

CO₂ emissions from red wood ant (*Formica rufa* group) mounds: Seasonal and diurnal patterns related to air temperature

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Red wood ant (*Formica rufa* group) mounds release high amounts of carbon dioxide (CO₂). As red wood ants and other invertebrates living in mounds are poikilothermal organisms, their metabolism and therefore CO₂ emissions are affected by changes in temperature. Thus, seasonal or diurnal changes in air temperature could affect CO₂ emissions from mounds. We found that seasonal mound CO₂ emissions and air temperature were correlated, both peaking in mid-summer. In contrast, diurnal CO₂ emissions and air temperature were inversely correlated, as we observed highest C fluxes during the night when air temperature was lowest. This CO₂ 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 CO₂-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 CO₂ 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 CO₂ 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 CO₂ emissions from red wood ant mounds was found to be minor on an ecosystem level (Risch *et al.* 2005). Since CO₂ 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 CO₂ emissions from their mounds. Therefore, our objectives were to examine how air temperature affects daily and seasonal CO₂ 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 km² 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 km² 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 composition (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.).

CO₂ measurements

We selected four mounds in each of the four stand types for this study, resulting in a total of 16 mounds (Table 2). CO₂ 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 CO₂ emissions and air temperature. Air temperature was measured over a 45

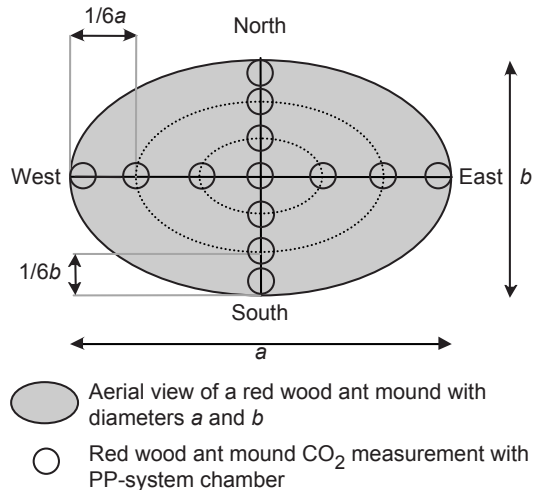


Fig. 1. Red wood ant mound CO₂ emission sampling design.

minute period with a portable temperature sensor placed in the shade 50 cm above the soil surface 10 m away from the mound.

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 CO₂ 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 CO₂ 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

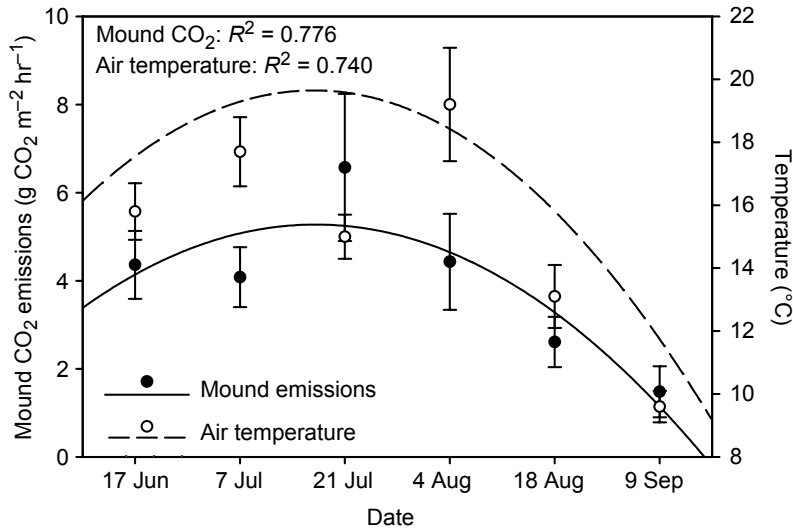


Fig. 2. Average CO₂ emission rates from red wood ant mounds, and average air temperature on six sampling dates between mid June and beginning of September 2003. Regression equations are polynomial (quadratic). Error bars = standard errors, $n = 16$.

Seasonal measurements

As CO₂ emissions among the stand types were not significantly different (Risch *et al.* 2005), we averaged CO₂ 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 CO₂ emission and the date of the year, and air temperature and date of the year.

Diurnal measurements

We normalized CO₂ emission rates and air temperature data for each measuring date and mound to remove seasonal effects of changes in CO₂ 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 CO₂ emission and time of day, and air temperature and time of day.

Results and discussion

Seasonal patterns in red wood ant mound CO₂ emissions

The highest CO₂ 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 CO₂ emissions are linked to temperature. In a laboratory experiment Holm-Jensen *et al.* (1980) showed that the CO₂ 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 CO₂ 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 pupae (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 CO₂ emissions would be the highest in mid-summer, same as ant emissions. The same relationship would probably

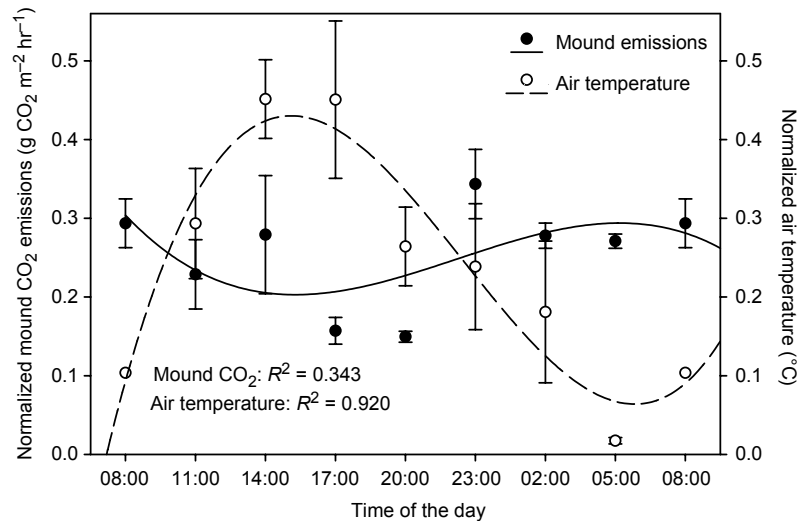


Fig. 3. Average daily CO₂ emission rates from red wood ant mounds, and average daily air temperature. Regression equations are polynomial (cubic). Error bars = standard errors, $n = 4$.

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 CO₂ emissions

The diurnal CO₂ 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 CO₂ emissions.

Elevated CO₂ 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 nighttime 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 CO₂-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 CO₂

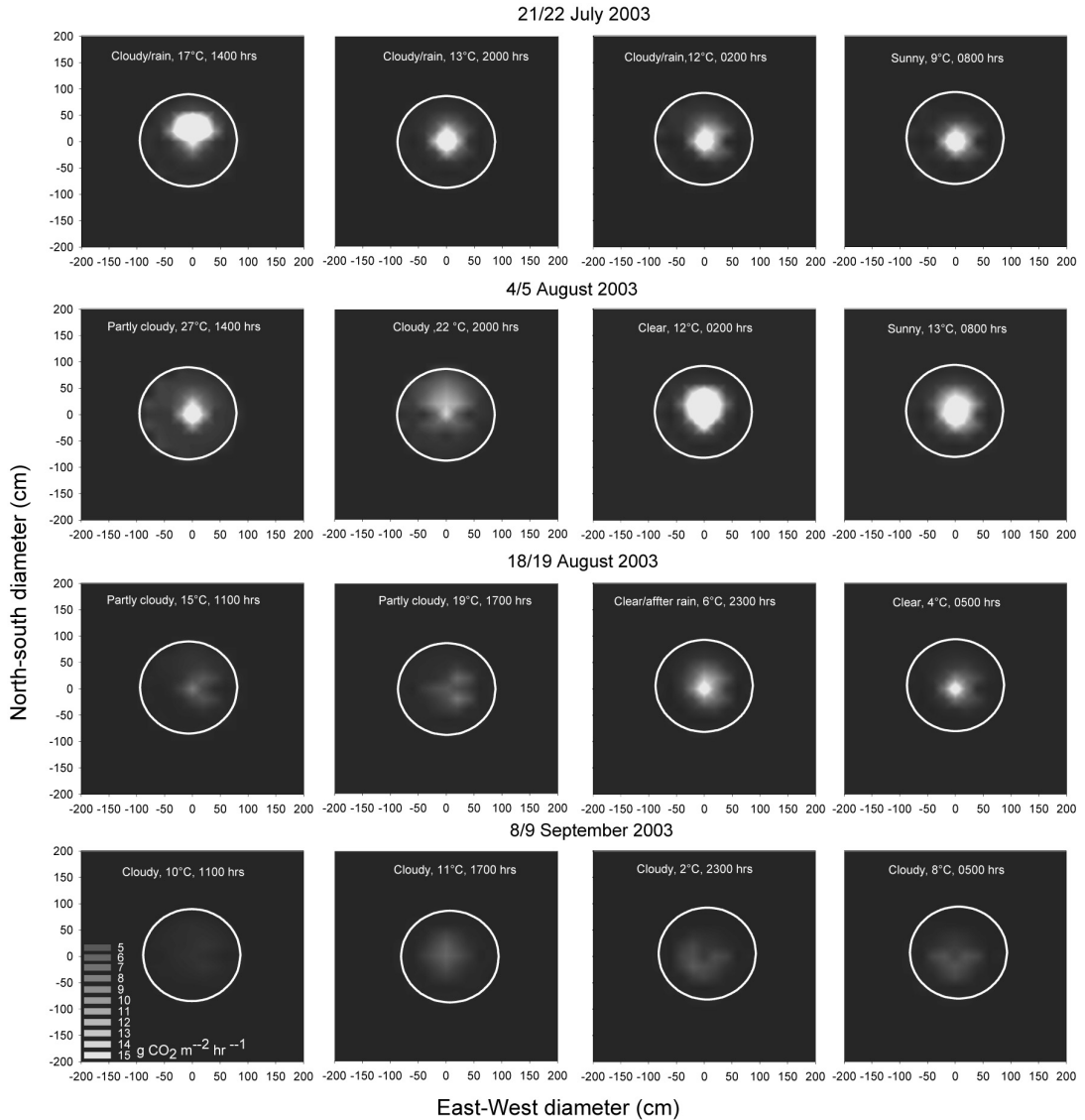


Fig. 4. CO₂ emission of one red wood ant mound measured at four different times during the day between 21 July and 9 September 2003. The white ellipse indicates the aboveground basal extent of the mound (aerial view). Data points between the 13 sample locations were calculated by interpolation of the surrounding sample points. CO₂ emissions ranged from 5 g CO₂ m⁻² hr⁻¹ (dark gray) to 15 g CO₂ 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 CO₂ emissions at any time during the day, and not only at night.

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