Applied Soil Ecology 101 (2016) 101–106

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil

Forest-built nest mounds of red wood ant *Formica aquilonia* are no good in clear fells

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ARTICLE INFO

Article history:
Received 2 November 2015
Received in revised form 12 January 2016
Accepted 25 January 2016
Available online 3 February 2016

Keywords:
Ants
Humidity
Hymenoptera
Insulation
Thermal capacity

ABSTRACT

Temperature and humidity conditions affect the growth and success of ectotherm insects. Red wood ants of the *Formica rufa* group are able to regulate the temperature of their nests to be close to the optimum, typically higher than ambient in northern latitudes and higher elevation. The mound-shaped nests are constructed from organic particles (needles, sticks, etc., plant material) and from soil particles. Nest mounds typically have a relatively dry inner structure but moister surface layer which may help the ants to insulate nests against cooling winds. Forest clear felling exposes nest mounds to direct sunlight, drier microclimate and increased wind. We studied whether clear felling affects the nest surface moisture and temperature conditions. We found that i) nest surfaces were significantly drier in clear fells than in forests, ii) a high height/diameter ratio and an increase in the nest volume increases surface dryness in clear fells but not in forests, iii) the nest temperatures relative to ambient temperature was higher in forests than in clear fells, and iv) the relative temperature increased with increasing moisture content of nest surface layer. The drying nest material and more unstable inside temperature may have adverse effects not only on the red wood ants themselves, but also for nest-dwelling soil organisms and myrmecophiles that live in red wood ant nests. In addition, changes in moisture and temperature could have effects on the rate of decomposition and nutrient turnover.

1. Introduction

Insects are ectotherms and thus their growth and reproduction is affected by the temperature of their habitat (Ratte, 1985; Atkinson, 1994; Chown and Nicolson, 2004). In addition, insects are generally small-sized, thus vulnerable to desiccation (Chown and Nicolson, 2004). Social insects, such as ants, bees, social wasps and termites are able to adjust the temperature-humidity conditions in their nests by the nest structure or by active ventilation (e.g., Jones and Oldroyd, 2006).

Red wood ants of the *Formica rufa* group actively regulate the nest temperatures during summer season from April to September (Kadochová and Frouz, 2014). Temperature inside nest mounds is typically markedly higher than ambient (Frouz, 2000; Frouz and Finér, 2007; Sorvari and Hakkarainen, 2009; Carpenter et al., 2013; Kadochová and Frouz, 2014). These ants build relatively big nest mounds from organic particles (needles, sticks, etc. plant material) and soil particles. Organic material is mostly collected from the forest litter layer and soil particles are mostly excavated from beneath the nest mound. The volume of nest mounds can reach over several cubic meters in large cases (e.g., Seifert, 1991 Wuorenrinne, 1994), but is usually smaller. Nests in shaded older forests are often larger than mounds in open sun exposed habitat patches or young forests (Sorvari and Hakkarainen, 2005; Kilpeläinen et al., 2008).

The nest mounds vary in moisture and temperature patterns. Temperatures vary more in dry nest mounds than in moist mounds in red wood ant *Formica polyctena* that has been proposed to be due to a lower thermal capacity of dry nests (Frouz and Finér, 2007). The thermal and moisture conditions of nests seem to vary with habitat type, e.g., nests in shaded forests are moister and have different diurnal temperature regime than nests in open patches (Frouz, 2000; Frouz and Finér, 2007).

In forest nest mounds, the nest surface layer is typically moister than inner parts of the nest (Laakso and Setälä, 1997, 1998; Elo et al., 2016, in press). This phenomenon has been proposed to be due to the heat produced in the inner nest by decaying organic material and the ant's own body activity. When the heat from the inner nest meets the colder ambient air from the surface it

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http://dx.doi.org/10.1016/j.apsoil.2016.01.019
0929-1393/

Table 1
The diameter, height, nest shape index (height/diameter) and relative moisture content of the surface layer of studied *Formica aquilonia* ant nests in different sites in central Finland. Minimum–mean–maximum are presented for diameter, height, shape index, volume and moisture.

Site	Habitat	Diameter (m)	Height (m)	Shape index	Volume (m^3)	Moisture (%)
1	Clear fell	1.00–1.24–1.48	0.23–0.36–0.54	0.20–0.29–0.38	0.16–0.30–0.61	8.2–32.6–52.5
	Forest	0.95–1.17–1.60	0.40–0.59–0.85	0.38–0.51–0.80	0.19–0.45–1.14	45.3–60.8–67.2
2	Clear fell	1.35–1.71–2.10	0.48–0.70–1.20	0.24–0.41–0.57	0.48–1.17–2.77	6.1–13.9–24.3
	Forest	0.75–1.63–1.90	0.35–0.61–0.80	0.27–0.39–0.47	0.10–0.95–1.51	53.6–59.5–64.0
3	Clear fell	0.70–1.21–1.70	0.30–0.40–0.53	0.23–0.34–0.47	0.08–0.34–0.68	8.2–14.9–30.6
	Forest	0.85–1.23–1.58	0.35–0.40–0.48	0.25–0.34–0.46	0.13–0.34–0.55	34.2–44.2–53.0

condenses increasing moisture at the surface (Rosengren et al., 1987; Hölldobler and Wilson, 1990). The moist surface layer of a nest mound may prevent cooling wind from penetrating the inner layers of the nest. Drying of the surface layer may thus have adverse effects on the temperature regulation of the nest mound (Sorvari, 2016).

Forest management practices, such as clear felling, affect the shadiness of forests to a great extent and thereby should affect the temperature regimes inside the nest mounds. Accordingly, diurnal variation in nest inside temperatures has been found to be higher in forest clearings than in forest interiors (Rosengren et al., 1979; Sorvari and Hakkarainen, 2009). While Sorvari and Hakkarainen (2009) suggested this to be due to the drier nest mounds in clear fells, the moisture content of the nest material was unfortunately not measured at that time and the relationship between temperature variations and nest moisture was therefore not confirmed. Forest clear felling has been shown to decrease the production of sexual offspring, size of workers and survival rate of colonies (Sorvari and Hakkarainen, 2005, 2007a,b, 2009; Sorvari et al., 2014). These may partly be caused by poor temperature conditions inside the nests.

Due to higher temperature and litter biomass compared to surrounding forest litter layer, ant nest mounds form an ideal environment for decomposers such as bacteria, fungi and soil animals, which may be many times more abundant within nest mounds than in adjacent soil (Laakso and Setälä, 1997, 1998). These organisms recycle the organic material back to inorganic substances and nest mounds commonly have higher phosphorus, nitrogen and carbon concentrations than the adjacent soil (Kilpeläinen et al., 2007). Therefore the nest mounds of red wood ants have an ecological function as hot spots of litter decomposition and nutrient turnover in boreal and temperate forests (Lenoir et al., 2001; Frouz and Jílková, 2008; Frouz et al., 2016). The nest mounds do not only maintain good conditions for decomposition, but they can also form a refuge for decomposer organisms during winter period since the temperature inside mounds tends to maintain above zero (Rosengren et al., 1987). Changes in the temperature and moisture properties of these mounds in summer period could have effects on the decomposer fauna and thus also on the rate of decomposition and nutrient turnover. In larger scale, these can have effect for the tree growth and thus recovery of ecosystem after a disturbance like forest clear-felling (Setälä and Huhta, 1991; Jílková and Frouz, 2014; Jílková et al., 2015a).

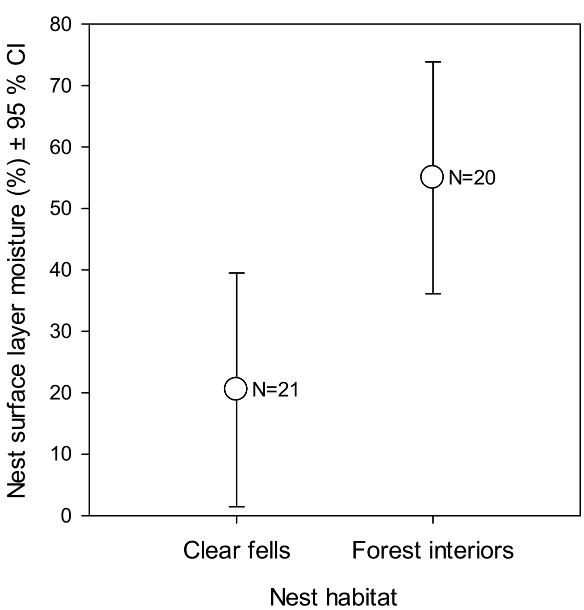

Fig. 1. Moisture content, i.e., percentage of water in the fresh biomass of the red wood ant (*Formica aquilonia*) nest mound surface was lower in clear fells compared to forests in central Finland ($P < 0.0001$).

Our aim in this study was to find out 1) if the moisture content of ant nest mounds differs between natural forest and clear-fell areas, 2) whether there is an association between nest surface moisture and nest inside temperature, and 3) whether these are affected by habitat and nest mound shape and volume differences.

2. Material and methods

2.1. Study species and study areas

The studied nest mounds belonged to the red wood ant *Formica aquilonia* Yarrow (1955), a member of *F. rufa* group. *F. aquilonia* is a forest-dwelling species inhabiting both the edges and interiors of conifer forests. The largest mounds are usually located inside forests (Kilpeläinen et al., 2008). The species forms colonies with multiple nest mounds (Rosengren and Pamilo, 1983), a situation called polydomy. The nest mounds can reach a height over 2 m and diameter over 3 m, however they are usually smaller (e.g., Wuorenrinne, 1994).

The study was conducted on three different sites located near the town of Kuopio in central Finland (WGS84: 62°52′: 27°29′). Each site contained a clear felled forest stand and a bordering non-felled stand (side by side). The study stands were dominated by Norway spruce (*Picea abies*) mixed with Scotts pine (*Pinus sylvestris*) and birches (*Betula pendula*,*B. pubescens*). The scrub layer was dominated by bilberry (*Vaccinium myrtillus*). The clear felling occurred one to three years before the study. The three sites (clear fell–forest pairs) were spatially well separated from each other (min 3.9 km, max 6.5 km). Seven nest mounds per clear fell and seven nest mounds per forest were sampled, except in one forest where only six suitable nest mounds of *F. aquilonia* were found. The minimum basal diameter of 0.70 m was used as a selection criteria as well as the occurrence of seemingly vital *F. aquilonia* colony, i.e., the deserted or semi-deserted and young (small) post-harvesting nests were not used in this study. The total number of studied nest mounds was 41. The first clear fell–forest