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Performance of *Acyrthosiphon pisum* (HARRIS) (Homoptera: Aphididae) on pea varieties (*Pisum sativum* L.) with emphasis on the relationships between aphid growth and reproductive parameters

G. MORAVVEJ[1] & A. AHMADIAN YAZDI[2]

[1] Dept. of Plant Protection, Faculty of Agriculture, Ferdowsi University of Mashad, Iran, Tel: 0098-511-6080038, Fax: 0098-511-8787430 (e-mail: moravej@um.ac.ir, moravvej2000@yahoo.co.uk).

[2] Agricultural Research Centre of Khorasan Razavi, Mashad, Iran.

Abstract

The performance of the aphid *A. pisum*, reared on nine *P. sativum* varieties, was assessed using mean relative growth rate of aphids (MRGR), number of pigmented embryos (NPE) and pre-reproductive adult weight. The result indicated that MRGR as a measure of growth for *A. pisum* should be used with caution particularly if assessed over a time as short as three days. Over the range of varieties used, there was a highly significant relationship between pre-reproductive adult weight and NPE. The latter, providing an estimate of initial reproductive rate, is a valuable method for the fast assessment of *A. pisum* performance on its host plants. The results indicated that the variety Onward had the highest antibiotic resistance, and other varieties were almost equally susceptible.

Keywords: Pea aphid, reproduction, pigmented embryos, mean relative growth rate

Introduction

The aphid *Acyrthosiphon pisum* (HARRIS) attacks a range of leguminous plants. Studies of varietal resistance to this species were first done more than 80 years ago, and apparently RUSSEL & MORRISON (1924) were the first to observe differences in resistance of pea varieties. A wide range of assessment methods for resistance to *A. pisum* has been used. The earliest investigations were based on simply recordings of numbers of aphids on test varieties, usually in field or glasshouse conditions (SEARLS, 1932), and often took a long time. MALTAIS (1937; 1950; 1951), for instance, reported aphid population counts for a period of 13 years on six pea varieties. More recently, the research has focused on the basis of resistance in order to correlate chemical or

physiological characteristics of plants with the degree of observed resistance (FEBVAY *et al.*, 1988; GIROUSSE & BOURNOVILLE, 1994; RAHBE *et al.*, 1988; SANDSTROM & PETTERSSON, 1994). Investigations related to varietal resistance to *A. pisum* provided different results in terms of the degree of resistance. MARKKULA & ROUKKA (1971), SOROKA & MACKAY (1991) and SANDSTROM (1994) found that there were small differences between pea varieties, but CARTIER (1963) and NEWMAN & PIMENTEL (1974) reported substantial differences in resistance between certain varieties. These differences might be due to the use of different assessment methods, resulting in measuring different components of resistance (SANDSTROM, 1994).

The consequences of resistance based on antibiosis mechanisms in plants are reduced growth and reproduction of an insect. Therefore, assessments of the degree of resistance are mostly based upon measurements of growth and reproductive performance of the insect. Typical measurements are mortality, growth rate, generation time, adult weight, fecundity and longevity. Some parameters have been identified which represent a combination of two or more of these measurements. The most important of such parameters are: mean relative growth rate (MRGR) (FISHER, 1921; RADFORD, 1967; VAN EMDEN, 1969, 1972) giving an indication of development time and weight increase, and intrinsic rate of natural increase (r_m) (BIRCH, 1948; SOUTHWOOD, 1978; VEHRS *et al.*, 1992) representing survival, fecundity and pre-reproductive time.

In the present study, the growth and reproduction of *A. pisum* on nine commercial *Pisum sativum* L. varieties were studied under laboratory conditions using MRGR, pre-reproductive adult weight and number of pigmented embryos (NPE). The aim was to identify varieties that show some degree of antibiotic resistance for further investigations. Over the range of varieties used, the relationships between the different measured variables were assessed and some problems regarding assessment methods for *A. pisum* are highlighted.

Materials and Methods

All experimental plants were maintained in a controlled temperature (CT) room with a 16-8 h light-dark cycle, 23-18°C day-night temperature, 55-80% relative humidity and photosynthetic photon flux density (400-700 nm) of 80-130 and 300-550 $\mu mol.m^{-2}.s^{-1}$ measured at the surface and 50-cm above the bench, respectively. Nine commercial varieties of peas (*P. sativum*) were used: Chopale, Grafila, Princess, Hurst Greenshaft (Hurst G.), Meteor, Onward, Kelevedon Wonder (Kelevedon W.), Little Marnel (Little M.), and Fortune. The first three varieties (obtained from W. A. Church Ltd. Bures Suffolk) were semi-leafless, having relatively large stipules, and the leaflets converted to tendrils. The others had normal leaves. Hurst G. and Meteor seeds were obtained from Unwins Seeds Ltd, Histon, Cambridge (UK) and Sharpes International Seeds Limited, Sleaford (UK), respectively. The last four varieties were obtained from Suttons Seeds Ltd, Torbay (UK).

The seeds were surface-sterilised by immersion in 6% (v/v) hypochlorite, soaked in water overnight and germinated in vermiculite in an incubator (26°C). After 3 days, 60-95% of seeds germinated. Two-day old seedlings, selected for size uniformity (within each variety), were transferred individually into 10-cm diameter plastic pots containing washed fine sand, which had been saturated by nutrient solution. The nutrient solution was a modified formulation based on Rorison nutrient solution (RORISON & ROBINSON, 1986). The plants were watered daily with nutrient solution; 25 ml in the first week, 50 ml in second week, 75 ml in the third week and 100 ml per pot thereafter. The drained solution was discarded.

A clone of *A. pisum* was established on *P. sativum*, var. Meteor, by a single parthenogenetic apterous aphid taken from a long-established colony. The aphid stock culture was kept in a 75×50×50 cm screen cage in the CT room under the same conditions as the experimental plant culture. The aphids were maintained on 2-3-week old plants of Meteor grown in potting compost watered every other day with tap water. Aphid performance was assessed on the 20-24 day old plants by estimates of MRGR, adult weight and NPE. In order to avoid the effects of preconditioning by the aphid culture host plant, about 6 days before each experiment, second instar nymphs (DIGILIO, 1995) were removed from culture plants and placed on pea plants of each of the varieties at the same age as the experimental plants. When adult, groups of 10-15 apterae were transferred into transparent-plastic dish cages (76×44×19 mm) enclosing leaflets and tendrils of the penultimate (the fifth or sixth) nodes of experimental plants. After four hours, the adults were removed, leaving 6-10 nymphs per dish-cage, this being regarded as a replicate. A group of 3-6 randomly selected nymphs per dish-cage was weighed on an electro micro-balance (with the precision of 1 μg) and then returned to their cage. Their mean weight (μg/aphid) (0-4 hours after birth) was recorded as the birth weight (0-day old). Weighing of aphids, randomly taken from each cage, was also done on the third and sixth days of nymphal development. Finally, 24-36 hours later, individual weights of pre-reproductive apterous adults were recorded.

MRGR for a group of aphids was calculated from the following formula (FISHER, 1921; RADFORD, 1967): MRGR ($\mu g.\mu g^{-1}.day^{-1}$) = [(Log $_e$ final weight) – (Log $_e$ initial weight)]/ ($t_2 - t_1$). In the present study, for calculation of $MRGR_1$, the weights of nymphs at birth and the 3rd day were considered as initial and final weights, respectively. For calculation of $MRGR_2$, the weights of nymphs at the 3rd and 6th days were used as initial and final weights, respectively. For calculation of total MRGR, the weights of nymphs at birth and the 6th day were regarded as initial and final weights, respectively. The term ($t_2 - t_1$) was considered as 3 days (for $MRGR_1$ and $MRGR_2$) or 6 days (for $MRGR_{total}$).

The NPE of weighed apterous adults was counted through dissecting each aphid using the novel method of immersion in the emulsifier, 0.02 % Triton X100. The terminal abdominal segment with the cauda was cut off from the body end, and while holding the thorax with a blunt-tip needle, the complete

reproductive system (usually along with the digestive system) was dragged out using a spatula. The triton emulsifier dissolved the fat and enabled the pigmented embryos to be counted very quickly and conveniently.

A completely randomised design was used with each treatment (variety) replicated four times. During the first two weeks, some plants were discarded due to having damaged and diseased leaves, so after 20-24 days, measurements of aphid performance were carried out using unequal replication. The normality of the data was examined and confirmed by Kolmogorov-Smirnov test using the Minitab software. One-way analyses of variance (ANOVA) were conducted on the data of nymphal weight, MRGR, adult weight and NPE. Means for varieties were compared using Duncan's multiple range test; as the replications were different between varieties (3-4 replicates), the Harmonic Mean Sample size of 3.375 was used for comparisons (SPSS, 1998). Linear regression analyses and paired-t tests were performed on certain variables (explained in results).

Results

The mean weights of nymphs on different varieties are presented in Table 1. The ANOVA results showed that birth weight of aphids was not affected by pea variety ($F_{8, 22} = 0.968$, $P = 0.485$), while the third and sixth day weights were significantly different over the range of varieties ($F_{8, 22} = 6.216$, $P < 0.001$; $F_{8, 22} = 10.888$, $P < 0.001$, respectively). Duncan's multiple range test indicated that nymphs reared on Hurst G., Kelevedon W. and Fortune weighed significantly more than those reared on other varieties for three days ($P < 0.05$). After six days, nymphs attained the lowest weight on Onward (1412 μg) and Grafila (1473 μg) and the highest on Hurst G. (1848 μg), Kelevedon W. (1854 μg) and Princess (1827 μg).

MRGRs were calculated based on the weight increase of nymphs over the first three days ($MRGR_1$) and the last three days ($MRGR_2$) of rearing period as well as the whole experimental period ($MRGR_{total}$) (Table 2). The ANOVA results showed that the growth of aphids was significantly affected by pea varieties ($F_{8, 22\ (MRGR1)} = 2.606$, $P < 0.05$; $F_{8, 22\ (MRGR2)} = 5.307$, $P < 0.001$; $F_{8, 22\ (MRGR\ total)} = 3.233$, $P < 0.05$). The lowest growth rates in the first three days were exhibited by nymphs feeding on Little Marnel (0.522) and Onward (0.517), and the highest by those feeding on Hurst G. (0.632). In contrast, in the last three days, the lowest growth rates were observed on Fortune (0.330) and the highest on Chopale (0.443) and Princess (0.454). The total MRGR, calculated on the basis of the 6-day period, can also be considered as the average of $MRGR_1$ and $MRGR_2$. The lowest total MRGR was obtained with aphids feeding on Fortune or Onward (0.453), and the highest with those feeding on Hurst G. (0.507) and Princess (0.509) (Table 2).

The average NPE and pre-reproductive adult weight of aphids reared on different pea varieties are presented in Fig. 1. In the analyses of variance, differences in both NPE and adult weight were highly significant ($F_{8, 22} = 8.133$ and $F_{8, 22} = 9.737$, respectively; $P < 0.001$ for both). NPE was highest in

Table 1: Nymphal weights (μg.aphid^{-1}) (mean ± s.e., n=3-4, each replicate contained a group of 6-10 aphids) of *A. pisum* attained on *P. sativum* varieties.

Pea variety	Birth weight	Third day weight	Sixth day Weight
Hurst Greenshaft	88.9 ± 7.0	588.1 ± 8.9 a	1848.2 ± 50.4 a
Kelevedon Wonder	96.7 ± 7.0	589.2 ± 40.9 a	1854.5 ± 65.3 a
Princess	85.7 ± 2.3	469.3 ± 25.6 b	1827.4 ± 81.2 a
Chopale	91.2 ± 5.0	440.9 ± 22.8 b	1662.7 ± 46.1 b
Meteor	88.9 ± 1.8	444.0 ± 20.7 b	1555.8 ± 40.8 bc
Fortune	103.0 ± 6.9	579.0 ± 35.3 a	1555.5 ± 49.2 bc
Little Marnel	87.1 ± 7.5	415.7 ± 25.3 b	1506.8 ± 36.5 bc
Grafila	92.7 ± 3.8	475.6 ± 48.2 b	1473.0 ± 32.3 c
Onward	93.6 ± 5.6	439.4 ± 13.2 b	1411.8 ± 26.9 c

In the same column, means sharing the same letter do not differ at the 5% level (Duncan's multiple-range test).

Table 2: Mean relative growth rates (MRGR) (± s.e., n=3-4, each replicate contained a group of 6-10 aphids) of *A. pisum* on *P. sativum* varieties based on first 3 days ($MRGR_1$), last 3 days ($MRGR_2$) of nymphal period. Last column is total MRGR based on whole experimental period (6 days).

Pea variety	$MRGR_1$	$MRGR_2$	$MRGR_{total}$
Hurst Greenshaft	0.632 ± 0.021 a	0.382 ± 0.014 bc	0.507 ± 0.017 a
Kelevedon Wonder	0.603 ± 0.022 ab	0.383 ± 0.016 bc	0.493 ± 0.014 ab
Princess	0.566 ± 0.011 abc	0.454 ± 0.005 a	0.509 ± 0.004 a
Chopale	0.525 ± 0.022 bc	0.443 ± 0.011 a	0.484 ± 0.011 abc
Meteor	0.535 ± 0.015 bc	0.419 ± 0.019 ab	0.477 ± 0.007 abc
Fortune	0.576 ± 0.042 abc	0.330 ± 0.014 c	0.453 ± 0.015 c
Little Marnel	0.522 ± 0.024 c	0.430 ± 0.029 ab	0.476 ± 0.017 abc
Grafila	0.542 ± 0.036 bc	0.380 ± 0.028 bc	0.461 ± 0.006 bc
Onward	0.517 ± 0.022 c	0.389 ± 0.009 b	0.453 ± 0.013 c

In the same column, means sharing the same letter do not differ at the 5% level (Duncan's multiple-range test).

the aphids feeding on Hurst G. (19.6), Kelevedon W. (19.2) and Princess (18.2), and lowest on Onward (14.2). Similarly, the heaviest aphids were produced on the formers (1887, 1870 and 1847 μg, respectively) and the lightest ones on Onward (1438 μg). The regression of the NPE of individual aphids on their pre-reproductive weights was highly significant ($F_{1, 168}$ = 359.35, R^2 = 0.68, $P < 0.001$; Fig. 2). Over a range of varieties screened, highly significant relationships were found between $MRGR_1$, $MRGR_{total}$ and NPE of resulting adults, but not with $MRGR_2$ ($F_{1, 29\ (MRGR1)}$ = 34.85, $F_{1, 29\ (MRGR_{total})}$ = 46.96, $P < 0.001$ for both; $F_{1, 29\ (MRGR2)}$ = 0.28, P = 0.601) (Fig. 3). Thus the results indicated that estimates of MRGR based on either a 6-day period (R^2 = 0.62) or the first three days (R^2 = 0.55) of development were well correlated with the NPE of apterous adults.

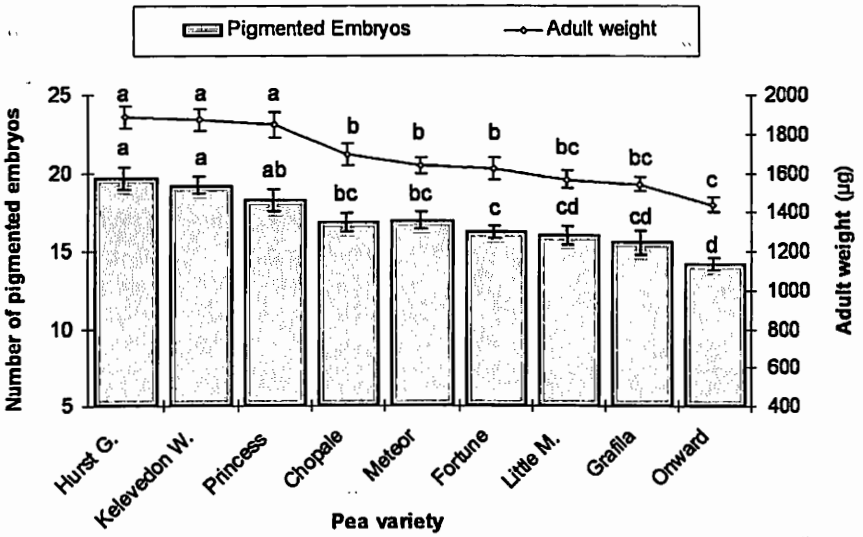

Fig. 1. Number of pigmented embryos and apterous adult weight of *A. pisum* reared on pea varieties, as mean ± s.e.; n=3-4 per variety, each replicate contained a group of 6-15 apterous adults. Within a variable, values sharing the same letter are not significantly different at the 5% level (Duncan's multiple range test).

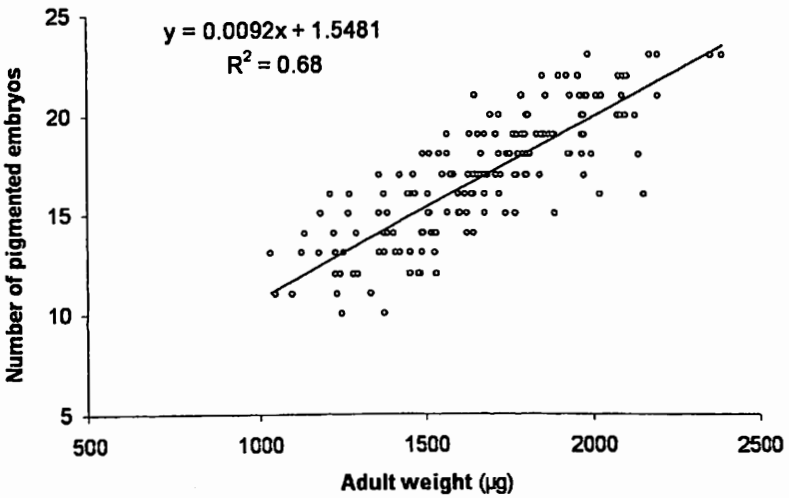

Fig. 2. Regression of number of pigmented embryos of apterous *A. pisum* aphids on adult weight before the onset of reproduction (pooled data from aphids reared on nine pea varieties).

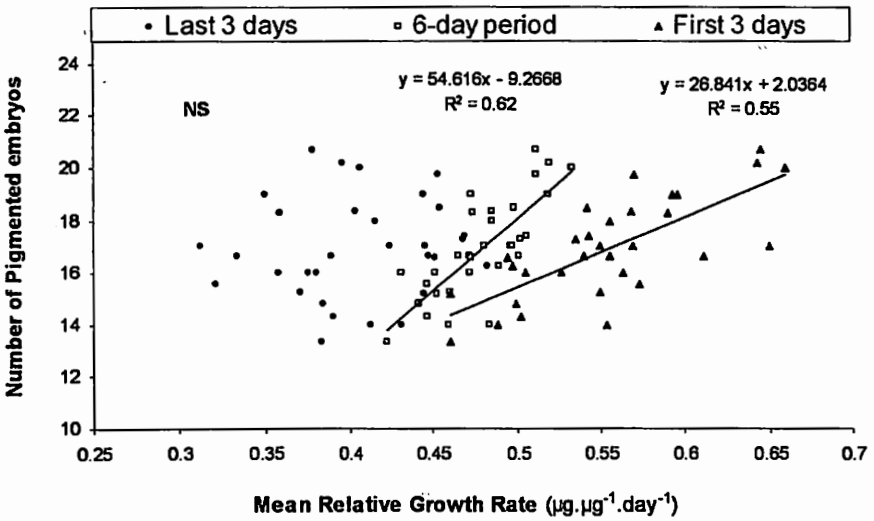

Fig. 3. Regression of number of pigmented embryos of apterous *A. pisum* on their mothers' mean relative growth rates (MRGR) based on different periods of developmental time (pooled data from aphids reared on all pea varieties). NS = non significant.

Discussion

MRGR as a measure of aphid growth performance has been used by many workers when comparing environmental treatments (LEATHER & DIXON, 1984; VAN EMDEN, 1969; VAN EMDEN & BASHFORD, 1971) or resistance of host plant species or varieties (GULDEMOND *et al.*, 1998; LEATHER & DIXON, 1984; SANDSTROM, 1994). The importance of this measure was fully explained by RADFORD (1967) and VAN EMDEN (1969, 1972) for screening tests of aphids subjected to various treatments. The speed of assessment, minimum handling of aphids and applicability of this technique in variable temperatures has been mentioned as three advantages when compared to adult weight or fecundity. The suitability of MRGR was reinforced when its good positive correlation with intrinsic rate of increase (r_m) was demonstrated for the aphid *Rhopalosiphum padi* (L.) (LEATHER & DIXON, 1984). Thus MRGR was proposed for quickly estimating r_m, (DIXON, 1985) which is considered as a valuable measure of population growth and reproduction (BIRCH, 1948; SOUTHWOOD, 1978). Similar correlations have also been demonstrated for apterous *A. pisum* in a previous work (MORAVVEJ, 2001). Comparing several aphid species, although GULDEMOND *et al.* (1998) confirmed the existence of highly significant and positive correlation between MRGR and r_m, these authors demonstrated that this relationship was influenced by aphid species. They also pointed out that MRGR, as an estimate of r_m must be used carefully.

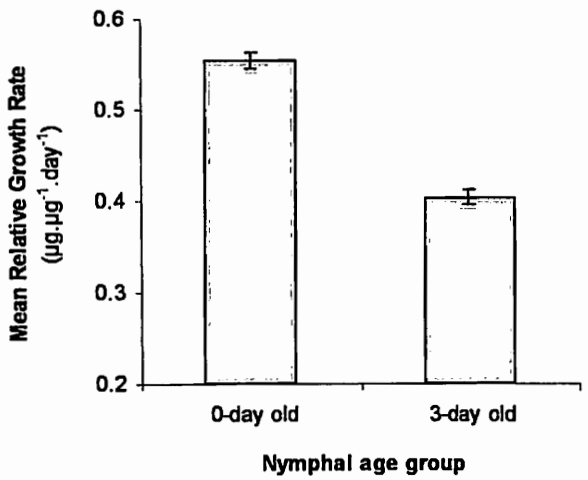

Fig. 4. Mean relative growth rates (mean ± s.e., n = 31) of *A. pisum* on *P. sativum* at birth (0-day old) and 3-day old nymphs (pooled data from aphids reared on nine pea varieties).

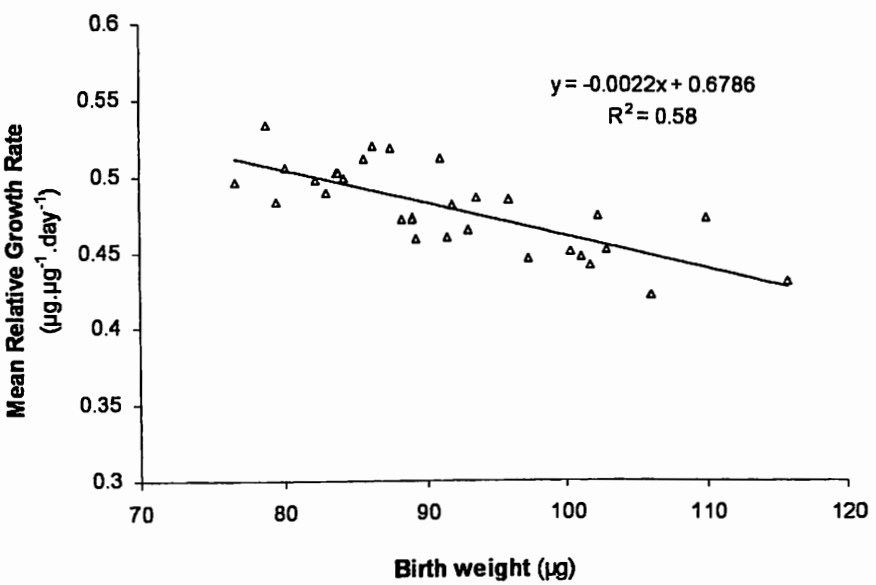

Fig.5. Regression of mean relative growth rate (based on 6-day period, $MRGR_{total}$) of apterous *A. pisum* reared on *P. sativum* on the weight of nymphs at birth (pooled data from aphids reared on nine pea varieties).

The present study (Fig. 3) demonstrates that, in controlled conditions, MRGR of *A. pisum* assessed during the first three days of the nymphal development correlated positively with the number of mature embryos in parent females, and that a better correlation was found when the assessment period was increased from three to six days. Therefore, if estimations of MRGR are based upon a time as short as three days, particularly at late developmental stage, the results might be misleading for assessing population growth. Older nymphs (mean weight of 488 μg) had significantly lower MRGR than the same individuals at birth (mean weight of 92 μg) (Paired-t test: $t = 10.26$, $P < 0.001$; Fig. 4). This indicates that the growth rate of aphids is not constant during nymphal development, as previously assumed (VAN EMDEN, 1969). The fact that MRGR of aphids varies with size has been neglected in most studies. This is due to high variation in the initial weights of test aphids which are usually nymphs born during 24 hours. Newborn nymphs, in this study, were deposited during 4 hours, resulting in a narrow range of size (76.7-115.7 μg), but even in such a short time, the results (Fig. 5) showed that there was a highly significant and negative correlation between birth weight and $MRGR_{total}$ ($F_{1,29} = 39.36$, $R^2 = 0.58$, $P < 0.001$). The importance of using aphids of similar size (weight) has been emphasized for accurate estimation of MRGR (VAN EMDEN, 1969; 1972).

NPE, often referred to as the number of mature embryos, indicates the initial reproductive rate. The assessment of NPE, although not undertaken in studies related to plant resistance to *A. pisum*, has been used in many ecological studies of several other aphid species (DEWAR, 1977; DIXON & DHARMA, 1980; KEMPTON *et al.*, 1980; LEATHER, 1980; LEATHER & WELLINGS, 1981).

A highly significant relationship was found between NPE and pre-reproductive adult weight of *A. pisum* (Fig. 2). A similar relationship has been shown in other aphids such as *Aphis fabae* SCOP. (DIXON & DHARMA, 1980), *R. padi* (LEATHER & WELLINGS, 1981), *R. insertum* (WALK) (DEWAR, 1977) and *Myzus persicae* (SULZ.) (KEMPTON *et al.*, 1980). The results (Fig. 1) revealed that on the most susceptible variety, Hurst Greenshaft, the largest adults (1887 ± 59 μg) were produced which had the greatest number of mature embryos (19.7 ± 0.7) in their ovaries, and that on the least susceptible variety, Onward, the smallest adults (1438 ± 34 μg) were associated with the least number of mature embryos (14.2 ± 0.4). Similarly, on *R. padi* and *A. fabae*, LEATHER *et al.* (1981) and DIXON (1980) respectively demonstrated that within each generation large individuals had more mature embryos than small ones at the time of moulting to the adult, and also had greater initial reproductive rates. The great variability of adult weight within and between different aphid species, its dependency to environmental factors such as temperature, and its lack of correlation with fecundity over a wide range of host plants have limited the use of adult weight in directly estimating population growth parameters. However, as the number of mature embryos can represent the initial reproductive rate of an aphid, it may be used in certain aphid species for estimation of r_m.

Conclusion

The present work focused on nine commercial *P. sativum* varieties and the aphid, *A. pisum,* with the aim of finding some degree of antibiotic resistance for subsequent research. Based on all three variables studied, namely total MRGR, NPE and adult weight, the four most divergent varieties, Hurst Greenshaft, Kelevedon Wonder, Grafila and Onward were chosen for further research. Of these, only the response of *A. pisum* to Onward has been reported before, in which some degree of resistance was noted (AUCLAIR, 1959; SEARLS, 1932). This is in agreement with the present results, although the assessment methods were different. The ranking of pea varieties based on $MRGR_1$ and $MRGR_2$ of aphids gave different outcomes (Table 2), which were dissimilar to the other measures. The present work was only concerned with a few parameters of aphid performance. Furthermore, although all the test varieties had the same chronological age, they might not represent the same physiological age when the tests were conducted. Thus, caution needs to be exercised when comparing these results with those of other workers or when choosing pea varieties for glasshouse or fieldwork.

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