

## REPORT

## Relative fitness of aphids: effects of plant quality and ants

B. Stadler,<sup>1\*</sup> A.F.G. Dixon<sup>2</sup>  
and Pavel Kindlmann<sup>3</sup>

<sup>1</sup>Bayreuth Institute for  
Terrestrial Ecosystem Research,  
University of Bayreuth, 95440  
Bayreuth, Germany.

E-mail: bernhard.stadler@  
bitoek.uni-bayreuth.de

<sup>2</sup>School of Biological Sciences,  
University of East Anglia,  
Norwich, NR4 7TJ, U.K. E-mail:  
a.f.dixon@uea.ac.uk

<sup>3</sup>Faculty of Biological Sciences,  
University of South Bohemia,  
Braníšovská 31, CS37005, České  
Budejovice, The Czech Republic.  
E-mail: pavel@entu.cas.cz

\*Correspondence:

E-mail: bernhard.stadler@  
bitoek.uni-bayreuth.de

## Abstract

We investigated the response of four species of aphids (*Metopeurum fuscoviride*, *Brachycaudus cardui*, *Aphis fabae*, and *Macrosiphoniella tanacetaria*) on tansy (*Tanacetum vulgare*) to plant quality and attendance by an ant, *Lasius niger*. The aphids experienced one of four different environments for two consecutive generations. Ant-attendance significantly affected the time needed to reach maximum fecundity only in *Me. fuscoviride* and plant quality in *Me. fuscoviride* and *B. cardui*. Maximum daily fecundity was positively affected by plant quality and the magnitude of the effect was inversely associated with the degree of myrmecophily. Ant-attendance had a positive effect on maximum fecundity only in the obligate myrmecophile, *Me. fuscoviride*. The intrinsic rate of population increase,  $r_m$ , on high quality plants, was lowest for the obligate myrmecophile, intermediate for the facultative myrmecophiles and highest for the unattended species. On high quality plants the fitness of *Me. fuscoviride* was more adversely affected by the developmental stage of the plant and absence of ants than that of *A. fabae* or *Ma. tanacetaria*, which were able to maintain a high relative fitness in all the environments. The implications for aphids experiencing different degrees of ant-attendance and seasonal changes in plant quality are discussed.

## Keywords

Ant-attendance, environmental change, fitness, myrmecophily, *Tanacetum vulgare*, tansy.

*Ecology Letters* (2002) 5: 216–222

## INTRODUCTION

For aphids the environment is highly unpredictable. This is especially true for those that feed on herbaceous plants or grasses. An aphid might develop on plants growing in good or nutrient-poor habitats; many herbaceous plants develop several shoots during a growing season and at any one time may have shoots that range in development from shoot extension to seed set or onset of senescence. Thus, spatially and temporally the members of an aphid clone are likely to encounter very different plant qualities. In addition, the prevailing temperature might affect the exploitation of high plant quality. In the field the fitness of *Cinara pruinosa* feeding on spruce of high quality in spring, at comparatively low temperatures, is equal to that of aphids on low quality plants at high temperatures in summer (Stadler 1997). Thus, the availability of high quality plants might not translate into fitness gains if temperature is low.

A further component in the life of aphids, which is likely to affect fitness, is ants. When associated with ants, aphids may incur direct costs (Stadler & Dixon 1999; Yao *et al.*

2000), associated with the need to maintain a honeydew composition attractive to ants (Fischer & Shingleton 2001; Yao & Akimoto 2001) or indirect costs in the absence of ants in the case of the obligate myrmecophiles (Stadler *et al.* 2001). It is unclear how changing environmental conditions (e.g. plant quality) and different degrees of association with ants interact and how these factors will affect fitness. It is reasonable to assume that obligate myrmecophiles will experience a strong decline in fitness in the absence of ants. However, the magnitude of this effect when feeding on different quality plants at different times in the season is unclear. Facultative myrmecophiles, in contrast, might be more flexible in their response to ant-attendance and the major selection pressure they experience could be the quality of their host plant. Ants do provide service functions like protection from natural enemies (Way 1963; Fowler & Macgarvin 1985), or hygienic services (Nixon 1951) when collecting honeydew, but no service is free. It is now widely acknowledged that these interactions depend on, e.g. the abundance and distribution of a mutualistic partner (Cushman & Addicott 1989; Stadler *et al.* 2001), alternative sugar

sources (Offenberg 2001) or density-dependent processes (Addicott 1979; Breton & Addicott 1992a; Sakata 1995). However, it is not clear what the fitness costs and benefits are in different environments and degrees of association with ants. For example, if the quality of the honeydew is affected by the quality of the host plant, this could have profound consequences for the fitness of facultative and obligate myrmecophiles. Breton & Addicott (1992b) investigated whether host plant quality mediated aphid–ant mutualism in the *Epilobium angustifolium*–*Aphis varians* system. They did not find a positive effect of ants on population growth or any evidence of a plant-mediated effect on aphid–ant interactions. However, they argue strongly for further experiments to disentangle the nature of fitness costs and benefits in mutualistic (tritrophic) associations.

The aim of the present study is to quantify these costs and benefits for four species of aphids feeding on poor and high quality plants of tansy (*Tanacetum vulgare*). Thus, in contrast to other studies, which investigated the effect of specific environmental conditions on aphid performance (Flatt & Weisser 2000; Fischer *et al.* 2001), we compare the fitness of different species of aphids in a range of environments. The aphids used were *Metopeurum fuscoviride*, *Brachycandus cardui*, *Aphis fabae* and *Macrosiphoniella tanacetaria*. Their mutualistic relationships with ants have been well studied. *Me. fuscoviride* is an obligate myrmecophile, *B. cardui* and *A. fabae* are facultative myrmecophiles, with the latter somewhat less intensively attended than *B. cardui* (Fischer *et al.* 2001), and *Ma. tanacetaria* is not attended. All of them feed on the upper parts of tansy, which reduces the obscuring effects of different feeding sites, and allows one to focus on the effects of plant quality and ant-attendance. To facilitate comparison we excluded the effects of variation in temperature, natural enemies and varying degrees of ant-attendance by making this study in a temperature-controlled greenhouse.

## MATERIALS AND METHODS

Stolons of tansy were collected in mid-April 2001 in a field close to Bayreuth University, cleaned of soil and divided into pieces of equal length. In total more than 40 plants were prepared for each treatment. The pieces of stolon were then planted in 2-litre pots in a mixture of sand, gravel and compost in equal volumes (= low quality treatment, LQ), or in compost only (= high quality treatment, HQ), in a greenhouse. In this way four different environments were created for the four species of aphids. All aphids were collected in the field in early spring and stock cultures were initiated for each species/treatment. After 6 weeks of growth at  $23 \pm 3$  °C and 18 : 6 L:D five to eight adults of *Me. fuscoviride*, *B. cardui*, *A. fabae* or *Ma. tanacetaria* were placed onto a single shoot (each species on separate plants) and left

to produce offspring for 24 h, after which the adults were removed. The offspring were reared together until they became adult. On the day of the adult moult single aphids from each cohort were transferred individually to a separate shoot on HQ- and LQ-plants, and their age-specific fecundity ( $m_{x,t}$ , number of offspring produced) and age-specific survival probability ( $l_{x,t}$ ) were monitored every day at the same time for the next 31 days or until the death of an aphid. If the body of a missing aphid was not found it was excluded from the analysis, because the reason for its disappearance was uncertain. Very few aphids were lost in this way. The minimum number of replicates in any analysis was five. A replicate was one individual per shoot. In a strict statistical sense this might not be viewed as a true replicate, because the shoots might be connected to a common stock. However, lateral shoots develop their own roots and in a biological sense may be as variable in quality as shoots of different plants. As mentioned in the introduction, at any particular time there are shoots at different stages of development, which provide a range of environments. Offspring were removed from the shoots every 2nd day to minimize disturbance. As a consequence, the number of offspring produced on a particular day was calculated as the difference between the number of offspring present on that day minus those present the day before ( $N_{t+1} - N_t$ ).

Workers of the ant *Lasius niger* either had access to the aphids or were excluded by means of a strip of sticky tape attached around the base of a shoot. In this way four environments were created for each species of aphid: high plant quality, with ants (HQ + A); high plant quality, ants excluded (HQ – A); low plant quality, with ants (LQ + A); and low plant quality, ants excluded (LQ – A). Ant workers were free to forage in the greenhouse and were given access to aphids (e.g. stock cultures). In addition, four *L. niger* colonies were kept in plexiglass containers and given exclusive access to one species of aphid in order to avoid conflict between ants from different colonies and to avoid the confounding issue of a preference for a specific aphid species. The ant colonies were given access to a different aphid species in the second generation. Ants always readily attended the aphids when access was allowed. Because there was only one adult aphid plus the offspring produced that day, such small colonies were usually attended by only one or two ants. Therefore, this experiment is not suitable to test for different degrees of ant-attendance or ant preferences for different aphid species. It was not possible to prevent ants eating aphids, which may have influenced the observed fecundity of the four species differently. In our experiments we never observed *L. niger* preying on first-instar aphids. However, in order to minimize the likelihood of this happening ants were repeatedly offered freshly killed insects as protein food. All ant colonies developed queens at the end of the experiment, indicating good rearing conditions.

In order to simulate the effect of a seasonal change in plant quality, these treatments were continued for two aphid generations. Individuals of the first generation on HQ-plants developed on plants at the shoot-extension to flower-bud developmental stages, whereas those of the second generation developed on flowering plants. Low quality plants developed more slowly and were only at the flower bud stage at the end of the experiment. Stock cultures were maintained under the same four environmental conditions. The second generation of aphids was again established by allowing actively reproducing individuals from the stock cultures to give birth to offspring for 24 h and then removing the adults. Over the complete experimental period temperature and light conditions were identical to those mentioned above.

#### Data analysis

In order to factor out random variability, fecundity data for each aphid were fitted using the following function:

$$y = a(x - d)e^{-b(x-d)^c} \quad (1)$$

where  $x$  is the age of the aphid,  $y$  is daily fecundity and  $a$ ,  $b$ ,  $c$  and  $d$  are parameters. Parameter  $d$  is the developmental time, while the other parameters determine the shape of the curve and the position of its peak (see eqns 2a and 2b below). Function 1 was chosen, because it is the simplest smooth function that has a triangular shape, typical of the fecundity curves of insects (Kindlmann *et al.* 2001).

The residual sum of squares was minimized using module SOLVER in EXCEL. As a measure of goodness-of-fit, the value of  $R^2$  was calculated, which also indicates the percentage of variation explained by the regression. From the parameter values, the expected age at which maximum fecundity is

achieved,  $X_{\max}$ , and the maximum daily fecundity,  $Y_{\max}$ , were calculated using the formulas

$$X_{\max} = \left(\frac{1}{bc}\right)^{\frac{1}{c}} + d \quad (2a)$$

$$Y_{\max} = a(X_{\max} - d)e^{-b(X_{\max} - d)^c} \quad (2b)$$

These were derived analytically from eqn 1 by equating the first derivative to zero and solving for  $x$ .

The potential instantaneous population growth rate,  $r_m$ , was calculated for each individual using the implicit Euler-Lotka equation

$$\sum_{x=0}^{\infty} m_x l_x e^{-r_m x} = 1, \quad (3)$$

where  $m_x$  is the daily fecundity at age  $x$  and  $l_x$  is the probability of survival to age  $x$ . When calculated for each individual,  $l_x = 1$  during the life of the individual, and  $l_x = 0$  at the instant of its death, so that eqn 3 simplifies to:

$$\sum_{x=0}^T m_x l_x e^{-r_m x} = 1, \quad (4)$$

where  $T$  is the life-span of an individual.

We looked for differences between species for each variable measured ( $X_{\max}$ ,  $Y_{\max}$  and  $r_m$ ) by means of a two-way ANCOVA with the factors: food quality and ants, and the covariate, generation. This approach was used because we were interested in the influence of plant quality and ant-attendance/absence. The developmental stage of the host plants (factor generation) is likely to be similar to variations in host plant quality and was thus factored out. Interspecific comparisons of  $r_m$ -values were done by means of one-way ANOVAS using the Bonferroni correction. Species were used

**Table 1** Results of the ANCOVA multiple comparisons test for four species of aphids. Factors were food quality (FQ) and ant-attendance (ANTS). The effect of different plant developmental stages (two aphid generations) is treated as a covariate. *Macrosiphoniella tanacetaria* is not ant-attended, therefore only one factor, FQ, is relevant for that species;  $X_{\max}$  is the time needed to reach maximum fecundity;  $Y_{\max}$  is the maximum daily fecundity; and  $r_m$  is the intrinsic rate of population increase

Aphid species	Factor	$X_{\max}$		$Y_{\max}$		$r_m$	
		<i>P</i>	d.f.	<i>P</i>	d.f.	<i>P</i>	d.f.
<i>Metopeurum fuscoviride</i>	FQ	< 0.001	1,37	< 0.001	1,37	< 0.001	1,37
	ANTS	0.022	1,37	< 0.001	1,37	< 0.001	1,37
	Interaction	0.034	1,37	< 0.001	1,37	NS	1,37
<i>Brachycaudus cardui</i>	FQ	< 0.001	1,36	< 0.001	1,36	< 0.001	1,36
	ANTS	NS	1,36	NS	1,36	NS	1,36
	Interaction	NS	1,36	NS	1,36	NS	1,36
<i>Aphis fabae</i>	FQ	NS	1,36	< 0.001	1,36	< 0.001	1,36
	ANTS	NS	1,36	NS	1,36	NS	1,36
	Interaction	NS	1,36	NS	1,36	NS	1,36
<i>Macrosiphoniella tanacetaria</i>	FQ	NS	1,17	< 0.001	1,17	< 0.001	1,17

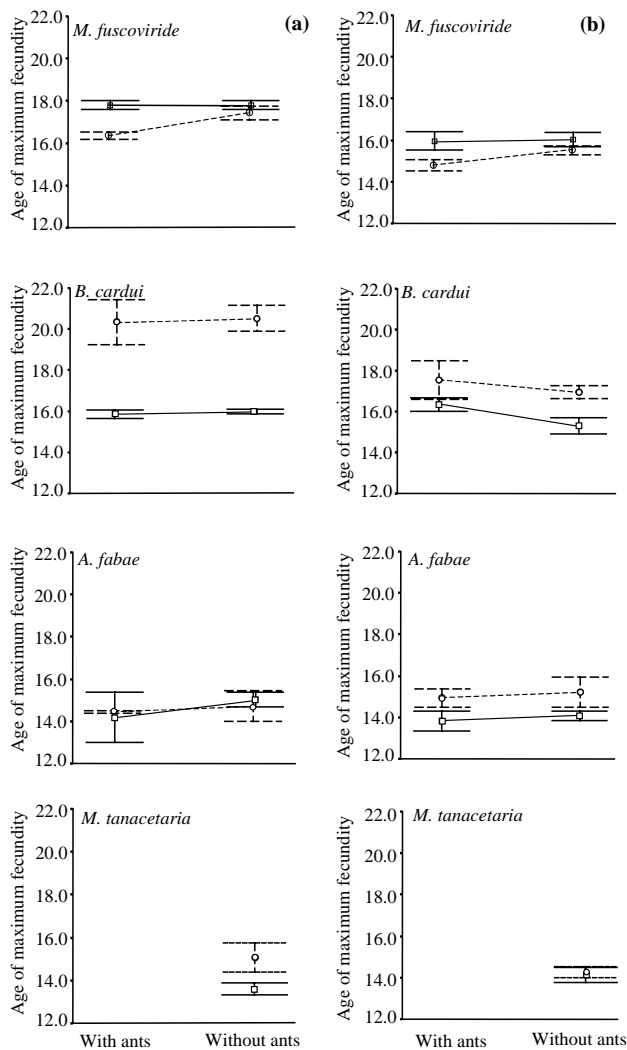
as factors and each treatment was analysed separately (HQ + A, HQ - A, LQ + A, LQ - A) for both generations.

**RESULTS**

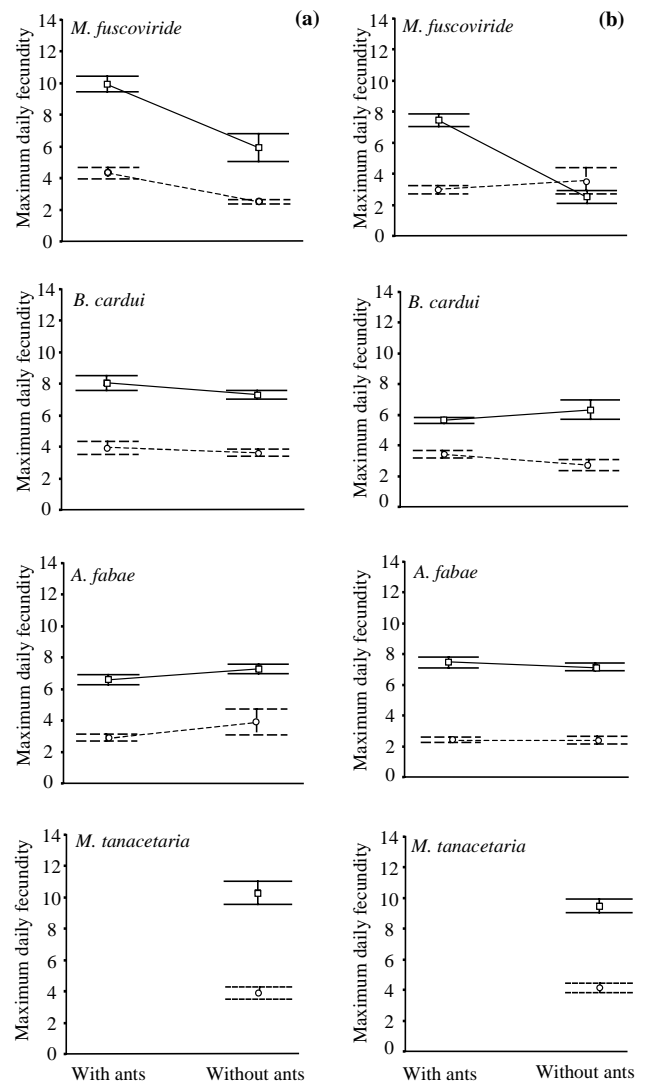
The function 1 fitted the data very well. On average, it explained 71.2% of the variability in the life-history data. Figure 1 and Table 1 show the differences in the age at which maximum fecundity was achieved ( $X_{max}$ ) both between aphids reared on high vs. low quality plants and between those ant-attended and not ant-attended. Age at which maximum fecundity was significantly

delayed when the aphids were reared on low quality plants. This is mainly because of the results for *B. cardui* and in part for *Me. fuscoviride* on plants at the shoot extension stage. The effect of ants on  $X_{max}$  was only significant in the obligate myrmecophile, *Me. fuscoviride*.

In contrast to the age at which maximum fecundity was achieved, the maximum fecundity ( $Y_{max}$ ) itself was much more strongly affected by the experimental design (Fig. 2, Table 1). In all species, fecundity was consistently and significantly lower in individuals reared on low quality plants compared to those reared on high quality plants, except for the second generation of *Me. fuscoviride*, when not



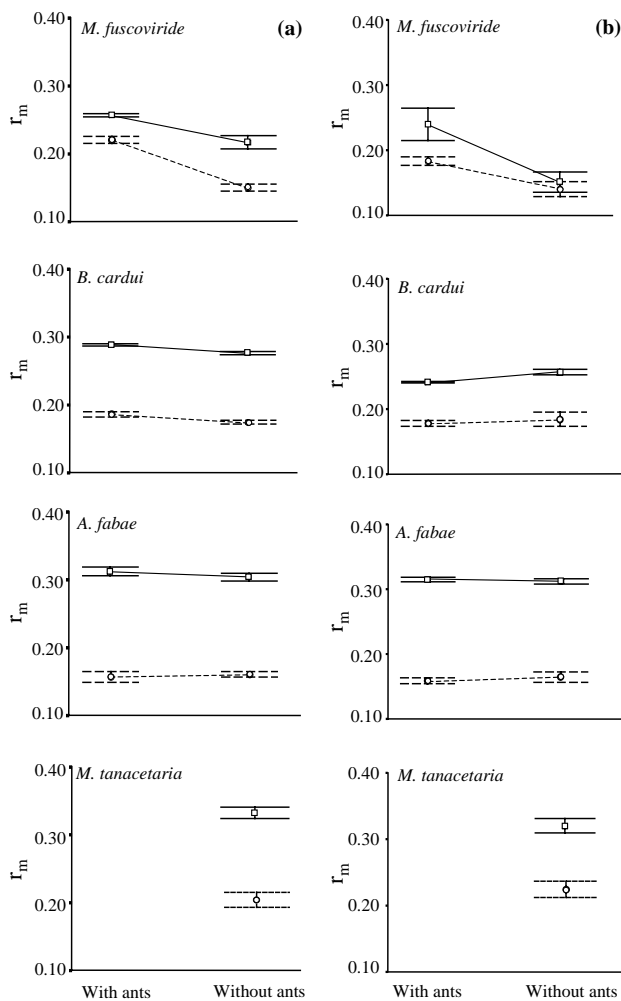
**Figure 1** Average age at which maximum fecundity was achieved (calculated from eqn 2a) for individual aphid species reared on high (solid lines) and low (dashed lines) quality plants, when ant-attended and not attended; (a) plants at the shooting and (b) flowering stages of development (means  $\pm$  SE).



**Figure 2** Average maximum daily fecundity (calculated from eqn 2b) for individual aphid species reared on high (solid lines) and low (dashed lines) quality plants, when ant-attended and not attended; (a) plants at the shooting, and (b) flowering stages of development (means  $\pm$  SE).

ant-attended. In all species, the total number of offspring produced declined by more than 50% when the aphids were feeding on low quality plants. Maximum daily fecundity was lower when aphids were not ant-attended in *Me. fuscoviride*, but not in *B. cardui* and *A. fabae* (no significant effect of the factor ants; Fig. 2, Table 1). In the first generation of *A. fabae* the maximum daily fecundity when not ant-attended tended to be higher than when ant-attended (Fig. 2a). Interaction terms between food quality and ant-attendance were significant only in *Me. fuscoviride*, which is a consequence of the strong drop in maximum fecundity when not ant-attended, especially on plants at the shooting stage (Fig. 2b).

A similar situation occurred when the impact of rearing aphids on high and low quality plants with and without ants,



**Figure 3** Potential instantaneous growth rate,  $r_m$  (calculated from eqn 4) for individual aphid species reared on high (solid lines) and low (dashed lines) quality plants, when ant-attended and not ant-attended; (a) plants at the shooting, and (b) flowering stages of development (means  $\pm$  SE).

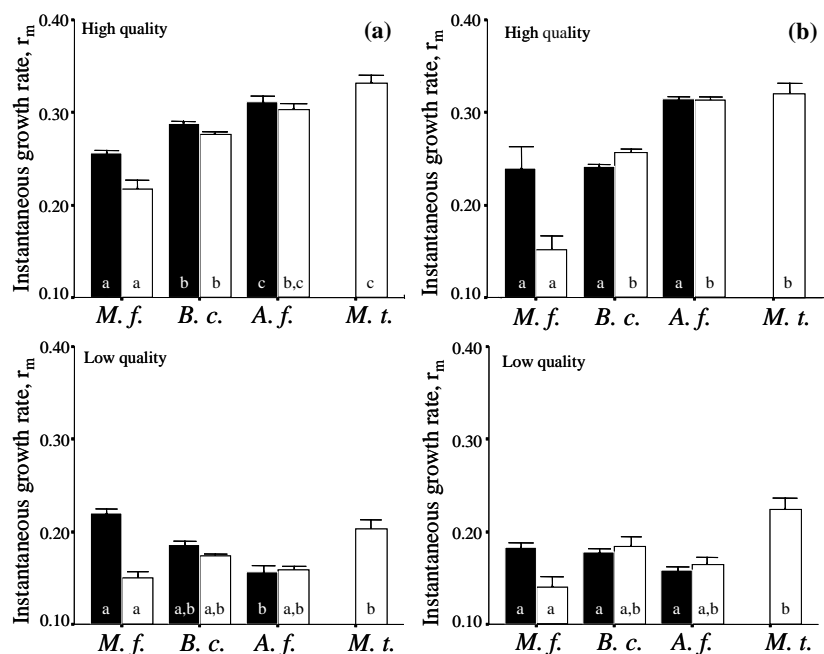
on an aphid's potential instantaneous population growth rate ( $r_m$ ) (which includes adult survival) was compared (Fig. 3, Table 1). The instantaneous population growth rate was consistently and significantly lower in individuals reared on low quality plants. Again, the only exception was the second generation of *Me. fuscoviride*, in which there was no difference between the fitness of aphids reared on HQ- and LQ-plants when not ant-attended. In general, with declining degree of myrmecophily, the effect of low plant quality became a more dominant factor reducing fitness. For example, when  $r_m$ -values were combined from the +A and -A treatments of the shooting stage, low plant qualities reduced the fitness of *Me. fuscoviride* by 14.1%, of *B. cardui* by 35.4%, of *A. fabae* by 50.0% and of *Ma. tanacetaria* by 38.9%.

The effect of ant-attendance on fitness was again most pronounced in *Me. fuscoviride*, and not present in *A. fabae* and *B. cardui* (Fig. 3, Table 1). The proportional increase in  $r_m$  when ant-attended was always much larger in *Me. fuscoviride*, especially when these aphids were reared on low quality plants at the shoot extension stage (Fig. 3a). Interaction terms were not significant.

The relative changes in  $r_m$ -values across species, experiencing different treatments were compared in Fig. 4a,b. For aphids on HQ-plants at the shoot extension stage the potential instantaneous population growth rates showed a significant increase from the obligate myrmecophile, *Me. fuscoviride*, to the unattended aphid, *Ma. tanacetaria*. The same trend is seen for aphids feeding on hosts at the flowering stage, although the differences were not significant at  $P < 0.001$ . Overall, when combining the  $r_m$ -values from the HQ and LQ treatment, e.g. at the shooting stage (Fig. 4a), the fitness increase due to ant-attendance was 23.5% in *Me. fuscoviride*, 5.4% in *B. cardui*, but only 0.3% in *A. fabae*. The facultatively attended aphid species suffered larger costs on LQ-plants when attended by *L. niger* than the obligate myrmecophile *Me. fuscoviride* (black columns in Fig. 4, HQ vs. LQ treatment). In absolute terms *Ma. tanacetaria* did best in three out of the four environments.

**Discussion**

The realized fitness of aphids is subject to a number of environmental constraints. Two of them, plant quality and ant-attendance have been investigated here. Plant quality and ants had relatively little effect on the age at which the aphids achieved maximum fecundity (Fig. 1), but greatly affected the maximum number of offspring they produced (Fig. 2). Therefore, age at maximum fecundity seems to be an invariant life-history characteristic for most species. On high quality plants the aphids produced most offspring and ant-attendance had the greatest positive effect on the obligate myrmecophile, *Me. fuscoviride*. Similar trends were observed in the intrinsic rates of population increase with



**Figure 4** Potential instantaneous growth rate,  $r_m$  (calculated from eqn 4) for individual aphid species reared on high and low quality plants when attended (black columns) and not attended (white columns) by *Lasius niger*; (a) shooting stage (b) flowering stage. Different letters within a particular group of columns (black, white) indicate statistical differences between species at  $P < 0.001$ , ANOVA, Bonferroni correction (means  $\pm$  SE).

aphids on HQ-plants always showing significantly higher  $r_m$ -values than individuals on LQ-plants. It is interesting to note that with decline in the strength of an aphid's association with ants the effect of plant quality increases. For example, the relative drop in fitness when feeding on HQ compared to LQ-quality plants was much larger in *Ma. tanacetaria* than in *Me. fuscoviride* (Fig. 3). Comparing fitness achieved in the best environment for each species, the potential population growth rates increased with decline in the strength of myrmecophily (Fig. 4). This might indicate that there are physiological costs to producing more or better honeydew. *Metopeurum fuscoviride*, e.g. is the only aphid that produces trisaccharides. It also produces the most honeydew (Völkl *et al.* 1999). Stadler & Dixon (1998) proposed a mechanism to account for the cost of the ant-attendance they observed in *A. fabae* on *Cirsium arvense*. In order to increase the production of honeydew when ant-attended, aphids have to feed at a rate that exceeds the optimum, and this reduces the efficiency with which they can assimilate amino-nitrogen from their food. In addition, Yao & Akimoto (2001) and Fischer & Shingleton (2001) showed that ant-attendance affects the sugar composition of honeydew in *Tuberculatus quercicola* and two *Chaitophorus* species, resulting in a reduced performance when ant-attended. Currently we do not know whether the fact that obligate myrmecophiles are less affected by plant quality

than facultative and unattended aphids, is mirrored in the composition of the honeydew of the aphids. We suspect that the composition of honeydew, when feeding on different quality plants, changes in different ways. For example, on low quality plants obligate myrmecophiles might reduce the costs of producing 'attractive' honeydew in order to maintain rather constant growth rates there, whereas unattended aphids have no such option to redirect resources. Thus we would predict bigger changes in the composition of the honeydew of obligate myrmecophiles, than of facultative myrmecophiles and unattended aphids, when feeding on plants of low quality. Unattended *Me. fuscoviride* feeding on HQ-plants at the shoot extension stage had approximately the same fitness as ant-attended individuals on low quality plants, which again indicates the relative importance of ants for this species. For individuals feeding on plants at the flowering stage the drop in fitness on unattended HQ-plants was even more pronounced in this species and fitness was not significantly different from that of aphids on LQ-plants (Fig. 3, top right). A likely reason is that when feeding on plants at the flowering stage this aphid had greater difficulty in disposing of honeydew. When not ant-attended they often became covered in honeydew or gave birth to dead offspring. No such difficulties were observed on the shooting stage. This implies that late in the season *Me. fuscoviride* becomes more

dependent on ants and/or that the composition of honeydew changes. None of the other species showed a stronger decline in fitness than *Me. fuscoviride* on HQ-plants when not ant-attended.

*Aphis fabae* and *Ma. tanacetaria* were able to maintain their population growth rates in the second generation, both on HQ- and LQ-plants (Fig. 4). The second generation of these aphids, unlike *Me. fuscoviride*, readily colonize newly developing secondary shoots, which may temporarily be of better quality. In contrast, *Me. fuscoviride* is relatively immobile when tended by ants and this may put them at risk of being killed if they have to produce less honeydew. Thus, the increased fitness costs incurred especially by *Me. fuscoviride* relative to the other aphid species in the course of the development of a host-plant may be because it cannot easily move to adjacent primary or secondary shoots.

Excluding the confounding effects of temperature and natural enemies reveals a complex mixture of costs and benefits for aphids when living on plants of different qualities and when entering into an association with ants. Because fitness is a relative measure, knowledge of the magnitude of the change in this trait for aphids experiencing changing environmental conditions should help us to understand the role of costs and benefits in the evolution of myrmecophily in aphids.

## ACKNOWLEDGEMENTS

We are indebted to two anonymous referees for suggestions and comments. Iva Dostalkova helped us with the statistics. Financial support was given by the German Ministry for Research and Technology (Fördernummer: BMBF No. PT BEO 51-0339476C). The European Science Foundation (programme LINKECOL) provided a travel grant to PK.

## REFERENCES

- Addicott, J.F. (1979). A multispecies aphid–ant association: density dependence and species specific effects. *Can. J. Zool.*, **57**, 558–569.
- Breton, L.M. & Addicott, J.F. (1992a). Density-dependent mutualism in an aphid–ant interaction. *Ecology*, **73**, 2175–2180.
- Breton, L.M. & Addicott, J.F. (1992b). Does host-plant quality mediate aphid–ant mutualism? *Oikos*, **63**, 253–259.
- Cushman, J.H. & Addicott, J.F. (1989). Intra- and interspecific competition for mutualists: ants as a limited and limiting resource for aphids. *Oecologia*, **79**, 315–321.
- Fischer, M.K., Hoffmann, K.H. & Völkl, W. (2001). Competition for mutualists in an ant–homopteran interaction mediated by hierarchies of ant attendance. *Oikos*, **92**, 531–541.
- Fischer, M.K. & Shingleton, A.W. (2001). Host plant and ants influence the honeydew sugar composition of aphids. *Funct. Ecol.*, **15**, 544–550.
- Flatt, T. & Weisser, W.W. (2000). The effects of mutualistic ants on aphid life history traits. *Ecology*, **81**, 3522–3529.
- Fowler, S.V. & Macgarvin, M. (1985). The impact of hairy wood ants, *Formica lugubris*, on the guild structure of herbivorous insects on birch, *Betula pubescens*. *J. Anim. Ecol.*, **54**, 847–855.
- Kindlmann, P., Dixon, A.F.G. & Dostálková, I. (2001). Role of ageing and temperature in shaping reaction norms and fecundity functions in insects. *J. Evol. Biol.*, **14**, 835–840.
- Nixon, G.E.J. (1951). *The Association of Ants with Aphids and Coccids*. Commonwealth Institute of Entomology, London, pp. 1–36.
- Offenberg, J. (2001). Balancing between mutualism and exploitation: the symbiotic interaction between *Lasius* ants and aphids. *Behav. Ecol. Sociobiol.*, **49**, 304–310.
- Sakata, H. (1995). Density-dependent predation of the ant *Lasius niger* (Hymenoptera: Formicidae) on two attended aphids *Lachnus tropicalis* and *Myzocallis kuricola* (Homoptera: Aphididae). *Res. Pop. Ecol.*, **37**, 159–164.
- Stadler, B. (1997). Egg distribution and survival of *Cinara pilicornis* (Hartig) on damaged and undamaged Norway spruce (*Picea abies*) (L.) Karst. *J. Appl. Entomol.*, **121**, 71–75.
- Stadler, B. & Dixon, A.F.G. (1998). Cost of ant-attendance for aphids. *J. Anim. Ecol.*, **67**, 454–459.
- Stadler, B. & Dixon, A.F.G. (1999). Ant attendance in aphids: why different degrees of myrmecophily? *Ecol. Entomol.*, **24**, 363–369.
- Stadler, B., Fiedler, K., Kawecki, T. & Weisser, W.W. (2001). Costs and benefits in for phytophagous myrmecophiles: when ants are not always available. *Oikos*, **92**, 467–478.
- Völkl, W., Woodring, J., Fischer, M., Lorenz, M.W. & Hoffmann, K.H. (1999). Ant–aphid mutualism: the impact of honeydew production and honeydew sugar composition on ant preferences. *Oecologia*, **118**, 483–491.
- Way, M.J. (1963). Mutualism between ants and honeydew-producing Homoptera. *Ann. Rev. Entomol.*, **8**, 307–344.
- Yao, I. & Akimoto, S. (2001). Ant attendance changes the sugar composition of the honeydew of the drepanosiphid aphid *Tuberculatus quercicola*. *Oecologia*, **128**, 36–43.
- Yao, I., Shibao, H. & Akimoto, S. (2000). Costs and benefits of ant attendance to the drepanosiphid aphid *Tuberculatus quercicola*. *Oikos*, **89**, 3–10.

Editor, S.D. Hacker

Manuscript received 21 September 2001

First decision made 2 November 2001

Second decision made 23 November 2001

Manuscript accepted 5 December 2001