

THE EFFECT OF NATIVE VEGETATION ON THE SUSCEPTIBILITY OF *ARISTOLOCHIA RETICULATA* (ARISTOLOCHIACEAE) TO HERBIVORE ATTACK¹

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Abstract. Plants growing in dense stands of native vegetation are often less susceptible to herbivore attack than isolated plants or plants growing in monoculture. Three mechanisms have been suggested that may account for this phenomenon: (1) maintenance of a complex predator fauna in dense vegetation; (2) inhibition by complex vegetation of the ability of an herbivore to discover its host plants; and (3) decreased residence time of herbivores on plants growing in diverse vegetation. This study demonstrates that for both adults and larvae of the pipevine swallowtail butterfly, *Battus philenor*, inhibition of discovery is the primary cause of decreased susceptibility of its host plants, *Aristolochia reticulata*, to attack when grown amid native vegetation. In addition, this study demonstrates that a seasonal decrease in the susceptibility of host plants to discovery by adults is correlated with a seasonal increase in the height and density of the native vegetation. A similar inverse correlation between vegetation structure and susceptibility to discovery by larvae was detected. However, seasonal changes in vegetation structure do not influence susceptibility to larval discovery. This differential effect of changing vegetation structure on searching efficiency is probably due to differences in the way larvae and adults search.

Key words: *Aristolochia*; *associational resistance*; *Battus*; *Big Thicket*; *discovery*; *herbivory*; *host-plant resistance*; *insect-plant association*; *oviposition*; *search behavior*; *swallowtails*.

INTRODUCTION

The susceptibility of plants to attack by specialized insect enemies is often greatly influenced by the structural and taxonomic complexity of the vegetation surrounding those plants (Pimentel 1961, Smith 1969, 1976, Tahvanainen and Root 1972, Root 1973, Atsatt and O'Dowd 1976, Kroh and Beaver 1978, Risch 1979). In general, an increase in vegetation complexity reduces susceptibility. Yet despite the apparent generality of this relationship and its implications for the evolution and population dynamics of plant-insect associations (e.g., Feeny 1976, Rhoades and Cates 1976), few investigators have attempted to determine the mechanisms that produce it. Root (1973) has suggested that any of three factors may be responsible for the generally observed inverse correlation between susceptibility of a plant to insect attack and the complexity of the surrounding vegetation: (1) diverse vegetation may maintain a complex predator fauna that can respond rapidly to the presence of herbivorous insects on a particular plant species; (2) insect herbivores may have a greater tendency to remain on plants growing in a simple background vegetation than on plants growing in a more complex vegetation; (3) insect herbivores may be less successful in locating host plants growing in a complex vegetational background than in

locating plants growing in a simple background. Although a few studies have reported that one of these factors may operate in the particular plant-herbivore association investigated (e.g., Lewis and Waloff 1964, Douwes 1968), in most studies the effects of variation in vegetational background are confounded with those of variation in host plant density. Moreover, the relative importance of all three factors in determining the overall effect of vegetation structure on susceptibility has seldom been assessed. Consequently, the primary objective of this investigation was to determine the extent to which each of the three factors listed by Root (1973) influences the susceptibility of one plant species to attack by its primary insect herbivore.

Although the kinds of gross experimental manipulations (e.g., total removal of all background vegetation) reported in this and other investigations can lead to changes in susceptibility of plants to herbivory, there is little evidence indicating that more subtle differences in the structure and composition of background vegetation can produce similar effects. One method of examining this question is to determine whether the changes in vegetation structure that occur over the course of a single growing season can affect susceptibility. This approach was adopted here. A secondary objective of this investigation was thus to determine whether seasonal changes in vegetation complexity are correlated with susceptibility of a plant species to herbivore attack. Moreover, an attempt was made to determine which of the three processes suggested by Root are affected by seasonal changes in background vegetation.

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The plant-insect association chosen for this study consisted of the pipevine swallowtail butterfly, *Battus philenor* (Papilionidae), and its primary host plant in east Texas, *Aristolochia reticulata* (Aristolochiaceae). This association offers several advantages for a study of this type. The system is simple, consisting of a host plant and only one major herbivore. Because other herbivores are rare, feeding damage can be attributed unambiguously to *B. philenor*. Both plant and herbivore are abundant, facilitating observation of interactions. Finally, ovipositing female butterflies can be followed easily in the field (Rausher 1978, 1980), permitting direct measurement of the success of the herbivore at locating its host plant.

METHODS

Study site and experimental organisms

This study was performed during March–August 1976 and March–July 1977 in an area of open longleaf pine upland habitat at the John Henry Kirby State Forest near Kountze, Texas. *Aristolochia reticulata*, along with its congener *A. serpentaria*, grow in the open pine woods of east Texas. The stem and leaves of the plant die back to the ground in the fall and the roots remain dormant throughout the winter. Some time in mid-March the plants begin producing a new stem and new leaves. Pipevine swallowtail pupae break diapause and emerge as adults to form the first brood just as the first new leaves are being produced by the host plant. First-brood females are common between about 15 March and 15 April (Rausher 1979a, 1981), during which time they search primarily for *A. reticulata* plants on which they lay small clusters of eggs (Rausher 1980). About 1 wk after oviposition, the eggs hatch and the first-instar larvae begin feeding. When a larva has consumed all edible foliage on a plant, it leaves that plant and moves on the ground through the vegetation until it locates another. A larva must often discover and feed on at least 25 different plants to obtain enough food to complete its development. An *A. reticulata* plant is thus susceptible to being discovered by both ovipositing first-brood females and their dispersing larval offspring.

Most of the surviving larvae pupate by early May. Around the 2nd wk in May a second brood of adults emerges and lays eggs until about 1 June. Although most second-brood females search preferentially for and lay most of their eggs on *A. serpentaria*, $\approx 20\%$ search for and lay eggs on *A. reticulata* (Rausher 1980). Larvae dispersing from *A. serpentaria* plants discover and feed on *A. reticulata* plants (Rausher 1979a). Consequently, *A. reticulata* plants are susceptible to discovery by both adults and dispersing larvae during the second brood as well as during the first. The larval offspring of second-brood females enter pupal diapause by early July and do not emerge again until the following spring.

Susceptibility of plants to oviposition

Experiment 1.—This experiment estimated the effect of natural vegetation surrounding a host plant on that plant's susceptibility to oviposition. In March 1977 the vegetation in an area ≈ 0.5 m in diameter surrounding each of 200 experimental (isolated) plants was clipped to the ground, while the vegetation surrounding 200 control plants was left undisturbed. After clipping, I measured the rate at which egg clusters appeared on plants in the two treatments by examining each plant every 4 d during the period 14 March–7 April (Brood 1, 6 census dates). Four hundred additional plants were assigned randomly to the two treatments in early May and were censused every 4 d during the the period 6–26 May (Brood 2, 5 census dates). Any eggs found during the censuses were removed, since the presence of eggs would have deterred oviposition during the subsequent 4-d period (Rausher 1979b). Because females normally oviposit only on plants with some newly produced foliage (Rausher 1979a), I estimated the probability that a plant in a particular treatment would have eggs laid on it during a 4-d period by dividing the number of plants having egg clusters at the end of that period by the number having young foliage. Young foliage is clearly distinguishable from old foliage; young leaves are light green, tender, flexible, and not markedly sclerophyllous, while old foliage is dark green, tough, rigid, and has markedly sclerophyllous veins. Although I may have misclassified a small fraction of plants, the bias was small and similar for both treatments and should thus not affect the results greatly.

Experiment 2.—This experiment compared, for isolated and control plants, the probability that a female would oviposit once she had alighted on a plant. During the first brood in 1977 females were followed in the field for up to 30 min. Over this period, $\approx 10\%$ of the plants on which females alighted were isolated plants. For each plant alighted upon I recorded the type of plant (e.g., isolated vs. control) and whether an egg cluster was deposited.

Experiment 3.—This experiment measured seasonal changes in the susceptibility of *A. reticulata* plants to discovery by searching females. During both broods in 1977 I followed females in the field and recorded the number of *A. reticulata* plants on which females alighted. A crude host plant discovery rate for each female was then obtained by dividing the number of plants on which she alighted by the amount of time she was observed. Searching females adopt one of two search modes by responding preferentially to either the broad, ovate leaves of *A. reticulata* or the lanceolate leaves of *A. serpentaria*; moreover, the search mode adopted affects the rate at which a female alights upon *A. reticulata* plants (Rausher 1978). Consequently, only females that searched preferentially for the leaves of *A. reticulata* were analyzed in this study (see

Rausher 1978 for method of determining searching preferences).

Because host plant discovery rates are directly proportional to host plant abundance (M. Rausher 1980 and *personal observation*), the host plant discovery rates measured in this experiment were divided by relative plant density to eliminate the effects of plant abundance. To calculate relative host abundance on a particular date, I marked 500 *A. reticulata* plants in September 1976. I then censused the plants weekly in 1977, beginning on 12 March. For each census date, relative host plant abundance was calculated as the fraction of plants that had one or more leaves and were thus presumably detectable by searching females. Relative abundances for dates between censuses were estimated by interpolation. Corrected host discovery rates were then obtained for each date by dividing the crude host discovery rate by the relative host plant abundance for that date. Differences between the corrected host plant discovery rates of first- and second-brood females are thus due to seasonal changes in factors that influence the probability that an individual plant is alighted upon by a searching female.

*Susceptibility of plants to discovery
and feeding by larvae*

Experiment 4.—This experiment measured the effect of natural vegetation on the susceptibility of host plants to discovery and feeding by larvae. In this experiment, the experimental (isolated) and control plants were the same as those used in Experiment 1. The plants were censused at approximately weekly intervals during the periods 30 March–27 April (Brood 1 plants) and 4–29 May (Brood 2 plants). During each census I recorded the number of leaves present on each plant and estimated, to the nearest quarter leaf, the amount of feeding damage to each leaf. Differences between censuses in number of leaves per plant and feeding damage per leaf thus estimate the number of new leaves produced or eaten during a census period. In addition, I recorded at each census whether a plant had any young foliage. The rate at which larvae discovered plants was estimated in two ways. For each census period, the first estimate used was the fraction of all plants that had sustained any feeding damage since the previous census. Since larvae tend not to feed on mature *A. reticulata* leaves as readily as on young leaves (Rausher 1979a, 1981), this technique may not reveal discovery of plants containing only mature foliage as readily as discovery of plants containing some young leaves. Consequently, this method of estimating host plant discovery rate may underestimate the true rate if a considerable fraction of host plants does not contain young foliage. To correct for this bias, I also estimated the probability of discovery during a given census period by the fraction of plants with young foliage at the beginning of the period that sustained feeding damage during that period.

Experiment 5.—This experiment attempted to determine if the susceptibility of host plants to discovery by larvae changes seasonally. In early April 1976, all host plants in each of two 16×16 m² plots were marked with surveyors' flags. In the center of each plot I established a 5×5 m² grid of stakes that served as release points for larvae. Each trial consisted of releasing on a given day one third-instar larva at each of the 25 release points and determining how rapidly the larvae appeared on the marked plants in the grid. Larvae were released at approximately 0900. All marked plants were examined at periodic intervals: every 30 min for the first 2.5 h, then every hour for the next 5 h and finally at 0900 the following day. Each time I examined a plant I removed any larvae that were present and recorded the number of larvae removed and the plant number. Three trials were performed on each plot on successive days at each of three times during the season: 16–18 April, 24–26 May, and 23–25 July. The first two periods correspond roughly to times of peak abundance of the larval offspring of first- and second-brood females, respectively. For each period I constructed from the data a curve representing the cumulative number of larvae appearing on marked plants vs. the time since the beginning of the experiment (Rausher 1979b). Differences in the cumulative discovery curves reflect different rates of discovery by larvae.

RESULTS

Susceptibility of plants to oviposition

The presence of natural vegetation around an *A. reticulata* plant greatly decreases the probability that eggs will be laid on it. The results of Experiment 1 reveal that during both broods eggs were laid on a significantly greater fraction of plants from which the surrounding vegetation had been removed than on control plants (Table 1). This difference was not due to a differential post-alighting response of females to the two types of plants. If anything, females that had alighted on a plant had a slightly lower probability of ovipositing if that plant was an isolated plant than if it was a control, but this difference is not significant (Table 2, $F = 0.31$, $P > .5$, G test, Sokal and Rohlf 1969).

Seasonal changes in susceptibility to oviposition

For the plants in Experiment 1, the Relative Susceptibility, defined as (fraction of control plants with eggs)/(fraction of isolated plants with eggs), estimates the degree to which the vegetation surrounding a plant reduces its probability of being oviposited upon. A Relative Susceptibility of 0.5, for example, means that during a given period control plants are half as likely to have eggs appear on them as are isolated plants. Because the isolated treatment is the same in the two

TABLE 1. Probability that eggs will appear on isolated and control plants over 4-d intervals during Broods 1 and 2 in 1977. Isolated plants had the vegetation removed in a 0.5-m diameter area surrounding the plant. Values for isolated and control plants differ significantly ($\chi^2 = 0$, $P < .05$ for each brood, sign test, Siegel 1956). Relative Susceptibility value (RS) for a given date is equal to (fraction of control plants oviposited upon)/(fraction of isolated plants oviposited upon). The difference in RS values for the two broods is highly significant ($U = 0$, $P < .01$, Mann-Whitney U test).

	Beginning date of 4-d census period	Fraction of plants oviposited upon		
		Isolated	Control	RS
Brood 1	18 Mar	.255	.020	.078
	22 Mar	.315	.294	.648
	26 Mar	.120	.056	.467
	30 Mar	.144	.105	.729
	3 Apr	.073	.016	.219
	7 Apr	.152	.039	.257
Brood 2	10 May	.275	.000	.000
	14 May	.457	.010	.022
	18 May	.586	.029	.049
	22 May	.244	.000	.000
	26 May	.300	.020	.067

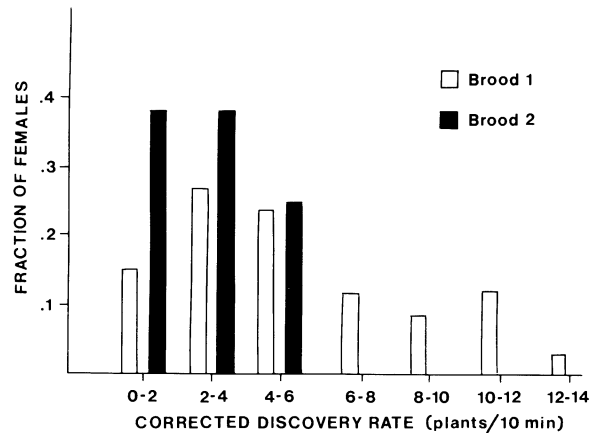


FIG. 1. Fraction of observed females searching preferentially for broad leaves (i.e., searching for *A. reticulata*) that discover host plants at the indicated rate. Discovery rates have been corrected for plant abundance (see Methods). Shaded bars: Brood 1 females ($N = 34$); open bars: Brood 2 females ($N = 8$). Difference between first- and second-brood females is highly significant ($t = 2.498$, Wilcoxon two-sample test, Sokal and Rohlf 1969).

broods, any changes in Relative Susceptibility between Broods 1 and 2 indicate a change in the susceptibility of control plants to oviposition.

Relative Susceptibility is significantly lower during the second brood than during the first brood ($\bar{x} = .400 \pm .115$ and $\bar{x} = .028 \pm .015$, respectively, Table 1, $P < .01$). This seasonal reduction in susceptibility of control plants to oviposition is paralleled by a reduction in the rate, corrected for host abundance, at which searching females alight on *A. reticulata* plants. First-brood females alight on more than twice as many plants per unit searching time as do second-brood females (Fig. 1).

Susceptibility of plants to larval discovery and feeding

In Experiment 4, the presence of vegetation surrounding an *A. reticulata* plant reduced the amount of feeding damage caused by dispersing larvae (Fig. 2A, B). During the period 30 March–27 April 1977, the number of leaves eaten per 100 plants was greater at each of the five census dates for isolated plants than

TABLE 2. Reaction of Experiment 2 females to plants on which they alighted. "Accept" indicates that a female oviposited, "reject" indicates she did not. The proportion of plants accepted does not differ for isolated and control plants ($G = 0.31$, $P > .5$).

Reaction	Type of plant	
	Isolated	Control
Accept	7	65
Reject	20	144

for control plants. The probability that these results would occur by chance under the null hypothesis that there is no difference between treatments in susceptibility to larval feeding is .031 (binomial probability). Similarly, during the period 4–29 May, the number of leaves eaten was greater in four out of five censuses for the isolated plants ($P = .187$ under the same null hypothesis). Taken together, these two experiments indicate a significant reduction in larval feeding damage due to the presence of vegetation around an *A. reticulata* plant ($\chi^2_4 = 10.28$, $P < .05$, Combined Probability Test, Sokal and Rohlf 1969).

One possible explanation for the greater feeding damage incurred by isolated plants is that dispersing larvae consume less foliage after discovering a plant surrounded by complex vegetation. This explanation is ruled out by the results depicted in Fig. 2C, D. During none of the 10 census periods was there any detectable difference between the number of leaves consumed per plant in the two treatments ($P > .05$ in all 10 cases, t test).

By contrast, there appears to be a slightly greater tendency for isolated plants to be discovered by dispersing larvae than for control plants (Fig. 2E–H). During the period 30 March–29 April, a greater fraction of isolated plants was discovered by larvae in all five census periods ($P = .031$ based on null hypothesis that plants in both treatments are equally susceptible to discovery). The results for the period 4–29 May are more ambiguous: during three of the five census periods a greater fraction of isolated plants was discovered ($P = .5$ based on same null hypothesis). Taken together, however, the results indicate a slight effect of neighboring vegetation on the probability that a

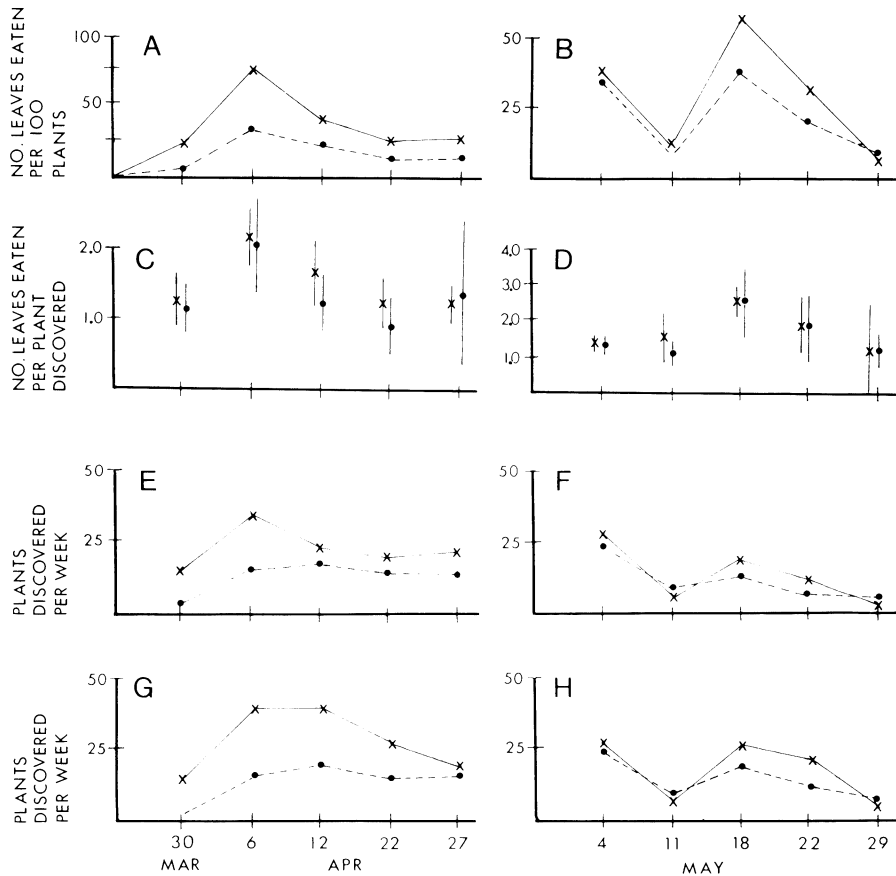


FIG. 2. Susceptibility of clipped and control plants to discovery and feeding by larvae. In all graphs, the open circles are control plants and the x's are clipped plants. A. Feeding damage to plants during the period 30 March–27 April. B. Same as A, 4–29 May. C. Mean number of leaves eaten per plant, 30 March–27 April. Only plants with greater than one quarter leaf eaten are included (see Methods). Vertical bars are 95% confidence intervals. D. Same as C, 4–29 May. E. Fraction of plants having new foliage 1 wk earlier that exhibit feeding damage received since the previous census (= fraction of plants discovered), 30 March–27 April. F. Same as E, 4–29 May. G. Fraction of all plants showing feeding damage (= discovered) since previous census, 30 March–27 April. H. Same as G, 4–29 May.

plant will be discovered by dispersing larvae ($\chi^2_4 = 8.4, P = .08$, Combined Probability Test). Moreover, this conclusion does not depend on the way in which host plant discovery rates were measured (e.g., compare E and F with G and H in Fig. 2).

Seasonal changes in susceptibility of plants to larval discovery

Although the presence of vegetation in the neighborhood of an *A. reticulata* plant reduces its probability of being discovered by dispersing larvae, a plant's susceptibility to discovery by a fixed number of experimental larvae does not appear to change during the season. The results of Experiment 5 suggest a tendency toward higher discovery rates early in the season (mid-April), (Fig. 3A, B). In Plot 1, for example (Fig. 3A), the mean number of larvae discovering host plants was greatest during the period 16–18 April, lower during the period 24–26 May, and the lowest during

the period 23–25 July. However, these differences are not significant ($F_{2,6} = 0.66, P > .5$ for number of larvae having discovered plants after 24 h; analyses of values for other times after larval release are also not significant).

A seasonal trend is less distinct in Plot 2 (Fig. 3B). During the first 2 h after larval release, the cumulative number of larvae discovering plants actually ran opposite the expected seasonal trend, and was greatest in the 23–25 July trials and lowest during the 16–18 April trials. By 7.5 h after release (1630), the mean number of larvae having discovered plants was similar for the April and July trials, but somewhat lower for the intervening May trials. None of these differences, however, were statistically significant ($F_{2,6} = 1.98, P > .2$ for values 24 h after release; values for other times were also not significantly different). Thus, there was no detectable seasonal increase in susceptibility of plants to larval discovery, though the rather high

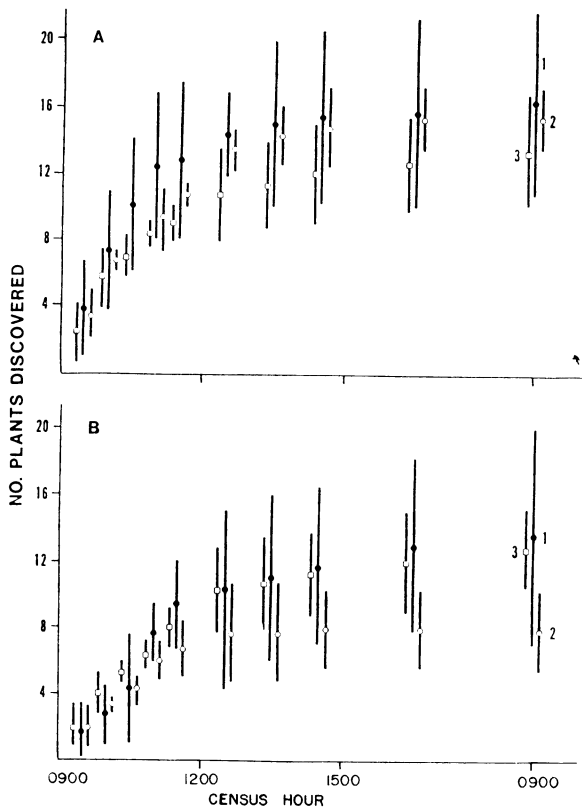


FIG. 3. Cumulative number of larvae appearing on marked plants by indicated time after release. Points plotted are means for three trials involving 25 larvae each. Bars are 95% confidence intervals. Solid circles: 16–18 April (Trial 1); open circles: 24–26 May (Trial 2); open boxes: 23–25 July (Trial 3). A. Plot 1. B. Plot 2.

variability within time periods precluded detection of subtle differences between periods.

DISCUSSION

The effects of native vegetation on susceptibility

Root (1973) has outlined several mechanisms whereby the presence of vegetation surrounding a plant could lower that plant's susceptibility to herbivory. These mechanisms include:

1) Greater predation on insects feeding on plants surrounded by natural vegetation: Diverse, dense stands of natural vegetation provide a broad spectrum of resources that maintains a complex predator fauna capable of responding to the appearance of herbivores on any given host within the stand. An herbivore feeding on plants surrounded by a dense stand of natural vegetation may thus have a lower survivorship rate than when feeding on the same plant species growing in sparse stands of vegetation, where the predator fauna is not nearly as large.

2) Greater susceptibility of host plants to discovery: By interfering with the ability of an herbivore to detect

its host plants (e.g., Tahvanainen and Root 1972), vegetation growing in association with hosts may reduce the probability that those hosts will be discovered by their specialist herbivores. The discovery rate of hosts growing in dense stands of vegetation would thereby be reduced, compared to the rate for the same hosts growing in relatively sparse or pure stands.

3) Greater residence time: Once an herbivore discovers a host plant that is surrounded by a dense stand of natural vegetation, that herbivore may have a lesser tendency to remain on that plant than if it had discovered a plant surrounded by little or no vegetation. Dense vegetation surrounding a host plant may, for example, create an unfavorable microclimate for the insect, inducing it to leave the plant. For ovipositing insects, the analogous mechanism would be a lower post-alighting probability of oviposition on hosts surrounded by natural vegetation than on hosts not thus surrounded.

In east Texas, greater susceptibility to discovery by searching females appears to be the primary cause of a greater number of egg clusters appearing on isolated plants than on controls. Neither increased predation (1) nor decreased probability of oviposition (3) on control plants explains the observed trends. Egg disappearance due to predation, for example, is minor. Other experiments conducted at the same time as these have shown that eggs laid on unmodified plants have a probability of only .15–.20 of disappearing over a 7-d period (Rausher 1979a, b, 1980). Since the plants in the experiments reported here were censused every 4 d, differences between egg disappearance rates on isolated and control plants are maximally 10%. Differential predation intensity on eggs in the two different treatments can thus account for only a small fraction of the nearly 100% difference in number of egg clusters found on the two types of plants during this study (Table 1). Experiment 2 (Table 2) demonstrated directly that the probability of oviposition, once a female has alighted on a plant, does not differ for isolated and control plants. Moreover, eggs are not mobile, so differences in residence time are irrelevant in this context. Differential rate of discovery by females thus appears to be the most reasonable explanation for the observed difference in susceptibility to oviposition.

Greater susceptibility of isolated plants to larval feeding is also due primarily to a greater probability of discovery by larvae. Greater predation and shorter residence time on control plants than on isolated plants can be eliminated as causes of the observed difference in feeding damage between the two treatments. If either of these explanations were true, larvae feeding on isolated plants would feed for longer periods on individual host plants than larvae feeding on control plants. A larva would thus consume a greater amount of foliage per discovered plant in the isolated treatment. The results do not support this expectation;

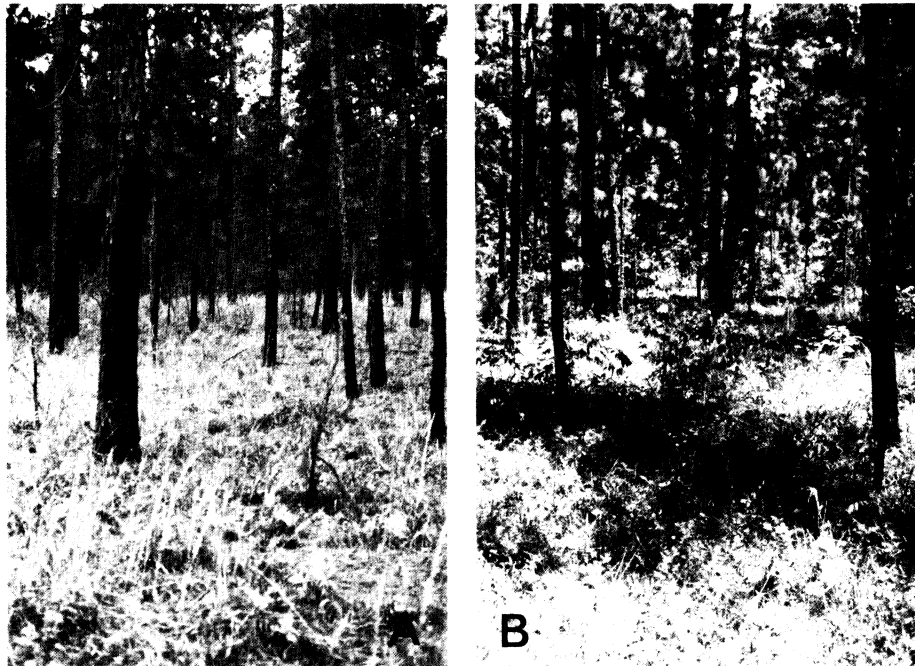


FIG. 4. Growth of native vegetation at Kirby Forest study site during the spring. A. Kirby Forest site in mid-March at beginning of first brood. Note sparse ground cover. B. Similar view in mid-May at beginning of second brood. Ground vegetation has grown considerably denser.

in fact, the number of leaves eaten per plant is remarkably similar for plants in the two treatments (Fig. 2C, D). Furthermore, my results indicate directly that isolated plants do indeed have a greater probability of being discovered by dispersing larvae than do control plants (Fig. 2E–H).

The mechanism by which the presence of vegetation surrounding a host plant interferes with its discovery is likely to be different for adults and larvae. Females of *B. philenor* are visually oriented searchers that use leaf shape as the primary cue for initiating the approach to a host plant; chemotactile and olfactory cues become important only after a female has contacted a plant (Rausher 1978). Moreover, females fly above the herbaceous vegetation and locate their host plants by looking down into it. The most likely way in which the presence of surrounding vegetation inhibits discovery by searching females is thus by masking the host plant foliage from the view of the females.

Larvae, by contrast with adults are not visual searchers. They locate new host plants by moving along the ground until they “bump into” a host plant with their palpi and/or antennae (M. Rausher, *personal observation*). Stems and leaves of non-host plants and other barriers encountered by searching larvae cause them to change their direction of movement and thus alter search behavior. It might be expected that such barriers would decrease the rate at which larvae search a particular area, both by slowing the rate of movement and by increasing the probability

that an area will be searched more than once. By decreasing the rate of search, barriers provided by native vegetation can be expected to decrease the probability that a given plant will be discovered by a larva before it is killed by predators, starves, or leaves the area of dense vegetation.

Seasonal changes in susceptibility of host plants

The results of this study demonstrate that the susceptibility of control plants to oviposition declines between Broods 1 and 2. Two explanations may be offered for this decline. It may be due, on the one hand, to a seasonal change in the searching behavior of *B. philenor* females. The predominant searching mode exhibited by females in east Texas shifts from preferential searching for *A. reticulata* during the first brood to preferential searching for *A. serpentaria* during the second (Rausher 1980). The observed seasonal change in Relative Susceptibility may be due at least partly to this simple behavioral change, if that change alters the relative probabilities that a female will perceive and alight on control and isolated plants.

In addition, the results of Experiment 3 suggest that the seasonal decrease in Relative Susceptibility is also at least partly due to changes in environmental characteristics that influence the probability that a plant will be discovered by a female. First-brood females alighted on more than twice as many plants per unit searching time as did second-brood females. Since this comparison involves only females with similar search-

ing behavior (i.e., females searching preferentially for *A. reticulata*) and the effects of host density have been removed, the seasonal decline in host plant discovery rates is most likely due to a seasonal decrease in the ability of females to perceive *A. reticulata* plants. Given the inhibitory effect of native vegetation on host location by females, it seems reasonable to conclude that changes in the height and density of the native vegetation are probably the most important factors leading to seasonal changes in host plant discovery rates, and hence to parallel declines in the susceptibility of plants to oviposition. During the first brood, the vegetation cover in the pine uplands of east Texas is relatively sparse and low; over the next 2 mo, however, growth is quite rapid, so that by the time of the emergence of the second brood, the vegetation is quite dense and tall (Fig. 4). This increase in density and height means there is more vegetation between the searching females and their host plants during the second brood than during the first. If the degree to which the vegetation masks host plants from view is proportional to the density or amount of foliage between butterfly and plant, as seems probable, then the seasonal increase in vegetation height should decrease the rate at which searching females discover host plants. Moreover, the susceptibility of unmanipulated plants should decrease relative to that of plants from which the surrounding vegetation has been removed. These two trends are precisely what I observed. These results therefore suggest that seasonal changes in the density and/or height of native vegetation can profoundly affect the success insects have at locating their host plants. One further implication of these results is that spatial variation in vegetation structure of a magnitude similar to that occurring seasonally may render some host plants in a population either more or less susceptible than others to discovery by specialized insect enemies. Such an interaction between herbivory and competitive environment may in turn be expected to influence the distribution and abundance of the host plant within its habitat.

Such effects need not necessarily occur, however. In this study, changes in the density of the native vegetation did not detectably decrease the efficacy of searching by *B. philenor* larvae. A likely explanation of this contrast with searching adults is that larvae encounter the barriers provided by natural vegetation at ground level. By mid-April, the time of the first larval release trials, the natural pine woods vegetation has not grown greatly in height, but most of the plants in the habitat have begun putting up shoots. The density and pattern of barriers to larvae searching at ground level are thus probably already established fairly early in the season and do not change greatly as the vegetation grows upward. Dispersing larvae therefore probably encounter a similar array of obstacles in May as in mid-April, a fact which would account

for their similar rates of host plant discovery at these times (Fig. 3).

Implications for host leaf shape

A final implication of the results of this study involves the interaction between visually oriented herbivores and morphological characteristics of their host plants. Gilbert (1975) and Barlow and Wiens (1977) have suggested that visually oriented herbivores can be potent selective agents causing plants to evolve leaf shapes that are cryptic against background vegetation. By resembling the foliage of other vegetation, these authors reason, a plant's leaves become less conspicuous to searching herbivores. Plants with such leaves are thereby more likely to escape detection by those herbivores than plants with more conspicuous leaves (i.e., leaves with shapes very different from the background vegetation). Although this hypothesis seems reasonable, there is little evidence demonstrating that the presence of background vegetation can interfere with the ability of a searching herbivore to locate its host plants visually. As I argued above, the results of this study indicate that natural vegetation to some extent masks host plants from the view of searching *B. philenor* females. Given this type of masking effect, it is not unreasonable to surmise that modification of a host plant's leaf shape to match the background vegetation more closely would improve the masking and render the plant even less susceptible to discovery. While it seems likely that this type of masking may at least partly explain the adaptive significance of leaf shape in plant species interacting strongly with visually oriented, coevolved insect herbivores (e.g., *Passiflora*, Gilbert 1975, *Aristolochia*, Rausher 1978), only subsequent investigations can confirm this hypothesis and reveal how generally it is applicable to other types of plants.

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