presence of earthworms (III).

The carbon losses in the leaching water were small in comparison with the losses through the respiration even when only organic layer was included in the micrososms (1.2-1.4% of the carbon respired; I, V). The earthworms did not consistently affect the amount of carbon in the leachates (I, II, V).

## 3.4 Release of nitrogen and phosphorus

In the absence of living plants, the earthworms increased the leaching of nitrogen from the soil (I, II, IV, V). In the microcosms with litter and humus layers only, most of the mineral nitrogen was in the form of ammonium (I). Addition of the mineral layer turned the balance to nitrate-N (II). In the presence of *A. velox,* when also the pH of the soil was raised with liming, most of the mineral nitrogen was in the form of nitrate (V). In every case, however, the earthworms increased the amount of prevailing form of mineral nitrogen in the soil (I, II, IV, V).

The birch seedlings effectively utilized the mineral nitrogen from the soil: amounts of extractable nitrogen were low and no differences were found between microcosms with and without earthworms (III, IV). Only the addition of mineral nitrogen fertilizer resulted in elevated concentration of ammonium-N in the soil (IV).

In the microcosms in which the earthworm biomass decreased, the decaying earthworm carcasses were an additional pool of nitrogen. However, the nitrogen in the dead biomass could not explain (although totally mineralized during the experiment) the differences in the nitrogen content between soils with and without earthworms (I, II, III).

No significant denitrification was found to take place in the soil. A parallel set of microcosms was kept considerably moister than the main microcosms, and no denitrification was found even in these (II).

The total nitrogen content (dry matter) of litter and humus was lower in the microcosms with than without earthworms. In the litter the nitrogen content increased with time from the initial figure, while in the humus it first increased and then decreased (II). In the limed humus, both with and without *A. velox,* the nitrogen content clearly decreased (V).

The influence of earthworms on the mineralization of phosphorus was insignificant in most experiments (I, II, IV, V). Only *L. rubellus,* and only in some cases, increased the amount of mineral phosphorus in the soil (I, II). In the microcosms including the mineral soil layer, the amount of phosphorus in the leaching water and in the mineral soil was below the limit of detection (II, IV).

## 3.5 Growth and nitrogen content of birch seedlings

Birch seedlings became well established in the microcosms, and grew fast (III). In the first experiment (III), the seedlings failed to become infected with mycorrhizal fungi, but in the second one a vigorous growth of mycorrhizae were found in the roots (IV).

Both epigeic (*L. rubellus*) and endogeic (*A. c. tuberculata*) earthworms increased the growth of the birch seedlings (III, IV). The growth increment was the greatest in the leaves, but *A. c. tuberculata* also enhanced the growth of stems and roots (IV). Neither the fertilization with mineral nitrogen nor the mixing of soil with the aid of "artificial worms" exerted significant effects on the growth (IV).

In the first experiment with plants (III), the total nitrogen concentration in the plants was significantly higher in the presence of earthworms (*L. rubellus*). This difference remained also in the fallen leaf litter. In the latter experiment (IV), the earthworms had no influence on the nitrogen concentrations of the plants, but because of the greater biomass, the total amount of nitrogen accumulated in the leaves was significantly greater in the presence of earthworms.

# 4 DISCUSSION

## 4.1 Development of earthworm populations

Mortality of *L. rubellus*, and to a certain extent also that of *D. octaedra*, induces some problems when evaluating the effects of earthworms on soil processes (I-III). Also in many other laboratory studies, the mortality of earthworms has turned out to be a problem (e. g. Atlavinyte et al. 1968, Marshall 1971, Graff & Makeschin 1980, McColl et al. 1982, Scheu 1987b). In long lasting microcosm experiments the earthworms may become stressed in artificially created environments without possibilities for habitat choices or migrations. In this study (experiments I-III) it is possible, however, that since all the specimens introduced were adults (because the identification of juveniles is uncertain), most of the earthworms may have died naturally due to their short lifespan. The populations, however, did not die out; cocoons and hatchlings were produced, but the growth of the new generation was rather slow (I, II). The dead earthworms did not contribute to the soil processes, but on the other hand, decomposing tissues served as additional nutrient source in the soil.

The survival, growth and reproduction of the earthworms was found to be directly associated with soil pH (IV). Laverack (1961) and Springett & Syers (1984) have also shown that the pH *per se*, rather than other factors associated with pH, determines the success of earthworms. According to literature (e.g. Edwards & Lofty 1977), the pH of the humus used in the experiments I-III was near the lower tolerance level for the species studied. It is possible that the earthworms suffered from the acidity of the organic layer when the natural heterogenous structure of the humus was broken by sieving (pockets of higher pH were disappered). The earthworms burrowed quickly into the homogenized humus, however, and the pH of the mineral soil under the humus was somewhat higher. Thus, some other factors than acidity must have mainly been responsible for the mortality of *L. rubellus* in the microcosms.

One possible factor, although not studied here, which influences the success of earthworms is the interaction with other soil animal groups. Earthworms can alter the population size and structure of other fauna and via versa (e.g. Haukka 1987: earthworms - enchytraeids; Hamilton & Sillman 1989: earthworms - microarthropods). There is also evidence that larger earthworm species may reduce the numbers of smaller ones (Huhta 1979).

The introduction experiment with *A. velox* in the present study showed that it would be possible to introduce new deep burrowing earthworm species to northern forests, but particular attention must be paid to the dispersal capacity of the species and to the acidity of the soil.

## 4.2 Effects of earthworms on soil pH

It has been demonstrated in several studies that the pH of earthworm casts is closer to neutral than that of bulk soil. Usually, the pH of the forest soil is below 7, and the pH of earthworm casts somewhat higher than in the surrounding soil (see the comprehensive review by Lee 1985). In this study the earthworms increased the soil pH with organic layer only, but decreased the pH when mineral soil was present under the organic layer although the initial pH was always below 7.

Earthworms may alter the soil pH in several ways. The increase of pH in earthworm casts derived from acid forest soils may result from excretion of ammonia or from the production of calcium carbonate in calciferous glands (Lee 1985). Robertson (1936) already found, however, that calciferous glands serve some other function than neutralization of dietary acids, and that the large resistant concretions of calcium carbonate observed in the oesophageal pouches have little effect on soil pH. Thus, it seems that calciferous glands assist in the regulation of tissue pH more than the pH in the gut (Piearce 1972).

It seems obvious that the effect of earthworms on pH is related to increased concentrations of mineral nitrogen in soils, and to changes in the ratio of ammonium to nitrate (I, II, V). The same conclusion was made by Robinson et al. (1992). The conversion of organic nitrogen to ammonia, and further to ammonium, temporarily increases the soil pH, while the oxidation of ammonium to nitrate decreases it (e.g. Binkley & Richter 1987). In the presence of plants (and in the field) the role of different forms of nitrogen is more complex. When taking up nitrogen from the soil, plants exchange nitrate ions to OH$^-$ and ammonium to H$^+$, which means an increase or decrease in pH, respectively. Thus, there are several reactions which determine the final outcome of different nitrogen forms in the soil pH (Mälkönen et al. 1990). That is why it is not enough to determine the pH of the casts *per se*, but what kind of effect these casts have on the pH of the soil in which they are deposited. In moderately limed soil earthworms seemed to have no effect on soil pH (IV, also in the study of Robinson et al. 1992), probably because other ions exerted greater effects on pH. It seems, however, that in certain circumstances earthworms can increase the soil pH, which in turn can enhance activity of microbes and nutrient uptake by plants. Moreover, it has also been found that the activity of earthworms can act as a buffer against the acidification processes (Scheu & Wolters 1991a).

## 4.3 Decomposition of organic matter

The effects of earthworms on decomposition are closely related to their effects on soil microflora. In the present study, only 20-30% of the increased soil respiration was estimated to be due to the earthworms' own metabolism, the rest being due to stimulated microbial activity. Normally, earthworms digest very little from their food (Lee 1985). Organic matter ingested by earthworms, while becoming finely ground physically, undergoes only minor chemical changes during passing through the gut. There is a general agreement that microbial biomass is not significantly changed during the gut passage (Scheu 1990, Daniel & Anderson 1992), but that the activity of microbes is greatly stimulated (Parle 1963, Syers et al. 1979, Scheu 1987a, Wolters et al. 1989, Elliott et al. 1990 & 1991, Wolters & Joergensen 1992). This has been observed as increased respiration, nitrification or denitrification in the gut and casts. The present study clearly demonstrated that earthworms stimulate microbial respiration when actively feeding and casting. It was found by Wolters et al. (1989) that incorporation by *A. caliginosa* cause an increase in bacterial and a decrease in fungal metabolism in the soil. Hanlon (1981) and Scheu (1990) concluded that the effect of decomposer invertebrates on the soil microflora depends on the nutrient status of the ecosystem. There is also evidence that the stimulation effects of earthworms on the soil microflora may loose its significance in acidified soils (Wolters & Joergensen 1992; on the other hand, see previous section of this thesis). This may greatly concern the boreal coniferous forests where the buffering capacity of soils is very low.

A recent study by Martin et al. (1992) demonstrates that earthworms assimilate, and therefore mineralize, preferentially easily decomposable organic compounds. It is obvious, however, that when deriving their energy from humus earthworms also contribute to the decomposition of native organic matter (IV). Very high assimilation efficiences (more than 50%) of highly palatable plant material observed by Dickschen & Topp (1987) for *L. rubellus* and by Daniel (1991) for *L. terrestris* indicate that litter-feeding earthworms may also have, under certain circumstances, a significant direct effect on decomposition.

## 4.4 Mineralization of nitrogen and phosphorus

Since earthworms excrete considerable amounts of nitrogenous products into the soil in casts, urine and mucoproteins (Lee 1983), it is obvious that earthworms can directly increase the amount of mineral nitrogen in soils. It should be noted that most of the excretion products are in a form readily assimilated by soil microbes. On the other hand, microbes are an important component of the diet of earthworms (Wright 1972, Piearce 1978, Cooke 1983). Wolters & Joergensen (1992) concluded that in beech forest soils, stimulation of nitrogen mineralization by earthworms could be explained by mobilization of nitrogen stored in the biomass of the microflora. Thus, it is obvious that both direct (excretion) and indirect mechanisms (earthworm-microbial interactions) partly explain the increased concentrations of mineral nitrogen in the presence of earthworms, and that there is an efficient recycling of nitrogen through earthworms, microbes and back to earthworms. This was shown to be the case also in coniferous forest soil (I, II, IV, V). There were, however, differences between the earthworm species. The contribution of the small epigeic *D. octaedra* to nutrient cycles was found to be insignificant (I). In the experiments where the earthworm biomass decreased (see section 4.1), the nitrogen released from decomposing tissues could not explain the increased amounts of nitrogen in the presence of earthworms (I-III).

Soil animals have been found to enhance nitrification or accelerate the onset of nitrification in laboratory incubations (McColl et al. 1982, Anderson et al. 1985, Scheu 1987b) and in the field (Anderson & Leonard 1988). The results of the present study show that when the circumstances are favourable for nitrification, earthworms enhance the activity of nitrifying microbes (II, V).

It has been shown that in agricultural and pasture soils denitrification can be higher in earthworm casts than in bulk soil (Svensson et al. 1986, Elliott et al. 1990, 1991). In coniferous forest soil with loose, well aerated structure, denitrification is obviously not an important route of nitrogen losses. This was supported by this study (II). No significant denitrification was observed with or without earthworms even when the soil was kept unnaturally wet.

Even though coniferous forest soils usually have a large storage of nitrogen, only about 1% of this is present in a mineralized form (e.g. Viro 1969). Thus, because of the low rate of nitrogen cycling, a deficiency of available nitrogen is usually the factor limiting tree growth (e.g. Kukkola & Saramäki 1983). On this background, the consistent stimulative role of earthworms in nitrogen mineralization deserves considerable attention (see below).

Increased amounts of mineralized phosphorus in earthworm casts and in soil with earthworms have been observed by many authors (e.g. Sharpley & Syers 1977, Mansell et al. 1981, Mackay et al. 1983). The mechanisms behind the effects of earthworms are mainly physical (Mansell et al. 1981, Mackay et al. 1983). In addition, Bogatyrev et al. (1983) and Cline et al. (1985) found that phosphorus mineralization is mainly due to chemical transformations in litter and soil. Results of the present study suggest that activity of earthworms do not significantly affect phosphorus mineralization in coniferous forest soils, and that phosphorus release may substantially be a non-biologically mediated process.

## 4.5 Effects of earthworms on plant growth

The positive effects of earthworms on plant growth and productivity have been extensively documented, but mainly in arable and grassland soils (Hopp & Slater 1949, Atlavinyte et al. 1968, van Rhee 1977, McColl et al. 1982, Stockdill 1982, Hoogerkamp et al. 1983, Curry & Boyle 1987). Direct evidence on the influence of earthworms on tree growth has been reported only in a few studies. In these cases, the effect of earthworms has been slightly positive (Zrazhevskii 1958, Marshall 1971). In the present study, both *L. rubellus* and *A. c. tuberculata* significantly enhanced the growth of birch seedlings in coniferous forest soil. Obviously there are several factors through which earthworms affected the growth. The elevated mineral nutrient concentration in soils throughout the growing period in the presence of active earthworms is undoubtedly of major importance. Other factors induced by earthworms, like higher $CO_2$ concentrations in the air, higher amounts of growth promoting substances in the soil, and changes in the physical structure of the soil may also be important, but were partly excluded in the second experiment (IV). It was also found that continuous fertilization with mineral nitrogen (the level of application corresponded to the amount increased by earthworms) would not necessarily increase the plant growth. Anderson & Leonard (1988) concluded that a large part of the nitrogen mobilized by macro-invertebrates is taken up by plants. It has been also pointed out that the enhanced nitrogen mineralization due to earthworms and the nutritional needs of plants are in good synchrony, especially in soils where nitrogen is a limiting factor for plant growth (Lavelle et al. 1992). These observations were supported in the present work.

It is possible that earthworms consume living plant roots (Cortez & Bouché 1992), and when present in high numbers could decrease the plant production, particularly in the root system, by overgrazing (Hameed et al. 1993). It is not obvious, however, that this kind of overgrazing could be common in the field, but in the microcosm studies it should be taken into account.

Alterations of nitrogen availability by soil animals may also affect the resource allocation of plants. Microfaunal grazing in the rhizophere (Clarholm 1985, Kuikman & van Veen 1989), and burrowing by endogeic earthworms (Wolters & Stickan 1991) accelerated the plant growth, increased the shoot to root ratio and decreased the fine root production. On the other hand, van Rhee (1977) found in the apple orchard more fine tree roots in soils with earthworms than in soils without them. In the present study the litter-feeding earthworms increased (III), while the endogeic ones did not affect the shoot to root ratio of birch seedlings (IV). It has been suggested that plants growing in soils with good nutrient status invest less of their production to root growth than do plants in nutrient poor environment (McClaugherty et al. 1982).

There are only a few data available on the influence of earthworms on the nutrient content of plants, and in most cases no effects have been found (Marshall 1971, MaColl et al. 1982, James & Seastedt 1986). In this study, the nitrogen concentration of the birches, and particularly in their leaves, was significantly increased in the presence of *L. rubellus*. Thus, the seedlings growing in the worm-worked soil derived benefit of the improved nutrient status not only by increasing the biomass production but also by producing biomass with higher nutrient content.

## 4.6 Impact of different earthworm species

Epigeic (*L. rubellus*) and endogeic (*A. c. tuberculata*), as well as anecic (*A. velox*) earthworms highly influenced the decomposition processes in microcosms with coniferous forest soil. The small epigeic species *D. octaedra* had only a slight impact on the processes, but its effect on the incorporation of leaf litter was unexpectedly high (I). Scheu (1987c) concluded that in a beech forest endogeic earthworms have the greatest effect on nutrient cycling through their burrowing activity. In the present study also the relative importance of epigeic and anecic species was found to be high.

Incorporation of litter from the soil surface and organic matter from the humus layer to the mineral soil by earthworms can lead to the formation of a mull soil (Scheu & Wolters 1991a,b). On the other hand, acid precipitation may decrease the rate of litter mineralization on the soil surface, which may lead to an accumulation of leaf litter and maintenance of a mor soil structure. Thus, the "cooperation" between litter-feeding epigeic and anecic (removing litter from the soil surface) and geophagous endogeic (mixing different materials) earthworms could lead to the formation or maintenance of a mull soil structure in forests which in turn would lead to higher productivity of the ecosystem. This hypothesis is worthy of studying with field experiments also in extreme habitats, like coniferous forests.

It is most probable that of the species studied here only the epigeic ones can survive and establish themselves in coniferous forest soils without any manipulation. The establishment of the deep burrowing species would require at least manipulation of the soil pH. The results of this study suggest, however, that it would be of theoretical and practical interest to carry out field experiments on the impact of both native, introduced and managed earthworms on the soil processes in the coniferous forests.

# 5 CONCLUSIONS

This laboratory study clearly showed that the presence or absence of one soil animal group, like earthworms, can have significant effects on the function of soil ecosystem. Earthworms accelerate the decomposition of organic matter and render the mineralization of nutrients more effective in fresh coniferous forest soil. Mineralization of nitrogen due to earthworms is in synchrony with plants' needs, and mineral nutrients are not lost from the soil. It was found that earthworms affect the soil processes both directly and indirectly. The results showed, however, that indirect effects (observed as increased microbial respiration and nitrification) are in crucial importance.

The results derived from the microcosm experiments carried out in the laboratory should be applied to the field conditions with care. Although the microcosms used in the present study were quite heterogenous in their structure (both biotically and abiotically), the complexity of interactions within the biotic compartment as well as that between biotic and abiotic compartments was partly lacking.

It has been hypothesized by Anderson et al. (1983) that coniferous forests are conservative in the utilization of nitrogen for sustained productivity, and smaller changes in the fluxes may have a greater significance for forest processes than in e.g. deciduous forests. Thus, because management practices can influence soil animal populations and community structure (Huhta 1979, Huhta et al. 1986b), it would be worth to study the bioturbation effects of earthworms in the field conditions also in coniferous forests. It has been found that the greatest absolute growth increase after nitrogen fertilization is in the forests of medium productivity (as the soil studied here) (Mälkönen et al. 1990). Nitrogen deficiency is not significant in the most fertile forests, where diverse earthworm fauna is normally well established in high numbers.

All of this implies that also earthworms should be taken into account when effects of silvicultural practices are studied in coniferous forests, or when new alternative, "more ecological", silvicultural methods are searched. Setälä (1990) has recently shown that the structure of a faunal community (earthworms were excluded) has a great effect on forest soil processes. A diverse fauna enhances decomposition and nutrient mineralization more than a simple one. Thus, the diverse soil fauna including earthworms would ensure the health and productivity of the soil and moreover the health and productivity of the whole forest ecosystem.

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## Yhteenveto

### Lierojen vaikutus kangasmetsämaan orgaanisen aineen hajotukseen ja ravinnekiertoihin

Tutkimuksen tavoitteena oli selvittää kokeellisesti, mikä merkitys lieroilla on tuoreen kangasmetsän hajotuksessa, ravinnekierroissa ja kasvien kasvussa. Tutkittuja lajeja olivat kangasmetsän pintamaassa luontaisesti elävät metsäliero (*Dendrobaena octaedra*) ja onkiliero (*Lumbricus rubellus*). Lisäksi tutkittiin millainen vaikutus lievästi kalkitun metsämaan hajotusprosesseihin on syvemmällä maassa elävällä peltolierolla (*Aporrectodea caliginosa tuberculata*) ja isokokoisella Ranskasta tuodulla lierolajilla (*Aporrectodea velox*).

Tutkimuksen kokeet tehtiin kokonaisuudessaan laboratoriossa, jossa kangasmetsän maaperää jäljiteltiin tiivisti suljettavissa koeastioissa (mikrokosmoksissa). Maaperä sisälsi joko homogenisoidut karike- ja humuskerroksen tai edellisten lisäksi myös mineraalimaakerroksen. Kahdessa koesarjassa mikrokosmoksiin istutettiin lisäksi koivuntaimi (tutkittavina lierolajeina olivat onki- ja peltoliero). Puoleen koeastioista lisättiin tietty määrä tutkittavaa lierolajia toisen puolen ollessa kontrolleina. Kaikissa koeastioissa oli metsämaan luontainen mikrobisto ja vaihteleva määrä muita maaperäeläimiä kuin lieroja. Kokeet olivat pitkäkestoisia (vähintään useita kuukausia kestäviä). Koeastiat säilytettiin kasvukammioissa, joissa vuorokausi- ja vuodenaikaisrytmiikan säätö (lämpötila, valo, kosteus) oli mahdollista.

Lierojen vaikutusta hajotukseen ja ravinteiden kiertoon tutkittiin mittaamalla säännöllisesti maan biologista aktiivisuutta (hiilidioksidituottoa). Tietyin väliajoin koeastioiden maata kasteltiin sadetta jäljitellen, ja maan läpi uuttuneesta vedestä mitattiin uuttuneiden ravinteiden määrät ja pH. Kokeiden lopussa maan eri kerroksista mitattiin pH, orgaanisen aineen pitoisuus ja ravinnepitoisuudet sekä laskettiin eläinten määrät. Kasvien kasvua ja ravinnepitoisuutta käytettiin myös keskeisenä lierojen vaikutuksen mittarina.

Kaikilla lierolajeilla oli mitattava vaikutus maan hajotusprosesseihin, pienikokoisella metsälierolla tosin harvoin merkitsevä. Säännön mukaan lierot lisäsivät maan mikrobiston aktiivisuutta ja nopeuttivat typen vapautumista orgaanisesta aineesta. Lierojen aktiviteetti (syöminen-ulostaminen ja sekoitustoiminta) edisti myös nitrifikaatiota (ammoniumtypen muuttumista nitraattitypeksi). Fosforin kiertoon lierojen vaikutus oli vähäinen.

Lieroilla oli selkeä vaikutus maan happamuuteen. Humus- ja karikekerroksessa ne vähensivät merkitsevästi happamuutta, mutta kun humuksen alla oli mineraalimaata, vaikutus oli päinvastainen johtuen todennäköisimmin lisääntyneestä nitraattitypen määrästä.

Sekä onki- että peltoliero nopeuttivat yksiselitteisesti koivuntaimien kasvua. Onkilierolla oli lisäksi positiivinen vaikutus kasvin (erityisesti lehtien) typpipitoisuuteen. Maan typpilannoitus tai mekaaninen, lierojen toimintaa jäljittelevä sekoitus, eivät saaneet aikaan vastaavaa kasvunlisäystä koivuntaimissa.

Ranskasta peräisin olevalla isokokoisella lierolajilla tehtiin pienimuotoinen istutuskoe maastossa. Lajin todettiin kestävän hyvin Suomen talviolot; lierot ovat eläneet toisella istutuspaikalla kuusi vuotta ja lisääntyneet hyvin, mutteivat ole kuitenkaan levinneet istutuspaikalta ympäristöön.

Tutkimus osoitti, että lieroilla on huomattava vaikutus maaperän hajotustapahtumiin ja maan kasvukuntoon myös esiintymisalueensa äärilaidoilla. Lierojen läsnäollessa mikrobiston aktiivisuus lisääntyy ja ravinteiden kierto maassa nopeutuu ja tehostuu. Kasvien osoitettiin hyödyntävän tehokkaasti parantuneet kasvuolot. Vastaavanlaisia tutkimuksia on aikaisemmin tehty lähinnä vain lauhkean ja lämpimän ilmaston pelto- ja lehtimetsämailla. Nyt kehitetyt mikrokosmostekniikat elävine puuntaimineen ovat myös edistystä alan tutkimuksessa. Tutkimuksen tulokset osoittavat, että jo yhdellä eläinryhmällä voi olla suuri merkitys maaperän hajotusprosesseissa ja sitä kautta koko ekosysteemin toiminnassa. Tulokset antavat myös aiheen sekä perusekologisiin että ympäristönhoidollisiin jatkotutkimuksiin kenttäoloissa.

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# ORIGINAL PAPERS

# I

# Effects of earthworms on decomposition processes in raw humus forest soil: a microcosm study

by

Jari Haimi & Veikko Huhta

Biology and Fertility of Soils 10: 178-183, 1990

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# II

# Influence of a litter feeding earthworm, *Lumbricus rubellus*, on soil processes in a simulated coniferous forest floor

by

Jari Haimi & Mustapha Boucelham

Pedobiologia 35: 247-256, 1991

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## III

# Growth increase of birch seedlings under the influence of earthworms - a laboratory study

by

Jari Haimi, Veikko Huhta & Mustapha Boucelham

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# IV

# Effects of endogeic earthworms on soil processes and plant growth in coniferous forest soil

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Jari Haimi & Mark Einbork

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# V

# Effects of an introduced earthworm *Aporrectodea velox* on nutrient dynamics of forest soil

by

Jari Haimi

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# Effects of an introduced earthworm Aporrectodea velox on nutrient dynamics of forest soil

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## Abstract

Aporrectodea velox (Bouché), an earthworm species endemic in France, was introduced to an abandoned field and a forest site (both conifers and deciduous trees) near Jyväskylä, Central Finland. The earthworms established themselves only in the forest where they survived for more than six years. During that time they reproduced, but migrated only a few meters from the initial point of introduction.

Effects of A. velox on decomposition and nutrient cycling in humus-rich forest soil were studied in a laboratory experiment. A. velox gained weight during the experiment, and had a positive influence on the microbial respiration as well as on the mineralization of nitrogen. Nitrification rate was high in the soil both with and without earthworms, but it was enhanced by the feeding activities of the earthworms. A. velox had a negative influence on the soil pH, which was artificially raised by liming before the experiment.

## 1. Introduction

Rate of active dispersal of earthworms is usually regarded as slow, and possibly there are large areas which more species could have colonized if they had only managed to migrate there. This kinds of areas are obviously common at northern latitudes where there are many kinds of impassable barriers for dispersal (acid and dry coniferous forests, large bog areas, distance with regard to the relatively short time after the last glaciation, etc.).

Man is undoudtedly playing an important role at least in long distance migrations of earthworms (Lee 1985). There are several examples in which earthworms, either intentionally or accidentally, have successfully been introduced into new areas. The populations have been observed to disperse from the original introduction sites, and their activities have been found to increase the soil fertility (van Rhee 1969; Stockdill 1982; Hoogerkamp et al. 1983; Ghilarov & Perel 1984). The fact that earthworms enhance decomposition and nutrient cycling in the soil makes it reasonable to manipulate the earthworm fauna by man.

The earthworm fauna of fresh coniferous forests in Fennoscandia consists of few species, mainly living in the upper layers of soil. Most of the species common in Southern and Central Europe can obviously not survive the cold winters of Fennoscandia. Furthermore, the acidity of coniferous forest soils undoubtedly makes them unfavourable for most of the species. There may, however, be some species whose environmental requirements could be met in the soil of northern forests. Huhta (1979) has shown that the native endogeic <u>Aporrectodea caliginosa</u> can be managed in coniferous forest soils with simple practices (liming or addition of leaf litter). Springett (1985) suggested that it may be important for the long-term soil fertility if the earthworm fauna includes a range of species occupying different ecological niches. In addition, it has recently been observed that earthworms might have significantly higher potential for migration than previously believed (Mather & Christensen 1992). These observations led to a question: would it be possible to add new deep burrowing (anecic) species to northern forest soils?

An anecic species <u>Aporrectodea velox</u> (Bouché) was chosen for the experiments, because it burrows very deep (mixing the soil horizons), lives in fairly unfertile soils in north-eastern France, and has a long lifespan as abult (Bouché 1972). It is also an important species in transformation of leaf litter (Rafidison 1982). The effects of this species on nutrient cycling and decomposition of organic matter in fresh coniferous forest soil were studied in a laboratory experiment. In order to get results comparable with those from similar studies with native species (Haimi & Huhta 1990, Haimi & Einbork 1992), the same experimental design was used.

## 2. Material and methods

### 2.1. Microcosm experiment

The soil used in this experiment was the same as that in previous experiments with native earthworm species (Haimi & Huhta 1990). Raw humus from a moist coniferous forest near the town of Jyväskylä, Central Finland, was sieved through a 5-mm mesh and mixed thoroughly. The initial organic matter content of the humus was 76.1 %, carbon content 41.6 %, nitrogen content 1.10 % and pH 4.15. Before the start of the experiment, pH of the homogenized humus was raised to 6.0 with lime ($Ca(OH)_2$), because the soil was initially too acid for A. velox (Bouché 1972). Birch leaf litter (Betula pendula) was collected soon after snowmelt. Its carbon content was 51.3 % and nitrogen content 1.33 %.

A layer of alcathene beads was spread on the bottom of six plastic vessels, each 0.085 $m^2$ in area. Fine nylon mesh (0.07 mm) was placed on this layer, and 400 g of humus (fresh mass, 194 g in dry mass) was spread on the mesh in each vessel. The humus was lightly packed and covered with a 3-mm mesh. 15 g of birch leaf litter (dry mass) was added on the coarse mesh, and further 2 g was added after 16 weeks. Two or three specimens of A. velox were introduced into each of three vessels (mean biomass 17.6 g f.m.). The specimens originated in Vosges, France (48°N and 6°E), and they were provided by Dr. M. B. Bouché. During the experiment, the vessels were incubated in a climate chamber in darkness at a constant temperature ($15 \pm 1$ °C).

The vessels had lids with four holes covered with 0.25 mm mesh. Each vessel had also a hole in the bottom, through which leaching water was collected for analyses, and two holes in the walls for air flow. The evolution of $CO_2$ in the vessels was measured weekly with an infra-red carbon analyzer (URAS 7N). During the measurements, lids without holes were used, and an air current was conducted through the vessels into the analyzer (for a more specific description, see Haimi & Huhta 1990).

The vessels were irrigated four times during the experiment (at weeks 4, 7, 11 and 16), and destructively sampled after 19 weeks. $NH_4^+$-N, $NO_3^-$-N, total N (including soluble organic, inorganic and particulate nitrogen) and $PO_4^{3-}$-P were analysed photometrically from the leachates (see Haimi & Huhta 1990). The amount of carbon in the leachates was determined using the URAS 7 N after burning subsamples (50 $\mu$l) at + 950°C. At the destructive sampling the nutrient content of humus was analysed from KCl-extractions in the same way as from the leachates (Haimi and Huhta 1990).

### 2.2. Introduction experiment

Ten adult specimens of A. velox were introduced to two different kinds of habitats near Jyväskylä (62°N and 25°E) on May 28, 1986. One was an abandoned field with low macrofaunal activity in the soil. Only a sparse population of A. caliginosa tuberculata was present at the site. Litter produced by the ground layer vegetation had been accumulated on the soil surface. pH of the topsoil was 4.9 (SD 0.1) and organic matter content was 12.1(0.4)%. Another habitat was a mixed forest site (birch, pine and alder). pH of the soil was 6.0 (0.1), and organic matter content 27.5(0.7)%. At this site, A. c. tuberculata, Lumbricus rubellus and Dendrobaena octaedra were found.

At both sites a hole was dug into the soil and the earthworms were placed on the bottom of the hole. The earthworms were carefully covered with soil in order to prevent predation by birds.

Both sites were checked at least twice a year over a period of six years. Castings on the soil surface were counted and the rate of dispersal was measured. After four years the populations were sampled with the formaline method.

## 3. Results

### 3.1. Effects of A. velox on the soil processes

The biomass of A. velox increased during the laboratory experiment by an average of 23 % [4.1(SD 1.8)g fresh mass with gut content]. The carbon loss from the system was greater in the presence of A. velox, mainly due to higher losses in $CO_2$ (Table 1).

The earthworms consumed 15.5(0.6)g of leaf litter during the experiment [mass loss of litter was 5.7(0.6)g in the controls]. pH of the soil decreased both with and without the earthworms, but less in the absence of them (Tables 2 and 3).

The amount of mineral nitrogen in the leachates from the humus was higher with A. velox than without it (Table 1). $NO_3$-N was elevated at most irrigations. During the experiment, the nitrogen content of humus (dry matter) decreased clearly both with and without A. velox; after 19 weeks the nitrogen-% was 0.83(0.10) with earthworms, and 0.77(0.04) without them (initially 1.10). At Week 19 there was more KCl-extratable total-N and $NO_3^-$-N but less $NH_4^+$-N in the humus with A. velox (Table 3). There were no significant differences in the amounts of $PO_4^{3-}$-P in the leachates, nor in the KCl-extracts.

A. velox altered the structure of the humus; their castings formed stable aggregates in the soil. The water holding capacity of worm-worked and control soil was compared by measuring the water content of soil samples both one hour and 24 hours after sinking them in water. The soil in the presence of A. velox contained 83.3(3.0)% of the water after 24 hours, while the figure was 65.8(2.6) in the control soil. At the end of the experiment, there were 196(85) nematodes per one gram of soil (dry mass) in the presence of earthworms, and 415(352) nematodes per gram in the controls.

### 3.2. Establishment of populations in the field

Activity of A. velox is relatively easy to observe because it produces big pipe-like casts onto the soil surface. Five months after the introduction only four castings were found at both sites. In the abandoned field the earthworms did not survive over the first winter; no fresh castings were found in 1987 or later on. At the forest site the population survived, but the activity was low over the years 1987 and 1988.

In 1989 and 1990, the activity of *A. velox* increased at the forest site. In the spring 1990 more than 10 big fresh castings were counted at the introduction site. The dispersal of earthworms had been minimal, only 3-4 meters. In June 1990 an earthworm sample was taken using the formaline method from an area of 2 $m^2$ at the introduction point. Fifteen juveniles of A. velox were caught. Other species found were L. rubellus (24 ex.), A. c. tuberculata (1 ex.) and D. octaedra (1 ex.). Adults of A.

velox did not emerge to the soil surface. In September 1991, 15 big fresh castings of A. velox were observed at the introduction site. The population had dispersed no more than five meters.

## Discussion

A. velox affected positively the soil processes, as did the native species in the previous experiments (Haimi & Huhta 1990, Haimi & Einbork 1992). In addition, A. velox had a strong influence on the soil structure. This anecic species can effectively mix materials between different soil horizons, as was observed in the field where big amount of mineral soil was brought up onto the soil surface. In the laboratory experiment the biomass of A. velox increased, even though it was initially high in relation to the amount of substrate [207 g (f.m.) m²]. The effect of A. velox on the soil pH was opposite to that of the indigenous earthworm species (Haimi & Huhta 1990). The pH of humus had been raised with lime to ca. 6.0, but it continued to rise above neutrality during the first few weeks. The negative effect of A. velox on the pH was at least partly connected to their positive effect on the amount of $NO_3^-$-N in the humus. Nitrification occurred both with and without the earthworms, obviously due to the increased pH, and it was accelerated by the function of *A. velox.* The enhancement of nitrification indicates the importance of indirect effects of earthworms in the nitrogen cycles (cf. Anderson et al. 1985). The higher concentration of ammonium in the leaching water in the presence of A. velox may at least partly be due to direct effect (excretion) of earthworms.

Leaching of nitrogen was much higher both in the controls and in the presence of A. velox, compared to the experiments with unlimed humus and the species L. rubellus and D. octaedra, while the amounts of nutrients in the KCl-extractions were of the same order of magnitude. A greater proportion of the KCl-exractable total N was in mineral form in comparison with the previous experiments (Haimi & Huhta 1990). The higher pH of humus in the present experiment undoubtedly favoured the microbes responsible for the mineralization of nitrogen. This is supported by the higher level of microbial respiration in the present experiment.

The present experiment showed that A. velox would be able to live at the northern latitudes, and withstand cold winters (frost penetrating deep into the soil). The low pH in coniferous forest soils may prevent, however, the establishment of this species. The reasons why A. velox did not become established in the abandoned field remained obscure. Shortage of suitable food and adverse soil conditions at the depths to which this species burrows may be among possible factors.

We know little about the competition between earthworm species (Lee 1985). More research is needed on interactions between native and newly introduced earthworms. Nevertheless, although the population density of A. velox was very high, and they altered the soil structure at the introduction site, they did not compete out (eliminate) the native species. If a native anecic species, such as *L. terrestris*, had existed at the site, competion for food and space would have been more obvious.

There are published observations on the rate of migration only for a few earthworm species. van Rhee (1969), Stockdill (1982), and Hoogerkamp et al. (1983) showed in their introduction experiments that the endogeic species A. caliginosa can spread 6-10 meters per year. The anecic L. terrestris spread 4.5 m/y on an average (Hoogerkamp et al. 1983). Langmaid (1964) observed a much faster dispersal of several lumbricids in acid podsol soils in Canada. Mather & Christensen (1992) have recently reported observations which imply relatively high mobility of several species of earthworms. They suggested that surfage migration is a normal resource-seeking activity, not necessarily connected to adverse conditions in the soil. They concluded that slow colonisation rates observed previosly are from sub-optimal habitats (introductions into areas which were devoid of earthworms). It is not sure, however, whether the surface migration leads to colonisation of new areas or do the earthworms return close to the area they started from. Rate of population expansion of A. velox seemed to be extremely slow in comparison with the common species mentioned above. The population exploits the same small area for several years. It is obvious that weak migration capacity of A. velox explains at least partly its restricted distribution in France (endemicity). Thus, A. velox would not be a good candidate for larger scale introductions.

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Table 1. Cumulative leaching (4 irrigations) of N and P from humus with and without A. velox (mg per vessel; mean and SD). Mean loss of C (g per vessel) calculated from the weighed mass loss (W), cumulative respiration (R), and total C leached (L). n = 3; $NO_3^-$-N and Total N were analysed from pooled samples. Significant differences are indicated by asterisks (Student's t-test: ** $P<0.01$).

| | Without A. velox | With A. velox |
|---|---|---|
| $PO_4^{3-}$ | 0.8(0.1) | 1.3(0.4) |
| $NH_4^+$ | 1.9(0.1)** | 4.0(0.4) |
| $NO_3^-$ | 6.6 | 29.6 |
| Total N | 16.4 | 48.7 |
| Carbon losses | W:7.29(0.49) | W:10.94(1.79) |
| | R:6.96+L:0.09 | R:7.77+L:0.11 |

Table 2. pH values of the leachates with and without A. velox (mean and SD). Significant differences as in Table 1 (n=3).

| | Without A. velox | With A. velox |
|---|---|---|
| Week 4 | 7.29(0.03)** | 7.11(0.05) |
| Week 7 | 7.33(0.04) | 6.89(0.36) |
| Week 11 | 7.02(0.13)** | 6.40(0.06) |
| Week 16 | 6.68(0.09) | 6.59(0.18) |

Table 3. pH and amounts of nutrients (KCl-extraction, mg per vessel, mean and SD) in soil with and without A. velox after 19 weeks' incubation. n = 3 for all. Significant differences as in Table 1 (* $P<0.05$, ** $P<0.01$).

| | Without A. velox | With A. velox |
|---|---|---|
| $PO_4^{3-}$ | 18.8(0.3) | 20.7(1.3) |
| $NH_4^+$ | 6.2(3.3) | 1.4(0.6) |
| $NO_3^-$ | 55.0(3.4) ** | 106.6(13.5) |
| Total N | 100.2(6.0)* | 144.2(19.6) |
| pH | 6.85(0.04)** | 6.62(0.07) |