

Dissertationes Forestales 66

Wood ants (*Formica rufa* group) in managed boreal forests: implications for soil properties and tree growth

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Academic dissertation

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ABSTRACT

Mound-building ants, and especially wood ants (*Formica rufa* group), are wide-spread key species that affect ecosystem functioning in several ways in the boreal forests of Eurasia. Forest clear-cutting harms wood ants, but the colonies gradually recover and multiply as forest succession proceeds. Thus their impact on ecosystem functioning may change with stand age. The objectives of this thesis were to study 1) the distribution of wood ants in boreal forests, 2) the role of wood ant mounds in the distribution of nutrients and roots, and 3) the effect of wood ant-aphid mutualism on the growth of Norway spruce (*Picea abies* L. Karst.). The 3rd National Forest Inventory data from the 1950s was used to study the distribution of ant mounds along major ecological gradients in Finland. Ecosystem-scale studies were conducted in 5-, 30-, 60- and 100-year-old Norway spruce dominated stands in eastern Finland.

The highest mound densities were found in spruce- and birch-dominated mature forests on medium-fertile sites in southern Finland. Ant mounds were more numerous and larger in older than in younger stands. More mound-building ant species were found in younger stands, while *F. aquilonia* Yarr. was the only species in the oldest stands. Most ant mounds were situated near stand edges. Carbon (C), nitrogen and phosphorus concentrations were higher in ant mounds than in the surrounding soil. More fine roots were found in the mineral soil under ant mounds than in the surrounding mineral soil. Ant mounds contributed only a small proportion of the total C and nutrient pools and root biomass in forest soil. Ant-aphid mutualism significantly reduced the radial growth of individual spruce trees in the 30-year-old stands only. Overall, the impact on spruce growth was marginal at the stand level. However, wood ants increased the heterogeneity in the spatial distribution of C, nutrients, roots, and tree growth.

Keywords: Norway spruce, nutrient content, roots, spatial distribution, species turnover, succession

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Joensuu, April 2008
Jouni Kilpeläinen

LIST OF ORIGINAL ARTICLES (I–V)

The thesis is based on the following articles, which are referred to in the text by their Roman numerals.

- I. Kilpeläinen, J., Punttila, P., Sundström, L., Niemelä, P. & Finér, L. 2005. Forest stand structure, site type and distribution of ant mounds in boreal forests in Finland in the 1950s. *Annales Zoologici Fennici* 42: 243–258. <http://www.sekj.org/PDF/anz42-free/anz42-243.pdf>.
- II. Kilpeläinen, J., Punttila, P., Finér, L., Niemelä, P., Domisch, T., Jurgensen, M. F., Neuvonen, S., Ohashi, M., Risch, A. C. & Sundström, L. 2008. Distribution of ant species and mounds (*Formica*) in different-aged managed spruce stands in eastern Finland. *Journal of Applied Entomology* 132: 315–325. doi: 10.1111/j.1439-0418.2007.01244.x.
- III. Kilpeläinen, J., Finér, L., Niemelä, P., Domisch, T., Neuvonen, S., Ohashi, M., Risch, A. C. & Sundström, L. 2007. Carbon, nitrogen and phosphorus dynamics of ant mounds (*Formica rufa* group) in managed boreal forests of different successional stages. *Applied Soil Ecology* 36: 156–163. doi:10.1016/j.apsoil.2007.01.005.
- IV. Ohashi, M., Kilpeläinen, J., Finér, L., Risch, A. C., Domisch, T., Neuvonen, S. & Niemelä, P. 2007. The effect of red wood ant (*Formica rufa* group) mounds on root biomass, density, and nutrient concentrations in boreal managed forests. *Journal of Forest Research* 12: 113–119. doi: 10.1007/s10310-006-0258-z.
- V. Kilpeläinen, J., Finér, L., Neuvonen, S., Niemelä, P., Domisch, T., Risch, A. C., Jurgensen, M. F., Ohashi, M., & Sundström, L. Does the mutualism between ants (*Formica rufa* group) and *Cinara* aphids affect Norway spruce growth? Manuscript.

I participated in designing the study and was responsible for collecting the field data for the last four papers. I wrote the first manuscripts of the papers I–III and V, and analysed the data in paper IV and participated in the writing work. Articles I–IV are reprinted with kind permission of the publishers: Finnish Zoological and Botanical Publishing Board (I), Wiley-Blackwell (II), Elsevier (III) and Springer (IV).

CONTENTS

ABSTRACT.....	3
ACKNOWLEDGEMENTS.....	4
LIST OF ORIGINAL ARTICLES (I-V).....	5
1 INTRODUCTION.....	7
1.1 Wood ant distribution.....	7
1.2 Role of wood ants in forest ecosystems.....	9
1.3 Objectives of the thesis.....	11
2 MATERIAL AND METHODS.....	11
2.1 3rd National Forest Inventory data (I).....	11
2.2 Intensive studies (II–V).....	12
<i>Study stands (II–V)</i>	12
<i>Ant mound survey (II)</i>	13
<i>Carbon and nutrient and root sampling (III–IV)</i>	13
<i>Norway spruce growth (V)</i>	15
3 RESULTS AND DISCUSSION.....	17
3.1 Distribution of ant mounds in boreal forests (I).....	17
3.2 Distribution of ant species and mounds in Norway spruce stands (II).....	18
3.3 Carbon and nutrient concentrations and pools of wood ant mounds (III).....	19
3.4 Root distribution in wood ant mounds (IV).....	20
3.5 Effect of ant-aphid mutualism on Norway spruce growth (V).....	21
3.6 Implications of wood ants for the prerequisites of tree growth.....	22
4 CONCLUSIONS AND FUTURE RESEARCH NEEDS.....	24
REFERENCES.....	25

1 INTRODUCTION

1.1 Wood ant distribution

Hölldobler and Wilson (1990) stated that "the neglect of ants in science and natural history is a shortcoming that should be remedied, for they represent the culmination of insect evolution, in the same sense that human beings represent the summit of vertebrate evolution." However, ants are much older than humans since they evolved more than 100 million years ago. Some 12 200 ant species in 20 subfamilies have been described so far (Bolton 2003). Ant species diversity is enormous especially in the tropics where dozens of ant species can be found in a single tree (e.g. Longino *et al.* 2002). About 60 ant species can be found in Finland (Söderman and Vikberg 2002; Vepsäläinen 2002; Czechowski and Radchenko 2006), and 12 of them build mound nests (Collingwood 1979; Punttila *et al.* 1991; 1994a; Punttila 1996; Seifert 2000; Mabelis and Korczynska 2001; Sundström *et al.* 2005).

Mound-building ant species are wide-spread in the boreal forests of Eurasia (e.g. Gößwald *et al.* 1965; Baroni Urbani and Collingwood 1977; Reznikova 2003). Wood ants of the *Formica rufa* group (*F. aquilonia* Yarr., *F. polyctena* Först., *F. rufa* L., *F. lugubris* Zett. and *F. pratensis* Retz.) are extremely common in many forest habitats and can be found throughout Finland from the hemi-boreal to the sub-arctic zone (Wuorenrinne 1974; Rosengren *et al.* 1979; Laine and Niemelä 1989). *F. aquilonia*, *F. polyctena* and *F. lugubris* are abundant throughout the whole country (Wuorenrinne 1974; Baroni Urbani and Collingwood 1977; Rosengren *et al.* 1979; Laine and Niemelä 1989; Punttila and Kilpeläinen 2008), whereas *F. rufa* occurs mainly in the hemi- and south-boreal forests (Wuorenrinne 1974; Punttila and Kilpeläinen 2008). On the average, three mounds per hectare occur on the most common forest site types in Finland (Wuorenrinne 1974; Rosengren *et al.* 1979; Domisch *et al.* 2005), and the mounds are often inhabited by several hundreds of thousands ants (Hölldobler and Wilson 1990). Other mound-building species, *F. uralensis* Ruzs., *F. truncorum* Fabr., *F. exsecta* Nyl., *F. fennica* Seifert, *F. forsslundi* Lohm., *F. pressilabris* Nyl., *F. suecica* Adlerz, are common in young, open forests, meadows or mires (Collingwood 1979; Punttila *et al.* 1991; 1994b; Punttila 1996; Punttila and Haila 1996; Seifert 2000; Mabelis and Korczynska 2001).

Colonization of an area by ants depends on the habitat requirements and the dispersal and colonization capacities of the species, as well as potential species interactions (Vepsäläinen and Pisarski 1982). The ant species composition also changes with stand age: pioneering ant species capable of independent colony establishment (e.g. *F. fusca* L.) are followed by species employing temporary social parasitism during colony founding (e.g. monogyne wood ant species). Later on, because of the intensified competition among the established colonies, only spreading through colony budding may remain a competitive colonization strategy (e.g. as in polygyne wood ant species) (Rosengren and Pamilo 1983; Punttila *et al.* 1991; Rosengren *et al.* 1993; Punttila *et al.* 1994b; Seppä *et al.* 1995; Punttila 1996; Punttila *et al.* 1996; see also Oinonen 1956). Long-range dispersal ability is generally considered to be better in monogyne (one queen) and weakly polygyne (a few queens) species, whereas short-range dispersal through the formation of bud nests dominates in polygyne (several queens per colony) species (Rosengren and Pamilo 1983; Rosengren *et al.* 1993; Sundström *et al.* 2005). Monogyne and monodomous (single nest colony) wood ant species (most Finnish populations of *F. rufa*, *F. lugubris*, *F. pratensis*) are more common in younger stands and fragmented mature forests, whereas polygyne and polydomous species (*F. aquilonia*, *F. polyctena*) thrive in continuous mature forests (Rosengren and Pamilo 1983; Savolainen and Vepsäläinen 1988; 1989; Punttila 1996; Sundström *et al.* 2005). The species composition correlates simultaneously

with the light conditions in the forest such that monogyne wood ants often dominate up until canopy closure, whereas larger mature stands in particular are often dominated by highly polygyne wood ants (Punttila 1996). Presumably, sufficiently large wood ant colonies can thermoregulate their large mounds and thrive in shady habitats more efficiently than small colonies (Coenen-Staß 1980; Rosengren *et al.* 1987; Punttila 1996; Frouz 2000; Sorvari and Hakkarainen 2005).

Most of the boreal forests in Fennoscandia are managed, and forest succession starts from clear-cutting. This can be destructive for wood ant colonies because, in addition to mechanical damage, it removes food resources, changes the micro-climate and alters the foraging routes, for instance (Rosengren and Pamilo 1978; Rosengren *et al.* 1979). The vitality of ant colonies decreases after clear-cutting and ants often abandon their mounds within a few years (Domisch *et al.* 2005; Sorvari and Hakkarainen 2005). Gradually the colonies recover and multiply along with the development of the forest stand (Punttila *et al.* 1991; Punttila 1996; Sorvari and Hakkarainen 2007). After stabilisation, ant mounds remain active in the same locations for several years, even for decades (Hölldobler and Wilson 1990).

Although the general distribution of wood ant species is fairly well known owing to the extensive studies carried out in many Eurasian countries (*e.g.* Baroni Urbani and Collingwood 1977; Seifert 1991; Reznikova 2003), the data are rarely based on systematic sampling across all forest site types and successional stages. In Finland, however, a national ant mound inventory was carried out as a part of the 3rd National Forest Inventory (NFI3) in the beginning of the 1950s in order to assess the density of the ecologically dominant wood ants of the *Formica rufa* group (Ilvessalo 1951; 1956) which, at the time, were considered to play an integral role in the pest control of managed forests (Adlung 1966). Wuorenrinne (1974) and Rosengren *et al.* (1979) have earlier analyzed subsets of the NFI3 data with respect to the number of ant mounds, and assumed that the data mainly encompassed the *Formica rufa* group. The authors found the highest occurrences and densities of ant mounds in medium-fertile, medium-dense, mixed forests in southern Finland, and concluded that factors related to vegetation, food resources and climate were the main determinants of mound distribution. The NFI3 data including ant mound numbers were reanalysed in the current study. Here the occurrence and density of ant mounds were studied on mineral soils throughout the whole mainland Finland, except in the northernmost parts, and a larger range of habitat attributes were included in the analysis. Although forest management and its intensity, and therefore also forest structure, have changed considerably since the 1950s (Valtanen 1996; Löfman and Kouki 2001), these data provide an opportunity to study the large-scale variation of mound occurrence and density along the major ecological gradients in boreal forests.

The distribution of ants at the landscape or ecosystem scale has been studied widely since the 1940s (*e.g.* Sudd *et al.* 1977; Klimetzek 1981; Levings and Traniello 1981; Laine and Niemelä 1989). Light has been often found to be a key factor determining nest locations (*e.g.* Klimetzek 1970), but competition (*e.g.* Cushman *et al.* 1988), slope aspect (*e.g.* Doncaster 1981), slope steepness, elevation, fire frequency (Risch *et al.* 2008), humidity, vegetation and soil characteristics (*e.g.* Lorber 1982) have also been shown to play important roles. In contrast to the earlier stand-level studies on the distribution of mound-building ants, forest age, nest locations, nest sizes and ant species are included in this study. Forest management likely affects ant species assembly, colony vitality, mound number, size, form and location (Punttila 1996; Domisch *et al.* 2005; Sorvari and Hakkarainen 2005; 2007). In particular, the density, size and location of ant mounds and also ant species determine the magnitude and the spatial distribution of ant activities as key species in forest ecosystems. The magnitude of ant effects may change with stand age.

1.2 Role of wood ants in forest ecosystems

Wood ants are considered to be key species in boreal forests due to their great abundance and the multitude and magnitude of their roles in the ecosystem: they cycle and aggregate carbon (C) and nutrients (e.g. Frouz *et al.* 1997; Folgarait 1998; Laakso and Setälä 1998; Lenoir *et al.* 2001; Risch *et al.* 2005), mix soil and alter its structure (e.g. Pokarzhevskij 1981), affect invertebrate (e.g. Way and Khoo 1992; Karhu and Neuvonen 1998; Laakso and Setälä 2000; Martikainen *et al.* 2000; Hawes *et al.* 2002; Punttila *et al.* 2004) and vertebrate distributions (e.g. Haemig 1992; 1994; Aho *et al.* 1999; Jäntti *et al.* 2007), and plant production (e.g. Wellenstein 1980; Rosengren and Sundström 1991; Mahdi and Whittaker 1993; Atlegrim 2005) (Figure 1). Wood ants defend their large territories against other ant species, especially against other territorial and aggressive species (Mabelis 1984; Savolainen and Vepsäläinen 1988; 1989). They are also a food source for other animals (e.g. Elgmork and Kaasa 1992; Swenson *et al.* 1999) and support various myrmecophiles (e.g. Päivinen *et al.* 2002).

Carbon and nutrient concentrations in ant mounds can be higher than those in the surrounding soil (Zakharov *et al.* 1981; Lenoir *et al.* 2001; Risch *et al.* 2005) due to the extensive flow of invertebrate prey, honeydew and seeds, and mound constructing material (litter, resin) into the mound (Stradling 1978; Rosengren and Sundström 1987; Stradling 1987; Rosengren and Sundström 1991), and the high number of nitrogen-fixing bacteria, earthworms and decomposer microbes living in the mounds (Frouz *et al.* 1997; Laakso and Setälä 1998; Stadler *et al.* 2006). Obviously the type of material used for construction also affects the chemical properties of ant mounds. The total C and nutrient pools in ant mounds, however, are likely to increase with stand age because ant mound and ant densities are higher in older stands (Sorvari and Hakkarainen 2005; 2007), and the ants have had longer time to build larger mounds. Studies carried out in temperate and alpine forests in Europe indicate that wood ants can play a significant role in nutrient cycling and aggregation (Frouz *et al.* 1997; Risch *et al.* 2005). Now the element concentrations and pools of wood ant mounds were studied for the first time in boreal forests (but see Laakso and Setälä 1998). Unlike the studies on active ant mounds in temperate, hemi-boreal and subalpine areas (Zakharov *et al.* 1981; Lenoir *et al.* 2001; Frouz *et al.* 2005; Risch *et al.* 2005), the below-ground mound parts and different stand ages are also included here.

Root distribution in ant mounds has not been studied earlier in boreal forests (see Karhu and Neuvonen 1998; Kristiansen and Amelung 2001). High nutrient concentrations and elevated temperatures, together with better aeration, might favour root growth and nutrient uptake in wood ant mounds. Since mound density is high in the boreal forests of Fennoscandia, the mounds might influence the variation in root distribution and growth in these forests. Changes in mound vitality might alter the chemical and physical conditions in the mounds and, consequently, the impacts of mounds on root growth. Furthermore, the bulk density of a mound could represent an indicator of ant colony vitality because, in recently clear-cut sites, weakened colonies may not be able to maintain their mounds in good shape and sufficiently aerated, resulting in higher average bulk densities of the mounds in clear-cut sites than in mature sites (Domisch *et al.* 2005). Dense and less active mounds can decompose faster than dry and porous active mounds (Lenoir *et al.* 2001). Thus forest management, ant colony vitality, bulk density, decomposition, C and nutrient concentrations and root distribution in ant mounds could be related.

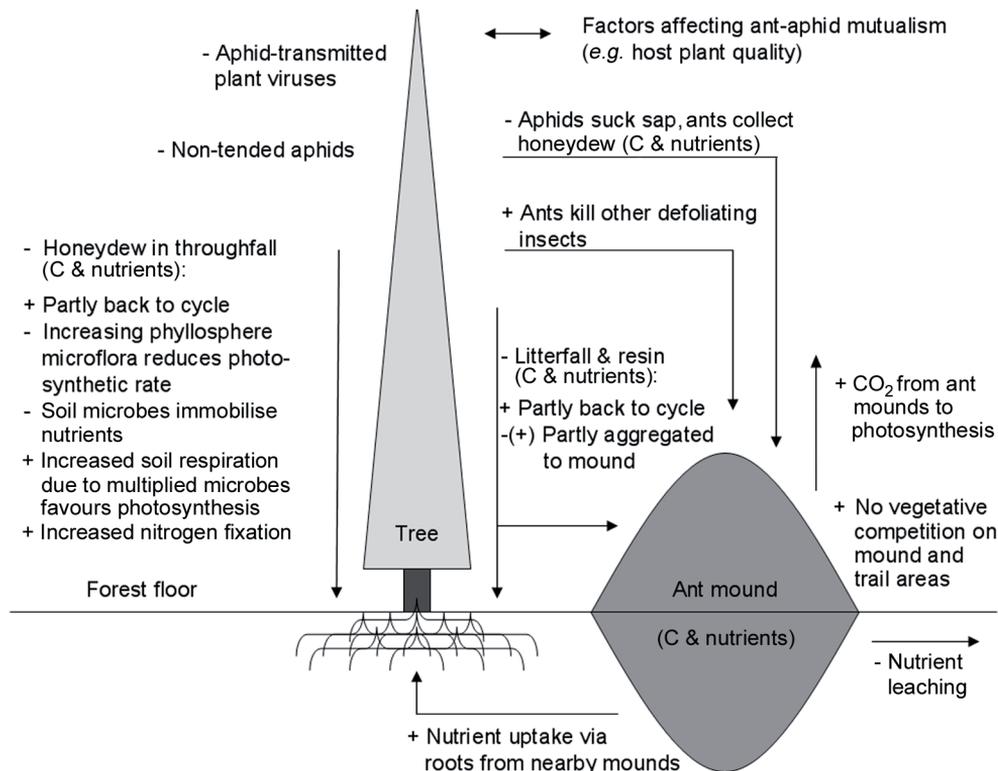


Figure 1. Schematic diagramme of the factors related to the effects of ant-aphid mutualism on tree growth. Signs + and - indicate assumed positive and negative effects.

Many ant species have mutualistic relationships with aphids feeding on the phloem sap of a wide variety of plants (e.g. Way 1963; Buckley 1987; Stadler and Dixon 2005; Styrsky and Eubanks 2007). Wood ants protect aphids (on conifers mainly *Cinara* spp.) from predators and, in return, are supplied with honeydew excreted by aphids. The removal of carbohydrates from the phloem by aphids can reduce tree growth. Ants may predate on other insects more intensively in mutualistic relationships with aphids than otherwise (Way 1963), which would also be beneficial for the host plants. The net effect of ant-aphid mutualism on plant growth is the sum of the direct loss caused by sap sucking and the indirect gain due to ants preying on other non-tended herbivores. The net effect on plant growth is likely to be positive when the populations of herbivores not tended by ants are high, whilst ant predation on small herbivore populations does not compensate for the growth losses caused by sap sucking (e.g. Styrsky and Eubanks 2007). Conifers, unlike deciduous trees, have only a few defoliating insects, and these seldom cause severe damage and consequent growth reduction in Fennoscandia. Thus ant-aphid mutualism most probably has a mainly negative effect on the growth of conifers. The effect of ant-aphid mutualism on Norway spruce was studied here for the first time by determining growth at both the tree and ecosystem levels (cf. Laakso and Setälä 2000; Frouz *et al.* 2008) and by controlling experimentally the ant-aphid mutualism (Styrsky and Eubanks 2007).

Ants and aphids can affect tree growth in several negative and positive ways, and through a number of factors (Styrsky and Eubanks 2007), such as the chemical defence of host plant (Sipura 2002), birds (Mooney and Linhart 2006; Mooney 2007), aphid saliva (Miles 1999),

aphid-transmitted plant viruses (Ng and Perry 2004; Goggin 2007), and honeydew in relation to phyllosphere microflora (Stadler and Müller 1996) and soil microbes (Dighton 1978; Petelle 1984; Grier and Vogt 1990; Reynolds and Hunter 2001; Stadler *et al.* 2001; Stadler *et al.* 2004; Stadler *et al.* 2006), and these factors can interact with the effects of ant-hemipteran mutualism on plant fitness (Figure 1). In this study only the net effect of ant-aphid mutualism on tree growth was considered and no attempt was made to distinguish between the different factors affecting tree growth.

1.3 Objectives of the thesis

The objectives of the thesis were:

- 1) to study large-scale variation in the distribution of ant (*Formica* spp.) mounds along major ecological gradients in Finland (I), and to study the spatial distributions of ant mounds, their dimensions and ant species in Norway spruce (*Picea abies* L. Karst.) stands of different ages (II),
- 2) to determine how C and nutrient concentrations and pools and root distribution in wood ant (*Formica rufa* group) mounds change with forest stand age in Norway spruce stands (III, IV), and
- 3) to assess the effect of mutualism between wood ants and aphids on the growth of Norway spruce in stands of different ages (V).

2 MATERIAL AND METHODS

2.1 3rd National Forest Inventory data (I)

Data from the 3rd National Forest Inventory (NFI3) were used to study the large-scale distribution of ant mounds. NFI3 was carried out during 1951–1953 as a line survey (Ilvessalo 1951; 1956). The data included a range of variables describing forest characteristics and the number of ant mounds on a total of 6570 0.1 ha circular sample plots on mineral soils (Figure 2). The log-likelihood ratio test was used to test whether the numbers of sample plots with and without at least one ant mound (mound occurrence) were distributed in similar proportions across stands of different site type, dominant tree species, forest density, forest age and development classes. To investigate the relationships between habitat attributes and the density of ant mounds per 0.1 ha, the data were processed by Poisson regression analysis. Hierarchical partitioning (Chevan and Sutherland 1991; Mac Nally 1996; Walsh and Mac Nally 2004), which produces the average independent and joint contribution of each explanatory variable to the goodness-of-fit of the full model, was used to assess the relative importance of each selected explanatory variable.

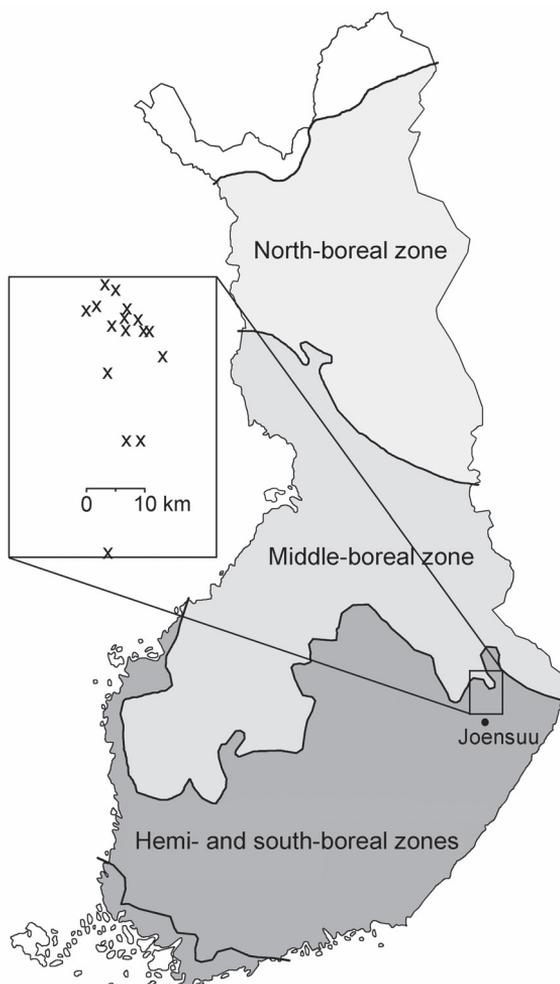


Figure 2. The 3rd national forest inventory data covered the grey tone areas. Crosses depict the location of the intensive study stands. Vegetation zones from Kalela (1960) and Ahti et al. (1968).

2.2 Intensive studies (II–V)

Study stands (II–V)

More detailed studies on the ant mounds and the effects of ant-aphid mutualism on tree growth were conducted in four stand age classes (5, 30, 60 and 100 years) on sites of the medium-fertile Myrtillus type (Cajander 1949) in and near the Koli National Park (29°52' E, 63°04' N, 160 m a.s.l.) (Figure 2). In each age class four replicate stands (2.3–11.3 ha) were selected. The stands were selected so that the size of the homogeneous tree stand was maximized and, correspondingly, the proportion of stand edge minimized. The stands were dominated by Norway spruce with an admixture of Scots pine (*Pinus sylvestris* L.), silver and downy birch (*Betula pendula* Roth. and *B. pubescens* Ehrh.), European aspen (*Populus tremula* L.), European alder (*Alnus incana* (L.) Moench) and, especially in the 5-year-old stands, rowan

(*Sorbus aucuparia* L.). Although only spruce was planted in the 5-, 30-, and 60-year-old stands, deciduous trees and pines were numerous in the young stands. The 100-year-old stands were naturally regenerated because planting was rare at the time of establishment. The soil type on the sites was haplic podzol (Soil map... 1990) on glacial till, and the organic layer was on the average 7 cm thick (Table 1).

Ant mound survey (II)

In the summer of 2003 the location, diameter, height, direction of the longest slope, an estimate of illumination (well-lit, open location; moderately shaded; heavily shaded by trees or other structures), and mound activity (active or abandoned) were determined on all mounds in the study stands. Above-ground ant mound volumes were calculated using the equation of a half ellipsoid (e.g. Risch *et al.* 2005). Ant samples were collected from all active mounds, and species identification was performed using a variety of taxonomic keys and research papers (e.g. Dlussky and Pisarski 1971; Douwes 1981; 1995; Czechowski and Douwes 1996; Seifert 2000; Czechowski *et al.* 2002; Goropashnaya *et al.* 2004a; 2004b).

To test for the differences in mound numbers of different ant species among the stand age classes, the chi-squared test was used for *F. aquilonia* and the other ant species pooled. The expected mound numbers in the stand age classes were adjusted according to the stand size. As the mounds of species other than *F. aquilonia* were very rare in the data, only *F. aquilonia* was taken for further analysis. To compare the densities (ha^{-1}) and volumes of *F. aquilonia* mounds among forest age classes, one-way anova and Bonferroni post hoc test were used. The mound volumes in different light conditions were tested in a similar way. To test for differences in mound numbers with their longest slopes facing in different directions, the chi-squared test was used. Mound volumes within 10 m from the stand edges and more than 10 m away from the stand edges were compared with the paired-samples t-test. The paired samples t-test was also used to compare the percentages of ant mounds within 10 m from the stand edges and the percentages of stand areas within the edges. The ant mounds in stands were considered as stationary and homogeneous spatial point patterns. To explore whether ant mounds were distributed randomly, regularly or were clustered within each stand, a transformation of Ripley's K function with an isotropic edge correction was applied (Baddeley and Turner 2005). To test whether the distribution of ant mounds differed from a homogeneous Poisson process selected to represent complete spatial randomness, a Monte Carlo test with 999 simulations was used. The absolute value of the sum of the transformed K function values was selected as a test quantity (Heikkinen 2006).

Carbon and nutrient and root sampling (III–IV)

Eight sample mounds from different mound volume classes were selected in each stand age class (32 mounds in total) (Table 1). In each stand one to three mounds and their surroundings were sampled. Three core samples were taken from the above-ground parts of each mound. One below-ground soil sample was taken under each of the three above-ground ant mound samples down to a depth of 21 cm. Four samples were taken from the organic layer and mineral soil at points 3 m from the ant mound edge in north, west, south and east directions. The thickness of the organic layer was measured.

Table 1. The density and volume of active and abandoned ant mounds, the height of spruces in the 5-year-old stands (h), the basal-area-weighted diameter of spruces in the older stands ($d_{1,3}$), spruce stem number, the percentage of spruces visited heavily by ants, the number of mounds and their surroundings sampled for carbon and nutrients (element) and roots, the number of mounds surrounded by the experimental trees (growth), and the thickness of the soil organic layer in the individual study stands.

Stand number	Age class (years)	Active mounds (ha^{-1})	Aband. mounds (ha^{-1})	Active volume (dm^3)	Aband. volume (dm^3)	$d_{1,3}$ (5-16) (cm)	h (1-4) (cm)	Stems (ha^{-1})	Heavy visit (%)	Element mounds	Root mounds	Growth mounds	Organic layer (cm)
1	5	4.6	0.6	91	30	44	1760	3.0	2	2	2	2	6
2	5	4.0	0.8	131	192	53	1425	3.1	3	3	3	1	5
3	5	0.6	0.1	302	5	60	1857	0.7	1	1	1	1	5
4	5	0.9	2.5	548	360	52	1867	1.4	2	2	2	1	9
5	30	5.3	0.4	212	5	12.9	1933	0.7	2	2	2	2	8
6	30	1.6	0.0	262	-	15.1	944	1.6	1	0	0	1	6
7	30	1.7	0.2	301	99	15.3	1122	1.4	2	2	1	1	7
8	30	4.2	0.9	218	143	16.1	1007	1.6	3	3	3	1	5
9	60	4.4	0.2	173	272	14.5	1111	1.3	2	2	2	2	10
10	60	9.7	0.5	763	219	17.1	867	2.0	2	2	2	1	6
11	60	5.7	1.5	264	255	30.0	429	7.0	2	2	2	1	9
12	60	2.0	0.8	399	369	22.8	600	3.8	2	2	0	1	5
13	100	4.9	0.6	1825	1125	18.6	1333	1.4	2	2	2	2	7
14	100	2.7	0.4	1023	42	21.2	450	4.7	2	2	1	1	8
15	100	3.3	0.4	859	1474	27.9	424	6.6	2	2	1	1	5
16	100	5.6	1.4	450	260	30.0	517	5.8	2	2	1	1	9

Mineral soil samples (E horizon and the upper part of the B horizon) were taken below the sampled organic layer in the same way as the soil sampling under the ant mounds. Stones and large roots (diameter > 20 mm) were separated from the samples and their mass and volume were subtracted from the samples. All living fine (diameter < 2 mm) and coarse (diameter 2–20 mm) roots were separated manually from the samples. The roots, mound material and soil samples were dried separately to constant mass at 40 °C, and then weighed. The samples taken from soil below the ant mounds and from the mineral soil were sieved through a 2-mm sieve, and both fractions were weighed. Nutrients were determined on the <2 mm fraction. The samples from the ant mounds and organic layer and root samples were milled before analysis. For nutrient analyses, the root samples were combined by stand age class. Element concentrations (g g^{-1}) were determined with standard methods used at the Finnish Forest Research Institute. The C and nutrient pools in the ant mounds were calculated by multiplying the average C and nutrient concentrations of the sampled ant mounds (the elements of roots were included) in each stand by the ant mound mass (g ha^{-1}). The element concentrations of roots (g g^{-1}) were multiplied by the root biomass (g per mound base area, m^2) in order to obtain the amount of elements in the roots per area (g m^{-2}). Root biomass density was determined as a percentage of the mound material or soil. Roots were separated from 25 mounds and their surrounding soil (Table 1).

Linear mixed models and Bonferroni multiple comparisons were used to test for differences in element concentrations, C/nitrogen (N) ratios and bulk density of mound and soil between the fixed factors, stand age classes and sample loci, and their interaction. Forest stand was used as a random factor. Among the sample loci, 1) ant mounds vs. soil organic layer, and 2) soil under ant mound vs. mineral soil, were tested separately. The same analysis was performed for the element pools m^{-2} . Root biomass and biomass density were tested in a similar way except that site * sampling location was also used as a random factor. The element concentrations and amounts in roots were compared between sample location with linear mixed models, where sampling location and root diameter class were fixed factors. The results were presented separately for fine roots and coarse roots. One-way ANOVA and Bonferroni multiple comparisons were applied to compare the element pools ha^{-1} of ant mounds between stand age classes.

Norway spruce growth (V)

Five medium-sized wood ant mounds were selected in each stand age class (Table 1). Ten of the most heavily-visited (by ants) and ten similar-sized non-visited spruces were selected within 20 m from each of the 20 ant mounds, to give a total of 100 trees in each stand age class. The access of ants to half of the heavily-visited and non-visited trees was blocked. Ant traffic was monitored regularly during 2004–2006. In the 5-year-old stands the number of ants currently present on the seedlings was counted. In the 30-, 60- and 100-year-old stands the number of ants passing breast height during the monitoring period of five minutes was recorded. The experimental trees without blocking were classified into two “Traffic” classes: half of the trees were classified as heavily-visited and half as lightly-visited. During the study, part of the initially non-visited trees changed to heavily-visited and part of the heavily-visited trees changed to lightly-visited. The six different tree groups in the experiment were combined into the variable “Tree group” (see Table 3 in V). The heights and breast height diameters of the experimental trees were measured in the beginning and at the end of the study. In the 30-, 60- and 100-year-old stands, the radial growth prior to and during the study were determined on increment cores taken at breast height on the trees.

To assess the effect of ant-aphid mutualism on height (5-year-old stands) and radial growth (30-, 60-, and 100-year-old stands) of experimental trees during the experiment, general linear models in which “Tree group” was a fixed factor and stand a random factor were used. In the 5-year-old stands, the seedling height in the beginning of the study was used as a covariate. The mean annual radial growth during ten years before the experiment was used as a covariate in the 30-, 60- and 100-year-old stands. To test the effect of blocking of ant traffic on tree growth, the trees visited heavily before and during the experiment were contrasted with the trees where the heavy ant traffic before the experiment was blocked during the experiment (“Block contrast”). To test whether the ant traffic prior to the experiment was still related to growth, the trees with light traffic before were contrasted with the trees with heavy traffic during the experiment (“Visit contrast”). To test the relationship between ant traffic during the experiment and growth, the trees with heavy ant traffic before and during the experiment were contrasted with the trees with light ant traffic before and during the experiment (“Traffic contrast”). The differences (%) in annual height (5-year-old stands) and radial growth (older stands) between the heavily-visited spruces and the spruces where the ant traffic was blocked were calculated.

Stand volume growth was estimated in each stand using data collected from systematically located tree sample plots in autumn 2003 and 2006. There was a total of 23 and 48 sample plots in the 5-year-old and older stands, respectively. In the 5-year-old stands, the heights of the spruce seedlings (height > 20 cm) were measured (Table 1). In the older stands, the breast height diameters ($d_{1.3}$) of the spruces ($d_{1.3} > 4$ cm) were measured (Table 1) and a part of the trees were taken as sample trees that were measured also for height and diameter at 6 m height (d_6) and cored for increment samples in autumn 2006. The KPL program was used to calculate tree stand characteristics (Heinonen 1994). The numbers of ants currently on the measured seedlings and on 0.5 m trunk parts at breast height on the older measured trees were counted several times during 2003–2006. The distances between tree sample plots and the nearest ant mounds were determined.

To estimate the proportion of heavily-visited spruces in each stand the number of ants on the trees within 20 m distance from one of the five selected ant mounds in each stand age class was counted. These data, together with the data from the tree sample plots, were used to fit regression models in which the proportion of heavily ant-visited spruces on a sample plot was explained by the distance from the nearest active ant mound. Stand-specific proportions of heavily-visited trees were calculated with the models in which surfaces indicating distances from the nearest active ant mounds created for each stand with ArcGIS 9.0 were used as explanatory variables.

The impact of ant-aphid mutualism on the annual stand volume growth was estimated. First, stand volume was calculated with ants present and without ants. Then, the change in stand volume (volume without ants – volume with ants present) was compared to the annual stand volume growth without ants. Laasasenaho’s (1982) volume model for Norway spruce was used to calculate the volume of a spruce tree with a mean diameter weighted by the stem basal area in each stand. The stand volume with ants present was calculated by multiplying the average tree volume with the number of spruce trees per hectare. The stand volume without ants was calculated by increasing the diameter of the heavily-visited trees with the estimated ant-aphid effect. In the 5-year-old stands the impact of ant-aphid mutualism on height growth was calculated in a similar way.

3 RESULTS AND DISCUSSION

3.1 Distribution of ant mounds in boreal forests (I)

The mean mound density across the entire country in the 1950s was 2.5 mounds ha⁻¹, and 3.1, 2.4 and 1.5 mounds ha⁻¹ in the hemi- and south-boreal, middle-boreal and north-boreal zones, respectively. The results were consistent with those of previous studies using subsets of the NFI3 data (Wuorenrinne 1974; Rosengren *et al.* 1979). The mound densities in Eurasian boreal forests are one magnitude higher than those in central European lowlands (see overview in Risch *et al.* 2005) and in North America (see overview in Risch *et al.* 2008). Here latitude contributed the most to the explained variation in the ant mound density. The decreasing density towards the north could be due to the lower fertility and productivity (Tamminen 1991), colder climate and shorter growth season, higher altitude, increased proportion of pine-dominated stands and other changes in forest stand structure (*e.g.* age class distribution), as well as to the turnover of ant species towards the north. The occurrence and density of ant mounds were highest on the medium-fertile sites and lowest on very infertile and rocky sites. Fertile sites most likely offered more diverse food resources, and a greater diversity of aphid species, and therefore could maintain a higher mound density than less fertile sites (Rosengren *et al.* 1979). Mound density was high also on fine sandy soils, which have good aeration and water holding capacity (Westman 1991) and thus promote plant production. Fine sandy soils can also have favourable temperature and overwintering conditions for ants.

In contrast to pine-dominated forests, birch- and spruce-dominated forests had a high occurrence of ant mounds. This was related to site type because birch and spruce dominated the most fertile and pine the least fertile sites. The high occurrence and density of ant mounds in spruce-dominated stands could be attributable to the presence of polygyne species of the *F. rufa* group, which are able to colonize and survive in these shady stands (Rosengren and Pamilo 1983; Punttila 1996). Moreover, a mixture of other tree species in spruce-dominated stands could offer diverse, continuous food resources throughout the whole foraging period of ants (Müller 1960; Rosengren and Sundström 1987; Laine and Niemelä 1989; Mahdi and Whittaker 1993).

Mound occurrence was generally lower in the youngest development classes than in the older classes. In addition to changes in illumination, clear-cutting removes the main resource, *i.e.* aphid trees, changes the ecological conditions and provides new habitats for open-country species (see Rosengren and Pamilo 1978; Vepsäläinen and Wuorenrinne 1978; Rosengren *et al.* 1979; Punttila *et al.* 1991; 1996; Punttila 1996; Sorvari and Hakkarainen 2004; 2005; 2007). On the other hand, mound density does not directly indicate the welfare of mound-building ants because forest thinning that leads to better illumination may promote ant colony founding (Rosengren *et al.* 1987; Punttila 1996), and logging often leads to colony budding in polygyne wood ant species (Rosengren *et al.* 1979; Sorvari and Hakkarainen 2005).

Forest management and structure have changed dramatically since the 1950s and this has most probably affected the ant mound density and species composition. Despite prohibited in the 1940s (Mikola 1984), selectively logged stands were still found in the NFI3. Currently, for instance, soil preparation might reinforce the devastating effects of clear-cutting through physical damage to the mounds, whereas thinning that increases light may increase the mound numbers. The reduced stand size of managed forests and the accretion of edge habitats (Löfman and Kouki 2001; 2003) may increase the mound density by providing favourable conditions for colony establishment (Klimetzek 1973; Punttila 1996). The increased proportion of young stands (Peltola 2006), and the isolation and smaller size of mature stands, may have favoured

monogyne or weakly polygyne nesting strategies at the expense of obligately polygyne ones (*sensu* Sundström *et al.* 2005), and increased the mound density of open-country species (Punttila 1996).

3.2 Distribution of ant species and mounds in Norway spruce stands (II)

In the studied spruce-dominated stands, the overall density of active and abandoned mounds was 3.8 and 0.7 per ha, respectively (Table 1). This is in good agreement with the earlier findings that ant mound density is higher than the average on spruce-dominated medium-fertile stands in Finland (I). In total, 16% of all the 452 mounds were abandoned, while most active mounds were inhabited by *F. aquilonia* (94%). Together with the other species of the *F. rufa* group (*F. rufa*, *F. polycтена* and *F. lugubris*), wood ants inhabited 97% of all the active mounds. The rest of the mounds were inhabited by *F. exsecta* and *F. pressilabris*. In these data, polydomous *F. aquilonia* dominated in all stand age classes, but the number of its mounds in the 60- and 100-year-old stands was twice that in the 5- and 30-year-old stands. The other mound-building species were concentrated in the younger age classes. Thus the species turnover along the stand age gradient was clear, but less evident than expected on the basis of earlier studies (Punttila 1996). These results suggest that, if polydomous colonies survive the decline in food resources after clear-cutting, they can to a large extent prevent other territorial ant species from colonizing the area (*cf.* Vepsäläinen and Pisarski 1982; Punttila 1996; Punttila *et al.* 1996). This is particularly evident in small and narrow clear-cut areas, where a polydomous ant colony may easily move its population in or close to the edge of more favourable older forest habitats through nest budding (Sorvari and Hakkarainen 2005).

In this study, both the mean mound volume and the mound volume per area increased from 0.3 m³ and 0.4 m³ ha⁻¹ in the 5-year-old stands to 1 m³ and 4 m³ ha⁻¹ in the 100-year-old stands. Thus, the ant worker population, as indicated approximately by the mound size (Seifert 1991; Martikainen *et al.* 2000; Liautard *et al.* 2003), increased along the stand age gradient. The variation in the volume of active mounds was lowest in the 30-year stand age class, where the old withering mounds have already been abandoned, and was highest in the 100-year stand age class, where bud nests were formed around large mounds.

In this study, mound height relative to its diameter increased with stand age and thus with degree of shadiness. This agrees with the observation that, in shaded conditions, higher ant mounds are better able to collect diffused light than flatter mounds (Andrews 1927; Lange 1959; Martin 1975; Sudd *et al.* 1977; Bretz 2004). On the other hand, the presence of flat mounds in the seedling stands could be partly attributable to mound compaction (Domisch *et al.* 2005; III). The longest slopes of the mounds faced south, as has been reported in Ireland (Breen 1979). This suggests that exposure to the sun is important in ant colony founding and survival. The finding that mounds were slightly smaller (*i.e.* younger) in well-lit locations and near stand edges in the oldest stands agrees with the suggestion by Punttila (1996), that polydomous colonies are able to spread through step-by-step dispersal utilizing canopy openings. Eventually, an ant population large enough to thermoregulate the mound can also survive in shaded conditions after tree-canopy closure (Rosengren *et al.* 1987; Punttila 1996). Polydomous colonies that exchange resources among mounds may survive better in shaded conditions than monodomous ones (Rosengren and Pamilo 1983; Punttila 1996).

In all stand age classes, *F. aquilonia* mounds were concentrated at the stand edges, and in permanently open locations by road sides and shores. Nearly half of the mounds were concentrated within 10 m from the stand edges, while this zone represented only one quarter of the stand area. The aggregation of ant mounds in edge habitats is common, as found *e.g.*

in planted forests in England (Sudd *et al.* 1977). The spatial distribution of ant mounds was significantly clustered only in some stands, and was most probably caused by the polydomous colonies of *F. aquilonia* and the concentration of ant mounds in edge habitats. A clustered nest spacing is common in polydomous ant species (*e.g.* Cerdá *et al.* 2002). In seedling stands, where light is more uniformly distributed and more ant species are specialized for different habitats (Punttila *et al.* 1991; Punttila *et al.* 1996), the spatial distribution might be more regular. Ants can minimize intra-specific competition by regular nest spacing, especially when the nest density is high (Cushman *et al.* 1988 and references therein). In the older sites the mound density was relatively high, which might partly explain why the distributions were not as clustered as expected. On a broader scale, ant mounds are apparently aggregated in these old-forest fragments (*cf.* I).

In addition to inter- and intra-specific interaction, abiotic factors also affect the spatial distribution of ant mounds. For example, topography may gain importance at a larger scale, whereas species interactions are more likely to play a role at a smaller scale (Crist and Wiens 1996 and references therein). Hence, in addition to the factors studied here (stand age, proximity to edge, illumination), several other factors such as altitude, slope steepness and the main slope direction of the terrain may influence mound locations at the forest stand scale. These variables had narrow ranges in the data and thus, had only minor impacts on mound distribution. Other studies, however, have shown that ant mounds are concentrated on south-exposing slopes (*e.g.* Laine and Niemelä 1989), and on the sunny sides of forest trails (Douglas and Sudd 1978).

3.3 Carbon and nutrient concentrations and pools of wood ant mounds (III)

The C, N and phosphorus (P) concentrations and C/N ratio in the above-ground parts of the ant mounds were comparable to those reported in temperate, boreal and subalpine coniferous forests (Zakharov *et al.* 1981; Lenoir *et al.* 2001; Risch *et al.* 2005). Both the C and P concentrations were higher in the above-ground ant mound material than in the surrounding organic layer. The ant mound material is selectively collected from the forest floor by ants. Norway spruce needle litter, which is a common mound-building material, usually has lower N and P concentrations (Berg *et al.* 1991; Johansson 1995; Lundmark-Thelin and Johansson 1997; Berg *et al.* 2000) than the ant mound material (Zakharov *et al.* 1981; Lenoir *et al.* 2001; Frouz *et al.* 2005; Risch *et al.* 2005; III), and therefore the presence of other ant mound material explains the higher nutrient concentrations. Ant mounds contain relatively more resin particles (Lenoir *et al.* 1999) and food remains than the surrounding organic layer. The soil microbe (Frouz *et al.* 1997; Laakso and Setälä 1998) and root composition (Farji-Brener 2000; IV) of ant mounds also differ from those in the surrounding soil, and they may have an impact on the C and nutrient concentrations. Ant mounds can have a higher N-fixing bacterium assemblage compared to the surrounding organic layer (Frouz *et al.* 1997), but this was probably not the case here because the N concentrations were similar in the ant mounds and in the surrounding organic layer. Laakso and Setälä (1998) found a larger soil animal biomass, suggesting a higher amount of resources, in ant mounds than in the surrounding forest soil in Finland, but no differences in the N and P concentrations between the surface layers of ant mounds and the surrounding litter layer. Ants themselves have also been reported to increase the leaching of dissolved organic C and N from litter (Stadler *et al.* 2006). Furthermore, the organic layer comprises the whole decomposition continuum from litter to humus, while the material in the ant mounds is less decomposed and, according to the higher C/N ratio (Berg and McLaugherty 2003), younger in the ant mounds than in the organic layer. The higher C, N and extractable

P concentrations in the soil under the ant mounds compared to the surrounding mineral soil might be explained by the input of organic material caused by the mixing activity of the ants. Here nutrient concentrations in the organic layer did not decrease with stand age, which was opposite to the earlier findings in boreal forests in southern Finland (Tamminen 1991). At the same time, the C concentrations in the ant mounds increased slightly with stand age.

The bulk densities in the above- and below-ground parts of the ant mounds were lower than in the surrounding soil. The interior of the mounds of the *Formica rufa* group is known to have a porous structure with ant tunnels and chambers, and the mineral soil under the mounds is also mixed with organic matter by the ants, resulting in a lower bulk density. There were no significant stand-age related differences in the bulk densities of the ant mounds, although the bulk density seemed to be highest in the seedling stands. This might indicate reduced ant activity in the recently clear-cut sites, which leads to accelerated decomposition (*cf.* flat mounds in seedling stands, II).

Carbon and nutrients accumulated in the ant mounds with stand age. The C, N and P pools in the above-ground mounds of the 100-year-old stands were 180, 4 and 0.3 kg ha⁻¹, respectively. The contribution of ant mounds to the total C, N and P pools in the forest soil was thus under 1%, which is less than that in sub-alpine forests in Switzerland, where it was 0.6–5 % of the C and N pools in the organic layer depending on the forest type (Risch *et al.* 2005). The pools in ant mounds are negligible when extrapolated to the ecosystem level. However, ant mounds increase the spatial heterogeneity in the distribution of C, N and P in forest soil. Further, the aggregation of ant mounds in stand edges (II) may increase the already high productivity of forest edges. Ant mounds located near the stand edges accumulate resources both from inside the stand and from the surrounding habitats, and become sources of nutrients after abandonment. Nutrients become first available to plants that have roots in and under the mounds (IV).

3.4 Root distribution in wood ant mounds (IV)

Fine and coarse roots accounted for < 1% of the dry mass of the mound material, and around 3% of the dry mass of the organic layer of the surrounding forest soil. The total root biomass (fine and coarse roots together) in the above- and below-ground parts of the mounds and the surrounding organic and mineral soil layers was 905±198 g m⁻² (mean ± SE) and 658±68 g m⁻², respectively. The root biomass obtained here was comparable with that reported in other studies in boreal forests (Steele *et al.* 1997; Vanninen and Mäkelä 1999; Makkonen and Helmisaari 2001). With a mound density of 4.5 ha⁻¹ and an average basal area of 1.4 m², the total root biomass in ant mounds was 6 kg ha⁻¹ compared to a biomass of 6600 kg ha⁻¹ in soil, which indicates that the contribution of mound roots to the total root biomass is only 0.1%. Given that wood ant mounds contain more nutrients than the surrounding soil (*e.g.* Pokarzhevskij 1981; Lenoir *et al.* 2001; Frouz *et al.* 2005; Risch *et al.* 2005; III), it was expected that the better nutrient conditions, together with the higher aeration and temperature (Rosengren *et al.* 1987), would result in better root growth in wood ant mounds. In contrast, the root biomass density (%) was lower in the above-ground mounds than in the organic layer. The relative dryness of wood ant mounds (Laakso and Setälä 1997; Frouz 2000; Lenoir *et al.* 2001) most probably limits root growth. Another possible explanation is that the formic acid produced by wood ants might also inhibit root growth (*cf.* Frederickson *et al.* 2005). Fine root biomass (g m⁻²) and biomass density (%) were higher in the soil below the mound than in the surrounding mineral soil. Coarse root biomass under the mounds was also higher than in the mineral soil in the 5- and 30-year-old stands. These results are in agreement with those

of Karhu and Neuvonen (1998), who found more roots in the mineral soil close to wood ant mounds than further from the mounds. This suggests that root nutrient uptake in the soil below the mounds can also be important. In abandoned ant mounds, however, the uptake may be even higher. Kristiansen and Amelung (2001) reported that abandoned wood ant mounds had a higher root density than the surrounding soil. The increased moisture content in abandoned mounds can accelerate organic matter decomposition and nutrient mineralization, thereby enhancing the growth and nutrient uptake of roots in abandoned ant mounds. The density of abandoned mounds was here 0.7 ha^{-1} , suggesting only a small addition to the effects of active mounds on root distribution. On the other hand, the effect of ant mounds lasts even for several decades in each location (Hölldobler and Wilson 1990).

The N, calcium (Ca), potassium (K), P, sulphur (S), magnesium (Mg), zinc (Zn) and copper (Cu) concentrations were higher in the fine and coarse roots in the above-ground mounds than in the organic layer, and the lead (Pb) concentration was lower in the fine roots than in the surrounding organic layer. The amounts of K and P were higher in the fine and coarse roots in the mounds than in the organic layer. The roots in the mounds accounted for nearly 0.2% of the N, Ca, K, P, S and Mg pools in the total roots at the stand level. Karhu and Neuvonen (1998) also reported higher foliar N concentrations in trees growing in wood ant mounds compared to those growing far from mounds. Current results suggest that nutrients from the organic matter aggregated in mounds over a large area could be utilized by the surrounding trees via roots. Thus ant mounds increase spatial variation in root distribution at the stand level.

Stand age was not found to have an effect on root biomass and density in this study, except that the fine root biomass density in the soil below ant mounds and in the surrounding mineral soil was higher in the 60- than in the 5-year-old stands. Earlier studies have shown that root biomass in the soil decreases immediately after clear-cutting, and then gradually increases to the pre-cutting levels (Palviainen *et al.* 2005). The same might be true for the roots in ant mounds.

3.5 Effect of ant-aphid mutualism on Norway spruce growth (V)

In this study the main results on the effects of ant-aphid mutualism on tree growth were based on a manipulative experiment (“Block contrast”) and they therefore provide more convincing evidence of the causality between ant-aphid mutualism and tree growth than correlative studies (here “Visit and Traffic contrasts”) (see Styrsky and Eubanks 2007). Contrary to expectations, ant-aphid mutualism increased the height growth of individual spruce seedlings by 16% during the three-year experiment ($p = 0.100$). In earlier studies the ant-aphid mutualism or aphids alone have had mainly a negative relationship with the growth of conifer seedlings (Fox and Griffith 1977; Holopainen and Soikkeli 1984; Holopainen *et al.* 1993; Straw *et al.* 1998; 2000; Smith and Schowalter 2001; Straw *et al.* 2002), as well as with the growth of deciduous tree seedlings (Dixon 1971; Banks *et al.* 1991). The increased height growth of seedlings may result merely from the fact that aphids select the fastest-growing trees (Fox and Griffith 1977). Changed allocation patterns in stem *vs.* root growth, or overcompensation in growth, may also explain the observed pattern (*e.g.* Agrawal 1998; Vanderklein and Reich 1999; Stowe *et al.* 2000; Offenberg *et al.* 2005). Overcompensation, meaning that lightly-defoliated plants grow more than intact plants, is possible in spruce seedlings with partly free growth but not in older spruces with predetermined growth (Kramer and Kozłowski 1979; Grossnickle 2000). Here the ants and aphids may have induced the overcompensation because spruces do not have many significant defoliating insects. At the stand level, however, the increase in the height growth of the seedlings was small: 1.2% or about 0.2 cm.

In the 30-year-old stands, the radial growth of heavily-visited spruces was 7% lower than that of the spruces where the ant traffic was blocked. At the stand level, this resulted in 0.05% annual volume growth losses, corresponding to $0.008 \text{ m}^3 \text{ ha}^{-1}$. The impact on stand growth was negligible, because only 1–7% of the trees were heavily-visited (Table 1). In the older stands the differences in similar comparisons were not significant. However, in the 60-year-old stands the spruces that were heavily-visited prior to the experiment grew 6% less than the ones visited lightly prior to the experiment. This may indicate that the ant-aphid mutualism has long-term effects on the growth of mature spruces, as has been reported also for aphid-infested Sitka spruce (Halldórsson *et al.* 2003). A similar negative relationship between ant-aphid mutualism and the growth of mature Scots pines (Klimetzek and Wellenstein 1978; Wellenstein 1980; Rosengren and Sundström 1991) and Norway spruces (Frouz *et al.* 2008) has also been reported earlier. In this study the reduction in radial growth of the 30-year-old spruces was only 7%, while it was 20% in 50-year-old Scots pines in a correlative study by Rosengren and Sundström (1991). Several reasons can account for the difference. Only part of the annual tree biomass production is allocated to the stem, and the proportion is higher in pine than in spruce (Finér 1989). Trees allocate a significant amount of their annual production into fine roots (Helmisaari *et al.* 2002). The assimilates can be reallocated and the growth effects in stems might be observable later than in roots and, accordingly, the growth reductions become long-lasting (Smith and Schowalter 2001). Furthermore, the study of Rosengren and Sundström was carried out in southern Finland where the active season of ants and aphids is longer than that in eastern Finland. More honeydew may be collected from Scots pine than from Norway spruce (Zoebelein 1956). In addition, the past growth of the trees, which was found to be a significant covariate, was not taken into account in their study.

The growth responses due to the blocking of ant traffic were not significant in the 60- and 100-year-old trees possibly because they grew so slowly that it was difficult to detect the effect during the three-year study period. On the other hand, the host trees of ant-aphid mutualism can change remarkably from year to year (Vepsäläinen and Savolainen 1994), although the heavily-visited trees usually remain the same during consecutive years (Rosengren 1977). If host trees change and if ant-aphid mutualism has long-term effects (more than a growing season) on tree growth (Smith and Schowalter 2001; Halldórsson *et al.* 2003; V), then the effect of mutualism can be higher than predicted because the growth of current host trees is compared to possible former host trees that might still have reduced growth rates.

3.6 Implications of wood ants for the prerequisites of tree growth

The C and nutrient concentrations and pools, and the biomass, density and element concentrations of roots in wood ant mounds, and the net effect of wood ant-aphid mutualism on tree growth, were examined in this study. Although C and nutrient pools in wood ant mounds are relatively modest at the stand scale (Risch *et al.* 2005, III), a considerable proportion of elements may be cycled through wood ant mounds in forest ecosystems (Frouz *et al.* 1997). However, the element fluxes through mounds or different processes related to ant-aphid-tree interactions were not studied here (*cf.* Figure 1). The achieved results, however, enable me to make an approximate generalization of the ecological impacts of wood ants (as listed in the Introduction), *viz.* the implications of wood ants for soil properties and tree growth in managed boreal forests. The overall ant mound density in the 1950s doubled from 1.5 mounds ha^{-1} in the north-boreal zone to the 3.1 mounds ha^{-1} in the hemi- and south-boreal zones (I). Thus the absolute ecological impacts of wood ants in the north-boreal zone are about one half of those in the hemi- and south-boreal zones. The highest mound densities, and thus the

largest ecological impacts, can be found in medium-fertile sites (I) and stand edges (II). The ant worker force surrogated by mound density and size increased with stand age (I, II). Thus the impact of ants is larger in older than in younger stands. This was seen in the increase of element pools in ant mounds with stand age (III). In Finland, the ecological impacts are largest and spatially widest in the polygyne top competitor *F. aquilonia* (II, Punttila and Kilpeläinen 2008).

Wood ant activity may have both positive and negative direct and indirect effects on tree growth, and the effects can have different magnitudes near wood ant mounds and further away from them (Table 2). As illustrated in Figure 1 and supported by articles III and IV, trees may take up nutrients from ant mounds. The nutritive effect is most probably larger in older stands due to the larger nutrient pools in active ant mounds (III) (Table 2), although nutrient uptake may be larger from abandoned or almost abandoned ant mounds that are common in recently clear-cut stands especially (Kristiansen and Amelung 2001, IV). The aggregation of organic matter into mounds may theoretically have a slightly harmful effect on the trees that shed the organic matter, but this effect might be minimal (Table 2). However, the direct effect of sap sucking by aphids supported by ants apparently outweighs the nutritive effect of ant mounds (as shown in the case of active ant mounds in V) that most probably occurs only in the immediate vicinity of ant mounds (Karhu and Neuvonen 1998; Frouz *et al.* 2008) (Table 2). Based on the manipulative treatment, wood ant-aphid mutualism (the combined effect in Table 2) reduced the growth of Norway spruce trees significantly only in the 30-year-old stands (V). The trees most often visited by ants are usually within 20 m from active ant mounds (Rosengren and Sundström 1991, V). If the trees affected by ants and aphids grow slower, then the trees further away from ant mounds may potentially obtain a slight competitive benefit, and thus wood ants may slightly reduce the difference in growth rates between more productive stand edge and the less productive stand interior (Table 2).

Table 2. Nutritive effects of active wood ant mounds and the effect of sap sucking by ant-tended aphids on Norway spruce growth near mounds, far from mounds and their combined effect at the stand level in different stand age classes (see V for growth details). Signs + and - indicate plausible positive and negative effects and the number of signs the magnitude of the effect.

Age (years)	Nutritive effect		Sap sucking		Combined at the stand level
	Near	Far	Near	Far	
5	+	0/-	++	0/-	(+)
30	+	0/-	---	0/+	-
60	++	0/-	---	0/+	0
100	++	0/-	---	0/+	0

4 CONCLUSIONS AND FUTURE RESEARCH NEEDS

This thesis gives, for the first time, stand-level information about the role of wood ants in the distribution of carbon, nutrients and roots and about the effects of ant-aphid mutualism on tree growth in managed boreal forests. Generally it was found that mound-building ants prefer certain habitat attributes and, as a result, their distribution is not even across Finland or even across individual forest stands. At the same time, the absolute effects of wood ants as key species are higher in southern than in northern Finland, higher in older than in younger stands, and higher in stand edges than in stand interiors. Because the studied roles of the key species are most efficient in the near vicinity of ant mounds, it can be concluded on the basis of this study that ant mounds increase the spatial variation of carbon and nutrient concentrations and pools in the forest floor, root distribution and nutrient uptake, and tree growth in boreal forest ecosystems. Their contributions were, however, small at the stand level.

Forest management practices and forest stand structure have changed considerably since the time when the NFI3 was carried out in the 1950s. The latest NFI10 also includes an ant mound survey, with species identification and the recording of mound size and colony vitality. The new data will give more detailed information on the distribution of ant species and their abundance, as well as on habitat preferences in Finland. The results can also be compared with the NFI3 data. In regards to wood ants, the most prominent change since the 1950s has been the increase in forest fragmentation, with diminishing stand size and an increasing proportion of different kinds of edge habitats. Fragmentation can, to a certain extent, increase the density of wood ant mounds by providing new, well-lit areas for colonisation. This study suggested that the currently small clear-cut areas with *e.g.* retention trees are maybe not as detrimental as the earlier larger clear-cut areas. Another eye-catching change since the 1950s has been the drainage of mires, which has created new habitats for wood ants but has been detrimental for mire specialists. The NFI10 will also add knowledge about mire ants, which have so far attracted relatively little research. In addition to these issues, the edge habitats, the proportion of which is constantly increasing and where ecosystem functioning is faster and where wood ant mounds also aggregate additional resources, need more research.

More research is also needed on nutrient dynamics related to wood ants. Additional studies designed to quantify nutrient dynamics between mounds and surrounding trees in comparison to other nutrient fluxes, such as litterfall and throughfall including honeydew, are needed to determine the impact of wood ant mounds on nutrient cycling in more detail (see Figure 1). A longer growth monitoring period with stand level manipulations would be needed to more accurately evaluate the impact of ant-aphid mutualism on tree growth. Aphids should also receive more attention in studies on aphid-tending ants. Furthermore, nobody knows what a changing climate will bring with it!

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