Ann. Zool. Fennici 42: 269–275 ISSN 0003-455X
Helsinki 28 June 2005

Accumulation of phosphorus in nests of red wood ants *Formica s. str*.

Jan Frouz[1]*, Jiří Kalčík[1] & Pavel Cudlín[2]

[1)] *Institute of Soil Biology ASCR, Na sádkách 7, CZ-37005 České Budějovice, Czech Republic (*e-mail: frouz@upb.cas.cz)*
[2)] *Institute of Landscape Ecology ASCR, Na sádkách 7, CZ-37005 České Budějovice, Czech Republic*

Received 1 Nov. 2004, revised version received 18 Feb. 2005, accepted 1 Mar. 2005

Frouz, J., Kalčík, J. & Cudlín, P. 2005: Accumulation of phosphorus in nests of red wood ants *Formica s. str*. — *Ann. Zool. Fennici* 42: 269–275.

Here we summarize recent data on the accumulation of phosphorus in nests of wood ants as compared with that in the surrounding forest soil, and discuss mechanisms that cause this phenomenon. Moreover, we also indicate questions for future research. Various species of red wood ants (*Formica s. str*.) in a wide geographic area show an apparent increase of phosphorus content in their nests. Remarkably, this increase mainly entails the forms of phosphorus which are potentially available for plants or microflora, whereas the increase in total phosphorus content is less pronounced. This increase in available phosphorus is mainly attributable to release from food brought to the mound, release by decomposition of organic matter in the nest and a shift in pH of the nest material from acidic to neutral, which supports the stability of available forms of phosphorus. The effect of increased availability of phosphorus in wood-ant nests in the surrounding forest ecosystem is not quite clear and requires further attention.

Introduction

Phosphorus often belongs to limiting nutrients, particularly in coniferous forests, not only owing to low content, but also owing to low availability in acidic soils (Wood *et al*. 1984, Prescott *et al*. 1992). Nevertheless, phosphorus content in nests of several ant species has been reported to be higher than in the surrounding soil (Dlusskij 1967, Czerwinski *et al*. 1971, Petal *et al*. 1977, Frouz *et al*. 2003). The aim of this review is to summarize recent data on the role of wood ants in phosphorus cycling in coniferous-forest ecosystems. We will focus on the following main questions: (1) How large are the differences in phosphorus content between ant nests and the surrounding soil? (2) What factors cause the accumulation of phosphorus in ant nests? We also indicate areas that we assume promising for future research.

Methods and data

A variety of methods have been used to study the accumulation of phosphorus in ant nests, but here we focus in particular on the description of methods used in papers published in other languages than English, as well as some unpublished data presented in this paper. Most studies dealing with the effect of ant nests on the content of nutrients compare values from various parts of the nest with those in the surrounding soil (Table 1). Soil consists of several layers, which differ in their physical and chemical composition (Leeper & Uren 1993). Moreover, the soil material in ant nests is not homogeneous either, but consists of several strata (Dlusskij 1967). This raises the question which strata to choose for comparison. Here we use the term "soil" for the organic soil horizon (a mixture of fermentation and humus layers). In ant hills we distinguish between the central part of the nest and the soil rim. The central part of the nest typically has a conical shape and is constructed from needles, small branches and other plant material. The surface layer usually consists of finer material, whereas the deep layers comprise larger pieces of plant material. The soil rim that typically surrounds the central part of the nest, is slightly elevated above the surface of the surrounding soil, and consists of mineral soil and fine organic material excavated in the course of burrowing chambers and corridors in the underground part of the nest (Dlusskij 1967). Unless otherwise stated, nest samples, both from the central part and the soil rim, as well as samples of surrounding soil were taken from surface layers (depth 0–15 cm). Because samples taken from the same location are not statistically independent we used the parametric paired *t*-test for comparing phosphorus contents in nest mounds and the surrounding soil. Unfortunately, some older papers, (Malozemova & Koruma 1973, Zacharov *et al*. 1981) did not provide adequate statistical test results. Apart from the literature data we also include some of our unpublished results on the spatial distribution of available phosphorus at various distances from the nest (Fig. 1a). The location was a spruce forest on cambisoil near the town of Tabor (Czech Republic). Samples were taken with the soil corer in a net of sampling points (Fig. 1a) on a transect through a nest of *Formica polyctena*. Samples were dried, homogenized and sieved through a 2-mm screen and the available phosphorus was extracted from a fraction > 2 mm using the exchange resin method (Macháček 1986). The phosphorus content in extracts was measured as described in Watanabe and Olsen (1965).

Unless otherwise indicated, the term available phosphorus refers to the chemical forms of phosphorus that are believed to be potentially available for most of plants and soil microflora. However, the factors affecting the actual use of phosphorus by plants may interact in many complex ways so that apart from the amount of available forms of phosphorus also other factors such as plant species and environmental conditions may affect the usage of phosphorus (Brady & Weil 1999).

To find out whether the additional supply of available phosphorus supports plant growth, we tested the growth rate of seedlings of *Picea abies* under different regimes of phosphorus supply in the laboratory (Table 2). The seedlings were grown in soil taken from a soil rim of *Formica polytena* and from the surrounding soil 1 and 3 m from the soil rim. Soil samples were taken in April 1992 in a spruce forest on cambisoil

Table 1. The content of total and available phosphorus (mg kg^{-1}) in nests of three *Formica* species, and the top layer of the surrounding forest soil. An asterisk (*) indicates that the phosphorus content is significantly higher in the nest (pairwise *t*-test: $p < 0.05$).

Species	Locality	*n*	Total P (mg kg^{-1})			Available P (mg kg^{-1})		
			soil	nest		soil	nest	
				rim	central part		rim	central part
F. polyctena[1]	Spruce forests, Czechia	18	901 ± 548	1179 ± 710*	–	76 ± 149	321 ± 290*	–
F. aquilonia[2]	Spruce forest, Russia	5	1030	1080 ± 225	1732 ± 409	20	61 ± 21	368 ± 104
F. pratensis[3]	North Kazachstan	1	–	–	–	24	39	144
F. lugubris[3]	North Kazachstan	1	–	–	–	24	139	218
F. polyctena[3]	North Kazachstan	1	–	–	–	24	96	174

[1] Frouz & Kalčík 1996, [2] Zacharov *et al.* 1981, [3] Malozemova & Koruma 1973.

near the town of Šluknov (Czech Republic). The substrates from individual sampling points were placed in 10 pots (i.e. 30 pots in total) 6 × 6 cm, 5 cm deep, and 13 seeds of *P. abies* were sown in each pot. The pots were kept in an outdoor plastic shelter and watered regularly for 120 days (June–September). At the end of the experiment the proportion of survivors was recorded and 240 randomly selected seedlings (8 from each pot) were harvested, divided in root, stem (wood) and needles. This material was first dried at 60 °C for 24 h, and then weighed to the nearest 0.1 mg. The values from all eight seedlings obtained in each pot were then averaged and these mean values for individual pots were used in future statistic calculations. The differences in survival and the weight of individual parts were compared with one way ANOVA with an LSD post hoc test using SPSS 10.0 software package.

Content and availability of phosphorus in wood ant nests and its effect on plants growth

Many studies have shown that nutrient contents in mound material or in excavated soil around the nest entrance is higher that in the surrounding soil in a variety of ant species (Dlusskij 1967, Czerwinski, *et al.* 1971, Petal *et al.* 1977, Petal 1978, Pokarzhevskij 1981, Frouz & Kalčík 1996, Frouz *et al.* 2003, Wagner *et al.* 2004; Table 1). In particular, phosphorus is one of the elements that occur at higher content in ant nests as compared with that in the surrounding soil. Frouz and Kalčík (1996) found that the soil rim of *F. polyctena* mounds had a significantly higher content in total, available, and water-soluble phosphorus than the surrounding soil (total phosphorus: $t = -4.44$, d.f. = 17, $p = 0.0004$; available phosphorus: $t = -4.63$, d.f. = 17, $p = 0.0002$; water soluble phosphorus: $t = -9.24$, d.f. = 17, $p < 0.0001$; Table 1). The elevation in phosphorus content in the nest (nest – soil difference) varied

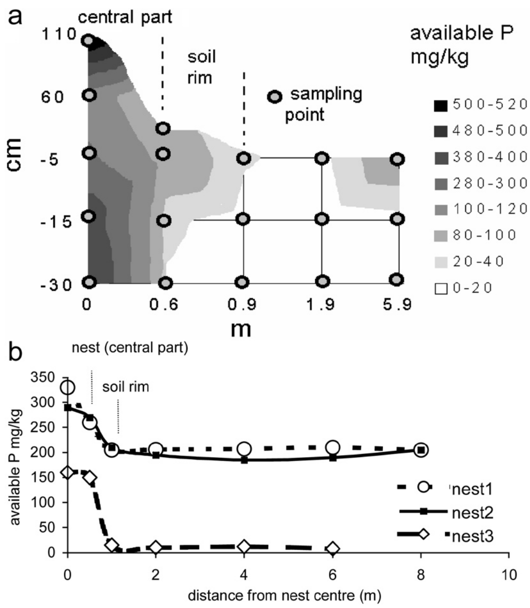

Fig. 1. Distribution of available phosphorus in (**a**) a transect across a *Formica polyctena* nest, and (**b**) the top soil layer (depth of 0–5 cm) at various distances from the nest center.

Table 2. The survival and dry mass (average ± S.D.; S.D. refers to variability between pots) of spruce (*Picea abies*) seedlings grown for one season on substrate taken from a *Formica polyctena* nest soil rim, and the surrounding forest soil 1 and 3 m from the nest. Statistically homogeneous groups are marked by the same letter LSD test ($p < 0.05$).

Substrate	Survival (%)	Dry mass (mg) of		
		roots	wood	needles
Soil rim	62.3 ± 15.5	34 ± 7a	22 ± 7a	43 ± 13a
Soil 1 m from nest	53.1 ± 13.5	16 ± 4b	8 ± 6b	19 ± 4b
Soil 3 m from nest	51.5 ± 13.3	12 ± 3b	9 ± 3b	16 ± 5b
Total degree of freedom	29	29	29	29
d.f. within groups	27	27	27	27
d.f. between groups	2	2	2	2
$F_{2,27}$	1.52	51.15	16.64	23.47
p	0.24	< 0.0001	< 0.0001	< 0.0001

depending on the form of phosphorus so that the available forms were relatively more abundant than total phosphorus in the nest material (Table 1). For example, total phosphorus content was about 1.3 times, whereas the available phosphorus content was 4 times higher in nest mounds of *F. polyctena*, than in the surrounding soil (Table 1; Frouz & Kalčík 1996). This difference is even more pronounced for water-soluble phosphorus, the content of which was six times higher in the nest material than in the soil (13 ± 9 mg kg^{-1} in soil and 81 ± 37 mg kg^{-1} in soil rim of the nest; Frouz & Kalčík 1996). Thus, ants not only affect the overall content but also the availability of phosphorus. The greatest increase in available phosphorus content occurred in the center of the aboveground part of the nest, whereas the elevation in available phosphorus content was less pronounced in the deeper and peripheral parts of the nest (Fig. 1a). The elevation of phosphorus contents was typically restricted to the nest itself and the soil rim surrounding the nest (Fig. 1). A similar pattern has also been found in other species of *Formica* ants (Zacharov *et al.* 1981, Malozemova & Koruma 1973; Table 1) and mounds of other ant species such as soil mounds of *Lasius niger* (Frouz *et al.* 2003).

Zacharov *et al.* (1981) compared two *F. aquilonia* nests of different ages and roughly calculated the changes in total amount of phosphorus contained in the two nests by multiplying the amount of phosphorus per unit weight with the estimated weight of the nest (Zacharov *et al.* 1981). Based on these data an entire 2-year-old nest of *F. aquilonia* was estimated to contain 10 g of available phosphorus and a 10-year-old nest about 75 g of available phosphorus, an increase of about 65 g in 8 years. Not only the absolute content of nutrients, but also the relative content of phosphorus, increased with nest age. The 2-year-old nest contained 250 mg kg^{-1} of available phosphorus whereas the 10-year-old nest contained 550 mg kg^{-1} (nest age was known from an annual inventory of nests in the locality; Zacharov *et al.* 1981). Kristiansen *et al.* (2001) found that after abandonment of the nest mound the content of available phosphorus in the nest material decreased, but even 10 years after the abandonment the soil below nest contained more available phosphorus than the surrounding soil.

High content of available phosphorus in ant nests, and perhaps also other changes in nest material, may support plant growth. This assumption was tested in the seedling growth experiment (Table 2). The root, stem and needle biomass of *P. abies* seedlings grown in substrate taken from *F. polyctena* nest soil rim were significantly higher as compared with those grown in soil taken 1 and 3 m from the nest (Table 2) (LSD post hoc test: $p < 0.0001$, d.f. = 20 in all cases in both comparisons for all three variables, root, stem and needle; Table 2). By contrast, the stem, root and needle biomass did not differ between seedlings grown in soil taken 1 and 3 m from the nest, respectively (Table 2). Seedling survival did not differ significantly between any of the three treatments (Table 2).

Mechanisms affecting content and availability of phosphorus in wood ant nests

Given that elevated levels of especially available phosphorus can be found in nest mounds of ants, the question arises by which mechanisms this occurs. Ants can modify the chemical content of nest material by: (i) soil mixing, i.e. the mixing of soil material from deeper and surface layers through excavation activities, (ii) enrichment of nest material by nutrient rich residues of food and excreta of ants, (iii) transport of organic matter into the ant nest as a building material (Baxter & Hole 1967, Kloft 1978, Frouz *et al.* 2003). All these processes may affect both the overall amount and the availability of individual chemical elements. Availability can be, in addition, affected by acceleration of the decomposition of organic matter as well as changes in the pH mediated by the ants.

Soil mixing was proposed by Baxter and Hole (1967) as an important mechanism contributing to nutrient enrichment. However, as pointed out by Kristiansen *et al.* 2001, soil mixing itself is unlikely to cause the increase in phosphorus content in nests of wood ants, because deeper soil layers unaffected by ant activities contain less phosphorus than top soil layers (Fig. 1a). Continuous import of organic material into the nest may, however, cause nutrient enrichment in the soil below the nest, and soil excavation and mixing may support nutrient enrichment in the soil rim.

Transport of food into the nest undoubtedly adds an important enrichment source of nutrients (Kloft 1978). Wood ants of the genus *Formica* bring into their nests large amounts of food (e.g. Oekland 1930, Wellenstein 1952, Holt, 1955, Horstman 1974, Rosengren & Sundström 1987, 1991, Gobel 1988, Frouz *et al.* 1997). The amount of honeydew brought into a nest ranges from 43 to 719 kg of fresh honeydew or 10–200 kg of sugar (Oekland 1930, Wellenstein 1952, Horstman 1974, Gobel 1988). The input of prey may be impressive as well, e.g. Holt (1955) reports 456 g of prey brought into a wood ant nest per day. Frouz *et al.* (1997) estimated the annual input of phosphorus contained in food into nests of *F. polyctena* as 345 g of phosphorus per nest per year (270 g from prey and 75 g from honeydew).

The bulk of the nest material in wood ant nest mounds consists of plant material, such as needles, small branches, etc., which also contains considerable amounts of phosphorus. The same plant material also occurs in the surrounding soil but in a much thinner layer. For example, Zacharov *et al.* (1981) state that the litter layer in a spruce forest near Moscow is 0–2.5 cm, whereas the volume of plant residues in five investigated nests of *Formica aquilonia* in the same forest ranged between 6 and 58 l, and the area of these nests between 0.35 and 0.75 m^2. When the nest volume is divided by the nest area, we can calculate that a nest represents a continuous layer of material 1.7–8 cm thick.

When focusing not only on the total amount of nutrients but also on their availability, then not only litter accumulation but also litter decomposition becomes important. Using the litter bag technique Frouz *et al.* (1997) found out that spruce needles decomposed more than twice as fast in *F. polyctena* nests as in the surrounding soil. Consequently, the release of available phosphorus from litter may be up to 10 fold in ant nests as compared with that in the surrounding soil (Frouz *et al.* 1997). The high decomposition rate found in that study was accompanied by high density and activity of decomposing microflora (Frouz *et al.* 1997). High densities and/or activities of decomposers, both microflora and invertebrate fauna, have repeatedly been reported in *Formica* nests (Gorny 1976, Coenen-Stass *et al.* 1980, Laakso & Setälä 1998). However, microbial activity in *Formica* nests is strongly dependent on nest material moisture; microbial activity is low in dry nests and increases dramatically with increasing moisture of the nest material (Frouz 2000, Lenoir *et al.* 2001). The high decomposition rate observed by Frouz *et al.* (1997) is thus probably not ubiquitous but limited only to moist ant nests. A study of moisture distribution in more than 60 nests in the Czech Republic indicated that only 36% of the investigated nests had their moisture level higher than 30% (expressed as volume-to-volume ratio) (Frouz 1996). The nest moisture may play an important role not only in decomposition but also in the maintenance of nest temperature and understanding the pattern of nest moisture is a promising field for future research.

When the moisture is optimal, microbial activity in *Formica* nests may be enhanced by high temperatures. Ants of the genus *Formica* maintain throughout the activity period a relatively constant temperature in their nest (Raignier 1948, Rosengren *et al.* 1987, Frouz, 2000), which may be on average more than 10 °C higher than the temperature of the surrounding soil (Frouz 2000). An increase in nest temperature of about 10 °C may increase the microbial activity more than 3 fold (Frouz *et al.* 1997). Moreover, the decomposition of coniferous litter is often limited by nutrient deficiency (a low amount of nitrogen and phosphorus in relation to carbon), and by a high content of slowly decomposable substances (Millar 1974). Thus the input of additional nutrients, such as nitrogen and phosphorus with food and excreta may accelerate decomposition. Food residues and excreta may also add easily available organic material, such as sugars or amino acids, which may accelerate the decomposition of slowly decomposable substances (priming effect).

The availability of phosphorus in ant nests may increase also indirectly by a modification of other soil properties, in particular pH. The availability of phosphorus is highest in neutral or slightly acid soil. In alkaline soil phosphorus binds to calcium, whereas in acidic soil it binds to iron and aluminum and so it becomes unavailable to plants (Leeper & Uren 1993, Brady & Weil 1999). The pH in ant mounds tends to shift towards neutral values, i.e. the pH value increases in acidic and decreases in alkaline soils (Dlusskij 1967, Malozemova & Koruma 1973, Frouz *et al*. 2003). This pH shift may increase the availability of phosphorus (Brady & Weil 1999).

Future research

The fact that ants accumulate significant amounts of phosphorus in their nest material, which is potentially available to plants, is well documented. This raises several new questions from a forest ecosystem perspective. For instance, do wood ant nests form hot spots, which enable local acceleration of nutrient turnover, or do they act as traps for nutrients extracted from the surrounding ecosystem and bound in nest material? If ant nests perform both these functions, what conditions determine whether the nests serve as a source or sink of nutrients? The accumulation of phosphorus and other nutrients in ant mounds may in fact be associated with some depletion of these nutrients in the surrounding environment through imported food and nest building material (Frouz *et al*. 1997). Large amounts of nutrients incorporated in honeydew collected from surrounding trees are continuously extracted from the environment and brought to a mound (Oekland 1930, Wellenstein 1952, Horstman 1974, Rosengren & Sundström 1987, Gobel 1988, Frouz *et al*. 1997). Ants are known to increase honeydew production by aphids (Gobel 1988, Rosengren & Sundström 1991) and this increase in tree exploitation by aphids may decrease tree growth (Rosengren & Sundström 1991). The effect of ant–aphid interaction on tree growth may be very complex, it may be affected by the presence of other herbivores, etc. (*see* Rosengren & Sundström 1991 for more detailed discussion) and require future attention.

The extent to which plants are able to use phosphorus accumulated in nest material, and its effect on plant growth, is also poorly understood. Wood-ant nests are usually not covered by herb vegetation, so this potential source of phosphorus may mainly benefit the trees growing around the nest. Indeed, our laboratory experiment showed that when grown in soil collected from the soil rim of an ant nest spruce seedlings reach a greater biomass of root, stem (wood) and needle tissue, whereas survival of the seedlings remains similar to those grown in soil collected 1–3 m away from a nest mound (Table 2). These results are, however, not directly applicable to field conditions as the outcome may also depend on moisture conditions in the nest (*see* above) and eventually on removal of seedlings by ants. An unresolved question is also to what extent mature trees can penetrate with their roots under the nest and use the accumulated phosphorus. A further question is whether phosphorus uptake by plants growing on an active nest mound changes after the abandonment of the mound?

Acknowledgements

This study was supported by research plan AV0Z60660521. The authors are pleased to thank two anonymous referees for their helpful comments.

References

Baxter, F. P. & Hole, F. D. 1967: Ant (*Formica cinerea*) pedoturbation in a prairie soil. — *Soil sci. Am. Proc*. 31: 425–428.

Brady, N. C. & Weil, R. R. 1999: *The nature and properties of soils*. — Prentice Hall, Upper Saddle River.

Coenen-Stass, D., Schaarschmidt, B. & Lamprecht, I. 1980: Temperature distribution and calorimetric determination of heat production in the nest of the wood ants *Formica polyctena* (Hymenoptera, Formicidae). — *Ecology* 61: 238–244.

Czerwinski, Z., Jakubczyk, H. & Petal, J. 1971: Influence of ant hills on the meadow soils. — *Pedobiologia* 11: 277–285.

Dlusskij, G. M. [Длусский, Г. М.] 1967: [*The ants of genus Formica*]. — Nauka, Moskva. [In Russian].

Frouz, J. 1996: The role of nest moisture in thermoregulation of ant (*Formica polyctena*, Hymenoptera, Formicidae) nests. — *Biologia, Bratislava* 51: 541–547.

Frouz, J. 2000: The effect of nest moisture on daily temperature regime in the nest of *Formica polyctena* wood ants. — *Insectes Sociaux* 47: 229–235.

Frouz, J. & Kalčík, J. 1996: The role of ants for availability of phosphorus in spruce plantation. — In: Kalčík, J. & Macháček, V. (eds.), *Proceeding of national conference about study of phosphorus and other elements*: 75–80. Institute of Soil Biology, České Budějovice.

Frouz, J., Holec, M. & Kalčík, J. 2003: The effect of *Lasius* *niger* (Hymenoptera, Formicidae) ant nest on selected soil chemical properties. — *Pedobiologia* 47: 205–212.

Frouz, J., Šantrůčková, H. & Kalčík, J. 1997: The effect of wood ants (*Formica polyctena* Foerst) on the transformation of phosphorus in a spruce plantation. — *Pedobiologia* 41: 437–447.

Goebel, S. 1988: *Freilanduntersuchungen an Waldameisenkolonien in Eichen -und Fichtenbestünden im Hinblick auf die Populations- dynamik von Rinderläusen (Aphidina) und deren Hönigproduction so wie die Auswirkungen auf die Insectenfauna*. — Ph.D. thesis, Albert-Ludwigs Universität, Freiburg.

Gorny, H. 1976: Eine pedoekologishe Probleme der Wirkung von industriellen Inision Waldstandorte. — *Pedobiologia* 16: 27–35.

Holt, S. J. 1955: On the foraging activity of the wood ant. — *J. Anim. Ecol.* 24: 1–34.

Horstmann, K. 1974: Untersuchung uber den Nahrungswerb der Waldameisen (*Formica polyctena* Foerst) im Eichenwald. III. Jahresbilanz. — *Oecologia* 15: 187–204.

Kloft, W. J. 1978: *Okologie der Tiere*. — UTB Ulmer, Stuttgart.

Kristiansen, S. M., Amelung, W. & Zech, W. 2001: Phosphorus forms as affected by abandoned anthills (*Formica polyctena* Förster) in forest soil: sequentional extraction and liquid state ^{13}P-NMR spectroscopy. — *J. Plant. Nutr. Soil. Sci.* 164: 49–55.

Laakso, J. & Setälä, H. 1998: Composition and trophic structure of detrital food web in ant nest mounds of *Formica aquilonia* and in the surrounding forest soil. — *Oikos* 81: 266–278.

Leeper, G. W. & Uren, N. C. 1993: *Soil science. An introduction*. — Melbourne University Press, Carlton.

Lenoir, L., Persson, T. & Bengtson, J. 2001: Wood ant nest as potential hot spots for carbon and nitrogen mineralisation. — *Biology and fertility of Soils* 34: 235–240.

Macháček, V. 1986: Verification of a new method of determining the rate of phosphorus release from the soil. — *Plant production* 32: 473–480.

Malozemova, L. A. & Koruma, N. P. [Малоземова, Л. А. & Корума, Н. П.] 1973: [The effect of ants on soil]. — *Ekologija* 4(5): 98–101. [In Russian].

Millar, C. S. 1974: Decomposition of coniferous leaf litter. — In: Dickinson, C. H. & Pugh, G. J. (eds.), *Biology of plant litter decomposition*: 105–128. Academic Press, London.

Murphy, J. & Riley, J. P. 1965: A modification of a single solution method for the determination of phosphate in natural waters. — *Anal. Chim. Acta* 27: 31–36.

Oekland, F. 1930: Wieviel Blattlauszucker verbraucht die Rote Waldameise. — *Biol. Zbl.* 50: 449–459.

Petal, J. 1978: The role of ants in ecosystems. — In: Brian, M. V. (ed.), *Production ecology of ants and termites*: 293–325. Cambridge Univ. Press, London.

Petal, J., Nowak, E., Jakubczyk, H. & Czerwinski, Z. 1977: Effect ants and earthworms on soil habitat modification. — *Ecol. Bull.* 25: 501–503.

Pokarzhevskij, A. D. 1981: The distribution and accumulation of nutrients in nests of ant *Formica polyctena* (Hymenoptera, Formicidae). — *Pedobiologia* 21: 117–124.

Prescott, C. E., Corbin, J. P. & Parkinson, D. 1992: Immobilisation and availability of N and P in the forest floor of fertilized rocky mountain coniferous forest. — *Plant and Soil* 143: 1–10.

Raignier, A. 1948: L'économie thermique d'une colonie polycalyque de la Fourmi des bois *Formica rufa polyctena* Foerst. — *La cellule* 51: 279–368.

Rosengren, R. & Sundström, L. 1987: The foraging system of a red wood ant colony (*Formica* s. str.) — collecting and defending food through an extended phenotype. — *Experientia Supplementum* 54: 117–137.

Rosengren, R. & Sundstrom, L. 1991: The interaction between red wood ants, *Cinara aphids*, and pines. A ghost of a mutualism past? — In: Huxley, C. R. & Cutler, D. (eds.), *Ant–plant interactions*: 81–91. Oxford University Press, Oxford, New York & Tokyo.

Rosengren, R., Fortelius, W., Lindström, K. & Luther, A. 1987: Phenology and causation of nest heating and themoregulation in red wood ants of the *Formica rufa* group studied in coniferous forest habitats in southern Finland. — *Ann. Zool. Fennici* 24: 147–155.

Wagner, D., Jones, J. B. & Gordon, D. M. 2004: Development of harvester ant colonies alters soil chemistry. — *Soil Biol. Biochem.* 36: 797–804.

Wellenstein, G. 1952: Zur Ernhrungs biologie der Roten Waldameise. — *Zeitshrift fur Pflanzenkrank und Pflanzenshutz* 59: 430–451.

Wood, T., Borgman, F. H. & Voilght, G. T. 1984: Phosphorus cycling in a northern hardwood forest: biological and chemical control. — *Science* 223: 391–393.

Zacharov, A. A., Ivanickova, E. F. & Maksimova, A. E. [Захаров, А. А., Иваничкова, Е. Ф. & Максимова, А. Е.] 1981: [Accumulation of elements in nests of red wood ants]. — *Pedobiologia* 21: 36–45. [In Russian with English summary].