

Bt cotton and modern insecticide adoption decreases *Helicoverpa* spp. population recruitment in a subtropical cropping system

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Abstract

Extensive crop sampling for *Helicoverpa* spp. pupae was undertaken (2017–2021) to provide insights as to how pest population dynamics have altered in a subtropical cropping system following the introduction of transgenic Bt cotton and newer generation insecticides for pulse production. Previously (1996–1999), a pattern of year-round population cycling and build-up was identified to occur between summer cotton (non-Bt) and winter chickpea, enabled by widespread resistance to broad-spectrum insecticides used at the time. Current pupae sampling was unable to recover pupae from Bt cotton, suggesting this crop had become a population sink rather than a source for *Helicoverpa* spp. Pupae were less abundant in pulses, with monthly counts varying from 0 to 3192/ha in chickpea being a fraction of previous densities that ranged from 10,000 to 100,000/ha whilst pupae were not detected in mungbean crops. Poor survival (0%–39.5%) of pupae collected from chickpea, likely due to sub-lethal insecticide exposure during the larval stage, further limited population recruitment. The highest densities of pupae (up to 18,666/ha) were routinely recovered from unsprayed pigeon pea grown as refuges for Bt cotton resistance management, although *Tachinid* spp. parasitoids caused increasing pupal mortality with refuge age. This study suggests that the high control efficacy afforded by transgenic Bt traits incorporated into cotton and newer insecticides used on pulse crops has provided a form of area-wide management that may explain suppression of *Helicoverpa* spp. pupae densities compared to levels previously recorded across the cropping system.

KEYWORDS

area-wide management, IPM, pupae, resistance management

1 | INTRODUCTION

Helicoverpa armigera (Hübner) and *Helicoverpa punctigera* (Wallengren) are major pests of cotton (*Gossypium hirsutum* L.) in Australia and occur at economically damaging levels every year (Downes et al., 2017). These species are also major pests of several

pulse and grain field crops (Brier et al., 2008; Fitt, 1989). Transgenic cotton cultivars that express toxins derived from *Bacillus thuringiensis* (Bt) were approved for use in Australia during the mid-90s for the control of *Helicoverpa* spp. and to reduce insecticide dependence (Downes et al., 2017; Fitt, 2000). A key concern for this technology was that target pests can develop resistance to the bacterial

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toxins due to the continual selection pressure that occurs during the life of the crop and across multiple seasons (Mahon et al., 2007; Tabashnik et al., 2003). Therefore, Bt cotton growers in Australia are compelled to adhere to a range of on-farm practices that underpin a resistance management strategy (Knight et al., 2021). These practices include prescribed sowing windows and harvest end dates to limit pest generational exposure, a refuge crop in close proximity to the Bt cotton crop to generate additional susceptible alleles and dilute potentially resistant ones, and post-harvest cultivation of Bt-cotton fields during winter to control diapausing *Helicoverpa* spp. pupae and thus potentially eliminate inter-season transfer of resistant alleles (Baker & Tann, 2014; Downes et al., 2017; Knight et al., 2021).

Pupal diapause is highly irregular in subtropical Central Queensland (CQ) (Sequeira & Playford, 2001), rendering post-harvest *Helicoverpa* spp. pupae destruction by cultivation ineffective compared to temperate regions. Approval to grow Bt cotton in this region was postponed until a detailed ecological study was undertaken to better understand *Helicoverpa* spp. population dynamics and identify appropriate alternate resistance management measures (Sequeira, 2001; Sequeira & Playford, 2001). Temporal pupae abundance measured under various crops grown within the cropping system strongly suggested that *Helicoverpa* spp. populations were primarily recruited within and exchanged between conventionally grown (sprayed non-Bt) summer cotton and winter chickpea (*Cicer arietinum* L.) crops with lesser exchange occurring between other crops such as soybean and sunflower (Sequeira, 2001).

Cotton production has markedly changed since this study, with the ubiquitous use of Bollgard II® cotton since 2004 followed by triple Bt protein, Bollgard® 3 since 2016 (Knight et al., 2021). Current varieties provide high control efficacy of *Helicoverpa* spp., with the requirement for chemical intervention having become rare (Downes et al., 2017; Wilson et al., 2013). Unsprayed pigeon pea (*Cajanus cajan* L.) comprising 2.5%–5% of the area sown to Bollgard 3 cotton are grown as a mandatory refuge requirement of the resistance management strategy (Knight et al., 2021). Outbreaks of silverleaf whitefly, *Bemisia tabaci* Middle East-Asia Minor 1 (MEAM1) in 2001 and subsequent control difficulties have resulted in a significant reduction in sunflower (*Helianthus annuus* L.) and soybean (*Glycine max* L.) production in CQ (Sequeira et al., 2009). The advent of newer insecticides for *Helicoverpa* spp. for which resistance is rare (Bird, 2015) provide control efficacy in pulse crops compared with older carbamate and pyrethroid compounds for which resistance became widespread during the 1990s (Bird, 2018).

Longer-term viability of *Helicoverpa* spp. management depends on maintaining both transgenic and conventional technologies used with an area-wide approach (Downes et al., 2017). In the CQ agricultural system, there have been changes to the types of crops grown and crop protection technologies used and it is likely that *Helicoverpa* spp. abundance will have been influenced by the use of Bollgard® cotton and newer insecticides. In the current study, we sampled pupae from a cross-section of crops between 2017 and 2021 to measure *Helicoverpa* spp. recruitment and enable

comparison with a historical survey undertaken by Sequeira (2001). A revised knowledge of inter-seasonal population dynamics can be used to inform ongoing resistance and area-wide management strategies.

2 | MATERIALS AND METHODS

Pupae assessments were made in commercial fields of host crops within the CQ cropping region located between Springsure (24.1161°S, 148.0886°E) in the south to Clermont (22.8230°S, 147.6383°E) in the north and Comet (23.6014°S, 148.5480°E) in the east between July 2017 until June 2021. The study focused on commercially-grown crops within this region that had been previously surveyed by Sequeira (2001) (Table 1). Unsprayed pigeon pea refuges were also included, but cannot be directly compared as they were not an industry-mandated requirement at the time of the previous survey. Cotton and associated pigeon pea refuges were predominantly sown during August and September and reached maturity in January. A smaller second sowing was undertaken by some growers each year during late November or December which attained maturity in May/June. Cotton and pigeon pea sampling therefore spanned both sowings with limited overlap between early and late crops: the October to January measurements corresponded with early-sown crops and February to May data align with later-sown crops.

The minor crops soybean, sunflower, navy bean (*Phaseolus vulgaris*) and Dolichos (*Lablab purpureus* L.) that were previously surveyed were not grown commercially during our study period.

Pupae were sampled by taking 20 × 1 m² quadrats per field on each sample occasion from the inter-row area utilizing the pupae excavation and recovery method described by Lloyd et al. (2008). Several transects >20m from the field boundary to avoid edge effects were made with random samples taken 20–40m apart. Sampling began when each crop neared or commenced florescence as this is when *Helicoverpa* spp. infestation (Sequeira & Playford, 2002; Wardhaugh et al., 1980) and recruitment (Titmarsh, 1993) becomes most likely. Sampling commenced at flowering for chickpea, mungbean (*Vigna radiata* L.), cotton and pigeon pea and from the tasselling or boot stage onwards for corn (*Zea mays* L.) and sorghum (*Sorghum bicolor* L.). Sampling continued approximately every 3 weeks until crop maturity. Below-average rainfall in 2018 and drought in 2019 impacted the areas planted to host crops. The number and diversity of crops available for assessment during this period were at times limited with many growers focusing production on smaller areas of higher margin crops (primarily cotton and chickpea).

To enable comparison with Sequeira (2001), the density of pupae sampled per hectare was calculated for each crop type every month; despite the underlying assumption that pupal density is evenly distributed across each field presenting a risk of over or underestimating abundance. This calculation was made by pooling the quadrat samples for each crop type per month to derive means as per below:

$$((\text{pre-pupae and pupae}) / \text{quadrat metres sampled per crop type}) \times (10,000).$$

TABLE 1 Emergence rate, species and mortality factors for undamaged pupae recovered during sampling.

Year	Crop	Fields sampled	Samples taken	Total pupae recovered	% Emerged as moths	% Dead (unknown causes)	<i>Helicoverpa armigera</i>	<i>Helicoverpa punctigera</i>	Total parasitism	% Contribution to parasitism	
										Ichneumonidae	Tachinidae
2017	Chickpea	7	580	7	14.3	85.7	57.1	42.8	0		
	Maize	1	60	6	83.3	16.7	100		0		
	Pigeon pea	4	200	92	26.1	49.6	16.7	83.3	24.3	22.7	77.3
	Sorghum	-	-	-	-	-	-	-	-	-	-
	Mungbean	-	-	-	-	-	-	-	-	-	-
Bt cotton	4	240	0								
2018	Chickpea	6	400	5	0	100	60	40	0		
	Maize	2	80	10	50.0	50.0	100		0		
	Pigeon pea	9	820	127	37.8	34.6	55.4	44.6	27.6	13.8	86.2
	Sorghum	1	60	3	33.3	33.3	100		33.3	100.0	0.0
	Mungbean	1	60								
Bt cotton	9	700	0								
2019	Chickpea	7	600	119	39.5	51.3	65.9	34.1	9.2	54.5	45.5
	Maize	-	-	-	-	-	-	-	-	-	-
	Pigeon pea	10	680	181	26.0	43.1	39.6	60.4	30.9	7.1	92.9
	Sorghum	5	240	0							
	Mungbean	-	-	-	-	-	-	-	-	-	-
Bt cotton	10	620	0								
2020	Chickpea	8	560	22	27.3	59.1	66.7	33.3	13.6	33.3	66.7
	Maize	4	200	29	58.6	34.5	100		6.9	0.0	100
	Pigeon pea	10	540	25	28.0	48.0	0	100	24.0	33.3	66.7
	Sorghum	2	60	0							
	Mungbean	4	180								
Bt cotton	10	500	0								
2021	Chickpea	-	-	-	-	-	-	-	-	-	-
	Maize	-	-	-	-	-	-	-	-	-	-
	Pigeon pea	5	380	83	25.3	48.2	47.3	52.7	26.5	29.4	70.6
	Sorghum	-	-	-	-	-	-	-	-	-	-
	Mungbean	5	200								
Bt cotton	5	260	0								

Note: -, no crops to sample.

Pupae not mechanically damaged during excavation were placed into individual 30 mL plastic cups and held in the laboratory at 24–25°C until moth emergence, parasitoid emergence or confirmation of pupae mortality. Pupae status (healthy, parasitised or dead) and emerging parasitoid genera were recorded.

Data were prepared for analysis by summing pupae counts across sampling dates for each crop by year and field and then dividing by the number of sampling quadrats taken. As no pupae were found in cotton or mungbean, these crops were excluded from the analyses. The 2021 data were also excluded from the analysis as pupae were only found in pigeon pea with other crops either not grown or having no pupae which could possibly bias the results. Genstat (VSNInternational, 2022) was used to conduct an unbalanced analysis of variance (ANOVA) using a general linear model due to different number of paddocks sampled across years and crops.

3 | RESULTS

Crop type and temporal pupae abundance throughout the study period are presented in Figure 1. Pupae could not be found during sampling of Bt cotton and mungbean crops (Figure 1) despite 2320 and 440 samples from 38 cotton and 10 mungbean fields respectively (Table 1). Pupal abundance varied significantly between the other crops ($F = 3.22$; $df = 3, 60$; $p = 0.029$) but not across years

or for the interaction between crop and year ($p > 0.05$) with pupae being more abundant in pigeon pea compared with chickpea and sorghum but not maize (Figure 2). Abundance of pupae under maize crops corresponded with late cob filling whilst pupae occurred in chickpea and pigeon pea crops throughout the flowering and pod-filling stages.

During sampling 709 undamaged pupae were assessed for emergence, species and mortality factors (Table 1). Both *H. armigera* and *H. punctigera* were recovered from chickpea and pigeon pea whilst only *H. armigera* were recovered from maize and sorghum. Moth emergence from pupae collected from chickpea ranged from 0% to 39.5% primarily due to high rates of pupal mortality from unknown causes with parasitism only accounting for 9.2% and 13.6% of mortality in 2019 and 2020 respectively. Moth emergence from recovered pupae ranged from 50.0%–83.3% for maize and 25.3%–37.8% for pigeon pea. Parasitism in pigeon pea accounted for 24.0%–30.9% of pupal mortality depending on the season (Table 1). Parasitism of pupae collected from the early and late sown pigeon pea refuges show a trend of increasing parasite activity over time as refuges aged (Figure 3).

Dry conditions impacted the availability of commercially grown crops, particularly during 2019 (Table 1). To provide context, annual rainfall for the town of Emerald (located centrally within the region) is provided for the year immediately prior and during our study combined with records the Sequeira (2001) study (Table 2).

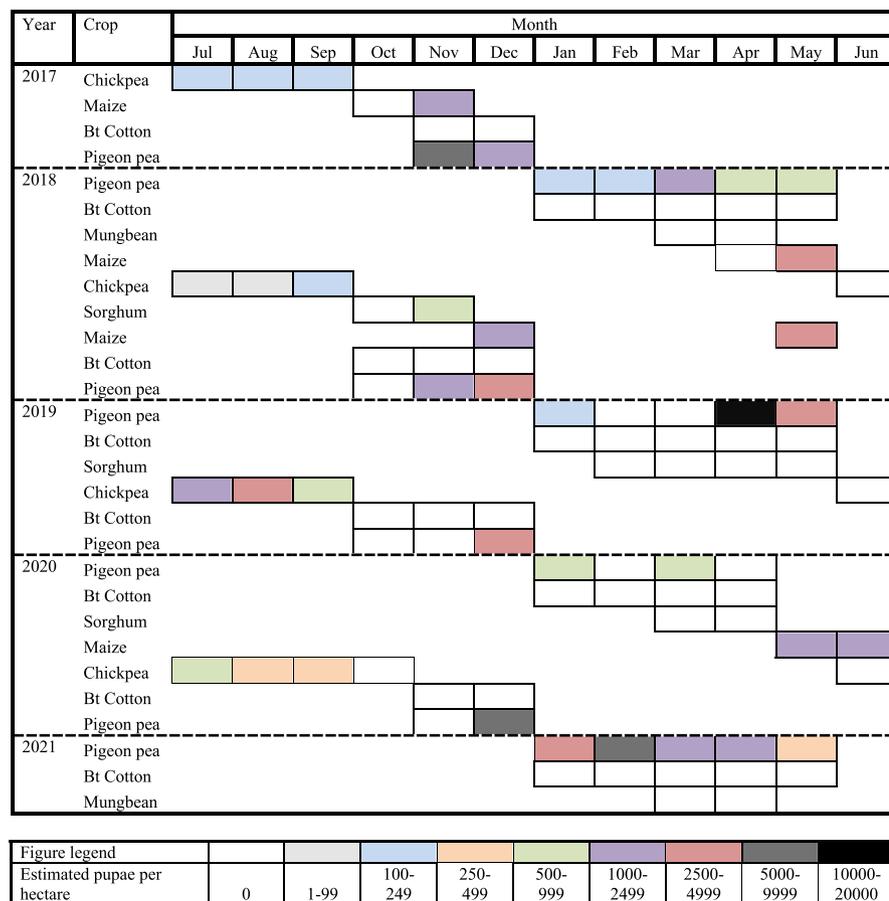


FIGURE 1 Abundance (pupae/ha) and temporal distribution of *Helicoverpa* pupae in relation to the crops grown and the cropping system in the Emerald area, 2017–2021. Estimates of pupal abundance for each crop are based on the number of pupae found in 20 random 1-m² soil samples per available fields each month. Individual crops were sampled up to five times at approximate 3-week intervals. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/jen.13118)]

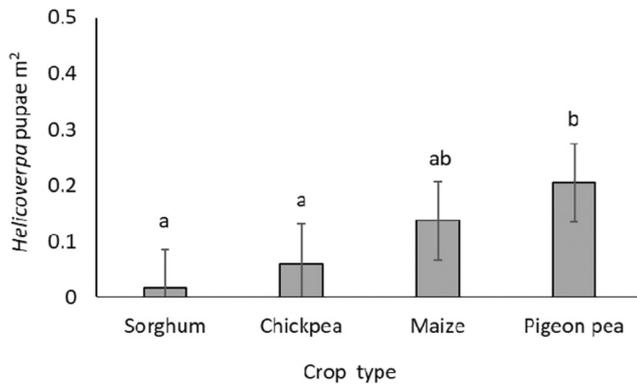


FIGURE 2 Mean *Helicoverpa* pupae abundance per m² quadrat samples across crop type throughout the study. Means with the same letter are not significantly different based on Fisher's least significant difference test ($p = 0.05$). Bars denote \pm mean SEM.

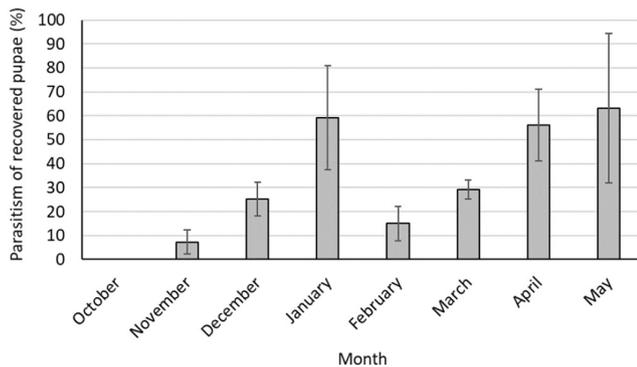


FIGURE 3 Parasitism of intact pupae recovered from pigeon peas each month between 2017 and 2021. Note that October to January data corresponds with early planted refuges whilst February to May is from late planting. Bars denote \pm mean SEM.

4 | DISCUSSION

Our objective was to compare *Helicoverpa* spp. recruitment ascertained via pupae sampling with an earlier study by Sequeira (2001) following the introduction of transgenic Bt cotton and newer generation insecticides within the CQ cropping system. The earlier study did not detail recovered pupae viability and therefore data presented in Figure 1 is based on an extrapolation of field sample data to allow comparison of pupae abundance despite the limitations outlined in the methods.

The overall abundance of pupae measured across crop types were non-existent to low (Table 1, Figures 1 and 2) and represent a stark departure from the pupae densities reported by (Sequeira, 2001). The former study found that cotton grown conventionally with insecticides was a major source for *Helicoverpa* spp. pupae recruitment, with monthly pupae density regularly exceeding 10,000/ha. However, we were unable to detect and recover any pupae from transgenic cotton despite extensive sampling (Table 1). As *H. armigera* oviposition behaviour is not altered by Bt expression, therefore making cotton a fatal host (Zalucki et al., 2012) the

TABLE 2 Annual recorded rainfall (mm) for study region spanning the historical (Sequeira, 2001) and current study periods. Annual deviation from mean rainfall denoted in (). Based on Australian Bureau of Meteorology station data from Emerald Airport 23.57 °S, 148.18 °E.

Year	Rainfall
1995 ^a	475 (-86)
1996	691 (129)
1997	416 (-146)
1998	982 (420)
1999	374 (-188)
2016 ^a	727 (165)
2017	612 (51)
2018	431 (-131)
2019	264 (-298)
2020	567 (6)

^aYear prior to study commencement.

widespread adoption of Bollgard® cultivars appear to have reduced the potential for cotton to act as a population source and instead has likely become a landscape level sink in CQ. This concurs with a study of *H. armigera* moth population dynamics in inland northern New South Wales, where cotton also represents a major component of the cropping system (Baker & Tann, 2016), that identified broad-scale moth suppression following the substitution of conventionally sprayed cotton with Bollgard II® Bt-expressing cultivars. Broad-scale adoption of Bt crops have shown similar suppressive effects on target pests in other regions of the world (Dively et al., 2018; Tabashnik et al., 2021; Wu et al., 2008).

Pupae density in chickpea (Figures 1 and 2) was a fraction of the 10,000–100,000/ha range reported by Sequeira (2001). The low viability of pupae recovered from chickpea due to unknown mortality factors ranging from 51.3% to 100% (Table 1) indicate that recruitment was lower than field counts suggest (Figure 1). During the study, growers were receiving high prices for chickpea and mungbean due to drought-related production shortfalls elsewhere in the Australian market. Insecticide spray action thresholds used by growers, account for commodity price versus the cost of control and therefore larvae are controlled more stringently when prices are high (GRDC, 2017, 2018a). The low density and high mortality of pupae recovered from chickpea and complete absence of pupae in mungbeans is thus potentially explained by the use of modern insecticides indoxacarb and chlorantraniliprole that have become widely used for pulse production to manage *H. armigera* (GRDC 2018b). Compared with older carbamate, pyrethroid and organophosphate insecticides for which efficacy was compromised by resistance in the 1990s (Forrester et al., 1993), these newer compounds provide high efficacy with resistance being still rare (Bird, 2018). Following application, chlorantraniliprole has been shown to have long-lasting residual activity on *Helicoverpa* spp. (Kuhar et al., 2010) and both this compound and indoxacarb are known to have sublethal effects on lepidopteran larvae through reduced pupation, pupal weight and adult emergence (Han et al., 2012;

Mahmoudvand et al., 2011). The characteristics of these commonly used compounds and the higher commodity value impetus for more stringent *Helicoverpa* spp. control in chickpea and mungbean during our study provide a plausible explanation for the very low rates of pupae recruitment compared to the 1990s and the subsequent mortality of recovered pupae.

Pupae abundance under maize and sorghum crops (Figures 1 and 2) were also well short of the density range of up to 49,999/ha reported by Sequeira (2001). Pupae recovered from maize had the highest rates of moth emergence compared with pupae recovered from other crops (Table 1) with spraying both less frequent and restricted to older less-effective compounds. A lack of pupae found in sorghum, particularly during 2019 and 2020 when no pupae were found (Table 1), was surprising given it is an attractive host for *H. armigera* during florescence and grain fill (Roome, 1975; Wardhaugh et al., 1980). Dry conditions, particularly in 2019 (Table 2) were considered a possible factor for low abundance in sorghum and maize. Irrigation was applied to all maize fields and a proportion of sorghum fields with all sampled crops producing harvestable yield and therefore likely to have attracted and supported infestation. During our study annual rainfall ranged from above average to well below and apart from a major divergence in year 3 was similar between studies (Table 2). Given the lack of difference ($p > 0.05$) for both pupae density across years or the interaction between crop and year it is unlikely that variable rainfall during our study was a primary cause for low pupal densities.

Analysis of crop scouting records prior to the introduction of Bt cultivars identified an annual pattern of linear increase for *Helicoverpa* spp. populations in the region's cotton fields over a 9-year period (Sequeira & Playford, 2002). Therefore, a more likely explanation for the low pupae numbers in sorghum and maize during our study is that Bollgard® cotton in which pupae recruitment was undetectably low (Figure 1, Table 1) markedly altered previous patterns of exchange between these overlapping crops.

Unsprayed pigeon pea refuges have become a minor but essential component of the cropping system since the release of Bollgard II® technology in 2003/2004 (Baker & Tann, 2014; Downes et al., 2017; Knight et al., 2021). Pigeon pea supported the highest pupae densities of the crops sampled during our study (Figure 1), however, it is the emergence of moths from pupae that is of critical importance for resistance management (Whitehouse et al., 2017). Overall moth emergence rates each season were low ranging from a quarter to a little over a third of recovered pupae (Table 1). A similar proportion was afflicted by parasitoids with Tachinids being predominant. The remainder died from unknown causes (Table 1). Epizootic outbreaks of baculovirus were observed periodically amongst larval populations inhabiting pigeon pea (Pers Obs). Baculoviruses have been found to reduce pupae fitness in other Lepidoptera (Myers et al., 2000) which may explain a portion of mortality observed which could not be attributed to specific causes.

Ideally, the emergence of moths from pigeon pea refuges should be synchronous with the emergence of rare resistant moths from

nearby Bt cotton crops (Baker et al., 2016; Whitehouse et al., 2017). The absence of pupae despite extensive sampling of Bollgard® 3 crops suggests that survival is rare (Figure 1) providing no direct indication as to when this could occur. Pupae production recorded in pigeon pea and other crops in this and the previous study demonstrate that *Helicoverpa* spp. are active throughout the entire period that cotton is grown and therefore the survival and emergence of rare resistant individuals from Bt cotton could occur at any time from first flower to crop maturity when cotton is morphologically likely to support larvae survival (Sequeira & Playford, 2001). Pigeon pea were therefore synchronously generating moths when survival could be expected in cotton (Figure 1). However, refuge effectiveness waned each season with crop age due to the increased activity of parasitoids (Figure 3) a factor observed elsewhere (Baker & Tann, 2014).

The greatly reduced pupae densities recorded in our study compared to Sequeira (2001) is most likely due to improved crop protection technology that currently prevents high level recruitment in cotton and chickpea. This partly supports the central hypothesis of Sequeira (2001) that chickpea and cotton production exacerbated the pest status of *Helicoverpa* spp. across CQ cropping system during the 1990s. However, this was a proximal association, ultimately caused by failing crop protection in both cotton and chickpea due to insecticide resistance.

Preserving the clear benefits that have accrued for growers due to new insecticides and Bt technology will be reliant on effective long-term preventative resistance management. The detection of a resistance mechanism for indoxacarb in *H. armigera* for which the primary fitness costs occur during diapause (Bird et al., 2020) would pose a greater risk for sub-tropical location such as in CQ where diapause is irregular. Therefore, adherence to insecticide usage advice based on annual resistance testing that aims to circumvent the development of resistance will remain critically important.

Our results also have implications for preventative Bt resistance management in CQ. To ensure the ongoing rarity of moths carrying resistance alleles known to exist within Australian *Helicoverpa* spp. (Mahon et al., 2007, 2012), dilution through the production of non-Bt exposed moths via refuges is an essential resistance management tactic. The waning of refuge effectiveness each season with crop age due to the increased activity of parasitoids (Figure 3) may need to be considered within the context of the resistance evolution modelling. The contribution of non-Bt exposed moths emerging from other crops and natural vegetation can be extensive and regarded as a positive for resistance management (Baker & Tann, 2013) but is valued conservatively within resistance evolution modelling due to the contribution being unstructured (Knight et al., 2021). Our data show that the contribution of *Helicoverpa* spp. originating from non-Bt crops should continue to be valued conservatively within resistance evolution modelling. Together with the historical comparison provided by Sequeira (2001), our study shows that when pests are resistant, host crops can act as major population sources within the landscape. When there are transgenic

resistant crops plus efficacious insecticides, these host crops instead act as major landscape-level sinks providing a form of area-wide management. Provided that crop producers utilize best management practices that strive to limit resistance, pest management can be sustainable.

AUTHOR CONTRIBUTIONS

Paul R. Grundy: Conceptualization; formal analysis; funding acquisition; methodology; project administration; resources; supervision; writing – original draft. **Gail Spargo:** Data curation; investigation; methodology; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

Available at Mendeley Data <https://doi.org/10.17632/mdbg4gwwpn.1>.

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