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The effect of plant quality and temperature on the fitness of *Cinara pruinosa* (Sternorrhyncha: Lachnidae) on Norway spruce

BERNHARD STADLER

Institute for Terrestrial Ecosystem Research, University of Bayreuth, 95440 Bayreuth, Germany;
e-mail: bernhard.stadler@bitoek.uni-bayreuth.de

Lachnidae, *Cinara*, environmental change, fitness, plant quality, temperature

Abstract. Many aspects in the life-history of aphids are critically dependent on the quality of their host plants and prevailing temperature. Therefore, the fitness of an aphid clone will depend on these parameters and will determine its ecological and ultimately its evolutionary success. Measuring and calculating the fitness of an organism in a natural environment is an important but also a difficult task, as many parameters that code for fitness need special assumptions, e.g. a uniform environment or stable age distribution. In this study, three aspects of environmental variability were considered: (a) the nutritional supply of the host plants (high- and low-quality plants), (b) the changes in host plant quality due to the endogenic life cycle of the host and (c) constant and variable temperature regimes. For each of three successive generations of *Cinara pruinosa* (Hartig) feeding on *Picea abies* (L.) Karsten, the change in fitness was determined by calculating the intrinsic rate of increase (r_m) and expected total reproductive success (ETRS) when the aphids were reared under greenhouse (constant temperature) or field (variable temperature) conditions. Nutritional supply, plant life cycle and temperature affected the fitness of aphids, with fluctuating temperatures obscuring the effects. As a consequence, differences in fitness values among treatments were most pronounced under the constant temperature regime of a greenhouse and less marked in the field. If plant quality varies but not temperature, the contribution to clonal fitness of early generations is overestimated in comparison to later generations. The limitations and consequences for the interpretation of fitness values of aphids are discussed.

INTRODUCTION

Central to the idea of natural selection and adaptation is the notion of fitness. The fitness an aphid clone is able to achieve in a given habitat or under variable environmental conditions depends on the ability of individual aphids of a particular generation to respond to such changes. However, it has been found notoriously difficult to find a universal measurement of fitness as all indexes appear to require either particular assumptions or data that are difficult to obtain (Roff, 1992; Stearns, 1992; Kozlowski, 1993). Therefore, any definition of fitness is regarded primarily as a problem-solving tool (Stearns, 1992) that may help to characterise some consequences of selection pressures on the performance of a population. The Lotka-Euler equation or intrinsic rate of increase (r_m) defines fitness for a population in a uniform environment and in a stable age distribution. Therefore, and for practical reasons, many r_m-values are determined in constant environments, e.g. at a particular temperature (see Gaston, 1988, for a review of r_m-values for many insect taxa). Aphids are usually short-lived and assumed to have developed generation-specific adaptations to their hosts (Wellings et al., 1980; Dixon, 1985; Stadler, 1992). Yet, as clonal organisms, individuals of any generation may encounter a range of host plants of different qualities due to a variable supply of the hosts with nutrients in different habitats, the endogenic changes in the life-cycle of their host plants or due to temperature fluctuations. Many species of the tribe *Cinarini*, such as *Cinara pruinosa* (Hartig) on Norway spruce are rather large and live for more than four weeks if they are not killed by natural enemies. They usually produce four to five generations in central Europe (Scheurer, 1964) depending on the parameters mentioned above. However, it is difficult to estimate the proportion of the fitness a particular individual will contribute to the fitness of a clone if the environmental parameters are not constant. Equally, the type of fitness definition used could influence predictions about life-history evolution (Benton & Grant, 1996). Aphids show a pronounced sensitivity to environmental changes (Hille Ris Lambers, 1966; Dixon & Glen, 1971; Watt, 1979; Leather & Dixon, 1981; Grüber & Dixon, 1988; Walters et al., 1988; Stadler, 1992). How this sensitivity to plant quality and temperature will translate to a change in fitness of a clonal organism is the objective of this paper.

With the help of two fitness measurements (r_m, as a deterministic measurement of fitness and expected total reproductive success as a dynamic measurement of fitness) that characterise the performance of aphids under locally constant (greenhouse) and variable (field) environmental conditions, the effect of plant quality and temperature is investigated.

MATERIAL AND METHODS

Fitness measurement of *C. pruinosa*

Ten 4-year old Norway spruce seedlings (non-clonal) were planted in pots either filled with high-quality soil (5 vol. compost soil, 2 vol. pumice, 2 vol. lava, 2 vol. peat-soil, 1 vol. loess, 2.5 kg/m^3 Osmocote fertilizer) or in sand without nutrients, in which the plants developed marked needle yellowing. These two extreme types of soil were chosen to follow aphid performance on trees of high and low qualities, similar to those they are most likely to encounter under natural conditions. After transfer to a greenhouse, each plant was infested with a single new born aphid (first instar larva), which was then reared to maturity. These aphids were offspring of a single fundatrix of *C. pruinosa* in order to investigate the phenotypic response of a clone to plant quality and temperature. On reaching maturity, the number of offspring produced at a particular age and the age specific survival rates were recorded for each individual. Each day, the newly born offspring were removed from the spruce seedlings. When offspring production ceased, one offspring was left on each tree which was again reared to maturity with age-specific survival and reproduction measured as in the previous generation. If an aphid failed to leave an offspring on a seedling that could be reared in the next generation, a first instar larva from another adult of the same clone was transferred to that tree prior to the start of the next generation. However, only aphids from the same treatment (high- or low-quality plants) were used as substitutes to account for possible maternal effects. In this way, three consecutive aphid generations were reared. The first generation developed during bud burst, the second during shoot elongation and the third after the shoot growth ceased. The temperature in the greenhouse was 19 ± 2°C and plants were watered according to their demands. To investigate the effect of variable temperatures during growth and reproduction on the fitness of aphids, a parallel treatment was set up at the experimental plot of the institute. Again, three consecutive generations of aphids were reared on high and low-quality plants and age-specific survival and reproduction measured. The temperature was recorded continuously two meters above ground. Aphids which disappeared before offspring reproduction were not substituted and not included in the analysis because it could not be determined whether they were lost by walking off the host plant or due to natural enemies. Lost aphids were only substituted prior to the rearing of the next generation.

Fitness calculations

The intrinsic rate of increase (r_m) was calculated for each aphid generation on plants of each treatment using the Lotka-Euler equation: $\Sigma m_x \cdot l_x \cdot e^{r_m x} = 1$, where l_x = age specific survival rate; m_x = age specific reproduction. The 95% confidence intervals were determined using a Jackknife method (Tukey, 1958;

Meyer et al., 1986; Hulting et al., 1990). For calculating statistical differences between r_m-values of aphids feeding on plants of different qualities, I followed Sachs (1984).

To determine the contribution of each age class to fitness, the expected total reproductive success (ETRS) was calculated. This was done by discounting offspring born to mothers of a particular age class by using the following equation: ETRS = $\frac{l(t+1,x)}{l(t,x)}[m(t,x)\exp^{r_m(x)(T-t)} + f(t+1,x)]$ (Stadler et al., 1994), where $l(t+1,x)/l(t,x)$ denotes the probability that an aphid survives the next day on a plant of developmental state x. $m(t,x)$ is the number of offspring produced on day t and $f(t+1,x)$ gives the fitness a mother gains on the following day. The discounting factor $\exp[r_m(x)(T-t)]$ accounts for the fact that offspring born early in adult life are of greater value to mothers than offspring born late, as the former are likely the first to reproduce. In this equation, local r_m's become local discount factors as generations are assumed to be discrete. T is the last day of life of the aphids in a particular generation.

RESULTS

In the greenhouse, the first generation of *C. pruinosa* started to reproduce on high-quality host plants on day 15 and reached the highest mean values in offspring numbers (m_x) three days after the beginning of reproduction (Fig. 1a). The number of offspring produced per day then declined until day 34. Aphids feeding on low-quality trees started to reproduce on day 16 of adult life and reached their maximum reproductive rate four days later. Offspring production ceased four weeks after birth. Age specific survival (l_x) of the aphids in both treatment groups ran almost parallel. The first aphids died 3.5 weeks after birth, the last one week later. The second generation of *C. pruinosa* invested significantly less energy in offspring. A maximum of three offspring was produced by aphids feeding on the high-quality plants two days after the beginning of reproduction, but for most of their adult life they only produced a single offspring per day. Aphids on poor quality plants did not show a pronounced peak in offspring production. In contrast to generation one, the second generation lived ten days longer. In the third generation, when shoot elongation had ceased, very few offspring were produced in both treatments, with the aphids on low-quality plants starting to reproduce more than a week after adult moult. Aphids on low-quality plants tended to live a few days longer than those on high-quality plants.

In the parallel experiment conducted under field conditions with fluctuating temperatures, similar differences between offspring production and survival were observed between aphids feeding on high- or low-quality plants (Fig. 1b). However, there were some noteworthy differences between the field and the greenhouse results. In generations one and two, offspring production started three weeks after birth. In generation one, however, the aphids showed a marked depression in their reproductive performance resulting from a cold period in mid/end of May. This effect, however, was less marked in aphids feeding on low-quality plants. The third generation of *C. pruinosa* feeding on plants, which had ceased shoot growth, started offspring production two days after adult moult, most likely a consequence of the higher temperatures at that time. However, they only lived for about one month and produced few offspring. No sexuals were produced in either experiment.

In Table 1, the generation-specific r_m-values and length of shoot growth are given for all six treatments. In the greenhouse, highest r_m-values were recorded at the time of bud burst and then declined. On low-quality trees, the highest values were also recorded for the first generation of aphids on actively growing buds. Statistically significant differences in r_m-values between aphids feeding on high and low-quality plants were only observed in the second and third generations (both greenhouse and field treatments) indicating that the

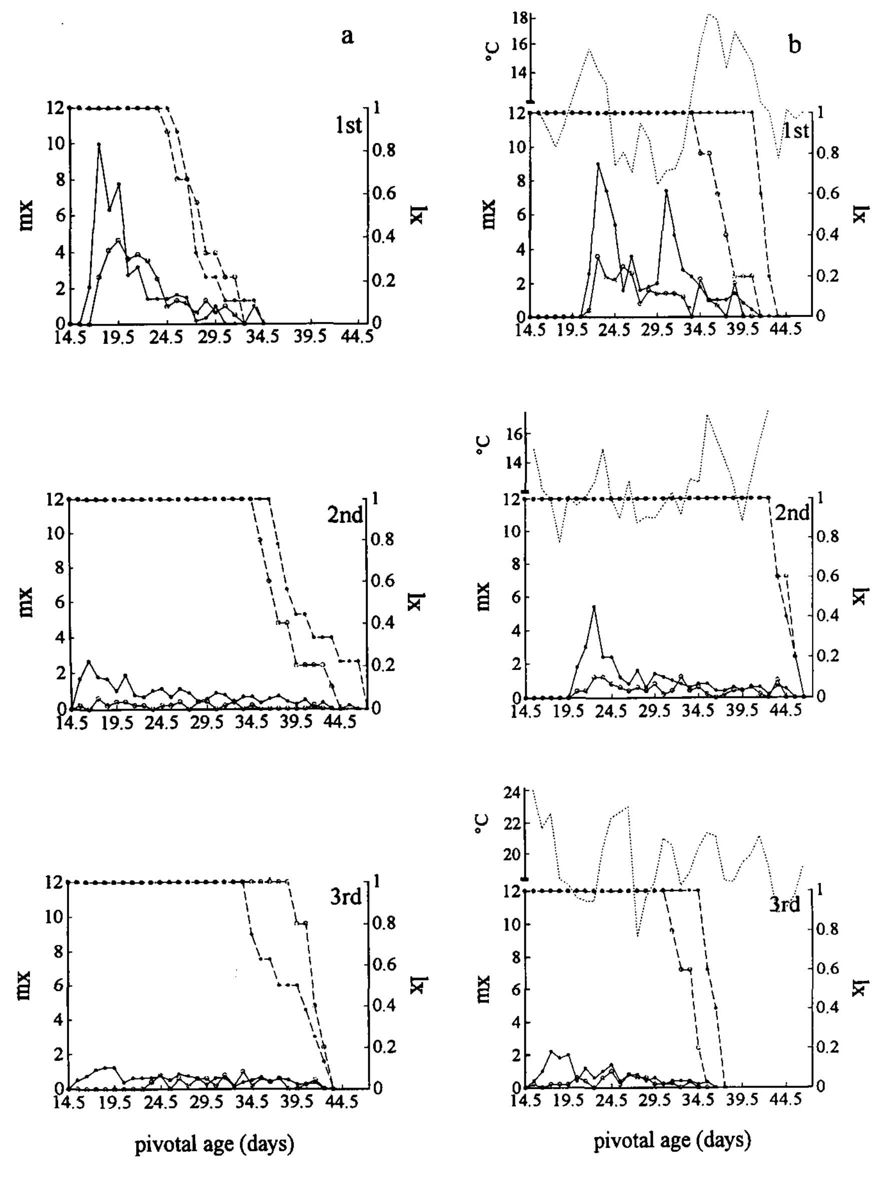

Fig. 1. Age-specific reproduction (m_x) (solid lines) and age-specific survival (l_x) (dashed lines) of *C. pruinosa* reared for three consecutive generations either on high (●) or low (○) quality plants. Series a – greenhouse (19 ± 2°C), 70% r.h.; Series b – field conditions with fluctuating temperatures. The experiments started in May (first generation) and ended in August (third generation). The first generation of aphids developed during bud burst, the second generation during shoot elongation and the third generation after shoot elongation ceased. Dotted lines give the mean daily temperature from continuous records.

decline in host quality occurs more quickly on seedlings that had a low nutritional supply. In the field, the effect of deteriorating plant quality, associated with the endogenic cycle of the host plant, was alleviated by the higher temperatures prevailing during summer. As a consequence, the range of r_m-values between successive generations of a particular treatment was more pronounced in the greenhouse. Differences in r_m-values between generations of a particular treatment were only statistically significant between the first and the following generations. The only exception was the low-quality treatment in the field, where no seasonal trend was found. Fluctuating temperatures obscured a pronounced seasonal decline in fitness values because aphids of the third generation started to reproduce one week earlier than aphids of the first two generations (see Fig. 1b).

TABLE 1. Intrinsic rate of increase (r_m) of *C. pruinosa* in three consecutive generations either on high- or low-quality spruce trees at different developmental stages (generation 1 – bud burst; 2 – shoot extension; 3 – end of shoot growth). 95% confidence intervals (CI) were calculated with the Jackknife procedure. Pairs of values in a row or column marked with an asterisk indicate statistical differences at $P < 0.01$.

Generation	Greenhouse (22°C)			Field (fluctuating temperature)		
	1	2	3	1	2	3
High-quality treatment						
n	9	9	8	5	5	5
Shoot growth (cm)	4.5	3.5	1	3	7.5	2
$r_m \pm$ 95% CI	0.19±0.01*	0.15±0.01 n.s.	0.12±0.02	0.15±0.01*	0.13±0.01 n.s.	0.13±0.01
	n.s.	*	*	n.s.	*	*
Low-quality treatment						
n	9	5	5	5	5	5
Shoot growth (cm)	1	1	0.5	1	1.5	0.5
$r_m \pm$ 95% CI	0.16±0.02 *	0.07±0.04 n.s.	0.07±0.02	0.12±0.03 n.s.	0.09±0.01 n.s.	0.08±0.01

The expected total reproductive success (ETRS) was used as an additional measurement of fitness to follow the contribution of particular age classes to the overall fitness. As with the r_m-values, the value of an offspring born now is compared with the value of an offspring born in the future. Offspring of generation one tend to be of greater value to a clone than offspring born to later generations (Fig. 2a–d). However, the magnitude to which that is true is different for different treatments. The difference in the ETRS of generation two and three relative to generation one was 87.0 ± 2.5% and 96.3 ± 0.8% on high-quality plants (Fig. 2a), and 98.9 ± 0.1% and 98.7 ± 0.3% on low-quality plants (Fig. 2b), in a constant temperature environment (fitness differences as percentage mean ± S.D. during the first five days of adult life). Under field conditions, these differences in fitness were consistently smaller: 64.2 ± 0.0% and 71.8 ± 8.1% on high-quality plants (Fig. 2c), and 78.4 ± 0.0% and 88.3 ± 0.8% on low-quality plants (Fig. 2d). Aphids that feed on plants with a poor nutritional supply always contribute less to the fitness of a clone than aphids of the same generations on high-quality plants, regardless of the prevailing temperature. Because the differences in ETRS of generation two and three relative to generation one are larger when temperatures are constant, both for the high-quality treatment and low-quality treatment (Fig. 2a,b compared to Fig. 2c,d), the contribution of generation one to the overall fitness might be overestimated while the contribution of later generations are underestimated. That is, when the temperature is held constant, the influence of plant quality on aphid fitness becomes larger than it actually is in nature.

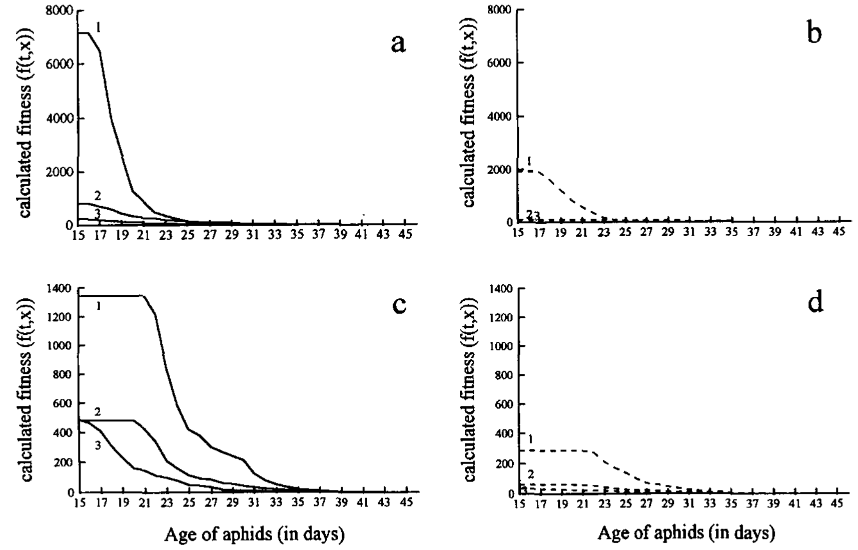

Fig. 2. Calculated fitness as expected total reproductive success (ETRS) for aphids on high-quality plants (a, c) and low-quality plants (b, d) from the greenhouse (a, b) and field experiments (c, d).

DISCUSSION

Producing offspring early in adult life is a central dogma for the fitness of aphids. The short-term measurement of numerical dominance can be approximated in several ways, for example by using the intrinsic rate of increase as one of the most prominent measurements (Partridge & Harvey, 1988) or a fitness function related to the concept of "reproductive value" (Fisher, 1930; Mangel & Clark, 1988). Ideally, for clonal organisms, such as aphids, the rate of increase should be calculated across all habitats the members of a clone encounter while considering the distribution of the offspring between habitats (Houston & McNamara, 1992; Sibly, 1995) or the sequence of different morphs (apterous, alates) (Weisser & Stadler, 1994). Due to the phenotypic plasticity of aphids, even within a particular generation of a clone, there is a range of possible fitness values that can be realised (Stadler et al., 1994). Therefore, for deriving reasonable evolutionary implications from particular fitness values, it is critical to determine the true fitness values for aphids of different generations within the life-cycle of a clone. This might be done more easily for autoecious compared to heteroecious species. However, measuring such values in a natural environment will be mandatory for the interpretation of selection pressures that operate on several life-history characters of aphids.

Temperature can have a canalising effect on the range in fitness values realised. E.g., the range from highest to lowest r_m-values (first to third generation) is 0.05 units lower in the field than under constant temperature conditions for both plant quality treatments. Thus, from greenhouse or growth chamber experiments, it might appear that there is less importance to selection on reproduction in later generations because when fitness is discounted offspring born early in adult life and in early generations are more important than offspring born to later generations. An aphid clone should always try to maximise offspring production in the first generation(s) and reproduce early in adult life because these offspring will be the first that reproduce and contribute to clonal fitness. That is, an aphid clone is likely to be selected for double discounting. Empirical data on the reproductive investment and offspring reproduction very much corroborate this view as it has been demonstrated that relatively more energy is allocated to reproduction in early generations compared to later generations (Taylor, 1975; Dixon & Dharma, 1980; Wellings et al., 1980; Stadler, 1995) and many aphids start to reproduce within the first few days of their adult life (Dixon, 1985). From the greenhouse results alone, one could assume that selection pressures on reproduction might be less severe in later generations because offspring of later generations will contribute proportionally less to the overall fitness of a clone. However, if large fluctuations of temperatures in early generations reduce the realised fitness during springtime, while higher temperatures in summer promote a larger contribution to fitness, then a strong selection pressure should act on later generations to maximise offspring reproduction. This should be true even if plant quality is deteriorating and its effect on fitness is severe (see e.g. constant temperature treatment). Whether prevailing selection pressures result in a programmed, generation specific response to fitness parameters is likely to depend on the magnitude in the fluctuation of environmental parameters during the life time of an aphid. The conclusions derived from life-history characters measured in a constant environment, however, might be considerably different from those of a variable environment.

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