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PLANT PLASTICITY, PHENOLOGY, AND HERBIVORE DISPERSION: WILD PARSNIP AND THE PARSNIP WEBWORM[1]

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Abstract. The influence of plant plasticity on the dispersion of a specialized insect herbivore was analyzed in an 8- to 9-yr oldfield. The parsnip webworm, *Depressaria pastinacella* (Lepidoptera: Oecophoridae), is a specialist on the flowers and developing seeds of the biennial herb *Pastinaca sativa* (Umbelliferae). The dispersion and abundance of larvae on isolated plants in mixed vegetation was compared with that on plants in patches in which flowering conspecific density was between 30 and 40 plants per m^2. On isolated plants the number of larvae per gram umbel was 50% higher at the peak of larval abundance, the cumulative proportion of plants attacked was 80% higher, and the cumulative proportion of umbels on each plant attacked was 40% higher than on high density plants. The dispersion of larvae within the study area was governed by the plastic response of plants to increasing plant density rather than by density *per se*. Successful oviposition was limited to unopened umbels. Isolated plants had more unopened umbels available at any one time and maintained this availability over a longer period of time than high density plants. Most umbels harbored only 1 larva. Hence, the number of umbels and the synchrony between presence of unopened umbels and moth oviposition period limited the number of early instar larvae.

Within-plant dispersion of larvae was related to the patterns of umbel size and the phenological staggering of umbel appearance of each plant. Experimental introduction of larvae onto plants either synchronously or asynchronously revealed these patterns. Only large-diameter umbels supported >1 larva, and these umbels were more common on isolated plants. Staggering of umbel production (or its simulation with asynchronous introductions) led to less aggregation of later instar larvae, because larvae arriving early preempted sections of umbel.

Key words: Depressaria; *herbivore dispersion; herbivore limitation; Illinois; Insecta; Lepidoptera;* Pastinaca; *plant density; plant plasticity; population; Umbelliferae.*

INTRODUCTION

Plant dispersion and density have been shown repeatedly to influence insect faunal composition and herbivore abundance (e.g., Luginbill and McNeill 1958, Dethier 1959, Pimentel 1961, Davis 1966, Way and Heathcote 1966, Janzen 1969, 1975, Tahvanainen and Root 1972, Wilson and Janzen 1972, A'Brook 1973, Root 1973, Platt et al. 1974, Cromartie 1975). However, changes in plant density are often accompanied by changes in plant size, shape and phenology (e.g., Thompson 1929, Harper and Gajic 1961, Yoda et al. 1963, Harper 1968, Putwain et al. 1968, White and Harper 1970, Pemadasa and Lovell 1974, Snell and Burch 1975, Bazzaz and Harper 1976). Under such situations, the simultaneous effects of varying patch density and plant plasticity must be considered and separated in analyses of the dispersion of insect herbivores.

In the present study we analyze how varying plant density, size, shape and phenology in *Pastinaca sativa* (Umbelliferae) influences attack of flowers and immature seeds by the parsnip webworm, *Depressaria pastinacella* (Duponchel) (Lepidoptera: Oecophoridae). We quantify the specific plant factors which influence within-field dispersion of the larvae. In addition, we describe the within-plant distribution and abundance of larvae under natural conditions and compare this with the dispersion of larvae experimentally introduced synchronously and asynchronously onto plants.

Plant shape, size and phenology have been well established as factors governing some insect herbivores, especially with regard to oviposition sites (e.g., Breedlove and Ehrlich 1968, Singer 1971, Breedlove 1972, Badawi et al. 1976, Rathcke 1976). The effect of these factors on larval or nymphal patterns of utilization of plants has been suggested by several studies (e.g., Heinrich 1971, Bryant and Raske 1975, Gilbert and Singer 1975, Kidd 1976*a*, *b*). However, analysis of these factors in the context of plant patchiness and plasticity is needed. Studies on the influence of plant plasticity and phenology together with analyses of plant chemistry, dispersion and density, and associational patterns with other plants (e.g., Feeny 1970, 1976, Tahvanainen and Root 1972, Root 1973, 1975, Cromartie 1975, Atsatt and O'Dowd 1976) are essential to an understanding of the mechanisms of arthropod-plant community organization in both contemporary and evolutionary time.

Natural history of host and herbivore

Pastinaca sativa is a biennial herb which occurs as a weed in disturbed areas throughout North America.

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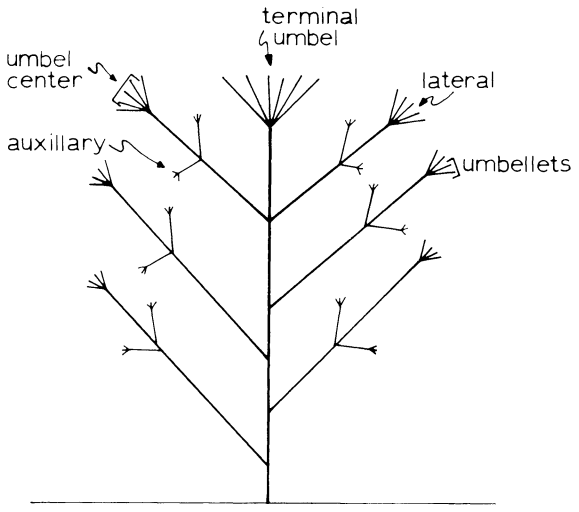

FIG. 1. General outline of the shape of *Pastinaca sativa*. Note that umbels decrease in size from the top to lower portions of the stem.

Originally from Eurasia, it has been naturalized in North America for at least 160 yr (Nuttall 1818). It grows naturally in a variety of dispersions and densities. In Illinois, seeds germinate in the spring and early summer. The first summer a plant develops a leaf rosette and a strong taproot. The following or some later spring it sends up a flowering stalk.

The terminology used to describe umbel arrangement is given in Fig. 1. Under natural conditions, umbels develop in the following order: terminal, upper lateral, auxillary and lower lateral. This is important for consideration of parsnip webworm distribution because only a few umbels on a plant are available for oviposition at any one time.

Depressaria pastinacella is an holarctic species which is restricted to a few host plants in the genera *Angelica*, *Heracleum*, and *Pastinaca*, all within the Umbelliferae (Hodges 1974). In the study area, the parsnip webworm was restricted to *P. sativa*, because other hosts do not grow nearby. One of us (J. N. T.) observed that larval populations in 1975 were high relative to 1974. This was the only oecophorid species on *P. sativa* and was the dominant herbivore (in terms of biomass) on the plants. Other herbivores on umbels were rare. The eggs were laid in unopened umbels from mid-May to early June. Each larva webbed and fed on the flowers and developing seeds. Webbing of an umbel by a larva generally preempted the umbel from other larvae because no remaining umbellets were close enough to permit a larva to web them together. If the umbel was large, 2 or more larvae would construct independent webs. If the stem was sufficiently large in diameter, the mature larvae bored into it to pupate, generally at the base of the lowest green leaf; larvae from plants with small stems pupated in the ground. Overwintering adults began to emerge in early July (Bethune 1870, Riley 1889, Brittain and Gooderman 1916, Clarke 1952).

METHODS

The study area was located in an 8- to 9-yr oldfield in the University of Illinois Ecological Research Area east of Urbana, Illinois. Flowering individuals of *P. sativa* grew singly or in patches up to 40 per m^2 over areas up to 30 m^2.

To compare the relative degree of utilization of high density and isolated plants by *D. pastinacella*, 60 rosettes in high density areas (30 or more/m^2) and 30 isolated plants, each in mixed vegetation and separated from conspecifics by at least 3 m, were tagged. High density plants were tagged in groups of three in 20 high density areas of the field.

The following parameters were monitored approximately every 4 days from 16 May to 30 June: basal stem diameter, number, phenological state and position on plant of umbels, and number and position on plant of larvae. Larvae were present on the plants from 20 May to 30 June.

Ten unmarked plants were chosen randomly and removed from both isolated and high density situations in the study area on 22 and 30 May and 7 June to estimate plant and umbel weight of the marked plants. High density plants were removed near but not within the marked quadrats. Plants were separated into roots, stems, leaves, and umbels (flowers, seeds and supporting structures), dried at 80°C to constant weight, and each component was weighed to the nearest 0.1 g. *Pastinaca sativa* has a large taproot which generally lacks large lateral roots. Thus, removal of virtually all root biomass was possible. Correlations between basal stem diameter and both total plant dry weight and umbel dry weight provided the basis for weight estimates for tagged plants from their basal stem diameters alone. Separate correlations were obtained for isolated and high density plants on each date, because growth patterns differed between the densities.

To analyze experimentally the intra-plant dispersion of larvae, 30 individuals of *P. sativa* were tagged on 26 May 1976 in a 150 m^2 plot in the study area. Plants were of different sizes and were separated from conspecifics by at least 2 m. *Depressaria pastinacella* females had not yet oviposited on any of the tagged plants. Each umbel on all tagged plants was given a permanent number in order to monitor larval dispersion.

Fifteen larvae were introduced synchronously onto each of 20 plants on 26 May to analyze how larvae would partition a plant if they were to begin development simultaneously. This would happen naturally if a number of umbels were available for oviposition at one time on a plant. For the experiment, second- and third-instar larvae were collected from another area of the field with a high larval population. Second- and third-instar larvae were used because it was difficult to

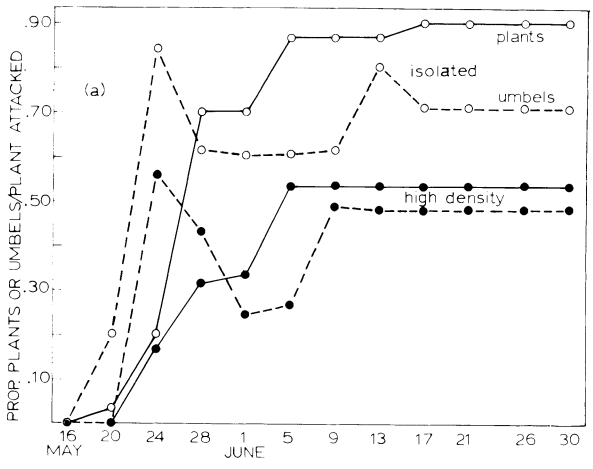

FIG. 2. Pattern of attack on *Pastinaca sativa* by *Depressaria pastinacella*. Cumulative proportion of plants (—) and umbels/plant (– – –) attacked; plants, differences significant on all dates after 24 May; umbels, all differences significant except 9 June.

establish first instars on new plants. Also, new first-instar larvae resulting from oviposition by females during the experiment could be identified easily as such and removed. Larvae were placed on the main stem approximately at the midpoint in height. This allowed the larvae to choose their final positions on the plant. Early on 27 May, additional larvae were added to each plant to compensate for failure of some larvae to become established successfully on the previous day, thereby bringing the total on each plant once again to 15 larvae.

Larvae were introduced 2 at a time over a period of 6 days on 10 other plants. This simulated the more normal situation in which larvae begin development on a plant over a period of days due to successive ovipositions in unopened umbels as they become available. Two second- or third-instar larvae were introduced onto each plant on the afternoon of 30 May following the same procedures for placement used in synchronous introductions. Subsequent introductions of second- and third-instar larvae were made 2× daily through 4 June, at which time 16 larvae had been introduced onto each plant. Positions of all larvae were noted 2× daily from 1–4 June and every day from 6–14 June, when the last larva had pupated.

In data analysis either $\log_{10}$ or square root transformations were used where appropriate for means with unequal variances or nonnormality of distributions. The test for equality of percentages (Sokal and Rohlf 1969) was used for comparisons of proportions. Standard errors on transformed data were replaced with asymmetric 95% confidence limits. Differences were tested using either *t*-tests or Chi-square tests.

RESULTS

Basal stem diameter was correlated significantly with both total plant dry weight and umbel dry weight for the unmarked plants collected on all three dates (number of correlations = 12; all $P < .05$; mean $r^2 = .87$; range of r^2 values: .51–.92). By using these correlations to estimate plant and umbel weights of marked plants from their basal stem diameters alone, isolated plants were shown to be significantly heavier in total weight and umbel weight (Table 1).

TABLE 1. Mean total plant dry weight and umbel dry weight (g) estimates ±95% confidence limits (C.L.) for marked isolated and high density plants on each observation date through June 9, after which plant and umbel weights levelled off. All weights, except umbel weight on May 20, were significantly higher on isolated than high density plants

		Plant wt (g)				Umbel wt (g)			
		Isolated (N = 29)		High density (N = 60)		Isolated (N = 29)		High density (N = 60)	
		$\bar{x}$	C.L.	$\bar{x}$	C.L.	$\bar{x}$	C.L.	$\bar{x}$	C.L.
			64.12		8.34		0.53		0.44
May	20	49.4		7.4		0.5		0.4	
			38.11		6.53		0.50		0.36
			55.98		7.53		3.11		0.39
	24	51.2		7.0		2.9		0.4	
			32.36		4.89		2.79		0.32
			72.78		9.68		3.12		0.73
	28	53.1		8.4		2.9		0.6	
			38.73		7.21		2.77		0.52
			73.11		9.02		3.11		0.70
June	1	53.7		7.3		2.9		0.6	
			39.45		5.90		2.72		0.51
			75.68		9.31		7.24		0.82
	5	59.8		8.2		6.0		0.7	
			47.32		7.26		4.63		0.65
			76.21		9.40		7.18		0.79
	9	61.1		8.5		5.9		0.7	
			48.98		7.71		4.70		0.61

Within-field dispersion

A significantly greater proportion of isolated plants was attacked by larvae (Fig. 2a, solid lines). This was related to the greater proportion of isolated plants which had unopened umbels throughout early June when many females were ovipositing and the greater number of unopened umbels per plant (Table 2). Fur-

TABLE 2. Proportion of isolated and high density plants with unopened umbels and mean number of unopened umbels/plant over period of *D. pastinacella* oviposition

	Isolated (N = 29)		High density (N = 60)	
Date	Unopened umbels	No. unopened umbels ($\bar{x}$ ± SE)	Unopened umbels	No. unopened umbels ($\bar{x}$ ± SE)
May 16	0.14	0.14 ± 0.07	0.22	0.28 ± 0.67
20	0.62	2.35 ± 0.64	0.71	1.82 ± 0.23
24	1.00	5.66 ± 0.80	0.97	2.80 ± 0.19
28	0.83	7.10 ± 1.52	0.90	3.45 ± 0.61
June 1	0.90	6.24 ± 1.26	0.73	2.23 ± 0.32
5	0.72	3.41 ± 0.89	0.48	1.92 ± 0.33
9	0.24	0.59 ± 0.38	0.00	0.00

TABLE 3. The number of larvae per gram umbel, obtained by dividing the number of larvae on all isolated or high density plants by the total umbel weight biomass estimate for that date. On 9 June larvae began pupating on both isolated and high density plants. Therefore, values for number of larvae per gram umbel are not given after this date

Date	Isolated (N = 29)			High density (N = 60)		
	Total umbel wt (g)	Larvae (n)	Larvae/gram umbel	Total umbel wt (g)	Larvae (n)	Larvae/gram umbel
May 20	14.9	1	0.1	25.5	...	...
24	86.2	26	0.3	22.8	12	0.5
28	86.1	133	1.6	44.7	26	0.6
June 1	85.6	170	2.0	42.8	28	0.7
5	188.1	277	1.5	48.0	48	1.0
9	187.4	214	1.1	46.4	41	0.9
13		72			13	
17		57			5	
21		14			...	
26		1			...	

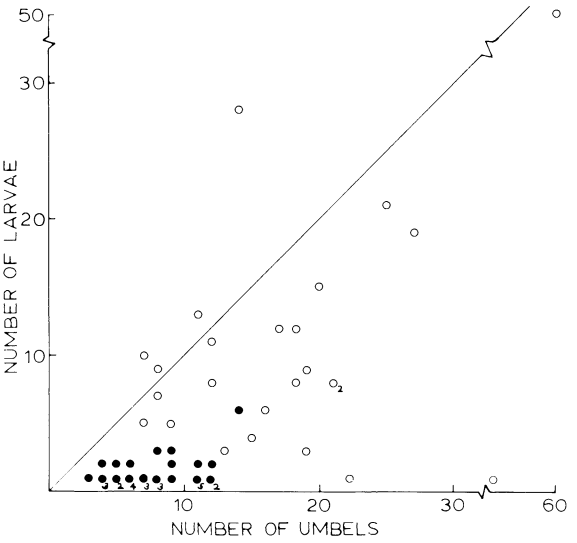

FIG. 3. Relationship between the total number of umbels on a plant through 1 June and number of larvae/plant on 5 June. The line has a slope of 1. Open circles represent isolated plants, closed circles high density plants. The number of larvae was generally less than the number of umbels present.

thermore, the proportion of umbels on each plant attacked by larvae was significantly higher on isolated plants (Fig. 2a, dashed lines). The peaks on 24 May for both isolated and high density plants resulted from *D. pastinacella* oviposition prior to the period of greatest umbel production.

The greater frequency of attack on isolated plants resulted in a greater number of larvae per gram umbel on isolated than on high density plants (Table 3). At the peak of larval abundance on 5 June, the number of larvae per gram umbel was 50% higher on isolated than on high density plants. Early instar larvae appeared on only one new plant after this date. Subsequent changes in the proportion of umbels attacked resulted from movements of late instar larvae tc new umbels. By 9 June, larvae were pupating, thereby lowering utilization of umbels on both isolated and high density plants after this date.

Within-plant abundance and dispersion

The maximum number of larvae per plant was limited by the number of umbels and especially by the synchrony between the presence of unopened umbels and *D. pastinacella* oviposition. Observations of larvae indicated that successful oviposition was restricted to unopened umbels. Unopened umbels were those in which the flower buds were not yet visible. All larvae found in open umbels were at least second instars. Except for terminal and some upper lateral umbels, only 1 larva developed per umbel. This meant that even with strong synchrony between presence of unopened umbels and moth oviposition, the number of larvae could seldom exceed the number of umbels. At the peak of larval abundance on 5 June, 93% of the discovered plants had fewer larvae than the total number of umbels on each plant on all previous observation dates (Fig. 3). The 4 exceptions were all isolated plants.

Larvae generally webbed the larger umbels on a plant, especially the terminal umbel when available. If a female oviposited in a relatively small, unopened umbel, the resultant larva moved to a larger umbel after the first instar or after the umbel was consumed. Webbing of an umbel by a larva often preempted use of that umbel by other larvae. Isolated plants more often supported >1 larva per umbel than high density plants. This appeared to be due to the large diameter of their umbels, especially the terminal umbels (Table 4). Plants with umbels harboring 3 or more larvae were uncommon and restricted to large-diameter umbels on isolated plants (Table 5).

The experimental introduction of larvae onto plants tested the hypothesis that aggregation of larvae on any umbel and the occasional, extreme aggregation of larvae in terminal umbels (Table 5; low density plants, 10 larvae per umbel) resulted from insufficient time for

TABLE 4. Mean terminal umbel diameter (in centimetres) ± SE. Plant growth was minimal after 9 June. Means are of marked plants whose terminal umbels were not webbed. NS = not significant

Date	Isolated		High density		Significance level (t-test)
	$\bar{x}$ ± SE	n	$\bar{x}$ ± SE	n	
May 16	0.0		0.0		
20	5.4 ± 0.41	6	4.3 ± 0.37	16	NS
24	11.6 ± 0.92	17	7.7 ± 0.38	41	.001
28	14.5 ± 0.80	20	9.2 ± 0.41	49	.001
June 1	17.3 ± 0.84	15	10.0 ± 0.37	45	.001
5	18.2 ± 1.28	15	10.8 ± 0.44	30	.001
9	18.8 ± 1.27	10	11.9 ± 0.63	17	.001

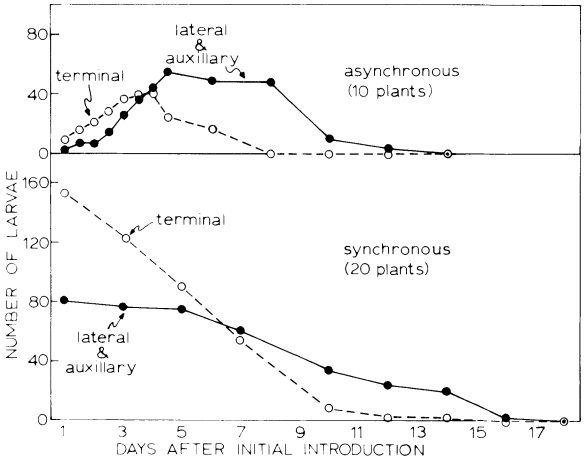

FIG. 4. Number of larvae on terminal versus all other umbels beginning with the day after introduction of larvae. Note the initial importance of terminal umbels under both treatments.

individuals to preempt sections of umbel because of heavy synchronous oviposition and high larval survival on the plant. This is more likely on isolated plants, because these plants generally have more umbels available for oviposition at any one time. This requires explanation. Active exclusion of larvae by other larvae was never observed. If 2 or more larvae arrived at an umbel at nearly the same time, their webs would often overlap, thereby creating a multi-larvae web. If a single larva, however, arrived at an umbel and had sufficient time to complete a web before other larvae arrived, the newly arrived larvae could not enter the already established web and there were seldom enough umbellets remaining for construction of a new web.

For both synchronously and asynchronously introduced larvae, the general pattern of larval positions on plants was similar in time. At the outset of both experiments, most larvae constructed webs in the terminal umbels (Fig. 4). As these umbels were consumed and/or preempted, larvae moved to lower umbels. Under both situations, every terminal umbel was utilized, emphasizing the importance of these umbels.

The dispersion of larvae on the umbels at the peak of larval abundance under both treatments was compared with a Poisson distribution and was found to be significantly clumped. This suggested that larvae were aggregated in the terminal umbel more than would be expected by random movement. If terminal umbels were excluded from the analysis, larvae were found to be distributed randomly over the remaining umbels. Therefore, differences in larval dispersion between synchronously and asynchronously introduced larvae centered on utilization of the terminal umbel.

Asynchronously and synchronously introduced larvae differed in the number of larvae which constructed webs in terminal umbels. As under natural conditions, the great majority of umbels with >2 larvae were terminal umbels under both experimental treatments (Table 6). However, larval abundance on terminal umbels of plants with asynchronously introduced larvae never reached the levels found on plants with synchronous introductions. The mean number of larvae per terminal umbel was significantly higher on plants with synchronously introduced larvae during the first 3 days than the mean for plants with asynchronously introduced larvae on any date (Fig. 5). This highly aggregated pattern which remained for a few days on plants with synchronous introductions was similar to the uncommon, aggregated pattern observed under natural conditions (Table 5; isolated plants).

Plants with asynchronously introduced larvae exhibited the more normal pattern of within-plant larval dispersion. A greater proportion of individual, asynchronously introduced larvae were able to preempt sections of the terminal umbel due to the longer time available to these larvae for web construction before other larvae arrived. On plants with asynchronously introduced larvae, a consistently greater proportion of webs on terminal umbels harbored only 1 larva than

TABLE 5. The distribution of larvae on discovered umbels. Note that most umbels supported only 1 larva and that only isolated plants ever supported >2 larvae. Numbers in parentheses indicate the number of those umbels which were terminal umbels

	Isolated						High Density	
	Larvae/umbel						Larvae/umbel	
Date	1	2	3	4	5 ...	10	1	2
May 20	1 (1)	...	...	...	...	...	...	...
24	26 (6)	...	...	...	...	...	12 (5)	...
28	125 (7)	4 (4)	...	...	...	...	26 (12)	...
June 1	152 (4)	4 (4)	2 (2)	1 (1)	...	...	28 (19)	...
5	226 (3)	6 (5)	2 (2)	2 (2)	3 (3)	1 (1)	40 (18)	4 (4)
9	180 (1)	4 (3)	3 (0)	3 (3)	1 (1)	...	33 (10)	4 (3)
13	61 (1)	4 (2)	2 (0)	...	...	...	13 (3)	...
17	49 (1)	4 (0)	...	...	...	...	5	...
21	14 (0)	...	...	...	...	...	...	...
26	1 (0)	...	...	...	...	...	...	...

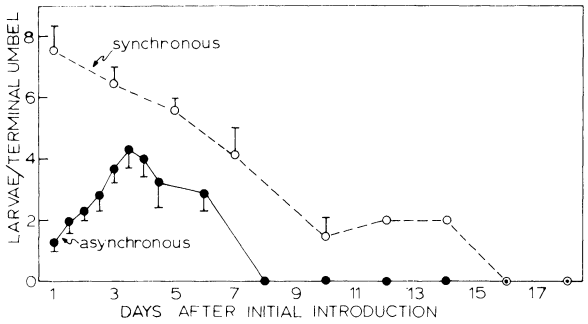

FIG. 5. Mean number of larvae per terminal umbel on plants with asynchronous and synchronous larval introductions. Vertical bars represent standard errors; only 1 plant in the synchronous introductions had larvae in the terminal umbel on the 12th and 14th day after introduction.

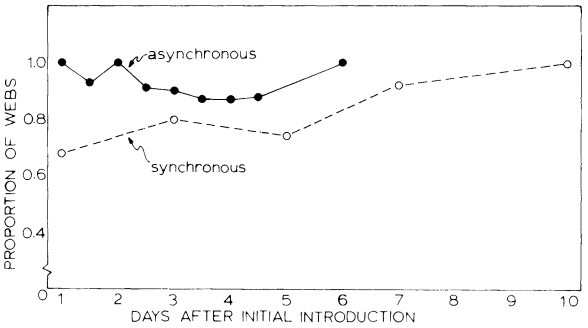

FIG. 6. Proportion of webs in terminal umbels maintained by a single larva from the day after introduction of larvae until the last larva had left the terminal umbel.

plants with synchronous introductions (Fig. 6). This limited the number of larvae which could utilize the terminal umbel. Few lateral and auxillary umbels harbored >1 larva (Table 6), because the smaller size of these umbels made them more likely to be preempted by a single larva than a terminal umbel. Hence, the sizes of umbels and the staggering in time of larvae on the plants greatly influenced within-plant larval dispersion.

DISCUSSION

The results indicate that plant plasticity in shape and phenology can govern the within-field and within-plant dispersion and abundance of a specialized insect herbivore. This may result either from insects searching for a particular host plant density or even, to some degree, from random search. If critical resources vary with plant density, a strong-flying insect, searching actively for host plants, may use patch density as a cue for finding resources in an acceptable state. This would lead to highest herbivore abundance relative to the amount of resource available at the density providing resources in the most acceptable manner, if this density was available in the cruising range of searching insects. Similarly, even through random search, herbivore abundance per unit of resource biomass would tend to be highest at the plant density that provided resources in the most acceptable manner. In either case, analysis of the plastic responses of plants is im-

TABLE 6. The distribution of larvae on discovered umbels on plants with synchronous and asynchronous larval introductions. Numbers in parentheses are the number of umbels in that category which were terminal umbels. N = 20 plants for synchronous introductions; N = 10 plants for asynchronous introductions. m = morning, a = afternoon

Date	Larvae/umbel												
	1	2	3	4	5	6	7	8	9	10	11	12	13
Synchronous													
May 28	73 (0)	5 (1)	...	3 (3)	2 (2)	3 (3)	1 (1)	2 (2)	1 (1)	2 (2)	2 (2)	2 (2)	1 (1)
30	58 (0)	6 (0)	4 (3)	3 (2)	2 (2)	1 (1)	3 (3)	4 (4)	3 (3)	1 (1)			
June 1	60 (0)	4 (2)	2 (1)	...	5 (5)	3 (3)	2 (2)	2 (1)	2 (2)				
3	59 (3)	3 (2)	1 (1)	4 (4)	...	...	1 (1)	...	1 (1)	...	...	1 (1)	
6	34 (1)	2 (1)	2 (2)										
8	21 (0)	2 (1)											
10	19 (0)	1 (1)											
12	1 (0)												
14	...												
Asynchronous													
June 1m	7 (5)	2 (2)											
1a	11 (4)	1 (1)	2 (2)	1 (1)									
2m	9 (2)	3 (3)	3 (3)	1 (1)									
2a	13 (1)	1 (0)	6 (6)	1 (1)	1 (1)								
3m	21 (1)	5 (2)	1 (1)	3 (3)	1 (1)	2 (2)							
3a	23 (1)	5 (1)	3 (1)	...	3 (3)	3 (3)							
4m	24 (2)	8 (1)	1 (1)	2 (0)	4 (4)	1 (1)	1 (1)						
4a	27 (4)	8 (1)	2 (0)	...	3 (2)	1 (1)	...	1 (0)					
6	37 (3)	6 (1)	1 (1)	2 (2)	1 (0)								
8	24 (0)	5 (0)	...	1 (0)									
10	10 (0)												
12	3 (0)												
14	...												

portant in dissecting the reasons for patterns of specialized herbivore dispersion with respect to host plant density.

In his resource concentration hypothesis, Root (1973, 1975) stated that herbivores are more likely to discover and remain on hosts growing in pure or dense stands and that the most specialized species reach higher relative densities in simple environments; as a result, species diversity (especially the evenness component) is reduced where hosts are more concentrated. According to the hypothesis, specialists utilize a greater proportion of the available resources in pure or dense stands, i.e., their herbivore loads should be higher. Cromartie (1975) found this to be true for some but not all crucifer specialists. For the parsnip webworm, larval numbers were lower per unit of umbel biomass on the near-monoculture, high-density plants than on the plants in mixed vegetation. This was because the important density-varying resources, availability of unopened umbels for oviposition and large umbels for larval development, were more common on isolated plants.

Several factors may restrict oviposition or survival of first-instar larvae to unopened umbels. *Pastinaca* flowers are visited by many insect species, a number of which are both pollen feeders and predators. Eggs and early instar larvae of *D. pastinacella* may be highly susceptible to attack by predators in open umbels. This may select for females which oviposit in unopened umbels. Other possible reasons for restriction of earliest instars to unopened umbels may be protection from dessication and mechanical or chemical limitation. The softer, unopened umbels may be more easily chewed or digested by first larvae than opened umbels and seeds.

Oviposition and development of early instar larvae in unopened umbels or inflorescences has been observed in other flower-feeding Lepidoptera. Clarke (1933) reported finding the young larvae of *Depressaria multifidae* in unopened umbels. Breedlove and Ehrlich (1968) found that oviposition of *Glaucopsyche lygdamus* (Lycaenidae) was restricted to immature inflorescences, and Breedlove (1972) suggested that, through this behavior, *G. lygdamus* may be resource limited.

The results illustrate how the interaction between patch density and plant plasticity can temper the effective response of a specialized insect herbivore to various host patches. In analysis of plant-herbivore interactions, this dimension of herbivore response must be considered together with associational resistance or enhancement (Tahvanainen and Root 1972, Root 1973, 1975, Atsatt and O'Dowd 1976) and apparency of plants to herbivores (Feeny 1975, 1976). The role of plant plasticity is magnified in considerations of insect community organization. Analysis of plant species diversity, dispersion, or density is insufficient to understand the effects of vegetation on insect species diversity or community organization. A knowledge of patterns of plant plasticity is essential to an understanding of how plants affect insect communities.

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