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Ant-root aphid relations in different plant associations

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ABSTRACT. The fauna of root aphids inhabiting the nests of ants in the xerothermal grassland and the moist meadow was investigated. In all plant clusters the total number of 14 aphid species was established. The highest variety of aphid species was observed in the nests of ants inhabiting the xerothermal grassland – 12 species were collected, while in moist meadow collected only 6 species were recorded.

Underground living aphids visited by ants in the oak-forest were also the subject of research. In the oak-forest only two species of root aphids were visited by three species of ants. The differences between the aphid faunas of the particular ant species are analysed with reference to the biology of both insect groups. In the case of oak-forest data is discussed with a view of foraging strategies and the interspecific competition between ants visiting aphids.

KEY WORDS: root aphids, ants, trophobiosis, plant association

INNTRODUCTION

The mutualistic relationship between some species of ants and the representatives of different hemipterans, especially Coccidoidea, Membracidoidea and Aphidoidea has been the subject of many researches, both aphidologists and myrmecologists (DELABIE 2001). Aphids are the most common ant-attended hemipterans in Europe. A detailed study of this relationship was conducted by WAY (1963) and PONTIN (1978). They showed that ants use aphids as a source of proteins and carbohydrates, at the same time defending them from predators and parasitoids, which result in the increase of their abundance.

Trophobiosis is a type of symbiosis, in which ants receive honeydew from aphids and other homopterans, as well as catepillars of certain lycaenid and riodinid butterflies, and in return provide these insects with protection. (WHEELER 1910, HÖLLDOBLER & WILSON 1990).

Root aphids, found in the ant nests, represent a set of interesting morphological features which distinguish them among others, overground living species of aphids. Their morphology is adapted to both the underground living conditions and to the requirements of trophobiotic relation with ants. For example, small size, short legs and antennae may be the adaptations to the underground life conditions (ZWÖLFER 1958). The lack of functional siphunculi designed for repelling the enemy (MONDOR et al. 2002), the lack of thick wax layer produced by special epidermal glands, dorsal position of anus and a short cauda, preventing a drop of honeydew from being thrown away for a longer distance, may be also the result of trophobiotic relation with ants (KUNKEL 1973). The above-mentioned may be the alternations which allow ant workers to take a droplet of honeydew (WAY 1963, STADLER & DIXON 1999). On the contrary, the species of aphids not attended by ants throw away the droplets of honeydew for a long distance.

In return for honeydew, aphids get the defence against the enemies or unfavourable weather conditions from ants, which get rid of the parasitic wasps and flies that lay eggs into the aphid bodies (STARY 1966, VÖLKL & MACKAUER 1993, RANA et al. 2002, STADLER 2002, HILL & HOY 2003). They also protect aphids from the attacks of predacious larvae of some beetles and neuropterans, preying on the unprotected aphid colonies and that may also be the reason why these aphids have their siphunculi reduced (aphids protected by ants do not need well-developed siphunculi) (MONDOR et al. 2002). Ants also move aphids to new plants being a better source of sap and where they can protect them more efficiently (COLLINS & LEATHER 2002). Finally, in a colder climate in the case of lacking a primary host, aphids may overwinter in the ants nests, moved on their secondary host by ants (PON-TIN 1978), which allows them to survive in the anholocyclic form.

It is known that not all aphids are attended by ants. The attended aphids show different degrees of dependence, from purely incidental relations to a very strong interdependence between trophobionts, though strict interspecific correlations have not been proved (SUDD 1987). ZWÖLFER (1958, after: SUDD 1987) lists 22 European species of underground living aphids found in the nests of 17 ant species. Although MUIR'S research (1959) in Western Scotland indicated that one ant species may cooccur with up to 7 species of aphids, in most of the ant nests only a single species of aphids are recorded.

Obviously, due to the aphid strong monophagy and oligophagy a significant relation exists between aphid fauna and the type of plant association in which they occur. Therefore it may be assumed that such a relation also develops among the aphids inhabiting ant nests in different plant associations. This kind of research was conducted in Denmark (GODSKE 1991, 1992) and Great Britain (MUIR 1959, PONTIN 1978), yet in quite homogenous assemblages of moist meadows.

This study aims at the description of fauna of root aphids either inhabiting ant nests in two different phytocoenoses (a xerothermal grassland and a moist meadow) or being visited by ants (in an oak-forest). Moreover, it attempts to provide qualitative and quantitative data describing interspecific relations between both groups engaged in trophobiotic relation.

STUDY SITE AND METHODS

The research was carried out at the territory of Piekary Śląskie and Bobrowniki [UTM: CA58], in the middle part of Middle-Triassic Ridge of Silesian Upland, in its central part. It lasted from 2005 to 2007, and was conducted in three types of plant associations:

1. The xerothermal grassland *Sileno-Phleetum* association (see BABCZYNSKA-SENDEK 2005) developed mainly on the soil formed from sand lying on limestone or from sand-gravelly soil. Dominant plants noted: *Phleum phleoides, Artemisia campestris, Hieracium pilosella, Peucedanum oreoselinum, Scabiosa ochroleuca, Centaurea scabiosa, Anthyllis vulneraria, Fragaria viridis, Euphorbia cyparissias, Sedum telephium.* It was localized in Bobrowniki at the southern slope of the hill about 330 MASL high (September 2006 and 2007).

2. The moist meadow belonging to the *Molinietum caeruleae* association (see MATUSZ-KIEWICZ 2002) situated in Piekary Śląskie, at the elevation of about 270 MASL in the valley of the Brynica river (September 2005 and 2006). Dominant plants recorded: *Molinia caerulea*, *Cirisium palustre*, *C.rivulare*, *Juncus effusus*.

3. The acid oak forest belonging to the *Molinio caeruleae-Quercetum roboris* plant cluster (see Matuszkiewicz 2002) also localized in Piekary Śląskie at the elevation of 280 MASL (September of 2006 and 2007). The dominant plant species: tree layer - Quercus robur, understory layer - *Frangula alnus, Corylus avellana*, herb layer - *Hieracium sabaudum, Luzula luzuloides, Pteridium aquilinum, Vaccinium myrtillus, Festuca gigantea, Poa compressa, Molinia caerulea*.

In the xerothermal grassland material was collected from all ant nests situated along the transect of overall length of 120 m and 1 m wide. Aphids were taken from the roots of plants covering the surface of anthills. The species of aphids covered by soil chambers but normally feeding on the overground parts of plants and being visited there by ants were not the subject of the study. In case of two species (*Acaudinum centaureae* and *Sipha maydis*) only these nests were counted in which aphids were feeding on the roots of their host plants, situated deep inside the ant-hill.

In the moist meadows much longer transect was made -450 m long and 1 m wide, because of the lower density of ant nests. The aphids were collected according to abovementioned the method.

In the forest, only the roots of all herbaceous plants and smaller shrubs growing along the transect were searched due to the difficulties in localization and penetration of the ant nests in the ground (fallen trees, nests under leaves or stones) and the lack of any plants overgrowing their surface. Because the density of nests in this area was also lower than in the xerothermal grassland (DEPA, unpubl. data), the transect was made 270 m long and 1 m wide.

Since the density of the nests in each site was different (DEPA, unpubl. data), it was necessary to make transects of different length so that the collected data could be numerous enough to be compared. The nest density was calculated on the basis of searching the squares method (PISARSKI & PETAL 1981) and the data was gathered during the research simultaneously conducted in the sites. The number of nests was given only in case of oakforest, since the percentage of ant nests served as a comparison with the percentage of aphid colonies visited by particular species of ants.

Additionally, for the oak-forest, the data about the daily activity of workers penetrating the ground surface was obtained, by the pitfall traps sampling. The pitfall traps were set during a simultaneously conducted research, on the 21.08 and 6.09. in 2006 and on 20.08. and 08.09. in 2007, and the search for aphids was carried out between these dates each year, at the beginning of September. Traps were set for 24 h, in a number of 50 each time, and were allocated randomly in the territory of the forest.

Due to the fact that the research was planned to be conducted in two parallel seasons of the two following years and gathering the aphids from the ant-hills caused an ample damage to the structure of the mound, each transect was divided thus during one year only a half of transect was searched. These actions were taken to avoid searching the mounds damaged in the previous season. Such damage might have affected the results, e.g. by the destruction of the plants covering the nest being the host plants for aphids.

RESULTS

Within the 251 ant nests searched in *Sileno-Phleetum* and *Molinietum caeruleae*, there were aphids found in 139 of them, belonging to the 14 species, total of 5 families of *Aphi-doidea*: *Pemphigidae*, *Anoeciidae*, *Drepanosiphidae*, *Lachnidae*, *Aphididae*. Ant nests abounded in species of *Pemphigidae* family (6 species) and only 1 species of *Drepanosi-phidae* occurred.

Sileno-Phleetum

In the xerothermal grassland the total number of 96 ant nests was searched. They belonged to 2 species of ants and include 90 nests with aphids (Table 1). There were 33 nests of *Lasius flavus* (F.) and 63 of *Lasius niger* (L.) searched and 12 species of aphids were found within these nests. In one nest of *L. flavus* and five nests of *L. niger* no aphids were found.

In the nests of *L. flavus* 10 species of aphids were found, most often it was *Tetraneura ulmi* (L.) (10 nests) and subsequently: *Forda marginata* KOCH, *Anoecia corni* (F.), *Trama troglodytes* HEYDEN, *Forda formicaria* HEYDEN, *Trama rara* MORDVILKO, *Pemphigus*

bursarius (L.), Anoecia nemoralis BÖRNER, Trama centaureae BÖRNER, Acaudinum centaureae (KOCH).

In nests of *L. niger* also 10 species of aphids were found, mostly *T. troglodytes* (20 nests) and *A.corni* (13 nests) as well as: *F. formicaria*, *F. marginata*, *A. nemoralis*, *Dysaphis angelicae* (KOCH), *A. centaureae*, *T. ulmi*, *Sipha maydis* KALTENBACH, and *Trama centaureae*.

plant association	Sileno- Phleetum		Molinietum caeruleae					
ant species	Lasius flavus	Lasius niger	Lasius flavus	Lasius niger	Myrmica rubra	Myrmica scabrinodis	Myrmica ruginodis	total
aphid species	Lasiu	Lasiu	Lasiu	Lasiu	Myı ru	Myi scabi	Myi rugi	
Forda formicaria	2	6						8
Forda marginata	5	4						9
Pemphigus bursarius	1		1					2
Geoica setulosa			2					2
Geoica utricularia			4					4
Tetraneura ulmi	10	2	8	2	1	4		27
Anoecia corni	5	13	4	16		1		39
Anoecia nemoralis	1	4	2	4				11
Sipha maydis		1						1
Trama centaureae	1	1						2
Trama rara	2							2
Trama troglodytes	4	20						24
Acaudinum centaureae	1	3						4
Dysaphis angelicae		4						4
nests with aphids	32	58	21	22	1	5		139
nests without aphids	1	5	1	5	78	14	8	112
total	33	63	22	27	79	19	8	251

Table 1. List of aphid species recorded from nests of ants in *Sileno-Phleetum* and *Molinietum-caeruleae* plant associations (numerals mark the amount of ant nests).

Molinietum caeruleae

On the territory of the moist meadow 155 ant nests were investigated belonging to 5 ant species. Aphids were found within 49 nests, including 21 (of 22) nests of *L.flavus*, 22 (of 27) nests of *L. niger*, 1 (of 79) nest of *Myrmica rubra* (L.) and 5 (of 19) nests of *M. scabrinodis* NYL. None of 8 investigated nests of *M. ruginodis* NYL. contained aphids.

Within the nests of *L. flavus* 8 species of aphids were recorded, most commonly *T. ulmi* (8 nests) as well as *Geoica utricularia* (PASSERINI), *A. corni, Geoica setulosa* (PASSERINI), *A. nemoralis, P. bursarius.*

Within the nests of *L. niger* only 3 species of aphids were collected, mostly *A. corni* (16 nests) as well as *A. nemoralis* and *T. ulmi*.

In one nests of *M. rubra* a few individuals of *T. ulmi* were found.

Within the nests of *M. scabrinodis* individuals of *T. ulmi* (4 nests) and of *A. corni* (1 nest) were found.

Quercetum roboris

In the oak forest 114 root aphid colonies were localized, 113 of them belonged to *T. ulmi* and one to *A. corni* (Table 2.). Among colonies of *T. ulmi* 26 of them were visited by workers of *L. platythorax* (SEIFERT, 1991), 49 by workers of *M. rubra*, 13 by *M. rugino-dis*, 1 by *L. flavus* and 24 were not visited by ants. One colony of *A. corni* was found and it was visited by workers of *L. platythorax*.

The qualitative composition of the root aphid fauna within the nests of ants presents the following: species belonging to the family Pemphigidae, mainly from genera *Geoica*, *Forda*, *Tetraneura* and family Anoeciidae were dominating. The analysis of the proportion of these occurrence for each aphid species attended by single ant species in different plant association reveals some differences in qualitative composition of aphid fauna (Fig. 1). A huge disproportion occurs in the case of presence of three aphid species: *T. ulmi*, *A. corni* and *T. troglodytes* within nests of *L. flavus* and *L. niger*. Interestingly, *T. ulmi* appeared more often in aphid fauna of *L. flavus* nests than of *L. niger*, in both the xerothermal grassland and the moist meadow. In the latter habitat *T. ulmi* was also dominant in the nests of both *Myrmica* species.

In the case of *A.corni* and *A. nemoralis*, both species shared a bigger part in the proportion of aphids in the nests of *L. niger* when compared to *L. flavus*. In both habitats and in the moist meadow the disproportion was even higher than in the xerothermal grassland. Finally, *T. troglodytes* which occurred only in the xerothermal grassland was dominant species in the nests of *L.niger*, while it occurred more rarely in the nests of *L. flavus*. Species of the genus *Forda* occurred with a similar proportion in the nests of both *Lasius* species, only in the xerothermal grassland. Species of the genus *Geoica* were reported only in the moist meadow occurring only in the nests of *L. flavus*.

In the case of oak-forest it was impossible to establish the connection between aphids and ants, since only one dominant species of root aphids was found. In this respect, the data gathered refer to the proportion of workers of different ant species attending root aphids and is compared to the proportion of ant nests counted in this habitat and to the activity of foraging workers (Fig. 3). Statistical analysis of two parameters (number of nests and number of aphid colonies visited) for *M. ruginodis* shows a significant difference of their values ($\chi^2 = 5.26$ df=1 p<0.05). On the contrary, *M. rubra* and *L. platythorax* more often attend aphid colonies when compared to the proportion of these species in a total number of ant nests. However, statistical analysis showed no significant difference between both parameters ($\chi^2 = 1.29$ df=1 p<0.3 for *M. rubra* and $\chi^2 = 0.36$ df=1 p<0.6 for *L. platythorax*). Similar pattern shows the comparison of the percentage of aphid colonies visited by particular ant species and the activity of foragers (Fig. 3.). The activity of foragers of *M. ruginodis* is higher than its share in visiting colonies of aphids while activity of *L. platythorax* is lower than its share in visiting colonies of aphids. The statistical analysis of number of aphid colonies visited by a particular species of ants and the activity of their foragers illustrates a significant difference in the case of *M. ruginodis* ($\chi^2 = 7.48$ df=1 p<0.01) and of *L. platythorax* ($\chi^2 = 42.24$ df=1 p<0.001) but not in the case of *M. rubra* ($\chi^2 = 0.36$ df=1 p<0.6).

Table 2. List of ant species visiting colonies of aphids, number of ant nests and their foraging activity in the oak-forest *Quercetum roboris*.

ant species aphid species	Lasius flavus	Lasplatius ythorax	Myrmica rubra	Myrmica ruginodis	not visited by ants	total
Tetraneura ulmi	1	26	49	13	24	113
Anoecia corni		1				1
total:	1	27	49	13	24	114
number of ant nests:		89	154	90		333
number of workers caught in pitfall traps:		41	256	128		425

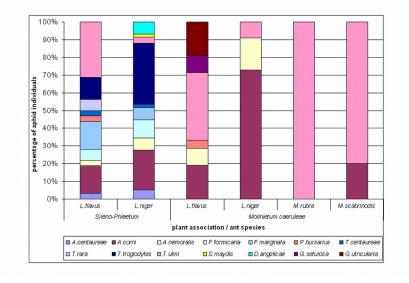


Fig. 1. Percentage of the particular species of aphids in the ant nests in the open habitats.

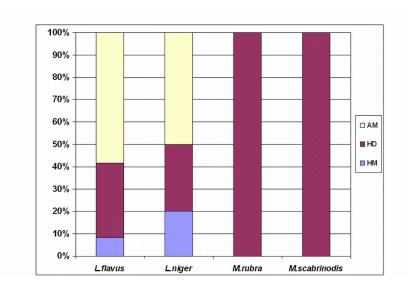


Fig. 2. Percentage of aphid species in the ant nests of the open habitats, with reference to their life cycle (AM – anholocyclic, monoecious; HD – holocyclic, diecious; HM – holocyclic, monoecious)

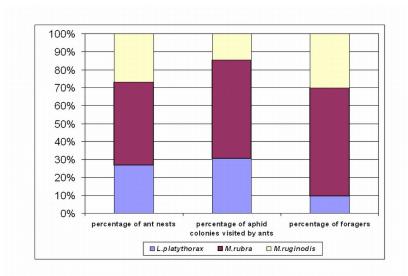


Fig 3. Shares of particular ant species in the oak-forest.

DISCUSSION

Obtained results generally agree with data about the aphid species inhabiting ant nests referred to in literature so far (ZWÖLFER 1958, MUIR 1959, PONTIN 1978). It is interesting that in the nests of L. flavus anholocyclic species was found more often than in the nests of L. niger (Fig. 2). In this study T. ulmi which occurs within nests of L. flavus more frequently is regarded as holocyclic (HEIE 1980), against SUDD'S (1987) suggestion, who referring to the PONTIN (1978), regards it as anholocyclic (although Pontin only indicates that the members of Pemphigidae occurring in the nests of ants may breed in anholocyclic way). With reference to present knowledge anholocyclic life cycle may be induced by climatic changes (RUSZKOWSKA 2007, RUSZKOWSKA & STRAŻYŃSKI 2007) in the part of holocyclic species population. According to Sudd, populations of anholocyclic species are totally dependent on ants (to reach high abundance and to overwinter) but the author does not give the explanation for this. Nevertheless, for a species such as L. flavus, being totally subterranean, anholocyclic aphids feeding only on one easily accessible host, are perfect source of food, available in the whole season and easy to be kept in the underground chambers of mound. Although in two colonies of T. ulmi, located in the oak-forest, winged morphs were found. It happens that ants bite the wings off to the alate forms of aphids (ZWÖLFER 1958) yet in this research such case was not reported.

On the other hand, workers of *L. niger* intensively penetrate the ground and overgrowing plants, taking advantage of the varied sources of food, including aphids feeding on the higher parts of plants. For this species root aphids are not the main source of food, and in spite of this, anholocyclic species are quite numerous and the difference in comparison to *L. flavus* is not significant.

The question raises why it happens that *A. corni* is more often collected from the nests of *L. niger* than *L. flavus*, and *T. ulmi* on the contrary? The answer could be the ability of virginoparae of *T. ulmi* mentioned by PONTIN (1978) and SUDD (1987) to breed in anholocyclic way, without changing the host plant. Sexuparae appearing in autumn may fly off on *Ulmus* sp., its primary host but still there are some parthenogenetic virginoparae staying in the nest. By the same time, virginoparae of *A. corni* do not possess such an ability, its individuals are obliged to fly off to the secondary host (*Cornus* sp.) in autumn (HEIE 1980) and in spring they are lacking on the roots of grasses, also in the ant nests e.g. of *L. flavus* (PON-TIN 1978). Only summer migrantes settle on different grasses and then they may be carried to the nests by workers of *L. niger* penetrating ground and herbs. Workers of *L. flavus* do not penetrate the ground surface so they rarely find colonies of *A. corni* settled by aphids themselves. Other anholocyclic species belonging to such a genera as *Forda* von HEYDEN and *Geoica* HART are also more often found in the nests of *L. flavus* than of *L. niger*.

Interestingly *T. troglodytes*, species anholocyclic and monoecious are more often found in the nests of *L. niger* than of *L. flavus*, though it should be theoretically preferred by the latter species. Also the presence of so called filter chamber in its digestive system (AU-CLAIR 1963, KLIMASZEWSKI et al. 1976), which helps to obtain higher concentration of the sugar in honeydew, does not seem to be the explanation of its different frequency in both species.

Determination of the species as holocyclic and anholocyclic may be problematic itself. The fact is, that some species which are anholocyclic in moderate climatic zone and feed only on one plant family as its host, in southern Europe are holocyclic and host alternating. Especially it refers to such a genera as *Forda* von HEYDEN and *Geoica* HART, so often occurring in the nests of *Lasius* ants. Southern Europe lays in a range of presence of both *Lasius* species, so it is very probable that these aphids (*Forda* spp. and *Geoica* spp.) occur in their nests there and this way, they increase the share of holocyclic and diecious species of aphids in ant nests. Most of the literature data concerning aphid fauna of ant nests, yet describes results of the research conducted in the moderate climatic zone (England – MUIR 1959, PONTIN 1978; NE France, Germany – ZWÖLFER 1958, Denmark – GODSKE 1991, 1992, Scandinavia – HEIE 1980). Therefore it is absorbing to undertake a further study in this matter in southern regions of Europe, where most of myrmecophilic aphids breed fully in their holocyclic way with the host alternation.

Considering other factors influencing the composition of aphid fauna within the ant nests, definitely the composition of phytocoenosis of given habitat matters as it defines the composition of the aphid community (HAŁAJ & WOJCIECHOWSKI 1996, 1998). For example, in this study aphids belonging to the genus *Trama* von Heyden occur only in the xerothermal grassland as it has significant amount of species of *Asteraceae* (*Taraxacum* sp., *Artemisia* sp., *Hieracium* sp.) which are hosts of those aphids (SZELEGIEWICZ 1978) and also *A. centaureae* appears only here as it feeds on *Centaurea scabiosa*, which is typical species for the xerothermal grasslands. In this respect the matter of relations between the aphid community and the fauna of root aphids in the ant nests should be the subject of further studies.

In the case of the oak-forest obtained data may be explained by different modes of foraging by particular ant species. In case of *L. platythorax*, which is quite recently recognised as a good species (SEIFERT 1991), it may be assumed, that underground foraging may play more important part for this species than for *M. ruginodis* and *M. rubra*. Although it shares significant position in the number of ant colonies in this habitat, it is least frequent in foraging activity. If so, it is easy to explain why number of root aphid colonies visited by this species is so significantly higher, than in the case of *Myrmica* species. Opposite situation may refer to *M. ruginodis*, which is significantly more numerous in foraging on the surface than in visiting underground living aphid colonies. Results for *M. rubra*, species of the largest niche width among *Myrmica* ants (SEIFERT 1988), suggest its well developed underground foraging activity.

Interspecific competition among ant species may also serve as the explanation of data obtained in the oak-forest. Research concerning interspecific competition among ants indicate, that there exists three-level hierarchy in their interspecific relations (VEPSÄLÄINEN & PISARSKI 1982, PISARSKI & VEPSÄLÄINEN 1989). The highest level is occupied by aggressive and territorial species, mainly of the genus *Formica* L. (CZECHOWSKI 1977), and the

lowest by submissive species e.g: of the Myrmica Latr. or Leptothorax MAYR genus (VEP-SÄLÄINEN & PISARSKI 1982). The intermediate level is occupied by ants non territorial but defending their food sources eg: Lasius niger (VEPSÄLÄINEN & PISARSKI 1982). Ants belonging to the highest level take over sources of food (in the experiments the baits with sugar) from species of lower level (MARKÓ & CZECHOWSKI 2004, CZECHOWSKI & MARKÓ 2005). As this behaviour affects epigean colonies of aphids (CZECHOWSKI 1985), it may also affect subterranean aphids. In such case, the higher would be the level of the given ant species, the more efficiently it could take over the colonies of aphids. Thus, the colonies of aphids occupied by the lower level ants should be less numerous than those visited by higher level ants. Moreover, ant species, which are in the lower levels of hierarchy are supposed to be more efficient in discovering ephemeral, randomly appearing sources of food (VEPSÄLÄINEN & PISARSKI 1982). On the contrary, higher levelled ants, especially territorial, show ability to discover and monopolise large food source (MARKÓ & CZECHOWSKI 2004). In this respect data concerning activity of foraging workers may indicate interesting differences in aphidophily of particular ant species. It may also be source of data referring to the interspecific hierarchy among ants. Since L. platythorax forages with low intensity it probably defends its aphid colonies or takes them over from lower levelled ant species, while aphid colonies visited by this species are quite frequent. Opposite situation concerns M. ruginodis - it probably does not defend its aphid colonies successfully since aphid colonies visited by this species are least numerous. M. rubra seems to retain intermediate position in this hierarchy, showing no statistical significant differences when comparing obtained data.

My observations pose difficulties in the case of free living root aphids because their cryptic mode of living requires drastic interference in both the condition of aphid host plant (if not its destruction) and the disturbance of the ant behaviour. It is also difficult to observe the competitive behaviour of workers foraging underground and measure their underground activity in the natural conditions. In this respect method applied in the case of oak-forest is far from accuracy, however it may provide interesting data serving for a better explanation of the relations between root aphids and ants.

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