

Effect of Plant Patch Shape and Surrounding Vegetation on the Dynamics of Predatory Coccinellids and Their Prey *Brevicoryne brassicae* (Hemiptera: Aphididae)

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ABSTRACT We assessed the effect of plant patch shape and surrounding vegetation on the density, emigration, and immigration of predatory coccinellids, and on the density of their aphid prey *Brevicoryne brassicae* (L.). Between spring 1997 and fall 1999, we set up square and I-shaped patches of *Brassica oleracea* Plenck surrounded by *Medicago sativa* L. or *Allium porrum* L. *Medicago sativa* is frequently used by coccinellids, whereas *A. porrum* is not. We used a factorial (2 × 2) randomized block design, and evaluated the density of coccinellids and aphids every 10 d. We also evaluated emigration and immigration of adult coccinellids through mark-recapture experiments. We quantified the population increase of aphids, and the final live mass of plants. All insects were more abundant in patches surrounded by *A. porrum* than in those surrounded by *M. sativa*, and coccinellids were occasionally more dense in square patches than in I-shaped ones. Coccinellids emigrated less from square patches, either surrounded by *A. porrum* or *M. sativa*, and immigrated more to patches surrounded by *A. porrum*. Aphids showed a higher population increase, and plants of *B. oleracea* ended up being heavier in patches surrounded by *A. porrum*, particularly in I-shaped patches. Surrounding vegetation and plant patch shape seem to have a direct effect on the density of coccinellids by modifying their immigration and emigration patterns, but also seem to have an indirect effect by changing plant growth and its effect on herbivore recruitment.

KEY WORDS ladybeetles, cabbage aphid, patch geometry, immigration, emigration

THE GEOMETRY OF plant patches and the nature of the surrounding vegetation may affect the population dynamics of associated animals (Stamps et al. 1987). Patch shape determines the length of patch edge directly in contact with neighboring habitats. Patches with high perimeter/area ratio (P/A) (e.g., elongated patches) have a higher proportion of plants in the edge compared with a patch of the same size with a low P/A ratio (e.g., square patches, Collinge 1996). Edges are analogous to a membrane across which organisms move (Wiens et al. 1985). Thus, more elongated patches may be more susceptible to interactions with outside habitats—and their associated organisms—than square ones (Collinge 1996), enhancing immigration and emigration.

In addition, the vegetation surrounding the patch may be radically different from that inside, and may directly influence the abundance of animals in the patch through its effect on immigration or emigration (Kareiva 1985). Host plant patches surrounded by nonhost plants may be more difficult to find and colonize by specialist herbivores and their predators than host plant patches surrounded by alternative host plants. Also, host plant patches surrounded by nonhost plants should be less abandoned than those sur-

rounded by host plants. This has been observed to occur with the chrysomelid beetle *Acalymma vittatum* (F.), which was more abundant in squash patches surrounded by nonhost tomato plants because of a lower emigration of beetles from these patches than from patches without surrounding tomato plants (Bach 1988).

The surrounding vegetation, also, may indirectly affect the abundance of animals inside patches by modifying their resources (Lawrence and Bach 1989). For instance, the growth of plants within a patch may depend on the neighboring vegetation (e.g., Bach 1988), triggering changes in populations of herbivores and predators. The effects of surrounding vegetation should be more pronounced in patches with high P/A ratio, whose plants are more exposed.

Patch shape and the surrounding vegetation may play especially important roles among herbivorous and predatory insects associated with crop fields. Predatory insects are usually found in large numbers in the vegetation adjacent to crop patches, which results in higher densities of these organisms on the crop (Sotherton 1985, Dennis and Fry 1992, Cowgill et al. 1993, Hausammann 1996, Hickmann and Wratten 1996). For instance, hoverfly predators were more abundant when cabbage crops were surrounded by *Phacelia tanacetifolia*, an annual plant that is a source of pollen for hoverflies (White et al. 1995). The higher abundance of natural enemies in the borders may increase the rates of parasitism or predation inside

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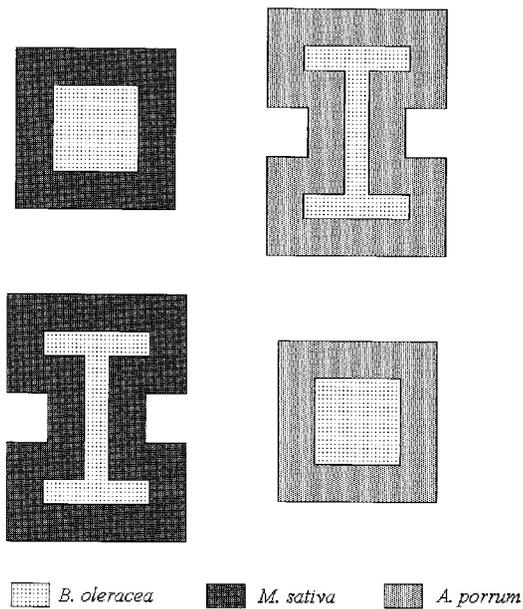


Fig. 1. Experimental patches for studying the effect of patch shape and surrounding vegetation on the dynamics of *B. brassicae* and Coccinellids. I-shaped and square patches of *B. oleracea* surrounded by *A. porrum* or *M. sativa* were set up using a 2×2 randomized block design, with 16 experimental patches distributed in four blocks.

patches and affect herbivore dynamics (Marino and Landis 1996).

In this article, we evaluate the effect of plant patch shape and surrounding vegetation on the density, emigration, and immigration of predatory coccinellids and on the density of their prey, the cabbage aphid *Brevicoryne brassicae* (L.), in patches of broccoli, *Brassica oleracea* variety *italica* Plenck. We studied three species of coccinellids present in the system: *Eriopsis connexa* (Germ.), *Hippodamia convergens* Guér., and *Hippodamia variegata* (Goeze). The first species is native and the other two were introduced to Chile for biological control programs (Montes 1970, Zúñiga et al. 1986). Coccinellids should emigrate less from lower P/A patches surrounded by a nonused vegetation. Therefore, they should reach higher abundance there, and have a greater effect on the density of aphids. Immigration may also be affected by plant patch shape and surrounding vegetation, and influence the standing density of coccinellids and aphids.

Materials and Methods

We conducted this study between spring 1997 and fall 1999 at the Instituto de Investigaciones Agropecuarias La Platina Research Station, Santiago, Chile. In November 1997 and 1998, we set up patches of 144 plants of *B. oleracea* varying in shape and surrounding vegetation: square patches and I-shaped patches surrounded by a 6-m wide border of *Medicago sativa* L. (alfalfa) or *Allium porrum* L. (leek) (Fig. 1). *B. ol-*

eracea plants were grown in speedlings in a greenhouse, where after they reached two to three true leaves they were transplanted onto the field. Plants were placed 1 m apart from one another. Surrounding crops were previously field-planted. *M. sativa* were sown in August 1997 at a 20 kg/ha seed density. The distance between rows was 18 cm. *A. porrum* was sown in a broadcasted seedbed system, and transplanted when they reached two to three true leaves in November 1997 and 1998. *M. sativa* was cut before transplanting *B. oleracea* plants.

We used a factorial (two shapes \times two surrounding vegetation) randomized block design, with 16 experimental patches distributed in four blocks. Square patches had a low P/A, with 30.6% of plants in the edge (i.e., the outermost row of plants) and the remainder up to 5.8 m from the edge, and I-shaped patches had a higher P/A, with 68.1% of plants on the edge and 31.9% up to 1.8 m from the edge.

We selected the surrounding vegetation based on its use by coccinellids: *M. sativa* provides a number of resources for coccinellids, including aphids and pollen, and would probably arrest more searching coccinellids than *A. porrum*, which has a few if any resources for these predator species. Neither of these crops serves as a host for *B. brassicae* (Prado 1991). Patches were irrigated every 10 d and kept free of weeds by manual removal. We quantified the density of larvae and adult coccinellids—the predatory stages—and apterous aphids every 10 d from December 1997 until March 1998 in 15 plants per patch, randomly selected each sampling date. Coccinellids were counted on the whole plant and aphids on one randomly selected leaf.

We also evaluated emigration and immigration of adult coccinellids (*E. connexa* and *H. variegata*) through mark-recapture experiments in one block. Individuals were collected from neighboring vegetation (nonexperimental crops) and marked in the pronotum with one dot of acrylic paint (Testor enamel, Rockford, IL.), with the color indicating the release location. To evaluate emigration, in January and April 1998 and January 1999 we released one marked ladybeetle on each *B. oleracea* plant (144 individuals per patch, with a total of 576 released ladybeetles in each experiment). To evaluate immigration, in January and April 1999 we released 680 marked ladybeetles in the surrounding vegetation of every patch (a total of 2,720 released ladybeetles in each experiment). After 2, 4, 6, 24, 72 and 120 h, we checked all *B. oleracea* plants and recorded the number and location of marked beetles. Immigrating beetles were recaptured to avoid overestimation of immigration events.

To evaluate the population increase of *B. brassicae*, in January 1999 we added 30–40 aphids to one leaf of five plants in every patch. We partially excluded predators (i.e., walking predators) by removing all neighboring leaves and adding tanglefoot to the base of the leaf. After 1 wk we counted the aphids. At the end of the experiment, we measured the final live mass of plants ($n = 15$ per patch) in all patches.

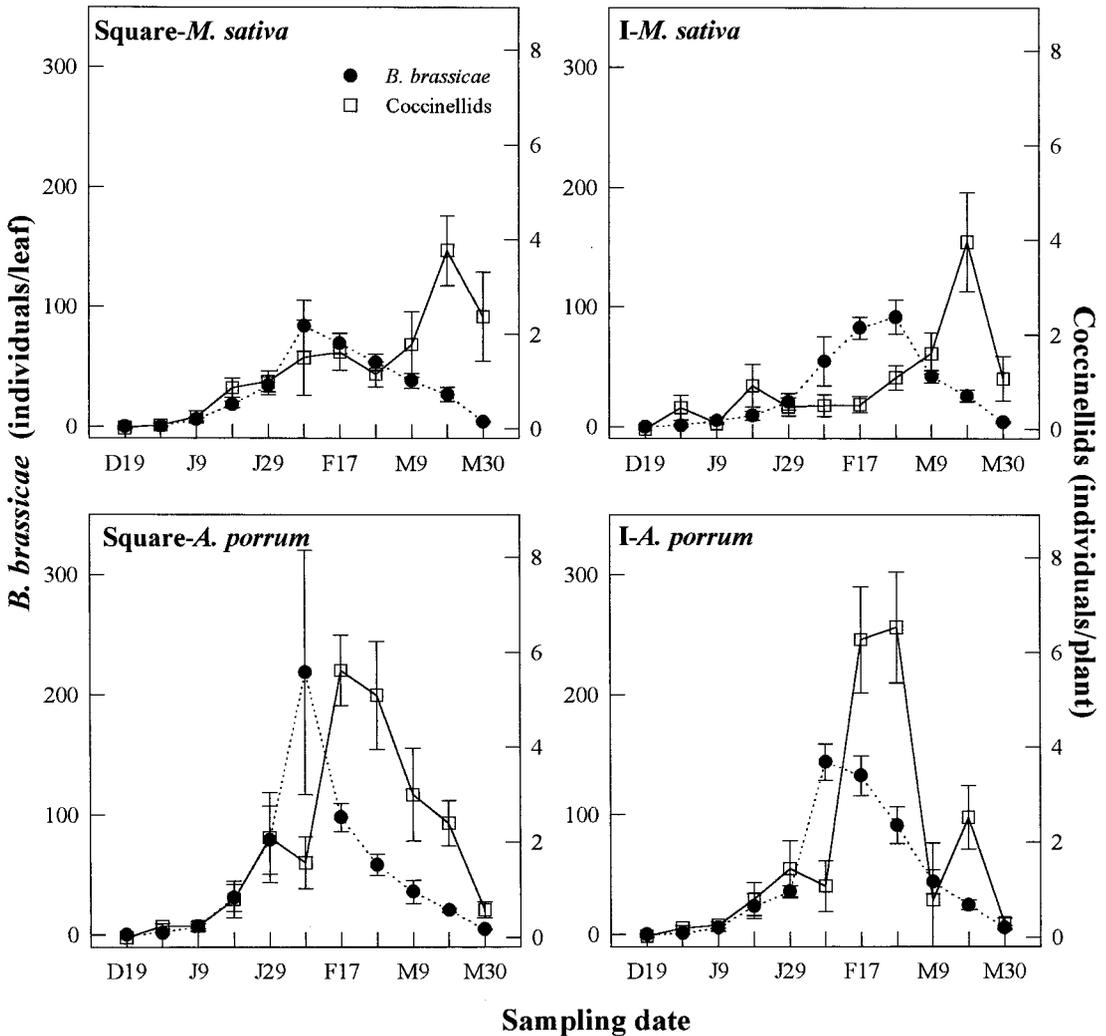


Fig. 2. Densities of *B. brassicae* and Coccinellids associated with patches of *B. oleracea* varying in shape and surrounding vegetation. Data are mean densities (from four blocks) ± 1 SE.

Densities of insects were analyzed using a factorial repeated-measures analysis of variance (ANOVA) (PROC GLM, SAS Institute 1996) with block, shape, surrounding vegetation and time (repeated measures) as variation sources. Because different plants inside patches are not statistically independent, we used mean density for statistical analyses. We normalized data through the transform $\sqrt{x_i + 0.5}$. Cumulative numbers of emigrants and immigrants were compared through chi-square analyses (Zar 1996). The recapture curves obtained from emigration experiments were analyzed by the Peto and Peto logrank test, a nonparametric test originally used to compare the shape of survivorship or removal rate curves (Pyke and Thompson 1986). In this case, recapture curves were considered analogous to survivorship curve. Differences in aphid population increase and final mass of plants were analyzed by two-way ANOVA, with each replicate consisting of the av-

erage value of a patch. Multiple comparisons used the Tukey honestly significant difference (HSD) test (Zar 1996).

Results

We found a significant effect of surrounding vegetation on the densities of both coccinellids and aphids but no consistent effect of patch shape was observed (Fig. 2; Table 1). The highest densities of coccinellids and *B. brassicae* were generally reached in patches surrounded by *A. porrum* (Fig. 2). Moreover, density peaks of coccinellids were not only higher but also earlier in patches surrounded by *A. porrum* than in patches surrounded by *M. sativa*. In all cases, the density curves of coccinellids showed a delayed response with respect to *B. brassicae*. *B. brassicae* was more dense in patches surrounded by *A. porrum*, especially in midsummer (February) when the highest

Table 1. Results of repeated-measures ANOVA for the effect of patch shape and surrounding vegetation on the densities of *B. brassicae* and Coccinellids associated with *B. oleracea*

Source of variation	MS	F	df	P
<i>B. brassicae</i>				
Blocks	6.42	1.30	3	0.3338
Shape	0.16	0.03	1	0.8614
Surrounding	36.69	7.41	1	0.0235
Shape * Surrounding	0.22	0.04	1	0.8370
Error (a)	4.94		9	
Time	180.30	69.83	10	0.0001
Shape * Time	4.91	1.90	10	0.1319
Surrounding * Time	8.26	3.20	10	0.0242
Shape * Surrounding*	0.31	0.12	10	0.9745
Time				
Error (b)	2.58		90	
Coccinellids				
Blocks	1.32	15.60	3	0.0007
Shape	0.06	0.69	1	0.4282
Surrounding	2.94	34.59	1	0.0002
Shape * Surrounding	0.37	4.35	1	0.0667
Error (a)	0.09		9	
Time	3.25	51.24	10	0.0001
Shape * Time	0.13	2.07	10	0.0353
Surrounding * Time	1.38	21.80	10	0.0001
Shape * Surrounding*	0.07	1.14	10	0.3446
Time				
Error (b)	0.06		90	

densities of aphids were reached. This pattern was independent of patch shape (Fig. 2; Table 1). Coccinellids were also significantly more dense in patches surrounded by *A. porrum* (February and early March), but this pattern reverses toward the end of March when they became more abundant in patches surrounded by *M. sativa*. Thus, there was a significant interaction between the effects of surrounding vegetation and time on the densities of coccinellids (Table 1). Although there was no global effect of patch shape on the densities of coccinellids, the significant interaction between shape and time indicates that in some dates (7 February and 30 March) coccinellids became more abundant in square patches (Fig. 2; Table 1).

The cumulative number of recaptured beetles in different patches during emigration and immigration experiments, and chi-square results are shown in Table 2. Adult coccinellids emigrated less from square patches, either surrounded by *A. porrum* (January 1998, 1999) or by *M. sativa* (January 1998 and April 1998; Fig. 3; Table 2; Peto and Peto logrank test Table 3). Even when a low

Table 2. Cumulative number of recaptured ladybeetles in different patches during six recapture events in emigration and immigration experiments

	Sq.- <i>M. sativa</i>	I- <i>M. sativa</i>	Sq.- <i>A. porrum</i>	I- <i>A. porrum</i>	χ^2 , P
Emigration ^a					
January 1998	70b	35a	99c	43a	40.9, < 0.001
April 1998	261a	150b	131b	149b	61.4, < 0.001
January 1999	166a	148a	201b	145a	12.0, < 0.01
Immigration ^b					
January 1999	2a	1a	32b	25b	50.3, < 0.001
April 1999	3a	0a	16b	11b	21.5, < 0.001

Letters after numbers indicate significant differences after subdividing chi-square analyses.

^a One marked ladybeetle was released on each *B. oleracea* plant (a total of 576 released ladybeetles in each experiment).

^b 680 marked ladybeetles were released in the surrounding vegetation of every patch (a total of 2,720 released ladybeetles in each experiment).

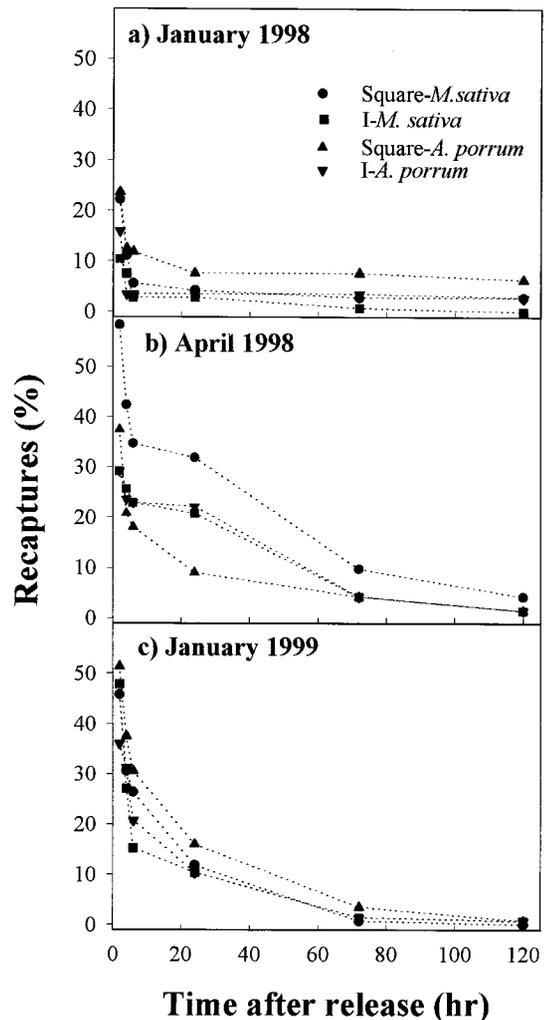


Fig. 3. Results from mark-recapture experiments for evaluating the emigration of *E. connexa* from patches of *B. oleracea* varying in shape and surrounding vegetation. Higher recapture percentages suggest lower emigration. (a) January 1998. (b) April 1998. (c) January 1999.

number of marked individuals were recaptured in the immigration experiment, it is possible to observe that both *E. connexa* and *H. convergens* adults immigrated

Table 3. Results of Peto and Peto's logrank test for the difference between recapture curves from emigration experiments run in January 1998, April 1998, and January 1999

	I-M. sativa	Sq.-A. porrum	I-A. porrum
January 1998			
Sq.-M. sativa	LR = 20.0*	LR = 1.7	LR = 8.7*
I-M. sativa		LR = 38.9*	LR = 6.0*
Sq.-A. porrum			LR = 16.9*
April 1998			
Sq.-M. sativa	LR = 26.4*	LR = 21.4*	LR = 27.4*
I-M. sativa		LR = 0.4	LR < 0.01
Sq.-A. porrum			LR = 0.6
January 1999			
Sq.-M. sativa	LR = 0.06	LR = 6.1*	LR = 3.5
I-M. sativa		LR = 4.4*	LR = 0.6
Sq.-A. porrum			LR = 8.5*

LR, logrank statistic which is compared with $\chi^2_{(1, 0.05)} = 3.84$. Any value above 3.84 indicates statistical difference between curves.
 *, $P < 0.05$.

more into patches surrounded by *A. porrum* than into patches surrounded by *M. sativa* (Fig. 4; Table 2).

Aphids displayed a greater population increase in patches surrounded by *A. porrum* than in patches surrounded by *M. sativa* (Fig. 5; Table 4), and *B. oleracea* plants ended up significantly heavier in patches surrounded by *A. porrum*, particularly in I-shaped patches (Fig. 6; Table 5).

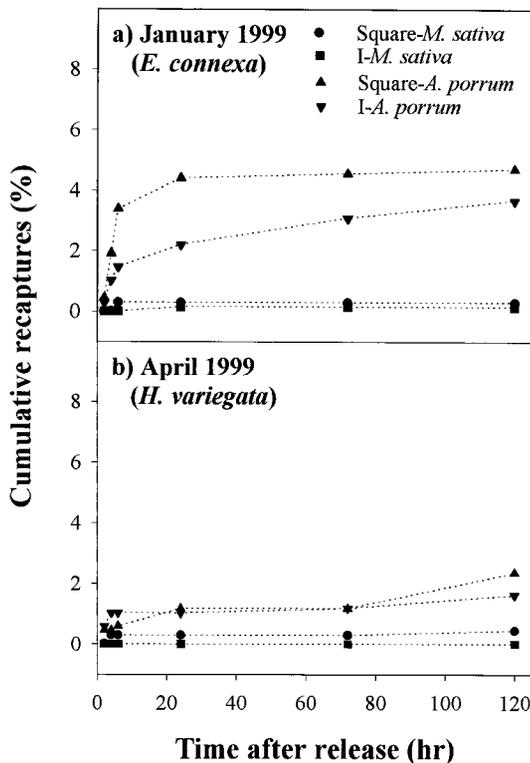


Fig. 4. Results from mark-recapture experiments for evaluating the immigration of Coccinellids into patches of *B. oleracea* varying in shape and surrounding vegetation. (a) Experiment run in January 1999 with *E. connexa*. (b) Experiment run in April 1999 with *H. variegata*.

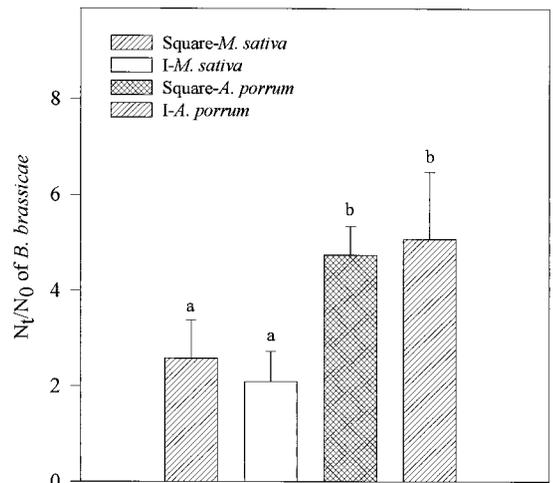


Fig. 5. Weekly population increase (N_i/N_0) of *B. brassicae* associated with patches of *B. oleracea* varying in shape and surrounding vegetation. Data are mean population increase (from four blocks) ± 1 SE. Different letters indicate significant differences ($P < 0.05$) according to Tukey HSD test.

Discussion

In all kinds of patches, coccinellids showed a delayed response with respect to *B. brassicae*, following the typical predator-prey curves, suggesting that coccinellid abundance was a consequence of aphid dynamics. Surrounding vegetation affected the density of coccinellids and *B. brassicae*, with higher peak densities in patches surrounded by *A. porrum*. These results support conclusions of other studies on the effects of surrounding vegetation on the density of herbivorous (e.g., Bach 1988, Lawrence and Bach 1989) and predatory insects (e.g., White et al. 1995) inside patches. Also, these results agree with previous studies regarding density patterns of *B. brassicae*, *E. connexa*, and *H. variegata* in patches surrounded by different kind of vegetation (Grez 1997). These species developed higher densities in subdivided patches of cabbage surrounded by weeds (including some wild crucifers) and in continuous patches (more cabbages between cabbage patches), than in subdivided patches surrounded by cloth barriers and mowed weeds (Grez 1997). In the first two arrangements, both aphids and coccinellids were able to use the surrounding vegetation and recognize the whole mo-

Table 4. Results of two-way ANOVA for the effect of patch shape and surrounding vegetation on the population increase of *B. brassicae*

Source of variation	MS	F	df	P
Block	5.70	2.19	3	0.1584
Shape	0.02	0.01	1	0.9253
Surrounding	26.65	10.25	1	0.0108
Shape * Surrounding	0.67	0.26	1	0.6296
Error	2.59		9	

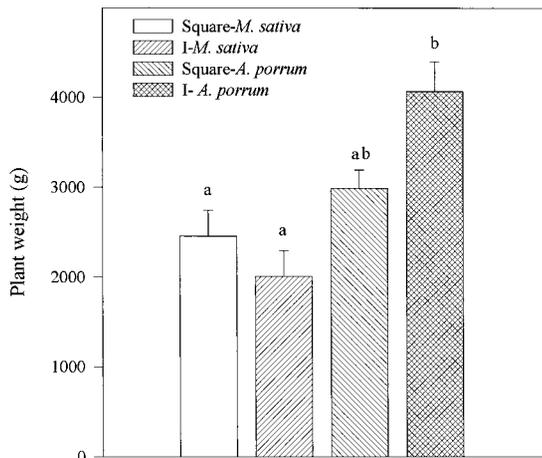


Fig. 6. Final weight of *B. oleracea* plants from patches varying in shape and surrounding vegetation. Data are mean weight (from four blocks) ± 1 SE. Different letters indicate significant differences ($P < 0.05$) according to Tukey HSD test.

saic of cabbage patches as a continuous habitat, with more concentrated resources (Root 1973), whereas in the third, surrounding habitat did not provide resources for them, probably determining the low density of these insects in cabbage patches (Grez 1997). Thus, surrounding vegetation seems to be crucial for the population dynamics of these herbivore and predatory species.

Plant patch shape had differential effects on aphids and coccinellids. On the one hand, plant patch shape did not affect the density of *B. brassicae*. Associated with patch geometry is patch size, with larger patches having lower P/A than smaller ones (Stamps et al. 1987). It has been shown that cabbage patch size has no effect on the density of *B. brassicae*, with aphids being equally abundant in square patches of 4, 16, 64, or 225 plants (Grez and González 1995). Therefore, it seems that P/A, given by patch shape (this study) or patch size (Grez and González 1995), does not determine the density of *B. brassicae*. However, coccinellids were occasionally more dense in square patches, suggesting that they can be affected by plant patch shape. These results were not only true for coccinellids, because lepidopteran species in this system were also affected by plant patch shape (Muriel 1999). Although the interaction between plant patch shape and surrounding vegetation was only marginally significant ($P = 0.0667$), coccinellids tended to be

more dense either on square patches surrounded by *A. porrum* (in midsummer) or in square patches surrounded by *M. sativa* (in late summer). Thus, surrounding vegetation seems to modulate the response of coccinellids to patch shape.

Plant patch shape, but not surrounding vegetation, affected the emigration of coccinellids as they emigrated less from square patches surrounded by *A. porrum* or *M. sativa* (see Tables 2 and 3). It seems that in square patches, with a low P/A ratio, coccinellids are less likely to reach the edges and abandon the patch, whereas in I-shaped patches, with a high P/A ratio, coccinellids would more probably emigrate as most plants are directly in the edge. This mechanism has been proposed to occur in herbivorous insects associated with differently sized patches, which also differ in P/A ratio (Kareiva 1985).

Surrounding vegetation affected the immigration of coccinellids as they immigrated more to patches surrounded by *A. porrum* than to patches surrounded by *M. sativa*. Contrary to *M. sativa*, which offers abundant resources to coccinellids, such as pollen or other species of aphids, *A. porrum* is not a profitable habitat for them. Therefore, coccinellids must abandon this kind of vegetation, resulting in a higher immigration to neighboring *B. oleracea* patches. In contrast, *M. sativa* vegetation may have been acting as a sink for coccinellids. Patch shape did not statistically affect immigration of coccinellids, but there was a tendency to a higher immigration to square patches surrounded by *A. porrum* than to I-shaped patches (see Fig. 4a). This result is contrary to our expectation, because immigration was supposed to be higher in I-shaped patches with higher P/A. Our results indicate that immigration was affected mainly by surrounding vegetation, contrary to emigration, which was affected mainly by patch shape. Therefore, both processes should be considered in empirical or theoretical studies of population dynamics in heterogeneous environments.

Brassica oleracea plants ended up heavier in patches surrounded by *A. porrum*, particularly I-shaped patches. This phenomenon may be the consequence of the differential exploitation of soil nutrient by *A. porrum* and *M. sativa*. At the end of the experiment, the soil of patches surrounded by *M. sativa* had three and two times less nitrogen and phosphorous than that of patches surrounded by *A. porrum* (3 versus 9 mg/kg nitrogen and 3 versus 7 mg/kg phosphorous, respectively), suggesting that *M. sativa* may have inhibited the growth of *B. oleracea*.

The highest growth of *B. oleracea* in patches surrounded by *A. porrum* may account for the highest population increase of aphids there. This, in turn, may have triggered higher immigration, lower emigration, and earlier aggregation of coccinellids in these patches. Previous studies have demonstrated that coccinellids tend to aggregate in regions of high prey density (Kareiva and Odell 1987). Thus, patches composed of bigger plants, such as those surrounded by *A. porrum*, may offer a higher resource concentration for herbivores (Root 1973), and trigger a density-dependent response of coccinellids. But, this bottom-up ef-

Table 5. Results of two-way ANOVA for the effect of patch shape and surrounding vegetation on the final weight of *B. oleracea*

Source of variation	MS	F	df	P
Block	539231.0	2.17	3	0.1610
Shape	589056.0	2.37	1	0.1578
Surrounding	6.0369E6	24.33	1	0.0008
Shape * Surrounding	1.9321E6	7.79	1	0.0210
Error	248117.0		9	

fect of *B. oleracea* growth, dependent of surrounding vegetation, cannot be interpreted as the only source of variation for coccinellid density, because beetles also responded to plant patch shape. Coccinellids were denser, tended to immigrate more, and emigrated less from square patches with smaller plants. Therefore, surrounding vegetation and plant patch shape seem to have a direct effect on the density of coccinellids by modifying their immigration and emigration processes, but also have an indirect effect resulting from changes in plant growth and its effect on herbivorous response.

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