

Egg-laying-site preferences of *Pterostichus melanarius* in mono- and intercrops

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Abstract

Increased vegetational diversity influences the behaviour of carabid beetles by changing plant-related abiotic factors. These abiotic factors (light, humidity and habitat structure) affect the selection of oviposition sites and egg survival of carabid beetles. In a field experiment, more larvae of *Pterostichus melanarius* (Illiger) (Coleoptera Carabidae) were caught in Brussels sprout intercropped with barley than in Brussels sprout alone. The influence of the presence of living barley and Brussels sprout plants on oviposition was studied in the laboratory. Also, the effects of wet/dry substrate, light/shadowed and structured/unstructured environment on the number of eggs laid were investigated under laboratory conditions. Results indicate a preference for moist, shadowed, structurally complex environments as egg laying sites. This preference results in significantly higher numbers of eggs laid by beetles in barley compared to Brussels sprout. Vegetation characteristics by themselves may influence egg-laying-site preferences, in addition to the availability of prey for adults and larvae in the different cropping systems. Vegetables intercropped with cereals provide a more favourable microclimate for the reproduction of *P. melanarius* than vegetables grown alone.

Key words: *Pterostichus melanarius*, abiotic factors, microclimate, egg laying, intercropping.

Introduction

Carabids are important generalist predators in agricultural fields (Luff, 1987; Lövei and Sunderland, 1996). Their biology and distribution are widely studied but information on their reproduction and larval ecology is limited (Booij *et al.*, 1996; Lövei and Sunderland, 1996). The reasons why a given habitat or microhabitat is preferred for oviposition are not understood (Powell *et al.*, 1995; Lee and Landis, 2002). High egg and larval mortality is often found and attributed to unfavourable abiotic conditions, predation and lack of adequate food (Heessen and Brunsting, 1981; van Dijk and den Boer, 1992). The mobility of carabid larvae is low (Lövei and Sunderland, 1996), so the decision of the female when selecting a site for egg laying is crucial for the survival of her offspring.

The distribution and activity of carabid beetles in different cropping systems have been studied extensively. Investigations usually show higher number of species and/or individuals in diversified cropping systems, compared to monocultures (e.g. Ryan *et al.*, 1980; Wiech and Wnuk, 1991; Armstrong and McKinlay, 1994; Booij *et al.*, 1997). However, how beetles are attracted to or arrested in these systems remains unknown. Adult carabid beetles are generally mobile and their life span is rather long, so probably they respond to quite different biotic and abiotic cues at different times of the season (Langmaack *et al.*, 2001). Also, some observations suggest a difference between the distribution (Thomas *et al.*, 1998) and the behaviour (Tréfás *et al.*, 2001) of male and female beetles that may refer to the different requirements of the sexes.

Increased fecundity as a result of increased vegetation diversity either within field (Zangger *et al.*, 1994; Chiverton and Sotherton, 1991) or at landscape level (Bommarco, 1997) has been shown in several cases.

This increased fecundity is generally presumed to be linked to better feeding conditions in more diverse agroecosystems. However, optimising food intake in order to maximise reproduction presumes a rather complex decision making system. Van Dijk and den Boer (1992) for example argue that polyphagous carabids, because of nervous restraints, will hunt in a simplistic manner, far from optimal foraging.

The possible relationship between optimal microclimatic conditions and reproduction success so far has not been investigated. The relationship between microclimate and beetle abundance is frequently referred to as a possible driving force behind carabid distribution. Many authors presume the important role of relative humidity and soil moisture and their relationship with plant structure in carabid habitat selection (Crist and Ahern, 1999; Thomas *et al.*, 1998; Honek, 1988; 1997; Speight and Lawton, 1976; Rivard, 1966). However, only few studies have shown a concrete relationship between a specific abiotic variable and carabid abundance (e.g. Asteraki *et al.*, 1995; Cardwell *et al.*, 1994), and very few investigated the mechanisms involved in detail.

The polyphagous carabid *Pterostichus melanarius* (Illiger) is a common autumn-breeding generalist natural enemy with larvae that overwinter in agricultural fields (Desender *et al.*, 1985; Luff, 1987). Being an open-field species, *P. melanarius* is not bound to field margins or boundaries for reproduction (Noordhuis *et al.*, 2001; Fadl *et al.*, 1996). The reproductive success of the species thus may depend greatly on the conditions for egg laying and larval survival within the field.

This work is part of a series of experiments in which we study how populations *P. melanarius* may benefit from intercropping (Tréfás *et al.*, 2001; 2003), and, as a result, may lead to lower pest populations. The results presented in this paper are focusing on egg-laying-site selection of *P. melanarius* in different vegetation types.

Following a trapping study where adults of the species had been caught in equal numbers in monocrops and intercrops (to be published elsewhere), we continued with field experiments aiming at evaluating the number of larvae in the same plots. Next, we did laboratory experiments to take a closer look at oviposition-site selection with special regards to abiotic factors, while feeding regimes were equal.

Materials and methods

Field experiment

Experimental plots were located at two sites, in Achterberg and Wageningen Hoog (the Netherlands), which are both research fields of the Laboratory of Entomology of Wageningen University. At both sites, 30 x 30 m plots of monocropped Brussels sprout (*Brassica oleraceae* L. var. *gemmifera* cv. Maximus) and Brussels sprout intercropped with spring barley (*Hordeum vulgare* L. cv. Video) were established, one plot per crop type at each site. Plots were separated by 15-m wide sown grass strips (*Lolium* species).

Brussels sprout plants were planted in the last week of May, at a row distance of 0.75 m and plant distance of 0.5 m; plants were 7 weeks old at planting. In the intercropped plots, sprout plants were planted immediately after the barley was sown. The arrangement of the intercropped plants followed the additive design, Brussels sprout was planted at the same row and plant distance as in the monocropped plots and three rows of barley (row distance = 0.125 m) were sown between the rows of the sprout plants. The grass strips around the plots were sown also in the last week of May.

The plots received no chemical treatment. Weeds were removed manually.

In each plot, 49 trapping stations were placed. The arrangement of the trapping stations followed a 7 x 7 grid design. Traps within the same row or column were placed 4.4 m from each other. Traps on the perimeter of the grids were located 1.8 m from the edge of the plots.

A trapping station consisted of two plastic dishes of 11 cm diameter and 7 cm depth. These dishes were sunk 0.5 m from each other so that their opening was completely level with the soil surface, and were connected by a plastic wall 0.2 m tall above ground, to enlarge trapping surface. Traps contained no preservatives. Trapping stations were dug in at the beginning of the growing season.

Larvae were collected weekly between 28 October and 25 November 2002, and were stored in 96% ethanol until identification. The sampling period was chosen according to the biology of *P. melanarius*. Third instar larvae of the species appear around the middle of October (Krehan, 1970) and, according to Traugott (1998), for most carabid species this is the instar that can be caught in the highest numbers. Larvae were identified using the key of Luff (1993).

Laboratory experiments

In the laboratory, two sets of experiments were carried out. The experiments were completed at the Department

of Crop and Weed Ecology, Wageningen University, the Netherlands.

Experiments with live plants

The experiments were completed in a climate chamber, from 19 September to 10 October 2003. Climate chamber settings followed the environmental conditions of mid-August in the Netherlands, the peak reproduction period of the species in this region (L:D = 14.5:9.5, RH 70% and 20 °C in the light period, RH 95% and 16 °C in the dark period). Light intensity was 365 mm/m²/s (400-700 nm) during the day period. To evaluate the effect of the presence of living plants on the egg laying of *P. melanarius*, 0.4 x 0.7 x 0.9 m plastic boxes were used. The bottom of the boxes was lined with potting compost in a layer of 0.2 m. Boxes were divided into two equal areas. Into one area, 20 laboratory-reared, 12-week-old barley plants were planted in a 4 x 5 grid. Into the other area, one laboratory-reared 12-week-old Brussels sprout plant (about 13 real leaves) was planted in the middle. 12-week-old barley plants represented the age of plants in the field in mid-August. However, 19-week-old Brussels sprout plants, the same age as those in the field in mid-August, were too large for experimental purposes. Two days after planting, the compost was sealed with a sheet of textile from above, to prevent beetles from laying eggs in the compost. In the textile, holes were made for the plants; the digging of beetles around or near plant stems was prevented by adhesive tape. Plants were watered every day, via a plastic tube that was inserted through the textile into the compost. On the surface of the textile, sand was distributed in an even, 1.5 cm layer.

Three of these boxes were used that corresponds to 3 replicates in space. Five female and five male beetles were released in the middle of each box, and left in the box for a week. Then the beetles were removed and the eggs were washed out of the sand.

After each week, new plants were planted in the boxes. The experiment was repeated 3 times. Each beetle was used only once. Beetles were fed daily with an excess amount of catfood (Edah own brand, with beef) placed in the middle point of the boxes on a petri dish lid. The sand in the boxes was watered twice a day, with 1.5 l water sprayed evenly over the surface.

Beetles for these experiments were trapped in winter wheat in August 2003 in dry pitfall traps, then kept in captivity, sexes separate, in groups of 15, in 19 x 13 x 5 cm plastic trays lined with wet potting compost, with an excess supply of catfood (Edah own brand, with beef), for a minimum of two weeks prior to the experiments, in the same climate chamber. Only coetaneous specimens were used.

Experiments on the influence of abiotic factors

In these experiments, the influence of different abiotic factors on egg laying was tested and no plants were involved. Experiments were carried out from 24 September to 30 October 2002, in a climate chamber with the same settings as previously described, in arenas of 1m², constructed of plastic. Arenas contained sand, in an

evenly laid, 1.5 cm thick layer.

Arenas were divided into two equal areas. Treatments, representing a choice situation, were applied on these areas as follows:

- I. dry substrate (no water) against wet substrate (watered twice a day, each time with 1 l of water sprayed evenly over the treatment area);
- II. shadow (a cardboard sheet placed in the way of light, 0.5 m above the area) against no shadow;
- III. structure (200 pieces of insulated steel wire (diameter 2 mm) fixed in a vertical position to the bottom of the area in a uniform distribution, the distance between adjacent wires being 2.5 cm) against no structure.

For each of these treatment pairs, two arenas were assigned (two replicates in space). Five female and five male beetles were released in each arena and left in the arena for a week. Feeding of beetles in the boxes was the same as in the first set of experiments. The substrate in the arenas was watered twice a day with 2 l water sprayed evenly over the whole arena, unless specified otherwise in the treatments. After one week the beetles were removed and eggs were washed out of the sand. The procedure was repeated each week during 5 weeks (5 replicates in time). The position of the arenas with different treatments within the climate chamber was changed after each week. Each beetle was used only once. Beetles were trapped in August 2002, in an alfalfa field in dry pitfall traps, then kept in captivity, the same way as described for the other set of experiments above.

Statistics

Results of the larval trapping were analysed with a Univariate ANOVA (General Linear Model, SPSS 10.0). Analysis was carried out on $\ln(n + 1)$ transformed data. The effects of vegetation type, experimental site and trapping week on the number of larvae trapped were analyzed.

In the egg laying experiments, egg numbers laid within treatments were summarized over replicates in space and time, the percentages of eggs laid in the different treatments were calculated and the χ^2 test was applied, with an expected ratio of 1:1.

Results

Trapping of larvae in field

Larvae were trapped in relatively low numbers during the four trapping weeks. At both research sites, i.e. in Achterberg and Wageningen Hoog, significantly more larvae were trapped in the intercrop of Brussels sprout and barley than in the monocrop of Brussels sprout ($P < 0.0001$, $DF = 1$, $F = 16.569$, table 1). More larvae were trapped in Wageningen Hoog than in Achterberg ($P = 0.011$, $DF = 1$, $F = 6.567$, table 1). Trapping week had a significant effect on the number of larvae trapped ($P = 0.002$, $DF = 3$, $F = .040$, table 1), but there was no relationship between plant type and trapping week ($P = 0.143$, $DF = 3$, $F = 1.814$).

Laboratory experiments

In the experiments with live plants, beetles laid significantly more eggs in areas planted with barley than in areas planted with Brussels sprouts ($P < 0.05$, $\chi^2 = 75.469$) (table 2).

In the experiments on the influence of abiotic factors on egg laying, significantly more eggs were laid in the wet substrate than in the dry substrate ($P < 0.05$, $\chi^2 = 59.063$) (table 3); in the shadow than in the normal light ($P < 0.05$, $\chi^2 = 49.648$) (table 3); and in the structured environment than in the unstructured environment ($p < 0.05$, $\chi^2 = 75.313$) (table 3). Differences between treatments seemed to be less pronounced in week 4; the number of eggs decreased drastically by week 5.

Table 1. Total and average number of *P. melanarius* larvae trapped in monocropped Brussels sprout (monocrop) and Brussels sprout intercropped with barley (intercrop) at the experimental sites in Achterberg and Wageningen Hoog, the Netherlands. Numbers in italics represent standard deviation.

	week	monocrop		intercrop	
		total number	number/trap	total number	number/trap
Achterberg	I	0	0	0	0
	II	0	0	0	0
	III	0	0	1	0.02 <i>(0.143)</i>
	IV	2	0.04 <i>(0.199)</i>	5	0.1 <i>(0.308)</i>
Wageningen Hoog	I	1	0.02 <i>(0.143)</i>	10	0.2 <i>(0.459)</i>
	II	0	0	1	0.02 <i>(0.143)</i>
	III	0	0	3	0.061 <i>(0.242)</i>
	IV	1	0.02 <i>(0.143)</i>	6	0.12 <i>(0.331)</i>

Table 2. Numbers of eggs laid by *P. melanarius* and their percentages in the different treatments in the laboratory experiments with live plants.

	treatment	barley	Brussels sprout	total
week	1	72 (78.3%)	20 (21.7%)	92 (100%)
	2	98 (69%)	44 (31%)	142 (100%)
	3	112 (70.9%)	46 (29.1%)	158 (100%)
	total	282 (71.9%)	110 (28.1%)	392 (100%)

Table 3. Numbers of eggs laid by *P. melanarius* and their percentages in the different treatments in the laboratory experiments on the effects of abiotic factors on the egg laying.

	treatment	wet substrate	dry substrate	total
week	1	62 (82.7%)	13 (17.3%)	75 (100%)
	2	39 (88.6%)	5 (11.4%)	44 (100%)
	3	45 (100%)	0 (0%)	45 (100%)
	4	40 (46.1%)	46 (53.5%)	86 (100%)
	5	1 (50%)	1 (50%)	2 (100%)
	total	187 (74.2%)	65 (25.8%)	252 (100%)
	treatment:	shadow	no shadow	
week	1	71 (69.6%)	31 (30.4%)	102 (100%)
	2	83 (83%)	17 (17%)	100 (100%)
	3	23 (62.2%)	14 (37.8%)	37 (100%)
	4	40 (55.5%)	32 (44.5%)	72 (100%)
	5	12 (63.2%)	7 (36.8%)	19 (100%)
	total	229 (69.4%)	101 (30.6%)	330 (100%)
	treatment:	structure	no structure	
week	1	91 (81.2%)	21 (18.8%)	112 (100%)
	2	42 (54.5%)	35 (45.5%)	77 (100%)
	3	64 (95.5%)	3 (4.5%)	67 (100%)
	4	21 (58.3%)	15 (41.7%)	36 (100%)
	5	19 (70.4%)	8 (29.6%)	27 (100%)
	total	237 (74.3%)	82 (25.7%)	319 (100%)

Discussion

In the larval trapping experiment in the field, significantly more larvae were trapped in the intercrop of barley and Brussels sprout than in the Brussels sprout monocrop. Though larvae of *P. melanarius* mainly occur in the soil (Noordhuis *et al.*, 2001; Sotherton, 1984; Wallin, 1985; Fadl *et al.*, 1996; Traugott, 1998), they also show some activity on the surface of the soil (Briggs, 1965; Desender *et al.*, 1985). The higher number of larvae trapped in the intercrop might be the result of either higher numbers present or of higher activity of the larvae in the intercrop resulting in higher catches. Below, we illustrate why we think this higher number really reflects higher population densities of larvae in the intercrop.

Neither the numbers of adult beetles trapped (Tréfás *et al.*, in preparation) nor the activity of the adults (Tréfás *et al.*, 2003) were different in the intercrop and Brussels sprouts. Thus, the higher number of larvae found in the intercrop of Brussels sprout and barley can indeed be a result of increased egg laying activity and not of a higher number of adults accumulated earlier in the plots. If intercropping increases fecundity and/or provides more favourable environment for egg laying, it means that even if the numbers of adults do not differ between

cropping regimes in a given year, diversified plant systems can have a significant positive effect on population levels in the next generation.

The results of the egg laying experiments in the laboratory show that females prefer to lay eggs in moist, shadowed, structurally diverse environments, either created completely artificially or induced by live plants.

In the laboratory experiments testing the effect of live plants on egg laying, beetles preferred barley to Brussels sprout for egg laying. Some field results support this observed preference for cereal plants, e.g. Bürki and Hausmann (1993) and Wallin (unpublished, cited by Wallin and Ekbom, 1988) found that autumn breeding species overwintering as larvae seemed to prefer dense cereal crops. Also Sotherton (1984) reported higher numbers of *P. melanarius* larvae in winter wheat than in either: cereal stubbles, turnip stubbles, field boundaries or woodlands. In the case of ground beetles breeding in the autumn, a mid-season redistribution within/between fields is suspected, caused by interrelated changes in plant cover and microclimate (Purvis and Fadl, 2002). The reproductive success of the species may significantly depend on its reaction to these changes (Purvis *et al.*, 2001). On a short range, *P. melanarius* adults were able to move between monocrops and intercrops on a daily base (Chapman *et al.*, 1999). The authors mention

preferable microclimatic conditions, i.e. more shadow and higher relative humidity, in a cabbage-clover intercrop compared to the cabbage monocrop and relate these to higher predator activity. Our findings indicate that beetles may move between contrasting vegetation types not only for foraging but also for egg laying. The design of our experiments did not enable us to define the scale at which such a selection might operate on the field.

In the laboratory experiments testing the effects of abiotic factors on egg laying, beetles preferred to lay eggs in moist, shadowed and structurally complex environments when compared to dry, structurally simple environments exposed to light. The influence of the soil moisture on the number of eggs laid by *Poecilus versicolor* (Sturm) and *Calathus melanocephalus* (L.) was mentioned by van Dijk and den Boer (1992). Also Aukema (1991) suspects the effect of substrate moisture on the egg laying site selection in *Calathus* species. Besides being able to choose between soil types, *Abax parallelepipedus* (Piller et Mitterpacher), a species known for primitive brood care, also preferred wet substrate when laying eggs (Symondson, 1994). Higher soil moisture correlated with higher numbers of trapped *P. melanarius* in the field experiments of Asteraki *et al.* (1995), but reproduction of the species was not considered in this experiment. Wet soil may promote the survival of eggs and young larvae; it was suspected for example in the case of *Pterostichus madidus* (F.) (Luff, 1994) or *Poecilus chalcites* (Say) (Lundgren *et al.*, 2005). Some carabid larvae survive rather long periods without food (Booij *et al.*, 1996; Luff, 1994; Heessen and Brunsting, 1981; Symondson, 1994) but under dry conditions they die very fast.

The effect of shadow on egg laying site preference is surprising, because *P. melanarius* is mostly nocturnal and is presumed to lay eggs in darkness. (In the case of *P. versicolor* and *C. melanocephalus* fecundity depended mostly on temperature also during the activity period (van Dijk and den Boer, 1992). Also, exposure to direct light in this case did not dry the substrate as it was watered regularly.

Another surprising result is the beetles' choice for the sites with vertical structures in the form of wires. Wires did not prevent the beetles in moving freely: it is highly improbable that they laid eggs around wires because they were "trapped" in the structured environment. Neither could the wires have provided any chemical cues that might have influenced the beetles' orientation. In the experiments with live plants females were observed to lay eggs almost solely at plant stems, at a depth of 2-3 cm (that is why plants and the compost had to be sealed from the beetles with a sheet of textile). This behaviour may explain the beetles' preference for a more structured environment in the experiments on the influence of abiotic factors. In a field experiment, the density of plant stems showed a positive relationship with the trapped numbers of ground beetles, among others also *P. melanarius* (Cardwell *et al.*, 1994). Though in the same experiment relative humidity and soil moisture did not show an obvious relationship with carabid numbers, the authors suggested that in sparse vegetation the soil

dries out faster which might cause the desiccation of larvae. Crist and Ahern (1999) also suspect the effect of vegetation structure on survival of carabid larvae through influencing microclimatic conditions.

Our egg-laying experiments in the laboratory were completed partially outside the main reproduction period of *P. melanarius*. According to Desender *et al.* (1985), the species will lay eggs for an elongated period in the laboratory if the temperature is sufficiently high and enough food is available. Males were used throughout the egg laying trials, as lack of males in other species prevented females to lay their eggs and even led to oosorption (e.g. Nelemans, 1987; Mols, 1993). A relatively high number of beetles per experimental unit was used to compensate for the possibly very high individual variation in egg production observed in the case of *P. melanarius* (Desender *et al.*, 1985; Wallin *et al.*, 1992) as well as other carabid species (e.g. van Dijk, 1983; Aukema, 1991; Nelemans, 1987; Zangger *et al.*, 1994; Symondson, 1994).

According to our results, the choice for oviposition sites by *P. melanarius* females is influenced by different abiotic factors, such as moisture levels of the substrate, light conditions and structural features. As these factors in a given microhabitat are defined by the plants, *P. melanarius* may be able to choose egg-laying sites according to the composition of the vegetation. Thus, when designing habitat management strategies for this species, and probably for other carabid beetles as well, one should consider the requirements of females for egg-laying sites.

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