Ann. Zool. Fennici 42: 283–290 ISSN 0003-455X
Helsinki 28 June 2005 © Finnish Zoological and Botanical Publishing Board 2005

CO_2 emissions from red wood ant (*Formica rufa* group) mounds: Seasonal and diurnal patterns related to air temperature

Anita C. Risch[1]*, Martin Schütz[1], Martin F. Jurgensen[2], Timo Domisch[3], Mizue Ohashi[4] & Leena Finér[3]

[1] *Swiss Federal Institute for Forest, Snow and Landscape Research, Zuercherstrasse 111, CH-8903 Birmensdorf, Switzerland*
* *Current address/corresponding author: Syracuse University, Department of Biology, 130 College Place, Biological Research Laboratory, Syracuse NY 13244, USA (email: arisch@syr.edu)*
[2] *School of Forest Resources and Environmental Science, Michigan Technological University, 1400 Townsend Drive, Houghton MI, 49931, USA*
[3] *Finnish Forest Research Institute, Joensuu Research Centre, P.O. Box 68, FI-80101 Joensuu, Finland*
[4] *University of Joensuu, Faculty of Forestry, P.O. Box 111, FI-80101 Joensuu, Finland*

Received 27 Oct. 2004, revised version received 9 Dec. 2004, accepted 17 Dec. 2004

Risch, A. C., Schütz, M., Jurgensen, M. F., Domisch, T., Ohashi, M. & Finér, L. 2005: CO_2 emissions from red wood ant (*Formica rufa* group) mounds: Seasonal and diurnal patterns related to air temperature. — *Ann. Zool. Fennici* 42: 283–290.

Red wood ant (*Formica rufa* group) mounds release high amounts of carbon dioxide (CO_2). As red wood ants and other invertebrates living in mounds are poikilothermal organisms, their metabolism and therefore CO_2 emissions are affected by changes in temperature. Thus, seasonal or diurnal changes in air temperature could affect CO_2 emissions from mounds. We found that seasonal mound CO_2 emissions and air temperature were correlated, both peaking in mid-summer. In contrast, diurnal CO_2 emissions and air temperature were inversely correlated, as we observed highest C fluxes during the night when air temperature was lowest. This CO_2 emission pattern can likely be explained by higher metabolic rates of ants resulting from their clustering, and increased numbers of ants in the mound when outside air temperature drops at night. Changes in microbial decomposition of mound organic matter or thermal convection of warm CO_2-rich mound air to the colder surface at night likely do not play a major role in the diurnal C fluxes observed in our study.

Introduction

Red wood ants (*Formica rufa* group) are commonly found in many European conifer and mixed conifer–hardwood forests (e.g., Gösswald 1989a, 1989b). Because of their wide occurrence, this group of ants has been the focus of extensive research on their social structure (e.g., Crozier & Pamilo 1996, Pamilo *et al*. 1997), geographical distribution and density (e.g., Kissling 1985), population dynamics and behavior (Klimetzek 1981), and their impact on biodiversity (Laakso

& Setälä 1997, 2000, Hawes *et al.* 2002). Even though the number of red wood ant mounds per hectare can be high (up to 18 mounds ha^{-1}) in certain forest types (Raignier 1948, Ceballos & Ronchetti 1965, Gris & Cherix 1977, Cherix & Bourne 1980), only recently their potential impact on soil carbon (C) and nutrient dynamics and CO_2 emissions has gained increased attention (Frouz *et al.* 1997, Lenoir *et al.* 2001, Risch *et al.* 2005).

Carbon and nutrient concentrations of mound material are higher than those of the forest floor and mineral soil (Frouz *et al.* 1997, Laakso & Setälä 1998, Lenoir *et al.* 1999, Risch *et al.* 2005), leading to increases in spatial heterogeneity of soil C and nutrients in ecosystems where these ants are found (Kristiansen & Amelung 2001). Red wood ant mounds were also reported to be "hot spots" for C emissions, with CO_2 originating from ants and other invertebrate respiration (Risch *et al.* 2005), and microbial activity (Coenen-Stass *et al.* 1980, Frouz 2000). However, the contribution to total CO_2 emissions from red wood ant mounds was found to be minor on an ecosystem level (Risch *et al.* 2005). Since CO_2 in red wood ant mounds is derived from biological processes, changes in environmental conditions could alter C emissions from these mounds. Red wood ants are known to keep temperature inside their mounds at higher levels than the outside air (Zahn 1957, Rosengren *et al.* 1987), but mound temperatures show fluctuations related to changes in air temperature (Heimann 1963, Rosengren *et al.* 1987). Since ants are poikilothermal organisms, diurnal or seasonal fluctuations in air temperature could affect CO_2 emissions from their mounds. Therefore, our objectives were to examine how air temperature affects daily and seaonal CO_2 emissions from red wood ant mounds.

Study area and methods

Study area

This study was conducted in the Swiss National Park, located in the southeastern part of Switzerland. The Park covers an area of 170 km^2 with elevations ranging from 1350 to 3170 m above sea level (m a.s.l.). Mean annual precipitation and temperature are 925 ± 162 mm and 0.2 ± 0.7 °C, respectively (average ± standard deviation, measured at the Park's weather station in Buffalora between 1904 and 1994 located at 1980 m a.s.l.). Fifty km^2 of the Swiss National Park are covered with conifer forests, which are composed of mountain pine (*Pinus montana* Miller), Swiss stone pine (*Pinus cembra* L.), European larch (*Larix decidua* Miller), Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.). Nearly pure stands of mountain pine are the early-successional forests, which are replaced by mixed-conifer stands. Most mixed forests contain all five conifer species, but stands dominated by larch/mountain pine are also found. The mixed forests are replaced by late-succession stone pine or stone pine–larch stands (Risch *et al.* 2003, 2004). A detailed description of the four stand types is

Table 1. Description of the four forest types found in the Swiss National Park (from Risch *et al.* 2003, 2004).

Stand type	Elevation (m a.s.l)	Canopy closure (%)	Stand height (m)	Stand age (years)	Basal area (m^2 ha^{-1})	Stand density (stems ha^{-1})
Mountain pine[1]	2006	43	14	165	25	1659
Larch/mountain pine[2]	1850	46	19	168	34	1275
Mixed[3]	1792	54	25	200	42	784
Stone pine[4]	1963	63	27	236	54	577

Species compsition (percentage of total basal area):
[1] *P. montana* 96%, *P. cembra* 2%, *L. decidua* 1%, *P. sylvestris* 1%
[2] *P. montana* 35%, *L. decidua* 62%, *P. abies* 1%, *P. sylvestris* 2%
[3] *P. montana* 17%, *P. cembra* 1%, *L. decidua* 32%, *P. abies* 34%, *P. sylvestris* 16%
[4] *P. montana* 3%, *P. cembra* 63%, *L. decidua* 25%, *P. abies* 8%, *P. sylvestris* 1%

given in Table 1. The total number of red wood ant mounds in the different stand types ranged from 6.0 to 13.3 per hectare (Table 2). For more detail on mound distribution within the four forest types, *see* Risch *et al*. 2005). Three different red wood ant species are found in the forests of the Swiss National Park: *Formica lugubris* ZETT., *Formica aquilonia* YARROW (Dethier & Chérix 1982) and *Formica paralugubris* (D. Chérix pers. comm.).

CO_2 measurements

We selected four mounds in each of the four stand types for this study, resulting in a total of 16 mounds (Table 2). CO_2 emissions were measured with a closed system soil respiration chamber (SRC-1, 15 cm high, 10 cm diameter) attached to a PP-System EGM-4 infrared gas analyser (PP-Systems, Hitchin, Hertfordshire, UK) by taking thirteen measurements on two transects across each mound (Fig. 1) every second week from late June until mid-September 2003 (6 sampling periods). As access into the Swiss National Park is normally not permitted at night, we were only able to sample two of the 16 mounds over a 24-hour period on a regular basis (Table 2). These measurements were conducted bi-monthly between July and mid-September. For the first half of this period we sampled at 0800 hrs, 1400 hrs, 2000 hrs, and 0200 hrs, then switched to 1100 hrs, 1700 hrs, 2300 hrs, and 0500 hrs in order to obtain a higher resolution of daily changes in CO_2 emissions and air temperature. Air temperature was measured over a 45 minute period with a portable temperature sensor placed in the shade 50 cm above the soil surface 10 m away from the mound.

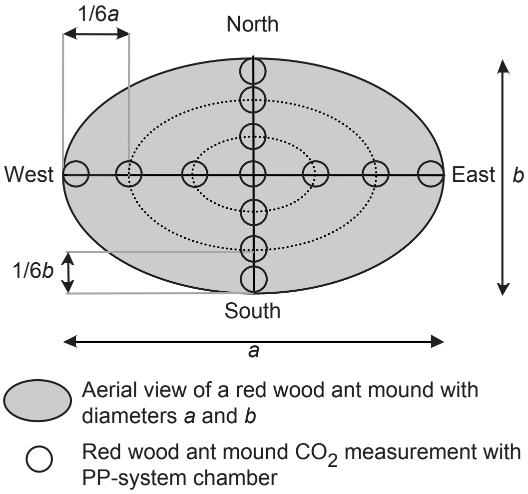

Fig. 1. Red wood ant mound CO_2 emission sampling design.

Statistical analyses

Previous calibration of our soil respiration chamber with a chamber system covering the entire mound (M. Ohashi *et al*. unpubl. data) indicated that the arithmetic mean of our mound measurements would give the best estimate for total mound CO_2 emissions. Therefore, we averaged the 13 measurements taken at each mound for each mound and sampling date.

Table 2. Average number of mounds per hectare in the four different stand types (from Risch *et al*. 2005), height and diameters of the 16 mounds (four per stand type) under study. Height = average from height measurements taken at the N, S, E, and W sides of the mound. D_{NS} = North–South diameter, D_{EW} = East–West diameter, Italics: mounds additionally sampled for CO_2 during the 24hr measurements.

Stand type	No. of mounds per ha (%)	Mound #1			Mound #2			Mound #3			Mound #4		
		Height (cm)	D_{NS}	D_{EW}	Height (cm)	D_{NS}	D_{EW}	Height (cm)	D_{NS}	D_{EW}	Height (cm)	D_{NS}	D_{EW}
Mountain pine	6.4	29	60	90	25	70	60	*44*	*110*	*120*	*90*	*175*	*175*
Larch/mountain pine	10.9	44	110	120	64	190	190	66	175	160	38	95	100
Mixed	13.3	48	155	135	62	160	135	58	155	180	69	205	180
Stone pine	6.0	48	170	120	53	180	135	69	220	215	91	210	230

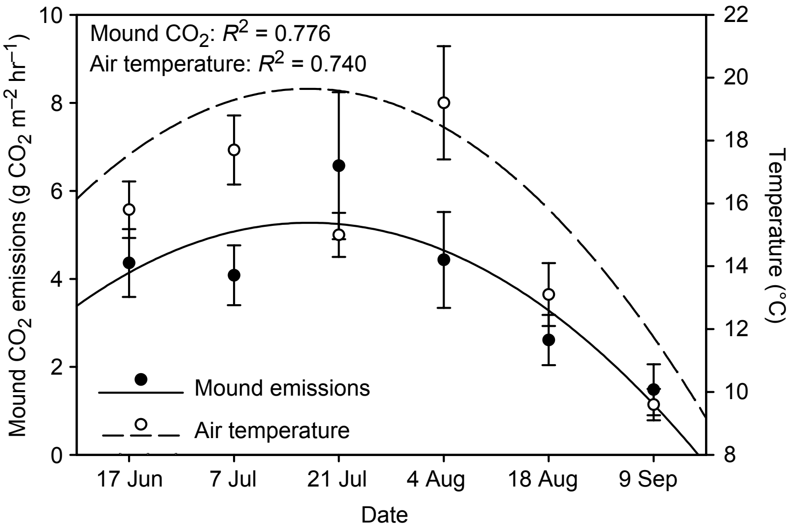

Fig. 2. Average CO_2 emission rates from red wood ant mounds, and average air temperature on six sampling dates between mid June and beginning of September 2003. Regression equations are polynomial (quadratic). Error bars = standard errors, *n* = 16.

Seasonal measurements

As CO_2 emissions among the stand types were not significantly different (Risch *et al.* 2005), we averaged CO_2 emission rates of all 16 mounds and the measurements for air temperature for each sampling day (arithmetic means). Regression analysis was used to assess the correlation between the red wood ant mound CO_2 emission and the date of the year, and air temperature and date of the year.

Diurnal measurements

We normalized CO_2 emission rates and air temperature data for each measuring date and mound to remove seasonal effects of changes in CO_2 emissions. Data from the two mounds were then averaged for each sampling time of the day, and regression analysis was used to assess the correlation between mound CO_2 emission and time of day, and air temperature and time of day.

Results and discussion

Seasonal patterns in red wood ant mound CO_2 emissions

The highest CO_2 emission rates were measured in mid-summer and the lowest in September, which closely followed the seasonal changes in observed air temperature (Fig. 2). Heimann (1963) and Rosengren *et al.* (1987) showed that nest temperatures in *Formica polyctena* (Foerst.) mounds were higher than the temperature of the surrounding air during their active season (April through October), but displayed strong seasonal patterns which closely followed changes in air temperatures. Since ants are poikilothermal organisms, their metabolic rates and therefore CO_2 emissions are linked to temperature. In a laboratory experiment Holm-Jensen *et al.* (1980) showed that the CO_2 production of *Formica rufa* L. workers increased with increasing temperature. Respiratory rates of red wood ants related to temperature have also been studied using changes in oxygen consumption instead of CO_2 release. Kneitz (1967) and Schmidt (1968) showed that oxygen consumption of *F. polyctena* increased at higher temperatures, as did metabolic heat production by red wood ant workers and pupea (Horstmann 1990). Increased oxygen consumption rates at higher temperatures were also reported for other *Formica* species (overview in Peakin & Josens 1978). Coenen-Stass *et al.* (1980) showed that microbial respiration in *F. polyctena* mound material increased with increasing temperature, and followed seasonal changes in nest temperature. Thus, microbial CO_2 emissions would be the highest in mid-summer, same as ant emissions. The same relationship would probably

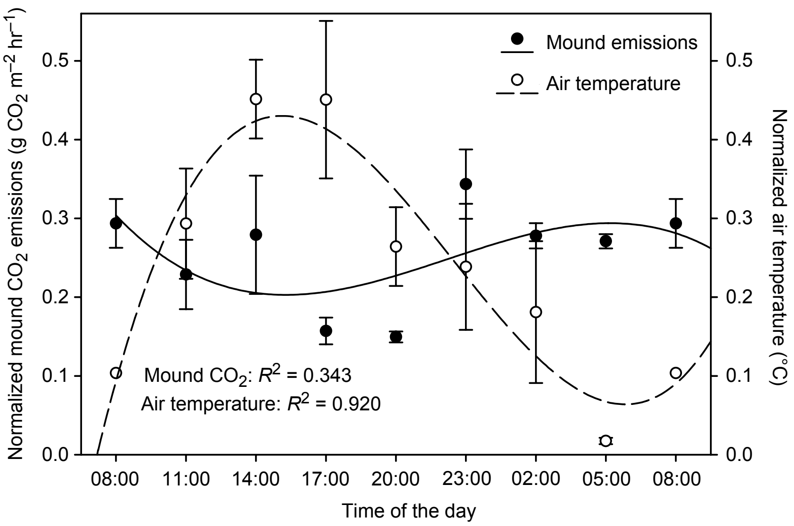

Fig. 3. Average daily CO_2 emission rates from red wood ant mounds, and average daily air temperature. Regression equations are polynomial (cubic). Error bars = standard errors, $n = 4$.

hold true for metabolic rates of other mound-inhabiting invertebrates, such as e.g., mites, beetles, or earthworms (Laakso & Setälä 1997, 1998), but we could not find any information on this subject in the literature.

Diurnal patterns in red wood ant mound CO_2 emissions

The diurnal CO_2 emission cycle was inversely correlated with air temperature. We found highest emissions during the night, when temperatures were lowest (Figs. 3 and 4). Greatest differences were found in August, when differences between day- and night-time temperatures were largest (Fig. 4). Mound temperatures show similar diurnal fluctuations as air temperatures (Heimann 1963), but the amplitudes in mounds are much lower than the ones in the surrounding air. This could be accomplished by ants clustering within the mound at night or during cold periods, which raises their respiration rate (Horstmann & Schmid 1986, Rosengren *et al.* 1987), and would increase night-time CO_2 emissions.

Elevated CO_2 emissions from red wood ant mounds could also be caused by more ants being present in the mounds at night (Finnegan 1973, Rosengren & Fortelius 1986, Hölldobler & Wilson 1990). Skinner (1980) reported that nest return rates of mound-building *Formica rufa* L. ants in England were strongly correlated with air temperature, being highest in the afternoon and lowest at midnight and noon. Similar temperature–nest activity patterns were also reported for *F. polyctena* in the Netherlands (de Bruyn & Kruk-de Bruin 1972) and in the Czech Republic (Frouz 2000). Zahn (1957) counted in- and outgoing red wood ants in artificial mounds and observed that the ants moved back to the nest when the air temperature dropped outside the mound. We did not count returning or leaving ants in our study, but observed lower activity during the night measurements.

Frouz (2000) hypothesized that higher night-time ant metabolism or ant density that cause increases in mound temperature could also trigger an increase in microbial activity, especially when the mound surface layer (0 to 15 cm) is wet (over 50% moisture content). Even though some of our measurements were conducted shortly after rain events, the C fluxes from our mounds always showed the same diurnal pattern with highest emissions during the night when air temperatures were at their minimum (Fig. 4). Therefore, we do not think that changes in microbial decomposition of the mound organic matter played a major role in our study.

Thermal convection of CO_2-rich subsurface air to the soil surface has occasionally been observed in forest ecosystems when air temperatures dropped below soil temperatures at night (Witkamp 1969). Thus, decreasing nightly air temperatures could potentially cause higher CO_2

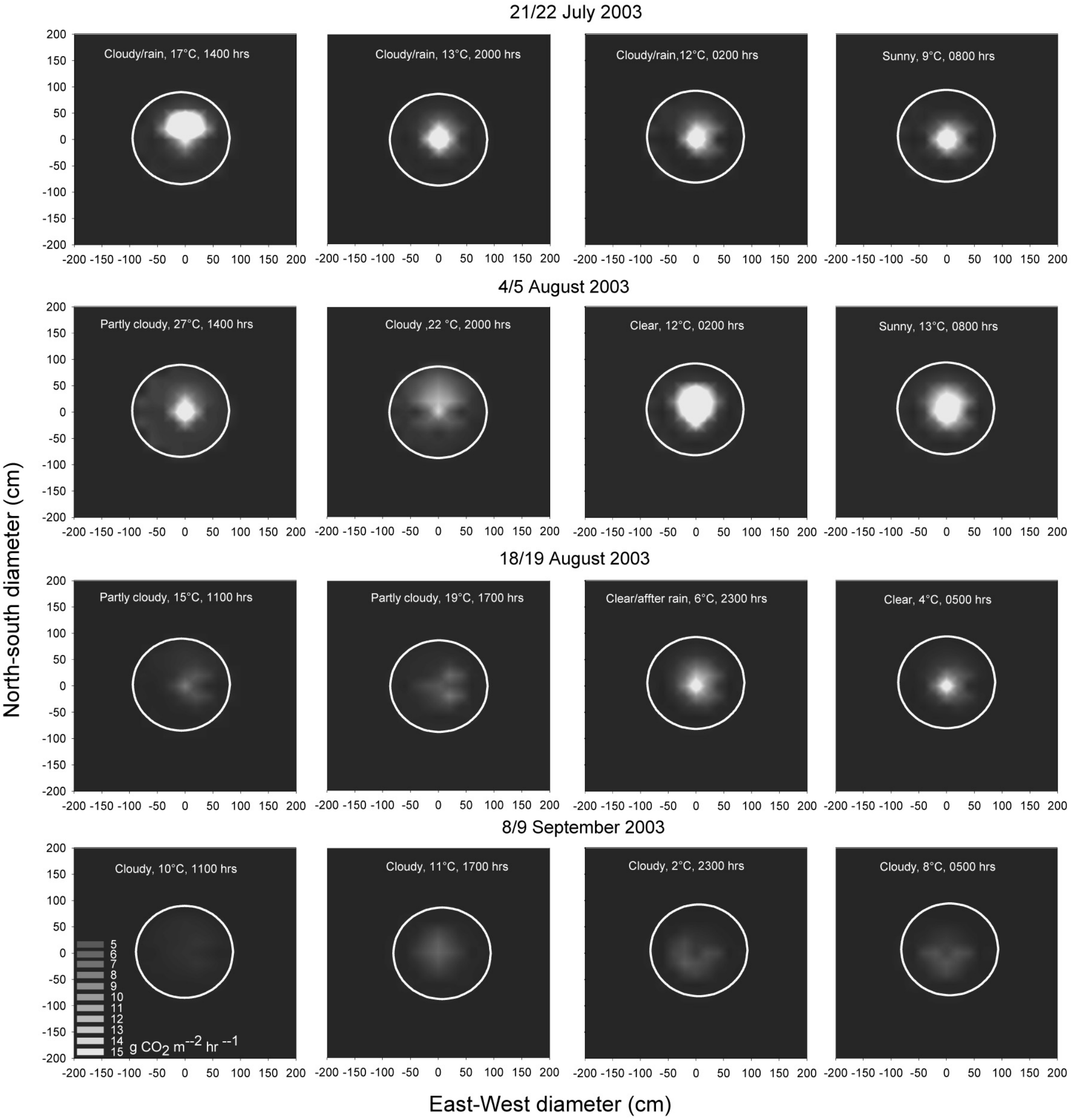

Fig. 4. CO_2 emission of one red wood ant mound measured at four different times during the day between 21 July and 9 September 2003. The white ellipse indicates the aboveground basal extent of the mound (aerial view). Data points between the 13 sample locations were calculated by interpolation of the surrounding sample points. CO_2 emissions ranged from 5 g CO_2 m^{-2} hr^{-1} (dark gray) to 15 g CO_2 m^{-2} hr^{-1} (light gray).

emissions from red wood ant mounds. However, diurnal changes in mound surface temperatures (0 to 10 cm) and air temperature follow the same pattern with mound surface temperatures always being higher (e.g., Heimann 1963, Frouz 2000). Thus, thermal convection would affect red wood ant mound CO_2 emissions at any time during the day, and not only at night.

Acknowledgements

This study was funded by the Swiss Federal Institute of Technology, Zurich (grant No. TH-1'/01-1), and the Academy of Finland (grant No. 200780). We express our gratitude to Wilhelm Fortelius and an anonymous reviewer for constructive comments on the manuscript and the staff of the Swiss National Park for the administrative and logistic support of our research.

References

Ceballos, P. & Ronchetti, F. G. 1965: Le formiche del grouppo *F. rufa* sui Piranei orientali spagnoli nelle province di Nerida i Gero. — *Estr. Mem. Soc. Entomol. Ital.* 45: 153–168.

Cherix, D. & Bourne, J. D. 1980: A field-study on a supercolony of the RWA *Formica lugubris* Zett. in relation to other predatory arthropodes (spiders, harvestmen and ants). — *Rev. Suisse Zool.* 87: 955–973.

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.

Crozier, R. H. & Pamilo, P. 1996: *Evolution of social insect colonies*. — Oxford University Press, Oxford, UK.

de Bruyn, G. J. & Kruk-de Bruin, M. 1972: The diurnal rhythm in a population of *Formica polyctena* Forst. — *Ekol. Polska* 20: 117–127.

Finnegan, R. J. 1973: Diurnal foraging activity of *Formica sublucida, F. sanguinea subnuda*, and *F. fossaceps* (*Hymenoptera: Formicidae*) in Quebec. — *Can. Entomol.* 105: 441–444.

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

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

Gösswald, K. 1989a: *Die Waldameise. Band 1. Biologische Grundlagen, Ökologie und Verhalten*. — AULA, Wiesbaden, Germany.

Gösswald, K. 1989b: *Die Waldameise. Band 2. Die Waldameise im Ökosystem Wald, ihr Nutzen und ihre Hege*. — AULA, Wiesbaden, Germany.

Gris, G. & Cherix, D. 1977: Les grandes colonies de fourmis des bois du Jura (groupe *Formica rufa*). — *Bull. Soc. Entomol. Suisse* 50: 249–250.

Hawes, C., Stewart, A. J. A. & Evans, H. F. 2002: The impact of wood ants (*Formica rufa*) on the distribution and abundance of ground beetles (*Coleoptera: Carabidae*) in a Scots pine plantation. — *Oecologia* 131: 612–619.

Heimann, M. 1963: Zum Wärmehaushalt der Kleinen Roten Waldameise (*Formica polyctena* Forest.). — *Waldhygiene* 5: 1–21.

Hölldobler, B. & Wilson, E. O. 1990: *The ants*. — Harvard University Press.

Holm-Jensen, I., Jensen, T. F. & Nielsen, M. G. 1980: The influence of temperature upon the rate of CO_2 production in enflurane anesthetized worker of ants of *Formica rufa* L. — *Ins. Soc.* 27: 180–185.

Horstmann, K. 1990: Zur Entstehung des Wärmezentrums in Waldameisennestern (*Formica polyctena* Förster; *Hymenoptera, Formicidae*). — *Zool. Beitr.* 33: 105–124.

Horstmann, K. & Schmid, H. 1986: Temperature regulation in nests of the wood ant *Formica polyctena* (*Hymenoptera: Formicidae*). — *Entomol. gener.* 11: 229–236.

Kissling, E. M. 1985: *Untersuchungen über die Biotopansprüche und einen allfälligen Rückgang von roten Waldameisen aus der Formica rufa-Gruppe in der Schweiz*. — Ph.D. thesis, No. 7801, ETH Zurich, Switzerland.

Klimetzek, D. 1981: Population studies on hill building wood-ants of the *Formica rufa*-group. — *Oecologia* 48: 418–421.

Kneitz, G. 1967: Stichproben zur jahreszeitlichen Dynamik des Waldameisenstaates. — In: Graff, O. & Satchell, J. E. (eds.), *Progress in soil biology: Proceedings of the Colloquium on Dynamics of Soil Communities*. Vieweg & Sohn, Braunschweig: 241–248. [In German with English abstract].

Kristiansen, S. M. & Amelung, W. 2001: Abandoned anthills of *Formica polyctena* and soil heterogenity in a temperate decidous forest: morphology and organic matter composition. — *Eur. J. Soil Sci.* 52: 355–363.

Laakso, J. & Setälä, H. 1997: Nest mounds of red wood ants (*Formica aquilonia*): hot spots for litter-dwelling earthworms. — *Oecologia* 111: 565–569.

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.

Laakso, J. & Setälä, H. 2000: Impacts of wood ants (*Formica aquilonia* Yarr.) on the invertebrate food web of the boreal forest floor. — *Ann. Zool. Fennici* 37: 93–100.

Lenoir, L., Bengtsson, J. & Persson, T. 1999: Effects of coniferous resin on fungal biomass and mineralisation processes in wood ant nest materials. — *Biol. Fertil. Soils* 30: 251–257.

Lenoir, L., Persson, T. & Bengtsson, J. 2001: Wood ants nests as potential hot spots for carbon and nitrogen mineralization. — *Biol. Fertil. Soils* 34: 235–240.

Pamilo, P., Gertsch, P., Thorén, P. & Seppä, P. 1997: Molecular population genetics of social insects. — *Ann. Rev. Ecol. Syst.* 28: 1–25.

Peakin, G. J. & Josens, G. 1978: Respiration and energy flow. — In: Brian, M. V. (ed.), *Production ecology of ants and termites*: 111–163. Cambridge University Press.

Raignier, A. 1948: L'économie thermique d'une colonie polycalique de la Fourmi des bois. — *La Cellule* 51: 279–367.

Risch, A. C., Nagel, L. M., Schütz, M., Krüsi, B. O., Kienast, F. & Bugmann, H. 2003: Structure and long-term development of subalpine *Pinus montana* Miller and *Pinus cembra* L. forests in the central European Alps. — *Forstw. Cbl.* 122: 219–230.

Risch, A. C., Schütz, M, Krüsi, B. O., Kienast, F., Wildi, O. & Bugmann, H. 2004: Detecting successional changes in long-term empirical data from subalpine conifer forests. — *Plant Ecol.* 172: 95–105.

Risch, A. C., Jurgensen, M. F., Page-Dumroese, D. S. & Schütz, M. 2005: The contribution of red wood ants to soil C and N pools and CO_2 emissions in subalpine forests. — *Ecology* 86: 419–430.

Rosengren, R. & Fortelius, W. 1986: Light:dark-induced activity rhythms in *Formica* ants (*Hymenoptera: Formicidae*). — *Entom. Gen.* 121: 221–228.

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

Schmidt, G. H. 1968: Einfluss von Temperatur und Luftfeuchtigkeit auf die Energiebildung während der Metamorphose verschiedener Kasten von *Formica polyctena* Foerst. (Hym.). — *Z. Angew. Zool.* 6: 61–109.

Skinner, G. J. 1980: Territory, trail structure and activity patterns in the wood-ant, *Formica rufa* (*Hymenoptera: Formicidae*) in Limestone woodland in north-west England. — *J. Anim. Ecol.* 49: 381–394.

Witkamp, M. 1969: Cycles of temperature and carbon dioxide evolution from litter and soil. — *Ecology* 50: 922–924.

Zahn, M. 1957: Temperatursinn, Wärmehaushalt und Bauweise der roten Waldameisen (*Formica rufa* L.). — *Zool. Beitr.* 3/2: 127–194.

This article is also available in pdf format at http://www.sekj.org/AnnZool.html