

POPULATION ECOLOGY

Effects of Host Plant Phenology on Oviposition Preference of *Crocidolomia pavonana* (Lepidoptera: Pyralidae)REBECCA R. SMYTH,¹ MICHAEL P. HOFFMANN, AND ANTHONY M. SHELTON²

Department of Entomology, Cornell University, Ithaca, NY 14853

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ABSTRACT Field studies have demonstrated mixed success in trap cropping to manage *Crocidolomia pavonana* (= *binotalis*) [F.], a major pest of cruciferous crops in Asia. A possible explanation for this is an influence of host plant phenology on oviposition preference. We tested this in simultaneous two-choice oviposition bioassays under laboratory conditions. In cylindrical cardboard experimental arenas, with 5-cm² leaf windows, individual *C. pavonana* females were offered eight sequential phenological stages of cabbage (*Brassica oleracea* L., Capitata group, cultivar Gloria) with a constant stage of preflowering Indian mustard (*Brassica juncea*, variety *rugosa*, cultivar Green Wave). Results showed a significant effect of cabbage developmental stage on oviposition preference. We continued with two-choice bioassays, using whole leaves, in screen cage experimental arenas. Females were offered the three most preferred phenological stages of cabbage and differing stages of four potential trap crop alternatives: preflowering Indian mustard; preflowering Chinese cabbage (*B. rapa* L., variety *pekinensis* [Lour.] Olsson); preflowering, flowering, and “with silique” sawi manis (*B. rapa*, variety *parachinensis* [Bailey] Tsen and Lee); and preflowering and flowering sayur pahit (*B. rapa*, variety *parachinensis* [Bailey] Tsen and Lee). Results indicated that the phenological stages of both plants had a significant effect on relative oviposition preference. However, patterns of preference changed in the context of the different plant species combinations. In addition, implicit hierarchical preference order was frequently contradicted. These results have implications for the improvement of trap cropping strategies to manage *C. pavonana* and for the potential success of biological control of *Plutella xylostella* [L.], where these pests occur in complex.

KEY WORDS trap crop, host selection, cultural control, plant–herbivore interactions, reproductive behavior

PRIOR TO THE ADVENT OF synthetic insecticides, *Crocidolomia pavonana* (= *binotalis*) [F.] was considered the foremost insect pest of crucifers in the Old World (Gunn 1925, Sison 1927, Ankersmit 1953). Its distribution ranged from South, West, and East Africa and Madagascar, through most of India, to Southeast Asia, the southwest Pacific, Guam, and Queensland, Australia, as it does today (USDA 1968, CAB 1979). After widespread application of insecticides to manage this and other crucifer crop pests, *C. pavonana* appeared less important. Studies were devoted to insecticide effectiveness (Smith 1975, Krishnakumar et al. 1986), and attention shifted to another crucifer pest, the diamondback moth, *Plutella xylostella* [L.] (Lepidoptera: Yponomeutidae).

The diamondback moth has become recognized worldwide because of its expanding distribution and capacity to rapidly evolve resistance to insecticides (Sun 1992). Recently, in some highland tropical areas,

there have been successful introductions and establishment of *Diadegma semiclausum* [Hellén] (Hymenoptera: Chalcididae) (Sastrosiswojo and Sastrohardjo 1986, Talekar 1996), a larval parasitoid that can provide effective management of diamondback moth. However, the suspension of regular insecticide applications, essential for conservation of the parasitoid population, seems to have permitted the resurgence of *C. pavonana*. A management strategy is needed for *C. pavonana* that is compatible with biological control of diamondback moth.

In Indonesia, for example, cabbage is cultivated on >30,000 ha, primarily in the highland regions of North Sumatra and West Java, where most farms are between 0.25–0.5 ha in size. In areas of North Sumatra, management of *C. pavonana* currently involves ≈28 insecticide applications per crop (Schellhorn 1995). The need for improved pest management is critical.

Attention to the reduction of insecticide use has renewed interest in *C. pavonana* field biology and ecology (Sastrosiswojo and Setiawati 1992, Shirai and Nakamura 1995). Three to four days after eggs hatch, larvae bore toward the center of the cabbage head and

¹ E-mail: rrs7@cornell.edu.

² Department of Entomology, Cornell University, NYSAES, Geneva, NY 14856.

become concealed by webbing. A single larva is capable of ruining an entire cabbage plant by damaging its apical meristem (Peter et al. 1986), which either kills the plant or causes it to develop multiple small loose heads.

Although egg and larval parasitoids have been tested, parasitism rates have been low ($\leq 11\%$) (Nagarkatti and Jayanth 1982, reviewed in Waterhouse and Norris 1987, Sastrosiswojo and Setiawati 1992, Saucke et al. 2000). Alternatives, such as pheromone mating disruption or entomopathogenic fungi (Hashim and Ibrahim 1999), are less feasible where economic resources, refrigeration, or transportation are limited. These conditions are prevalent where cabbage is grown in the highland tropics of the Old World.

Another environmentally compatible approach that has been considered is trap cropping. Previous studies in India (Srinivasan and Krishna Moorthy 1991), Indonesia (Prabaningrum and Sastrosiswojo 1994, Schellhorn 1995), and Guam (Muniappan and Marutani 1992) have reported mixed success. Some of their results, along with field observations, suggest an effect of host plant phenology on patterns of *C. pavonana* oviposition. Verification of a peak in host acceptance determined by host plant phenology could narrow the critical period for *C. pavonana* management and could improve trap cropping strategies.

The objective of this work was to distinguish an influence of host plant phenology from seasonal patterns of *C. pavonana* oviposition and to evaluate this in the context of several potential trap crops for cabbage. Whereas this study was designed so that any promising results could be incorporated into field methods in North Sumatra, a broader goal was to provide insights for refining trap cropping strategies for other production systems as well.

Materials and Methods

Plant Culture and Cultivars. Plants were grown in a glasshouse in Ithaca, NY, under natural light in the summer months or under Lumalux high pressure sodium lamps and a 12:12 (L:D)-h photoperiod. Cabbage plants were grown in 25-cm-diameter pots in Premier Pro Mix BX (Premier Horticulture, Québec, Canada) potting soil. Chinese cabbage plants were grown in 20-cm-diameter pots. All other plants were grown in 15-cm-diameter pots. Pete's (Grace-Sierra Horticultural Products, Milpitas, CA) water soluble fertilizer (20N:10P₂O₅:20K₂O) was administered to the soil in the plant pots at a 1:15 concentration once each week.

Crucifer cultivars were chosen for the following reasons. *Brassica oleracea* L. variety *capitata* cultivar Gloria (Kays and Dias 1996) is a commercial head cabbage commonly grown in the two major cabbage growing regions of Indonesia and elsewhere in Asia. "Gloria," known in North America as "Greenboy," seed was obtained from Reed's Seeds (Cortland, NY). Indian mustard (*Brassica juncea* [L.] Czernj. and Coss variety *rugosa* Bailey) (Kays and Dias 1996) has been

used as a trap crop with some success in both India (Srinivasan and Krishna Moorthy 1991) and Indonesia (Sastrosiswojo and Setiawati 1992). Indian mustard, cultivar Green Wave (Johnny's Selected Seeds, Albion, ME) was used. Chinese cabbage (*B. rapa* L. variety *pekinensis* [Lour.] Olsson) (Kays and Dias 1996) is commonly grown in Southeast Asia, is a known host plant of *C. pavonana* (Lever 1946), and was suggested by Muniappan and Marutani (1992) and Silva-Krott et al. (1995) as a trap crop for cabbage in Guam. Chinese cabbage, cultivar Lettuce Type (Johnny's Selected Seeds) was used. Sawi manis and sayur pahit (both *B. rapa* variety *parachinensis* [Bailey] Tsen and Lee) (Kays and Dias 1996) are believed to be North Sumatran landraces. They are leafy greens that are commonly found in household gardens in the highlands. These were suggested by North Sumatran cabbage farmers in 1995. Identification and increases of the North Sumatran cultivars were made at the USDA-ARS Plant Genetic Resources Unit, Cornell University, Geneva, NY.

Older Chinese cabbage plants usually showed drying leaf tips. Therefore, older plants were not considered representative of field plants and were not tested in bioassays. Because of the problem of powdery mildew, *Erysiphe polygoni*, in the greenhouse, insufficient sayur pahit plants reached silique stage and insufficient Indian mustard reached flowering stage without infection to include those phenological categories in the bioassays.

Cabbage plants were categorized in phenological stages (stages 2–8) similar to those described by Andaloro et al. (1983). A "stage 3-plus" was added to more narrowly define the interval of highest oviposition by *C. pavonana*. As grown under the greenhouse conditions described above, the phenological stages of cabbage and the four alternate host plants are defined in Tables 1 and 2.

Colony Initiation and Rearing. One hundred fifty *C. pavonana* pupae survived transport from Bogor, West Java, to Ithaca, NY, in November 1995. The pupae were from a colony that had been collected in the Puncak region of West Java less than 3 mo earlier. A minimum population size of ≈ 300 adults was maintained at all times for the 17 mo duration of the colony.

Female *C. pavonana* frequently will oviposit on wax paper or other smooth substrates. To avoid reduction in ovipositional host discrimination over generations, eggs saved for continuation of the colony were not taken from holding cages but only from those cages in which moths had access to host plant leaves. Each day, larvae were fed a mixture of at least two types of fresh crucifer leaves: cabbage, mustard, Chinese cabbage, rapeseed (*B. napus* L. variety *napus*), sawi manis, or sayur pahit. Pupal sex was determined for pretreatment standardization of mating status. See Smyth (1999) for details of rearing and sex determination.

Because *C. pavonana* is not known to exist in the New World and is a serious pest of crops that are widely grown in the United States, all experiments and rearing took place inside an environmental growth chamber, located in the USDA-approved ARS quar-

Table 1. Description of cabbage phenological stages

Cabbage stage	Time from planting	No. of true leaves	Description
2	≈4 wk	≤5	
3	5–6 wk	6–8	
3-plus	≈6 1/2 wk	9–10	
4	7–8 wk	11–12	Base of the stem and bases of all leaves still visible from above
5	9–11 wk	13	Base of the stem and bases of all leaves no longer visible from above, innermost heart leaves growing upright, concealed by outer leaves, and not yet forming a firm center
6	≈12 wk	>13	Innermost heart leaves growing upright, concealed by outer leaves, and forming a firm center
7	14–17 wk	>13	Inner heart leaves forming a firm ball ≤10 cm in diameter
8	>18 wk	>13	Firm round head visible

Time periods represent ranges within which plants reached morphologically described stages.

antine facility at Cornell University. The walk-in chamber measured 2.36 by 1.75 m and was maintained at $27.8 \pm 1.4^\circ\text{C}$, $54.6 \pm 5.7\%$ RH. The chamber was equipped with full spectrum lighting set to a photoperiod of 14:10 (L:D) h, including a pattern of 3 h of low intensity, 8 h of high intensity, and 3 h of low intensity during light hours. In addition, 1 h each of subjective dawn and subjective dusk were simulated with a single 30-W incandescent bulb (cylindrical cardboard arenas) or six 15-W incandescent bulbs (wire mesh cage arenas), thus reducing the period of total darkness to 8 h.

Pretreatment Protocol. Every 24 h, newly eclosed pairs of randomly selected virgin moths were placed in mating cages (cylindrical 0.75-liter cardboard containers), and 48 h later, pairs were randomly allocated to experimental arenas. If eggs were laid or if either moth died or became impaired before transfer from the mating cage to the experimental arena, the pair was not used in the study.

Two-Choice Preference Assays. We used simultaneous two-choice trials to assess relative acceptability of potential host plants at defined phenological stages. Two types of experimental arena were used (described below). Moth pairs remained together throughout. Leaves were replaced every 24 h in the late afternoon. Oviposition occurred at night, usually within 3–5 d of eclosion. Replicates in which death or impairment of either moth occurred before oviposition were omitted. Days from eclosion to oviposition, approximate numbers of eggs, and location of egg

mass(es) were recorded. A minimum of 20 replicates were conducted for each trial.

Oviposition Preference Between Preflowering Indian Mustard and Eight Phenological Stages of Cabbage. Preliminary bioassays (Smyth 1999) determined that cylindrical 3.78-liter cardboard containers (larger than mating cages) could serve as adequate arenas for two-choice oviposition preference tests. These were 18 cm high by 17.5 cm in diameter, with two 5-cm² windows cut opposite one another midway up each side. Dental wick soaked in 20% honey/deionized water solution in a small petri dish half was taped to the center of the base of each cardboard cylinder. Wick moisture was replenished daily with deionized water. Cylinder lid rims held fiber glass screening over the tops. The insides of arenas were lined with waxed paper. Cardboard cylinders were randomly situated daily such that each had equal access to light and neither leaf within an arena was illuminated more than the other.

Leaves were placed over the square window with the abaxial surface facing inward. All cut edges were covered with masking tape to reduce desiccation. An advantage to this design was that moths had access to equal surface areas of both leaf types. Cabbage leaves were cut each day from ≥10 randomly selected plants of the appropriate phenological stage. Leaves from preflowering Indian mustard were cut from distinct plants for each replicate each day. If one or more egg masses were found on or within 4 cm of a leaf window, it was considered a positive oviposition response.

Oviposition Preference Between Phenological Stages of Four Potential Trap Crops and Cabbage Stages 4, 5, and 6. After evidence for an effect of cabbage plant phenology on oviposition preference, we changed experimental arenas to 30.5 by 30.5 by 30.5 cm BioQuip "collapsible cages," with aluminum frames and 16 by 18 mesh aluminum screening. These permitted use of whole leaves in somewhat more natural conditions and testing of alternate hosts with smaller or delicate leaves that would have dried overnight without water in the leaf window arena. Dental wick soaked in honey water solution was placed in a small petri dish half in the center of each cage. Leaf petioles

Table 2. Description of alternate host plant phenological stages

Host plant	Preflowering	Flowering (terminal bud visible)	With Siliques
Indian mustard	5–8.5 wk	NA	NA
Chinese cabbage	5–7 wk	NA	NA
Sawi manis	≈6 wk	6–8 wk	>8 wk
Sayur pahit	<7 wk	>7 wk	NA

Time periods represent ranges within which plants reached morphologically described stages.

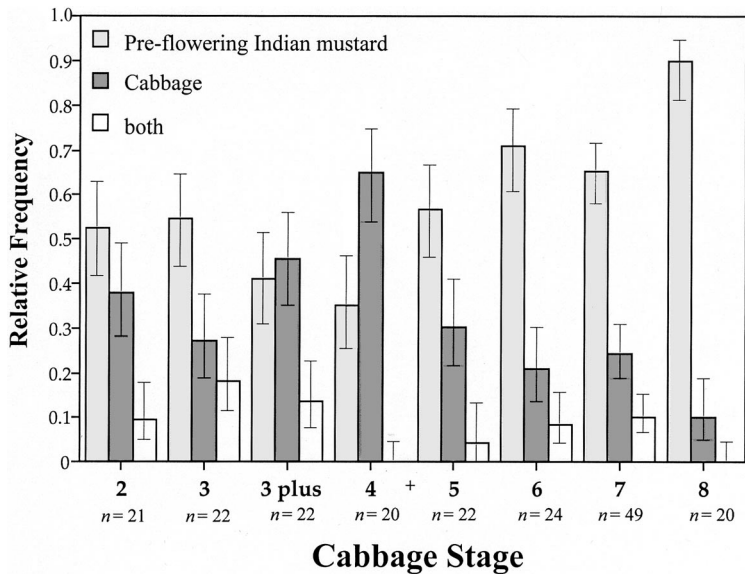


Fig. 1. Relative frequencies ($\pm 95\%$ confidence interval) of oviposition on eight phenological stages of cabbage, pre-flowering Indian mustard, or both in the paper can experimental arena. Significant differences between oviposition on cabbage and Indian mustard within trials are indicated by no overlap of confidence intervals. A significant difference ($P < 0.05$) in relative proportions of oviposition between sequential trials is indicated by +.

were placed in deionized water in Erlenmeyer flasks. Flask tops were covered with parafilm before petiole insertion to prevent moths from entering.

Given results from the leaf window bioassay, preliminary tests among cabbage stages (Smyth 1999), and field observations in 1995, we believed peak oviposition in the field to coincide with a time between the initiation of stage 4 and stage 6 in cabbage. We tested cabbage stages 4, 5, and 6 in combination with selected phenological stages of four additional host plants (Tables 1 and 2).

Leaves from cabbage and potential trap crop plants were matched as closely as possible with respect to surface area. Preliminary assays (Smyth 1999) determined that cabbage leaves 4–8 from the central growing heart were most preferred for oviposition by *C. pavonana*, and only these were used. Otherwise, cabbage leaf selection was as described for the leaf window bioassays. Alternate host leaves were cut from distinct plants for each replicate each day. Wilted leaves were replaced, and flasks were refilled with deionized water daily. Leaves were placed in diagonally opposed corners with adaxial surfaces facing the center of the cage. Cages were arranged on growth chamber shelves so that leaves alternated consistently and different plant types were not adjacent to each other.

Statistical Analyses. Because egg and egg mass number may vary between individual moths for factors not controlled in these experiments, neither was considered an appropriate sample unit. Observations were defined in terms of the location of the first egg masses laid in one night by individual moths, regardless of egg or egg mass number or days to oviposition. Although oviposition responses were recorded in four categories,

host plant A, host plant B, both, or other (e.g., on the petri dish or far from a leaf window), only the first three categories were analyzed statistically. This is because “other” was thought to be a construct of the experimental arenas, lacking biological significance. Responses in the category of “other” were rare ($\approx 0.01\%$) in the course of these experiments. Also, it is not known with what frequency *C. pavonana* would oviposit on “both” host plants in the field. If the survival of a single egg to third instar larva can ruin an entire cabbage plant, it may be argued that responses of “both” should be considered as damaging to the main crop as “cabbage only” responses. With this simplification, we would, however, lose information. The most objective treatment of “both” was to consider that response statistically independent. As expected, higher proportions of “both” responses generally occurred when preference was less distinct.

There are at least four questions of interest regarding these data. One is the effect of host plant phenological stage on oviposition preference. This was addressed by χ^2 analyses of the equality of proportions among all response categories in grouped trials (StatXact 1989). Series of trials involving multiple phenological stages of cabbage and constant stages of alternate hosts, e.g., cabbage stages 4, 5, and 6 versus flowering sayur pahit, were grouped and analyzed together. Series of sequential stages of alternate hosts with a constant cabbage stage, e.g., preflowering, flowering, and sawi manis with silique versus cabbage stage 4, also were grouped together. In addition, all three stages of cabbage versus all stages of sayur pahit and versus all stages of sawi manis were grouped and compared by χ^2 .

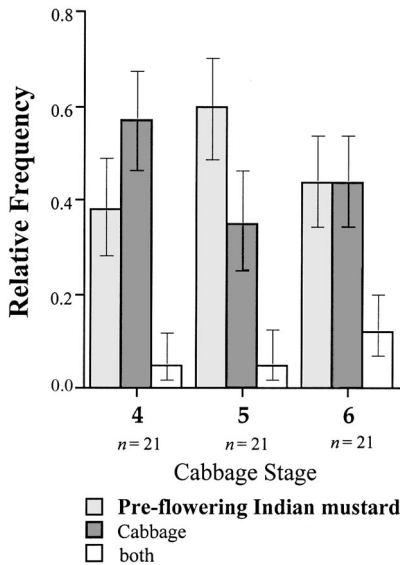


Fig. 2. Relative frequencies ($\pm 95\%$ confidence interval) of oviposition on phenological stages 4, 5, and 6 of cabbage, preflowering Indian mustard, or both, from two-choice tests in the screen cage experimental arena. Significant differences between oviposition on cabbage and Indian mustard within trials are indicated by no overlap of confidence intervals.

We examined the relative degree of change in host plant acceptance between phenological stages. Proportions of oviposition between pairs of sequential trials within a combined group were compared by χ^2 .

A third question is the within-trial difference between oviposition on cabbage and an alternate host at a particular phenological stage of each. This analysis was made by comparisons among asymptotic confidence intervals around within-trial proportions from multinomial distributions (StatXact 1989). Results are considered statistically significant when confidence intervals do not overlap.

Fourth, we considered whether preferences shown in series of two-choice assays can reflect hierarchical preference among more than two plant categories. For examination of preference hierarchy, within-trial comparisons also were made for each alternate host plant versus preflowering Indian mustard and preflowering sayur pahit versus flowering sawi manis.

Results

Oviposition Preference Between Preflowering Indian Mustard and Eight Phenological Stages of Cabbage. Developmental stage of cabbage significantly affected the probability of oviposition on cabbage when presented with preflowering Indian mustard ($\chi^2 = 27.50$; $df = 14$; $P = 0.017$). Differences between consecutive trials were significant only for stage 4 (cabbage preferred) and stage 5 (mustard preferred; $\chi^2 = 6.034$; $df = 2$; $P = 0.049$). Significant within-trial differences between choice of mustard or cabbage were found at stages 3 and 4–8 (Fig. 1). Of these, stage

4 was the only cabbage stage preferred over mustard. Between-trial differences between preflowering Indian mustard versus stage 4 cabbage, and compared with all other cabbage stage trials except 2 and 3-plus, were significant ($P \leq 0.02$).

Oviposition Preference Between Phenological Stages of Four Potential Trap Crops and Cabbage Stages 4, 5, and 6. Relative preference was significantly affected by phenological stage of cabbage (stages 4, 5, and 6 grouped) when presented with preflowering sayur pahit ($\chi^2 = 10.200$; $df = 4$; $P = 0.037$) and between cabbage stages 4 and 5 when presented with preflowering sayur pahit ($\chi^2 = 7.722$; $df = 2$; $P = 0.021$). Relative preference was marginally affected by stage of sayur pahit (preflowering and flowering) when presented with cabbage stage 4 ($\chi^2 = 4.863$; $df = 2$; $P = 0.088$).

Relative preference was marginally affected by phenological stage of sawi manis (preflowering, flowering, and with silique) when presented with cabbage stage 5 ($\chi^2 = 8.430$; $df = 4$; $P = 0.077$). Phenological stage of cabbage did not affect overall relative preference of any constant stage of sawi manis presented with cabbage, although changes in proportions were found between trials of flowering versus sawi manis with silique presented with stage 4 cabbage ($\chi^2 = 7.333$; $df = 2$; $P = 0.026$) and stage 5 cabbage ($\chi^2 = 7.494$; $df = 2$; $P = 0.024$). This was also seen between sawi manis w/ silique and stage 4 versus stage 5 cabbage ($\chi^2 = 5.961$; $df = 2$; $P = 0.051$) and stage 5 versus stage 6 cabbage ($\chi^2 = 6.488$; $df = 2$; $P = 0.039$). Relative proportions of oviposition on either preflowering Indian mustard or Chinese cabbage were not affected by phenological stages of cabbage.

In addition, significant changes in relative preference were found among all three stages of sawi manis together with cabbage stages 4, 5, and 6 ($\chi^2 = 26.40$; $df = 16$; $P = 0.048$). Relative proportions among all six trials between stages of sayur pahit and cabbage did not differ significantly.

Patterns of preference between cabbage and the alternate hosts varied. For example, cabbage stage 4 was the most preferred, and stage 5 was least preferred when presented in combination with Indian mustard (Fig. 2). Cabbage stage 5, however, was the most preferred when presented with both preflowering and flowering sayur pahit (Fig. 3). This pattern was consistent for sawi manis with silique as well, but not for other phenological stages of sawi manis (Fig. 4). Cabbage stage 6 was the most preferred cabbage stage when presented with flowering sawi manis but not when presented with preflowering or sawi manis with silique. Chinese cabbage was consistently chosen over head cabbage, and no significant differences were found between consecutive phenological stages of cabbage (Fig. 5).

Within-Trial Differences. Stage 5 cabbage was significantly preferred over preflowering sayur pahit, and both stages 4 and 5 cabbage were significantly preferred over flowering sayur pahit (Fig. 3). All three stages of cabbage were significantly preferred over

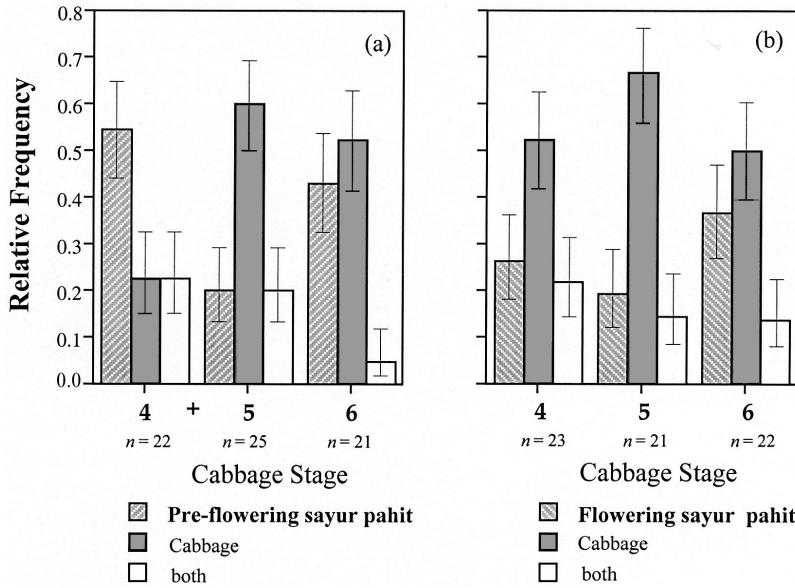


Fig. 3. Relative frequencies ($\pm 95\%$ confidence interval) of oviposition between (A) preflowering and (B) flowering sayur pahit and stages 4, 5, and 6 of cabbage, from two-choice tests in the screen cage experimental arena. Significant differences between oviposition on cabbage and sayur pahit within trials are indicated by no overlap of confidence intervals. A significant difference ($P < 0.05$) in relative proportions of oviposition between sequential trials is indicated by +.

sawi manis with silique, but none were preferred over other stages of sawi manis (Fig. 4).

Preflowering sayur pahit was significantly preferred over stage 4 cabbage (Fig. 3). Preflowering Indian mustard was significantly preferred over stage 5 cabbage (Fig. 2). Chinese cabbage was significantly preferred over stages 4 and 5 cabbage (Fig. 5).

Stage 4 cabbage was significantly preferred over stage 5 cabbage, and preflowering sayur pahit and flowering sawi manis were significantly preferred over

Indian mustard (determined by asymptotic confidence intervals, data not shown).

Discussion

By conducting these experiments in controlled environmental factors of light, humidity, and temperature, and with standardized physiological conditions of moth age, mating status, and previous host plant experience, we could distinguish differences in rela-

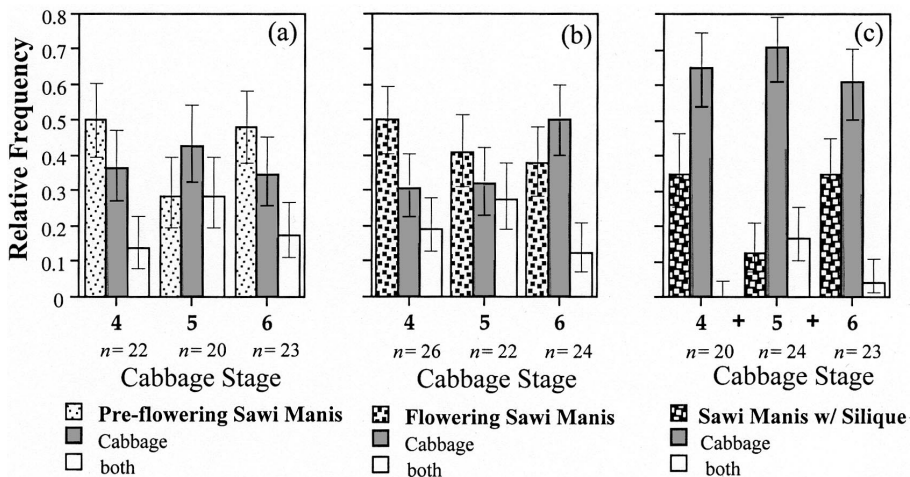


Fig. 4. Relative frequencies ($\pm 95\%$ confidence interval) of oviposition between (A) preflowering, (B) flowering, and (C) sawi manis with silique, and stages 4, 5, and 6 of cabbage, from two-choice tests in the screen cage experimental arena. Significant differences between oviposition on cabbage and sawi manis within trials are indicated by no overlap of confidence intervals. Significant differences ($P < 0.05$) in relative proportions of oviposition between sequential trials are indicated by +.

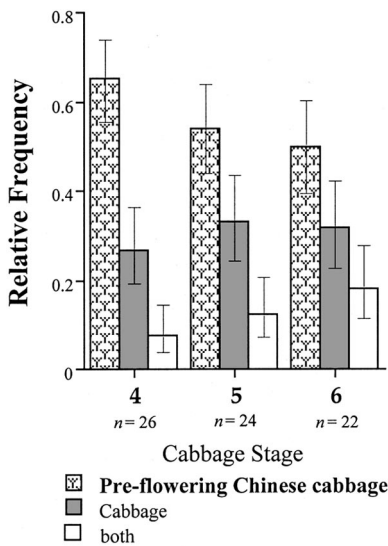


Fig. 5. Relative frequencies ($\pm 95\%$ confidence interval) of oviposition on phenological stages 4, 5, and 6 of cabbage, Chinese cabbage, or both, from two-choice tests in the screen cage experimental arena. Significant differences between oviposition on cabbage and Indian mustard within trials are indicated by no overlap of confidence intervals.

tive oviposition preference caused by host plant phenology without confounding seasonal and environmental influences. Peaks in oviposition on cabbage have been observed in the field, both in monocropped plantings and in combination with trap crops. Timing of these peaks ranged from 8 to 9 wk (Schellhorn 1995), 10 to 12 wk (Sastrosiswojo and Setiawati 1992), and 12 wk (Sudarwohadi 1975, Prabaningrum and Sastrosiswojo 1994) after sowing. Our data suggest that *C. pavonana* oviposition peaks in the field are correlated with host plant phenology. Given differences between laboratory and field environments, we cannot be certain with which cabbage stage oviposition peaks normally correspond.

In two-choice trials between consecutive phenological stages of cabbage and a constant preflowering stage of Indian mustard, in both the leaf window bioassay and the whole leaf bioassay, stage 4 cabbage was the only cabbage stage preferred over Indian mustard. It is interesting that what was defined as cabbage stage 4 lasted, on average, only 6 d for a given plant, while later cabbage stages lasted 2 wk or more. Stage 6 cabbage, however, was significantly less preferred than Indian mustard in the leaf window bioassay, but equally preferred in the whole leaf bioassay. The use of whole leaves, water-fed leaves, and attention to use of only the most preferred leaves from each cabbage head could account for differences in results from the two experimental designs.

As comparisons with other alternate host plants demonstrated, cabbage stage 4 is not invariably the most preferred stage of cabbage. None of the other three alternate host plants elicited the same pattern of response when tested against cabbage stages 4, 5, and

6. That oviposition peaks in field populations of *C. pavonana* may be correlated with stage 5 rather than stage 4 cabbage is not so consequential as is the dependence of patterns of preference on the combination of host plant species presented. Our results show that relative oviposition preference for *C. pavonana* females is contextual. The response to cabbage at a particular phenological stage is altered by the identity of the other host plant in the experimental arena and vice versa. This aspect of these results has implications for both trap cropping strategy and interpretations of insect sensory physiology. Various hypotheses of sensory integration with respect to host finding and host acceptance in insects have been studied and debated (e.g., Dethier 1971, Miller and Harris 1985, Städler 1984). Contextual results suggest that perception of both leaves (simultaneously or sequentially) influence host choice as opposed to simple host acceptance (Singer 1986).

We also note that expectations of hierarchical preference were frequently contradicted. Ordered sequences, where say A is preferred to B, and B is preferred to C, predict that A should be preferred over C, but this was not always borne out in sets of paired comparisons. For example, stage 4 cabbage was preferred over stage 5 cabbage (52 versus 26%, Smyth 1999), and stage 5 cabbage was preferred over preflowering sayur pahit (Fig. 3), but preflowering sayur pahit was preferred over stage 4 cabbage. Similarly, Indian mustard was preferred over stage 5 cabbage (Fig. 2), and stage 5 cabbage was preferred over preflowering sayur pahit (Fig. 3), but preflowering sayur pahit was preferred over Indian mustard (60 versus 25%).

Rejection of the assumption of hierarchical host plant preference on the part of *C. pavonana* raises the question of oviposition behavior in the setting of a relatively complex field. Among many factors, novel results could emerge because of varying host plant combinations. Although in our experiments, small cage size, multidirectional air currents, or crowding may have limited the range of host finding modalities normally employed by *C. pavonana* in nature, our data are consistent with results from several trap cropping field studies (Srinivasan and Krishna Moorthy 1991, Muniappan and Marutani 1992, Silva-Krott et al. 1995). These studies report *C. pavonana* oviposition on cabbage during only a short portion of the season when planted with a mustard trap crop, or directed entirely away from cabbage in the presence of alternate host plants, such as Chinese cabbage.

Our experiments were designed to evaluate preference around the time of highest oviposition by *C. pavonana* on cabbage, and trap cropping strategies may also be designed to protect cabbage plant primordia for this shorter period of time during the growing season. Although caution must be used in extrapolating laboratory results to the field, several approaches are suggested. Using as an example the plants that we tested, preference for sayur pahit was pronounced but brief, only occurring for the coincidence of stage 4 cabbage and the preflowering stage

of sayur pahit. Plants like Chinese cabbage were preferred over stages 4 and 5 cabbage. Perhaps Chinese cabbage and sayur pahit could be planted so as to synchronize preflowering stages with stage 4 cabbage. Preflowering Indian mustard was consistently preferred over stage 5 cabbage. The preflowering stages of Indian mustard and Chinese cabbage last a relatively long time. It would be possible to plant these to coincide with stage 5 cabbage, which lasts approximately 2 wk. In our study, preflowering sawi manis and Chinese cabbage tended to be preferred over stage 6 cabbage, although the differences were not significant. Alternate hosts like these might function simultaneously for protection of cabbage stage 6.

Because periods of highest preference of all of the host plants tested are ephemeral, trap crops would best be planted sequentially. In this way, highly attractive trap crops are more likely to be present throughout the time of highest cabbage susceptibility.

An additional aspect of alternate host plants like those we studied is their leafy, open plant structure. If oviposition were drawn away from cabbage to these alternate hosts, *C. pavonana* egg masses and larvae would be substantially more visible. Farmers would be able to find and eliminate them regularly. Although strategies such as this may at first sound complex, they could be feasible under circumstances like those in North Sumatra. Climatic conditions are consistent enough that plant development can be accurately predicted. Farmers focus attention on few crops and small land holdings, and they cultivate largely by hand.

Subtropical highland cabbage growers like those in North Sumatra face constant crop loss from *P. xylostella* and/or *C. pavonana*. Inasmuch as a combination of strategies that reduce losses caused by *C. pavonana* can be accomplished without interfering with the natural enemies that remedy *P. xylostella*, notable improvement will be made in the simultaneous management of both pests. Moreover, the advantages of reduced dependence on transportation and expense of pesticides, reduced residues on crops, and fewer health risks could be substantial. Further analyses of plant qualities that influence *C. pavonana* oviposition behavior could provide valuable insight for plant breeding strategies to reduce oviposition on cabbage.

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