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Can larvae of the pod-borer, *Helicoverpa armigera* (Lepidoptera: Noctuidae), select between wild and cultivated pigeonpea *Cajanus* sp. (Fabaceae)?

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Abstract

Experiments were conducted to observe the feeding and food selection-behaviour of different instars of the pod-borer *Helicoverpa armigera* (Hübner) in response to choices between the cultivated and a wild species of *Cajanus*. First and second instars fed upon a cultivated variety of *Cajanus cajan* in preference to a wild species, *C. scarabaeoides* and on flowers of *C. cajan*, rather than pods or leaves of *C. cajan*. First and second instars preferred pods of *C. scarabaeoides* with trichomes removed to pods with trichomes present. All instars fed upon pods of *C. cajan* rather than those of *C. scarabaeoides*. Solvent extraction of the pod surfaces affected the feeding of larvae, in some instances. They preferred the unextracted pods of *C. cajan*; the extracted pod of *C. scarabaeoides* (first and second instars) or the unextracted pod of *C. scarabaeoides* (fourth and fifth instars). Glass-fibre disc bioassays showed that the methanol, hexane and water extracts from the pod-surface of *C. cajan* stimulated the feeding of fifth instars. The experiments have shown that characteristics of *C. cajan*, such as either the compounds present or the type and distribution of trichomes on the plant surfaces, can determine the susceptibility of *C. cajan* to pod-borer larvae.

Introduction

Cajanus cajan (Fabaceae), pigeonpea, is a grain legume that provides a significant proportion of the daily protein requirements of people living in the semi-arid tropics (Nene *et al*., 1990). The majority of pigeonpea production (up to 80% of the total) is centred in India although it is also cultivated less intensively throughout Africa and in Latin America (Nene *et al*., 1990). It is grown on relatively poor soils and has the potential to provide up to three crops per year (Ranga Rao & Shanower, 1999). Insects are the major constraint to its production with more than 200 species known to feed upon the plant (Shanower *et al*., 1999). Financial losses have been estimated to be in excess of $520 million per annum (ICRISAT, 1992). One of the most significant pests of pigeonpea is *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae). Larvae of this moth feed primarily on flowers and pods (Shanower *et al*., 1999). Shanower *et al*. (1997) showed that larvae fed on pods of a *C. cajan* cultivar in a no-choice experiment consumed more food, gained weight more quickly, developed into larger adults and suffered lower mortality than those fed on pods of the wild genotype, *Cajanus scarabaeoides* (Fabaceae). Furthermore, Peter & Shanower (1996) found that the pod

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walls of *C. scarabaeoides* were more resistant to abrasion than pods of *C. cajan* and therefore prevented ingress of *H. armigera* larvae into the pods. These data indicate that *C. scarabaeoides* possesses characters that might make it resistant to predation by larvae of *H. armigera*.

The experiments presented below investigated the food-selection of larvae of *H. armigera* in response to cultivated *C. cajan* and wild *C. scarabaeoides*. The response of larvae of different ages to choices between the two species of *Cajanus* or between different plant structures was investigated. In addition, the effects of pod-surface chemicals and trichomes were investigated in binary choice experiments using pods of *C. cajan* and *C. scarabaeoides*. To establish the effects of compounds from the pod surfaces of *C. cajan* on the selection-behaviour of larvae of *H. armigera*, fifth instars were presented with extracts of the pod surface in a glass-fibre disc bioassay. The results are discussed in relation to the factors that make *C. cajan* susceptible to pod-borer and how these can be used for breeding less susceptible hybrids.

Materials and methods

Bioassays using plant material

Plant-choice experiments

The aim of this experiment was to observe the preference of first and second instars when presented with a choice between cuttings of a wild species *C. scarabaeoides*, (International Crop Research Institute for the Semi-Arid Tropics (ICRISAT) accession = ICPW 83) and a cultivar of *C. cajan* (ICRISAT accession = ICPL 87). Plant cuttings of similar size (approximately 30 cm long) and free from insect eggs and larvae, that had both pods and flowers present, were taken from plants of cv. ICPL 87 and cv. ICPW 83 growing in unsprayed field plots at ICRISAT, Patancheru, Andhra Pradesh, India. One cutting of cv. ICPL 87 and one of cv. ICPW 83 were placed into a 500 ml conical flask so that the cut end of the stem dipped into a 0.05 M sucrose solution (250 ml) to increase the longevity of the cuttings. The flask was placed within a circular wire frame (30 cm diameter, 60 cm high) and a plastic Petri dish containing 30 first and second instars was held within the cage and inverted over the plants so that larvae could abseil onto the plants. A netting sleeve was tied around the neck of the flask to enclose the frame and plants. This process was repeated until five replicates of 30 larvae had been prepared. Plants were kept in a growth chamber that was maintained at 12 h/27°C (light): 12 h/20°C (dark).

The distribution of larvae between plants and among plant parts was used as a measure of the preference of larvae. After five days the cuttings were thoroughly examined and the numbers of larvae on each plant and each plant part were recorded. The numbers of surviving larvae upon different plants and different structures were analysed with the χ^2 test, with equal distribution of larvae between the plants or among the plant parts as the expected values.

Detached plant part choice experiments

The aim of this experiment was to investigate the preference shown by different instars of *H. armigera* when presented with pods, flowers and leaves from ICPL 87. The distribution of first and second instars among pods, flowers and leaves was used to indicate the preferred plant part. Later instars tend to predate upon their conspecifics when in groups, so third to fifth instars were kept isolated during the experiments presented below. In these experiments, preference for plant parts was measured by recording the proportion of seeds eaten or the numbers of larvae consuming both the corolla and reproductive structures of flowers, termed 'whole flowers'. The calyx was excluded from this measurement as preliminary experiments indicated that very few of the insects attempted to feed on this structure. Branches removed from cv. ICPL 87 were examined to ensure that no eggs or larvae were present and divided into pods, flowers and leaves. Pods were taken from the tip of the branch. Newly opened flowers were taken from the apices of the plant and young leaves were removed from the first group below the inflorescence. Different instars of *H. armigera* were selected from a colony maintained on an artificial diet (Armes *et al*., 1992) at ICRISAT. First and second instar *H. armigera* or larvae 24–36 h since moulting into either the third, fourth or fifth instar were selected from the colony. A flower, a leaf and a pod were placed into a plastic Petri dish (9 cm diameter), on top of dampened filter paper and a mixture of first and second instar *H. armigera* (n = 10) were transferred to the centre of the dish using a paint-brush. Each dish was then sealed with its lid. This was repeated, with one larva per Petri dish, for third (n = 44), fourth (n = 30) and fifth instars (n = 20).

After 24 and 48 h the numbers of first and second instars on (or in) each plant part were recorded. For the third, fourth and fifth instars, the percentage of seeds eaten, as a proportion of those present in each pod and the numbers of larvae consuming whole flowers were recorded after 24 h. The distribution of first and second instars among the pod, flower or leaf was analysed (χ^2 test) with equal distribution among the three structures as the expected value. The proportion of seeds eaten by third, fourth and fifth instars was compared among instars with the Kruskal-Wallis test and between instars using the Mann-Whitney test (Siegel & Castellan, 1988).

Effects of extracts and trichomes from the surface of pods on the selection behaviour of H. armigera *larvae*

Preparation of extracts

The method used for the extraction of pod surface compounds was a modified version of that used by Shanower *et al*. (1997). Pod surface areas were measured using an area meter (LI-3000, LI-COR, Lincoln, Nebraska, USA) prior to extraction. Extracts of the pod surfaces of cv. ICPL 87 and cv. ICPW 83 were prepared by placing pods of a known surface area into 500 ml of either hexane, methanol (Analar® grade (Fisher Chemicals, Loughborough, UK)) or double-distilled water and stirring for 120 s with a glass rod. Each extract was then filtered using Whatman® No. 1 filter paper before being evaporated to dryness under vacuum. Extracts of cv. ICPL 87 were presented to larvae in the glass-fibre disc bioassay described below. Extracted pods were left in a fume cupboard for 2 h to allow any remaining solvent to evaporate.

Pod-choice experiments

Larvae of different ages were presented with a choice between pods of cv. ICPL 87 and cv. ICPW 83 to observe whether *H. armigera* larvae can select between pods of wild and cultivated species of *Cajanus*. One pod from cv. ICPL 87 and one pod from cv. ICPW 83, each containing five seeds, were placed into Petri dishes (n = 10) with 30, first and second instar *H. armigera*. The surface of pods of cv. ICPW 83 possess a dense covering of non-glandular trichomes, which occur rarely on the pod surfaces of cv. ICPL 87 (Romeis *et al*., 1999). The influence of pod trichomes on the selection behaviour of *H. armigera* larvae was investigated by presenting larvae with a choice between a pod from either cv. ICPL 87 or cv. ICPW 83 and a pod from cv. ICPW 83 from which pod surface trichomes had been removed. Pods were carefully shaved with a razor blade until no more non-glandular trichomes remained. Pods were inspected with a hand lens (× 10 magnification) following shaving and any pods that still had intact trichomes or that were cut or split, were discarded. The effects of compounds present on the pod surface on the preference shown by larvae were investigated by presenting larvae with choices between pods that had been surface-extracted in either hexane, methanol or water and unextracted pods. Solvents of different polarity were used to ensure that the maximum range of compounds were extracted from the pod surface. Groups (n = 10) of first and second instars (n = 30) were presented with each of the choices shown in table 1. This was repeated for individual third, fourth and fifth instars (n = 20), with the exception of choices 1, 2, 4, 5 and 6 (table 2) where ten replicates of fifth instars were tested. Larvae were aged and selected as described previously. Dampened filter paper was placed under the lid of each Petri dish to maintain the humidity.

After 24 h the distribution of first and second instars and the percentage of seeds consumed by third, fourth and fifth instars was recorded. The Wilcoxon Signed Rank test (Sokal & Rohlf, 1987) was used to compare the numbers of first and second instars on the different pods and the percentages of seeds eaten in each dish by third, fourth and fifth instars. Larvae (third, fourth and fifth instars) that had not consumed seed material were classed as not having taken part in the experiment and were excluded from this analysis.

Bioassay of pod-surface extracts from C. cajan *(ICPL 87) using glass-fibre discs*

Extracts of the pod surfaces of cv. ICPL 87 (prepared as described above) were redissolved in either hexane, methanol or water so that 100 μl of solution contained a quantity of extract equivalent to 3.46 cm^2 of pod surface: the area of a 2.1 cm (diameter) glass-fibre disc. This ensured that larvae were presented with a naturally occurring concentration of extract. Aliquots (100 μl) of the hexane extract were then pipetted onto individual glass-fibre discs (n = 15 for each extract) and the discs were left to air-dry for 24 h. Subsequently, each dry disc was weighed and placed into separate plastic Petri dishes (9 cm diameter) with a pre-weighed, untreated disc. Both discs were dampened with 100 μl of distilled water prior to the start of the bioassay, as previous observations showed that *H. armigera* larvae were less likely to feed upon dry discs. Furthermore, to decrease variability in their selection behaviour during the experiment *H. armigera* larvae that were 24–36 h into the fifth stadium were selected and deprived of food for 2 h prior to the bioassay (Simmonds *et al*., 1990). One larva of known age was placed into each Petri dish. All dishes were then moved into a growth-chamber maintained at 12 h/27°C (light): 12 h/20°C (dark).

Table 1. Choices of pod treatment presented to groups (first and second instar) or single third to fifth instar larvae of *Helicoverpa armigera*.

Choice number	Choice of pods presented to larvae	
1	ICPL 87	ICPW 83
2	ICPL 87	ICPW 83, shaved
3	ICPW 83	ICPW 83, shaved
4	ICPL 87	ICPL 87, extracted in hexane
5	ICPL 87	ICPL 87, extracted in methanol
6	ICPL 87	ICPL 87, extracted in water
7	ICPW 83	ICPW 83, extracted in hexane
8	ICPW 83	ICPW 83, extracted in methanol
9	ICPW 83	ICPW 83, extracted in water

ICPL 87, *Cajanus cajan*; ICPW 83, *C. scarabaeoides*. Some pods from ICPW 83 were shaved with a razor-blade to remove trichomes from the pod-surfaces. Pods were extracted in 500 ml of solvent, for 120 s, before being dried in a fume cupboard.

After 24 h the larvae were removed from the Petri dishes, and the glass-fibre discs dried and re-weighed. Only those larvae that had consumed > 1 mg of either the treated or control disc after 24 h were classed as having taken part in the experiment. Data for larvae that had taken part were used to calculate a feeding index: $FI = [(C - T)/(C + T)] \times 100$, where C and T are the amounts of the control and treated disc eaten, respectively (Simmonds *et al*., 1990). Feeding indices range from − 100 to +100. A stimulatory extract would be indicated by an FI of < 0 to − 100, whilst an FI of > 0 to 100 indicates that the extract does not stimulate feeding. The feeding indices between extracts were compared using the Mann-Whitney test. The amounts of control and treated discs eaten within a treatment were compared with the Wilcoxon Signed Ranks test.

Results

Bioassays using plant material

Plant choice experiments using first and second instar H. armigera

After five days all the surviving larvae (36 ± 3.4%) had congregated on cv. ICPL 87. The larvae were not evenly distributed among pods, flowers and leaves of cv. ICPL 87 (χ^2, $P < 0.01$). The majority of the surviving larvae (87 ± 4.1%) were recorded on the flowers, compared to 13 ± 4% on the pods, with no larvae on the leaves. In most instances, the larvae had burrowed through the petals into the centre of the flowers, evidenced by clearly visible holes in the petals.

Detached plant-part choice experiments

Young larvae (first and second instars) were not evenly distributed among the pods, flowers and leaves (χ^2, $P < 0.01$). The majority of first and second instars were found on or in the flowers of cv. ICPL 87 although some were found on the pods (fig. 1). There were no differences, among third, fourth and fifth instars, in the numbers of larvae consuming whole flowers (Kruskal-Wallis, $P > 0.05$). However, the amount of seed material consumed increased from the third to fifth instar (Mann-Whitney, $P < 0.01$) (fig. 2).

Table 2. Summary of the pods on which the majority of *Helicoverpa armigera* larvae of different ages congregated (first and second instars) or fed in significant numbers (third, fourth and fifth instars) when provided with a binary choice between pods of cv. ICPL 87 (*Cajanus cajan*) and/or ICPW 83 (*C. scarabaeoides*).

Pod-choice	Instar			
	First and second	Third	Fourth	Fifth
ICPL 87 vs. ICPW 83 (shaved)	ICPL 87	ICPL 87	ICPL 87	ICPL 87
ICPL 87 vs. ICPW 83 (shaved)	ICPW 83 (shaved)	=	=	=
ICPL 87 vs. ICPW 83	ICPL 87	ICPL 87	ICPL 87	ICPL 87
ICPL 87 vs. ICPL 87 (extracted in hexane)	=	ICPL 87	=	=
ICPL 87 vs. ICPL 87 (extracted in methanol)	=	ICPL 87	ICPL 87	=
ICPL 87 vs. ICPL 87 (extracted in water)	=	ICPL 87	=	=
ICPW 83 vs. ICPW 83 (extracted in hexane)	ICPW 83 extracted in hexane	=	=	ICPW 83 extracted in hexane
ICPW 83 vs. ICPW 83 (extracted in methanol)	ICPW 83 extracted in methanol	=	ICPW 83	=
ICPW 83 vs ICPW 83 (extracted in water)	=	=	=	=

=, no difference between the numbers of larvae on each pod or between the amount of seed consumed.

Effects of pod-surface chemistry and morphology on the behaviour of H. armigera *larvae*

Pod-choice experiments

Significantly more larvae were found on pods of cv. ICPL 87 than either cv. ICPW 83 or cv. ICPW 83 with pod-surface trichomes removed (cv. ICPW 83 shaved) (Wilcoxon Signed Rank, $P < 0.001$) (fig. 3). However, there were more larvae found on cv. ICPW 83 pods with surface trichomes removed than on the intact cv. ICPW 83 pods (Wilcoxon Signed Rank, $P < 0.05$) (fig. 3). Removal of the trichomes from pods of cv. ICPW 83 did not alter the preference of larvae for cv. ICPL 87. In contrast, first and second instars congregated on the pods of cv. ICPW 83 with trichomes removed rather than on the intact pods. More first and second instars were found on pods of cv. ICPW 83 extracted with either hexane or methanol than were found on unextracted pods (Wilcoxon Signed Rank, $P < 0.001$) (fig. 3). None of the first and second instars presented with a choice between pods of cv. ICPW 83 and cv. ICPW 83 (extracted in water) moved onto the pods.

These data indicate that the compounds extracted from cv. ICPW 83 into hexane and methanol are important in deterring larvae from feeding on pods of cv. ICPW 83. In contrast, there was no difference in the numbers of larvae found on cv. ICPL 87 pods and cv. ICPL 87 pods that had been extracted in either hexane, methanol or water (Wilcoxon Signed Rank, $P > 0.05$). A greater proportion of the seeds of cv. ICPL 87 was consumed by third, fourth and fifth instars than of either cv. ICPW 83 or of cv. ICPW 83 with pod surface trichomes removed (Wilcoxon Signed Rank, $P < 0.001$) (fig. 4.). Also, third instars consumed more whole seeds from cv. ICPL 87 than from cv. ICPL 87 pods that had been extracted in either hexane, methanol or water (Wilcoxon Signed Rank, $P < 0.001$) (fig. 4b). This indicates that compounds that stimulate the feeding of third instar *H. armigera* on cv. ICPL 87 are removed from the pod surfaces following extraction with hexane, methanol or water. In addition, a greater proportion of seeds from the unextracted pods of cv. ICPW 83 and cv. ICPL 87 were eaten by fourth instars (Wilcoxon Signed Rank, $P < 0.001$) (fig. 4b). More seeds of cv. ICPW 83 were consumed by fifth instars than those of cv. ICPW 83 pods extracted in hexane (Wilcoxon Signed Rank, $P < 0.001$) (fig. 4c). There were no other differences in the proportion of seeds consumed by third, fourth or fifth instars. Overall, the numbers of third, fourth and fifth instars feeding were reduced if both the choices were pods from cv. ICPW 83 (fig. 5). This indicates that in the absence of choice, larvae preferred not to feed on cv. ICPW 83.

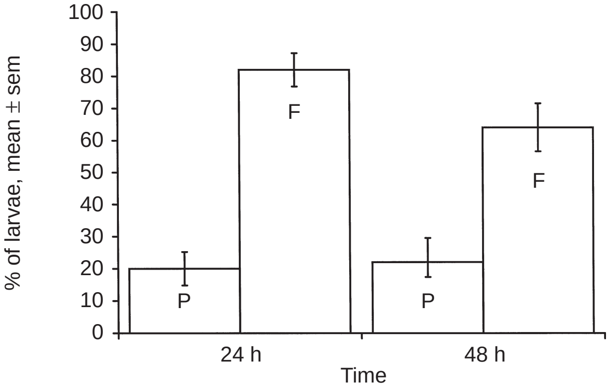

Fig. 1. Distribution (mean ± sem) of first and second instar *Helicoverpa armigera* recorded on pods and flowers of *Cajanus cajan* in a three-way choice bioassay after 24 and 48 h. P, pod; F, flower.

Bioassay of pod-surface extracts from C. cajan *using glass-fibre discs*

Each of the three extracts from the pod surface of *C. cajan* (cv. ICPL 87) stimulated the feeding of fifth instar *H. armigera*

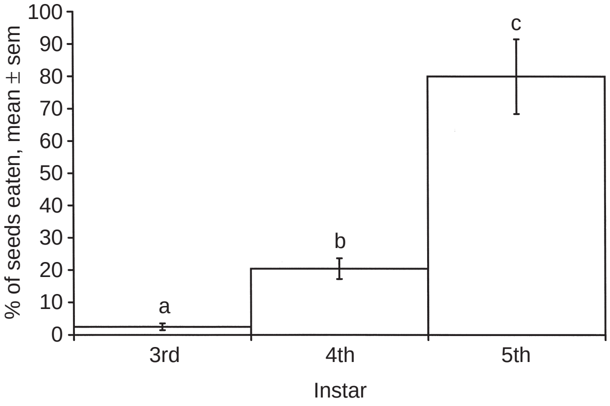

Fig. 2. Percentage of seeds eaten (mean ± sem) by third, fourth and fifth instar *Helicoverpa armigera* in three-way choice bioassays after 24 h. The percentage of seeds eaten by different instars was compared with the Mann-Whitney test. Different letters indicate significant differences. b > a, $P < 0.05$ and c > b and a, $P < 0.001$.

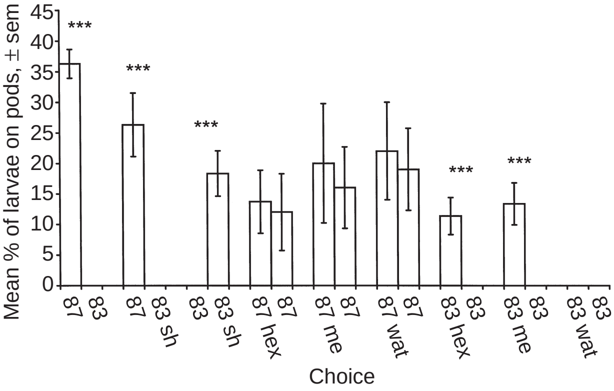

Fig. 3. Distribution (mean ± sem) of first and second instar *Helicoverpa armigera* found on pods in a pod-choice experiment after 48 h. The numbers of larvae on each of the pods were compared using the Wilcoxon Signed Ranks test. *** $P < 0.01$; 87, ICPL 87; 83, ICPW 83; hex, me, wat, pods extracted in hexane, methanol and water, respectively; sh, pod-surface trichomes removed.

when presented to them at a pod-surface-equivalent concentration. Feeding indices were −35 ± 16 (n = 15), −86 ± 5 (n = 14) and −65 ± 11 (n = 11) for larvae presented with the hexane, methanol and water extracts, respectively. More of each disc treated with the hexane, methanol or water extract was consumed when compared with its respective control (Wilcoxon Signed Rank, $P < 0.05$). The methanol extract was significantly more stimulating than the hexane extract (Mann-Whitney, $P < 0.01$), but not the water extract (Mann-Whitney, $P > 0.05$).

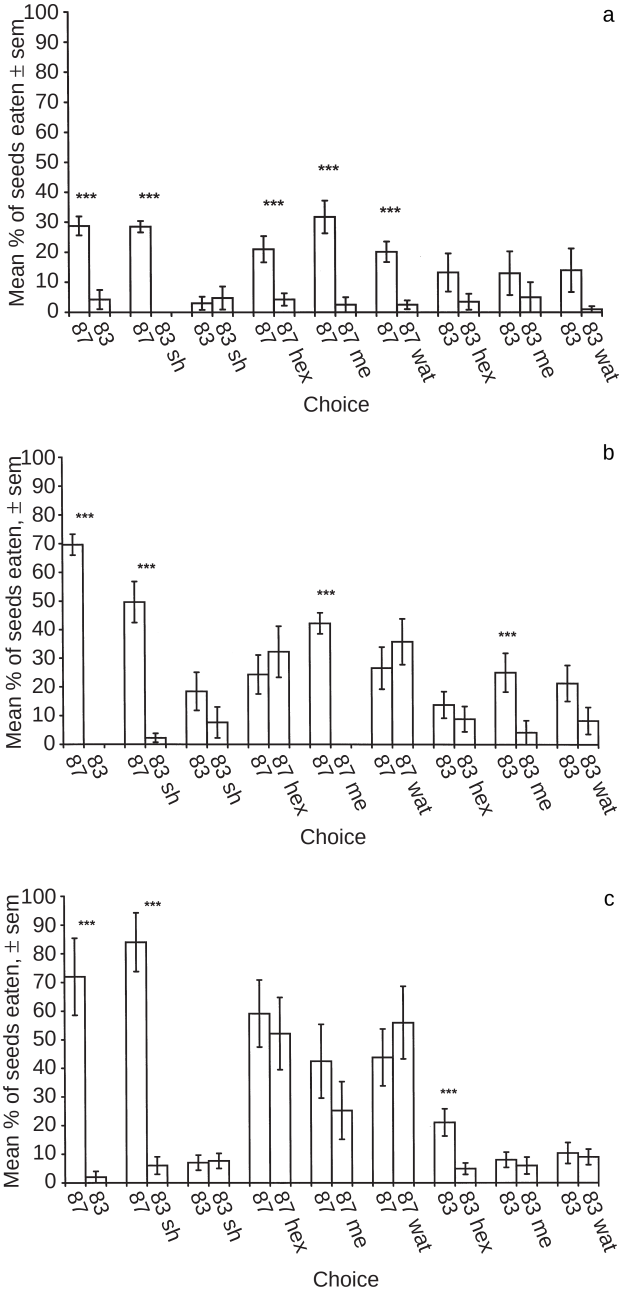

Fig. 4. Percentage of seeds eaten (± sem), by (a) third, (b) fourth and (c) fifth instars of *Helicoverpa armigera* when presented with binary-choices between *Cajanus* sp. pods over 24 h. The amounts of seed eaten were compared using the Wilcoxon Signed Ranks test. *** $P < 0.001$; 87, ICPL 87; 83, ICPW 83; hex, me, wat, pods extracted in hexane, methanol and water, respectively; sh, pod-surface trichomes removed.

Discussion

Larvae of *H. armigera* are able to select among different plant parts and between two different species of *Cajanus* in choice experiments. There were, however, differences in the responses at different developmental stages of the insect. Young larvae (first and second instars) congregate inside flowers of cv. ICPL 87 in preference to other plant structures. Young larvae are vulnerable to desiccation and predation so burrowing into flowers would offer first and second instars some protection. Later instars (third to fifth) show an increasing tendency to feed upon pods, switching from

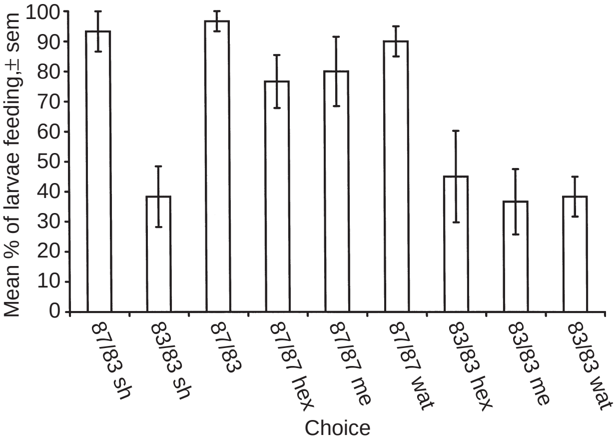

Fig. 5. Percentage (mean ± sem), of third, fourth and fifth instar *Helicoverpa armigera* consuming pod material during pod-choice experiments. The mean value was calculated from the proportions of third, fourth and fifth instars feeding. 87, ICPL 87; 83, ICPW 83; hex, me, wat, pods extracted in hexane, methanol and water, respectively; sh, pod-surface trichomes removed.

feeding primarily on flowers (third instars) to preferring pods (fourth and fifth instars). This could be due to changes in the nutritional requirements across instars. Older larvae of Lepidoptera have increased appetitive behaviour (Raubenheimer & Barton-Browne, 2000) and a need for more protein (Simpson *et al*., 1988). Blaney & Simmonds (1983) measured the quantity of an artificial diet eaten during the larval phase of *H. armigera*. They found that the amounts of food eaten during each instar, as a proportion of all the food consumed during the larval phase, were 0.08, 0.91, 5.7, 24, 31 and 40%, respectively for the first to sixth instars. Thus, the switch between the third and fourth instars from feeding on flowers to feeding primarily on pods reflects that pods, rather than flowers, would be more likely to provide the quantity and quality of nutriment required by fourth and fifth instars.

Sison & Shanower (1994) found that larvae reared solely on pods of cv. ICPL 87 throughout the larval phase developed more quickly into heavier pupae and larger and more fecund adults than other larvae reared upon flowers or leaves of the same genotype. Whilst the effect of food choice on the growth of larvae was not investigated in the present study, the data have shown that there are ontogenic differences in food selection behaviour during the larval phase which would not be apparent in single choice experiments. As larvae would contact the surfaces of flowers, pods and leaves before starting to either burrow into or feed upon these, it is likely that compounds on the surfaces of these structures could play a role in the selection behaviour of larvae.

In the pod-choice experiments all instars preferred to either congregate upon (first and second instars) or feed upon (third to fifth instars) pods of cv. ICPL 87 rather than cv. ICPW 83 (table 2). These data confirmed that *H. armigera* larvae are able to select what has been found to be the nutritionally more optimum food (Shanower *et al*., 1997) across instars, where a choice between cv. ICPL 87 and cv. ICPW 83 pods was provided (table 2).

Removal of the pubescence from the surface of cv. ICPW 83 pods resulted in first and second instars moving onto these pods in preference to intact pods of the same genotype. Pods of cv. ICPW 83 have a more dense covering of hair-like trichomes than cv. ICPL 87 (Peter *et al*., 1995). These pod surface hairs may present a significant barrier to feeding by young larvae. Some of the older larvae (third to fifth instars) fed upon pods of cv. ICPW 83 whether trichomes were present or removed from the pod surface.

Differences in pod chemistry, that resulted from extraction of pod-surfaces, affected the preference of *H. armigera* larvae. In general, first and second instars preferred to congregate upon pods of cv. ICPW 83 that had been surface extracted in organic solvents whilst older larvae (fourth and fifth instars) fed upon unextracted pods in preference to those extracted in methanol or hexane, respectively. Therefore, younger larvae (first and second instars) are deterred by compounds that are present on the pod surfaces of cv. ICPW 83. Conversely, it is possible that older larvae are deterred by what is left behind on the pod surfaces following extraction in methanol (fourth instars) or hexane (fifth instars) or, alternatively, by the removal of feeding stimulants into the solvents. The preference of first and second instars is not affected by differences in pod surface chemistry of cv. ICPL 87; third instars preferred to feed upon unextracted pods of cv. ICPL 87 and fourth instars were less likely to feed on cv. ICPL 87 pods that had been extracted in methanol. This indicates that compounds present on the pod surfaces of cv. ICPL 87 and cv. ICPW 83 have a role in the acceptance or rejection of a plant part by larvae of *H. armigera*. Identification of compounds, or groups of compounds, that mediate the preference shown by larvae could enable identification of varieties that lack stimulatory compounds or, conversely, that produce deterrent compounds.

There is a clear difference between the type and distribution of glandular trichomes on the pod-surfaces of cv. ICPL 87 and cv. ICPW 83 (Romeis *et al*., 1999). Type A trichomes (present only on pods of cv. ICPL 87) could produce attractants whilst type B trichomes (present in significantly greater numbers on the pod surfaces of cv. ICPW 83) could produce deterrent compounds. However, the responsiveness of the larvae to these compounds varies among instars.

Field data have shown that adult *H. armigera* do not lay eggs on cv. ICPW 83 when in a mixed cropping system, compared with 69 eggs per ten marked inflorescences of cv. ICPL 87 (Sharma *et al*., 2001). There are physical (Peter & Shanower, 1996) and nutritive differences between pods of cv. ICPL 87 and cv. ICPW 83 (Shanower *et al*., 1997) and one or both of these factors could contribute to the different levels of oviposition and feeding preference of larvae of *H. armigera*.

Results from the binary choice bioassay confirmed that the compounds extracted from the pod surfaces of cv. ICPL 87 by either hexane, methanol or water stimulated the feeding of fifth instars and the compounds extracted into methanol were the most stimulatory. Flavonols that affect the feeding behaviour of crop pests, such as the mite *Halotydeus destructor* (Tucker) (Acari: Eupodidae) have been identified from extracts of Fabaceae (Wang *et al*., 1998). Modification of the quantities and complement of these behaviour-modifying compounds in the Fabaceae has been suggested for developing cultivars of groundnut less susceptible to the aphid *Aphis craccivora* Koch (Hemiptera:

Aphididae) (Grayer *et al*., 1992) or *Spodoptera litura* (Fabricius) (Lepidoptera: Noctuidae) (Stevenson, 1993) and chickpea that is less susceptible to *H. armigera* (Simmonds & Stevenson, 2001). Since larvae of *H. armigera* would contact the compounds present on the pod surface before feeding commenced, it is likely that they would play a role in determining food selection and initiation of feeding. To establish whether pod-surface compounds of cv. ICPL 87 have a role in food selection, further work will attempt to characterize these compounds and determine their biological significance. Identification of compounds that play a role in making cv. ICPL 87 susceptible to pod-borer would provide breeders with tangible selection characters; choosing hybrids that lacked these stimulants may lead to the development of less susceptible varieties.

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The Convention on Biological Diversity and Product Commercialisation in Development Assistance Projects: A Case Study of LUBILOSA

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