Different-sized oak trees are equally protected by the aphid-tending ants

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Abstract Theoretical models predict that the ecological impacts of ants on plants will vary with the size of the plant, but experimental evidence supporting this hypothesis is lacking. Focusing on aphid-tending ants, *Lasius fuliginosus*, and host oak trees, *Quercus liaotungensis*, we surveyed the density of aphids on the leaves of different-sized trees and the relationship between the densities of aphids and ants on the leaves. We then evaluated the impacts of ants on small (diameter at breast height (DBH) < 5 cm) and large trees (DBH > 25 cm). The field survey showed that the density of ants on leaves was determined by the density of aphids and the latter was similar among different-sized trees; through an ant-exclusion treatment, we found that the impacts of ants on plants, aphids, caterpillars, and galls did not differ by the size of the tree. *L. fuliginosus* had a significant protective effect for *Q. liaotungensis*, but this effect did not convert to enhanced fruit production during the 2-year study period. Considering that size can be used as an indicator of a plant's ontogenetic stage, our results indicate that with similar densities of aphids and, in turn, ants on their canopy, trees at early and later ontogenetic stages are equally protected by aphid-tending ants.

Keywords Ant-aphid mutualism · Ant-plant interaction · Herbivory · Ontogeny · Biotic defense

Introduction

Protective ant-plant interactions have served as model systems in ecological and evolutionary research (Heil and McKey 2003). In those interactions, ants protect plants against herbivores, and in return, plants reward ants either directly with food body, extrafloral nectar, and domatia or indirectly with honeydew secreted by homopterans. Recent meta-analyses confirmed that both the direct and indirect ant-plant interactions have a wide range of ecological impacts, including positive impacts on plants and negative impacts on non-homopteran herbivores (Chamberlain and Holland 2009; Rosumek et al. 2009; Trager et al. 2010; Romero and Krichcheva 2011). However, knowledge on which factors moderate the ecological impacts of ants on plants is still lacking.

The impacts of ants on plants are assumed to vary across the plants' ontogenetic stages (Bronstein 1994; Boege and Marquis 2005; Baker-Méio and Marquis 2011). In direct ant-plant interactions, the impacts of ants on plants in earlier ontogenetic stages are assumed to be weaker because those plants offer limited rewards to the ants (Bronstein 1994; Heil and McKey 2003; Boege and Marquis 2005). The production of rewards like domatia may be particularly costly to plants during their earlier ontogenetic stages (Brouat and McKey 2001). Relatively larger or older plants are more effectively protected because they can better reward the ants (Val and Dirzo 2003; Trager and Bruna 2006). Furthermore, some defensive ants prefer to colonize larger trees as compared with smaller trees, which can lead to the "ontogenetic succession" of the impacts of ants on plants (Palmer et al. 2010; Stanton and Palmer 2011). However, there is also evidence that small myrmecophytic trees can be effectively protected by ants (Fonseca 1994). To our knowledge, no such evidence on the indirect ant-plant interaction mediated by

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homopterans has been reported. Thus, the role of plant size in ant-plant interactions is unclear and should be addressed more explicitly (Baker-Méio and Marquis 2011).

In indirect ant-plant interactions, homopteran is one of the key factors determining the density and ecological impacts of ants on plants (Heil and McKey 2003; Styrsky and Eubanks 2007). Even for myrmecophytic plants, the presence of homopterans can significantly change the impacts of ants on plants (Pringle et al. 2011). Therefore, factors impacting the performance of homopterans such as aphids on plants can also play an important role in indirect ant-plant interactions (Wimp and Whitham 2007; Mooney and Agrawal 2008). Homopterans may prefer plants of different ontogenetic stages. For example, previous researchers have found that aphids are more commonly seen on mature trees and that their fitness is much higher on mature trees as compared with juvenile trees (Kearsley and Whitham 1989). Therefore, if the density of aphids increases with the ontogenetic stages of plants, the impacts of the aphid-tending ants on plants may also be intensified. We currently know little about this issue because most related research has utilized plants of similar sizes as study subjects.

Considering that ant abundance can vary with tree size and that tree size can be used as a visual indicator of a plant's ontogenetic stage, we hypothesized that the impacts of ants on plants and herbivores are stronger for relatively larger trees. The ant *Lasius fuliginosus*, aphid spp. (*Lachnus tropicalis* and *Tuberculatus* sp.), and the oak tree *Quercus liaotungensis* were used to test this hypothesis. *L. fuliginosus*, a typical honeydew-collecting ant species, often has facultative mutualistic relationships with aphid species (Hopkins and Thacker 1999). Three relationships were evaluated to test our hypothesis: (1) the relationship between the densities of ants and aphids on leaves of the oak tree, (2) the relationship between the density of aphids on leaves and tree size, and (3) the ecological influences of aphid-tending ants on different-sized trees.

Materials and methods

Study site

The study area is located in the Beijing Forest Ecosystem Research Station (30°57'29N, 115°25'33E) of the Chinese Ecological Research Network (CERN), 100 km northwest from Beijing City, China. This area has a typically warm, temperate, continental monsoon climate with average annual precipitation of 500–650 mm. The mean annual temperature is 5–10°C. For the study site, we selected a slope (altitude 1,200–1,400 m) in a small watershed that is nearly 2 km south of the station. We chose this site because the distribution of the dominant oak tree, *Quercus liaotungensis*,

ranges from 1,020 to 1,770 m in elevation in this area (Zhang et al. 2006). Therefore, the study site covers the middle area of the distribution range of *Q. liaotungensis*. The study was conducted in a deciduous, broad-leaved forest from April to September in 2009 and 2010. The forest is an oak (*Q. liaotungensis*)-dominated, 80-year-old secondary forest with a few birches (*Betula* spp.), maples (*Acer mono.*), and shrubs (e.g., *Prunus* spp., *Vitex negundo* var. *heterophylla*).

Methods

Relationship between the densities of ants and aphids on leaves

According to previous pitfall trap sampling, *L. fuliginosus* was the only ant species at high abundance at the study site. The relationship between the densities of ants and aphids on leaves was surveyed in June 2009. We randomly located 30 individual trees along a transect line. For each tree, we selected a twig (the terminal part of a branch) with aphids present on the leaves and then counted the total number of aphids and their attending ants on six leaves of the twig (from the tip, we selected the first to the sixth leaves).

The densities of aphids on leaves of different-sized trees

Each month from May to September 2010, we surveyed the densities of aphids on the leaves of about 140 individual trees with DBH ranging from 1.8 to 42.8 cm. For each tree, we randomly selected a twig and counted the total number of aphids on six leaves of the twig (from the tip, we selected the first to the sixth leaves).

The effects of ants on herbivory, fruit production, and herbivore densities

We compared the impacts of ants on trees that varied largely in their DBH: DBH < 5 cm (small trees, with age < 15 years) and DBH > 25 cm (large trees, with age > 45 years). The small trees were saplings, and the large trees were adults. In April 2009, before the growing season of the oak, we randomly located 42 trees (20 small, DBH mean = 3.5 cm, SE = 0.2 cm, ranging from 1.8 to 4.9 cm; 22 large, DBH mean = 30.8 cm, SE = 1.1 cm, ranging from 25 to 42.8 cm), and in April 2010, we randomly located 53 trees (30 small, DBH mean = 3.5 cm, SE = 0.2 cm, ranging from 1.8 to 4.9 cm; 21 large, DBH mean = 31.3 cm, SE = 1.1 cm, ranging from 25 to 42.8 cm) on two transects along the slope. Two branches similar in size, height, and position were chosen on each tree. One was randomly set as an ant-exclusion branch, and the other as a control. An adhesive 5–10 cm in width was smeared at the base of the branch to prevent ant visitation. This adhesive was made of a

polymer resin mixture (Beijing Nonghaha S & T CO. LTD) and was nontoxic, harmless to plants, and non-attractive to insects. The adhesive was re-smearred every 2 months until the end of the study. Any bridges that could allow ants to climb onto ant-excluded branches were cut off.

From late May to September both in 2009 and 2010, the percentage of leaf area loss was calculated on a monthly basis. In each month, one randomly chosen twig was cut from both the ant-excluded and control branches of the focal tree. For each twig, the first to sixth leaves from the tip were collected. During the sampling period, a few branches were dead or missing, so the number of samples for each month was not exactly the same. All of the leaves were scanned by EPSON Perfection 4,870 Photo (EPSON America, Inc., USA) and then used to calculate the percentage of leaf area loss. The herbivore-damaged parts of each leaf were repaired using Adobe Photoshop CS2 (Adobe Systems Inc., USA) according to the expected shape. The original (a) and repaired (b) areas of leaves were calculated with WinFOLIA Basic 2004a (REGENT Instruments Inc., Australia). The percentage of leaf area loss was calculated as $L = (b - a)/b * 100\%$. The anti-herbivory effect of ants was calculated as the difference between the average percentage of leaf area loss on the ant-excluded and control branches of each tree. In September, both 2009 and 2010, the fruiting season of *Q. liaotungensis*, fruit numbers were counted from each ant-excluded and control branch. To exclude the impact of branch size, we counted the fruits from 10 twigs on each branch.

From May to September 2010, we recorded the monthly number of aphids, caterpillars, and galls on the six leaves collected in the leaf loss assessment experiment. The numbers were counted immediately after the leaves were cut off. For each category, the total numbers on the six leaves were used in the data analysis.

Statistical analysis

The relationship between the densities of ants and aphids on leaves was analyzed through regression analysis. A generalized linear regression model was used to test the impacts of DBH, month, and their interaction on the

densities of aphids (proc glm, SAS). The effects of ant exclusion, month, tree size, and their interactions on the percentage of leaf area loss, aphids, caterpillars, and galls were also analyzed by repeated-measures ANOVA (proc mixed, SAS) with month as the repeated variable. The impacts of DBH rank, month, and their interaction on the anti-herbivory effects of ants were also analyzed through repeated-measures ANOVA. We used one-way ANOVA to test for differences among ant-excluded and control branches at each census, with a sequential Bonferroni correction. The leaf loss data were square root transformed to normalize their distribution, and data on the anti-herbivory effects of ants were transformed by $\sqrt{x + 0.03}$. The effect of ants on fruit production was analyzed using the Kruskal–Wallis test. All analyses were conducted using the SAS statistical package (SAS Institute Inc.).

Results

Relationship between the densities of ants and aphids on leaves

There was a clear log-linear relationship between the densities of ants and aphids on the leaves of *Q. liaotungensis* (Fig. 1). The density of ants was largely determined by the density of aphids on leaves: 88% of the variance of ant densities can be explained by the abundance of aphids on leaves.

The densities of aphids on leaves of different-sized trees

The densities of aphids on leaves were not impacted by the size of the tree ($F_{1, 704} = 2.54$, $P = 0.11$; Fig. 1) or the interaction between tree size and month ($F_{4, 704} = 0.47$, $P = 0.76$). Aphid density was significantly influenced by month ($F_{4, 704} = 3.22$, $P = 0.01$).

The effects of ants on herbivory and fruit production

In the two consecutive growing seasons, ants significantly reduced plant herbivory, while tree size and its interaction

Fig. 1 The relationship between the densities of aphids and ants on the leaves of *Q. liaotungensis* ($n = 30$, left) and the density of aphids on the leaves of different-sized trees ($n = 714$, right) with DBH ranging from 1.8 to 42.8 cm. The density refers to the total abundance of individuals per six leaves

with ant-exclusion treatment had no significant effects on herbivory (Table 1). The interaction between ant-exclusion treatment and month significantly impacted herbivory in 2009, but not in 2010. In 2010, month had significant effects on herbivory (Table 1, Fig. 2).

The anti-herbivory effect of ants was not significantly different between the large and small trees in either year (in 2009, $F_{1, 43} = 0.24$, $P = 0.63$; in 2010, $F_{1, 52} = 2.13$, $P = 0.15$; Table 1, Fig. 3). Month significantly influenced the anti-herbivory effect of ants in 2009 ($F_{4, 147} = 3.09$, $P = 0.02$), but not in 2010 ($F_{4, 183} = 1.71$, $P = 0.15$). The interaction between month and DBH rank had no significant impacts on the anti-herbivory effects of ants in either year. During the growing season, ants decreased leaf loss for small trees by 2.43% in 2009 and 1.55% in 2010; for the large trees, ants decreased leaf loss by 1.38 and 2.96% in 2009 and 2010, respectively (Fig. 3). Ant exclusion had no significant effect on fruit production for large or small trees in the 2-year study (Fig. 4).

The effects of ants on herbivore densities on leaves

In general, ants had a significantly positive impact on the density of aphids, a negative impact on caterpillars, and no significant impact on galls. The two groups of trees hold similar densities of aphids, caterpillars, and galls on their leaves. The interactions between tree size and ant-exclusion treatment also had no significant impact on the densities of aphids, caterpillars, and galls (Table 2).

During the growing season, the aphid densities on leaves without ants decreased by 44.8 and 48.1% on the small and large trees, respectively, with no significant between-group difference ($F_{1, 53} = 0.03$, $P = 0.88$). The caterpillar densities decreased by 56.0 and 65.2% on the small and large trees, respectively, with no significant between-group difference ($F_{1, 53} = 0.56$, $P = 0.46$; Fig. 5). Galls started to occur on leaves in June for both the small and large trees. The interaction between tree size and month had a marginally significant impact on the density of galls

Table 1 Results of repeated-measures ANOVA testing the effects of ant exclusion, tree size, month, and their interactions on the leaf loss percentage of *Q. liaotungensis* in 2009 and 2010

Source	2009			2010		
	DF	F Value	Pr > F	DF	F Value	Pr > F
Treatment	1, 41	10.03	0.0029	1, 52	23.67	<.0001
Tree size	1, 41	0.10	0.7562	1, 52	1.03	0.3150
Month	1, 140	1.34	0.2598	4, 183	4.00	0.0039
Treatment*Tree size	1, 41	0.00	0.9976	1, 52	2.58	0.1141
Treatment*Month	4, 140	3.52	0.0090	4, 183	1.46	0.2155
Tree size*Month	4, 140	0.04	0.9974	4, 183	1.83	0.1241
Month*Treatment*Tree size	4, 140	1.48	0.2129	4, 183	1.02	0.3961

Fig. 2 The leaf loss proportion (Mean $\pm$ SE) on the ant-excluded (open symbols) and control (solid symbols) branches of *Q. liaotungensis* according to plant size in 2009 (upper) and 2010 (lower) (*means $P < 0.05$; **means $P < 0.01$; ***means $P < 0.001$)

Fig. 3 The anti-herbivory effect (Mean, SE) of ants on different-sized *Q. liaotungensis* during the growing season in 2009 and 2010 (no significant differences were detected between the small and large trees). *Positive values* mean that ants can reduce the leaf area loss of the plant; *negative values* mean that ants can enhance the leaf area loss of the plant

($F_{4, 187} = 2.44$, $P = 0.07$). On large trees, the impact of ants on galls seemed to be relatively stronger, although the interactive impact of ant-exclusion treatment and tree size on galls was not significant ($F_{1, 53} = 2.85$, $P = 0.10$).

Discussion

Fully evaluating the outcome of ant-plant interaction across the ontogenetic stages of plants is crucial for understanding the maintenance of the mutualism (Palmer et al. 2010). Through monitoring and experimental research, we showed that the ecological impacts of ant-aphid-plant interactions are not impacted by tree size. The small and large trees differed about ninefold in their mean DBH, but were equally protected by ants. In contrast to previous findings on the direct ant-plant interaction (Val and Dirzo 2003, Trager and Bruna 2006, Palmer et al. 2010), this study indicates that trees at different ontogenetic stages may be equally impacted by aphid-tending ants.

Fig. 4 Fruit production on the control and ant-excluded branches of *Q. liaotungensis* in 2009 and 2010 among trees of different sizes

This study demonstrates that trees in early ontogenetic stages can be as effectively protected by aphid-tending ants as mature trees. Previous studies have shown that some aphids, caterpillars, and predators show preferences for different-sized plants (Kearsley and Whitham 1989, Kaitaniemi and Ruohomäki 2001, Boege 2005, Castellanos et al. 2006). However, in our study, aphids on leaves showed no preference for trees with DBH varying from 1.8 to 42.8 cm (Fig. 2). In the aphid-mediated ant-plant interactions, aphid is the key factor that attracts ants (Heil and McKey 2003, Stadler and Dixon 2005, Styrsky and Eubanks 2007). In our study, about 88% of the variation of ant density on leaves can be explained by the density of aphids (Fig. 1). Considering that trees of different sizes hold similar levels of aphids on their leaves (Fig. 2), it is reasonable to predict that the densities of ants on leaves are also similar for trees of different sizes. In the ant-exclusion experiment, we also found that the densities of caterpillars on leaves were similar on different-sized trees (Table 2). For *Q. liaotungensis*, caterpillars are the main herbivores causing the leaf area loss in the study site (Yu et al. 2001). Because the outcome of the ant-herbivore interaction is often determined by the densities of ants and herbivores

Table 2 Results of repeated-measures ANOVA testing the effects of ant exclusion, tree size, month, and their interactions on the densities of aphids, caterpillars, and galls on the leaves of *Q. liaotungensis*

Variables	Source	DF	F value	Pr > F
Aphids	Treatment	1, 53	14.94	0.0003
	Tree size	1, 53	0.02	0.8816
	Month	4, 187	7.60	<.0001
	Treatment*Tree size	1, 53	0.03	0.8682
	Treatment*Month	4, 187	0.37	0.8326
	Tree size*Month	4, 187	0.08	0.9874
	Treatment*Tree size*Month	4, 187	0.36	0.8387
Caterpillars	Treatment	1, 53	12.84	0.0007
	Tree size	1, 53	0.38	0.5386
	Month	4, 187	3.83	0.0051
	Treatment*Tree size	1, 53	0.56	0.4588
	Treatment*Month	4, 187	0.78	0.5386
	Tree size*Month	4, 187	2.60	0.0373
	Treatment*Tree size*Month	4, 187	2.09	0.0837
Galls	Treatment	1, 53	2.26	0.1389
	Tree size	1, 53	2.32	0.1340
	Month	4, 187	1.44	0.2346
	Treatment*Tree size	1, 53	2.85	0.0975
	Treatment*Month	4, 187	0.54	0.6532
	Tree size*Month	4, 187	2.44	0.0669
	Treatment*Tree size*Month	4, 187	0.74	0.5278

Fig. 5 The aphid, caterpillar, and gall abundances on the leaves of the control (solid symbols) and ant-excluded (open symbols) branches in 2009 and 2010 among different-sized *Q. liaotungensis* (*means $P < 0.05$; **means $P < 0.01$)

(Chamberlain and Holland 2008), it is not surprising that the impacts of ants on herbivores and plants are similar among the large and small trees (Table 1, Figs. 2, 3).

Ants had a significant anti-herbivory effect on the host plants during the 2-year study period, but this protective effect did not convert to enhanced plant fitness. The fruit production of small trees, which are at earlier ontogenetic stages, was much lower than that of large trees (Fig. 4). In 2010, there was a coincidence between the abundance of caterpillars and leaf area loss on ant-excluded branches in August for the small trees and in June and July for the large trees (Figs. 2, 5). This suggests that the protective effect mainly results from the ant-caused decrease in caterpillar abundance. In our study, ants had no impact on plant reproduction (Fig. 4). A recent meta-analysis found that plants show certain levels of tolerance to herbivory in ant-plant interactions (Trager et al. 2010). For oaks, a previous study found that a 3% increase in herbivory could cause a significant reduction in fruits (Crawley 1985). In our study, ants reduced herbivory by 1.38–2.96%, but no enhanced fruit production was detected. Nevertheless, the increase in aphid abundance through ant tending can lead to intensified negative impacts on plants, such as infections by plant viruses (Styrsky and Eubanks 2007). A recent meta-analysis found that sucking insects like aphids have significant negative impacts on the growth, reproduction, and photosynthesis of plants (Zvereva et al. 2010). This is a possible reason why ant protection did not convert to enhanced fruit production of the oak. Considering the short time period of fewer than 3 years in our study and most similar studies (Chamberlain and Holland 2009, Rosumek et al. 2009), longer-term studies are needed to illuminate the effect of ants on plants (Palmer et al. 2008, 2010).

Although focusing on the herbivory-reducing effect, we find that the ecological impacts of aphid-tending ants are not impacted by tree size; plant size can still be an important factor impacting ant-plant interactions in many cases. The DBH of the smallest tree we considered in the study is 1.8 cm, and the impact of ants on even smaller trees is unknown. Seedlings are often more susceptible to chewing and sucking insects than saplings and adults (Boege and Marquis 2005, Zvereva et al. 2010). Therefore, it is possible that aphid-tending ants may play a role in the growth of seedlings. Plants with a large amount of resources for ants can influence the distribution patterns of ant nest in field (Wagner and Nicklen 2010). At our study site, *L. fuliginosus* often nests in holes at the basal part of bigger trees, so those large trees may play an important role in the colonization process of *L. fuliginosus*.

In conclusion, from the standpoint of anti-herbivory, we found that trees of different sizes can be equally protected by aphid-tending ants. Recent studies have highlighted the important role of ontogeny in interspecific interactions,

which means that individuals experience significant ontogenetic shifts both in type and strength of their interactions with other species (Boege and Marquis 2005, Palmer et al. 2010, Yang and Rudolf 2010). However, our study does not support this argument in the indirect ant-plant interactions mediated by aphids. To fully understand the role of ontogeny in the ant-plant interaction mediated by aphids, more detailed factors should be evaluated, such as the distribution pattern of different-sized trees and the succession process of ants in a community.

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