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SHORT COMMUNICATION

Decomposition of organic matter and nutrient mineralisation in wood ant (*Formica rufa* group) mounds in boreal coniferous forests of different age

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Abstract Wood ants (*Formica rufa* group) are dominating ecosystem elements of the boreal region due to their wide and abundant occurrence. They collect and concentrate organic material from the surrounding forest floor by building large above-ground mounds. These mounds have higher temperature and lower water content than the surrounding forest floor. We studied how these peculiar environmental conditions affected mass loss and carbon (C), nitrogen (N), phosphorus (P) and potassium (K) mineralisation of organic matter in boreal Norway spruce (*Picea abies* L. Karst.)-dominated mixed forest stands of four different age classes (5-, 30-, 60-, and 100-year-old) situated in eastern Finland using the litter bag technique. Norway spruce needle litter was incubated in inhabited and abandoned wood ant mounds as well as on the surrounding forest floor. We expected decomposition to be extremely slow due to the dryness of the mounds. Mass losses inside inhabited mounds were lower compared to the surrounding forest floor (on average 30 vs 50% after 2 years) but not as low as we expected, which might be a result of ant and microbial activity in the mounds. Decomposition in the abandoned mounds proceeded similarly as on the forest floor. Nutrient mineralisation proceeded more slowly in the ant mounds than on the surrounding forest floor. Mineralisation occurred for all studied nutrients in the ant mounds, except for N, which net amount remained stable during the years of the experiment. When wood ant mounds are abandoned and their porous and dry structure is no longer maintained by the ants, their decomposition is accelerated, and nutrients may be available for uptake by plants, although the nutrient mineralisation seems still to remain lower compared to the surrounding forest floor. However, eventually the mound material will be decomposed and nutrients mineralised, thus providing a nutrient hot spot increasing the heterogeneity of forest floor nutrient availability.

Keywords Carbon · Nitrogen · Mass loss · Needle litter · Norway spruce

Introduction

Mound-building wood ants (*Formica rufa* group) are dominating ecosystem elements of the boreal region due to their wide and abundant occurrence. They collect and concentrate organic material from the forest floor and resin by building large aboveground mounds. The concentrations of organic matter and nutrients are higher in these mounds

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than in the surrounding forest floor (Niemelä and Laine 1986; Frouz et al. 1997; Folgarait 1998; Laakso and Setälä 1998; Kristiansen et al. 2001; Lenoir et al. 2001; Frouz et al. 2005; Risch et al. 2005; Kilpeläinen et al. 2007), and environmental conditions differ from those of the forest floor, e.g. temperatures are higher inside the mounds during summer, and water content is lower throughout the year (Czerwiński et al. 1971; Pokarzhevskij 1981; Laakso and Setälä 1997; Frouz 2000; Lenoir et al. 2001). These dry conditions suppress a fast decomposition of organic material (Pokarzhevskij 1981; Lenoir et al. 2001). The higher temperatures in the mounds, on the other hand, may enhance decomposition.

One dominating component of the material in wood ant mounds in coniferous forests is needle litter (e.g. Wisniewski 1967) as it is produced in large quantities and is usually the largest fraction of aboveground litter in coniferous forests (O'Neill and De Angelis 1981) containing a relative dynamic pool of organic matter and nutrients and therefore has a central role in nutrient cycling. Decomposition is an important process for nutrient cycling in forest ecosystems. Particularly ants are able to modify the physical and chemical properties of the soil and litter (Pokarzhevskij 1981; Petal and Kusinska 1994; Frouz et al. 1997; Nkem et al. 2000; Frouz et al. 2003). Stadler et al. (2006) proposed that already the presence of wood ants may have an accelerating effect on litter decomposition on the forest floor through direct physical effect on needle litter and indirect trophic effects with aphids and micro-organisms.

Decreasing mound activity, whether for internal reasons such as the abandonment of the mound by ants or for external reasons, e.g. environmental changes due to clear-cutting, may lead to increased decomposition of mound material. The decomposition potential in ant mounds may turn effective when ant mounds are abandoned and their water content increases. Thus, more nutrients may become available for plants (e.g. Zacharov 1981). Wood ant mounds situated on clear-cut areas show lower vitality (Rosengren et al. 1979; Punttila et al. 1991), and ants may not be able to maintain the porous and dry structure of their mounds. These mounds are also subject to higher precipitation and may thus have also higher water content, which in turn could accelerate decomposition of mound material (Ohashi et al. 2007a), which in turn will enhance nutrient mineralisation and increasing spatial variability of nutrient availability.

To our knowledge, no studies into decomposition of standard organic matter in inhabited and abandoned wood ant mounds have been done so far. Therefore, the objectives of this study were (1) to compare mass losses from organic matter between inhabited and abandoned wood ant mounds and the surrounding forest floor, (2) to study the mineralisation of C and nutrients from inhabited and abandoned wood ant mounds in boreal forest stands via decomposition of organic matter and (3) to assess whether mass losses and nutrient mineralisation in ant mounds differ between forest stands of different age.

We predict that decomposition inside inhabited ant mounds will proceed more slowly, being nearly negligible in comparison to the surrounding forest floor, particularly due to the low water content in inhabited mounds. After abandonment, decomposition should accelerate due to increased water content. Decomposition in inhabited mounds situated on clear-cut areas should be accelerated as nest vitality and the maintenance of the dry and porous mound structure decreased owing to the presence of fewer ants.

Materials and methods

Study sites and experimental design

The study was carried out in the Koli National Park and vicinity, eastern Finland (29°5′E, 63°3′N, 160 m a.s.l.). Wood ant mounds (*Formica rufa* group) were inventoried in early summer 2003 in 16 forest stands (mean size 6.5 ha ±2.2 ha SD) of four age classes (5-, 30-, 60- and 100-year-old) on medium-rich site type (*Myrtillus*-type according to the Finnish classification system; Cajander 1949) dominated by Norway spruce [*Picea abies* (L.) Karst.]. The height and diameter of each mound was measured to calculate their base area and volume (a total of 382 mounds, on average 23.9±16.3 mounds per stand). One median-sized inhabited mound from each stand was selected for studying the decomposition of Norway spruce litter in ant mounds and the surrounding forest floor (Table 1). Litter bags were inserted also into abandoned mounds of similar size as the selected inhabited ones, but their decomposition was monitored only for 1 year, as we expected the differences to appear already during the first year. No similar-sized abandoned mounds were available in the 30-year-old stands, so no data are presented for this age class. In the other age classes, the number of abandoned study mounds varied from 2 (100-year old stands) to 4 (5- and 60-year-old stands). All selected inhabited mounds were colonized by *Formica aquilonia* Yarrow, except one mound in one of the 5-year-old stands that was inhabited by *Formica lugubris* Zetterstedt.

The litter bag technique was used to determine the mass losses of needle litter that was collected from the forest floor in a Norway spruce stand in Joensuu (29°49′E, 62°33′N). We used litter from the forest floor, as the ants collect fallen litter material for constructing their mounds. After drying at 40°C to a constant mass, exactly 0.500 g litter was put into polyester litter bags of size 5×5 cm^2 and mesh size 1 mm.

Table 1 Description of the study sites and their wood ant mounds

Age class (years)	Site characteristics			Inhabited mounds		Abandoned mounds	
	Mean area (ha)	Inhabited mounds (ha^{-1})	Abandoned mounds (ha^{-1})	Volume (dm^3)	Mound area (m^2)	Volume (dm^3)	Mound area (m^2)
5	5.8 (1.0)	2.5 (1.0)	1.0 (0.5)	660 (350)	2.02 (0.82)	277 (270)	0.97 (0.89)
30	5.1 (1.0)	3.2 (0.9)	0.4 (0.2)	365 (112)	1.21 (0.32)		
60	6.5 (1.5)	5.4 (0.7)	0.7 (0.3)	1,044 (463)	2.28 (0.70)	539 (193)	1.76 (0.55)
100	7.9 (1.3)	4.1 (0.7)	0.7 (0.2)	1,660 (959)	2.90 (1.18)	2,433	3.84

Standard errors are in parentheses.

The litter bags were placed vertically into the mound interior at three depths (top, centre and bottom) and horizontally on the surrounding forest floor at least 5 m away from the mound. The litter bags inserted into the mounds were sown as compartments of a longer strip for easier lifting and were inserted with help of a long metal tongue. The bags on the forest floor were replicated three times and were fixed onto the surface with Teflon-coated metal pins. For estimating the growth of the mounds due to input of litter material onto the mounds, litter bags were also fixed onto the mound surface of inhabited mounds. At each location, 192 litter bags were used, and thus a total of 576 litter bags were used in this study. The litter bags were set out in early June 2004 and were collected in late October and early June until 2006. At every date of retrieval, three litter bags were taken from each location in each stand.

We did not measure temperature from the mounds used in this study. However, we have extensive temperature data from other 20 wood ant mounds in the same forest stands (Ohashi et al., unpublished results). These data show that the average temperatures in ant mounds are significantly higher during summer months compared to the surrounding forest floor (23 vs 11°C) and are fairly similar between mounds. Mound temperatures did not depend on forest age nor mound volume, except that mounds in the 5-year-old sites had lower average temperatures during summer. The volumetric water content ($m^3\ m^{-3}$) of the mounds was measured at the end of the study period with a ThetaProbe sensor (type ML2x, Delta-T Devices, Cambridge, UK). The water content was 0.03 $m^3\ m^{-3}\pm0.005$ in active mounds, 0.10 $m^3\ m^{-3}\pm0.03$ in abandoned mounds and 0.22 $m^3\ m^{-3}\pm$ 0.02 in the forest floor.

Calculations and chemical analyses

After lifting in the field, the litter bags were brought into the laboratory; the remaining content was carefully removed and dried at 40°C until a constant mass, and was then weighed for mass loss. The mass losses were calculated relative to the initial mass of the litter material. The average values were calculated for the three locations of the forest floor of each site, rendering one value at each site (n=16) for the forest floor, as well as for the mound interior, as mound depth was not a significant factor. Then the mean±SE were calculated for each age class (n=4 for inhabited mounds and n=2–4 for abandoned mounds).

Some litter bags were damaged. Although the material should not have attracted the ants, they made holes in 15–20% of the litter bags inside the mounds. These bags were emptied to a certain degree, and in some of the bags, we found resin instead of the needles. All cases with damaged litter bags were excluded from our data.

The concentrations of K and P in the initial and remaining litter material were analysed with an IRIS ICP-spectrometer after dissolving in nitric acid and hydrogen peroxide (Luh Huang and Schulte 1985). C and N concentrations were analysed with a LECO CNH-600 analyser. The initial concentrations of C, N, K and P in the litter material were 502 mg g^{-1} (±2.9), 12.8 mg g^{-1} (±0.17), 2.06 mg g^{-1} (±0.15) and 0.70 mg g^{-1} (±0.05; average±SD, respectively). The nutrient amounts were calculated by knowing the nutrient concentrations as well as the mass of the remaining litter.

Statistical testing

To reduce heteroscedasticity, all data to be tested were ln-transformed. A linear mixed model analysis was used for determining whether there were any significant effects of time (four observations), stand age class (5, 30, 60 or 100 years) or location (inhabited or abandoned mounds or forest floor) on mass losses and nutrient concentrations of the remaining litter, as the residuals of each location at different observation times could not be assumed to be independent:

$$\begin{aligned} y_{ijk} = {} & \mu + \mathrm{location}_i + \mathrm{ageclass}_j + \mathrm{time}_k \\ & + (\mathrm{location} \times \mathrm{ageclass})_{ij} + (\mathrm{location} \times \mathrm{time})_{ik} \\ & + (\mathrm{ageclass} \times \mathrm{time})_{jk} + (\mathrm{location} \times \mathrm{ageclass} \times \mathrm{time})_{ijk} \\ & + \mathrm{site}_l + \varepsilon_{ijkl} \end{aligned} \tag{1}$$

where y is the variable to be explained (mass or nutrient loss), and location (i=1–3 for inhabited and abandoned mound or forest floor), age class (j=5, 30, 60 or 100) and time (k=1–4) were used as fixed effects. Time in months (with age class × location × site as subject variables) represented a repeated effect and site (l=1–16) a random effect. The residual of each location ijl at each time k is represented by ε_{ijkl}. A first-order autoregressive covariance structure was used for repeated effects. When the interactions between location and time or age class and time were statistically significant, pairwise Bonferroni post hoc comparisons were used to test for differences between locations or age classes within times. Statistical analyses were performed with Statistical Package for the Social Sciences (SPSS) 14.0.1 for Windows (SPSS, Chicago, IL, USA).

Results

Mass losses during the first year of observation were higher in abandoned mounds than in the inhabited ones (Fig. 1; $F_{1,16.5}$=8.469, P=0.010), and higher in the forest floor than in the inhabited mounds ($F_{1,27.8}$=87.12, P<0.001), whereas they were not different between abandoned mounds and forest floor ($F_{1,34.2}$=0.119, P=0.912). Mass losses of the needle litter increased with time at all locations (main effect of time $F_{3,68.5}$=31.89, P<0.001), being highest during the first period (June–October) and slowing down subsequently (Fig. 1). On average, the mass losses inside the mounds were 15–25% after 1 year and 25–43% after 2 years, relative to the initial mass.

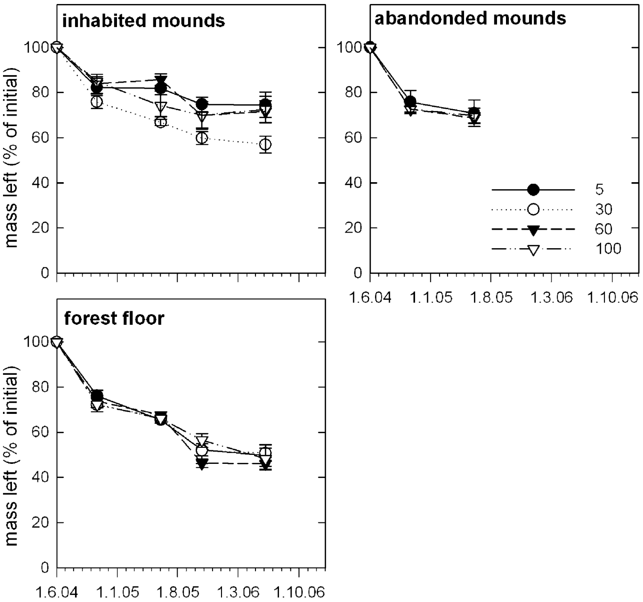

Fig. 1 Mass losses from Norway spruce needle litter in inhabited and abandoned wood ant mounds and the surrounding forest floor in 5-, 30-, 60- and 100-year-old Norway-spruce-dominated forest stands during a period of 2 years (1-year period for abandoned mounds). Standard errors are indicated (n=8–12)

The litter bags on the surface were covered soon with litter material that ants brought to the mound. After 2 years, the thickness of the new litter layer on individual mounds varied between 1 and 20 cm. On average, it was highest on the mounds in the 30-year-old forest stands (10 cm) and lowest on the mounds in the 5-year-old stands (1 cm), indicating that ants were the most active in the 30-year-old stands and least active in the 5-year-old stands.

The significant interaction between location and stand age ($F_{5,32.0}$=5.481, P=0.025) indicated that mass losses inside the mounds were highest in the 30-year-old forest stands (Fig. 1), and that stand age had no effect on mass losses from the litter on the forest floor (Fig. 1). The mass losses inside the mounds of the 5-year-old sites were not higher than inside the mounds of the other sites (Fig. 1). As stand age had no statistically significant effects on the changes of remaining nutrient amounts relative to the initial amounts, the results are presented pooled by stand age (effects of stand age for C: $F_{3,17.387}$=1.444, P=0.264; for N: $F_{3,17.668}$=0.250, P=0.861 and for P: $F_{3,15.241}$=0.616, P=0.615). An exception was K, where the effect of stand age was significant ($F_{3,15.786}$=6.569; P=0.004) indicating K losses were higher in the clear-cut stands (0.001<P<0.023).

Carbon losses from the litter were similar to the respective mass losses (Fig. 2). Practically no net release of N occurred from the litter in the inhabited ant mounds, whereas there was some release in the other locations: nearly 10% after 1 year in abandoned mounds and nearly 20% after 2 years in the forest floor (Fig. 2). The K amounts decreased faster than the remaining mass at all locations (Fig. 2). There were no differences between inhabited or abandoned ant mounds, but K disappeared faster on the forest floor than in the ant mounds (Fig. 2). The only location where P was mineralised already during the first year was the forest floor (Fig. 2). In both inhabited and abandoned ant mounds, no changes in P amount was detectable during the first year, but subsequently, the P amounts also decreased there (Fig. 2).

Nutrient losses in the inhabited and abandoned mounds were not statistically different, except for higher losses of K in the abandoned mounds (Fig. 2; effect of location $F_{1,50.2}$= 11.58, P=0.001). The variation between mounds was rather high and may thus mask the differences between locations, and no significant differences of nutrient losses relative to the initial amounts were found between abandoned mounds and forest floor, except for higher losses of K in the forest floor (Fig. 2; effect of location $F_{1,43.5}$=11.57, P=0.001). The nutrient losses from the litter in the forest floor were always higher than compared to those in the inhabited mounds (Fig. 2). The C/N ratio of the litter was at the

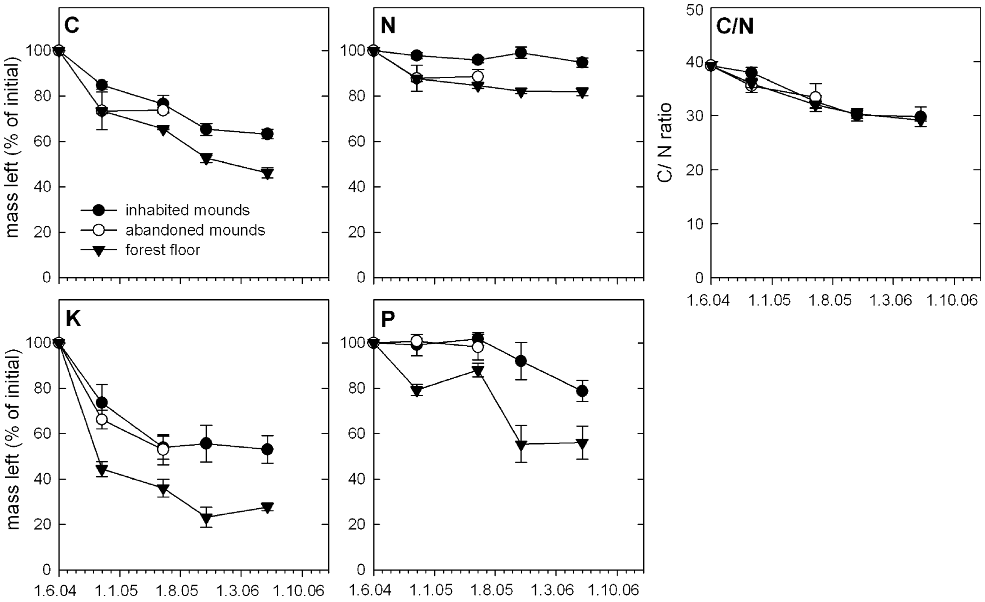

Fig. 2 Amounts of C, N, K and P and the C/N ratio in the remaining litter during decomposition of spruce needles in inhabited and abandoned ant mounds and the surrounding forest floor during a period of 2 years (1-year period for abandoned mounds). Standard errors are indicated (n=8–12)

beginning 39.3, and it decreased with time in the remaining litter (Fig. 2). The lowest values were found in the litter buried in the mounds in the 30-year-old stands (data not shown).

Discussion

In contrast to our first hypothesis, mass losses from the litter buried in inhabited wood ant mounds were on a level we considered to be surprisingly high taking into account the extreme dryness inside the mounds. On average, mass losses in the mounds were lower than on the surrounding forest floor observed in the present or earlier studies (e.g. Smolander et al. 1996; Vesterdal 1999; Albers et al. 2004; Palviainen et al. 2004). Frouz et al. (1997) observed that mass losses from organic material in wood ant mounds were more than six times higher compared to the surrounding forest floor. The higher mass losses may be attributed to the higher water content in their ant mounds (approximately 47%). Also different climatic conditions, different composition of mound material or nutrient concentrations of the organic matter could be reasons for these differences. Pokarzhevskij (1981) again concluded that decomposition rates in *Formica polyctena* mounds were undetectable, but nevertheless the mound material decomposed. Laakso and Setälä (1997; 1998), Pimenov and Pokarzhevskij (1975) and Stebayeva et al. (1977) found more decomposer microbes and a larger soil animal biomass in boreal wood ant mounds compared to the surrounding soil, indicating a higher decomposition potential and a higher amount of resources in ant mounds. It seems apparent that an ant-mound-specific microflora uses food waste (Golubev and Babjeva 1972). It may also use ant excrements and be well adapted to the dry conditions. The priming affect of ant activity could thus be another reason for the mass losses to be higher than we expected. Also the higher temperatures in ant mounds compared to the surrounding forest floor could be another reason for the mass losses we observed. Inhabited or abandoned mounds, respectively, showed similar mass losses, irrespective of stand age or mound size, with the exceptions of the inhabited mounds in the 30-year-old stands, where mass losses were higher than in inhabited mounds of the other stands. One possible explanation could be overall ant activity, as Stadler et al. (2006) observed that already the presence of ants had an effect on soil microbial activity. They suggested that ants could have an accelerating effect on litter decomposition through direct physical effect on needle litter and indirect trophic effects with aphids and micro-organisms. In our study, the mounds in the 30-year-old sites were the smallest but were also the most active ones in terms of mound building rapidity, indicating that the ants had affected the decomposition process also in our study and presumably most in the mounds of the 30-year-old stands.

In contradiction to our other hypothesis, mass losses from the litter buried in the mounds in the 5-year-old sites were similar to those in the older stands. Although the risk of being abandoned is higher in clear-cut areas (Punttila 1996), these mounds were still inhabited, although their activity was lower. Thus, we may presume that the mounds in the 5-year-old stands had lower average temperatures, but they had higher water content compared to mounds in older stands. This indicates that decomposition is not only dependent on temperature and water content but also on their interaction (e.g. Leirós et al. 1999).

Despite no differences in C/N ratios between mounds and forest floor, the N amount decreased in abandoned mounds and the forest floor, whereas in inhabited mounds, the net amount of the litter N remained unchanged. The binding of N to the lignin fraction and humification products during decomposition (e.g. Berg and Staaf 1981) could explain the relatively stable amount of N, but it does not explain the lower N net release of the litter buried in the inhabited mounds. Frouz et al. (1997) found a much higher number of N-fixing bacteria in wood ant mounds compared to the surrounding forest floor, which may be one explanation for this unchanged N amount. The relatively low C/N ratio in the litter, compared to freshly fallen spruce needle litter (Kurka et al. 2000), indicated that the litter had already started to decompose before our experiment. Although the litter had been subject to decomposition and leaching already on the forest floor before the experiment, the highly soluble nutrient K still showed higher losses compared to other nutrients. Losses of K were highest in the mounds and forest floor of the clear-cut stands, where the precipitation reaching the soil is higher than in the closed forest stands and some percolation of water may have occurred also through these mounds. One reason for the higher K losses from the litter compared to N and P could be that N and P, once mineralised, are immediately immobilised by the microflora inhabiting the litter. The mineralisation of P was slower in ant mounds compared to the forest floor. Also Frouz et al. (1997; 2005) found that P is being concentrated in wood ant nests, and consequently Kristiansen et al. (2001) observed higher P concentrations in abandoned ant mounds still after 5–10 years of abandonment.

The mounds of our study were very dry, and we may assume that practically no leaching of nutrients due to percolating water occurred. Still the amounts of nutrients in the litter decreased, except that of N in the inhabited mounds. The question then arises: “where do the nutrients go?” Tree roots do grow into the mounds (Ohashi et al. 2007b), but nutrient uptake by tree roots should be lower compared to the forest floor, where root density is much higher (Ohashi et al. 2007b). Another reason could be the mound microflora that needs N and P and is a strong competitor for nutrients (Setälä et al. 1998; Laakso et al. 2000). Thus, the majority of nutrients will remain in the mound, resulting in increased C and nutrient concentrations compared to the surrounding forest floor. This, in fact, has been shown by many studies (Niemelä and Laine 1986; Frouz et al. 1997; Folgarait 1998; Laakso and Setälä 1998; Kristiansen et al. 2001; Lenoir et al. 2001; Frouz et al. 2005; Risch et al. 2005; Kilpeläinen et al. 2007). Jakubczyk et al. (1972) and Petal et al. (1992) observed that *Myrmica* and *Lasius* mounds contained less Actinomycetes and microorganisms using mineral N but more fungi and cellulolytic microbes compared to the surrounding soil. Actinomycetes are better adapted to utilise the more difficult degradable compounds compared to most bacteria (McCarthy and Williams 1992). Czerwinski et al. (1971) and Jakubczyk et al. (1972) concluded that the lower decomposition rate in ant mounds is a result of the lower number of Actinomycetes in ant mounds compared to the surrounding soil. Jakubczyk et al. (1972) also showed that after abandonment of ant mounds, the number of Actinomycetes increased and that of other bacteria decreased relatively fast to levels prevailing in the surrounding soil. These results coincide with our observations that mass losses in abandoned mounds were similar to those on the forest floor but higher than in inhabited mounds, and may also explain the lower N mineralisation rate in inhabited mounds compared to abandoned mounds and the surrounding soil.

We can conclude that wood ant mounds represent “cold spots” of nutrient mineralisation (Ohashi et al. 2007a). When ant mounds are abandoned, their decomposition is accelerated, and nutrients are mineralised and available for uptake by plants, although the mineralisation seems still to remain lower compared to the surrounding forest floor. However, eventually the mound material will be decomposed and nutrients mineralised and thus provide a nutrient hot spot increasing the heterogeneity of forest floor nutrient availability.

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