HERBIVORY, PLANT DENSITY, AND PLANT REPRODUCTIVE SUCCESS: THE EFFECT OF BATTUS PHILENOR ON ARISTOLOCHIA RETICULATA

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Abstract. The pipevine swallowtail butterfly, Battus philenor, normally consumes ~45% of the annual leaf crop of its primary host plant in east Texas (USA). Aristolochia reticulata. Feeding by larvae significantly increases plant mortality and decreases plant growth rate. No direct effects of larval feeding on reproduction were detected, but a substantial decrease in seed production per plant is inferred from the increased mortality and decreased growth rates.

Plants grown experimentally at high density had the same probability of having eggs laid on them as did plants grown at low density. The actual number of leaves eaten per plant was also similar for plants grown at both densities. Larval feeding increased mortality and decreased plant growth rate by similar amounts at both high and low plant density. There was also no evidence that seed production was greater at one plant density than at another. The pipevine swallowtail thus does not appear to regulate the density of local patches of Aristolochia. These experimental results do not rule out the possibility of regulation by a numerical response of the butterfly to increases in host population densities throughout large areas of habitat.

These results suggest that the pipevine swallowtail has exerted a potent selective pressure molding the evolution of A. reticulata. Three characteristics of this plant species may be interpreted as adaptive responses to this pressure: tough, nutrient-poor leaves; underground flowering and fruiting; and a high root/shoot ratio.

Key words: Aristolochia; Battus; coevolution; herbivory; plant demography; predation; swallowtails.

INTRODUCTION

Many authors have suggested that herbivorous insects have greatly influenced the evolution and population dynamics of land plants (Fraenkel 1959, 1969, Gillett 1962, Ehrlich and Raven 1964, Feeny 1976, Rhoades and Cates 1976). One implication of this suggestion is that herbivorous insects commonly decrease the reproductive success or fitness of the plants on which they feed. Although there are numerous examples of seed-eating insects reducing the fitness of their host plants (e.g., Janzen 1971a, b, c, Green and Palmblad 1975, Moore 1978a, b), similar examples involving natural populations of foliage-feeding insects are uncommon or poorly quantified (Harper 1977; but see Janzen 1966, Cantlon 1969, Morrow and Lamarche 1978). We report here the effects of one foliage-feeding insect on the reproductive success and population dynamics of its primary host plant.

In this investigation we attempted to answer two questions. The first question was simply, “By how much does the insect lower the reproductive success of its host plant?” Previous attempts to answer this question using leaf-feeding insects have usually yielded ambiguous results. Much of the reason for this ambiguity is that investigators have usually resorted to artificial methods such as manual clipping of foliage and growing plants in greenhouses, weed-free monocultures, or other artificial environments (Knight and Hollowell 1962, Womack and Thurman 1962, Collins and Aitken 1970, Maun and Cavers 1971, Rockwood 1973, Cates 1975, Waloff and Richards 1977). The response of plants to herbivory in artificial environments may be quite different from their response in the natural conditions in which they have evolved, especially since one of the most important effects of herbivory may be to upset the competitive balance between two plant species or individuals (Sibma et al. 1964, Harper 1977). Furthermore, while experiments using artificial methods measure the effect of a certain degree of herbivory on an individual plant, they seldom take into account the fraction of plants in the population that normally experiences that degree of herbivory. Consequently, they do not measure the effects of natural herbivore populations on the populations of their host plants. This study was designed to alleviate these problems by transplanting experimental plants into their natural environment and by exposing them to natural populations of the herbivore.

The second question we attempted to answer in this investigation was, “Does plant density affect the degree to which the herbivore reduces plant reproductive success?” Several studies of leaf-feeding insects suggest that plants growing at high densities are subject to greater herbivore attack than plants growing at low densities (Dethier 1959, Cantlon 1969, Orians et al. 1975) and growing plants in greenhouses, weed-free monocultures, or other artificial environments (Knight and Hollowell 1962, Womack and Thurman 1962, Collins and Aitken 1970, Maun and Cavers 1971, Rockwood 1973, Cates 1975, Waloff and Richards 1977). The response of plants to herbivory in artificial environments may be quite different from their response in the natural conditions in which they have evolved, especially since one of the most important effects of herbivory may be to upset the competitive balance between two plant species or individuals (Sibma et al. 1964, Harper 1977). Furthermore, while experiments using artificial methods measure the effect of a certain degree of herbivory on an individual plant, they seldom take into account the fraction of plants in the population that normally experiences that degree of herbivory. Consequently, they do not measure the effects of natural herbivore populations on the populations of their host plants. This study was designed to alleviate these problems by transplanting experimental plants into their natural environment and by exposing them to natural populations of the herbivore.

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ute to the regulation of plant density. Other studies, by contrast, have shown that leaf-feeding insects may actually be found more commonly on plants growing at low densities (Pimentel 1961, Way and Heathcote 1966, A'Brook 1968, 1973, Heathcote 1969, Jones 1977). In this case, insect attack may act to promote a local increase in plant density rather than to limit it. In none of these studies, however, has the increased or decreased herbivore load that accompanies a change in plant density been shown either to increase or to decrease the reproductive success of the plants being attacked. Moreover, at least one study has revealed that different insects feeding on the same plant species may respond to plant density in opposite ways (Cromartie 1975). It is thus often difficult to predict the overall effect of plant density on the degree of herbivore reduction of plant reproductive success. By studying a simple system consisting of one major insect herbivore and one plant species and by measuring the effects of herbivory on various components of plant reproductive success, we attempted to determine whether the herbivore actually contributes to the regulation of the density of its host plant.

The plant-insect association we examined was the pipevine swallowtail butterfly, Battus philenor (Lepidoptera: Papilionidae), and its primary larval host plant in the Big Thicket region of southeast Texas, the Texas Dutchman's-pipe Aristolochia reticulata (Aristolochiaceae) (Scriber and Feeny 1976). Several characteristics of this association make it highly suitable for a study of this type. The association is very simple: B. philenor is the only important herbivore feeding on A. reticulata in southeast Texas. During three seasons of fieldwork we found only one other herbivore, a small, unidentified leaf-rolling caterpillar, feeding on A. reticulata. This caterpillar was very rare; in examining over 10,000 plants we saw fewer than 15 individuals. Because of the rarity of this insect and because its feeding damage is distinct from that caused by B. philenor larvae, most feeding damage can be attributed unequivocally to B. philenor. A second advantageous feature of the Battus-Aristolochia association is that the plants are small, erect, perennial herbs that reproduce entirely by seed. Their discrete growth form facilitates measurement of growth rates, mortality, and reproduction for individual plants.

The pipewine swallowtail is found primarily in the open pine upland habitat of southeast Texas, as is A. reticulata (see Watson 1975 for a description of the habitat). Normally B. philenor has two adult broods per year. The first brood emerges in mid-March, at which time females lay most of their eggs on A. reticulata. The eggs hatch =1 wk after being laid. One plant seldom has enough foliage to support the complete growth and development of a larva, which must search for other host plants after it eats all the edible foliage on the plant on which it hatches. Although a larva consumes much of the foliage of the plant on which it hatches, it obtains most of the foliage it consumes from subsequent plants. A second brood of adults emerges in mid-May. The females lay most of their eggs on a second food plant, Aristolochia serpentaria, also a small, erect, perennial herb that does not have enough foliage to support the complete development of a larva. Larvae produced by second-brood females must also locate additional food plants, a large fraction of which are A. reticulata. Consequently, A. reticulata suffers extensive damage from second-brood larvae even though second-brood females lay very few eggs on that species. Most larvae produced by second-brood females pupate by the 1st wk in July; very little feeding damage occurs after that time (see Rausher 1979, 1980) for further details of the natural history of B. philenor.

**Methods**

**Study area**

This study was conducted at the "Camp Waluta" study site on the J. A. Vickers survey tract in Hardin County, Texas (for a detailed description see Rausher 1979). The tract is located near Camp Waluta, =10 km north of Silsbee, Texas and 6 km west of Texas Farm Road 92. The area consists mostly of open longleaf pine woods (Fig. 1). We performed our experiments in an area of =100 ha that had been burned 4 yr prior to the study.

In east Texas, periodic fires maintain the natural longleaf pine disclimax by preventing the encroachment of species characteristic of the nearby beech-magnolia-loblolly forest (Watson 1975). Aristolochia reticulata is a characteristic fire-adapted species of the herbaceous layer in the open pine woods. Individual plants readily produce a new shoot and leaves after a fire and suffer little associated mortality (M. Rausher, personal observation). Populations of the pipewine swallowtail also do not appear to be greatly affected by occasional fires, probably because most fires occur between July and March when the butterfly is in pupal diapause (M. Rausher, personal observation). The normal pupation site for diapausing butterflies is on tree trunks several metres aboveground and out of danger from ground-level fires.

**Measurement of feeding damage effects**

Ideally, the effects of feeding damage should be measured by the reduction in lifetime reproductive success caused by feeding. By reproductive success we mean the average number of seeds a plant produces during its lifetime, starting as a seedling and taking both mortality and reproduction into account. Because A. reticulata plants may live for 20 yr or longer, however, direct measurement of lifetime reproductive success was not feasible. Instead, we attempted to measure the effects of natural levels of herbivory on three components of reproductive success: annual survivor-
ship, growth rate, and seed production per season. Feeding damage may lower any or all of these components and thus lower the reproductive success of plants exposed to herbivory below that of plants protected from herbivory. We also attempted to determine whether the effect of herbivory on these components varied at different plant densities.

_A. reticulata_ plants that had been collected in the field were washed, weighed, and transplanted into one of four treatment plots. The four plots were located in an area of open longleaf pine habitat in which _A. reticulata_ plants grew naturally. The plants were placed in the ground with as little disturbance to the natural vegetation of the plots as possible. All _A. reticulata_ plants growing naturally in the plots were removed prior to transplanting the experimental plants. Each plot consisted of plants grown at one of two densities and either protected from or exposed to _Battus philenor_. The four treatments were thus (1) high density—protected, (2) high density—exposed, (3) low density—protected, and (4) low density—exposed. The two densities used were 0.33 plants/m² and 4.0 plants/m². Within the pine upland habitat, naturally growing _A. reticulata_ plants are distributed somewhat patchily. The density values used in the experiment approxi-

mate the extremes of local density found in natural populations (Rausher 1979).

The protected plants had a 7.5 cm high circular aluminum barrier placed around them and sunk into the ground =1.23 cm. The outside surface of the barrier was coated with Tanglefoot (The Tanglefoot Company, Grand Rapids, Michigan), which prevented wandering larvae from crawling onto the plant. Once a week eggs that were laid on the protected plants were removed before hatching. There was no aluminum barrier surrounding exposed plants nor were eggs removed from them. Each plot contained 101 plants. In order to minimize traumatization of plants due to transplanting, the transplants were performed in December 1975, after the aboveground parts had died back to the ground and the roots were dormant. The plants remained dormant in the ground for 3 mo; in mid-March 1976, they began putting up new leaves at the same time as the undisturbed _A. reticulata_ plants in the habitat. Before transplanting, the plants had been assigned to plots such that each plot started with a similar frequency distribution of plant root masses. The position of each plant in a plot was marked with a 30 cm high numbered surveyor’s flag.

We recorded feeding damage by censusing all plants approximately every 7 d during the periods March–September 1976 and March–June 1977. During each census we recorded the number of eggs and larvae present on each plant. We also estimated to the nearest quarter the proportion of each leaf eaten. From these estimates we were able to reconstruct the history of each leaf on each plant throughout the season and hence determine for each plant the number of new leaves produced each week as well as the number of leaves eaten.

Plant growth rates were determined by measuring the gain in root mass over the course of the experiment. Root mass is an appropriate measure of plant size in _A. reticulata_ for several reasons. The root/shoot ratio is high (=2.3); the roots therefore make up a large fraction of the standing biomass of the plant. Root mass is also well correlated with reproductive effort and seed output (see below). Finally, root mass fluctuates less widely than the mass of the aboveground parts, which may decrease from some high value to zero in 1 d due to feeding by _B. philenor_ larvae. The roots of _A. reticulata_ have very few fine hairs that are lost when the plants are dug up. Moreover, the roots do not extend laterally or vertically > ≈15 cm. We could therefore recover virtually 100% of the roots when they were excavated.

After the plants were dug up in December 1975, and before they were transplanted, the roots were washed to remove adhering soil. They were then blotted dry, weighed, and transplanted into the treatment plots. An additional set of plants was cleaned, weighed, oven dried, and weighed again to determine the fraction dry mass. The plants that remained alive at the end of the

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Fig. 1. Longleaf pine (Pinus palustris) habitat, Camp Waluta study site, Hardin County, Texas.
experiment were dug up again in early July 1977. The soil was washed from their roots, which were then frozen and later freeze-dried. Growth rates were measured as the gain in dry mass.

Mortality rates were determined simply as the fraction of plants in each plot that had died by the end of the experiment. A plant was considered dead if no trace of it could be found when we attempted to dig it up for weighing at the end of the experiment. In practice, there was no ambiguity in determining whether a plant was dead or alive.

We measured plant reproduction in two ways. The total number of seeds produced by each plant was counted in June 1977. We also estimated the total reproductive expenditure of each plant by the dry mass of inflorescences it produced. Because *A. reticulata* flowers and fruits underground, reproductive structures could be counted and weighed only by digging up the plants. For this reason annual seed production and total reproductive expenditure were determined only during the 2nd yr, when all plants in all treatments were dug up.

**Seed-set as function of root mass**

In July 1976, during the period of peak seed production, 119 plants growing naturally outside the experimental plots were dug up. Each plant was separated into roots, stems, leaves, and reproductive parts, and the separate parts were oven dried and weighed. The seeds were dissected out of the fruiting capsules and counted to estimate the mean number of seeds produced per plant with a given root mass.

**Analysis of plant size distributions**

To estimate the effects of herbivory on the overall reproductive success of *A. reticulata* plants, we calculated first the expected root growth and, second, the expected number of seeds produced by a seedling over its 1st 20 yr of growth for plants exposed to and protected from herbivory. These estimates were obtained by using projection matrices, the values of which were determined by the data collected in the experiments described above. For plants with root dry masses initially <0.1 g (e.g., seedlings), the expected frequency distribution of root masses after a given number of years of growth was determined using a modification of standard growth matrix techniques (Leslie 1945, Lefkovitch 1965, Usher 1966, 1969, Hartshorn 1975). Each entry \( g_{ij} \) in such a matrix, \( G \), represents the probability that a plant originally in root mass class \( i \) would be in mass class \( j \) at the end of two growing seasons (the effective length of the experiment). A separate growth matrix was calculated for each density-herbivory treatment in the transplant experiment described above. In addition, the plants for each density treatment were pooled within each exposure treatment to yield a combined matrix for each of the two exposures. The entries \( g_{ij} \) for each treatment matrix were estimated simply by the fraction of plants initially in mass class \( i \) in that treatment that were in mass class \( j \) at the end of the experiment. Because some mortality may occur, the sum of the \( g_{ij} \) for any given \( i \) can be <1.0. Six different mass classes were used: 0–0.1, 0.1–0.2, 0.2–0.4, 0.4–0.8, 0.8–1.6, and 1.6–3.2 dry mass.

For a cohort of 100 plants initially in mass class 1 (0–0.1 g), the expected distribution among mass classes after \( 2n \) yr was found by the equation

\[
A_{2n} = A_0 G^n,
\]

where \( A_0 \) is the vector representing the initial distribution of individuals among size classes and is given by

\[
A_0 = (100, 0, 0, 0, 0, 0).
\]

\( A_{2n} \) is the vector representing the distribution of individuals among mass classes after \( 2n \) yr of growth, and \( G \) is the \( 6 \times 6 \) growth matrix as already defined. Because the experimental plants were in the ground for two seasons the growth matrix represents changes in plant size that occurred over a 2-yr period. Consequently, application of the matrix \( n \) times represents \( 2n \) yr of growth.

The expected number of seeds produced by a plant a given number of years after reaching mass class 1 was calculated using the size distribution matrices \( (A_{2n}) \). The equation used was

\[
m_{2n} = 2A_{2n} R',
\]

where \( m_{2n} \) is the total number of seeds produced by an initial cohort of 100 plants during the period \( 2n \) to \( 2n + 2 \) yr after reaching mass class 1, \( A_{2n} \) is the vector described above, and \( R \) is the \( 1 \times 6 \) reproductive vector. The expected number of seeds produced by an individual plant is \( (m_{2n})/100 \). \( R \) was calculated using the data collected from the 119 naturally growing plants described above. The plants were divided into the six mass class categories and the mean number of seeds produced per plant was calculated for the plants in each mass class. The factor two in Eq. 3 is necessary because \( R \) represents the number of seeds produced in 1 yr, while \( m_{2n} \) represents the number of seeds produced over a 2-yr period.

Ideally, a separate \( R \) matrix should have been obtained for each density-exposure treatment in the transplant experiment. The plants in these treatments produced few seeds during the 2nd yr of the experiment, however, making calculations of separate \( R \) matrices impossible. The use of a common \( R \) matrix ignores the possibility that the effect of herbivory on *A. reticulata* may be first to reduce annual seed production, with a reduction in growth rate also occurring only if herbivore damage is great enough. Estimating the effects of herbivores on seed production in this manner thus probably underestimates herbivore impact on plant reproductive success to some extent.
TABLE 2. Mean number of leaves eaten by larvae per week in exposed treatment plots.

<table>
<thead>
<tr>
<th>Density treatment</th>
<th>Year</th>
<th>High</th>
<th>Low</th>
<th>( P^* )</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1976</td>
<td>23.8</td>
<td>24.5</td>
<td>&gt;.10, NS</td>
</tr>
<tr>
<td></td>
<td>1976†</td>
<td>30.2</td>
<td>21.6</td>
<td>&gt;.10, NS</td>
</tr>
</tbody>
</table>

* Wilcoxon matched-pairs signed-ranks test (Siegel 1956).
† 14 March–4 July.
‡ 16 March–24 June.

the exposed treatments also produced new leaves rapidly during the first month of the season. In early April, however, the number of leaves per plant began to decrease and did not begin to rise again until late April or early May. Another decline in the number of leaves present began in late May or early June, with the number of leaves present beginning to increase again 2 or 3 wk later. These fluctuations in number of leaves present per plant occurred during the periods of peak abundance of fourth- (penultimate) and fifth- (ultimate) instar *B. philenor* larvae. The number of leaves present decreased when more leaves were eaten than were produced in a given week. As larvae entered the pupal stage fewer leaves were eaten, plants produced new leaves to replace those that had been eaten, and the number of leaves present began to increase again.

Plants growing at high density had neither a greater nor a lesser probability of being oviposited on than did plants growing at low density (Table 1). Ovipositing female butterflies thus do not appear to respond to local changes in plant density. Feeding damage does not appear to be affected by plant density either. For plants in the two treatments exposed to herbivory, the mean number of leaves eaten weekly did not differ significantly in either 1976 or 1977 (Table 2).

TABLE 3. Number and fraction (in parentheses) of *A. reticulata* plants dying in protected and exposed treatments between December 1975 and July 1977. Each treatment contained 101 plants.

<table>
<thead>
<tr>
<th>Density treatment</th>
<th>Exposure treatment</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Protected</td>
</tr>
<tr>
<td>High</td>
<td>1 (0.01)</td>
</tr>
<tr>
<td>Low</td>
<td>3 (0.03)</td>
</tr>
</tbody>
</table>

\( G \)-tests for differences in percentages (Sokal and Rohlf 1969):
1) High-protected vs. high-exposed treatments
\( G = 7.70, P < .01 \)
2) Low-protected vs. low-exposed treatments
\( G = 3.33, .05 < P < .10 \)
3) Overall, protected vs. exposed (high and low densities combined)
\( G = 10.01, P < .01 \)

**RESULTS**

*Feeding damage*

During most of the 1976 and 1977 seasons the plants in the two treatments exposed to *Battus philenor* larvae had only about half as many leaves as the plants in the two protected treatments (Fig. 2). The number of leaves in the protected treatments increased rapidly during the first month of the season. The rate of production of new leaves then decreased, although plants sporadically produced a few new leaves throughout the season, as is indicated by the more or less steady increase in number of leaves per plant. The plants in

TABLE 1. Number of plants oviposited on per 101 plants in exposed treatments. NS = not significant in this and all subsequent tables.

<table>
<thead>
<tr>
<th>Density treatment</th>
<th>Year</th>
<th>High</th>
<th>Low</th>
<th>( P^* )</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1976</td>
<td>25</td>
<td>21</td>
<td>&gt;.10, NS</td>
</tr>
<tr>
<td></td>
<td>1977</td>
<td>5</td>
<td>7</td>
<td>&gt;.10, NS</td>
</tr>
</tbody>
</table>

* \( G \) test (Sokal and Rohlf 1969).
Mortality rates

The effects of larval feeding on Aristolochia reticulata are immediately apparent when mortality rates are compared between exposed and protected plants. Over the 2 yr of the experiment, plants exposed to herbivory had a mortality rate of 9%, 4.5 times greater than the mean mortality rate for protected plants ($P < .01$, Table 3). Although the data in Table 3 cannot be tested for the presence of an interaction between density and exposure, exposure to larval feeding appears to increase plant mortality by similar amounts at both densities (6 vs. 8%). The mortality rates of protected plants are not significantly different at the two densities, while the mortality rates of exposed plants are identical at the two densities.

Growth rates

To compare the effect of larval feeding on plant growth rate, we converted the original fresh mass of each plant to dry mass using the formula

$$D = F \times \frac{D}{F},$$  \hspace{1cm} (4)

where $D$, $F$, and $D/F$ are dry mass, fresh mass, and fraction dry matter, respectively. Fraction dry matter was not constant, but, over the range of root masses we obtained, was correlated with original fresh mass. This relationship can be expressed by the following equation:

$$\frac{D}{F} = aF + b,$$  \hspace{1cm} (5)

where $F$ and $D$ have units of grams and $a$ has units of grams⁻¹. The values obtained for $a$ and $b$ were .01456 and .2535, respectively ($r = .58$, $n = 20$, $P < .05$). Consequently, by substituting (5) with these numerical values into (4), we obtained the original dry mass of a root from the equation:

$$D = F \times [0.01456F + .2535].$$  \hspace{1cm} (6)

In all four density exposure treatments there is a significant positive correlation between final and original root masses (Fig. 3). This result by itself is not surprising, since it means simply that small plants do not grow to be large plants in only 2 yr. To determine how much a plant with a given initial mass grew during the experiment, the regression line should be compared with the line $y = x$, which represents no growth and no loss in mass. Thus, the low-density, protected-treatment plants with initial masses $\leq 0.75$ g tended to increase in mass, since below that mass the regression line lies above the line $y = x$. By contrast, plants with original root masses $> 0.75$ g lost mass, on the average, although some clearly increased in size.

For both the high- and low-density plots the regressions for the exposed-treatment plants lie below those for the plants in the protected treatment (Fig. 3). The biological meaning of this relationship is that for a given initial root mass, the final root mass is greater for plants protected from herbivory. The significance of this difference in mass gain was tested by an analysis of covariance (ANCOVA) with original root mass as the covariate. Because the residual variances of the regressions of final dry mass on original dry mass for the four treatments were highly heteroscedastic ($F_{\text{max}4,87} = 4.64$, $P < .001$, Sokal and Rohlf 1969), the final dry masses were transformed to logarithms before performing the ANCOVA. Although the variances remained slightly heteroscedastic after the transformation ($F_{\text{max}4,87} = 1.93$, .05 $< P < 0.1$), the results should not be greatly affected, since analysis of variance procedures are not very sensitive to moderate heteroscedasticity (Sokal and Rohlf 1969). Preliminary analysis (using log-transformed data) of the four treatment slopes revealed that the slopes were homogeneous ($F_{3,36} = 1.33$, $P > .25$). A test for differences among adjusted means (y-intercepts) was therefore valid.

There is a highly significant effect of exposure treatment on regression intercept ($P < .0001$, Table 4).
Table 4. Analysis of covariance of final dry mass of roots on initial dry mass. Final dry masses have been transformed to logarithms to make the variances homogeneous.

<table>
<thead>
<tr>
<th>Source</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial mass</td>
<td>167.66</td>
<td>1</td>
<td>167.66</td>
<td>320.9</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>(covariate)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Exposure</td>
<td>54.4</td>
<td>1</td>
<td>54.4</td>
<td>104.13</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Density</td>
<td>3.3</td>
<td>1</td>
<td>3.3</td>
<td>6.35</td>
<td>&lt;.05</td>
</tr>
<tr>
<td>Interaction</td>
<td>0.02</td>
<td>1</td>
<td>0.02</td>
<td>0.04</td>
<td>&gt;.80, NS</td>
</tr>
<tr>
<td>(exposure ×</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>density)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Error</td>
<td>191.2</td>
<td>366</td>
<td>0.52</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>416.6</td>
<td>370</td>
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</tbody>
</table>

The growth rate of protected plants is thus greater than the growth rate of plants exposed to herbivory. There is also a weak but significant density effect ($P < .05$, Table 4). Plants growing at high density have a lower growth rate than plants growing at low density (mean y-intercepts are −2.25 and −1.87 for high- and low-density plants, respectively).

Plant density does not appear to influence the degree to which feeding by *B. philenor* larvae reduces plant growth rates. The low and nonsignificant interaction term in the ANCOVA ($P > .8$, Table 4) indicates that herbivory reduces growth rate by similar amounts at high and low plant density. This result is expected, since feeding damage is similar at both density treatments (Table 2).

**Reproduction**

When the plants in the four treatments were dug up at the end of the experiment, we found that none had produced seeds during the 2nd yr of the experiment. Consequently, seed production by plants exposed to and protected from herbivory could not be compared directly. Many plants in the protected treatments had begun to produce inflorescences, however, while very few in the exposed treatments had produced any (Table 5). To the extent that the expenditure involved in producing inflorescences is correlated with the number of seeds that a plant will produce later in the season, protected plants would appear to be more successful at producing seeds than plants unprotected from larval feeding.

**Plant size and reproductive success**

Because plants were not excavated during the 1st yr of the experiment, the number of seeds produced per plant was not determined. Nevertheless, during March of the 2nd yr of the experiment seven seedlings were found in the two protected-treatment plots, while none appeared in the plots exposed to herbivory. Since each of the seedlings was within 5 cm of a transplanted plant, each was probably produced by a protected plant in 1976. Although these numbers are too small for statistical analysis, they suggest that protected plants produce more seeds than exposed plants.

Table 5. Mean dry mass (mg) of inflorescences per *A. reticulata* plant in early July 1977. Abbreviations as in Figs. 2 and 3.

<table>
<thead>
<tr>
<th>Original root mass (g)</th>
<th>HE</th>
<th>HP</th>
<th>LE</th>
<th>LP</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.0–0.5</td>
<td>0</td>
<td>0.68</td>
<td>0.56</td>
<td>1.11</td>
</tr>
<tr>
<td>0.5–1.0</td>
<td>0</td>
<td></td>
<td>0.25</td>
<td>0.48</td>
</tr>
<tr>
<td>1.0–1.5</td>
<td>0</td>
<td>0.56</td>
<td>0.25</td>
<td>3.64</td>
</tr>
<tr>
<td>1.5–2.0</td>
<td>0</td>
<td>0.56</td>
<td>0.25</td>
<td>0.76</td>
</tr>
<tr>
<td>2.0–3.0</td>
<td>0</td>
<td>0.56</td>
<td>0.25</td>
<td>10.16</td>
</tr>
<tr>
<td>3.0–6.0</td>
<td>0</td>
<td>0.56</td>
<td>0.25</td>
<td>5.27</td>
</tr>
</tbody>
</table>
Table 6. Growth matrices for *A. reticulata* plants in protected and exposed treatments. Each entry \( x_{ij} \) is the probability that a plant initially in mass class \( i \) (rows) will be in mass class \( j \) (columns) after 2 yr. The values in the **Dead** column are the fractions of plants initially in the indicated size class that died during the experiment. The **Dead** column is not part of the growth matrix, \( G \), used in Eq. 1. Each matrix is based on 202 plants. Data for high and low density treatments combined.

<table>
<thead>
<tr>
<th>Dry mass of root at end of experiment (g)</th>
<th>0–0.1</th>
<th>0.1–0.2</th>
<th>0.2–0.4</th>
<th>0.4–0.8</th>
<th>0.8–1.6</th>
<th>1.6–3.2</th>
<th>Dead</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Protected plants</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0–0.1</td>
<td>.358</td>
<td>.377</td>
<td>.208</td>
<td>.038</td>
<td>0</td>
<td>0</td>
<td>.019</td>
</tr>
<tr>
<td>0.1–0.2</td>
<td>0</td>
<td>.275</td>
<td>.450</td>
<td>.200</td>
<td>.050</td>
<td>0</td>
<td>.025</td>
</tr>
<tr>
<td>0.2–0.4</td>
<td>0</td>
<td>.024</td>
<td>.220</td>
<td>.683</td>
<td>.024</td>
<td>0</td>
<td>.049</td>
</tr>
<tr>
<td>0.4–0.8</td>
<td>0</td>
<td>0</td>
<td>.079</td>
<td>.421</td>
<td>.500</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>0.8–1.6</td>
<td>0</td>
<td>0</td>
<td>.050</td>
<td>.200</td>
<td>.700</td>
<td>.050</td>
<td>0</td>
</tr>
<tr>
<td>1.6–3.2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>.750</td>
<td>.250</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><strong>Exposed plants</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0–0.1</td>
<td>.681</td>
<td>.064</td>
<td>.043</td>
<td>0</td>
<td>.021</td>
<td>0</td>
<td>.191</td>
</tr>
<tr>
<td>0.1–0.2</td>
<td>.450</td>
<td>.375</td>
<td>.050</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>.125</td>
</tr>
<tr>
<td>0.2–0.4</td>
<td>.051</td>
<td>.385</td>
<td>.333</td>
<td>.154</td>
<td>0</td>
<td>0</td>
<td>.077</td>
</tr>
<tr>
<td>0.4–0.8</td>
<td>.024</td>
<td>.171</td>
<td>.415</td>
<td>.317</td>
<td>.024</td>
<td>0</td>
<td>.070</td>
</tr>
<tr>
<td>0.8–1.6</td>
<td>0</td>
<td>.077</td>
<td>.115</td>
<td>.731</td>
<td>.077</td>
<td>0</td>
<td>.007</td>
</tr>
<tr>
<td>1.6–3.2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>.500</td>
<td>.500</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

The correlation between root mass and number of seeds produced, although highly significant \((P < .01)\), explains only \( \approx 16\% \) of the total variance in seed production. The great residual variation is due to the fact that some plants produce many seeds, while most other plants in the same mass class produce none. The cause of this large variation in seed production is not known, but in view of the extensive feeding by *B. philenor* larvae, it is likely that at least some of the variation is caused by differences in herbivore damage to individual plants.

*Plant growth rates and size distributions*

The results already presented demonstrate that feeding by *B. philenor* larvae under natural conditions significantly lowers the growth rate and survivorship of *A. reticulata* plants. The interaction of these two effects both decreases the probability that a seedling will survive to the size at which reproduction begins, and increases the time taken to reach that size. This interaction is easily visualized by examining growth matrices for plants in the exposed and protected treatments. Because plant density does not appear to influence the effects of herbivory on the components of plant reproductive success, and because the effect of plant density on growth rate is minor, the present analysis combines the plants in two density treatments to yield one pooled growth matrix for each exposure treatment. The results of comparing exposed and protected plants for each density treatment separately are very similar to those obtained by combining the data.\(^3\)

Examination of the pooled growth matrices (Table 6) reveals that for the plants in the protected treatments, most of the numbers above the main diagonal are large, whereas the numbers below the main diagonal are small. In other words, there are many more plants that increase in size than decrease. The plants in the exposed treatments show the opposite trend: numbers above the main diagonal are small, whereas those below the main diagonal are large. Consequently, many more exposed plants decrease in size than increase.

The long-term effect of *B. philenor* on *A. reticulata* is revealed by the fate of a cohort of young plants. The growth matrices and Eq. 1 were used to determine the size distribution, after a certain number of years, of an initial cohort of 100 plants with roots weighing between 0.0 and 0.1 g initially (size class 1). Plants protected from herbivory grow rapidly, as is indicated by the shift in the size distribution of the cohort (Fig. 5). Within 10 yr, 75% of the original cohort has reached the smallest size class at which reproduction is possible (0.4–0.8 g) and 91% of the cohort is still alive. After 20 yr a more or less stable size distribution is attained, with 82% of the cohort alive and virtually all individuals of reproductive size.

The size distribution of plants exposed to herbivory does not change nearly as rapidly as that of protected plants. After 10 yr <3% of the original cohort has analyses for each density treatment and the individual growth matrices for each density-exposure treatment. For a copy of this document, contact the senior author or order from ASIS/NAPS, Microfiche Publications, P.O. Box 3513, Grand Central Station, New York, New York 10017 USA.

\(^3\) See National Auxiliary Publications Service document \#3705 for 39 pages of supplementary material (results of
reached reproductive size and <40% of the cohort is alive. After 20 yr only 17% of the original cohort is alive and <2% are large enough to produce seeds. The frequency distributions shown in Fig. 5 may also be thought of as probability distributions for the likelihood that one seedling will be in a given size class after a given number of years.

Expected seed production

The expected number of seeds produced by a plant during its lifetime was estimated for plants protected from and exposed to feeding by *B. philenor* by using the calculated growth and reproductive matrices and Eq. 3. This estimate is an approximation of overall plant reproductive success that combines the effects of growth, mortality, and reproductive rates. Because Eq. 3 yields the expected number of seeds produced by an initial cohort of 100 seedlings, the values $m_{sp}$ were divided by 100 to obtain the expected number of seeds produced by an individual seedling. Once again, the density treatments were pooled to yield one value for each exposure treatment.

The reproductive vector, $R$, used in Eq. 3 is

$$R = (0, 0, 0, 1.44, 3.34, 9.18).$$

Each component $r_j$ corresponds to the mean number of seeds produced annually by an individual plant in size class $j$ (the size classes correspond to those used in Table 6). Plants with roots weighing <0.4 g (i.e., the first three size classes) do not produce seeds, while the mean number of seeds produced per plant increases steadily with size for plants in the three largest mass classes.

Because feeding by *B. philenor* larvae suppresses plant growth, a plant exposed to herbivory is expected to produce fewer seeds during its lifetime than a protected plant. This difference is already apparent within the 1st 20 yr of growth (Table 7). During the 1st 4 yr both exposed and protected plants set comparable numbers of seeds (0.14 vs. 0.11, respectively). During the next 2-yr period (years 4–6), however, a protected plant is expected to produce six times as many seeds as a plant exposed to herbivory (1.00 vs. 0.17). Within 10 yr the ratio has increased to 24:1 (3.34 vs. 0.14 seeds). This great difference in expected biennial seed production means that the cumulative number of seeds produced by a protected plant over a series of years is expected to be much greater than the number produced by a plant exposed to herbivory. After 10 yr, a protected plant is expected to have produced 11 times as many seeds (6.7 vs. 0.6) as one exposed to herbivory and after 20 yr, 29 times as many (29.8 vs. 1.03). This difference in expected reproductive success continues to increase after the 1st 20 yr, but is not depicted in Table 7.

The calculated difference between exposed and protected plants in number of seeds produced can only be an approximation. The reproductive matrix was calculated from plants that had been exposed to herbivory under natural conditions. It should therefore be
a good estimate of the reproductive matrix for the exposed plants in the experimental plots. The protected plants, on the other hand, may be able to produce more seeds because they have not had nutrients and other materials removed by feeding larvae. The reproductive vector, \( R \), would in that case underestimate the true matrix values for protected plants. Consequently, the effect of \( B. \text{ philenor} \) on seed production by \( A. \text{ reticulata} \) would also be underestimated. The projections based on these growth and reproductive matrices are also valid only if the plant growth, mortality, and reproductive rates measured in this study are representative of their long-term average values. Our observations over a 7-yr period (1972–1979) indicate little annual fluctuation in \( B. \text{ philenor} \) abundance, and hence suggest that the magnitude of herbivory measured in this 2-yr study is representative of that period. Extrapolation beyond 7 yr is obviously dangerous. Nevertheless, the projections illustrate well the magnitude of the impact of herbivory on \( A. \text{ reticulata} \) for the period in which this study was conducted.

**Discussion**

*Herbivory and reproductive success*

Severe defoliation of naturally growing *Aristolochia reticulata* plants by *Battus philenor* larvae is common in east Texas. During the years 1976 and 1977, for example, larvae consumed an average of 45.2 and 47.8% of the foliage of naturally growing plants (Rausher 1979). This degree of feeding damage is reflected in the results of this experimental study, which demonstrate that the pipevine swallowtail greatly reduces the reproductive success of its primary host plant in east Texas. One affected component of reproductive success is mortality. Extensive herbivore damage significantly increases the probability that an *A. reticulata* plant will die, as has been demonstrated for other plant species (see references in Kulman 1971). The risk that feeding damage will lead to mortality appears to be greater for young plants (Table 6). This result is expected (e.g., Janzen 1971), since small plants have fewer resources upon which to draw for producing new leaves after defoliation.

Larval feeding also reduces plant growth rates, or more precisely, root growth rates. As has been found for other plant species (Ellison 1960, Jameson 1963), the reduction in root growth due to defoliation may be due to any of several factors. When an *A. reticulata* plant is partly defoliated, it normally puts out new leaves within 2–3 wk. Much of the material used to produce the new leaves is probably transported from the roots (Jameson 1963). Defoliation therefore slows long-term growth by interspersing periods of accumulation of stored material with periods in which that material moves out of the roots into new leaves. Photosynthate manufactured by any uneaten leaves may also be diverted from the roots to the production of new leaves after defoliation (Gifford and Marshall 1973, Ryle and Powell 1975). Reduced growth rate may also be due to a reduction in leaf area caused by larval feeding, and hence to a decrease in the total amount of photosynthetic mass transported to the roots for storage. Finally, the reduction in leaf area may decrease the amount of nutrients absorbed by the roots (Jameson 1963). Our data do not permit us to determine the relative importance of these alternate factors.

Defoliation has been shown to reduce annual seed production, a third component of plant reproductive success, in many plant species (Knight and Hollowell 1962, Jameson 1963, Rockwood 1973, Cates 1975, Waloff and Richards 1977). In *A. reticulata* we could detect no differences in seed production between exposed and protected plants over a short period of 2 yr. We were able to show, however, that plants exposed to herbivory produce many fewer seeds as a result of the indirect effects of increased mortality and decreased growth rates. Because plants exposed to larval feeding grow more slowly, they take longer to reach reproductive maturity. Slow growth rates increase prereproductive mortality of exposed plants by causing them to remain longer in smaller size classes which are more susceptible to mortality from all sources (Table 6). As a consequence, a seedling exposed to *B. philenor* larvae has a much lower probability of reaching reproductive maturity, and hence of producing seeds, than does a plant protected from herbivory. Moreover, exposed plants have a much greater probability of decreasing in size than do protected plants (Table 6). Any given plant may reach reproductive size, produce seeds for a number of years, and then decrease in size due to larval feeding. Such a decrease in size increases the probability of mortality, and thus acts to decrease the average number of seeds produced by exposed plants that survive to reproductive maturity, compared to protected plants.

*Evolved defenses against larval feeding*

The decrease in reproductive success caused by the feeding of *B. philenor* larvae is likely to have been a potent selective force influencing the evolution of *A. reticulata*. At least three features of this plant species which differ from those found in most other species of *Aristolochia* can be interpreted as adaptations for deterring feeding by *B. philenor* larvae, although other selective forces may also have contributed to the evolution of these features.

The mature leaves of *A. reticulata* differ from those of the sympatric and closely related *A. serpentaria* in being tough, unpalatable to *B. philenor* larvae, and low in nutrients; these sclerophyllous leaves protect *A. reticulata* plants from feeding damage to some extent and are therefore probably an evolved defense
against larval feeding (Rausher 1979, 1981). They are obviously not a perfect defense, however, since sufficient feeding on immature leaves still occurs to cause a significant reduction in plant survivorship and growth rates.

The mortality risks associated with defoliation may also be responsible for the high root/shoot ratios of \( A. \) \textit{reticulata}. Monk (1966) reports root/shoot ratios of 0.2–0.5 for most perennial herbs, whereas the value for \( A. \) \textit{reticulata} is 2.29 (± 0.7) (M. Rausher, personal observation). An individual \( A. \) \textit{reticulata} plant has a very high probability of being severely defoliated at least once during a season. Under such circumstances, plants that put most of their photosynthate and reserve materials into shoot growth stand a great chance of losing those materials. By contrast, most \( A. \) \textit{reticulata} plants appear to limit shoot elongation in favor of root growth. When a plant is defoliated only a small amount of the plant biomass is removed and the plant can recover fairly easily.

Finally, underground flowering and fruiting by \( A. \) \textit{reticulata} may be an adaptation that minimizes seed predation by \( B. \) \textit{philenor} larvae. We have observed that larvae readily consume the flowers and developing seed capsules of \( A. \) \textit{reticulata} and other \textit{Aristochoia} species when they are offered in the laboratory. In nature, California populations of \( B. \) \textit{philenor} larvae commonly consume the developing aerial fruits of \( A. \) \textit{californica} even when much apparently edible foliage remains (M. Rausher, personal observation). In spite of underground fruiting in \( A. \) \textit{reticulata}, we have made similar observations in east Texas: we have seen two \( A. \) \textit{reticulata} plants that produced basal inflorescences lying on the surface of the ground. In each case \( B. \) \textit{philenor} larvae first ate all edible foliage on the plant and then consumed all developing seed capsules before dispersing in search of other plants. If this behavior is typical, feeding by \( B. \) \textit{philenor} larvae would probably destroy a large fraction of \( A. \) \textit{reticulata} seeds if they developed aboveground. By producing subterranean flowers and fruits, \( A. \) \textit{reticulata} plants probably avoid such extensive seed predation. In doing so, however, they have probably sacrificed much of their potential for outcrossing and seed dispersal. Because little is known about pollination or seed dispersal in \( A. \) \textit{reticulata}, we can say little about the consequences of such a sacrifice to the population biology of this plant species.

\textit{Plant density and reproductive success}

Although the pipevine swallowtail has a demonstrable effect on the reproductive success of \( A. \) \textit{reticulata}, this study has revealed no effect of plant density on herbivory. Plants grown at high densities had the same number of leaves eaten by \( B. \) \textit{philenor} larvae as plants grown at low density. Plant density also did not influence the effects of herbivory on plant mortality rate or on plant growth rate. Finally, there was no evidence to suggest that plant density affects the degree to which herbivory reduces annual seed production by \( A. \) \textit{reticulata} plants. Thus, at least within the range of densities used in these experiments and found in natural populations, the degree to which feeding by the pipevine swallowtail reduces the reproductive success of its host plants does not appear to be influenced by plant density.

It would be a mistake to conclude from these results, however, that \( E. \) \textit{philenor} does not regulate the density of \( A. \) \textit{reticulata} in east Texas. Density regulation of plants by herbivorous insects can occur in at least two ways. Insects may respond behaviorally to small-scale, local variation in plant density by selectively foraging in high-density patches of host plants (Pimentel 1961, Way and Heathcote 1966, A’Brook 1968, 1973, Cantlon 1969, Janzen 1970, Root 1973, Cromptie 1975, Orians et al. 1975, Jones 1977). Behavior of this type is akin to the nonrandom foraging of many insect predators and parasitoids (e.g., see Hassell 1978) and can lead to similar stabilization of prey (host plant) populations. Herbivorous insects may also regulate the density of their host plants through a numerical or generation response to increases in plant density. An increase in host plant density may promote greater survival of insects dispersing from one plant to another (Dethier 1959) and thus an increase in insect abundance in subsequent generations; this increase could in turn lead to greater plant mortality or decreased plant reproduction (Dempster 1971). When this effect operates throughout the habitat occupied by insect and host, the density regulation that occurs is analogous to classical models of prey regulation by predators (e.g., Varley et al. 1973, Hassell 1978). A similar numerical response may also occur within small patches of host plant. Within a patch, for example, high host plant density may promote the survival of larvae dispersing between plants and may lead to a greater amount of feeding damage per plant than occurs in patches of low host density.

In this investigation we have examined the behavioral and numerical responses of \( B. \) \textit{philenor} to increases in plant density only in areas up to several square metres. We found no evidence for either a behavioral response to local variation in plant density or for a within-patch numerical response of larvae. It is therefore unlikely that \( B. \) \textit{philenor} acts to regulate the density of small patches of host plant. Whether long-term regulation of plant density over much larger areas of habitat occurs is as yet an unanswered question. In conclusion, we would like to amplify a comment made by Wilson (1964) in a review of the biological control of introduced weeds by insects. He concluded that in most successful cases of biological control, a biologist viewing the plant at equilibrium with its herbivores would have little reason to suspect that insects had a significant impact on the plant. Our experience with the \textit{Battus-Aristochoia} system leads us to be-
lieve that this conclusion about exotic plant-insect interactions may often apply to natural plant-insect associations as well. A biologist casually examining Aristolochia plants in east Texas might not suspect B. phileenor had such a marked effect on the reproductive success of its host plants. Some feeding damage is evident, but much is not. Early in the season, for example, larvae often eat all of the leaves on a plant and chew the stem down to the ground, leaving no above-ground structures to betray the fact that an entire plant has been eaten. Even when a larva does not eat all the leaves on a plant before leaving it, feeding damage is often not conspicuous, since larvae tend to consume all of a leaf before feeding on another. Finally, the growth of new leaves as replacements for those removed by larvae tends to make feeding damage even less evident. Nevertheless, the impact of B. phileenor on its host plants is obviously great. Moreover, exclusion of B. phileenor doubles the amount of foliage present on experimental plants. We believe that this type of cryptic feeding damage is more common in nature than is frequently suspected; as Harper (1977) points out, however, it will normally be revealed only by careful quantification and by perturbation experiments.

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LITERATURE CITED


