ECOSYSTEMS

The Role of Wood Ants (*Formica rufa* group) in Carbon and Nutrient Dynamics of a Boreal Norway Spruce Forest Ecosystem

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ABSTRACT

Wood ants (*Formica rufa* group) are regarded as keystone species in boreal and mountain forests of Europe and Asia by their effect on ecosystem carbon (C) and nutrient pools and fluxes. To quantify the impact of their activity on boreal forest ecosystems, C, nitrogen (N), phosphorus (P), potassium (K) and calcium (Ca) pools and fluxes in wood ant nests (WAN), and soil were assessed along a 5-, 30-, 60-, and 100-year-old Norway spruce (*Picea abies* L. Karsten) dominated successional gradient in eastern Finland. Amounts of C and nutrients in WAN increased with stand age, but contained less than 1% of total C and nutrient pools in these stands. The CO_2-efflux from nests was also insignificant, as compared to CO_2-efflux from the forest floor. Annually, the amount of C brought by wood ants into their nests as honeydew, prey and nest-building materials ranged from 2.7 to 49.3 kg ha^{-1} C, but this is only 0.1–0.7% of the combined net primary production of trees and understorey in boreal forests. The difference between wood ant nest C inputs and outputs was very small in the younger-aged stands, and increased in the older stands. Carbon accumulation rates in nests over a 100 year period are estimated to be less than 10 kg ha^{-1} a^{-1}. In contrast to C, annual inputs of N, P, and K are larger compared to wood ant nest nutrient pool size, ranging from 3 to 6% of the annual tree stand and understorey uptake. This indicates a more rapid turnover and transport of N, P, and K out of WAN, and suggests that wood ants increase the cycling rate of these nutrients in boreal forests.

Key words: ant nest; carbon balance; honeydew; element cycling; *Picea abies*; prey; succession; turnover.

INTRODUCTION

Wood ants (*Formica rufa* group) are keystone species in boreal and mountain forests of Europe and

Asia (Hölldobler 1960; Rosengren and others 1979; Laine and Niemelä 1980), as they are considered to be ecosystem engineers that affect carbon (C) and nutrient pool sizes and fluxes (for example, Jones and others 1994; Risch and others 2005). They transfer C and nutrients from the forest floor to their nests and from the nests back to the forest floor and from the tree canopy to nests (Figure 1). The area of forest floor and the number of trees affected by ants as well as the magnitude of the element transfer depend on the nest density (number and size of nest ha^{-1}), colony size (number and size of workers), the extent of the foraging area and the length of the growing season available for the foraging within the forest ecosystem (for example, Savolainen and Vepsäläinen 1988; Sorvari 2009). Wood ants collect plant litter, preferably conifer needles, twigs and resin from the forest floor to build large, long-lived nests on the soil surface (for example, Wisniewski 1967; Lenoir and others 1999). The diet of wood ants consists of elements collected from different trophic levels: honeydew excreted by aphids (Hemiptera, Aphidina) living in the tree canopy, and invertebrate prey from both the canopy and forest floor (Hölldobler and Wilson 1990; Rosengren and Sundström 1991; Domisch and others 2009). As compared to prey, honeydew is low in nutrients and mostly used as an energy source. In contrast, prey is mainly needed for brood production (Deslippe and Savolainen 1994).

Although many studies have estimated C and nutrient budgets in boreal forests including tree, understory and soil components (for example, Mälkönen 1974; Helmisaari 1995; Finér 1989,

1991; Finér and others 2003), none have included ant nests or their C and nutrient fluxes. A few studies have assessed C and nutrient pools in wood ant nests (WAN) (Pokarzhevskij 1981; Risch and others 2005; Kilpeläinen and others 2007), or C and nutrient fluxes related to wood ant activity (Zoebelein 1954; Horstmann 1974; Wellenstein 1980; Frouz and others 1997; Domisch and others 2009). These studies clearly indicate that C and nutrient pools in WAN are a very small component of total amounts in the forest floor or mineral soil in boreal forests. However, WAN are localized C and nutrient "hot spots", whose importance to nutrient cycling may depend on the successional stage of the forest stand (Ohashi and others 2012).

Earlier studies show that the amounts of phosphorus (P) and nitrogen (N) transferred to WAN as honeydew and prey at the ecosystem level are 10–60% of soil inputs from aboveground litterfall (Frouz and others 1997; Domisch and others 2009). This indicates that nutrients transferred to WAN may be a significant ecosystem nutrient flux, especially in young stands where annual tree litterfall is small. Although the C and nutrient balances of WAN must be positive to allow the nest to grow in size as the colony ages, we could not find studies in which both pools and fluxes of WAN (as shown in Figure 1) were used to estimate C and nutrient accumulation rates in different-aged stands. Such information is important to understand the role of WAN imports and exports on C and nutrient fluxes and cycling during stand succession after clear-cut harvesting, which is the major disturbance agent in boreal forests of Europe at present.

Therefore, the objectives of this paper are to: (1) estimate the C, N, P, potassium (K) and calcium (Ca) pool sizes, fluxes and accumulation rates in WAN during forest succession and wood ant colony development in different-aged Norway spruce (*Picea abies* L. Karsten) stands, and (2) assess C and nutrient fluxes of WAN in relation to fluxes from other stand components during the growth and development of a Norway spruce forest ecosystem. This was accomplished by accessing comprehensive, 3-year datasets of C and nutrient pools and fluxes of WAN, and soil in Norway spruce-dominated stands in eastern Finland.
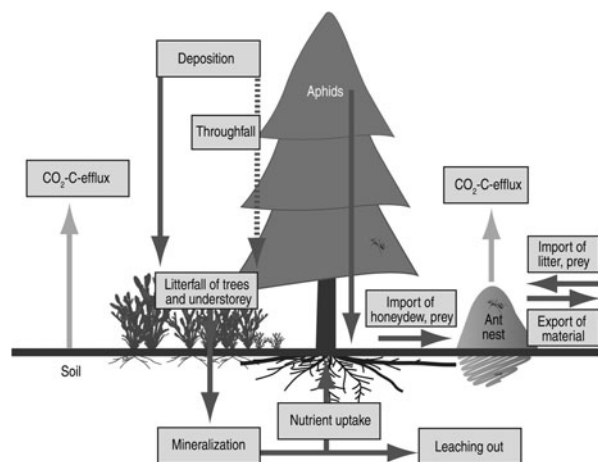

Figure 1. A schematic presentation of the carbon and nutrient pools and fluxes related to wood ant nests in forest ecosystems. Evidence for and estimates of different pools and fluxes are given in the results.

MATERIALS AND METHODS

Study Sites

Most of the information used was obtained from a series of published studies carried out in 16 Norway

spruce-dominated forests of different successional stages in eastern Finland (29°52′N, 63°04′E). The tree stand, ant nest characteristics, and study methods are described in detail by Kilpeläinen and others (2008, 2009), soil and ant nest properties by Kilpeläinen and others (2007), Ohashi and others (2007a) and Domisch and others (2008), CO_2-effluxes by Domisch and others (2006) and Ohashi and others (2007b, 2012), and ant dietary spectrum and the selection of host trees by Domisch and others (2009, 2011). The age classes of the stands were 5, 30, 60, and 100 years, with each age class having four replicates. The numbers of active WAN varied among age classes, ranging from 2.5 to 5.4 ha^{-1}. Tree stem volume and volume growth in different-aged stands ranged from 0 to 324 m^3 ha^{-1} and 0–13.7 m^3 ha^{-1} a^{-1}, respectively (Kilpeläinen and others 2008; Kilpeläinen and others 2009). More detailed stand information is given in Table 1.

Carbon and Nutrient Pools and Fluxes

Vegetation

Pool sizes and fluxes of C and nutrients in living trees, understory, WAN, and soil were estimated separately for all of the stands.

Tree stem volumes measured in autumn 2003 and 2006 in the Norway spruce stands (Kilpeläinen and others 2008) were used to calculate C and nutrient pools in the aboveground components of living trees with the equations from Palviainen and Finér (2011) for boreal forests. Stumps and coarse root biomass and C pools were estimated in a similar manner using the equations of Lehtonen and others (2004), assuming a woody biomass C content of 50%. Because no equations were available for stumps and roots of deciduous trees, the equations for Scots pine were used. The nutrient pools of trees, stumps, and coarse roots were estimated by multiplying biomass weights with the nutrient concentrations presented by Finér (1989). Fine root C and nutrient pools were obtained from

the study of Ohashi and others (2007a) in the Norway spruce stands. Carbon and nutrient content of fine root turnover were estimated to be 0.74% of the standing fine root biomass (Finér and others 2011). The annual accumulation of C and nutrients in tree biomass was calculated as follows:

$$A_i = \text{Pool}_{i2006} - \text{Pool}_{i2003}/3 \qquad (1)$$

where A_i is the annual accumulation of C, N, P, K or Ca (kg ha^{-1} a^{-1}), and Pool$_i$ is C, N, P, K, or Ca pool (kg ha^{-1}) in tree biomass in 2006 or in 2003, respectively, and 3, the number of growing seasons.

The C pool of the understory was estimated with the biomass equations presented by Muukkonen and Mäkipää (2006) for boreal forests, and assuming a 50% biomass C content. Understory nutrient pools were obtained using nutrient concentrations of Kubin (1983) for boreal Norway spruce-dominated forests. The C and nutrient content of understory litterfall was estimated to be 25% of the standing biomass, as presented by Mälkönen (1974) for boreal forests.

Tree litterfall totals were estimated using the equations of Saarsalmi and others (2007, Table 4, Eq. 1). The amount of litterfall on the top of the WAN was assumed to be proportional to nest basal area, and assumed to have a C content of 50%. Nutrient content of litterfall was calculated using concentrations presented by Ukonmaanaho and others (2008).

WAN and Soil

Pool sizes of C and nutrients in WAN and soil were published by Kilpeläinen and others (2007) and Ohashi and others (2007b). The input of C, N, P, K, and Ca as honeydew, prey, and to the WAN in each of the 30-, 60- and 100-year-old forest age stands was obtained from a study by Domisch and others (2009), which was based on measurements from one medium-sized nest for 3 years (2003, 2004,

Table 1. Mean (±SD) Stand Characteristics in the Four Stand Age Classes ($N = 4$)

Age (years)	Area (ha)	Number of active nests (ha^{-1})	Basal area of active nests (m^2 ha^{-1})	Stem volume				Volume growth (m^3 ha^{-1} a^{-1})
				Spr. (%)	Pine (%)	Dec. (%)	Total (m^3 ha^{-1})	
5	5.8 (2.0)	2.5 (2.1)	2.0 (0.9)				0	0
30	5.1 (2.0)	3.2 (1.8)	2.6 (1.3)	79	6	15	163 (34)	16.3 (4.9)
60	6.5 (3.0)	5.4 (3.2)	6.6 (6.5)	84	10	6	229 (73)	12.4 (2.3)
100	7.9 (2.5)	4.1 (1.4)	8.7 (4.5)	73	20	7	324 (49)	9.8 (7.0)

Spr. = Norway spruce = Picea abies, Pine = Pinus sylvestris L., Dec. = deciduous trees, mainly Betula pendula Roth

and 2005). Similar measurements were taken in 2003 and 2005 for one medium-sized wood ant nest (0.13 m^3) in one of the 5-year-old stands and in all of the stands in 2003, 2004, and 2005 for all nest-building materials (unpublished data).

The CO_2-efflux from WAN was obtained from the study of Ohashi and others (2012) in the four stand age classes of the Norway spruce stands. Carbon and nutrient inputs and C outputs as CO_2 from nests were extrapolated to stand level by multiplying the results obtained per nest with the nest density (number of WAN ha^{-1}) for each stand. Carbon and nutrient pools in soil and WAN were obtained from Kilpeläinen and others (2007), and soil C output (including fine roots) as CO_2 was taken from Ohashi and others (2012) who did the measurements in all of the Norway spruce stands.

RESULTS AND DISCUSSION

Changes in WAN Carbon Pools and Fluxes with Stand Age

Carbon pools

WAN contained between 36 and 233 kg ha^{-1} C, and pool size was correlated with the age of the Norway spruce-dominated stands (Table 2). Although WAN age could not be determined in these stands, it was assumed they were the same as the stand age. The only other studies on wood ant nest C pools were by Pokarzhevskij (1981), who reported a dry weight of 350 kg ha^{-1} (corresponds to app. 175 kg ha^{-1} of C) of Formica polyctena WAN in a 50-60-year-old temperate oak forest of the Russian Kursk region, and by Risch and others (2005), who found 130–990 kg ha^{-1} of C in WAN of Swiss subalpine conifer forests varying in age from 165- to 236-years-old. The size of the C pools seems to correlate positively with the volume of wood ant nest (Figure 2), which increases with stand age (Rosengren and others 1979; Vepsäläinen and Savolainen 1994; Sorvari and Hakkarainen 2005; Kilpeläinen and others 2005; Sorvari 2009). Wood ant nest age and nest C accumulation rates can increase by stand age (Table 3). The processes which control C accumulation in nests with increasing stand age were increased C input by wood ants and litterfall (Table 3), and the decrease in nest decomposition rate (Domisch and others 2008). An increase in wood ant nest C accumulation rate with increasing stand age also agrees with observations that ant population size correlates with nest size, which increases with stand succession (Sorvari and Hakkarainen 2005).

As shown in Table 2, WAN are small C pools ($<0.1\%$) even in the youngest forest age classes, where soil and understorey were the main C pools. Small wood ant nest C pools were also found in Swiss subalpine forests (Risch and others 2005), contributing only between 0.6 and 5% to total soil C pools. Even though C pools in WAN were insignificant at the ecosystem level, their C content was 6–10 times higher on an area basis (g m^{-2}) than the forest floor in the Finnish Norway spruce stands, and 3–12 times higher in Swiss subalpine forests (Risch and others 2005).

Carbon Inputs

Carbon is carried by wood ants into the nests as honeydew, prey, resin, and plant litter. Additional C is added to nests from aboveground litterfall and fine root growth (Domisch and others 2009; Figure 3). Honeydew was the most important C input, whereas plant material brought into the nests by wood ants and litterfall accounted for 12 to 44% of the annual nest C input. No other study reported the C content of litter inputs to WAN, but the amounts of litter components transported by wood ants in these Norway spruce stands agree with mass proportions reported for a wood ant colony in a Finnish Scots pine forest (Rosengren and Sundström 1991). Gibb and Johansson (2010) found that wood ants harvest 18.8, 11.7, and 24.4 kg ha^{-1} dry mass of honeydew during July in clear-cut (1–4-years-old), middle-aged (30–40 years) and old (80–100 years) Swedish boreal forests. Assuming that half of the annual honeydew input occurs in July, and is two-thirds of the total C input (Figure 3) and using a C concentration for dry honeydew of 43% (Domisch and others 2009), the annual C inputs to WAN in northern Sweden are 24, 15, and 31 kg ha^{-1} in clear-cut, middle-aged, and old stands, respectively. The C honeydew estimates for the middle-aged and old stands are within the 95% confidence intervals of our Norway spruce stands, but honeydew inputs in the Swedish clear-cut stands are higher than the estimate for our seedling stands. The WAN present in the Swedish forests might have survived a few years after clear-cut harvest, and consequently, honeydew transport remained at a relatively high level. However, food resources were reduced in our young Norway spruce seedling stand, and honeydew harvesting was decreased (Punttila and others 1991; Punttila 1996; Domisch and others 2005; Sorvari and Hakkarainen 2007). The amounts of honeydew carried into WAN are higher in temperate forests, where a total of 13–216 kg ha^{-1} a^{-1} (dry mass) has been reported from a relatively small number of stands (Horstmann 1974;

Table 2. Mean (±SD) Carbon, Nitrogen, Phosphorus, Potassium and Calcium Pools (kg ha^{-1}) in Wood Ant Nests (Including Above- and Belowground Components of Living Trees, and Understorey) and Soil Organic Layer in the Norway Spruce Stands of Four Age Classes ($N = 4$)

	5 Years	30 Years	60 Years	100 Years
Carbon				
Nests	36 (20)	40 (19)	135 (146)	233 (143)
Vegetation	2083	72901	93789	126449
Soil	32745 (5703)	25074 (3438)	29579 (4594)	27526 (2397)
Nitrogen				
Nests	1.06 (0.56)	1.40 (0.54)	4.12 (4.60)	6.25 (3.56)
Vegetation	39.4	437.3	511.6	650.8
Soil	2203 (434)	2109 (243)	2313 (813)	1814 (157)
Phosphorus				
Nests	0.036 (0.022)	0.045 (0.018)	0.154 (0.173)	0.255 (0.187)
Vegetation	20.0	67.5	90.7	101.9
Soil	52.7 (18.2)	45.7 (5.8)	43.3 (13.6)	38.4 (6.1)
Potassium				
Nests	0.076 (0.056)	0.100 (0.038)	0.274 (0.236)	0.630 (0.455)
Vegetation	37.3	216.3	260.7	321.5
Soil	122 (68)	117 (40)	83.4 (22.8)	71.9 (10.2)
Calcium				
Nests	0.247 (0.135)	0.821 (0.343)	1.520 (1.645)	2.284 (1.555)
Vegetation	73.8	476.0	558.7	674.4
Soil	364 (169)	358 (158)	272 (114)	267 (92)

Wood ant nest and soil data were taken from Kilpeläinen and others (2007)
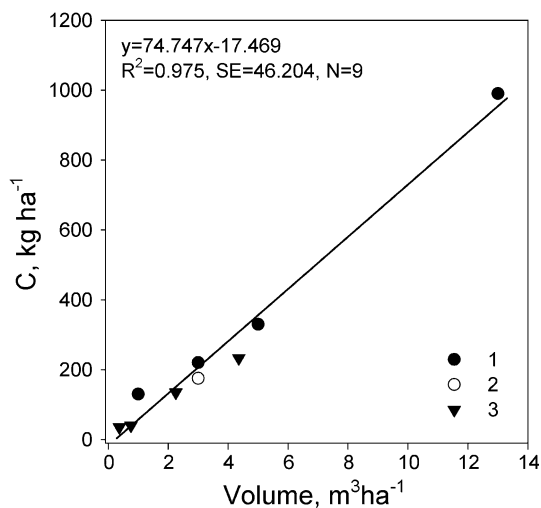

Figure 2. Carbon (C) contents of wood ant nests in different forests in relation to nest volume (*1*) Kilpeläinen and others (2007), (*2*) Pokarzhevskij (1981), (*3*) Risch and others (2005).

Wellenstein 1980; Frouz and others 1997 and references therein).

Total C inputs into WAN from honeydew and prey seem to increase with the age of the stand (Figure 3), as does the tree stand productivity from the 5-year-old stands compared to the older ones

(Tables 1, 3). Because the availability of phloem sap for aphids is related to the productivity of the forest (Stadler and Michalzik 1998; Stadler and others 1998), site quality can also affect the amounts of honeydew C carried by wood ants into their nests. It has been shown that the availability of food plays an important role in determining the abundance and sexual productivity of ant colonies (Deslippe and Savolainen 1994). The C transported to WAN is a reallocation of C within the ecosystem, and is an insignificant (0.1–0.7%) amount of the C fixed annually in net primary production (trees and understorey combined) in boreal forests. This explains why the harvesting of honeydew C from Norway spruce canopies was not found to reduce tree growth at the ecosystem level (Kilpeläinen and others 2009).

Carbon Outputs

As shown in Table 3, CO_2-efflux from WAN in Finnish Norway spruce forests increased with stand age (Table 3). Such a stand age effect was not observed in older Swiss subalpine forests (Risch and others 2005), where the age varied from 165 to 236 years. Most of the CO_2-efflux likely comes from wood ant respiration, and a lesser amount from microbial decomposition of nest organic matter and

Table 3. Mean (±SD) Annual Carbon Fluxes (kg ha^{-1} a^{-1}) in Wood Ant Nests, Aboveground Parts of Trees, Understorey, Roots and Soil Organic Layer in the Norway Spruce Stands of Four Age Classes ($N = 4$)

Flux	5 Years	30 Years	60 Years	100 Years
Nests				
Input	2.7 (2.0)	12.4 (7.1)	36.7 (22.3)	49.3 (16.5)
Output	3.3 (1.6)	9.6 (5.6)	17.6 (10.4)	17.9 (5.9)
Trees				
Accumulation	0	7011 (1998)	4968 (981)	3697 (1733)
Litterfall	0	591 (50)	692 (157)	678 (78)
Roots				
Litterfall	227	252	283	322
Understorey				
Litterfall	870	1287	1635	1948
Soil				
Output	8360 (3035)	10738 (502)	9670 (1449)	11096 (1134)

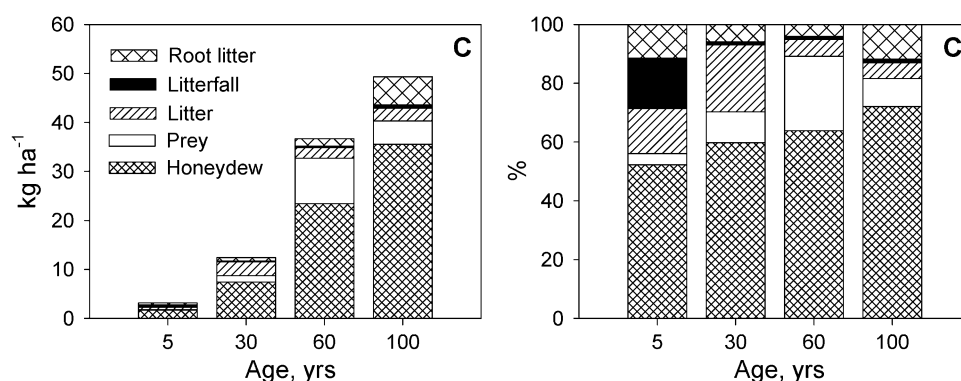*Soil carbon fluxes were taken from Ohashi and others (2012)*

Figure 3. Annual input of carbon (C) in the wood ant nests as honeydew, prey, litter (mainly needles and resin) and litterfall (needle and fine roots) in the different stand age classes. Inputs of honeydew and prey to the nests are taken from Domisch and others (2009).

fine root respiration (Risch and others 2005; Domisch and others 2006; Ohashi and others 2007b). However, WAN in temperate forests may have higher moisture contents than WAN in boreal forests (Frouz and others 1997; Domisch and others 2008), and organic matter mineralization in these nests could contribute more to total nest CO_2-efflux.

In contrast, no stand age-dependent trend was found in the CO_2-efflux from the forest floor in the Finnish boreal or Swiss subalpine forests where, however, all the study stands were much older (165–236 years). The proportion of wood ant nest CO_2-efflux in total forest soil CO_2-efflux increased with stand age in Norway spruce forests, but the contribution was marginal in both ecosystems: 0.03–0.5% in Norway spruce stands (Ohashi and others 2012) and 0.7–2.7% in the subalpine forests (Risch and others 2005) and the proportions would have been even smaller if the CO_2-effluxes from soil coarse woody debris would have been measured in the studies and included in the forest soil CO_2-effluxes (Palviainen and others 2010).

Carbon Budget

The balance between C inputs and outputs as CO_2 was near zero in the two youngest stand age classes, and somewhat positive in the two oldest age classes (Table 3); however, these C balance estimates do not include C outputs in nongaseous forms. To increase size and maintain nest vitality, the long-term C balance of nests is positive, otherwise nests would gradually collapse. These estimated annual nest C accumulation rates are close to the combined inputs of litter by wood ants and litterfall on the nest surface (1–11 kg C ha^{-1} a^{-1} in boreal forests), both of which decompose slowly (Lenoir and others 2001, 2003; Domisch and others 2008). In contrast, C inputs from honeydew and prey are rapidly consumed, and quickly lost as CO_2 by wood ant respiration. Similar C accumulation rates (1–7 kg C ha^{-1} a^{-1}) were also calculated by dividing the nest C pools by the age of the stands. The comparable figures obtained with these different methods indicate that the long-term C

accumulation rates of WAN in boreal forests are less than 10 kg ha^{-1} a^{-1}.

Changes in Wood Ant Nest Nutrient Pools and Fluxes with Stand Age

Nutrient Pools

Similar to C, wood ant nest pools of N, P, K, and Ca in Finnish Norway spruce increased with stand age (Table 2). Except for Ca, the nutrient pools increased with nest volume (Figure 4). Nutrients in nests were a very small component of total nutrient pools ($<1\%$) in the boreal forests. However, on a local area basis (g m^{-2}), the nutrient content of WAN in Finland and Switzerland were 3–11 times

higher than in the forest floor (Risch and others 2005, Kilpeläinen and others 2007).

Transport and Accumulation of Nutrients

The annual input of nutrients to WAN in boreal Norway spruce forests followed the same stand age related pattern as C (Table 4). More than 90% of N, P and K were brought into nests as honeydew and prey, which have higher nutrient concentrations than plant litter used in nest construction (Domisch and others 2009, Figure 5). Honeydew supplied most of the N, P, and K to nests (59–84%), whereas Ca contributions were similar for honeydew and prey. However, Ca concentrations were higher in
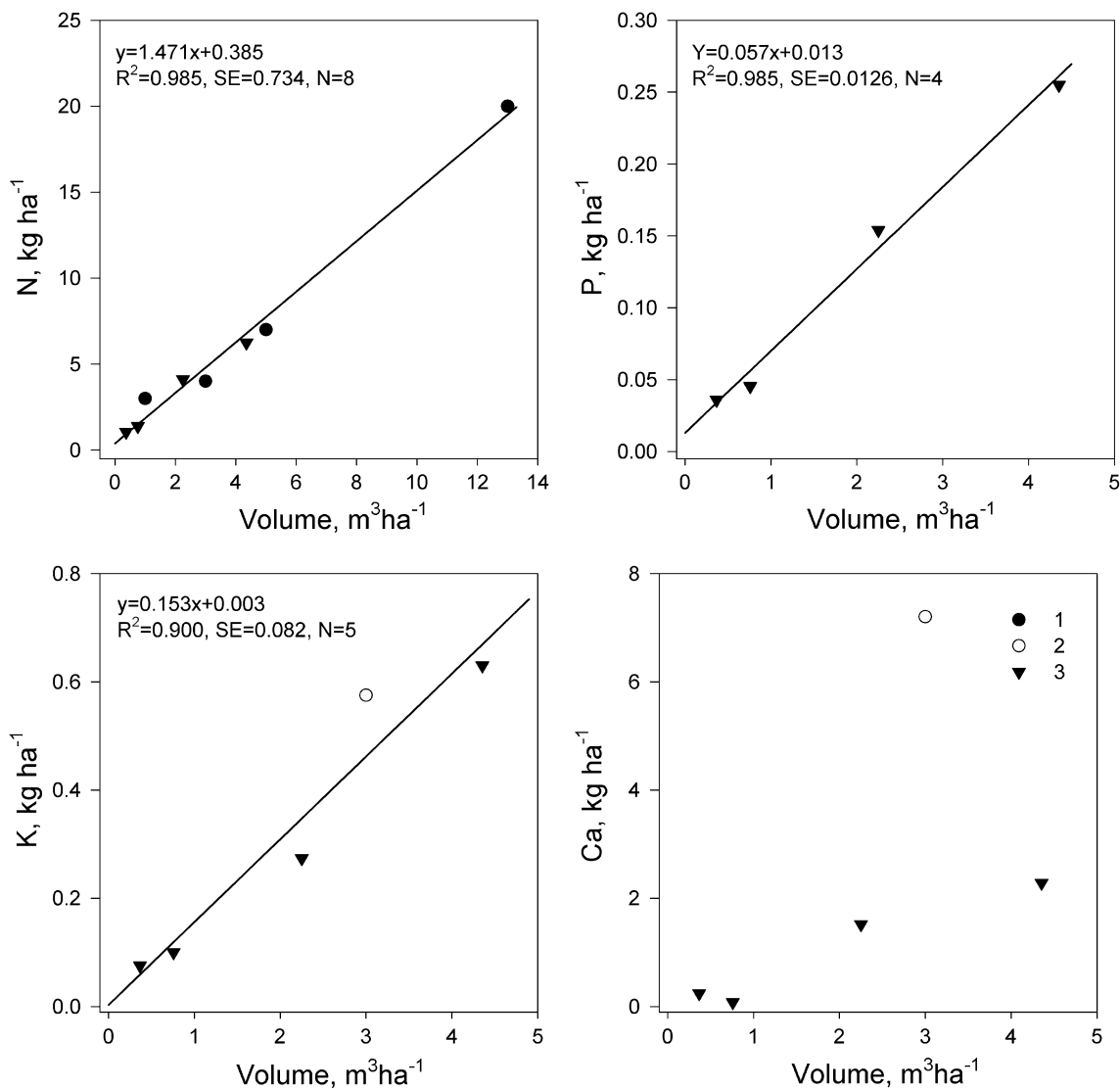

Figure 4. Nitrogen (N), phosphorus (P), potassium (K) and calcium (Ca) contents of wood ant nests in different forests in relation to nest volume (*1*) Kilpeläinen and others (2007), (*2*) Pokarzhevskij (1981), (*3*) Risch and others (2005).

wood ant nest litter than honeydew and prey, and supplied 27–73% of nest Ca. Frouz and others (1997) reported that the annual input of P into WAN was 1.725 kg ha^{-1} in a temperate Czech Republic Norway spruce plantation, and 78% was transported as prey instead of honeydew. This was higher than in Finnish boreal forests, and is likely due to higher wood ant nest density in the Czech plantation (0.2% of the soil surface area), compared to 0.02–0.09% in the Finnish stands. In a German oak forest, N input to WAN as honeydew was 0.7 kg ha^{-2} a^{-1} (Horstmann 1974), which is

Figure 5. Annual transport of nitrogen (N), phosphorus (P), potassium (K) and calcium (Ca) by wood ants into nests as honeydew, prey, litter (mainly needles and resin), and from litterfall on the nest surface in the different stand age classes. (Fine roots were not included, because the root nutrient uptake was assumed to take place inside the nests). Inputs of honeydew and prey to the nests are taken from Domisch and others (2009).

comparable to the two younger boreal Norway spruce age classes. We could not find any other studies in the literature which measured WAN nutrient inputs.

Table 4. Mean (±SD) Annual Nitrogen, Phosphorus, Potassium and Calcium Fluxes (kg ha^{-1} a^{-1}) in Wood Ant Nests, Living Trees, Understorey, Roots and Soil Organic Layer in Norway Spruce Stands of Four Age Classes ($N = 4$)

	5 Years	30 Years	60 Years	100 Years
Nitrogen				
Nests				
Input	0.20 (0.16)	1.11 (0.64)	4.87 (2.88)	4.86 (1.60)
Trees				
Accumulation	0	38.4 (10.7)	25.2 (6.5)	17.4 (8.2)
Litterfall	0	14.9 (1.26)	17.7 (4.0)	16.7 (1.9)
Understorey				
Litterfall	4.7	5.25	5.9	6.7
Roots				
Litterfall	15.2	22.5	28.5	34.0
Phosphorus				
Nests				
Input	0.020 (0.016)	0.100 (0.057)	0.488 (0.288)	0.320 (0.105)
Trees				
Accumulation	0	3.91 (1.04)	2.51 (0.64	1.68 (0.81)
Litterfall	0	1.75 (0.15)	2.08 (0.47	1.97 (0.23)
Understorey				
Litterfall	0.55	0.61	0.68	0.77
Roots				
Litterfall	1.31	1.94	2.47	2.94
Potassium				
Nests				
Input	0.039 (0.031)	0.169 (0.139)	0.755 (0.448)	0.522 (0.172)
Trees				
Accumulation	0	16.6 (4.4)	10.8 (2.4	7.33 (3.6)
Litterfall	0	6.94 (0.59)	8.21 (1.87)	7.80 (0.89)
Understorey				
Litterfall	1.32	1.46	1.64	1.87
Roots				
Litterfall	2.37	3.51	4.45	5.30
Calcium				
Nests				
Input	0.007 (0.007)	0.078 (0.045)	0.148 (0.088)	0.149 (0.050)
Trees				
Accumulation	0	37.6 (10.0)	23.7 (5.3)	15.6 (7.8)
Litterfall	0	6.1 (0.5)	7.2 (1.6)	6.8 (0.8)
Understorey				
Litterfall	1.14	1.26	1.42	1.61
Roots				
Litterfall	5.13	7.58	9.63	11.48
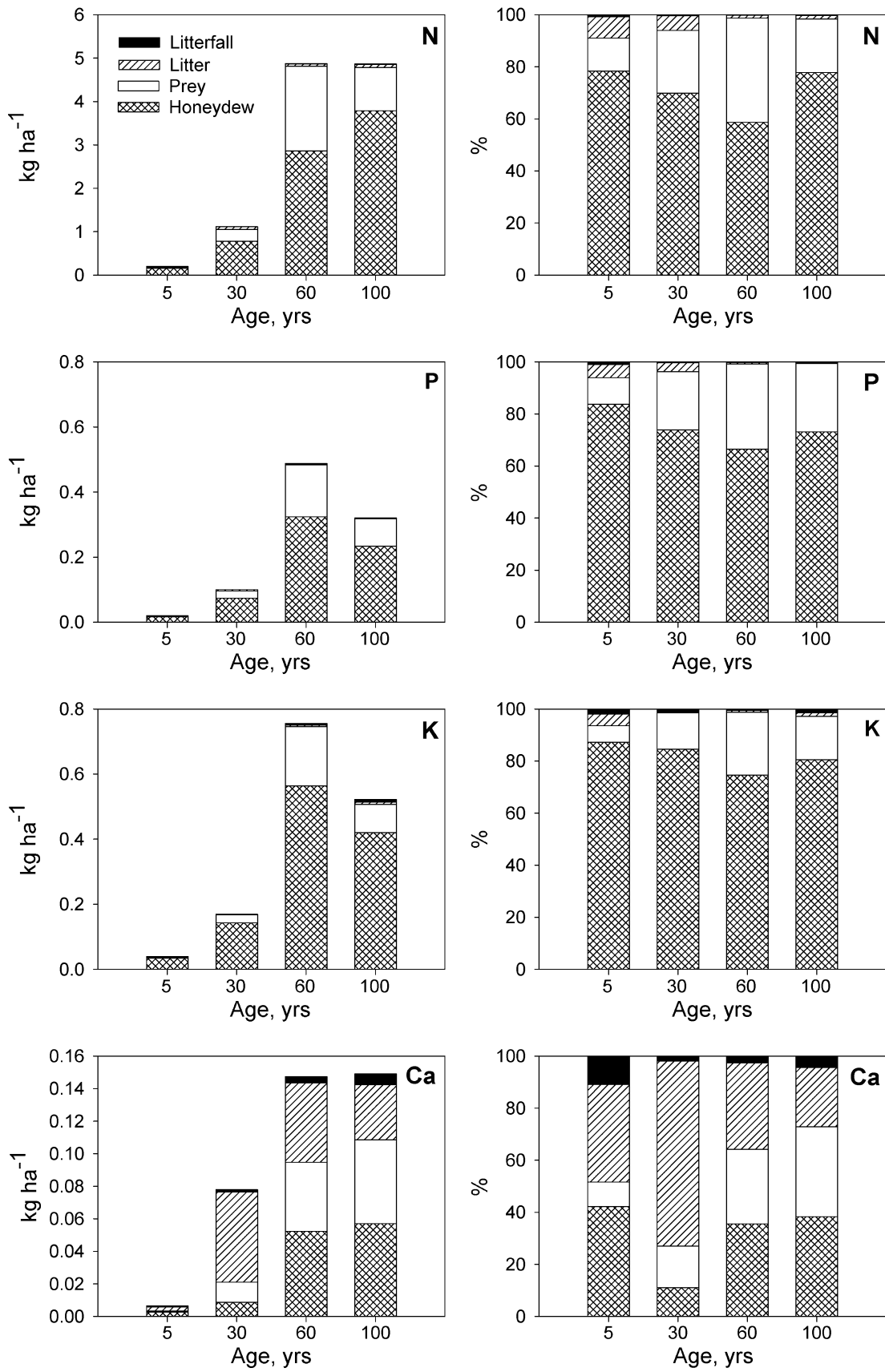
The annual transport of N, P, and K into WAN was large compared to the amounts of nutrients already in the nests (Tables 2, 4). This indicates that nutrients are rapidly cycled, and there is a continuous flow of nutrients out of the nests. We do not have any information on the magnitude of these nutrient flows, but there are a number of pathways by which nutrients are removed from WAN: (1) ants remove waste material (for example, dead bodies of ants, prey remains, seeds, and so on) to garbage dumps outside the nest (Mabelis 1979; Gorb and others 2000; Czechowski 2008 and references therein), (2) ant-propagule production (sexual production, that is, gynes and males) varies from year-to-year and may constitute a large proportion of all reproductive investments of a colony as was in a monogynous population of *Formica exsecta* where an average of 73% of the spring brood and 85% of its biomass were sexuals which leave the natal nest for dispersal (Vitikainen and others 2011), in contrast to the monogynous colonies, in polygynous colonies the produced gynes mostly stay in their natal, often multiple-nest colony, (3) predation on ants both on the nest, especially in early spring by brown bear and woodpeckers (Rolstad and others 1998; Swenson and others 1999) and on the foraging territory by ants (Mabelis 1979) and other predators, (4) other soil fauna in the WAN (Laakso and Setälä 1998; Lenoir and others 2003) move nutrients to the surrounding soil and dispersing myrmecophiles to other ant colonies (for example, Päivinen and others 2002), (5) roots growing inside WAN (Ohashi and others 2007a) translocate nutrients from WAN to the aboveground, and (6) the fungi translocate nutrients from decomposing nest organic matter into the surrounding soil (Berg 1988; Boddy and Watkinson 1995). The leaching of nutrients out of WAN is probably insignificant, and does not exceed nutrient input from atmospheric deposition, because only the uppermost nest layers are affected by rainfall and the rest of the nest remains dry (Frouz 1996; Lenoir and others 2001; Domisch and others 2008). The mineralization of N and P from litter used for nest building is slow (Domisch and others 2008), indicating that the N and P cycling rates are accelerated by wood ant activity. This might be especially important in boreal forests, where N is often a growth-limiting nutrient (for example, Tamm 1991). Eventually WAN are abandoned, the moisture content of nest organic matter increases, and they become hot spots for nutrient mineralization (Lenoir and others 2001; Domisch and others 2008).

The annual transport of N, P, and K to WAN was 3–6% of the combined total annual flux in trees and understory for the two oldest Norway spruce age classes, whereas the proportions were smaller (~1%) in the two youngest age classes (Table 4). The corresponding proportions for Ca fluxes were even smaller, varying between 0.2 and 0.6% in the different stand age classes. Frouz and others (1997) calculated that more than 30% of the annual P flux from the aboveground tree components to soil in a temperate Norway spruce plantation is mediated through WAN. If we make a similar calculation for the Finnish boreal Norway spruce forests, 22–23% of N and 14–19% of P fluxes from trees were annually transported through WAN.

WAN as Carbon and Nutrient Hot Spots

The impact of wood ants in forest ecosystems is spatially heterogeneous, and dependent on the extent of their foraging area and nest density. Based on a literature review by Risch and others (2005), the number of WAN in most European forests is less than 5 ha^{-1} and seldom is greater than 15 ha^{-1}. The recent national forest inventories in Finland show that the average wood ant nest density of active nests is 3.19 ha^{-1} (Punttila and Kilpeläinen 2009). During forest succession wood ant nest density varies less than nest size (Punttila 1996; Kilpeläinen and others 2008), which increases with stand age (Domisch and others 2005; Kilpeläinen and others 2008). Changes in wood ant species composition during forest succession also affect ant population size (Punttila 1996; Kilpeläinen and others 2008).

The number and distribution pattern of WAN increased the spatial variability of C and nutrients in boreal Norway spruce forests, because their C and nutrient content (g m^{-2}) was 6–10 times higher than in the forest floor. The foraging distance of wood ants from their nests depends on the ant species and the size of the colonies. Early successional stands have a higher diversity of wood ants and other nest-building ant species, and the nests (and colony population sizes) of these species are usually much smaller than in later successional stands (Kilpeläinen and others 2008; Sorvari 2009). The foraging distance of smaller wood ant populations in younger stands extends only 10 m from their nests, whereas in late successional stands with larger colonies of species such as *Formica aquilonia*, the dominant wood ant in Finnish Norway spruce stands, foraging distances are much greater (Kilpeläinen and others 2008; Sorvari 2009; Table 5). Using the equation presented by Sorvari (2009):

$$Y = 22.006 \times x + 14.985 \qquad (2)$$

Table 5. Foraging Distances of Wood Ants in Different Types of Forests Reported in Literature

Forest type	Wood ant species	Foraging distance (m)	Reference
Temperate			
Several forest types	*Formica rufa* group	25–30 m	Adlung (1966)
Pinus sylvestris	*F. polyctena*	>60 m	Wellenstein (1980)
Hemiboreal			
P. sylvestris, mature	*F. polyctena*	<150 m	Vepsäläinen and Savolainen (1994)
Boreal			
P. sylvestris, pole stage	*F. rufa, F. aquilonia*	20 m	Domisch and others (2011)
P. sylvestris, sapling stage	*F. aquilonia, F. lugubris, F. polyctena*	20 m	Domisch and others 2011
Betula pendula, pole stage	*F. aquilonia, F. lugubris*	20 m	Domisch and others (2011)
B. pendula, sapling stage	*F. rufa, F. pratensis, F. aquilonia*	20 m	Domisch and others (2011)
P. sylvestris, Picea abies, B. pendula, sapling stage	*F. exsecta*	<10 m	Sorvari (2009)
P. abies, B. pendula, mature forest	*F. aquilonia*	<150 m	Sorvari (2009)
Subarctic			
B. pubescens	*F. aquilonia*	15–20 m	Laine and Niemelä (1980)

where Y is the distance to the most distant tree used for foraging (m), and x is basal area of the nest (m^2), the average foraging distances in the 5-, 30-, 60- and 100-year-old Norway spruce stands are 33, 33, 41 and 61 m. Therefore, wood ants foraged in 85% of the total stand area in the youngest age classes, and 100% of the stand in the older age classes. However, in reality, the distribution of wood ant activity in their foraging area is highly uneven (for example, Figure 2 in Savolainen and Vepsäläinen 1989 and Figure 1 in Niemelä and others 1992), and nest densities are at their highest near forest edges (Kilpeläinen and others 2008).

In Finnish boreal Norway spruce forests only a very small proportion of trees (0.01–2.3%) is visited by wood ants (Kilpeläinen and others 2009; Domisch and others 2011). As expected, the percentage is higher near WAN, where up to 60% of the trees are visited within 20 m of the nest (Vepsäläinen and Savolainen 1994; Domisch and others 2011). This indicates that the C and nutrient inputs to WAN come from very few trees, the growth of which is significantly affected by ants harvesting honeydew (Kilpeläinen and others 2009). The indirect effects of wood ants on canopy throughfall, soil nutrient mineralization, hunting of invertebrates for prey, and C and nutrient fluxes in and out of nests can also impact the growth of other trees in the stand not used by wood ants to tend aphids for honeydew (for example, Stadler and others 2004; Jurgensen and others 2008).

Conclusions

Wood ants had little impact on C pool size and efflux in different-aged Norway spruce stands in Finland. Carbon accumulation rates in WAN over a 100-year period are estimated to be less than 10 kg ha^{-1} a^{-1}. The annual transport of N, P, and K into nests was large compared to nest pool size and 3–6% of the annual stand uptake, which indicates that these nutrients are rapidly cycled, and there is a continuous flow of nutrients out of nests. Thus, WAN are localized ''hot spots'' for nutrient cycling, and can affect the spatial distribution of C and nutrient fluxes within boreal forest ecosystems.

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