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Spatial Distribution and Impacts of Moth Herbivory on Northern Pitcher Plants

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Abstract - Larvae of two noctuid moths, *Exyra fax* and *Papaipema appassionata*, are obligate herbivores of *Sarracenia purpurea* (northern pitcher plant). We studied the relationship between presence of these larvae and plant size, the spatial clustering of herbivory, and effects of herbivory on subsequent plant size at Harvard Pond in central Massachusetts. Plants fed upon by *E. fax* were larger than uneaten plants, were clustered in the study area, and decreased in size after a year relative to uneaten plants. The few plants fed upon by *P. appassionata* were similar in size to the overall population, and were clustered only in 2003. Limited mobility of adult moths and plant size preference may account for clustering of herbivory by *E. fax*, whereas larval mobility may account for clustering of herbivory by *P. appassionata*.

Introduction

In insect species for which larval mobility is low, parental oviposition site selection can affect larval survivorship, leading to a selective advantage for adults that make good ovipositional choices. The characteristics of a good oviposition site vary among species, life histories, and habitats (see reviews by Crawley 1983, Thompson and Pellmyr 1991). Larval survivorship of many butterflies and moths increases with host plant mass, and females of some species are more likely to oviposit on larger plants (e.g., Zangerl and Berenbaum 1992). Herbivory generally reduces plant growth rate, reproductive ability, and size, and increases susceptibility to further damage and disease (see reviews by Anderson 1987; Crawley 1983, 1989). However, some studies indicate that herbivory can lead to increased growth and fruit production in plants (Lennartsson et al. 1998, Paige 1999).

Larvae of *Exyra fax* (Grote) (Noctuidae; pitcher plant moth) and *Papaipema appassionata* (Harvey) (Noctuidae; pitcher plant borer) are host-specific herbivores of *Sarracenia purpurea* L. (Sarraceniaceae) (northern pitcher plant). Because *S. purpurea* is a carnivorous plant that uses each leaf both for photosynthesis and for nitrogen acquisition, it is an excellent organism on which to study the effects of herbivory. Herbivory of the leaves results in a loss of energy and nutrients to the plant. The low mobility of *E. fax* adults (Jones 1921), the patchy distribution of plants, and the overall environment at our research site provide the opportunity to observe the effects of spatial variation in host availability on herbivore distribution.

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The goal of this study was to describe patterns of occurrence of *E. fax* and *P. appassionata* among peat islands at Harvard Pond in Central Massachusetts and the effects of their larvae on plant growth. We examined whether herbivory by these moths on *S. purpurea* plants showed any spatial distribution patterns. We hypothesized that the spatial pattern of herbivory by both species of moth would be clumped because of the limited mobility of adults of *E. fax* and the possibility that a single *P. appassionata* larvae can feed upon multiple plants (Rymal and Fokerts 1982). If this was the case, and individual larvae were distributed randomly throughout the bog and fed upon multiple nearby plants, herbivory would be clustered despite the random distribution of larvae. We also hypothesized that moths were more likely to feed upon larger plants and that herbivory would lead to reduced plant size the following year.

Study Species

Sarracenia purpurea

The northern pitcher plant is a long-lived perennial herb that grows in bogs and fens in the eastern United States and Canada (Fish and Hall 1978, Folkerts and Folkerts 1996, Hepburn et al. 1920, Jones 1921). *Sarracenia purpurea* is a carnivorous plant characterized by distinct pitcher-shaped leaves that collect rainwater in which captured prey drown. In most species of pitcher plants, the mouth of each pitcher is partially obscured by a stiff hood that protrudes over the pitcher opening and prevents rainwater from entering the pitcher chamber. In *S. purpurea*, however, the hood is oriented vertically, allowing rainwater to fill the pitcher chamber. A single stiff keel runs along the plant from the petiole to the lip of the leaf mouth, directly opposite the hood (Arber 1941, Hepburn et al. 1920). Rosettes consist of 3–10 leaves that live 1–2 years, although the rosette may persist for decades by growing new leaves each year. New leaves grow continuously at the average rate of one leaf per 20 days during the 16-week growing season in Massachusetts (Fish and Hall 1978).

Exyra fax and *Papaipema appassionata*

There are few pitcher-plant herbivores (Rymal and Folkerts 1982). The chief herbivores are larvae of two species of noctuid moths, *Exyra fax* and *Papaipema appassionata*. Signs of herbivory by larvae of both species are distinctive and are easily recognizable in the field (Fig. 1).

Exyra fax is a host-specific herbivore of *S. purpurea* that, as a larva, feeds on the interior surface of the pitcher chamber (Folkerts and Folkerts 1996, Jones 1921, Lafontaine and Poole 1991, Rymal and Folkerts 1982). Leaves showing signs of herbivory by *E. fax* often contain drainage holes drilled at the base of the petiole. The drainage hole prevents the leaf from filling with water and thus makes it unable to capture prey, but it does not kill the plant (Fish 1976, Folkerts and Folkerts 1996, Rymal and Folkerts 1982). *Exyra fax* larvae employ two methods for closing the top of the pitcher chamber. The first and most common method is to spin a web of fine silken threads across the pitcher chamber near the pitcher mouth. The second method is to cut a fine girdle around the leaf just under the ridge at the opening of the chamber. The tissue above the girdle dies and shrivels inwards, closing the pitcher opening.

Once inside a sealed pitcher chamber, *Exyra* larvae eat the leaf from within while preserving the outer epidermis (Folkerts and Folkerts 1996; Jones 1904, 1921). At a distance this appears as yellow patches most easily observed on the underside of the leaf (Figs. 1A and 1C). Close inspection reveals that feeding occurs within the pitcher and is concentrated on the leaf underside away from the keel. As the larva eats, the pitcher chamber fills with ruddy-colored frass (D. Atwater, pers. observ.). It is unknown how many leaves a larva will eat before it pupates. Pupae suspend from the pitcher wall by a silken web (Folkerts and Folkerts 1996, Jones 1921).

Adults of *E. fax* have a variable ruddy coloration with black and ivory blotches or bands thought to serve as camouflage when they rest within the

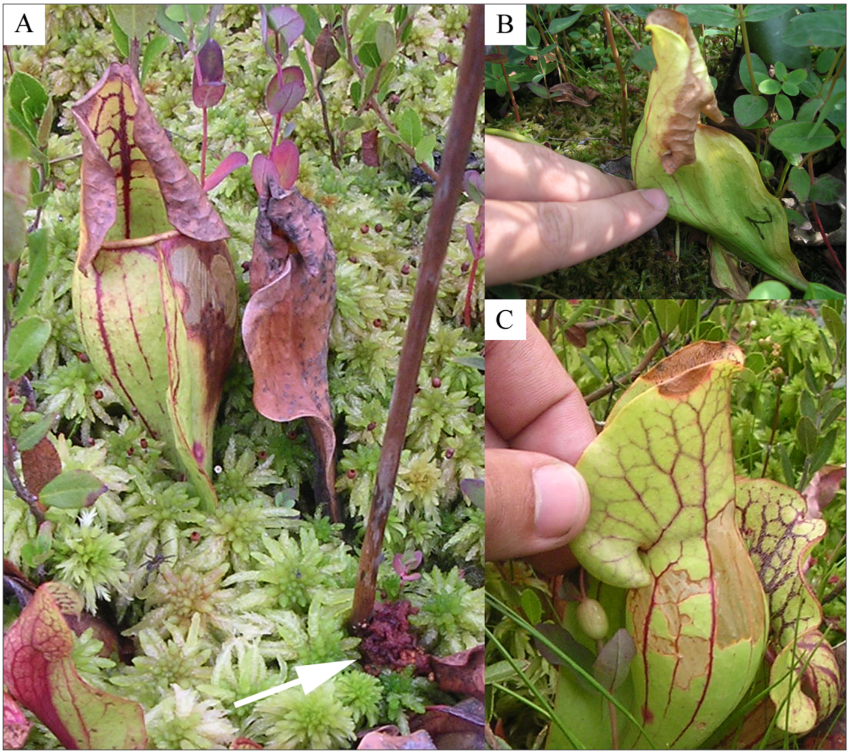

Figure 1. Signs of herbivory by *E. fax* (A and C) and *P. appassionata* (A and B). Destruction of the epidermis by *E. fax* herbivory is visible as light patches on the leaf surface in A and C. The wilting of leaves in A and B are characteristic signs of herbivory by *P. appassionata*. Frass evacuated by the feeding *P. appassionata* larva is visible in A (arrow).

interior of drained pitcher plant leaves. Females are hypothesized to fly either infrequently or over short distances, as only males are typically found outside of the plants at night (Jones 1921). During the day, both males and females rest motionless in the drained leaf. Mating occurs within the pitchers (Folkerts and Folkerts 1996, Jones 1921). Eggs of *E. fax* are small, round, and yellowish in color (Folkerts and Folkerts 1996, Jones 1921). According to Folkerts and Folkerts (1996), eggs are laid separately, several to a pitcher. Jones (1921), however, observed that eggs are laid in batches of 5–15, and one batch is deposited per plant. Eggs are laid below the opening of the pitcher chamber on the interior wall of a previously drained leaf.

From New Jersey southwards, *E. fax* is multivoltine. Further north, including in Massachusetts, it is univoltine (Brower and Brower 1970, Folkerts and Folkerts 1996). Larvae overwinter as third instars, and pupate in early summer the following year (Brower and Brower 1970).

Papaipema appassionata is listed as an endangered species in Connecticut and Indiana, is listed as threatened in the Commonwealth of Massachusetts, is a species of concern in Rhode Island, and is considered rare by the State of New Jersey. The State of New York and the Province of Ontario list the status of *P. appassionata* as unknown, and the species is not listed in any other states or provinces within its range.

Little is known about *P. appassionata* due to the rarity of the species. *Papaipema appassionata* larvae feed below ground and their effects on the rhizome of *S. purpurea* are cryptic in spite of the fact that herbivory eventually causes the death of the entire rosette (Brower and Brower 1970). One observable effect of *P. appassionata* herbivory is characteristic wilting of the plant (Figs. 1A and 1B). Wilting begins at leaf edges and spreads inwards until the entire leaf is yellow and soft. Throughout the season, more leaves in the rosette wilt until all the leaves die, turn black, and disintegrate (D. Atwater, pers. observ.). Another observable effect of *P. appassionata* herbivory is the accumulation of frass at the center of the rosette. The frass is granular and is a deep maroon color (Brower and Brower 1970, Rymal and Folkerts 1982). It is distinguishable from that of *E. fax* both by its location relative to the host plant and by its color.

Larvae reach 4 cm and are reddish-brown with discontinuous longitudinal white stripes (Bird 1903, Brower and Brower 1970). In late summer, larvae leave their burrows to pupate at the base of the plant (Bird 1903). Adults fly late in the year and lay eggs singly (Brower and Brower 1970). Adults have yellow wings with maroon flecks and a 3.8-cm span. At the center of each forewing are two groups of small white dots (Brower and Brower 1970, Rymal and Folkerts 1982). Though *P. appassionata* occurs most commonly with *S. purpurea*, it can occasionally be found feeding on other *Sarracenia* spp. (Rymal and Folkerts 1982). However, no other species of *Sarracenia* occur naturally north of North Carolina (Gleason and Cronquist 1991).

Methods

Study site

This research took place at Harvard Pond in Petersham, MA (42º30'N, 72º2'W; elevation 252 m above sea level). This artificial pond was created in the 1800s by the construction of two dams on Riceville Creek. We conducted our research in the southwestern portion of the pond, which is shallow and dotted with buoyant *Sphagnum* islands dominated by *Chamaedaphne calyculata* L. (Ericaceae; leatherleaf). This portion of the pond is wet year-round, and the contours of the buoyant islands do not change despite small fluctuations in water depth that occur continuously throughout the year (the site is illustrated and described in more detail by Butler et al. 2005). There were 62 islands in the 2000-m^2 area used in this study. The islands ranged in size from 0.1 m^2 to 60 m^2 and averaged 7 m^2. Twenty-eight islands had pitcher plants large enough to measure (pitcher mouth opening ≥ 2 cm).

Data collection

Data were collected between July 29 and August 15, 2003 and again the following year on August 14, 2004. In 2003, a flag was placed at the center of each island in the study site. We mapped the location of each island using transect tapes and compass, and determined their spatial positions (in Cartesian coordinates) relative to the first island sampled.

The shape of each island was mapped by choosing multiple points on the island perimeter that were roughly descriptive of the shape of that island. The distance and bearing of each of these points was found relative to the flag at the center of the island. These data were then converted to Cartesian coordinates, and the area of each enclosed polygon was used as a measure of island size.

To map the locations of the pitcher plants on each island, we found the distance and bearing from each plant on the island to the flag at the center of the island. The location of each plant was converted to Cartesian coordinates in the same coordinate system described above. Only plants with pitcher mouth diameters ≥ 2 cm were used.

Height and mouth diameter measurements were taken on the largest leaf of the plant (see Ellison and Gotelli 2002 for an illustration of these measurements). Mouth diameter (W) was measured as the longest diameter of the pitcher's mouth. Leaf height (H) was measured as the distance from the base of the petiole to the top of the hood along the mid-vein. Rosette size (R) was measured as the total number of leaves in the rosette. We recorded the presence of damage to the plant by both species of moth, and in the case of herbivory by *E. fax*, we recorded the number of leaves fed upon (E).

Leaves were scored as fed upon by *E. fax* if they contained no water and had one or more of the following characteristics: loss of interior leaf tissue with preservation of the outer epidermis, the presence of light brown frass in the leaf, or wilting of the hood of the chamber ascribed to girdling. Plants were scored as fed upon by *P. appassionata* if rust-colored frass was visible at the center of the rosette. Occasionally, light brown frass interpreted to be that of *E. fax* was found by the base of the leaves at or near the center of the rhizome. This was thought to be *E. fax* frass that spilled out of the leaf and onto the ground. In all cases in which such frass was found outside the leaves, at least one of the leaves of the rosette matched the characteristics of herbivory by *E. fax*. All plants scored as fed upon by *P. appassionata* also showed signs of characteristic leaf wilting or leaf death presumably caused by damage to the rhizome (Brower and Brower 1970). The following year (2004), leaf diameters, leaf height, rosette size, herbivory by *E. fax*, and herbivory by *P. appassionata* were measured for each plant that could be relocated with confidence.

Statistical analysis

We used Pearson correlation matrices to establish relationships among rosette size, leaf height, mouth diameter, and number of leaves per rosette with herbivory by *E. fax* in both 2003 and 2004. Bonferroni corrections were used to determine α values appropriate for each matrix ($\alpha = 0.050$/number of pair-wise correlations). We then performed two principal components analyses to produce an overall plant-size score (S) for each year. To determine how many principal components to use for further analyses, we used the Kaiser criterion, removing any components with eigenvalues < 1.0. We then performed two-sample *t*-tests comparing the plant-size scores from 2003 grouped by presence/absence of *E. fax* herbivory in 2003, and the plant-size scores from 2004 grouped by presence/absence of *E. fax* herbivory in 2004. Linear regressions were used to test for a relationship between plant size and herbivory in 2003 and in 2004. We divided the number of leaves per rosette fed upon by *E. fax* (E) by the total number of leaves in the rosette (R) to determine the fraction of leaves fed upon (E% = E / R).

To test whether the damage was distributed homogeneously across the islands, we performed two Kruskal-Wallis tests with fraction of leaves fed upon per plant (E%) and the principal component score (S) containing plant size as the response variables and island as the factor.

We used paired *t*-tests to test for differences in R, H, and W for each plant from 2003 to 2004. To test for a relationship between change in size and presence of herbivory by *E. fax* in 2003, regressions were performed with change in R, change in H, and change in W each as a response variable and percent of leaves per plant fed upon by *E. fax* as the predictive variable. All of the preceding analyses were performed using Minitab Release 14.

To determine whether the occurrence of herbivory in the plant population was clustered, we performed a nearest-neighbor analysis. The nearest-neighbor distance (NN) for any given plant is the distance from that plant to the closest neighboring plant. Mean NN was calculated for plants fed upon by *E. fax* and *P. appassionata* in both years. We used Monte Carlo simulations to determine if the observed mean was significantly different from that expected if herbivory was randomly distributed among plants. To calculate the expected mean NN for the number of plants *n* in the population damaged by moths, we randomly selected n plants from the entire population, calculated the NN value for those plants, and repeated the procedure 1000 times. If the observed mean NN for the n plants is smaller than 95% of the simulated mean NNs for the 1000 random samples of size n from the entire population, then we can say that the observed mean is more clustered than would be expected with probability (p) = 0.05. This analysis allowed us to distinguish a clustered distribution of herbivory from a random distribution despite the fact that the plants themselves are spatially clustered.

Results

In 2003, we found a total of 153 rosettes distributed among 28 of 62 islands in the study area (Table 1). Of those plants, 51 were fed upon by *E. fax*, 4 were fed upon by *P. appassionata*, and 1 was fed upon by both species. Seventeen islands containing a total of 69 pitcher plants were revisited in 2004. Among those 69 plants, 16 could not be found again. Among the 53 remaining plants, 33 were fed upon by *E. fax*, 6 were fed upon by *P. appassionata*, and 1 was fed upon by both species. Sixteen of the plants with herbivory by *E. fax* and one plant fed upon by *P. appassionata* in 2004 had no herbivory in 2003. The others showed signs of herbivory by *E. fax* in 2003. Eleven of the plants sampled in 2003 were so close together that it was impossible to precisely relocate them, making it impossible to determine whether they had changed size between 2003 and 2004. Ten of these plants were fed upon by *E. fax* in 2003, and all 11 were fed upon in 2004. Leaf morphology was impossible to measure for 3 plants in 2003 and 4 plants in 2004 due to wilting associated with *P. appassionata* herbivory.

Pearson correlations showed significant positive correlations among leaf height, mouth diameter, rosette size, and number of leaves fed upon by *E. fax* in 2003 and 2004 (Table 2). Principle component scores (Table 3) differed between plants fed upon by *E. fax* and plants not fed upon in 2003

Table 1. Matrix of plants in 2004 (columns) and 2003 (rows) categorized by presence of herbivory by *E. fax* (E) and *P. appassionata* (P). Totals are listed for each row and column. Total remeasured = the number of plants from each category that were remeasured in 2004.

	No feeding: 2004 ($n = 13$)	E only: 2004 ($n = 33$)	P only: 2004 ($n = 6$)	E and P: 2004 ($n = 1$)	Not found: 2004 ($n = 16$)	Not searched for: 2004 ($n = 84$)	Total
No feeding: 2003 ($n = 97$)	12	15[*]	1	1	11	57	97
E only: 2003 ($n = 51$)	1	18[**]	5[†]	0	1	26	51
P only: 2003 ($n = 4$)	0	0	0	0	3	1	4
E and P: 2003 ($n = 1$)	0	0	0	0	1	0	1
Total	13	33	6	1	16	84	153
Total re-measured	13	22	2	1	0	0	38

[*] One plant could not be positively relocated due to proximity to neighboring plants.

[**] Ten plants could not be positively relocated due to proximity to neighboring plants.

[†] Four plants could not be remeasured due to wilting.

($p < 0.001$) and in 2004 ($p < 0.001$). In both years, plants that were fed upon were larger than plants that were not fed upon. Among all plants surveyed in 2003, the number of leaves fed upon by *E. fax* increased ($p < 0.001$, $r^2 = 0.15$) and the percent of leaves per rosette fed upon by *E. fax* increased ($p < 0.001$, $r^2 = 0.10$) with increasing plant size. With plants that were not fed upon by *E. fax* larvae removed from the analysis, a significant relationship remained between plant size and number of leaves with

Table 2. Pearson correlation matrix containing number of leaves in rosette (R), largest-leaf height (H), largest-leaf width (W), and number of leaves fed upon by *Exyra fax* per plant (E) in 2003 (n = 150) and 2004 (n = 38), and Pearson correlation matrix containing change in number of leaves in rosette (dR), change in largest-leaf height (dH), and change in largest-leaf mouth diameter (dW) between 2003 and 2004 (n = 38). Coefficients for each cross are listed above p-values. The Bonferroni correction ($\alpha = 0.050/k$) is used to determine α for each matrix.

	R	H	E	dR	dH
Pearson Correlation for 2003 ($\alpha = 0.008$)					
H	$.40^{**}$				
E	$.24^{*}$	$.26^{*}$			
W	$.30^{**}$	$.59^{**}$	$.43^{**}$		
Pearson Correlation for 2004 ($\alpha = 0.008$)					
H	$.42^{*}$				
E	$.50^{*}$	$.55^{**}$			
W	.01	.26	$.47^{*}$		
Pearson Correlation for 2004–2003 ($\alpha = 0.017$)					
dH				.22	
dW				.01	.38

$^{*}p < \alpha$

$^{**}p < 0.001$.

Table 3. Results of principle components analyses of number of leaves in rosette (R), largest-leaf height (H), and largest-leaf mouth diameter (W) in 2003 (n = 150) and R, H, and W in 2004 (n = 38). Components are listed in columns. Eigenvalues are listed in the first row followed by the contribution of the listed component to the model. The coefficients applied to each variable are listed next to the variable name under each component.

		S1	S2	S3
2003	Eigenvalue	1.8853	0.7402	0.3945
	Proportion	0.622	0.247	0.131
	Cumulative	0.622	0.869	1.000
	R	-0.491	-0.851	0.184
	H	-0.634	0.204	-0.746
	W	-0.597	0.483	0.640
2004	Eigenvalue	1.4999	0.9958	0.5043
	Proportion	0.500	0.332	0.168
	Cumulative	0.500	0.832	1.000
	R	0.601	0.526	-0.602
	H	0.706	0.004	0.709
	W	0.375	-0.851	-0.368

herbivory ($p = 0.008$, $r^2 = 0.01$, $n = 53$) but disappeared between plant size and percent of leaves fed upon in the rosette ($p = 0.316$, $r^2 = 0.00$, $n = 53$).

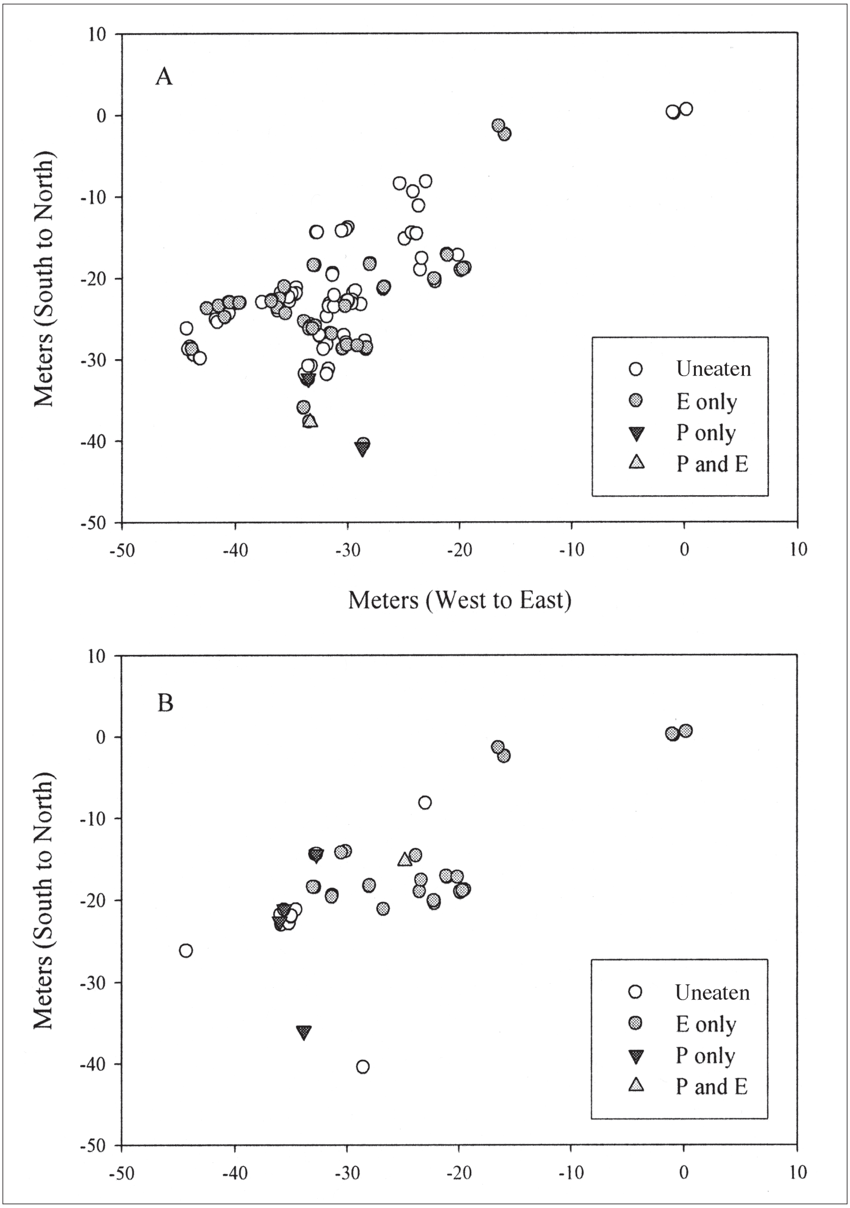

Figure 2. Distribution map of *Sarracenia purpurea* plants in the study area in 2003 (A) and 2004 (B). Open circles represent uneaten plants, light gray closed circles represent plants with herbivory by *Exyra fax* (E only), gray inverted triangles represent plants with herbivory by *Papaipema appassionata* (P only), and light gray triangles represent plants with herbivory by both *E. fax* and *P. appassionata*. North is in the positive Y direction and east is in the positive X direction. Scale is in meters.

Of the plants fed upon by *P. appassionata* in 2003, only 2 plants could be measured. In both cases, 6 leaves were present in the rosette. Average height (± standard deviation) of the largest leaf was 10 ± 1.4 cm and average mouth diameter was 2.3 ± 0.4 cm. In 2004, seven plants were fed upon by *P. appassionata*, three of which could be measured. Those plants averaged 4.3 ± 0.6 leaves, had a largest leaf height of 14.3 ± 2.3 cm, and had a leaf diameter of 2.2 ± 0.3 cm.

The distribution of herbivory by *E. fax* was more strongly clustered than would be expected if plants were selected at random (Fig. 2). The mean NN for plants fed upon by *E. fax* in 2003 was 0.673 ± 1.090 m (n = 53). This value is less than the expected mean NN of 1.165 ± 0.233 m (p = 0.008). The mean NN of plants fed upon by *E. fax* the following year was 0.424 ± 0.651 m (n = 33), also smaller than the expected mean NN of 1.302 ± 0.329 m in 2004 (p = 0.002). In 2003, the mean NN for plants fed upon by *P. appassionata* (2.183 ± 2.931 m, n = 5) was lower than expected (6.510 ± 2.887 m, p = 0.033). However, in 2004, the observed mean NN for plants fed upon by *P. appassionata* (2.625 ± 3.473 m, n = 7) did not differ significantly from the expected value of 5.545 ± 2.263 m (p = 0.108).

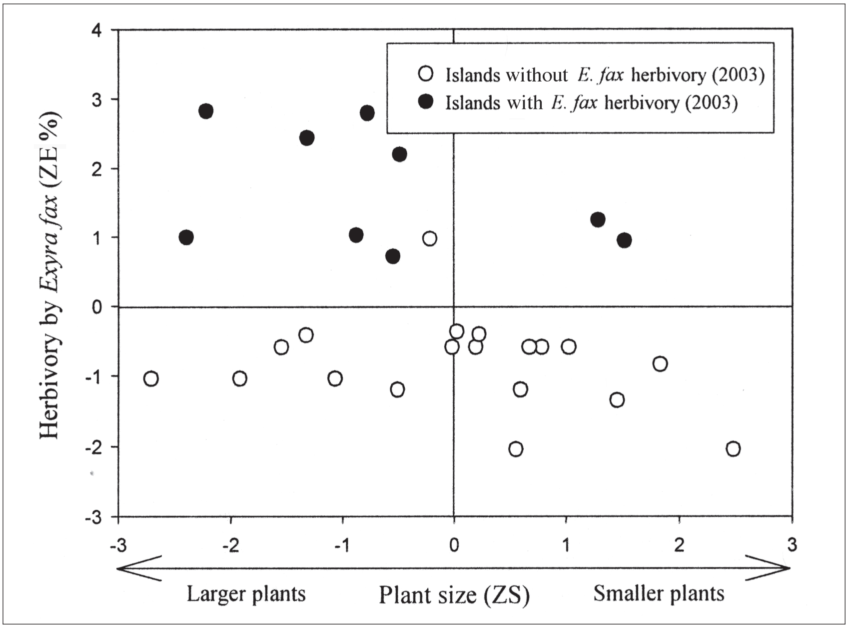

Figure 3. Damage vs. size of plant for each island. Herbivory is represented as Z-values (ZE%) calculated using Kruskal-Wallis test with percent of leaves per plant fed upon (E%) by *E. fax* in 2003 as the response variable and island as the factor. Plant size is represented as Z-values (ZS) calculated using a Kruskal-Wallis test with first plant size component score (S) from 2003 as the response variable and island as the factor. Open circles represent islands containing only uneaten plants, and closed circles represent islands containing at least one plant with herbivory by E. *fax*.

In 2003, 14 of the 28 plant-bearing islands contained plants with herbivory by *E. fax*. The same year, only 3 islands bore plants fed upon by *P. appassionata*. Those islands were within 6.7 m of one another and were located in the far southwestern portion of the research area. *Exyra fax* larvae fed upon plants on 10 of 17 revisited islands in 2004. The percent of leaves with herbivory by *E. fax* differed significantly from island to island ($p < 0.001$, $n = 150$, $df = 27$). *Papaipema appassionata* larvae fed upon plants on 4 islands, and those islands were more widely distributed across the research area than the islands with *P. appassionata* herbivory in 2003.

The principle component score of the plants in 2003 also differed from island to island using the same test ($p = 0.009$, $n = 150$, $df = 27$). Islands with large median plant size had higher incidence of *E. fax* herbivory than islands with small median plant size (Fig. 3). In 2003, of 14 islands with large plants, 8 were free of herbivory by *E. fax*. In 2004, 5 of those 8 islands were revisited, and 4 of them were newly settled by moths of *E. fax*.

Paired *t*-tests revealed no overall difference in rosette size ($p = 0.871$, $n = 38$), largest-leaf height ($p = 0.729$, $n = 38$), or largest-leaf diameter ($p = 0.599$, $n = 38$) among plants sampled in 2003 and 2004. We found no significant relationship between proportion of leaves fed upon in 2003 and change in rosette size ($p = 0.344$, $n = 38$) or height of largest leaf ($p = 0.741$, $n = 38$). However, the mouth diameter of the largest leaf declined significantly from 2003 to 2004 as the proportion of leaves fed upon in 2003 increased ($p = 0.006$, $r^2 = 0.17$, $n = 38$).

Discussion

We found that *E. fax* larvae were more likely to feed upon large plants, and that plants with herbivory by *E. fax* were unevenly distributed throughout the study area. However, among only those plants with herbivory by *E. fax*, per-leaf probability of herbivory was not correlated with increased plant size. This suggests that moths selected plants above a threshold plant size and that moths were selecting oviposition sites on a per-leaf and not a per-plant basis. We were unable to detect any plant-size preference trends for *P. appassionata* larvae due to the morphological consequences of damage by those larvae and the low sample size in this study.

We found spatial clustering of herbivory by both species of moths in 2003, and for herbivory by *E. fax* in 2004. Herbivory distribution would appear clustered if individual larvae attacked multiple neighboring plants, even if the larvae themselves were distributed randomly throughout the study area. It is unknown how many leaves larvae of *E. fax* or *P. appassionata* can consume during a lifetime or the degree to which larvae of either species move among plants. We note that ≈ 42% of the plants surveyed in 2003 had only one leaf fed upon by *E. fax* and that, of the 11 plants farther than 1 m from the nearest neighboring plant, five (45%) had only one leaf with *E. fax* herbivory. These data suggest that *E. fax* larvae do not require multiple leaves to feed and that larval movement is not a factor in herbivory clustering. In 2003, three plants fed upon by *P. appassionata* were within 6 cm of one another, and in 2004, a different three plants fed upon by *P. appassionata* were within 4 cm of one another. It is unclear whether this is due to a single larva feeding upon multiple rhizomes (see Rymal and Folkerts 1982) or to parental ovipositional choice. It is also possible that the clustering of *P. appassionata* observed in 2003 is an artifact of the small sample size, together with the fact that the distribution of *P. appassionata* was more limited within the study area in 2003 than in 2004, when spatial clustering was no longer detectable.

Certain individual islands possessed higher levels of *E. fax* herbivory than other islands and those islands also possessed large plants. However, more than half of the islands with large plants were also entirely free of *E. fax* herbivory. If adults were highly mobile, they would be expected to find each large plant in the study area with equal likelihood. Instead, they oviposited only upon certain islands. Our data support the hypothesis that limited mobility of *E. fax* adults leads to a clustered distribution of herbivory (Jones 1921). We note that several of the islands with large plants and no presence of *E. fax* in 2003 recruited populations of *E. fax* in 2004, suggesting that low adult mobility reduces but does not eliminate the chance of emigration to a new island.

We found evidence that *E. fax* herbivory plays a role in controlling year-to-year variation in plant size. Rosette size and leaf height did not change as a function of herbivory by *E. fax*, but plants with many leaves that were fed upon in 2003 had smaller mouth diameters in 2004 than plants with lesser herbivory. The effects of feeding by *E. fax* are known to prevent the pitcher from filling with water. When a leaf loses its ability to contain water, it also loses its ability to directly obtain nitrogen from captured prey. The resulting loss of nutrients could cause a reduction in production (i.e., leaf size) the following year.

Given the apparently low mobility of *E. fax* adults and the presumed high mobility of *P. appassionata* larvae, it would be interesting to monitor spatial changes in moth population structure. Herbivory by *P. appassionata* is sporadic, and the distribution of herbivory might be hard to predict from year to year. The distribution of *E. fax* moths could follow a more predictable pattern. It may be that once an island is settled, larvae quickly inhabit all suitable plants. Plants may then reduce in quality to the point at which the island is no longer habitable. The population would then either emigrate or suffer a loss in size. This would lead to a dynamic interaction in which metapopulations of *E. fax* moths reduce resource availability on an island until the metapopulation either dies or scatters. Afterwards, the plants on that island could recover to habitable size until they were fed upon again. A long-term study tracking the spatial and temporal distribution of herbivory across the bog could address this hypothesis.

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