ABSTRACT  It has been claimed that plant architecture can alter aphid reproductive rates, but the mechanism driving this effect has not been identified. We studied interactions between plant architecture, aphid density, environmental conditions, and nutrient availability on the reproduction of pea aphids \textit{(Acyrthosiphon pisum (Harris))} using four near-isogenic peas \textit{(Pisum sativum L.)} that differ in morphology. Manipulations of aphid density (1, 5, and 10 adults per plant) allowed us to examine any effects of plant morphology on crowding and consequently reproduction. Pea morphology per se did not alter pea aphid crowding, as measured by mean nearest neighbor distance, and there was no effect on reproduction. In addition, reproduction increased with increasing adult density, indicating positive density dependence. In a separate experiment, peas were fertilized to determine whether differences between nutrient availability of the four different morphologies might drive any observed differences in aphid reproduction. Although plant nitrogen content was altered by fertilization treatments, this did not have an impact on aphid reproduction. Greenhouse experiments, however, suggested that pea morphology can interact with environmental conditions to reduce aphid reproduction under some conditions. We conclude that plant morphology only influences aphid reproduction when environmental conditions are less than optimal.

KEY WORDS  plant morphology, density dependent, fertilization, environmental conditions, reproduction

Many authors have focused on the effects of insect density (Underwood and Rausher 2000, Agrawal 2004), environmental conditions (Dixon 1973), and the phytochemistry of plants (van Emden 1966, Bentz and Townsend 2001) on herbivore performance, but the physical properties of plants can also affect insect herbivore population growth, reproduction, and survival (Kareiva and Sahakian 1990, Soroka and MacKay 1990). Our objective was to study how plant architecture, aphid density, environmental conditions, and available nutrients of pea plants \textit{(Pisum sativum L.)} affect the reproduction of pea aphids \textit{(Acyrthosiphon pisum (Harris))}. Researchers working with this system have recorded contradictory effects of plant morphology on pea aphids. Although some authors report a strong influence of pea architecture on aphid population growth (Soroka and MacKay 1990), others find little or no impact (Legrand and Barbosa 2000). However, Soroka and MacKay (1990) used six different cultivars of field peas, whereas Legrand and Barbosa (2000) used near-isogenic peas of a single cultivar. It is possible that the effects reported by Soroka and MacKay were caused by differences between cultivars, such as smaller-scale morphological differences (e.g., differences in surface wax). It is also possible the experiments by different authors included uninvestigated interactions between morphology and other important factors. We aimed to gain more insight by simultaneously studying several possible mechanisms through which plant morphology could affect herbivore performance, using four near-isogenic peas of a single cultivar that have different architectures.

Plant architecture is the size and design of a plant. The two major determinates of plant morphology are the spread of plant tissue through different positions in space, and the variety of plant structures (Lawton 1986, Cloyd and Sadof 2000). Stem and leaf dimension, branching angles, surface complexity, and canopy spacing are all important architecture characteristics of a plant that might influence insect herbivores. For example, plant architecture partly determines the surface area that is available to an insect herbivore, which in turn determines the availability of resources.

Some authors have found that fecundity, population growth rate, and longevity of herbivores are affected by plant architecture. In laboratory studies on different cultivars of field peas, Soroka and MacKay (1991) reported lower pea aphid longevity and total fecundity on the semileaftless cultivar \textit{Tipu} but found no effect of morphology on population growth rates. Sandström and Pettersson (1994) also found a significant reduction in fecundity on a leafless pea cultivar, and in addition, reported reduced population growth...
rates of pea aphids on this cultivar. However, they report that another leafless cultivar had one of the highest population growth rates, which suggests that cultivar-specific differences unrelated to gross morphology may play a role. When using near-isogenic peas that differed in morphology, Kareiva and Sahakian (1990) found only a slight, nonsignificant reduction in the population growth rate of aphids on leafless plants compared with normal plants. Similarly, Legrand and Barbosa (2000) reported no significant effect of the architecture of isogenic peas on fecundity or population growth of pea aphids, but did report some impact on longevity.

Because plant surface area can be altered by plant architecture, it is also possible that any reported effects of morphology are actually caused by differences in surface area, and consequently, the strength of any density-dependent regulation of aphid growth parameters. In many species of aphids, population growth is strongly affected by density (Underwood and Rausher 2000, Agrawal 2004, Rhainds and Messing 2005). For example, density-dependent processes regulate the population growth of Aphis gossypii Glover, the melon aphid, on taro (Rhainds and Messing 2005). Moreover, it is also possible that alteration of surface area with differences in morphology varied between the different cultivars used in these studies.

None of the authors working with the pea plant–pea aphid system measured the surface area of the plants used. The different experimental methods used also produced widely varying aphid densities. For example, Legrand and Barbosa (2000) removed aphid offspring every 48 h, whereas Soroka and MacKay (1991) allowed aphids to reproduce until death and did not remove offspring. Consequently, the results of Soroka and MacKay (1991) may be related to a significant negative density-dependent effect of plant architecture, whereas those of Legrand and Barbosa (2000) may reflect a lack of such effects.

Architecture can also alter the movement rates of herbivores. Structure that causes reduced movements could increase crowding and therefore alter the effective per capita access to resources. That is, the local density of aphids may be higher on a given plant morphology because the plant shape tends to restrict offspring to the vicinity of their birth. Increased aggregation on the plants can increase intraspecific competition that may increase mortality, lower reproductive success, and increase the rate of dispersal to a less dense location (Dixon 1973, Day 1986, Klindman and Dixon 1996). None of the authors working with the pea aphid system measured aphid crowding, so it is not certain if this mechanism lies behind reported effects of plant morphology.

More obviously, plant architecture can also determine how much shelter is provided by the plant against adverse weather conditions. Pea aphid performance (Dixon 1973, Bursell 1974), population dynamics, and seasonal occurrence are affected by temperature (Campbell et al. 1974, Logan et al. 1976, Schowalter 2000). The effects of ambient temperature can interact with host plant characteristics to affect development, fecundity, and mortality (Morgan et al. 2001). Host plant architecture could provide more or less protection from suboptimal temperature, precipitation, humidity, and sunlight. For example, it has been suggested that semileafless morphologies of peas can increase pea aphid exposure to detrimental environmental conditions because of the openness of the canopy (Soroka and MacKay 1990). A comparison between field studies (Soroka and MacKay 1990) and various laboratory studies (Legrand and Barbosa 2000) is complicated by this potential interaction, and we note that, in controlled conditions, authors seem less likely to report large effects of pea morphology on aphid reproduction or population growth rates (Kareiva and Sahakian 1990, Legrand and Barbosa 2000, Soroka and MacKay 1991).

Finally, one of the most important plant characteristics for performance of insect herbivores is the amount of plant nutrients and/or secondary compounds. There is a positive correlation between the amount of nitrogen in plants and the fecundity, reproduction rates, and population growth of herbivorous insects (van Emden 1966, Bentz and Townsend 2001, Sudderth et al. 2005). The nitrogen content in phloem is low compared with other plant parts, so aphids must concentrate nitrogen from their diets for growth and reproduction (Auclair et al. 1957). Nitrogen fertilization has been used to determine the effect of nitrogen availability on plants and sap-sucking insects (Montllor 1991). Nevo and Coll (2001) found a positive correlation between nitrogen fertilization and population growth rate in the melon aphid, Aphis gossypii Glover, on cotton plants, Gossypium hirsutum L. This effect can also be seen when aphids are fed on artificial diets. In a study on pea aphids, ingestion rates increased in diets that contained added amino acids compared with diets without them (Srivastava and Auclair 1974).

This relationship between nutrition and fecundity suggests that studies that have reported significant effects of plant architecture on aphid reproduction may have confounded differences in plant nutrition with differences in morphology. For example, nutrition may vary between cultivars. Sandström and Pettersson (1994) found no difference between the amino acid concentration of a number of pea cultivars, but it is possible that differences in nutrients may appear under particular environmental conditions (e.g., low soil nutrients). In addition, nutrients may differ between plants of the same cultivar with different morphologies because photosynthetic energy gained is determined by plant structure. For example, a leafless plant has a reduced area to collect energy compared with a broad leaf blade morphology. It also seems likely that some structures are more energetically costly to construct. Even in studies in which near-isogenic peas were used (Kareiva and Sahakian 1990; Legrand and Barbosa 2000), it is possible that plants with different morphologies differed in nutrient status. As a result, it is unclear whether any observed correlations between plant architecture and herbivore success is caused by plant morphology per se or
is the result of indirect impact through changes in plant nutrition.

The motivation for this study was to determine the mechanisms that interact with plant architecture to alter aphid reproduction. By simultaneously examining effects of morphology, aphid density, environmental conditions, and plant nutrients on a single cultivar of near-isogenic peas, we hoped to determine the explanation for the contrasting results in the literature. We tested three hypotheses. First, if density dependence is important in regulating aphid reproduction, we expect reproductive rates to be reduced on leafless mutants at high aphid densities, as reported by Kareiva and Sahakian (1990) and others but that reproduction rates would be unaffected by pea morphology at low aphid densities, as suggested by Legrand and Barbosa (2000). This hypothesis is based on the idea that one impact of morphology is to modify the density-dependent regulation of population growth by altering either plant surface area or aphid crowding. We also tested the hypothesis that plant morphology may alter aphid reproduction rates only under suboptimal environmental conditions, which could explain discrepancies between field and laboratory studies (Soroka and MacKay 1990, Legrand and Barbosa 2000). Finally, we tested the novel hypothesis that alteration in aphid reproduction with plant morphology is caused by indirect effects of plant nutrition.

Materials and Methods

The pea plant (Pisum sativum) is ideally suited to study the effects of plant architecture because pea morphology is modified by simple, naturally occurring mutations. We used a near-isogenic line of peas that has reduced stipules (Cv. Frogel), which was obtained from the USDA–ARS Western Regional Plant Introduction Station, Pullman, WA. The morphologies of peas are altered by mutations in the genes af (afila) and tl (acacia). “Normal” (AfAfTlTl genotype) has normal, compound leaves with one to two pairs of leaflets and a number of tendrils. “Tendril” or af (afafTlTl) has leaflets replaced by tendrils (also called “afila”). In “leaflet” or tl (AfAfNlTl), tendrils are converted into leaflets (also called “acacia”). “Parsley” (afafTlTl) has an interaction between the af and tl mutations. It has tiny leaflets and branching petioles (Fig. 1). Phloem-sucking species are ideal for examining effects of plant structure on insect herbivores, because these herbivores have little impact on the structure during feeding. We used pea aphids (Acyrthosiphon pisum) from a laboratory population that was founded with individuals purchased from Carolina Biological Supply (Burlington, NC). At 20–25°C, aphids mature after growing 7–9 d and molting four times (Campbell and MacKauer 1975). Parthenogenic adults produce live young 1 d after maturing and produce 5–15 young per day for ~7 d. We reared pea aphids in the laboratory on fava beans (Vicia faba) and peas (Pisum sativum cultivar Little Marvel) in mesh rearing containers (Bugdorm II; BioQuip products, Rancho Dominguez, CA). The temperature in the laboratory ranged from 18 to 24°C with a photoperiod of 16:8 (LD).

We quantified plant architecture by measuring surface area and fractal dimension. The fractal dimension characterizes the architecture or morphology of a plant (Morse et al. 1985, Gunnarsson 1992, Gee and Warwick 1994) by giving an indication of how completely an object appears to fill space. For example, we expect a lower fractal dimension for morphologies that have a linear and branching structure and a high fractal dimension for those plants with more leaf tissue and less branching.

We produced two-dimensional (2D) projections of the plants by scanning them on a photo scanner (model 3490: Epson Perfection, Long Beach, CA) and converting the image into binary format. We calculated the fractal dimension from the binary file using the box-counting dimension routine in the Frac-Lac 2004 plug-in for the NIH distributed software package Image-J (http://rsb.info.nih.gov/ij/). The box-counting dimension has been well established as a measure of plant architecture (Gunnarsson 1992, Gee and Warwick 1994). The use of 2D projections to analyze 3D structure is based on the projections theorem (Marstrand 1954), which states that the fractal dimension ($D_f$) in $n - 1$ dimensional space is equal to $D_f = 1$, where $n$ is the Euclidean dimension. Experimental studies also have shown that the fractal dimension of 2D projections of root systems and plant structure is correlated with the 3D estimates (Nielson et al. 1997, Walk et al. 2004).

We calculated the surface area of individual plants by analyzing a scan where the tissue of the whole plant was cut into pieces of approximately the same size.
This technique reduces the probability of tissue overlap, which would cause an underestimate of the surface area. Preliminary analysis indicated that tendril plants have a surface area about half that of the other morphologies. As a result, we used two tendril plants compared with one of the other morphologies for all experiments. The fractal dimension was calculated by analyzing individual leaflets with a small piece of attached stem from a given plant (similar to pieces in Fig. 1). Scanning the entire uncut plant gives an overestimate of fractal dimension because of plant tissue overlapping on the scanner. However, scanning the entire plant cut into pieces gives an underestimate because of the increased number of edges included in the estimation.

**Experiment 1: Architecture and Density Effects on Reproductive Rates.** To determine how plant architecture and aphid density may influence pea aphid reproductive rates, we examined the total reproduction of 1, 5, or 10 mature aphids on a single plant (or two tendril plants) over 72 h. Plants were grown in a growth chamber (model PGR15; Conviron, Winnipeg, Manitoba, Canada; 16 L:8 D photoperiod; light levels = 480 μmol; 18.15°C temperature regimen) until they were ≈30 d old (≈20 cm tall). All experimental plants were grown in Fafard 52 mix in 5 in deep by 4 in wide pots. At the end of the growth period, plants were placed in experimental enclosures, which consisted of a circular pot with a piece of circular styrofoam that had a square pot embedded in it. This pot was used to hold a potted plant. A piece of circular acrylic tubing topped with fine mesh (Anti-Viral insect screen; International Greenhouse, Danville, IL) enclosed each experimental plant to prevent the escape of the experimental organisms.

We placed 1, 5, or 10 adult aphids that were 7 d old (±8 h) on the peas to simulate the effects of increased crowding, and the enclosures remained under lights for 72 h. At the end of this period, the number of offspring and their spatial distribution on the peas were recorded. There were a total of 25 replicates for each pea morphology.

To measure the spatial distribution of the aphid nymphs, we took digital photos of a cluster of aphids in a 2 by 2-cm² sampling area. The aphids within the sampling region were marked with a dot in Adobe Photoshop. The x,y coordinate of each point was calculated using the particle counter in ImageJ. A SAS macro created by Moser (1987) was used to calculate the mean nearest neighbor distances. All statistical analysis was completed in SAS (SAS Institute 2007).

**Experiment 2: Architecture and Environmental Effects on Reproductive Rates.** To determine whether plant morphology interacts with environmental conditions to affect aphid reproduction, two sets of greenhouse experiments were conducted. The conditions in the greenhouse were more variable than those in the laboratory, and therefore aphids experienced both higher and lower temperatures. In addition, the pea aphids were subjected to direct sunlight and varying humidity levels. One set of greenhouse experiments was conducted from 6 to 9 February 2008, and a second set of experiments was conducted from 21 to 24 April 2008. February experiments had lower maximum and minimum temperatures than April experiments and lower insolation (refer to Table 1 for more information on environmental conditions). For ≈30 d, six plants of each of three pea morphs (normal, leaflet, and parsley) were grown on a greenhouse bench that had capillary matting and drip lines to supply water (note that there was insufficient seed to conduct experiments on tendril plants). Each of the plants was enclosed with clear acrylic tubing that was topped with antiviral mesh. These enclosures could have increased temperature and humidity experienced by the plants and aphids compared with the surrounding greenhouse environment. Five adult aphids aged 7 d (±8 h) were placed on each morph for 72 h, and the number of offspring were counted.

**Experiment 3: Architecture and Nitrogen Effects on Reproductive Rates.** We examined aphid reproduction on the four pea morphs crossed with a nitrogen fertilization treatment to determine whether there is an interaction between nutrient availability and plant architecture that may affect pea aphid reproduction. Plants received either no fertilization (control) or low (0.22 g/1.1 liter per pot) or high (0.88 g/1.1 liter per pot) levels of ammonium sulfate applied to the soil as a granular form during initial planting. Only nitrogen fertilizer was used because it has been shown that fertilization of peas with phosphorus and potassium is not particularly effective (McKenzie et al. 2001a, b). The plants were grown in a growth chamber (model CEC-3610; pH environmental; 16 L:8 D photoperiod with 18.15°C temperature regimen) until they were ≈30 d old. A single adult aphid aged

<table>
<thead>
<tr>
<th>Date</th>
<th>Outside temperature (°C)</th>
<th>Solar radiation (W/m²)</th>
<th>Greenhouse temperature (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Minimum</td>
<td>Maximum</td>
<td>Minimum</td>
</tr>
<tr>
<td>Feb.</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6 Feb. 2008</td>
<td>1</td>
<td>18</td>
<td>630</td>
</tr>
<tr>
<td>7 Feb. 2008</td>
<td>-2</td>
<td>13</td>
<td>800</td>
</tr>
<tr>
<td>8 Feb. 2008</td>
<td>-7</td>
<td>-2</td>
<td>830</td>
</tr>
<tr>
<td>9 Feb. 2008</td>
<td>-12</td>
<td>-2</td>
<td>410</td>
</tr>
<tr>
<td>April</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>21 April 2008</td>
<td>7</td>
<td>23</td>
<td>1,310</td>
</tr>
<tr>
<td>22 April 2008</td>
<td>12</td>
<td>24</td>
<td>1,330</td>
</tr>
<tr>
<td>23 April 2008</td>
<td>12</td>
<td>25</td>
<td>1,150</td>
</tr>
<tr>
<td>24 April 2008</td>
<td>14</td>
<td>25</td>
<td>900</td>
</tr>
</tbody>
</table>
The surface area of the pea plants was determined by acid digestion followed by Inductively Coupled Plasma (ICP) Emission Spectrometry. Analysis completed by the STAR lab at the Ohio State University.

**Table 2. Mean surface area (cm²) ± SE and mean fractal dimension of the four different pea morphologies with three different initial adult densities**

<table>
<thead>
<tr>
<th>Morphology</th>
<th>Adult density</th>
<th>Surface area (cm²)</th>
<th>Fractal dimension</th>
</tr>
</thead>
<tbody>
<tr>
<td>Normal</td>
<td>1</td>
<td>230 ± 23</td>
<td>1.54 ± 0.014</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>270 ± 22</td>
<td>1.54 ± 0.014</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>240 ± 18</td>
<td>1.54 ± 0.015</td>
</tr>
<tr>
<td>Leaflet</td>
<td>1</td>
<td>250 ± 25</td>
<td>1.60 ± 0.0072</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>240 ± 16</td>
<td>1.60 ± 0.0086</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>220 ± 18</td>
<td>1.60 ± 0.0083</td>
</tr>
<tr>
<td>Parsley</td>
<td>1</td>
<td>230 ± 21</td>
<td>1.49 ± 0.0010</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>200 ± 23</td>
<td>1.48 ± 0.013</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>170 ± 21</td>
<td>1.47 ± 0.015</td>
</tr>
<tr>
<td>Tendril</td>
<td>1</td>
<td>230 ± 25</td>
<td>1.46 ± 0.015</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>220 ± 27</td>
<td>1.44 ± 0.013</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>220 ± 23</td>
<td>1.41 ± 0.015</td>
</tr>
</tbody>
</table>

**Fig. 2.** Mean number of offspring per adult (±SE) for initial number of adults and pea morphologies. There is a significant increase in per capita reproduction with an increase in adult aphid number.

7 d (±8 h) was placed on each pea morph in the experimental enclosures previously described for 72 h, and the number of offspring produced was determined. There were a total of eight replicates for each pea morphology.

To determine plant response to the fertilizer treatments, after the aphids were removed, the experimental plants were dried for 16–20 h in a dehydrator. Percent nitrogen was determined by combustion analysis and the total concentration of major elements was determined by acid digestion followed by Inductively Coupled Plasma (ICP) Emission Spectrometry (analysis completed by the STAR lab at the Ohio State University).

**Results**

**Experiment 1: Architecture and Density Effects on Reproduction.** The surface area of the pea plants was not significantly different between any of the experimental treatments (two-way analysis of variance [ANOVA], $F_{1,288} = 1.31, P = 0.2168$; Table 2), which suggests that the area available to the aphids was similar across all four pea architecture. The fractal dimension of the pea morphologies was significantly different (two-way ANOVA, $F_{3,288} = 97.23, P < 0.0001$; Table 2). A Tukey’s comparison of means indicated that all four morphologies differed from each other.

Plant morphology had no significant effect on the per capita reproduction of pea aphids ($F_{3,288} = 0.30; P = 0.8241$; Fig. 2). These results are consistent with those of Legrand and Barbosa (2000) but were generated using a different experimental protocol. There was a significant difference in the number of offspring per adult for different initial adult densities ($F_{2,288} = 9.53; P < 0.0001$). A Tukey’s comparison of means indicated that there was a positive effect of density on the reproduction of pea aphids. Levene’s test for homogeneity of variance was significant ($F_{1,288} = 2.20; P = 0.0147$), but Welch’s weighted ANOVA indicated that there was a significant effect on mean reproductive rate when the unequal variances were accounted for ($F_{11,113} = 2.21; P = 0.0186$). There was no significant interaction between plant morphology and initial adult density that affected aphid reproduction ($F_{0,288} = 0.69; P = 0.6594$).

Plant architecture did not alter the crowding of aphids. The tendril morph with an initial adult density of five individuals had the highest mean nearest neighbor distance (mean = 0.00036 ± 0.00013 cm), whereas leaflet with an initial adult density of one individual had the lowest (mean = 0.00018 ± 0.000021 cm). However, a two-way ANOVA indicates that plant morphology and initial adult density had no significant effect on the mean nearest neighbor distances ($F_{7,32} = 0.93; P = 0.4974$).

**Experiment 2: Architecture and Environmental Effects on Reproduction.** Analysis of the February greenhouse data indicated that there was no significant difference in aphid reproduction between the pea morphologies (one-way ANOVA, $F_{2,115} = 0.7681; P = 0.7681$; Fig. 3). Analysis of the April greenhouse data indicated that there was a significant difference in aphid reproduction between the morphologies (one-way ANOVA, $F_{2,12} = 5.50; P = 0.0161$; Fig. 3). Tukey’s comparison of means indicated that pea aphids on the leaflet morph had a significantly higher reproductive rate compared with pea aphids on the parsley morph. There was no difference in reproductive rates between normal and leaflet plants.

**Experiment 3: Architecture and Percent Nitrogen Effects on Reproduction.** There was a significant effect of fertilization on the percent nitrogen in the pea plants (two-way ANOVA, $F_{2,172} = 4.89, P < 0.0001$; Fig. 4a). Nitrogen was significantly greater in the 0.88 g fertilization treatment, and the leaflet morphology had significantly higher nitrogen levels than parsley or tendril plants, whereas normal plants had more nitrogen than tendril plants. A smaller number of replicates had sufficient tissue for phosphorus and potassium analysis. Plant morphology and fertilization treatment had no effect on phosphorus content ($F_{1.47} = 0.88; P = 0.5651$; Fig. 4b). The potassium content of leaflet and normal plants was significantly less than that of...
tendril plants \( (F_{3,47} = 6.36; P = 0.0010; \text{Fig. 4c}) \) but did not differ between the fertilization treatments \( (F_{2,47} = 0.74; P = 0.4836) \). However, examination of Fig. 4c does suggest that the higher potassium of tendril plants may have been caused by a different response to the fertilization regimen that we were unable to detect statistically.

We were unable to maintain similar surface area across the different morphologies in the fertilization experiment (two-way ANOVA, \( F_{3,84} = 3.96; P = 0.0108 \)). A Tukey’s comparison of means indicated that leaﬂet and normal plants were signiﬁcantly larger than two tendril plants. The leaﬂet morph was also signiﬁcantly larger than parsley. However, plant surface area did not vary systematically between fertilization treatments \( (F_{2,84} = 0.04; P = 0.9623) \). The fractal dimension of the different peas followed the same pattern as previously observed in experiment 1. The leaﬂet morphology had the highest fractal dimension followed by normal, parsley, and tendril, respectively \( (F_{3,84} = 3.47; P = 0.0197) \). However, Tukey’s analysis of the means indicated that there was only a signiﬁcant difference between the leaﬂet and tendril morphologies. There was no effect of the fertilization on fractal dimension \( (F_{2,84} = 2.33; P = 0.1038) \).

Plant morphology and nitrogen fertilization had no signiﬁcant effect on aphid reproduction (two-way ANOVA, \( F_{11,84} = 1.11; P = 0.3611; \text{Fig. 4d} \)). In addition,
multiple linear regression indicated that there was no linear relationship between aphid reproduction and percent nitrogen, surface area, or fractal dimension ($F_{3,52} = 0.31; P = 0.8179; r^2 = 0.0176$). The peas responded to the fertilization treatment but this did not alter the reproduction of aphids.

Discussion

Our analysis with near-isogenic peas suggests that plant morphology only affects pea aphid reproduction when environmental conditions are suboptimal. Aphid density does have an effect on reproduction. Increasing the initial adult density caused an increase in per capita reproduction across all pea morphologies, but density and aphid crowding did not interact with plant architecture to alter reproductive rates. Finally, the pea nitrogen levels increased with fertilization, but this had no effect on the reproduction of aphids.

Plant morphology had no effect on pea aphid reproduction when surface area is controlled (Fig. 2). These results are consistent with those of Legrand and Barbosa (2000) who also used near-isogenic peas and found no effect of plant morphology on several aphid performance parameters. However, these results may be inconsistent with several studies that have reported differences in aphid population growth on different plant morphologies. Kareiva and Sahakian (1990) also used isogenic peas and found that aphid population growth was slightly reduced on a leafless pea compared with a normal pea when the density of pea aphids is high. Soroka and MacKay (1990) and Sandström and Pettersson (1994) compared different cultivars of peas with differing morphology and reported that pea aphid fecundity and longevity was significantly reduced on semileafless pea cultivars. However, direct comparison to this work is complicated by the possibility that different cultivars differed in factors other than gross morphology (e.g., surface wax).

In our study, we controlled for plant surface area and found that there was no effect of plant morphology on aphid crowding that could have altered density-dependent impacts on reproductive rates. In fact, increasing the number of adult aphids caused increased reproduction or positive density dependence. Agrawal et al. (2004) also found positive density dependence in a study on milkweed aphids on 18 species of milkweed in the field. However, these authors did not identify the possible causes. We speculate that this effect may have resulted from increase resource flow because of increased aphid feeding. It has also been shown that increased aphid damage by *Diuraphis noxia* Kurjiumov, the Russian wheat aphid, increases the concentration of essential amino acids in wheat (*Triticum aestivum* L.), resulting in a nutritionally enhanced diet (Telang et al. 1999).

It is possible that negative density dependence could have an impact on aphid reproduction that interacts with plant shape, where aphid densities are higher than those studied here. Such negative density dependence could possibly explain the reported reductions in pea aphid longevity and population growth rates on semileafless peas. Because tendril plants (i.e., semileafless) were observed to have the smallest surface area in our study, they are most likely to produce negative density-dependent controls of reproduction at higher aphid densities. It is possible that the effects observed by other authors were driven by negative density dependence that differed between morphs, but which was not observed in our study because of lower aphid densities or controlled surface areas. However, the mean nearest neighbor distances measured in this study were not significantly different between the morphologies. Therefore, it seems unlikely that the different pea morphologies will have an impact on aphid crowding at higher densities. If surface area is controlled, we predict that negative density dependence will not interact with pea morphology even at high aphid densities.

We found that plant morphology alters aphid reproduction under greenhouse conditions. In the February greenhouse experiments, with cool temperatures and low insolation, there was no effect of plant morphology on aphid reproduction, but in the April greenhouse experiment, with warm temperatures and high insolation, there was a significant effect of morphology on aphid reproduction. The aphids on the leaflet morph had significantly higher reproduction compared with those on the parsley morph (Fig. 3). Dunbar et al. (2007) have shown that at high temperatures (35°C) symbiotic gut bacteria are killed, which causes aphids to become sterile because of the lack of essential nutrients for reproduction. We suggest that the leaflet morph could be providing some protection against high temperatures and direct sunlight, possibly preventing desiccation or sterilization that occurred on the parsley morph. Soroka and MacKay (1990), who worked with different cultivars in field conditions, also suggested that a semileafless cultivar exposed aphids to adverse weather conditions because of the openness of the canopy.

Plant structure and percent nitrogen did not have an effect on pea aphid reproduction. Different pea morphologies did differ in nutrients, and the pea plants did respond to the highest fertilization treatment. Peas in the highest fertilization treatment (0.88 g N) had the highest percent nitrogen in all of the morphologies compared with the control and the 0.22 g N treatment. The leaflet morph had the highest percent nitrogen followed by normal, parsley, and tendril, respectively (Fig. 4a). Phosphorus and potassium did not differ between fertilization treatments; however potassium levels did differ between pea morphologies (Fig. 4b and c). Tendril plants had greater potassium levels than leaflet or normal morphologies. However, pea aphids did not respond to changes in plant nitrogen or differences in potassium (Fig. 4d).

These results are inconsistent with other reports of positive effects of nitrogen on herbivore growth, development, and reproduction (van Emden 1966, Janson and Ekblom 2002, Sudderth et al. 2005), but those studies were not conducted on nitrogen-fixing plants such as peas. It may be that the aphids are not significantly nitrogen limited on these types of plants and...
thus there is no impact of nitrogen on reproduction. In support of this hypothesis, we note that the nitrogen content of our plants was a little higher than the nitrogen content found in a pea variety that is susceptible to aphid infestation with a mean total percent nitrogen of 3.128 (Maltais 1951). Similarly, Sandström and Pettersson (1994) found that amino acid composition did not differ significantly between five pea genotypes and aphid reproduction was not determined by nitrogen levels.

In conclusion, we found no evidence pea morphology per se could affect pea aphid reproduction. Some previous studies (Soroka and MacKay 1990, Sandström and Pettersson 1994) that report differences in aphid reproduction or population growth with differences in pea morphology have compared different cultivars. Different cultivars of peas could have different allelochemicals or surface waxes that impact aphid reproduction. By using a line of near-isogenic peas that differ in morphology, we eliminated the possibility that any observed effects were driven by differences between pea cultivars.

Our examination of the interaction of morphology with other factors also suggest that it is unlikely that differences in aphid crowding or plant nutrients between morphologies occur. However, we do not claim that all previous reported effects of morphology on pea aphid reproduction were actually caused by cultivar differences. Although not conclusive, our April greenhouse experiment suggests that pea morphology may interact with environmental conditions to alter aphid reproduction. We found the lowest reproductive rates on peas that provided the lowest amount of shelter for aphids. Soroka and MacKay (1990) also suggested a simple explanation for alteration in aphid population growth rates across cultivars with different morphologies under field conditions. We conclude that environmental exposure that varies with plant morphology or negative-density dependence that depends on plant surface area are two possible explanations for the effects reported by Soroka and MacKay (1990), Sandström and Pettersson (1994), and Kareiva and Sahakian (1990).

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