

# Pea Aphid (Homoptera: Aphididae) Fecundity, Rate of Increase, and Within-Plant Distribution Unaffected by Plant Morphology

ANA LEGRAND<sup>1</sup> AND PEDRO BARBOSA<sup>2</sup>

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**ABSTRACT** Plant morphology has been shown to influence the biology of herbivores through changes in oviposition behavior, feeding preferences, and plant tenure times. The goal of the work herein was to establish whether or not differences in plant morphology can affect the performance and distribution of the pea aphid, *Acyrtosiphon pisum* (Harris), on peas, *Pisum sativum* L. Fecundity and intrinsic rate of increase were the selected parameters to measure the aphid's performance. Genetic near-isolines of the garden pea were used to determine the effect of plant morphology on the pea aphid. The use of genetic near-isolines eliminates as much as possible confounding effects, such as phytochemicals, that could occur when comparing different plant species or cultivars. Four plant lines differing in leaf morphology (*Normal*, *af*, *tl*, and *af tl*) and two lines with normal and reduced stipules (*Normal* and *st*) were tested. Changes in plant morphology did not have a significant effect on pea aphid total fecundity or intrinsic rate of increase. Although there were no changes in fecundity caused by plant morphology, longevity was significantly influenced both by leaf type and stipule size. The morphology of the leaf did not affect the within-plant distribution of the pea aphid on three plant lines tested.

**KEY WORDS** *Acyrtosiphon pisum*, plant-herbivore interactions, plant morphology, genetic near-isolines

MANY INTRINSIC CHARACTERISTICS of plants such as nutritional value, secondary chemistry, and morphology can influence the fecundity, growth, and survival of insect herbivores (Slansky and Feeny 1977, Norris and Kogan 1980, Montllor 1991). Several examples highlight the role of plant morphology on plant-herbivore interactions. First, plant morphology can influence herbivore distribution as a result of changes in oviposition behavior. Herbivores may use plant morphology as a cue. For example, the butterfly *Battus philenor* L. has been shown to form a search image for particular leaf shapes as they search for their larval host plant (Rausher 1978). Further, herbivore feeding preferences (Rivero-Lynch et al. 1996) and plant tenure time (Vaughn and Hoy 1993) can differ as a result of differences in leaf shape. The shape of plant structures such as trichomes has been shown to be the basis of insect resistance in some crop plants (Norris and Kogan 1980). Lastly, plant architecture can influence the sectorial transport of plant nutrients and therefore affect the resource base available to a herbivore (Watson and Casper 1984, Marquis 1996).

The goal of the work herein was to establish whether or not differences in plant morphology can affect the performance and distribution of a herbivore using the pea aphid, *Acyrtosiphon pisum* (Harris), on peas, *Pisum sativum* L. Considerable research has been

conducted on the demographics of the pea aphid (Frazer 1972, Hutchison and Hogg 1984, Zeng et al. 1993), as well as on the effect of temperature, photoperiod, and different plant species and cultivars on its development (Kenten 1955, Kilian and Nielson 1971, Soroka and Mackay 1990a, Soroka and Mackay 1991, Kaakeh and Dutcher 1993, Sandström 1994, Sandström and Pettersson 1994). In an investigation of the effect of pea cultivars, Soroka and Mackay (1991) found that a semileafless cultivar (leaflets in this cultivar are substituted by tendrils) reduced the survivorship and longevity of the pea aphid. Albeit inconsistently, fecundity was also reduced when the semileafless cultivar was compared with normal leaf cultivars. These data suggested that plant morphology, through the presence of leaflets, could have an impact on the pea aphid. However, in other studies, leafless cultivars did not always result in a reduction in fecundity and in the intrinsic rate of increase. Sandström (1994) and Sandström and Pettersson (1994) found that only one of three leafless cultivars examined consistently resulted in a reduction of fecundity and rate of increase. The other two leafless cultivars were either not significantly different or resulted in an increase (as compared with normal leaf cultivars) in the above performance parameters. Using two pea lines that only differed by two mutant genes, Kareiva and Sahakian (1990) found that pea aphid population growth was hardly reduced (on average <10%) on leafless/reduced stipule plants as compared with the normal leaf/normal stipule plants.

<sup>1</sup> Department of Plant Science, University of Connecticut, 1376 Storrs Road, U-67, Storrs, CT 06269-4067.

<sup>2</sup> Department of Entomology, 4112 Plant Science Building, University of Maryland, College Park, MD 20742.

The results of the aforementioned studies are difficult to compare and to ascribe a cause and effect relationship because differences in the aphid's performance could be caused by nonmorphological (e.g., chemical) factors in the cultivars tested. For instance, Kareiva and Sahakian (1990) who used two isogenic lines of the same cultivar did not find a large difference in the aphid population growth between the leafless and normal leaf plants. Therefore, in this study we undertook an investigation of the importance of plant morphology using genetic near-isolines of the garden pea. The isolines differ substantially in the shape and size of leaves and stipules. The use of genetic near-isolines eliminates, as much as possible, confounding effects of phytochemical differences or other changes that could affect aphid performance. The performance parameters measured include aphid fecundity and intrinsic rate of increase.

We also recorded the location of aphids on a plant because feeding position could affect reproduction and survival both through direct physiological mechanisms or ecological mechanisms. Changes in feeding location can alter the access to nutrients thus influencing herbivore fecundity and development (Ralph 1976, Larson and Whitman 1991). Further, herbivore behavioral responses could be modified. Pea aphid feeding on plant stems were more responsive to alarm pheromone preceded by simulated vibration of plant substrate than aphids feeding on leaf undersides (Clegg and Barlow 1982). Finally, changes in feeding location can alter vulnerability to environmental conditions (Norris and Kogan 1980). Reports on the distribution of the pea aphid within plants note the aphid was more often observed on leaves than on stems of broad bean, *Vicia faba* L. (Salyk and Sullivan 1982), and that it tended to concentrate on the bud with only 8–10% of the aphids found on the stem of broad beans (Lowe 1971). Similarly, pea aphids were found in significantly greater proportion on leaf undersides than on stems while feeding on peas with normal wax. Yet the proportion of aphids feeding on stems tended to increase when they were on reduced-wax plants (Eigenbrode et al. 1998).

The location of the pea aphids was studied by observing the within-plant distribution of apterous aphids colonizing a plant. This is important because adult apterae can move from plant to plant when the plants touch or when they are on the ground and climb a plant. Apterous pea aphids may colonize plants from the ground more than other aphid species because their propensity to drop from plants when disturbed (Niku 1975, Dill et al. 1990, Chau and Mackauer 1997, Losey and Denno 1997) and their movement orientation to vertical structures such as sticks or stems (Niku 1972). Moreover, apterous pea aphids have been shown to disperse among plants when active predators are present (Roitberg et al. 1979). Information is lacking as to how plant morphology influences the location of the pea aphid. Thus, the objectives of the work presented here were to determine the effect of plant morphology on the total fecundity and intrinsic rate of increase of the pea aphid, and to deter-

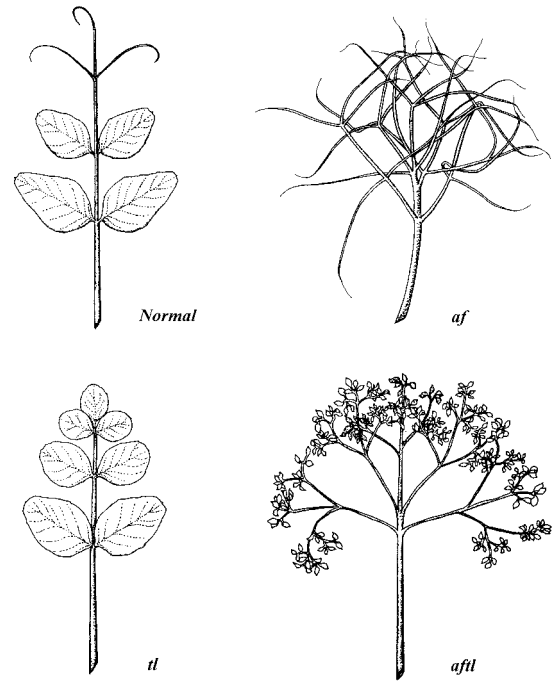


Fig. 1. Leaves of the *Normal*, *af*, *tl*, and *aftl* near-isogenic lines of pea, *Pisum sativum* L. The *Normal* leaf type is composed of the rachis, two pairs of leaflets, and terminal tendrils. The *af* leaf has all leaflets substituted by tendrils. The *tl* leaf mutant is composed of a rachis and only leaflets. The *aftl* leaf mutant is composed of a highly branched rachis and tiny leaflets.

mine the effect of plant morphology on the settling location choice by apterae pea aphids as they contact the plant from the ground.

### Materials and Methods

**Plant Material.** Peas, *Pisum sativum* L., exhibit mutations that influence the form of the leaf and the stipule. The normal pea plant may be altered considerably in its morphology by the mutant genes *af* (afile), *tl* (acacia), and *st* (reduced stipule) (Wehner and Gritton 1981). These genes are probably the best studied leaf mutant genes in *P. sativum*, are highly specific in their action, and do not show a wide range of pleiotropic effects (Murfet and Reid 1993). The combinations of these genes and their interaction produce eight morphological plant types. Genetic near-isolines for these eight genetic types (in the genetic background 'New Line Early Perfection' cultivar) were used for our experiments. A description of each isolate follows and the four leaf types and two stipule types are illustrated in Figs. 1 and 2. (1) *Normal* (*AfAfTlTlStSt* genotype): This plant has a normal pea leaf which is compound, consisting of a leaf stalk (rachis), two to three pairs of leaflets followed by an unpaired number of tendrils (Khovostova 1983). Stipule size is normal. (2) *Afile* or *af* (*afafTlTlStSt*): The

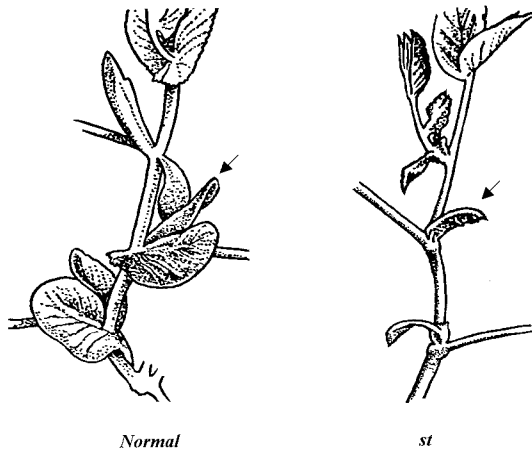


Fig. 2. Stipule types of the *Normal* and *st* (reduced stipule) near-isogenic lines of pea, *Pisum sativum* L. The *st* plants exhibit stipules in the form of two narrow wings around the stem (indicated by arrow).

*af* allele replaces leaflets with tendrils (Wehner and Gritton 1981). Stipule size is normal. (3) *Acacia* or *tl* (*AfAftltStSt*): The *tl* allele causes the conversion of tendrils into additional leaflets (Khovostova 1983). This type of leaf is also known as acacia leaf or multifoliate. Stipule size is normal. (4) *afil* (*afafiltStSt*): The interaction of *af* with *tl* results in the minute leaflet phenotype, which is a plant with highly branched petioles and tiny leaflets (Wehner and Gritton 1981). It is also known as the parsley leaf type. Stipule size is normal. (5) Reduced stipule or *st* (*AfAftltstst*): This plant has the normal leaf type but the *st* allele narrows the stipule to the shape of narrow wings. This gene does not have any effect on leaf blades and it is located in chromosome III (Khovostova 1983). (6) *tlst* (*AfAftltstst*): This combination of *tl* and *st* results in a phenotype that looks the same as the acacia type (*tl*) but with reduced stipules. (7) *afst* (*afafiltstst*): This plant looks the same as *afila*, but has reduced stipules. Both *afila* (*af*) and *afst* types have less lodging than the *Normal* type and may yield as many peas (Wehner and Gritton 1981). (8) *afilst* (*afafiltstst*): The same description as in the *afil* type applies here. However, stipules are reduced.

**Insects.** For this study, aphids were collected from pea plots planted at the University of Maryland Research Farm in Upper Marlboro, MD. A laboratory colony was established by bringing in apterous adults (green morph) from separate locations from the field. The initial collections occurred in April 1995. Additional collections took place in spring 1996 and aphids were incorporated into the laboratory colony. The aphids were kept on the Wando pea cultivar (normal foliage). Plants used to maintain the aphid colony were grown in a greenhouse. Aphid colonies were kept in Plexiglas cages at  $21 \pm 2^\circ\text{C}$  under cool white fluorescent lamps at a photoperiod of 16:8 (L:D) h. Voucher specimens (# UCMS-V2000.1) were placed in the Research Collection of the Connecticut State

Museum of Natural History, University of Connecticut, Storrs.

**Pea Aphid Performance.** The eight morphological near-isolines described above were used to test the effects of plant morphology on aphid total fecundity and intrinsic rate of increase. A factorial completely randomized block design was used with the following treatments combinations: four leaf shapes (*Normal*, *af*, *tl*, and *afil*) combined with *Normal* or reduced stipule (*st*). This resulted in a total of eight treatments (*Normal*, *af*, *tl*, *afil*, *st*, *afst*, *tlst*, and *afilst*). Each treatment was replicated three times per block, giving a total of 72 observations. The experimental unit was a single apterous female placed on the bud (developing leaf enclosed by stipule) of the plant as a newly born nymph (4–8 h). At the start of the experiment, two such nymphs were placed on the bud; and after 24 h, one nymph was removed. The eight aphids used for one set of treatments came from the same aphid mother. The blocks consisted of replicates in time, which were conducted three times (29 July 1996, 31 December 1996, and 14 April 1998) in the same plant growth chamber with Sylvania Gro-Lux (Danvers, MA) wide spectrum plant lights at  $21 \pm 1^\circ\text{C}$ , 60% RH, and a photoperiod of 16:8 (L:D) h.

Seeds of all eight plant types were planted in germination trays using 300S growing media (Pro-Gro Products, Elizabeth City, NC). Fifteen to 20 d after planting, seedlings were transplanted to 15 cm wide plastic pots with the same growing media. White sand was used to cover the surface of the growing media. Plants within a block were 27 d old (with 9–10 nodes), 28 d old (with 9–10 nodes), and 29 d old (with 10 nodes), for blocks 1–3, respectively. Plants were placed individually within cages constructed of transparent polycarbonate sheets bent to form a cylinder (60 cm tall, 30 cm in diameter). The cylinders were placed on a tray with white sand and they had white organza mesh on top. Cages were randomly positioned within the chamber and every week their position was rerandomized until the end of the experiment. The following four measurements were taken for each aphid: (1) number of days until a nymph matured to an adult and produced nymphs, (2) number of nymphs produced every 2–3 d (nymphs were removed as they were counted), (3) total progeny produced until death of aphid mother, and (4) longevity of aphid mothers (done only for block 1).

Data on fecundity and longevity were tested to determine if assumptions of normality and homogeneity of variances were met. To test the null hypothesis that fecundity is the same on all eight types of plants, analysis of variance (ANOVA) was conducted using PROC MIXED (PROC MIXED, SAS Institute 1996a). For the statistical model, maternal line of the aphids was treated as a random effect and it was nested within a block, which was treated as a fixed effect. Plant type was also treated as a fixed effect. To obtain the denominator degrees of freedom, the general Satterthwaite approximation was requested in PROC MIXED. The data on longevity were tested with an ANOVA using PROC GLM (PROC GLM, SAS Insti-

tute 1990). *P* values for multiple comparisons were adjusted using the Scheffé procedure (PROC MIXED, SAS Institute 1996b). Least-squares means and their corresponding standard errors are reported for data on fecundity and longevity because there were three missing observations.

The intrinsic rate of increase ( $r_m$ ) was calculated using the equation  $r_m = 0.74 (\ln M_d)/T$  (Wyatt and White 1977), in which *T* is time from birth to onset of reproduction,  $M_d$  is the reproductive output per original female during a period equal to *T*, and 0.74 is a correction factor. The above equation has been used by several workers to calculate  $r_m$  for aphids (Leather and Dixon 1984, Sandström 1994, Sandström and Pettersson 1994, Soroka and Mackay 1991). The resulting  $r_m$  values have been shown to agree closely with values calculated using the method of Birch (1948), and fall within the same 95% confidence interval (Wyatt and White 1977). This  $r_m$  value was calculated for each aphid, and these values were used as the response variable, without transformation, in the ANOVA.

**Aphid Within-Plant Distribution.** To assess the effect of leaf morphology on the settling location of adult apterae the following experiment was conducted in five time blocks. Each block consisted of nine plants per treatment. In this case, only the *Normal*, *tl*, and *afil* morphological isolines were tested because they presented striking differences in leaf shape. To minimize effects of crowding on the settling choice of aphids, only 10 adult apterae aphids per plant were placed on the first stem segment of the plants. However, to test many aphids on an individual plant, three groups of 10 aphids were sequentially tested on a given treatment plant per block. Plants within a block had 9–10 nodes and expanded only about one new leaf during the block period. The observations for each individual plant were pooled, thus totaling 30 aphids per plant per treatment. Plants were placed individually inside the same cages used previously in experiments on aphid fecundity.

After 24 h, each plant was searched and aphids were removed. The following location categories were scored for each aphid: plant bud, leaf, stem, and stipule. The location was defined as the place where the aphid was seen feeding. If the aphid dropped before scoring its position, was found dead, or not found at all, it was scored as missing. Blocks 1–4 were conducted in a plant growth chamber (same as described above) at  $21 \pm 1^\circ\text{C}$ , 60% RH, and a photoperiod of 16:8 (L:D) h. Block 5 was conducted on a laboratory bench at  $21 \pm 2^\circ\text{C}$  and received sunlight from two windows. The start dates for blocks 1–5 were 18 January, 24 February, 1 June, 6 July, and 27 July 1998, respectively.

Compositional analysis (using multivariate ANOVA was used to compare the proportions of aphids at each location among the three plant types. This method is necessary because there are four locations to consider and the proportions of aphids on each location are not independent from each other and must add to 1 (Aitchison 1986). The proportion of aphids on the stem was used to center all the other locations by dividing the proportion of each location by the stem propor-

**Table 1.** Effect of pea leaf morphology and stipule size on total fecundity and intrinsic rate of increase ( $r_m$ ) of *A. pisum* apterae (LS means  $\pm$  SEM)

	Fecundity	$r_m$
Leaf type		
<i>Normal</i>	97.4 $\pm$ 3.22	0.386 $\pm$ .008
<i>af</i>	98.6 $\pm$ 3.14	0.398 $\pm$ .008
<i>tl</i>	95.9 $\pm$ 3.22	0.387 $\pm$ .008
<i>afil</i>	102.8 $\pm$ 3.22	0.399 $\pm$ .008
Stipule size		
<i>Normal</i>	100.1 $\pm$ 2.52	0.394 $\pm$ .007
<i>st</i>	97.3 $\pm$ 2.44	0.391 $\pm$ .007

tion. A log transformation of these ratios makes them linearly independent (Aitchison 1986). Any zero proportion was converted to 0.01. These transformed data were used then to test the effect of plant type on the settling location of the aphid. Multivariate ANOVA in PROC GLM (PROC GLM, SAS Institute 1990) was used for the test. The proportions of aphids missing were analyzed to test for any plant effect.

In addition, when aphids were on a leaf, their within-leaf location was scored as either being on the rachis (and rachioles in the case of the *afil* plant) or leaflet. These data were calculated as the number of aphids found on leaflets or rachises. A chi-square analysis was conducted on a  $3 \times 2$  contingency table with plant type as rows and locations as columns.

## Results

**Pea Aphid Performance.** Changes in plant morphology did not have a significant effect on pea aphid total fecundity or intrinsic rate of increase (Table 1). The *P* values from the ANOVA were all  $>0.13$  with the exception of the block effect in the analysis of the effect of leaf morphology and stipule size on the intrinsic rate of increase. Because there was no significant interaction between leaf type and stipule size, only main effects means are reported. Even though there were no changes in fecundity caused by plant morphology, longevity was significantly influenced both by leaf type ( $F = 7.2$ ;  $df = 3, 14$ ;  $P = 0.0037$ ) and by stipule size ( $F = 20.88$ ;  $df = 1, 14$ ;  $P = 0.0004$ ). The leaf by stipule interaction was not significant ( $F = 0.41$ ;  $df = 3, 14$ ;  $P = 0.7473$ ). The pea aphids lived the shortest time when they were on the *af* plants and on the *Normal* stipule plants (Table 2). For the longevity data, the number of observations per treatment was only three. However, the lack of significant interaction between leaf type and stipule size provides hidden replication. That is, the leaf type factor is essentially replicated six times and the stipule size factor is replicated 12 times. Nevertheless, the effect of plant morphology on longevity was measured only in one experiment. Adult pea aphid longevity ranged from 21 to 43 d.

**Aphid Within-Plant Distribution.** The MANOVA test criterion (Wilk's lambda) indicated that there was no significant effect of leaf morphology on the settling locations of the aphids ( $F = 1.3344$ ;  $df = 6, 252$ ;  $P = 0.2422$ ). Aphids settled on stem, stipule, leaf, and bud

**Table 2.** Effect of leaf morphology and stipule size on the longevity (LSMeans ± SEM) of *A. pisum* apterae

	Longevity (days)
Leaf type	
<i>Normal</i>	34.2 ± 1.48a
<i>af</i>	26.8 ± 1.48b
<i>tl</i>	32.9 ± 1.65a,b
<i>afil</i>	36.4 ± 1.65a
Stipule size	
<i>Normal</i>	29 ± 1.17a
<i>st</i>	36.2 ± 1.04b

*P*-values for multiple mean comparisons were adjusted using Scheffé procedure. Within a main effect, LS means followed by a different letter are significantly different at the  $\alpha = .05$  level.

with almost identical proportions for all the three plant types (Table 3). The percentage of missing aphids was not significantly different because of plant type. The mean was 13% for all treatments. Aphids were observed reproducing on the location where they settled. Aphids scored as being on the leaf were further classified according to position within the leaf. The numbers of aphids per leaf varied from one to four. There were no significant differences in the number of aphids found on leaflets versus rachises when the three types of plants were compared ( $\chi^2 = 1.618$ ,  $P = 0.445$ ). The data were pooled across plant type and the mean percentage (±SEM) of aphids settling on leaflets was 66% ± 1.6 and the mean proportion for aphids settling on rachises or rachioles was 33% ± 1.6.

**Discussion**

Morphological changes of the pea isolines did not alter the total fecundity and the intrinsic rate of increase ( $r_m$ ) of the pea aphid nor its location within the plant. When different plant species and cultivars are compared, the pea aphid can exhibit significant differences in fecundity and  $r_m$  (Soroka and Mackay 1990a, 1991; Kaakeh and Dutcher 1993; Sandström 1994; Sandström and Pettersson 1994). The literature indicates that the  $r_m$  values for the pea aphid range from 0.109 to 0.401 when plant species are compared (Sandström and Pettersson 1994); 0.324–0.402 and 0.288–0.318 when pea cultivars are compared (Sandström and Pettersson 1994, Soroka and Mackay 1991, respectively) and 0.241–0.465 when light and temperature are manipulated (Siddiqui et al. 1973). The  $r_m$  values from this experiment fall in the upper range and the differences are small when compared with the

**Table 3.** Settling locations of *A. pisum* apterae on plants with different leaf morphology

Plant Type	Stem	Stipule	Leaf	Bud
<i>Normal</i>	0.37 ± 0.019	0.22 ± 0.012	0.32 ± 0.019	0.09 ± 0.009
<i>tl</i>	0.35 ± 0.021	0.22 ± 0.011	0.32 ± 0.022	0.11 ± 0.014
<i>afil</i>	0.355 ± 0.018	0.19 ± 0.012	0.355 ± 0.019	0.10 ± 0.012

Numbers indicate mean proportions (Mean ± SEM) out of 30 aphids tested.

range of values stated above. Thus, although  $r_m$  for the pea aphid can vary, we have shown that the morphology of the plants alone is not likely to have an impact on the fecundity and rate of increase of the pea aphid.

Although reproductive performance was unaffected, plant morphology did have an effect on longevity of the pea aphid apterae in the one experiment in which this was measured. However, these differences did not appear until most of the reproduction had been completed. Most of reproductive output occurs before 20–25 d, whereas differences in longevity affected survival from 26 to 36 d. The differences in longevity as a result of leaf type may be caused by the microclimate experienced by the aphids while on the plants. Aphids lived the shortest time on the *af* leaf type. On these plants, aphids are the most exposed to the radiant heat of the growth chamber lights and hence they may experience a higher temperature and lower humidity. Temperature changes have been shown to influence insect survival (Benedict and Hatfield 1988) and temperature and longevity are inversely related for the pea aphid (Campbell and MacKauer 1977). The reduction in longevity caused by larger stipule size was unexpected. One plausible explanation is that aphids on average had easier access to the plant's bud on the reduced stipule plants. The size of the normal stipule could slow or hinder the movement of the aphids to the bud relative to what is achieved on the reduced stipule plants. This would result in an enhanced access to young plant tissue, which could affect longevity.

Parallel to the results on aphid performance, plant morphology did not influence pea aphid location within the plant. The leaf morphology did not affect the choice of settling location by the pea aphid; pea aphids settled in almost equal proportions on the three leaf types tested. They also did not discriminate between stems and leaves. One alternate explanation is that they did not have sufficient time to discriminate between plant parts. They were allowed access to the plants for 24 h. However, previous observations indicated that once an aphid settled in one location and began reproducing, it remains there from 1 to 7 d (unpublished data). Moreover, a test conducted to see if after 48 h the aphids would move from their previously scored locations showed no change (A.L., unpublished data). Although there were no differences in aphid location when the three types of plants were compared, the aphids did discriminate among parts of leaves of any plant type. Once the aphids entered the leaf, 66% of them chose to settle in the leaflet structures as compared with rachises or rachioles. This difference of position within the leaf could have consequences for the aphid's performance, its effect on the plant's nutrient flow, or its susceptibility to natural enemies.

In conclusion, these laboratory experiments show that changes in pea leaf morphology and stipule size do not influence the reproduction and intrinsic rate of increase of the pea aphid. Similarly, location of the pea aphid was not influenced by the leaf morphology of *Normal*, *tl*, or *afil* plants. Nevertheless, plant morphol-

ogy could mediate the effect of other factors influencing the aphid population. For instance, plant morphology could have an effect on a herbivore through changes in the effectiveness of its natural enemies (Gardner and Dixon 1985, Kareiva and Sahakian 1990, Grevstad and Klepetka 1992, Clark and Messina 1998). Moreover, plant morphology could legislate the effect of weather conditions. In field studies, Soroka and Mackay (1990b) found that a leafless cultivar (similar to *af* in this study) supported less pea aphids than other normal cultivars. They proposed that the substitution of leaflets for tendrils reduced the preferred space for aphid population development and made them more vulnerable to weather conditions. In this example, predator exclusion experiments suggested that increased predation on the leafless cultivar was not the cause for the reduction in aphid numbers. Further work should assess the influence of plant morphology as a factor mediating the action of biotic and abiotic factors. Hence, the lack of a physiological effect of plant morphology on the pea aphid should simplify the experimental isolation of ecological effects.

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