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Within-plant distribution of *Helicoverpa armigera* (Hübner) and *Helicoverpa punctigera* (Wallengren) (Lepidoptera: Noctuidae) eggs on irrigated soybean

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Abstract The corn earworm (*Helicoverpa armigera*) and the native budworm (*H. punctigera*) are major pests of irrigated soybean in southern New South Wales and northern Victoria. Information on the within-plant distribution of eggs is required to assist in the development of appropriate sampling techniques for these pests and to determine possible effects on the control achieved by insecticides. Field-cage experiments were conducted to determine the within-plant distribution of the eggs of both species throughout the development of a soybean crop. The distribution of eggs in the field was also recorded from commercial crops of soybean. The results indicate that the majority of eggs of both species are laid on fully expanded leaves in the top 20 cm of the crop canopy at all growth stages, except pod fill. This distribution resulted from a preference for leaves and the top of the canopy, combined with the dominance of leaves as potential oviposition sites. There was a strong preference for the lower surfaces of the leaves, with the upper surface rarely preferred. During the reproductive development of the crop, *H. armigera* exhibited a strong preference for the developing flowers and pods, while *H. punctigera* showed a preference only for fully developed pods. The preference for flowers and pods, combined with the increase in the proportional area of leaves in the lower regions of the canopy, led to a decrease in the proportion of eggs laid in the top 20 cm of the canopy as the crop developed. Although the two species tended to lay eggs on different plant structures, the vertical distribution of eggs within the canopy was similar. The results are discussed in terms of the development of appropriate sampling techniques and possible effects on insecticidal control.

Key words field cage, oviposition, pest management, preference, sampling.

INTRODUCTION

The corn earworm, *Helicoverpa armigera* (Hübner) and the native budworm, *H. punctigera* (Wallengren) (Lepidoptera: Noctuidae) are both regarded as major pests of irrigated soybean (*Glycine max* L.) in southern New South Wales (NSW) and northern Victoria (Colton *et al.* 1995). *Helicoverpa punctigera* tends to be the most abundant species during the early part of the season and *H. armigera* towards the end of the season (Duffield 1998), but oviposition by both species occurs throughout the development of the crop.

There is limited information about the oviposition behaviour of these species on soybean in Australia. As a soybean crop develops, new structures such as flowers and pods become available for oviposition. Research conducted in the United States with other species of *Helicoverpa* and *Heliothis* indicates that the within-plant distribution of eggs changes as these developing fruiting bodies become preferred oviposition sites (Hillhouse & Pitre 1976; Terry *et al.* 1987).

Information on the within-plant distribution of eggs is required to assist the development of appropriate sampling techniques for *Helicoverpa* on soybean in Australia. A similar situation occurred on cotton, where *Helicoverpa* oviposition was shown to be concentrated in the top 20 cm of the crop canopy from fruiting onwards (Mabbett & Nachapong 1984). This enabled egg-based sampling plans to be developed, which focus on the plant terminal (top 20 cm) rather than the whole plant (Dillon & Fitt 1995), thereby reducing the time required to sample the crop, while maintaining accuracy.

In addition to possible impacts on sampling, the distribution of eggs within the canopy may also influence the control achieved by insecticides. The deposition of insecticides by both aerial and ground equipment is reduced towards the lower regions of a soybean canopy (Hutchins & Pitre 1984, 1985). Accordingly, if there is a shift in the distribution of eggs during the season, the overall efficacy of insecticides may change.

For these reasons it is important to characterise the pattern of oviposition of the two species, and determine whether the distribution of eggs changes as the crop develops. The present paper describes the results of a field cage experiment designed to provide information on the distribution of *H. punctigera* and *H. armigera* eggs on soybean during the development of the crop.

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MATERIALS AND METHODS

Field-cage experiments were conducted at the CSIRO Land and Water Research Station, Griffith, NSW. Soybean cv. Hooper sown on 28 November 1998 on 1.3-m beds, with a row spacing of 0.95 m and plant density of 290 000 plants per ha was used for the trial. No insecticides were applied to the experimental crop for the duration of the experiments. Irrigation and fertiliser applications followed commercial practice. An additional site at farm 8, Coleambally, NSW was used for a single experiment. Untreated soybean cv. Hooper grown to a similar configuration was used for this release.

Moths were released into cages enclosing the soybean crop in the field. Each cage consisted of a metal frame 0.7 m by 0.7 m at the base and 1.4 m in height, covered with white 50% shadecloth (Sarlon^{TM}). The cages were erected over a single row of soybean to enable free flight of the moths around the enclosed crop. Background *Helicoverpa* populations were low (< 2 eggs per plant), but a visual inspection of the crop was made prior to enclosure and any *Helicoverpa* eggs and larvae on the crop were removed. The *Helicoverpa* released were reared from locally collected eggs and larvae. Moths were released into the cages between 16.00 and 18.00 h and recovered after 36 h. The number of moths released per cage varied according to availability, and ranged from 2 to 10 mated females per cage. Five cages were used for each species on each of six release dates.

The procedure was repeated at five growth stages described by Fehr *et al.* (1971): V3 (early vegetative, 17 December 1998); V9 (late vegetative, 7 January 1999); R2 (full bloom, 21 January 1999); R4 (pod set, 2 February 1999); and R6 (pod fill, 5 March 1999 and 25 March 1999). *Helicoverpa armigera* were unavailable for the release at V3. For the V3 and V9 releases, 24-h-old mated females were used while subsequent releases used 3-day-old mated females. An additional release was performed at R6 at the second trial site due to poor oviposition in the first release.

After 36 h, plants were visually inspected for eggs. The distribution was divided into three vertical categories: < 20 cm; 20–60 cm; and > 60 cm down from the top of the canopy. Each category was divided into plant structures: terminal and growing tips (including unexpanded leaves); fully expanded leaves (upper and lower surface recorded separately); stem (including petioles); flowers; and pods.

On the day of release 15 plants (five adjacent plants from three locations) from the same row as the field cages were destructively harvested at ground level. The plant material was partitioned into the same height–structure classes as mentioned in the previous section. The surface area of each class was determined using a leaf area meter (Li-Cor Portable Model LI-300; Li-Cor Inc., USA). The recorded area was doubled to provide an estimate of the total surface area. The exception was the expanded leaves, where the upper and lower surfaces were regarded as separate structures. When plant material was too thick to be fed into the meter, the outline of the structure was traced onto paper and the paper fed through the meter.

In addition to the field-cage experiments, limited data were also collected from commercial soybean crops during the same time period. Ten fields were visited during the vegetative (V3-V9), flowering and early pod fill (R1-R3), and pod fill (R4-R7) stages. Three row metres of crop were harvested from each field at ground level. The plants were inspected in the laboratory and the position of any *Helicoverpa* eggs was recorded using the system described earlier. The eggs were not identified to species and the height of the crop and the area of the plant structures were not recorded.

Statistical analysis

The observed egg distribution was compared with that expected from the proportional surface area of the different height–structure classes using chi-squared analysis. Chi-squared analysis was also used to compare the egg distributions of the two species. Classes in which the expected number of eggs was < 5 were pooled.

A standardised residual was used to determine whether preferences existed for the different height–structure classes (after Terry *et al.* 1987), where

$$r = (\text{observed} - \text{expected})/(\text{expected})^{1/2}$$

A positive residual indicates a preference for that plant structure relative to its surface area, while a negative value indicates a non-preference.

RESULTS

A total of 702 *H. punctigera* and 2045 *H. armigera* eggs was recorded in the field cage experiments, and 380 *Helicoverpa* eggs were found in the field monitoring. Due to low and erratic numbers, the data for the different species from individual field cages on each release date were pooled. Data from the two releases at R6 were also pooled.

Crop growth

As the crop developed, the proportional area of the top 20 cm of the canopy declined. It constituted the entire area at V3, when the plants were less than 20 cm high, but declined to approximately 30% by R6 (Fig. 1). The surface area of the portion of canopy between 20 and 60 cm increased as the crop developed, accounting for more than 50% of the area from R4 onwards. The percentage of the canopy more than 60 cm below the top of the crop peaked at 7% of the total area at R6.

Leaves accounted for the largest proportion of the surface area of the crop, ranging from 89% at growth stage V3 to 74% at R6. The proportional area of stems remained relatively constant, ranging from 9 to 15% throughout the development of the crop. The proportion of the total surface area that was accounted for by the terminal and growing tips declined from 5% at V3 to 0% at R4, when growth of the canopy ceased. Flowers accounted for a maximum of 0.3% of the available area at R2, while the surface area of pods increased from 2% at R4 to 13% at R6.

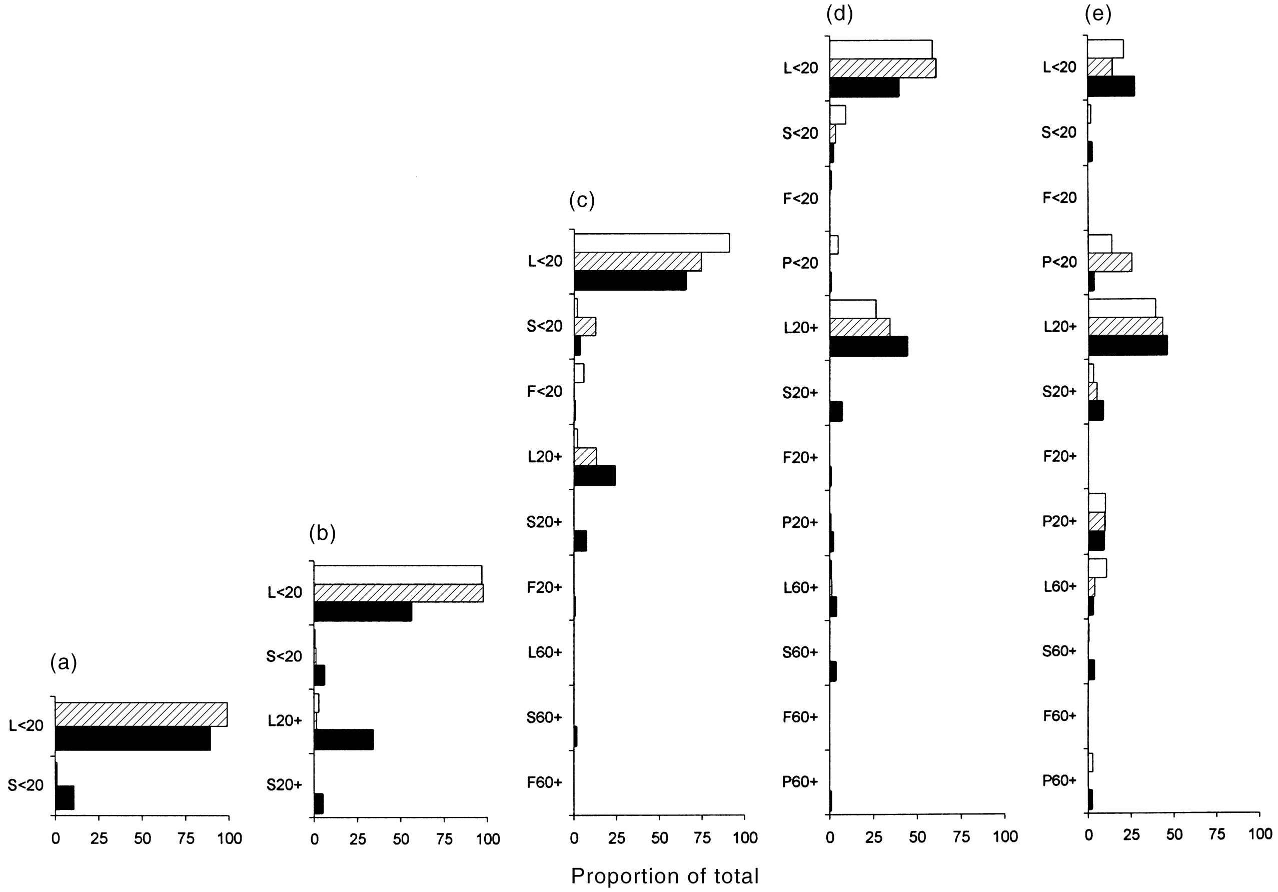

Fig. 1. Distribution of surface area and *Helicoverpa* spp. eggs in field cage experiments on different height–structure classes at five soybean growth stages: **(a)** V3; **(b)** V9; **(c)** R2; **(d)** R4; **(e)** R6. (■), surface area; (▨), *H. punctigera*; (□), *H. armigera*. Structure class: L, leaves; S, stems, terminal and growing tips; F, flowers; P, pods. Height class: < 20, 0–20 cm from top; 20+, 20–60 cm from top; 60+, > 60 cm from top.

Table 1 Height preference as expressed as standardised residuals (after Terry *et al.* 1987) based on the proportion of the surface area of the different height classes and the proportion of eggs laid

Height class	Statistics	Growth stage V3 Hp	 V9 Hp	 Ha	 R2 Hp	 Ha	 R4 Hp	 Ha	 R6 Hp	 Ha
< 20 cm			**4.71**	**4.56**	**2.25**	**3.60**	**3.60**	**4.99**	**1.43**	**0.82**
20–60 cm			–5.96	–5.76	–3.16	– 5.18	–2.40	–3.59	–0.59	–1.34
> 60 cm					–1.02	– 1.02	–2.19	–2.31	–1.28	**2.27**
Height	χ^2		115.0	475.0	21.7	77.9	35.5	55.5	2.9	63.9
	d.f.		1	1	1	1	2	2	2	2
	P		***	***	***	***	***	***	NS	***
Species	χ^2		1.1				7.4		5.7	
	d.f.		1				1		2	
	P		NS				*		NS	

Hp, *Helicoverpa punctigera*; Ha, *H. armigera*.

NS, $P > 0.05$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

There were insufficient degrees of freedom to enable χ^2 analysis for differences between species at R2 due to group values being < 5.0.

Bold font indicates a preference.

Table 2 Structure preference as expressed as standardised residuals based on the proportion of the surface area of the different structures and the proportion of eggs laid

Structure class	Statistics	Growth stage								
		V3	V9		R2		R4		R6	
		Hp	Hp	Ha	Hp	Ha	Hp	Ha	Hp	Ha
Leaf		**1.03**	**0.99**	**1.04**	–0.14	**0.42**	**1.05**	–0.09	–1.58	–0.50
Stem		–2.46	–2.83	–3.07	–2.12	–2.89	–2.81	–0.55	–2.27	–2.39
Terminal and growing tip		–1.74	–0.70	–0.22	**11.66**	–0.03	**2.29**	–0.56		
Flower					–0.57	**9.22**	–0.47	**1.12**		
Pod							–1.08	**1.68**	**6.07**	**3.61**
Structure	χ^2	12.7	17.9	92.5	6.5	16.7	17.2	5.7	32.5	159.0
	d.f.	2	1	1	1	1	2	2	2	2
	P	**	***	***	*	***	***	*	***	***
Species	χ^2		0.2		8.5		20.7		3.1	
	d.f.		1		1		2		1	
	P		NS		**		***		NS	

Hp, *Helicoverpa punctigera*; Ha, *H. armigera*.
NS, $P > 0.05$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.
Bold font indicates a preference.

Table 3 Height–structure preference expressed as standardised residuals based on the proportion of the surface area of the different height–structure classes and the proportion of eggs laid

Height class	Structure class	Statistics	Growth stage								
			V3	V9		R2		R4		R6	
			Hp	Hp	Ha	Hp	Ha	Hp	Ha	Hp	Ha
< 20 cm	Terminal and growing tip		–1.7	–0.7	–0.2	**14.6**	**0.3**	**3.6**	–0.4		
	Leaf		**1.0**	**5.6**	**5.5**	**1.1**	**3.2**	**3.5**	**3.1**	–2.4	–1.1
	Upper leaf surface		**3.4**	**0.8**	0.3	–4.4	**0.7**	–1.3	–2.2	–3.3	–2.1
	Lower leaf surface		–1.9	**7.1**	**8.1**	**6.0**	**3.8**	**6.2**	**6.6**	–0.1	**0.4**
	Stem		–2.5	–1.9	–2.2	**0.5**	–1.0	**0.1**	**6.1**	–1.4	–0.3
	Flower					–0.3	**16.6**	0.3	**2.7**		
	Pod							–0.4	**11.4**	**13.7**	**6.7**
20–60 cm	Terminal and growing tip					–0.4	–0.4	–0.3	–0.3		
	Leaf			–5.6	–5.3	–2.2	–4.5	–1.5	–2.7	–0.4	–0.9
	Upper leaf surface			–3.7	3.8	–3.2	–3.0	–3.3	–3.6	–0.3	–3.7
	Lower leaf surface			–4.1	3.7	**0.2**	–3.3	**1.3**	–0.2	–0.3	**2.3**
	Stem			–2.2	–2.2	–2.6	–2.6	–2.5	–2.5	–1.2	–1.9
	Flower					–0.5	–0.5	–0.3	–0.3		
	Pod							–0.9	–1.3	**0.4**	**0.4**
> 60 cm	Terminal and growing tip					–0.2	–0.2	–0.3	–0.3		
	Leaf							–1.2	–1.4	**0.8**	**5.3**
	Upper leaf surface							–1.3	–0.7	–1.1	**1.9**
	Lower leaf surface							–0.5	–1.3	**2.3**	**5.5**
	Stem					–1.0	–1.0	–1.7	–1.7	–1.7	–1.7
	Flower							–0.3	–0.3		
	Pod							–0.6	–0.6	–1.3	**0.6**
	Height–structure	χ^2	30.3	180.8	910.2	137.4	82.8	119.2	95.7	30.5	910.5
		d.f.	3	5	5	5	5	7	5	6	11
		P	***	***	***	***	***	***	***	***	***
	Species	χ^2		3.5		250.3		28.1		13.5	
		d.f.		2		3		5		5	
		P		NS		***		***		*	

Hp, *Helicoverpa punctigera*; Ha, *H. armigera*.
NS, $P > 0.05$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.
Bold font indicates a preference.

Egg distribution

More than 85% of the eggs laid by both species were on structures in the top 20 cm of the canopy up to R2 (Fig. 1). The proportion of eggs laid in the top 20 cm then declined to 64% and 39% at R4 and R6 for *H. punctigera*, and 73% and 36% at R4 and R6 for *H. armigera*, respectively. More than half the eggs laid at R6 were laid in the 20–60-cm portion of the crop canopy.

At all stages of the crop's development the majority of eggs laid by both species were on the leaves. The proportion of eggs laid on the leaves, however, declined as the crop developed. For *H. punctigera* it declined from 99% to 61% from V9 to R6, respectively, and from 99% to 70% for *H. armigera* at the same growth stages. With the exception of growth stage R6, less than 10% of eggs were laid on other plant structures. During R6, however, 35% and 26% of the eggs laid were on pods by *H. punctigera* and *H. armigera*, respectively.

Leaves in the top 20 cm of the canopy received more than half of all eggs laid by both species at all growth stages with the exception of R6, when a higher proportion of the eggs were laid on leaves 20–60 cm into the canopy.

Both species demonstrated a preference for structures in the top 20 cm of the canopy at all growth stages (Table 1). This means that a higher proportion of eggs were laid in the top 20 cm than that expected by the proportional surface area of the plant structures. A non-preference was shown for the lower sections of the canopy, with the exception of *H. armigera* at R6 for the >60-cm section. This resulted in highly significant ($P < 0.001$) differences between the observed egg distribution of both species and that expected by the available surface area (Table 1), with the exception of *H. punctigera* at R6. Significant ($P < 0.05$) differences were detected only between the height preferences of the two species at R4.

During the vegetative stages (V3–V9), eggs were preferentially laid on the leaves in relation to their surface area, compared to the stems. No differences were detected in the patterns of the two species ($P > 0.05$; Table 2). At R2 and R4, structures in the top 20 cm other than leaves were also preferred, along with the underside of leaves 20–60 cm into the canopy (Table 3). *Helicoverpa armigera* exhibited a strong preference for flowers in the top 20 cm during R2 and R4 (Table 3), which was reflected by an overall preference for flowers (Table 2). This preference was not shown by *H. punctigera*. *Helicoverpa armigera* demonstrated a preference for pods in the top 20 cm at R4, and both species exhibited a preference for pods in the top 60 cm of the canopy at R6 (Table 3). A preference for pods at distances over 60 cm from the top of the canopy was also shown by *H. armigera* at R6.

The differences in the preference for flowers and pods exhibited at R2 and R4 resulted in significant differences ($P < 0.01$) being detected between the distribution of eggs of the two species in terms of both the structure (Table 2) and height–structure (Table 3) classes. Significant differences were not detected in the egg distribution of the two species at R6 in terms of plant structure (Table 2) although a significant ($P < 0.05$) height–structure difference was recorded.

More than 60% of the eggs recorded in the field were laid on structures in the top 20 cm at all growth stages (Fig. 2). The majority of eggs were laid on leaves during the vegetative and flowering growth stages, while during pod fill the majority of eggs were laid on the pods. Due to the limited nature of the data recorded, statistical analysis was not conducted on the field data.

DISCUSSION

The results of our study demonstrate that the within-plant distribution of *H. armigera* and *H. punctigera* eggs on soybean reflects a combination of a preference for different plant structures at specific distances into the canopy, and of the available surface area of those structures.

The majority of eggs laid by both species in the field cages were laid on fully expanded leaves in the top 20 cm of the canopy at all growth stages except pod fill (R6), a pattern supported by the field data. This distribution reflected a preference for leaves and the top of the canopy, combined with the dominance of leaves compared to other plant structures in terms of their surface area, and therefore the availability of oviposition sites. The preference for leaves was characterised by a strong preference for their lower surfaces. Similar preferences for the underside of leaves in the top portion of the

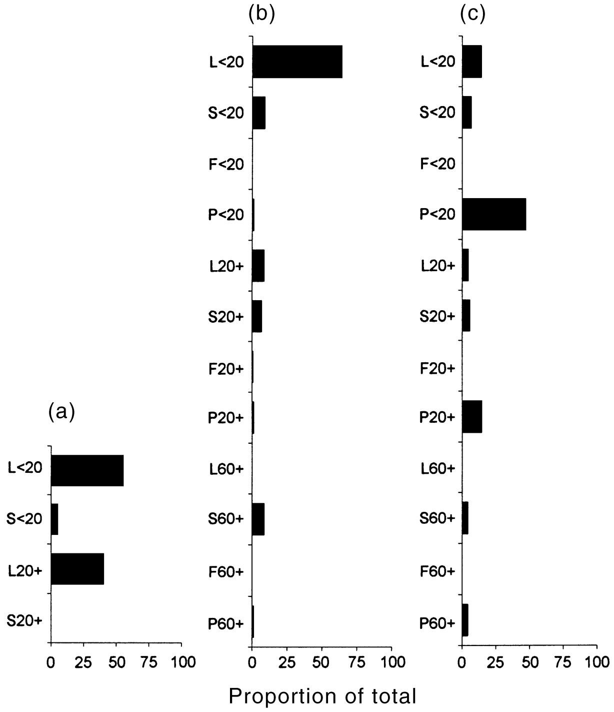

Fig. 2. Distribution of *Helicoverpa* spp. eggs in commercial soybean crops on different height–structure classes during different growth stages: **(a)** vegetative (V3–V9); **(b)** flowering (R1–R3); **(c)** pod fill (R4–R7). Structure class: L, leaves; S, stems, terminal and growing tips; F, flowers; P, pods. Height class: <20, 20 cm from top; 20, 20–60 cm from top; 60+, >60 cm from top.

canopy have been recorded for both these species on cotton (Mabbett & Nachapong 1984; Hassan *et al.* 1990), and for species of *Heliothis* on soybean in the United States (Hillhouse & Pitre 1976; Terry *et al.* 1987). The preference for the underside of the leaves has been attributed to higher densities of leaf pubescence on the under-surface compared to the upper surface (Hillhouse & Pitre 1976; Navasero & Ramaswamy 1991).

Helicoverpa armigera exhibited a strong preference for the developing flowers and pods, while *H. punctigera* showed a preference only for fully developed pods. Preferences for the developing fruiting bodies have also been demonstrated for *Helicoverpa* spp. on cotton (Mabbett & Nachapong 1984; Hassan *et al.* 1990; Jallow *et al.* 1999) and for *Heliothis virescens* (F.) oviposition on soybean (Hillhouse & Pitre 1976). Flowers and pods are preferred larval feeding sites on soybean (Eckel *et al.* 1992), and oviposition on or close to these structures may promote larval growth and survival. The mechanism for this preference for flowers and pods is poorly understood, but the availability of nectar for adult feeding (Adjei-Maafo & Wilson 1983) and a concentration of chemical cues in the fruiting structures that promote oviposition (Jallow *et al.* 1999) are likely to be contributing factors.

Cultivar differences in leaf structure such as leaf hairiness can influence oviposition preference and subsequent egg distribution (Navasero & Ramaswamy 1991). Morphological differences in the cultivars grown in south-eastern Australia are not large, however, and it would be expected that the oviposition patterns recorded on cultivar Hooper in the present study would not differ significantly from that on other cultivars grown in the region.

These results have implications for the sampling of *Helicoverpa* in soybean. The finding that a high proportion of the eggs of both species are laid within the top 20 cm of the canopy offers the opportunity to develop a sampling plan similar to that developed for cotton, where terminals (top 20 cm) are assessed alone (Dillon & Fitt 1995). Egg-based sampling plans enable insecticide applications to be targeted on the egg or the early instar larvae. Specifically targeting early instar larvae is critical because the levels of resistance of *H. armigera* populations (in the region) to the main insecticide groups currently used are high and increasing (Forrester *et al.* 1993; Gunning *et al.* 1996), making control of late-instar larvae difficult. In addition there is a rapid decline in the age-specific susceptibility of both species to some of the biological insecticides, compatible with integrated pest management, recently registered in soybean (Duffield & Jordan 2000). If an egg-based sampling plan using counts from the top 20 cm of the canopy was developed, it would need to be growth-stage dependent due to the changing proportion of eggs laid in the top portion of the canopy, especially at pod fill.

The deposition of insecticides applied using ground and aerial spray equipment decreases in the lower portions of a soybean canopy, due to reduced spray penetration (Hutchins & Pitre 1984, 1985). On cotton, similar spray patterns lead to reduced efficacy of conventional insecticides against *Helicoverpa zea* (Boddie) eggs in the lower portions of the canopy (Farrar & Bradley 1985). Accordingly, the control achieved by insecticides may decrease as the crop develops and a greater proportion of the eggs are laid further into the canopy. However, although the two species we studied may oviposit on different plant structures, the vertical distribution of eggs within the canopy is similar. This suggests that, in the absence of insecticide resistance, the control achieved by insecticides would not be expected to differ between the species.

Our results also suggest that the observed differences in the oviposition patterns of the two species are unlikely to mean that sampling based on the vertical distribution of eggs within the canopy need be adjusted for the different species. For the same reason, within- and between-season variation in the relative abundance of the two species would also not be expected to influence egg-based sampling plans in any significant way.

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