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The Influence of Vegetational Diversity on the Population Ecology of a Specialized Herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae)

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Summary. The population ecology of *Phyllotreta cruciferae* Goeze, a flea beetle which is an important pest of cole crops (*Brassica oleracea*) in central New York was studied in experimental gardens of differing vegetational diversity over a three year period. Adult beetles were more abundant on collards (*B. oleracea* var. *acephala*) grown in monocultures than on those grown adjacent to natural vegetation. The emergence of individuals forming the new annual generation was also greater in the pure stands. Predators and parasites appeared to have a negligible influence on the adult beetles in both habitats. Further experiments demonstrated that monocultures were colonized more rapidly and experienced greater feeding damage than stands in which collards had been interplanted with tomatoes and tobacco. Choice experiments in the laboratory showed that chemical stimuli given off by non-host plants (tomato, *Lycopersicon esculentum*, and ragweed, *Ambrosia artemisiifolia*) interfered with the host finding and feeding behaviour of *P. cruciferae*. These results indicate that vegetational diversity can exert a direct influence on populations of phytophagous insects.

We conclude that the environmental capacity (*Determination* in Schwerdtfeger's terminology) of diverse natural communities is lower than that of natural or man-made monocultures. The "associational resistance" resulting from the higher taxonomic and microclimatic complexity of natural vegetation tends to reduce outbreaks of herbivores in diverse communities.

Introduction

One of the major characteristics of most agricultural and silvicultural ecosystems is their low biotic diversity. These simple systems are often so susceptible to the outbreaks of herbivorous insects that continuous production of high quality crops is practically impossible without extensive use of chemical pesticides (e.g., Knipling, 1966; Janzen, 1970a). In diverse natural communities, on the other hand, outbreaks rarely occur (e.g., Vouté, 1946; Pimentel, 1961). A typical pattern of faunal changes associated with the simplification of a natural system has been described by Bey-Bienko (1961). He reported a decline in total insect

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species and an increase in the frequency of population outbreaks when virgin grass steppe was ploughed and converted into a wheat field. Many important crops, such as sorghum, maize, sugar cane and cotton, have been invaded by pests that had previously been inconsicuous feeders on wild, native plants (Uvarov, 1964). The cacao plant, *Theobroma cacao*, has been plagued by pests since it was transferred from its native American rain forests into commercial plantations (Tinsley, 1964; Clark *et al.*, 1967). Cacao was also introduced into West Africa where difficult pest problems appeared after about thirty years. Similarly, teak growing in the original forests of Indonesia was seldom injured by insects, but serious infestations of a scolytid beetle, *Xyleborus destructor*, developed when the natural forests were replaced by teak plantations (Kalshoven, 1952).

The well documented outbreaks of insects in the northern temperate and coniferous forests occur in areas where a single tree species forms extensive monoculture of even age. The spruce budworm, *Choristoneura fumiferana*, causes the most damage in pure, old stands of balsam fir (Tothill, 1923; Morris, 1963) and the European pine looper, *Bupalus piniarius*, is much more destructive in pure pine stands than in mixed woods (Engel, 1939, 1942). Damage by white pine weevil, *Pissodes strobi*, is insignificant where its major host grows as a subdominant in mixed forests (Graham, 1926).

These trends appear to be characteristic of simple, natural communities as well. Thus in subarctic regions, where vegetational diversity is naturally low, outbreaks frequently occur in primeval forests (Schwerdtfeger, 1957; Palm, 1959; Nuorteva, 1963). The highly diverse forests of the tropics, on the other hand, are believed to be relatively free of herbivore outbreaks if the vegetation is not simplified by cutting (von Hassel, 1925; Schneider, 1939; Eidman, 1943).

Although there is an apparent relationship between the simplicity of vegetation and its vulnerability to herbivore attack, the basic reasons for this are not clear. Many ecologists maintain that larger and more diverse populations of predators and parasites prevent the rapid increase of herbivore populations in diverse communities (e.g., Schneider, 1939; Voûté, 1946). This concept has been examined theoretically by MacArthur (1955) and Margalef (1970). Paine (1966) has shown that predators are important in controlling the abundance of intertidal organisms and in maintaining diversity and stability in intertidal communities. Van Emden (1965) observed increased predation on the cabbage aphid, *Brevicoryne brassicae*, in the vicinity of a diverse uncultivated field. Similarly, predation on the larvae of *Pieris rapae* on brussels sprouts, *Brassica oleracea* v. *gemmifera*, was higher in unweeded than in weeded plantings (Dempster, 1969). In Poland the mortality of larvae of the Colorado beetle, *Leptinotarsa decemlineata,* and potato feeding aphids was higher near woods and uncultivated field edges than in the center of extensive cultivated fields (Galecka, 1966; Karg, 1969). These authors suggest predation as the probable cause of this mortality. According to some observations, parasitism on the eggs and pupae of the pine looper is higher in mixed than in pure pine stands (Friedrichs, 1930; Friedrichs *et al.*, 1940). The thorough analysis by Engel (1939, 1942) on the mortality of all stages, however, revealed that the overall generation mortality was higher in pure stands where, nevertheless, the pine looper was considerably more abundant than in mixed stands. Similarly, Root (1973) has shown that the herbivore load is lower on collards, *B. oleracea* v. *acephala,* grown in diverse habitats than in those grown in monocultures. In this case concentration of food was apparently the primary factor responsible for the development of high herbivore populations.

The present work concerns some of the questions raised by Root's investigation (1973) of the arthropod fauna associated with *B. oleracea.* The behaviour and population biology of the dominant herbivore in this association, *Phyllotreta cruciferae,* was followed for three years. The influence on this species of various factors associated with habitat diversity provided the focus for the investigation.

History and Habits of *P. cruciferae*

The flea beetle, *P. cruciferae,* was probably introduced into North America from Eurasia early in the present century (Milliron, 1953; Brown, 1967). It is a serious pest of cruciferous crops on both continents. Its host range consists of numerous crops and weeds of the family *Cruciferae* (Heikertinger, 1925; Newton, 1928; Jones and Jones, 1964). The most favored hosts, however, are in the genus *Brassica.* Many *Brassica* spp. contain the mustard oil, allyl isothiocyanate, a powerful attractant to the adults of *P. cruciferae* (Dobson, 1956; Matsumoto, 1970; Feeny *et al.*, 1970).

In early spring the overwintering adults disperse to their cruciferous hosts; mainly weed species at first and then cultivated crops somewhat later (Newton, 1928; Root and Tahvanainen, 1969). Eggs are laid on the soil around the stems of the host plants during May and June. Larvae feed on the roots of the host and pupate in the soil (Newton, 1928). On cultivated *B. oleracea* in central New York, the new generation starts to emerge in July. The emergence reaches a peak in late August or in early September (Tahvanainen, 1972). This species, which rasps small pits in the foliage of its hosts, is usually the most serious pest of cole crops in our area (Root and Skelsey, 1969). In the fauna associated with collards, herbivore load is directly related and herbivore species

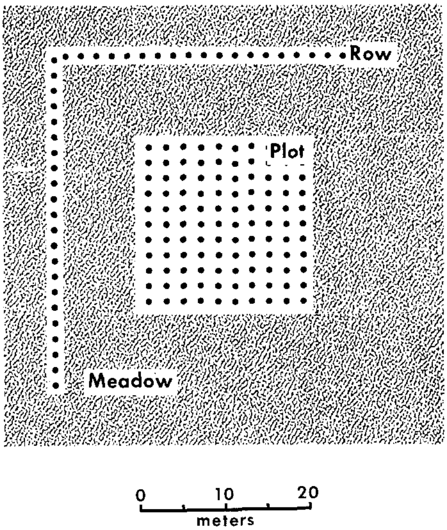

Fig. 1. Layout of an experimental *B. oleracea* garden

diversity is inversely related to the biomass of this one species (Root, 1973).

Population Trends in Simple and Diverse Habitats

Experimental Plots and Sampling. Gardens of collards were set out in 1968, 1969, and 1970, near Ithaca, New York. The gardens were similar to those used by Root (1973) and were located in the same meadow. Each experimental unit consisted of a 21 × 21 m central plot and a perimeter row separated from the plot by a 12 m wide strip of meadow vegetation (Fig. 1). The collards in the central plot formed a monoculture while those in the perimeter row were bounded on both sides by diverse vegetation. The plot and row were ploughed, disked and fertilized in the same manner and were kept free of weeds throughout the growing season. In 1968, two experimental gardens, called East and West, were established. The East garden was used in all three summers, the West garden only during 1968. Collard seedlings (two months old) were transplanted into the gardens during the first week in June each year. The rows were 102 cm apart in the plots. The distance between adjacent plants in the rows was 46 cm in both of the experimental habitats.

Populations of *P. cruciferae* were followed by taking samples at 10 to 15 day intervals from June through October. Samples were always taken during the early afternoon; rainy or particularly windy days were avoided. The sample unit was one collard. Plants in the four rows around the edges of the central plots were not sampled. During 1968 and 1969, samples were taken by counting all flea beetles on a number of randomly selected collard plants. The sample size varied according to the density of *P. cruciferae*. In early summer, when the density of flea beetles was low, samples of up to 100 plants were taken. With increasing population density, the number of plants sampled was reduced to 10. This appeared to be a realistic comprise that provided reliable estimates for the amount of effort that could be spent in sampling (see also Mukerji and Harcourt, 1970). In 1970, samples were taken with a vacuum net [D'Vac Vacuum insect net (Model 1) with 3 HP engine on back-pack, D'Vac, Co., Riverside, California] using the same general plan as before. To compare the efficiency of field counting and D'Vac sampling, samples in the East garden were taken in 1970 on July 25 (50 plants) and August 18 (30 plants). From the D'Vac samples, the density of *P. cruciferae* was estimated to be 27 individuals per plant in July and 280 individuals per plant in August. Field counts gave a similar estimate in July and a 12% lower estimate in August. Apparently the D'Vac is somewhat more effective than visual counts at high beetle densities. It is felt, however, that the difference is within reasonable limits and both methods yield satisfactory results for following population trends in the two habitats.

On every other sampling date during 1968 and 1969 some, or all, of the collards on which counts had been made were cut at ground level, oven dried at 80° C, and weighed. Removing all of the plants that were examined early in the season would have seriously depleted stand density. Plant weights were determined on every sampling date during 1970.

Emergence cages were used to estimate the size of the new generation of *P. cruciferae* developing on the collards. Five cages were placed in both the monoculture and the perimeter row of the East garden each summer. The cages, each covering one collard plant, were placed in the field before the start of the emergence and kept in operation till the end of the growing season. The structure of the cages and the details of the sampling procedure are described elsewhere (Tahvanainen, 1972).

Results. The results are presented in Table 1 and Fig. 2. Collard growth was usually somewhat better in the plot than in the perimeter row. The reason for this is not completely understood. It is possible that the physical condition of the soil in the rows was not as favorable as in the plots which could be disked more effectively.

The number of *P. cruciferae* per collard was higher in the monocultures on all 38 sampling dates. On only one of the 19 sampling occasions for which collard weights were determined was the number of beetles per 10 g of collard higher in the diverse habitat. During succes-

Table 1. Sampling schedule, plant weights, and the abundance of *P. cruciferae* on collard plants in monoculture plots and diverse rows of the East garden

Year and sampling date	No. of collards sampled/weighed[a]	Average dry weight (g) of collard		No. of *P. cruciferae* per 10 g (dry wt.) of collard	
		Plot	Row	Plot	Row
1968					
June 10	100/—	—	—	—	—
21	100/20	2.4	2.5	4.04	0.40
July 2	100/—	—	—	—	—
12	50/20	18.0	15.2	2.52	0.39
23	30/—	—	—	—	—
Aug. 7	20/20	61.5	49.2	20.67	13.61
20	20/—	—	—	—	—
Sept. 7	12/12	84.0	78.4	57.99	34.39
23	12/—	—	—	—	—
Oct. 12	15/15	102.1	100.0	15.89	6.78
1969					
June 9	50/—	—	—	—	—
16	50/20	3.2	3.0	8.50	8.86
27	30/—	—	—	—	—
July 11	20/20	36.1	38.0	3.89	1.94
21	20/—	—	—	—	—
Aug. 7	15/15	125.4	103.8	20.27	10.38
Sept. 1	10/10	110.0	88.1	75.22	39.40
21	10/—	—	—	—	—
Oct. 14	15/15	164.6	149.8	17.15	8.61
1970					
July 1	25/15	7.5	7.8	3.97	2.32
17	15/15	44.9	36.5	5.12	3.03
Aug. 6	15/15	163.7[b]	132.2	20.60	2.26
19	15/15	143.7	116.4	17.95	6.16
Sept. 1	15/15	130.5[b]	100.0	58.36	20.85
11	15/15	151.4	149.0	96.22	11.87
22	15/15	141.6	144.9	78.51	19.59
Oct. 5	15/15	245.5[b]	174.4	30.70	13.07
20	15/15	145.0	141.6	20.60	8.52

[a] Equal numbers of collards were sampled and weighed in the plot and in the row.

[b] Significant (5% level) difference in collard weights between plot and row. Calculated by use of Wilcoxon's two-sample rank-sum statistic (Alder and Roessler, 1968).

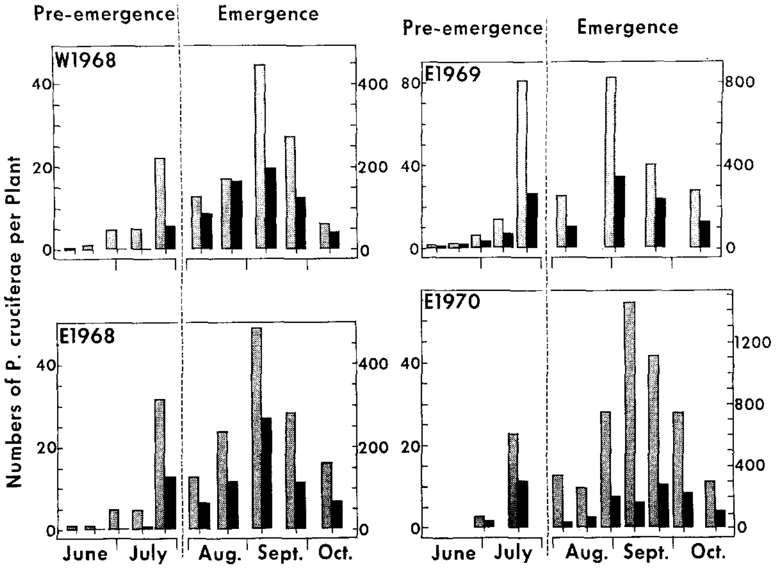

Fig. 2. Seasonal abundance of *P. cruciferae* on collard plants in monoculture plots (gray bars) and diverse rows (black bars) in the West garden in 1968 (W1968) and in the East garden in 1968, 1969, and 1970 (E1968–E1970). The scale for the pre-emergence period is on the left and for the emergence period on the right

sive years in the East garden, the average number of *P. cruciferae* per collard was 2.3, 2.2, and 4.4 times higher in the monoculture than in the diverse habitat. In the West garden the same ratio was 1.8 during 1968.

In Fig. 2 the season is divided into a pre-emergence period and an emergence period. The former covers the time from the planting of the collards until the start of the emergence of the new generation. Thus the population before the emergence period consists entirely of immigrants. The peak abundance of *P. cruciferae* occurs at the end of August or the beginning of September, coincident with the peak emergence of the new generation.

There are considerable differences in the size of *P. cruciferae* populations between years. The relative differences between the simple and diverse habitats, however, remain approximately the same. The number of beetles seems to increase in successive years (Fig. 2). This may reflect the growth of the local population in response to five years of extensive collard cultivation in the study area.

The size of the emerging generation is shown in Table 2. Two to four times as many beetles emerged in the monoculture as in the diverse stand. Except for the higher emergence in the diverse habitat during

Table 2. Emergence of the new generation of *P. cruciferae* in the East garden. Each figure represents the seasonal total per collard based on the average of five emergence cages

Year	No. of *P. cruciferae* per collard	
	Plot	Row
1968	2805.20	654.20
1969	2544.70	1165.20
1970	2702.20	617.20

1969, there is little difference in the size of the new generation in successive years.

The Role of Predators and Parasites

Evidence of predation was sought during the hundreds of hours spent counting flea beetles in the field. Practically no predation was observed on adults. A few beetles were occasionally caught in spider webs, but they showed no sign of having been eaten by the spiders. Some carabid beetles, mostly nocturnal species, that were captured in pit fall traps during August, 1970, had parts of flea beetles in their intestines. It is probable, however, that the carabids were eating flea beetles which were especially vulnerable because they had also fallen into the traps. Natural encounters between flea beetles and carabids are probably infrequent because the former tend to remain on the upper, vertical leaves of the collards at night and the latter are poor climbers.

Adults of *P. cruciferae* were parasitized by larvae of the braconid, *Microctonus vittatae*. This parasitoid is a North American species which has recently extended its host range from native flea beetles to attack the introduced *P. cruciferae* (Smith and Peterson, 1950; Loan, 1967). Data on the abundance of *M. vittatae* adults are summarized in Table 3. In 1966, 1967 and 1968, *M. vittatae* was sampled by "capturing" individual collard plants and the arthropods resting on them in large plastic bags (the procedure is more fully described in Root and Skelsey, 1969). This method, however, appeared to be rather ineffective for quick-moving insects. Therefore, additional samples were taken in 1967 and 1970 with a vacuum net. The estimates obtained with the latter method are higher (Table 3). The relative differences between the habitats were similar with both methods. Densities of *M. vittatae* were low in both habitats, but somewhat higher in the monoculture.

The incidence of parasitism by *M. vittatae* was determined by dissecting *P. cruciferae* adults. This method proved to be better than rearing

Table 3. Abundance of the adults of *M. vittatae* on collard plants in monoculture plots and diverse rows

Year	Sampling dates	No. of collards sampled		No. of *M. vittatae* per collard	
		Plot	Row	Plot	Row
Plastic bag samples					
1966	6/21, 7/5, 7/20, 8/3, 8/17, 8/30, 9/13	104	104	0.01	0.009
1967	6/27, 7/11, 7/18, 7/26, 8/2, 8/8, 8/15, 8/22, 8/29, 9/14	223	224	0.03	0.03
1968	7/8, 7/22, 8/5, 8/19, 8/21, 9/3	144	48	0.27	0.08
De'Vac samples					
1967	7/20, 8/4, 8/18, 9/1, 9/14	240	240	0.28	0.08
1970	7/24, 7/28, 8/6, 9/1	84	84	0.79	0.16

Table 4. Percentage of *P. cruciferae* parasitized by *M. vittatae* on collard plants in monoculture plots and diverse rows

Date	Number of *P. cruciferae* dissected		Percentage of *P. cruciferae* parasitized	
	Plot	Row	Plot	Row
1968				
June 28	250	250	18.0	12.8
Aug. 30	300	250	2.0	0.4
1969				
July 4	200	200	14.0	8.0
1970				
July 1	200	200	9.0	11.0
Aug. 25	200	200	1.0	1.5

the parasites through because of the high mortality of flea beetles under laboratory conditions (Smith and Peterson, 1950). The early samples were taken before the new generation of *P. cruciferae* began to emerge (Table 4). The samples taken in late August tend to coincide with the emergence peak of the host. The incidence of parasitism was relatively low. The percentages observed in the early samples were similar to those reported by Loan (1967) from Ontario, Canada. In late summer, however, parasitism dropped to extremely low levels, reflecting the recent, large emergence of the host. Parasitism was somewhat higher in the monocultures in 1968 and 1969, but differences between the habitats were relatively minor.

It appears that predators and parasites, although possibly causing significant overall mortality in flea beetle populations on the study area, were not responsible for the consistent differences in *P. cruciferae* densities in the two experimental habitats. Predation on the soil inhabiting larvae of the beetle was not investigated. Since the soil in both treatments was worked in the same way, it is assumed that the larval mortality caused by predation was similar in the two habitats.

Host Colonization and Utilization

The life cycle of *P. cruciferae* on collards can be roughly divided into the following phases: colonization, feeding and reproduction, and emigration. The density of beetles on a host plant can be affected by the efficiency of host finding and colonization, by the success of feeding and reproduction, and by the rate of attrition due to emigration and extrinsic mortality factors. Each year the *P. cruciferae* populations in the monoculture were approximately twice as dense as in the diverse habitat at the close of the preemergence period (Fig. 2). This indicates, especially since predation and parasitism appeared to be similar in both habitats, that the efficiency of host finding and colonization were enhanced by conditions in the monocultures. The large populations that aggregated in the pure stands may then have caused the subsequent differences in densities. This hypothesis was tested in the field during 1969 and 1970, and the details of the process were further examined in the laboratory during 1970.

Field Experiments

Methods. While the results of the population survey indicated that differential colonization played a critical role, there were features in the plot-row design which made it difficult to evaluate the impact of particular factors. For instance, the sizes of the treatments were different, there being 1000 plants in the monocultures and only 200 plants in the diverse stands. Also the dispersion of hosts differed between treatments, those in the monoculture being laid out in a solid block, those in the perimeter rows in narrow strips. To avoid complications arising from these kinds of variables, field experiments were designed in which the treatments were similar in size and shape. The designs of the plots are shown in Fig. 3. In 1969 a collard monoculture and a mixed stand were

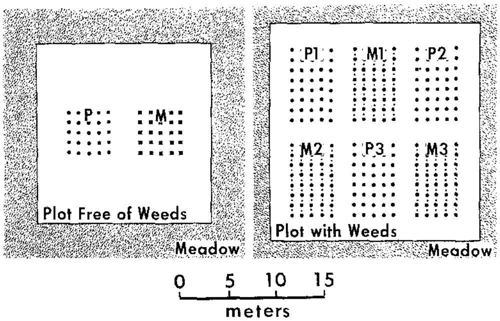

Fig. 3. Left: Layout of 1969 diversity experiment. Monoculture (*P*) consists of pots with two collard plants in each, and diverse stand (*M*) of pots with two collards and one tomato in each. Right: Layout of 1970 diversity experiment. Monocultures (*P1–P3*) with collards only. Diverse plots (*M1–M3*) with collards (big dots) and tomatoes and tobacco (small dots)

established in the middle of an old 21 × 21 m experimental plot. The monoculture consisted of 25 large (41 cm high) clay pots, each containing two collard plants. These pots were buried in the soil in five rows; the spacing pattern was the same as in the survey experiments. The mixed stand, which was adjacent to the monoculture, differed only in that each clay pot contained one tomato seedling in addition to the two collards. Tomato was chosen because it is not a normal host of *P. cruciferae* and it grows well in this experimental situation. The plots were established on June 10 and the colonization of collards by *P. cruciferae* was followed thereafter until the end of July. The beetles were counted on all collards in both treatments at 5 to 10 day intervals. At the end of the experiment, the collards were oven dried and weighed.

Because of the small size of the treatments and lack of replicates in the 1969 pot experiment, a more extensive experiment was carried out in 1970. Again an old 21 × 21 m experimental plot was used (Fig. 3). It was divided into six subplots which were planted on June 6. Each subplot contained 5 rows of collards and each row contained 16 plants spaced as in the survey plots. On three of the subplots, tomato and tobacco (*Nicotiana tabacum*) seedlings were planted alternately in the rows between the collards. The other three subplots were maintaiend as collard monocultures. Initially the mixed stands contained twice as many individual plants as the monocultures. To avoid excessive shading and crowding in this situation, the mixed stands were gradually thinned so that both treatments contained the same total number of plants after four weeks. The subplots were kept free of weeds during the experiment, but the space between and around subplots was left unweeded. The development of *P. cruciferae* populations was followed by taking samples with a vacuum net. Five sets of samples were taken in early summer. Every collard sampled was also dried and weighed. The rest of the collards were left in the field and six emergence cages, three in each treatment, were set out on August 6 to estimate the relative sizes of the new generation. The feeding damage caused by flea beetles was estimated near the end of the pre-emergence period (July 26) by counting the number of holes (pits) on a 2 cm wide strip across the leaf. Fifteen randomly selected leaves from each treatment were examined for this purpose.

Results. In 1969, flea beetle populations built up more rapidly in the monoculture (Table 5). Average plant weights were significantly higher in the mixed stand at the end of the experiment (2.5% level, Wilcoxon's two-sample rank-sum statistic). The monocultures sustained much higher flea beetle loads during 1970 (Table 6). On 26 July 1970 there were an average of 5.4 feeding holes per 1 cm^2 of leaf surface in the monocultures and 1.4 holes per 1 cm^2 in the mixed stands. The size of the new generation, based on the catches from emergence cages, was larger in the monocultures where 1322.5 beetles emerged per plant during the 1970 season. In the mixed stand only 432.3 beetles emerged per plant.

Table 5. Colonization of collards by *P. cruciferae* in the 1969 pot experiment. Each figure represents the number of *P. cruciferae* per pot based on the average of 25 replicates

	Sampling dates										
	June					July					
	16	18	23	26	28	4	9	13	17	23	30
Collards alone	0.12	0.40	3.88	6.92	5.72	7.40	4.84	9.32	16.56	23.12	46.00
Collards with tomatoes	0.00	0.08	1.04	3.96	2.24	3.80	0.36	2.32	12.04	10.04	25.45

These experiments, together with the results of the survey, suggest that the observed differences between the monocultures and the diverse habitats were caused by differential colonization by *P. cruciferae*. Since the experimental treatments were designed so that microlimates and the dispersion of the hosts were as similar as possible, we suspected that the presence of non-host plants interfered with the orientation and host utilization of these beetles. Since host finding by *P. cruciferae* is almost

Table 6. Population buildup of *P. cruciferae* in collard monocultures (subplots P1–P3) and in mixtures of collard, tomato and tobacco (subplots M1–M3) in 1970 field experiment[a]

		Sampling date				
		June 26	July 13	July 24	Aug. 6	Aug. 18
No. of *P. cruciferae* per collard	P1	0.42	18.80	155.60	466.00	230.80
	P2	1.42	31.60	215.20	366.60	165.40
	P3	1.00	20.20	181.80	386.00	165.60
	M1	0.14	14.40	80.80	101.80	62.40
	M2	0.28	10.40	53.60	149.80	66.80
	M3	0.14	13.20	72.40	134.80	77.80
No. of *P. cruciferae* per 10 g (dry wt.) of collard	P1	1.33	10.37	22.46	40.00	24.60
	P2	8.11	11.67	30.96	32.21	19.69
	P3	7.04	9.52	48.87	36.62	21.78
	M1	0.36	4.17	8.95	9.67	5.19
	M2	0.92	5.14	7.60	11.48	5.68
	M3	0.38	4.59	12.29	16.04	8.80
Average weight of collard	P1	3.14	18.12	69.25	116.48	93.80
	P2	1.75	27.06	69.50	113.80	84.00
	P3	1.42	21.20	37.20	105.40	76.00
	M1	3.85[b]	34.50[b]	90.25	105.26	120.14
	M2	2.85	20.22	70.50	130.40	117.40
	M3	3.64	28.70	58.87	84.02	88.38

[a] On June 26, 7 collards and on all other sampling dates, 5 collards were sampled in each subplot.

[b] Significant (5% level) difference in collard weights between monocultures and mixed stands. Calculated by use of Wilcoxon's two-sample rank-sum statistic (Alder and Roessler, 1968).

exclusively guided by chemical stimuli, namely mustard oils produced by its cruciferous hosts (Görnitz, 1953, 1956), it seemed likely that the decreased colonization in mixed stands was caused by repellant or masking chemical stimuli originating from non-host plants.

Laboratory Experiments on Chemical Interference

Various chemical compounds in plants, especially the so-called secondary plant substances, are often involved in the host selection and feeding response of phytophagous insects (Thorsteinson, 1960; Fraenkel, 1969; Hsiao, 1969). Most research has been done on attactants and feeding stimulants. Recently, however, it has been found that repellants and feeding deterrents may be equally important (Harley and Thorsteinson, 1967; Hsiao and Fraenkel, 1968; Feeny, 1970). Since almost all the work on the relationships between insects and secondary plant substances has been conducted in the laboratory, very little is known about the interactions between the numerous attractants and repellents which insects constantly encounter in diverse natural communities (Whittaker and Feeny, 1971). A few observations indicate, however, that the odors from non-host plants can greatly complicate host utilization by herbivorous insects and their primary parasites. Brues (1920) noted that certain cabbage feeding butterflies are repelled by the odor of tomato plants. Tirrell (1970) has successfully used mixed plantings of garden crops in order to avoid pest problems (also see Philbrick and Gregg, 1966). The efficiency of primary parasites which are attracted to the odor of the food plant of their phytophagous hosts can be influenced either by the presence of non-host plants in the vicinity (Monteith, 1960) or by growing the host insect on different food plants (Streams *et al.*, 1968; Read *et al.*, 1970).

Methods. Choice experiments were used to test the influence of non-host plants on the feeding behaviour of *P. cruciferae*. Simple chambers were built by melting together three plastic dishes (diameter 10.3 cm, height 6.4 cm). There was a 1.3 cm passage slip between adjacent sections (Fig. 4). A hole, closed with a cork, was placed in the bottom of the middle section. "Windows" covered by Dacron screening placed in the sides of all three sections permitted air to circulate through the chambers. Experiments were conducted in a laboratory where humidity and temperature were not controlled. The small leaves to be tested were placed in small rubber capped plastic vials filled with water. The vials were then buried in a wooden flat filled with odorless sand. The vials were arranged so that when the chamber was placed over them, the treatments to be compared occupied opposite end sections of the chamber. Four chambers (replicates) were used at a time; the relative positions of experimental treatments were chosen randomly for each trial. Fifteen *P. cruciferae* adults, taken from the field 2 hours before the experiment, were placed in the chambers through the hole of the middle section between 6:30 and 8:00 p.m., and left for 12 hours. The feeding by the beetles on collard leaves was measured by placing a nylon screen with 1 mm mesh over the leaf and counting all the feeding pits that covered at least half of an opening in the screen.

Four treatments were tested, each with ten trials of four replicates. In every treatment there was a young collard leaf in one end section of the choice chamber; in the opposite end section were placed the following combinations:

Treatment No. 1: One collard leaf together with two intact tomato leaves.

Treatment No. 2: One collard leaf together with two intact ragweed, *Ambrosia artemisiifolia,* leaves.

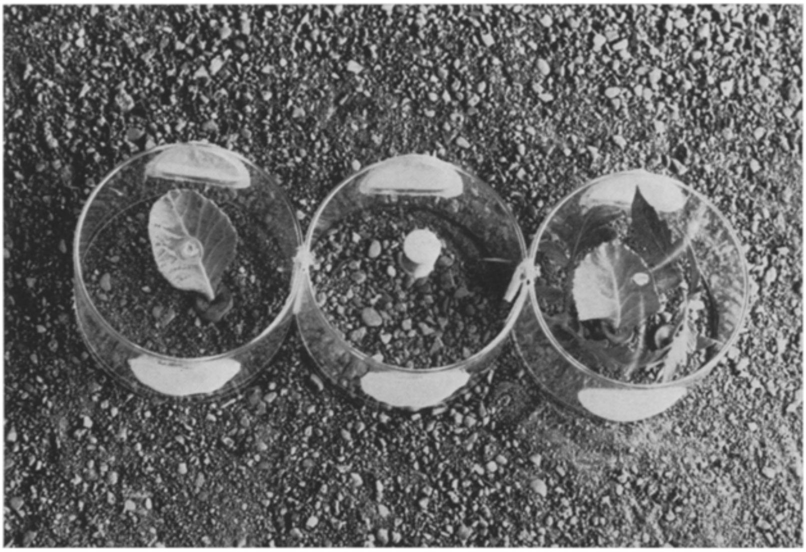

Fig. 4. Choice chamber placed over test plants. One collard leaf is in the section at the left and one collard leaf and two tomato leaves are in the section at the right

Treatment No. 3: One collard leaf together with two small plastic vials stuffed full of wadded tomato leaves, the latter vials covered with a thin layer of sand.

Treatment No. 4: One collard leaf together with two small plastic vials stuffed full of wadded ragweed leaves, the latter vials covered with a thin layer of sand.

Tomato leaves were tested because this plant was used in the field experiments. Ragweed was selected because it was one of the most abundant wild plants around the edges of the experimental gardens. The treatments with leaves stuffed in vials were included in order to determine how odor alone, in the absence of normal visual or tactile stimuli from non-host leaves, might influence the beetles' feeding behavior.

Results. In all treatments, the collard leaf that was kept alone was preferred over the collard leaf that was associated with non-host material (Table 7). The stuffed non-host leaves had almost the same influence as the intact ones. There was considerable variation in overall feeding between different trials. This was apparently caused by the varying temperatures of the laboratory; temperature fluctuated between 69° F and 85° F during the experimental period. Also differences in the physiological state of beetles collected in the field at different times may have influenced the results.

Table 7. Numbers of feeding holes made by 15 *P. cruciferae* in collard leaves over a 12 hour period. The beetles were given a choice between collards alone and collards accompanied by non-host materials. Each figure represents the average of four replicates

Trial	Collard alone	With intact tomato	Collard alone	With intact ragweed	Collard alone	With stuffed tomato	Collard alone	With stuffed ragweed
1	43.8	13.1	51.0	18.0	93.5	13.5	92.1	7.2
2	51.1	22.8	149.6	14.4	52.0	5.3	74.6	23.8
3	35.7	46.2	101.2	3.5	51.7	22.8	118.3	11.8
4	82.5	21.1	75.2	28.1	55.0	8.0	93.6	15.6
5	44.8	4.3	71.1	5.4	63.7	15.0	116.9	5.2
6	98.8	5.8	102.2	1.6	54.7	30.2	76.2	6.0
7	62.4	0.4	78.2	45.2	76.7	9.3	65.4	9.5
8	91.2	0.0	85.6	18.8	56.5	11.1	69.1	18.4
9	99.9	11.4	89.8	49.1	82.7	15.9	90.7	18.2
10	115.9	6.4	84.6	21.0	102.4	35.4	78.4	11.8
Mean ratio	5.5:1		4.3:1		4.1:1		6.9:1	
Trial period	Aug. 26–Sept. 10		Aug. 1–13		Sept. 12–26		Aug. 13–26	

These experiments demonstrate that the proximity of a non-host plant can greatly decrease the utilization of collards by *P. cruciferae*. Since the movements of these beetles could not be followed easily in the choice chambers, it was difficult to judge if active repulsion or merely a feeding inhibition were involved in the interference. We noticed, especially when ragweed was used, that the beetles tended to concentrate in the section containing collard by itself immediately after the experiment was started. This suggests direct repulsion. The strong influence of the buried, stuffed non-host leaves indicates that interference was effective on the olfactory level. In the treatments with intact non-host leaves, interference through contact chemostimuli may also have taken place. It is not known which chemical compounds in tomato and ragweed leaves were involved in the process.

Discussion

The Influence of Vegetational Diversity

Recent research has revealed that even polyphagous insect herbivores, such as grasshoppers, exhibit preferences for plants containing characteristic attractants and feeding stimulants and lacking repellants and feeding deterrents (Hsiao and Fraenkel, 1968; Fraenkel, 1969; Haskell and Mordue, 1969; Hsiao, 1969). In other words, herbivorous insects tend to feed selectively on the plants that are available. This selectivity probably arises during the course of coevolution between herbivores and plants: in response to herbivore pressure, plants may differentiate and develop various defense mechanisms to which herbivores may develop, in turn, specialized adaptations (Ehrlich and Raven, 1965; Whittaker, 1969; Whittaker and Feeny, 1971).

In natural situations, vegetation is usually composed of mixtures of numerous, unrelated plant species. This means that herbivorous insects, when seeking their preferred food plants, may encounter a wide spectrum of chemical stimuli which emanate from plants. Many of these stimuli are likely to be repellant or inhibiting. Our experiments with a specialized herbivore have shown that even the slight increase in vegetational diversity produced by interplanting non-host plants can drastically decrease colonization efficiency and subsequent population density. While the experiments involved only one phytophagous insect and a small proportion of the plant species it encounters in the field, it is probable that the masking and antagonism of host stimuli are widespread in nature. Both electrophysiological and behavioral studies have shown that the sensory system of phytophagous insects responds to a wide variety of chemical stimuli and that the mixing of chemicals can cause antagonism and eventual breakdown in patterns of orientation, feeding and reproduction (Schoonhoven and Dethier, 1966; Hsiao and Fraenkel, 1968; Dethier and Schoonhoven, 1969; Haskell and Mordue, 1969; Ishikawa *et al.*, 1969).

In diverse natural communities, individuals of most plant species are widely scattered and relatively rare. Consequently the distance between individuals may itself hinder the effective utilization of plants by phytophagous insects (von Hassel, 1925; Schneider, 1939; Janzen, 1970b). Dethier (1959) has shown that the mortality of dispersing larvae of the butterfly, *Melitea harrisii*, increased sharply with increasing distance between the individuals of the host plant. The importance of distance, however, may be greatly augmented when combined with a parallel increase in complexity, in which neutral or repellant stimuli dilute the potency of specific, host-finding cues. Douwes (1968) observed that when the host plants of *Cidaria albulata* were randomly distributed among other plants in the field, the butterfly landed randomly on both non-hosts and hosts; but when the same number of hosts were growing in patches, the landings on hosts occurred relatively more often. Clearly in sparse, random dispersions of the host, the chemical stimuli that induce landing seemed to become "lost" in the environment.

In addition to their high taxonomic diversity, most natural plant communities have a relatively complex physiognomy and associated pattern of microclimates. In vertically stratified stands of trees or field vegetation, different parts of the same plant may be situated in different temperature, moisture and light regimes. Since insects exhibit species-specific preferences for different microclimates (Cloudsley-Thompson, 1962; Schwerdtfeger, 1963), the herbivores must seek out appropriate strata within the community. Thus it seems likely that insects may experience further difficulty in locating and remaining in small, favorable spots if microclimatic conditions are highly fractioned.

A natural community, such as a meadow, can be treated as a compound system composed of smaller, component communities (Root, 1973). The arthropods associated with different plant species represent important components in terrestrial systems. The available information indicates that the biotic, structural and microclimatic complexity of natural vegetation greatly ameliorates the herbivore pressure on these individual components, and consequently, on the system as a whole. Thus, it can be said that in a compound community there exists an "associational resistance" to herbivores in addition to the resistance of individual plant species. If the complex pattern of natural vegetation is broken down by growing plants in monocultures, most of this associational resistance is lost. As a result, specialized herbivores which are adapted to overcome the resistance of a particular plant species, and against which the associational resistance is most effective, can easily exploit the simplified system. Population outbreaks of such herbivores are thus more likely to occur in monocultures where their essential resources are highly concentrated (Watt, 1965; Root, 1973).

Determination and Limitation of Herbivore Populations in Simple and Diverse Systems

Although there are few comparative data on the regulation of phytophagous insects in different habitats, it is widely accepted that biotic agents, especially predators and parasites, exert more effective control in diverse than in simple communities (Schneider, 1939; Vouté, 1946; Elton, 1958; Huffaker and Messenger, 1964). Ecologists have suggested a wide variety of mechanisms by which herbivore populations are controlled (e.g. Nicholson, 1954, 1958; Milne, 1957; Solomon, 1964; Huffaker, 1966). Among these diverse opinions, there seems to be some agreement that both density-dependent and density-independent forces are involved in the process. Hairston *et al.* (1961) and Slobodkin *et al.* (1967) have proposed that herbivores, as a trophic level, are usually controlled by predation in terrestrial systems. This argument, however, has been disputed by Murdock (1966) and Ehrlich and Birch (1967) who stress the role of other factors, such as weather, availability of food, availability of resources other than food and self regulatory mechanisms.

Population control has been described by Clark *et al.* (1967) in terms of "life systems" which incorporate the properties of the subject species as well as its effective environment. Wilbert (1962) and Schwerdtfeger (1969) have developed similar integrated models of population control. According to Schwerdtfeger (1969), two groups of functionally different processes, which he calls determination and limitation, set the abundance of an organism. Determination includes such environmental qualities as climate, physical structure of the habitat, and the absolute amount and dispersion of food, which together with the ecological properties of the subject species define the environmental capacity of a particular locality. These kinds of determinative factors set the upper limit of density, i.e. the maximum amplitude of fluctuation that an organism can attain. Limitation, on the other hand, consists of all subtractive processes which tend to oppose the realization of the maximum environmental capacity. These subtractive processes can be perfectly density-dependent, imperfectly density-dependent, or density-independent. Perfectly density-dependent factors, such as intraspecific competition and in some cases predation and parasitism, are the true regulatory factors (simple regulatory circle) while imperfectly density-dependent and density-independent factors, such as weather and often predation, act as a combination of regulation and random mortality (complex regulatory circle). Limitation operates by decreasing fertility and immigration and increasing mortality and emigration. Even though the distinctions between some aspects of determination and limitation and between some density-dependent and imperfectly density-dependent factors are not always clear, this model clarifies the usually ignored coaction of determinative and limiting forces in population control. The model makes it clear that under the same relative intensities of subtractive factors (limitation), completely different densities may be maintained in two localities or at different times in the same locality if the environmental capacities (levels of determination) are different.

In the case of *P. cruciferae*, there was little difference in the relative intensity of predation and parasitism in the two experimental habitats, but the density of this beetle was, nevertheless, much higher in the monocultures. While the role of intraspecific competition could not be fully evaluated, it appears that the impact of regulatory processes was about the same in both habitats. On the other hand, both field and laboratory experiments showed that colonization and food utilization by this herbivore were lower in mixed stands where the chemical stimuli used in host finding and feeding were masked by the complex environment. This means that the collards in mixed stands had a lower environmental capacity (lower determination) as measured by the behavioral and ecological properties of *P. cruciferae*. Huffaker (1966), working with citrus feeding mites in the laboratory, has demonstrated a close relationship between the complexity of a system and the level of population determination.

Furthermore, Huffaker showed that the same regulatory factor, intraspecific competition, caused characteristic population fluctuations around the mean density at each level of environmental determination. In laboratory populations of flour beetles (Holdaway, 1932) and water fleas (Terao and Tanaka, 1923), variations in such basic conditions as temperature and humidity significantly alter the level of determination.

The differential roles of determination and limitation have been rarely and only partially evaluated in the field (Clark, 1964; Morris, 1964; Carne, 1969). Andrewartha and Birch (1954) emphasize the determinative factors while most recent work has been focused on the regulatory aspects of population control (e.g., Miller, 1959, 1960; Morris, 1959, 1963; Auer, 1961; Neilson and Morris, 1964; Varley and Gradwell, 1965; Southwood, 1967).

Even though analysis of regulatory factors alone makes it possible to understand, and even to predict, the pattern of temporal changes in a particular locality, an awareness of environmental determination is necessary if we are to explain differences in mean population levels and the amplitudes of fluctuation in different habitats (see Morris, 1964). For instance, Engel (1939, 1942), found that while mortality of the European pine looper was slightly higher in pure pine stands, its densities were several times higher in this situation than in mixed woods. Engel apparently failed to realize that his data for the number of eggs per female and for the number of eggs laid per tree indicated that the much higher level of determination in pure stands was responsible for the differences in abundance. Reviewing numerous case histories from forest entomology, Graham (1956) and Tothill (1958) suggest that increased colonization, food utilization and reproduction of specialized feeders may be the primary reason for the severity of insect outbreaks in simple, homogeneous forests of the northern hemisphere.

The strong influence of plants and plant assemblages on the population biology of phytophagous insects is also seen in the reciprocal phenomenon, the impact of insects on plants and vegetation. Ehrlich and Raven (1965) have described how herbivore pressure can induce taxonomic diversification of plants through time. Similarly, as has been pointed out by Ridley (1930), Gillett (1962), Bullock (1967), Harper (1969) and Janzen (1970b), herbivores may be important agents in creating and maintaining vegetational diversity in space. Single species stands of plants, if not protected by special climatic conditions or provided with superior defense and high tolerance for attack, tend to become seriously damaged by specialized feeders and will be replaced by mixtures of several plant species. Eventually the state will be reached where the utilization rate of herbivores and the dispersion of the host are in equilibrium; in this state both the plant and the herbivore may be rather rare but still interacting (Huffaker, 1966; Harper, 1969). Although this kind of process, especially if close to equilibrium, is difficult to assess, several examples have been recorded in natural situations (Huffaker, 1957). In numerous successful cases of biological control of weeds, reduction of the target species and parallel increases in vegetational diversity have been followed in detail (e.g., Simmonds, 1934; Dodd, 1940; Huffaker and Kennett, 1959).

Thus, our experiments with *P. cruciferae* and a bulk of direct and circumstantial evidence in the literature indicate that, for phytophagous insects, the environmental capacity (determination) of diverse natural vegetation is lower than that of natural or man-made monocultures. In the past, the effect of low determination levels in diverse systems has often been credited to regulatory processes, specifically to predators and parasites. Similarly, the inefficiency of predation has commonly been cited for the occurrence of outbreaks in simple systems when high determination levels may have been the fundamental cause.

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