

Sequential flowering of neighboring goldenrods and the movements of the flower predator *Epicauta pennsylvanica*

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Summary. As neighboring plants flower sequentially, do flower feeders preferentially remain in the area, rather than move to another area with flowering plants? I examined the movements of the meloid beetle *Epicauta pennsylvanica*, a flower predator specializing on *Solidago*, in four types of replicated experimental plots – monocultures of *Solidago altissima*, or *S. altissima* interplanted with members of the same genus, same family, or different taxonomic orders. I released marked beetles only in the “genus” plots, which contained four species of *Solidago*, two that bloom before *S. altissima*. The number of beetles in the genus plots declined steadily as *S. altissima* came into flower in all the plots; the total number of beetles in all the plots remained fairly constant. I found no evidence that plant neighborhoods affected beetle distribution. Beetles foraging on the early blooming *Solidago* species did not remain in the genus plots as *S. altissima* came into flower. In addition, beetles that left the genus plots did not differentially accumulate in any of the other plot types, even though one type of plot was a monoculture with four times the density of *S. altissima* than the other plots.

Key words: Flowering phenology – Facilitation – Resource concentration – *Epicauta pennsylvanica* – *Solidago*

Facilitation of pollinators (Rathcke 1983) can occur if plant species flowering early in the season support pollinators that would otherwise be unavailable for later flowering species (Baker 1963; Baker et al. 1971; Heinrich and Raven 1972). Waser and Real (1979) term this phenomenon sequential mutualism, and document an example. Hummingbirds are major pollinators of *Delphinium nelsonii* and *Ipomopsis aggregata*. When early-blooming *D. nelsonii* was unusually rare in two consecutive seasons, migrating hummingbirds did not remain in the area to pollinate the later-flowering *I. aggregata*.

The abundance patterns of non-pollinating insects can also depend on the phenology of neighboring plants. Sequentially available populations of different plant species, whether interplanted or simply nearby, can provide agricultural insect pests (e.g. Root and Tahvanainen 1969; Tamaki et al. 1975a) and their natural enemies (e.g. Sluss 1967;

Flaherty 1969; Atsatt and O’Dowd 1976) with a continuous supply of resources. For example, Tamaki et al. (1975b) showed that the density of the redbacked cutworm, *Euxoa ochrogaster*, was lower in asparagus fields without weeds than with weeds. These cutworms hatched before most asparagus came up; only in weedy fields was there plentiful food for early instar larvae.

Just as the presence of early-flowering species may boost local pollinator populations foraging on later-flowering species, the presence of early-flowering plants may also increase local populations of insect flower predators. I investigated facilitation of flower predators with *Epicauta pennsylvanica* DeGeer (Coleoptera: Meloidae). Adults of this blister beetle feed destructively on *Solidago* (goldenrod) flowers, consuming anthers, stigmas, and other soft flower parts (Werner et al. 1980; unpublished work). The beetles spend the day on flowers and the night in the litter near the base of their host plants (Mathwig 1968).

Using marked beetles, I investigated facilitation in four kinds of experimental plots, all containing *Solidago altissima* L. (Asteraceae). One kind of plot also contained two other species of *Solidago* that bloom before *S. altissima*. If facilitation occurred, I would expect that the marked beetles, which were released in the plots with the early flowering goldenrods, would remain in these plots as *S. altissima* came into flower in all the plots.

This experiment also provided an opportunity to test Root’s (1973) “resource concentration hypothesis.” According to this hypothesis, population densities of insects should be higher in areas with a high resource concentration because insects are likely to find a pure or dense stand of host plants, and short movements are not likely to take herbivores out of such stands. If *E. pennsylvanica* respond to resource concentration, I would expect beetles that left the genus plots to have preferentially accumulated in the plots with the highest resource concentration.

Methods

I worked in experimental plots established at Cedar Creek Natural History Area in Bethel, MN, by Drs. P.A. Morrow and D.W. Tonkyn in 1982. Within each plot there are 169 *Solidago altissima* (Asteraceae) plants in the “S” position, each with six nearest neighbors (Fig. 1). By changing the species of the neighboring plants in the A, B, and C positions, four types of plots were created. In the “species” plots the A, B, and C neighbors are all *S. altissima*, resulting

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SPECIES PLOTS

A, B, C, S *Solidago altissima* L.

GENUS PLOTS

S *Solidago altissima* L.
 A *Solidago nemoralis* Ait.
 B *Solidago missouriensis* Nutt.
 C *Solidago rigida* L.

FAMILY PLOTS

S *Solidago altissima* L.
 A *Liatris aspersa* (Michx.) Greene
 B *Aster ericoides* L.
 C *Helianthus laetiflorus* Pers.

ORDERS PLOTS

S *Solidago altissima* L. (Asterales)
 A *Monarda fistulosa* L. (Lamiales)
 B *Lespedeza capitata* Michx. (Fabales)
 C *Asclepias tuberosa* L. (Gentianales)

Fig. 1. Detail of the planting design of the plots. A, B, and C represent the neighboring species of *S. altissima*, S

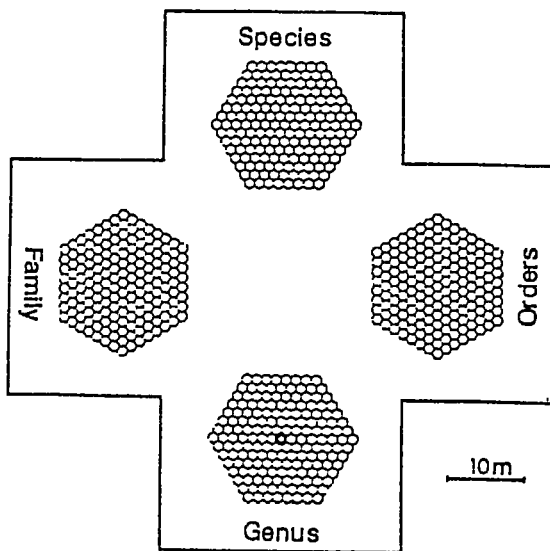
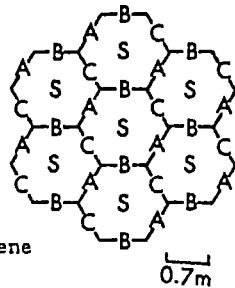


Fig. 2. Layout of one of the three blocks of experimental plots. The star marks the point where beetles were released

in a monoculture. There are three types of polycultures in which the A, B, and C neighbors are three species from 1) the genus *Solidago*, 2) different tribes or subtribes of the Asteraceae family, 3) different orders. These are called the "genus," "family," and "orders" plots, respectively. All the plant species are perennials native to North America, and co-occur naturally in tall grass prairie.

Figure 2 shows the layout of the experimental plots. There are three replicate blocks of the four plots. Each plot is 21 m across and contains 721 numbered and mapped plants; each plant is 0.7 m from each of its six nearest neighbors. The ground between plants was cultivated to remove weeds.

The plants grew vigorously in the plots, and were trimmed so that conspecifics were roughly the same size. The *S. altissima*, which were commonly close to a meter tall, were trimmed to three stems per plant. The average height of the *S. altissima*, and the percentage of *S. altissima* in flower, did not vary significantly among plot types (P.A.

Morrow and D.W. Tonkyn, unpublished work). Almost all the *Solidago* flowered.

Epicauta pennsylvanica forage on all four species of goldenrod in the genus plots. Censuses and observations in the plots in 1983 indicated that beetles forage equally often on blooming *S. altissima*, *S. missouriensis*, and *S. nemoralis*; *S. rigida* is less preferred (R.J. Goldberg, unpublished work).

On August 8, 1984 I collected all the *E. pennsylvanica* I could find (approximately 400) from the two early blooming goldenrod species, *Solidago nemoralis* and *Solidago missouriensis*, in the three replicate genus plots. There were no *E. pennsylvanica* in any of the other plots, because *S. altissima* – the only *Solidago* in the other plots – was not yet in flower. I collected another 200 *E. pennsylvanica* from other fields at Cedar Creek, and divided the beetles into three groups of 200. I marked each beetle with two dots of "Testor's" model paint on one elytron, using a different color for each group. The beetles were caged overnight in a 15 degree C incubator, and released between 6:15 and 6:30 A.M. on August 9. Each group of 200 beetles was released near the center plant of one of the three genus plots (Fig. 2). The beetles were released on white paper, so that any dead beetles would be easy to find.

Between 8:30 and 10:30 A.M. on the day of release, the *E. pennsylvanica* in all the plots in all the blocks were visually censused (visually recaptured) and their locations recorded on maps. Because the black beetles stand out against the yellow goldenrod flowers, they were easy to sight. Dead beetles at the release points were counted and removed (there were 10). Beetles were recensused on August 11, 13, 15, 17, and 21. Six to eight people usually participated in the censuses; all but one census was completed in two hours. Immediately after each census, in each genus plot, I categorized the flowering stage of 30 *S. altissima* "S" plants and three neighbors (one "A", one "B", and one "C" plant) of each of the 30.

The census data were analyzed with the statistical package IVAN (Weisberg and Koehler 1982) on the University of Minnesota's Cyber 74 computer. Before performing statistical tests, count data were square root transformed and proportion data were arcsin square root transformed.

Results

Approximately 80 percent of the *S. nemoralis* and *S. missouriensis* plants in the genus plots were in flower at the beginning of the experiment (Fig. 3). The percentage of *S. missouriensis* in bloom declined steadily, while the percentage of *S. nemoralis* in bloom remained fairly constant throughout the experiment. Approximately 10 percent of the *S. altissima* and *S. rigida* in the genus plots were in flower at the beginning of the experiment; the percentage of these two species in bloom increased steadily. This flowering phenology corresponded to that of natural populations of these species at Cedar Creek Natural History Area. An additional census on the day of the last census showed that the percentage of *S. altissima* in flower in the species, family, and orders plots was comparable to that in the genus plots.

Approximately 50 percent of the beetles were not recaptured in any of the plots during the first census, several hours after the beetles were released. Censuses in 1983 indicated that the 200 beetles released per plot was not an ab-

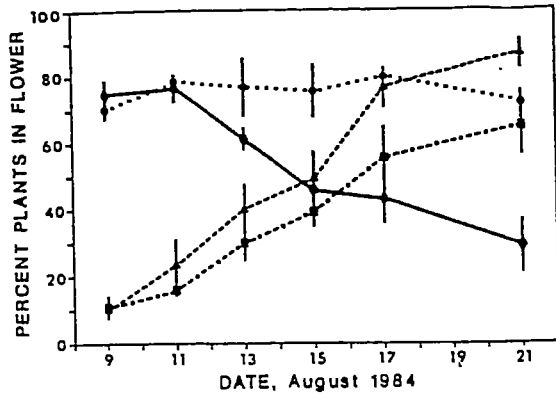


Fig. 3. Percentage of the four species of *Solidago* in the three genus plots, in bloom during the censuses (\pm s.e.). Each point represents 90 plants. (..... *S. altissima*, *S. nemoralis*, — *S. missouriensis*, - - - - *S. rigida*)

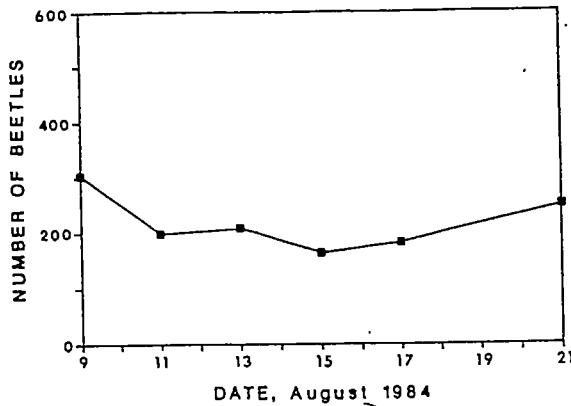


Fig. 4. Total number out of 600 released beetles that were recaptured in all the plots in all the blocks

normally high plot density. But since the 200 beetles were actually released around one plant, the local beetle density was probably high enough to cause many of the beetles to leave. The total number of beetles recaptured after the first census in all the plots in all the blocks did not, however, decline (Fig. 4). On average, 37 percent of the marked beetles were recaptured per census. A repeated measures ANOVA on the total number of beetles recaptured per block (no matter where they were released) did not have a significant census effect (Table 1a), and the linear contrast from the census effect was not significant ($P=0.48$). I also used a repeated measures ANOVA to analyze the change over time (starting with the first census) in the number of marked beetles remaining in the plot where they were released. There was a significant census effect (Table 1b, $P=0.0005$). The linear and quadratic contrast from the census effect were both significant ($P<0.0001$, $P=0.02$, respectively). Thus, although the number of beetles recaptured per block did not decline, the number of marked *E. pennsylvanica* remaining in the genus plot in which they were released declined in a nonlinear fashion over time (Fig. 5).

Resource concentration is a function of stand purity and density. Because the species plots were monocultures, and the density of *S. altissima* in the species plots was four times that in the family and orders plots, the resource con-

Table 1a, b. Repeated measures ANOVA's on the number of beetles recaptured. The data in (a) and (b) were square root transformed. (a) Analysis of the total number of marked beetles censused per block. (b) Analysis of the number of marked beetles censused in the genus plot in which they were released.

Source	d.f.	Mean square error	F	P
a				
Block	2	7.50		
Census	5	3.56	0.87	0.53
Error	10	4.07		
b				
Block	2	7.59		
Census	5	28.54	12.23	0.0005
Error	10	2.33		

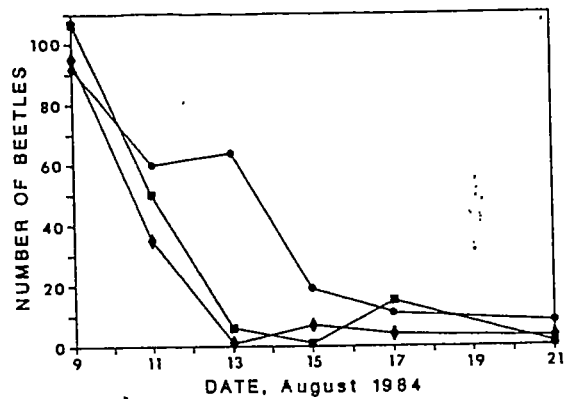


Fig. 5. Number of marked beetles recaptured in the genus plot in which they were released. Each curve represents one replicate genus plot

centration in the species plots was higher than in the family and orders plots. To examine the effect of resource concentration on beetle movement, I performed a third repeated measures ANOVA on the number of marked beetles censused in these plots (all the plots other than the genus plots; data includes beetles released in one block and recaptured in another). The number of beetles in the species, family, and orders plots increased linearly over time (Table 2a, census effect, $P=0.0001$; linear contrast from census effect, $P<0.0001$) - beetles were emigrating from the genus plots (Fig. 6). Although the average number of beetles recaptured per census was lower in the family plots than in the species and orders plots (mean \pm s.e. = 6.2 ± 2.7 for the family, vs. 14.5 ± 10.7 for the species and 13.9 ± 8.4 for the orders plots), there was not a significant plot effect, nor was there a significant plot \times census interaction (Table 2a). Because there are four times more *S. altissima* in the species plots than family and orders plots, I also performed a similar ANOVA on the number of *E. pennsylvanica* per *S. altissima*, with similar results (Table 2b). The number of beetles per *S. altissima* increased linearly over time (Table 2b, census effect, $P=0.0004$; linear contrast from census effect $P=0.0002$). Although there were fewer beetles per *S. altissima* in the species plots than in the family and orders plots (0.11 ± 0.07 , 0.15 ± 0.17 , and 0.24 ± 0.29 , respectively), the

Table 2a, b. Repeated measures ANOVA's on beetles recaptured in the species, family, and orders plots. a Analysis of the number of marked beetles censused in the species, family, and orders plots. Square root transformed data. b Analysis of the number of beetles per *S. altissima* in the species, family, and orders plots. Arcsin square root transformed data

Source	d.f.	Mean square error	F	P
a				
Block	2	1.09		
Plot	2	7.75	0.91	0.47
Error 1	4	8.48		
Census	5	17.54	7.26	0.0001
Plot × census	10	3.40	1.40	0.22
Error 2	30	1.97		
b				
Block	2	0.008		
Plot	2	0.086	3.51	0.13
Error 1	4	0.024		
Census	5	0.067	6.23	0.0004
Plot × census	10	0.017	1.62	0.15
Error 2	30	0.321		

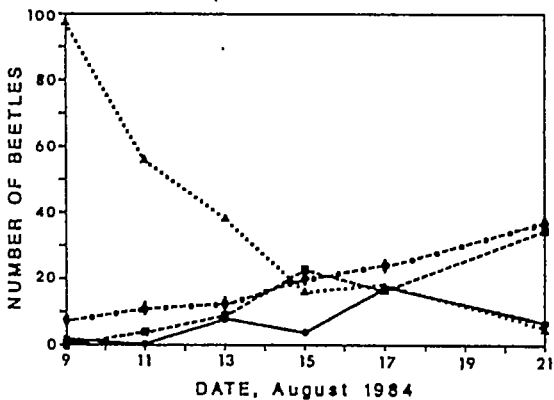


Fig. 6. Average number of marked beetles recaptured in the species (■), family (●), orders (◆), and genus (▲) plots. $N=3$. Data includes beetles released in one block and recaptured in another. Standard errors are omitted from the figure because they are large; they are given in the text for the overall plot means

plot effect was again not significant. In short, I found no evidence that after the beetles left the genus plots, they differentially accumulated in the species, family, or orders plots. The standard errors for the mean numbers of beetles in the plots were large: the statistical power for the tests of plot effect were low (approximately 0.20 for Table 2a, approximately 0.55 for 2b). But, the fact that the species plot had the lowest number of beetles per *S. altissima* suggests that the absence of a resource concentration effect was not just a problem of power.

The beetles not only spread out over the different plot types (analysis above), they also did not remain in the particular blocks in which they were released (Fig. 7). A repeated measures ANOVA on the number of beetles recaptured per block, that were released in a different block.

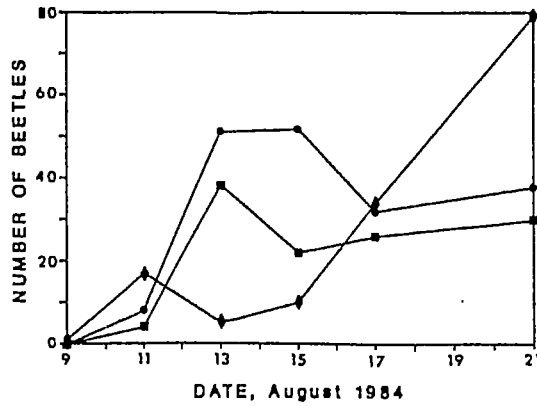


Fig. 7. Number of marked beetles recaptured in a block, that were released in the other two blocks. Each curve represents one replicate block

Table 3. Repeated measures ANOVA on the number of recaptured beetles per block, that were released in a different block. Square root transformed data

Source	d.f.	Mean square error	F	P
Block	2	1.35		
Census	5	16.04	5.55	0.01
Error	10	2.89		

increased linearly with time (Table 3: census effect, $P=0.01$; linear contrast from census effect, $P=0.0006$).

Discussion

I found no evidence that the presence of early flowering species causes local flower predator populations to remain in the area and feed on later flowering species. *E. pennsylvanica* feeding on early blooming goldenrods in the genus plots showed no tendency to remain in these plots to feed as *S. altissima* came into flower in all the plots.

My results are only relevant to the spatial scale at which I worked (Heads and Lawton 1983; Kareiva 1983; Weins 1986; Wiens et al. 1986). There may be different behavioral mechanisms governing insect movements between plants at different spatial scales (Stanton 1983). In fact, the only way we can distinguish what an animal considers a patch is by studying variation in the animal's movement patterns. In this experiment there were three spatial scales at which the beetles might react: within plots (0.7 to 1.4 m between flowering goldenrods), within blocks (10 to 25 m between plots), between blocks (60 to 240 m). Figure 6 shows that a large fraction of the beetles left the genus plots and distributed themselves among the other plots. Fig. 7 shows a comparable effect for blocks. In each census, over a period of thirteen days, the percentage of beetles recaptured did not decline, and averaged a relatively high 37 percent (Fig. 4). Thus, although the experiment was fairly large for an ecological manipulation, the beetles' free movement among plots and blocks suggests that the beetles regarded the entire experiment as one large goldenrod patch.

If I had worked on a larger spatial scale, my results might have been different. If *E. pennsylvanica* forages ran-

domly within a patch, and a plot is smaller than a patch, then the proportion of goldenrod fed on in a plot will vary inversely with goldenrod density. This is because the beetles will on average spend equal amounts of time in all parts of the patch. (See Heads and Lawton (1983) for a definition of patch based on this idea.) Thus, the absence of a resource concentration effect and the lower density of beetles I observed in the species plots may simply reflect that plot size was smaller than patch size. Furthermore, I have found marked *E. pennsylvanica* one to two km from where I had released them less than one week earlier. It is possible that if there were no early blooming goldenrods in a large area (many square kilometers), then the number of *E. pennsylvanica* feeding on the later blooming *S. altissima* in this area might be reduced.

Because *E. pennsylvanica* feeds destructively on flowers, it shares characteristics with both destructive insect herbivores and flower feeding insect pollinators. Although pollinator visitation rate does not always increase with the local density of flowering plants (Schmitt 1983), it is commonly assumed that the density and proximity of flowering plants influences pollinator foraging behavior because of pollinator energetic constraints (e.g. Thomson 1981; Heinrich and Raven 1972; Cibula and Zimmerman 1984). The movements of *E. pennsylvanica* showed no evidence of such energy constraints. The beetles did not simply move from early flowering goldenrods to the nearby *S. altissima* in the genus plots, nor were beetles that left the genus plots recaptured more frequently in the species plots, which had four times the density of *S. altissima* as the family and orders plots. However, there are notable differences between *E. pennsylvanica* and most insect pollinators. Unlike bees, the most widely studied pollinators, sexual behavior may complicate *E. pennsylvanica*'s foraging behavior. Furthermore, because *E. pennsylvanica* consumes more of a flower than just nectar and pollen, this beetle probably can obtain considerably more energy per flower than a pollinator; the cost of plant to plant movement may be comparatively small.

A number of studies, primarily comparisons of monophagous insects in agricultural systems, support Root's resource concentration hypothesis (reviewed in Perrin 1977; Stanton 1983; Andow 1986); insect herbivores differentially accumulate in pure or dense stands of host plants. However, *E. pennsylvanica* that left the genus plots showed no response to increased resource concentration in the species plots. Furthermore, *S. rigida* and a few remaining *S. nemoralis* and *S. missouriensis* were in bloom along with the *S. altissima* in the genus plots. Censuses of naturally occurring beetles in the experimental plots in 1983 indicated the (*E. pennsylvanica*) forage equally often on *S. altissima*, *S. missouriensis*, and *S. nemoralis*; *S. rigida* is less favored (R.J. Goldberg, unpublished work). Thus the beetles that emigrated from the genus plots to the family or orders plots went to plots with a lower resource concentration.

In conclusion, I found no evidence in this study that plant neighborhoods play a role in the distribution of *E. pennsylvanica*. (Goldburg (1986) found, however, that *E. pennsylvanica* were more strongly attracted to *S. altissima* surrounded by non-flowering, rather than flowering, non-goldenrods.) *E. pennsylvanica* did not remain in the genus plots as *S. altissima* came into flower in all the plots, nor did the movements of beetles that left the genus plots reflect patterns of resource concentration.

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