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Early-season floral bud loss has little impact on the maturity, yield, and lint quality of high-yielding Bt cotton crops

Paul R. Grundy ⓘ | **Kerry L. Bell**

Department of Agriculture & Fisheries, Crop & Food Science, Toowoomba, Queensland, Australia

Correspondence
Paul R. Grundy, Department Agriculture & Fisheries, Crop & Food Science, PO Box 102, Toowoomba, QLD 4350, Australia.
Email: paul.grundy@daf.qld.gov.au

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Abstract

Protecting floral buds (squares) from insect damage in cotton during early growth is a priority for crop managers despite unclear implications for yield potential and increased system risks from early-season insecticide use. This study was conducted to determine the compensatory responses of high-yielding *Bacillus thuringiensis* (Bt) cotton, *Gossypium hirsutum* L. cultivars, following manual square damage across 30 experiments, spanning different seasons and environments under commercial production conditions. Square removal from the first five sympodia (fruiting branches) before flowering reduced yield by 9% in one experiment, increased yield by 9%–12% in three experiments and had no effect in the remaining experiments. The most damaging treatment, with squares removed twice across 10 sympodia, reduced yield in just nine experiments by 10%–23%. Lint strength and length remained high, exceeding Australian market preferences. Micronaire decreased with later or more severe square loss particularly in shorter season environments, but economic impact varied. Compensatory growth following pre-flowering square loss increased fruiting site production without raising total biomass or boll proportion commensurately and caused only minor boll opening delay (<4 days). Yield compensation occurred through increased boll retention at the first position on upper canopy sympodia and more distal positions on remaining sympodia and was un-reliant on growth of additional mainstem sympodia. Square loss impacts were greater after commencement of flowering or when pre-flowering losses continued during the early-flowering period. Crop managers can have confidence to reduce pre-flowering pesticide use without jeopardizing high yields, which may produce additional systems benefits.

Plain Language Summary

This study examined how high-yielding Bt cotton plants react when their flower buds (squares) were damaged across a series of 30 experiments. Removing the squares before flowering reduced the cotton yield by 9% in one experiment but increased it by 9%–12% in three others. In most cases, it had no effect. The worst damage, removing

Abbreviation: Bt, *Bacillus thuringiensis*.

buds twice from many branches, reduced the yield by 10%–23% in some experiments. Despite this, the quality of the cotton stayed high, meeting Australian standards. When squares were lost, the plants managed to produce additional squares elsewhere in the canopy, with no meaningful delay for subsequent harvest. The impact was bigger if squares were lost during or after flowering started. Farmers can use fewer pesticides before flowering without risking lower yields.

1 | INTRODUCTION

Cotton, *Gossypium hirsutum* L., is a polycarpic plant that can compensate square (fruiting bud) and boll (fruit) loss through the production of additional fruiting structures (Mauney, 1986; Pettigrew et al., 1992), retention of subsequent fruiting positions that would otherwise be shed (Bednarz & Roberts, 2001; Stewart et al., 2001), or by increasing boll size (Sadras, 1995). This can enable recovery from pest insect damage or environment-induced fruiting structure abscission often without yield loss or substantially delayed crop maturity (Grundy et al., 2020; Sadras, 1996a,b; Wilson et al., 2003). Average irrigated cotton lint yields in Australia have increased by 33.6 kg ha^{-1} year^{-1} over five decades with a 5 year average of 2483 kg ha^{-1} for irrigated crops (Conaty & Constable, 2020). New cultivars and improved management have accelerated yield gain threefold since the mid-1990s (Liu et al., 2013). This inexorable yield increase has caused crop managers to question previously accepted tolerances for pest damage, and in the absence of updated management guidelines, they may be inclined to increase insecticide inputs.

Helicoverpa spp. (Lepidoptera: Noctuidae) and the green mirid, *Creontiades dilutus* Stål (Hemiptera: Miridae), are the primary pests that cause square loss in Australia (Khan, 2000; Lei et al., 2003; Sadras, 1996a). Since the introduction of transgenic *Bacillus thuringiensis* (Bt) cotton cultivars (Bollgard—Bayer) in Australia, *Helicoverpa* spp. is largely controlled without the need for insecticide prior to crop damage occurring (Wilson et al., 2018). However, *C. dilutus* is uncontrolled by Bt and remains a significant pest of concern. Economic thresholds were developed for mirids at the commencement of the Bollgard II cotton era (Farrell & Johnson, 2005; Khan et al., 2006) but grower adoption of these management guidelines is variable and below expectations (Sequeira, 2019; Whitehouse, 2011). Annual surveys between 2010 and 2017 found that a third of early-season insecticide sprays had been applied to below threshold populations of mirids (Sequeira, 2019). Low confidence in economic thresholds and damage compensation following square loss coupled with multi-tasking weed spraying operations are stated reasons for below threshold spraying (Sequeira, 2019; Whitehouse, 2011). However, insecticide application has associated risks of environmental pollution, selection of resistance in target

and non-target pests, and reduction of beneficial arthropods, thereby contributing to secondary pest outbreaks (Wilson et al., 1998). Avoiding below threshold insecticide application is therefore important for sustainable pest management.

Understanding compensatory response can inform pest management thresholds and avoid uneconomic insecticide use (Wilson et al., 2009). The artificial removal of fruiting structures is demonstrated to produce the same crop response as insect damage in cotton crops (Brook et al., 1992a,b) with numerous studies utilizing simulated damage to test underlying assumptions for pest thresholds in cotton (Bednarz & Roberts, 2001; Lei & Gaff, 2003; Lu et al., 2012; Pettigrew et al., 1992; Stewart et al., 2001; Wilson et al., 2003). Effective yield compensation for square loss prior to flowering is a common theme in these studies with instances of yield loss being attributable to continued fruit loss during flowering or where delayed crop maturity coincided with season length constraints. Bednarz and Roberts (2001), who undertook a particularly detailed study of yield compensation and associated fruiting dynamics, did conclude that compensation capacity for cotton grown under commercial conditions would be more varied due to climatic or regional factors. None of the aforementioned studies measured crop damage response across both multiple seasons and climatically diverse regions under commercial conditions.

With the increase in yield coupled with production expansion into higher latitude environments that have a shorter season due to cooler spring and autumn conditions, particularly since the advent of Bollgard II and Bollgard 3 cultivars in Australia (Knight et al., 2021), some managers are dismissive of previous crop compensation and threshold studies and instead actively manage for high square retention despite the aforementioned environment, resistance, and beneficial arthropod disturbance risks.

In an effort to resolve these concerns, we imposed artificial square removal experiments within commercially grown irrigated cotton fields, spanning full and shorter season environments across multiple seasons. Measurements of biomass production and partitioning, fruiting site production and retention, crop maturity, lint yield, lint quality components, and within-canopy boll distribution were made to better understand and describe compensation processes relevant to high-yielding commercial scenarios.

2 | MATERIALS AND METHODS

Experiments were implemented within commercially grown irrigated cotton fields at multiple locations spanning sub-tropical central Queensland (23.5° S) to shorter season temperate/Mediterranean climate of southern New South Wales (34.5° S). A key objective was to assess compensation ability without any specific tailored crop management inputs that might encourage yield recovery. Therefore, each experiment was managed according to the crop production requirements of the broader field area, which was indicative of the undamaged control plots for each experiment. Inputs were applied by producers to each field with the objective of achieving maximum yield potential. In particular, defoliation and harvest were conducted according to the status of the broader field at each experiment site. Therefore, compensation that was reliant on delayed maturity could not occur. Transgenic Bt cotton expressing Cry1AC, Cry2AB, and Vip3a (Bayer—Bollgard 3) were grown at each site. Each field was checked regularly by a professional agronomist for the presence of pests, which were controlled according to standard industry thresholds (CottonInfo, 2018). Locality, sowing date, cultivar, row spacing, and picking date for each experiment site are provided in Table 1.

All experiments utilized a randomized block design with four replications. The majority of experiments were implemented as core sites with treatment plots measuring 10-m × 4 rows wide. This plot size enabled periodic crop biomass sampling without compromising subsequent yield assessment. The remaining experimental sites where resourcing did not allow biomass assessment were implemented as single row × 10 m plots that were assessed for yield parameters only. At each experiment, replicate blocks were laid out contiguously end to end. Two untreated rows were placed between treatment rows, and plot ends were separated by a 2 m bare earth buffer allowing unimpeded access to each plot. As each experiment was located within commercial fields, care was taken to avoid placing treatment rows in machinery tramlines from intersecting plots. On occasion this necessitated increasing the between-plot row buffers to four instead of two rows.

Square damage was imposed on specific fruiting branches (sympodia) at two stages of crop development, forming three damage treatments for comparison with an undamaged control (Table 2). Damage treatment 1 (Sympodia [S] 1–5) was implemented when at least 50% of the plants in the plots had produced six sympodia, with a total of 11–13 mainstem nodes, and were 7–14 days from commencement of flowering. Damage treatment 2 (S6–10) was implemented when at least 50% of the plants in the plots had produced 11 sympodia, with a total of 16–18 mainstem nodes, 7–14 days following commencement of flowering. Damage treatment 3 (S1–10) combined damage treatments 1 and 2 on the same plants at each occasion (Table 2).

Core Ideas

- Compensation for pre-anthesis floral bud loss is effective under commercial conditions at very high-yield levels.
- Yield recovery was effective across seasons and environments and unaided by crop management intervention.
- Early-season square loss did not cause meaningful crop maturity delay or loss of lint quality.
- More stringent early-season pest management is unnecessary to preserve potential lint yields = >2700 kg/ha.
- Crop protection inputs that preserve fruiting structures are better targeted from anthesis onward.

Every plant within the treatment plot rows was artificially damaged. When implementing damage, all squares present were removed from appropriate sympodia utilizing a small pair of point-nosed pliers to "pinch" the bud, squashing the internal structures. The damaged squares subsequently aborted 2–4 days later along with a small proportion of squares that directly detached during damage implementation. Very small pinhead squares (<3 mm) were left intact as it is difficult to do this without also damaging underlying meristem tissue. When implementing the second damage incident on treatment S1–10, any compensatory squares that had grown on sympodia 1–5 were left intact.

Only one experiment was implemented in 2018 with a key objective of training a number of personnel to ensure consistent implementation of experiment methodology across the geographically spread locations used for the remainder of the study.

At core experiments, aboveground biomass was measured when damage was implemented and at subsequent intervals being approximately 3 weeks post first flower, cut-out, first open boll, and just prior to defoliation. On each occasion, 1 m of crop row was sampled from a designated row in each plot and was partitioned into stems (including petioles), leaves, squares, and bolls (green, unharvestable, and open) prior to drying for 5–7 days in a forced draught oven at 80°C. Partitioning enabled the contribution of each plant part, or groups of parts, as a proportion of total biomass to be calculated. Fruit were defined as bolls from the day of anthesis until when the boll wall sutures had begun to split, after which they were defined as open bolls. The total number of fruiting sites (fruiting structures present and sites with missing fruit) and bolls remaining at maturity was recorded for these samples. Final retention was calculated by dividing the final boll number present by the total number of fruiting sites

TABLE 1 Experiment site details spanning 2018–2022.

Location (nearby municipality) and year	Latitude	Longitude	Environment	Sowing date	Cultivar	Row spacing (m)	Picking date
2018							
Goondiwindi[a]	28.3421	150.1626	Full season	Nov. 3, 2018	Sicot 746B3f	1	Apr. 8, 2019
2019							
Emerald[a]	23.3246	148.0235	Full season	Aug. 8, 2019	Sicot 748B3F	1	Jan. 30, 2020
Dalby[a]	27.1520	151.1455	Full season	Nov. 22, 2019	Sicot 748B3F	2	Jun. 10, 2020
Brookstead[a]	27.4326	151.2428	Full season	Oct. 29, 2019	Sicot 748B3F	1	May 7, 2020
Goondiwindi[a]	28.3741	150.1648	Full season	Nov. 6, 2019	Sicot 748B3F	1	May 10, 2020
Whitton[a]	34.3450	146.1105	Shorter season	Oct. 10, 2019	Sicot 746 B3F	1	May 29, 2020
2020							
Comet[a]	23.3642	148.3103	Full season	Aug. 4, 2020	Sicot 748B3F	1	Apr. 15, 2021
Norwin[a]	27.3521	151.2200	Full season	Nov. 5, 2020	Sicot 746B3F	2	May 24, 2021
Cecil Plains	27.3508	151.1554	Full season	Oct. 30, 2020	Sicot 748B3F	1	May 26, 2021
Brookstead[a]	27.4326	151.2428	Full season	Oct. 9,2020	Sicot 746B3F	1	May 4, 2021
St. George	28.0533	148.4212	Full season	Nov. 30, 2020	Sicot 748B3F	1	Apr. 28, 2021
Mungindi	28.5850	149.0318	Full season	Oct. 20, 2020	Sicot 748B3F	1	May 11, 2021
Goondiwindi[a]	28.3711	150.1648	Full season	Nov. 4, 2020	Sicot 748B3F	1	May 25, 2021
Moree	29.2330	149.4601	Full season	Oct. 15, 2020	Sicot 748B3F	1	–
Warren	31.4103	147.4506	Shorter season	Oct. 12, 2020	Sicot 748B3F	1	Apr. 23, 2021
Trangie	32.0325	148.0302	Shorter season	Oct. 18, 2020	Sicot 748B3F	1	May 10, 2021
Benerembah	34.2458	145.5246	Shorter season	Oct. 4, 2020	Sicot 714B3F	1	May 11, 2021
Whitton[a]	34.3515	146.1133	Shorter season	Oct.10, 2020	Sicot 714B3F	1	May 29, 2021
Leeton[a]	34.3648	146.2507	Shorter season	Oct. 8, 2020	Sicot 714B3F	1	May 21, 2021
2021							
Comet[a]	23.3714	148.3057	Full season	Aug. 3, 2021	Sicot 748B3F	1	Feb. 8, 2022
Cecil Plains[a]	27.3508	151.1554	Full season	Oct. 15, 2021	Sicot 606B3F	1	May 15, 2022
Brookstead[a]	27.4326	151.2428	Full season	Oct. 10, 2021	Sicot 748B3F	1	May 20, 2022
St. George	28.0616	148.4228	Full season	Oct. 6, 2021	Sicot 748B3F	1	Apr. 28, 2022
Goondiwindi[a]	28.3333	150.1645	Full season	Nov. 20, 2021	Sicot 746B3F	1	May 25, 2022
Moree	29.2303	149.4607	Full season	Oct. 6, 2021	Sicot 748B3F	1	Apr. 11, 2022
Wee Waa	30.0831	149.3542	Shorter season	Oct. 25, 2021	Sicot 606B3F	1	Apr. 29, 2022
Trangie	32.0236	148.0234	Shorter season	Nov. 3, 2021	Sicot 748B3F	1	May 10, 2022
Whitton[a]	34.3455	146.1138	Shorter season	Oct. 10, 2021	Sicot 714B3F	1	May 11, 2022
Leeton (site 1)[a]	34.3648	146.2507	Shorter season	Oct. 12, 2021	Sicot 746B3F	1	May 10, 2022
Leeton (site 2)[a]	34.3644	146.2508	Shorter season	Oct. 12, 2021	Sicot 606B3F	1	May 12, 2022

[a]Core sites with larger plot size that enabled biomass sampling. Dash (–) denotes site unable to be picked due to storm damage just prior to lint harvest, assessment of total biomass, maturity and boll size were completed prior to storm damage.

TABLE 2 Treatment structure and sympodia (S) (counting from ground up) from which squares were either damaged and subsequently aborted or left intact.

Sympodia	Treatment 1 (S1–5)	Treatment 2 (S6–10)	Treatment 3 (S1–10)	Control
1–5	Damaged	Intact	Damaged	Intact
6–10	Intact	Damaged	Damaged	Intact

produced. Dates of first flower and first open boll were defined according to the presence of one occurrence per meter of crop row. Cut-out was defined when there were less than four nodes above white flower (Bourland et al., 1992). All samples were weighed immediately after drying; masses are presented on an oven-dry basis.

The maturity profile of bolls within treatment plots leading up to defoliation and picking was determined by counting, hand harvesting, and then weighing open bolls from 2 m of row within each plot every 6–9 days from first open boll to complete crop maturity. The term "pickable" described bolls where all or a significant proportion of the boll was open, with the lint unfurled and available for machine spindle. Relative maturity of the crop among the treatments was assessed by estimating the date when 60% of bolls were open, which is a method for timing of chemical defoliation of cotton (Bange & Milroy, 2000; Snipes & Baskin, 1994). The Brookstead site in 2020 was unable to be accessed routinely due to flood water for regular maturity picking and was therefore excluded from the maturity picking analysis.

The intra-canopy distribution of boll number and size was measured using a segmented hand-picking technique, in the majority of experiments, just prior to harvest on 2 m of crop row. The canopy was compartmentalized into the following sections that were handpicked separately:

1. first position bolls (P1) on sympodial branches 1–5;
2. first position bolls (P1) on sympodial branches 6–10;
3. first position bolls (P1) on sympodial branches 11–15;
4. first position bolls (P1) on sympodial branches 16 and above;
5. outer position bolls across all sympodial branches; and
6. bolls on the monopodial branches.

Yield was determined in the core experiments by picking an entire 10 m row with a single-row spindle picker. In some core experiments, picking machinery was unavailable, and handpicking was utilized instead on 10 m of row. For the experiments with a single row, the remaining 6 m of row subsequent to maturity and segmented picking assessment was handpicked and combined to provide a measure of yield for 10 m of row. Handpicked yields were reduced by 10% to account for likely inefficiency associated with mechanical harvest. The Moree experiment site in 2020 was damaged a day before scheduled picking by a severe storm that prevented final yield assessment but not all other previous measures. Lint yield was calculated by ginning a 400 g subsample with a 10-saw laboratory mini-gin. The turnout measurements were adjusted for each experiment using the commercially ginned crop average from field area that each experiment was located in. Typically, mini-gin lint fraction results were 3–4 percentage points higher than those measured during industrial-scale gin processing. Lint samples were collected to measure fiber

length (mm), micronaire (a measure of fiber fineness and maturity, µg in.$^{-1}$), and fiber strength (g tex^{-1}). Fiber quality was measured using a high volume instrument operated by a commercial fiber classer (Proclass).

The traits of interest that were analyzed include numbers of bolls m^{-2}, total fruiting site m^{-2}, final boll retention percentage, mean boll weight, lint yield kg ha^{-1}, total biomass g m^{-2} and boll fraction, days from sowing until 60% open bolls, and lint quality (fiber length, strength, and micronaire). Analyses of these traits, across experiments, were performed using linear mixed models and fitted with restricted maximum likelihood. The factorial combination of damage treatments and experiment were fitted as fixed effects and block was fitted as a random effect. For traits partitioned into different canopy sections, a section term was also included in the factorial combination, while plot was added to the random effects. Separate block and residual variances were fitted for each experiment.

Supplementary analysis to examine the influence of year and environment on the traits of interest was undertaken to assist with meaningful interpretation. Experiments were defined as either full or shorter season based on location above or below 30.0° S (Table 1). These subsequent analyses were then conducted on each trait, whereby the (fixed) treatment structure was extended to consider the nesting of experiments within environment.

Additionally, to compare just the undamaged control and the S1–5 damage treatment, across experiments for relevant traits, an embedded factorial structure was used to isolate that comparison and its interactions.

All analyses were performed in Genstat (22nd Edition, VSN International, 2022), whereby the level of significance was set at 5% for all testing. Significant effects were further explored using the protected least significant difference test.

3 | RESULTS

The interaction between environment, experiment and damage treatment, and year, experiment, and damage treatment was significant ($p \leq 0.05$) for lint yield, fiber length, time to maturity, and biomass, and therefore treatments were compared within each experiment.

The impact of the damage treatments on yield was limited with no significant ($p > 0.05$) reductions from any of the damage treatments at 18 of the 29 picked experiment sites (Table 3). Treatment S1–5 in which squares were removed pre-flowering significantly ($p = 0.002$) reduced yield by 9% in one experiment (Leeton location 2020), but conversely increased ($p \leq 0.05$) yields by 10%–14% in three experiments compared with the undamaged control (Table 3), and had no significant effect in the remaining 25 experiments.

The only yield increase for the remaining damage treatments occurred at St. George in 2021, with the S6–10 and

TABLE 3 Lint yield for each experimental site.

Location and year	Control	S1–5	S6–10	S1–10	Fprob	LSD
2018						
Goondiwindi	2274	2267	2492	2347	0.151	111.0
2019						
Emerald	2605	2589	2454	2531	0.396	103.8
Dalby	1823	1779	1891	1791	0.340	71.5
Brookstead	2260	2272	2340	2336	0.811	118.9
Goondiwindi	2689	2596	2737	2618	0.805	180.8
Whitton	2537	2688	2447	2531	0.779	265.4
2020						
Comet	2826	2840	2978	2722	0.266	135.0
Norwin	2538	2492	2448	2456	0.973	240.7
Cecil Plains	2805b	3100a	2835b	2951ab	0.040	100.4
Brookstead	2200	2262	2287	2401	0.722	199.5
St. George	2621	2709	2646	2648	0.725	89.5
Mungindi	2931	3199	2965	2871	0.482	243.5
Goondiwindi	3208a	3110a	3013ab	2829b	0.043	127.4
Moree	–	–	–	–		–
Warren	2789a	2758a	2659ab	2404b	0.041	136.1
Trangie	2890	2997	2652	2972	0.076	140.3
Benerembah	2586a	2602a	2585a	2256b	0.040	130.6
Whitton	2685	2556	2457	2185	0.352	305.0
Leeton	3137a	2853b	2710b	2476c	0.001	99.4
2021						
Comet	3206	3295	3278	3150	0.907	251.4
Cecil Plains	2582a	2723a	2308b	1977c	0.001	75.4
Brookstead	1831	1780	1856	1599	0.577	222.4
St. George	3157b	3241ab	3325a	3370a	0.049	76.6
Goondiwindi	2535b	2818a	2387b	1970c	0.001	163.4
Moree	3316a	3482a	3224ab	2898b	0.017	163.4
Wee Waa	3076b	3516a	2703c	2712c	0.001	145.5
Trangie	2763	2670	2505	2419	0.249	194.9
Whitton	3006	2887	3040	2840	0.743	239.8
Leeton (site 1)	2880	2722	2746	2700	0.250	102.1
Leeton (site 2)	3165a	3009ab	2958b	2737c	0.009	103.3

Note: Moree experiment 2020 was lost to storm damage a day prior to scheduled picking. When there are significant overall treatment effects in an experiment (Fprob ≤ 0.05), treatment means for damage treatments with the same letter are not significantly different.

Abbreviations: LSD, least significant difference; S, sympodia.

S1–10 treatments being 5%–6% greater ($p = 0.049$) than the control. Yield was reduced by these damage treatments by 7%–14% at four experiment sites for S6–10 and by 12%–23% at nine experiment sites for S1–10 (Table 3).

The lint quality picked from all experiments and treatments exceeded the Australian market preference (no economic penalty) for fiber length and strength. Fiber length ranged from 1.11 to 1.33 with significant differences ($p \leq 0.05$) between treatments occurring at only three experiments (Table 4). Fiber strength was well above base grade of 26 g tex^{-1} for all plots in all experiments, ranging from 29 to 35.8, with significant treatment differences ($p \leq 0.05$) occurring in three experiments (Table 4). There was no consistent trend between damage treatments and these parameters across experiments.

Micronaire was the most responsive fiber characteristic to the damage treatments with significant reductions ($p < 0.05$) occurring in seven experiments primarily in response to the most damaging S1–10 treatment (Table 3). The interaction for environment × damage treatment was significant ($p = 0.007$)

TABLE 4 Parameters for lint quality at experimental sites where significant damage treatment differences occurred (Fprob ≤ 0.05).

Location and year	Control	S1–5	S6–10	S1–10	Fprob	LSD
	Length					
Goondiwindi 2018	1.19c	1.19bc	1.21b	1.23a	0.003	0.017
Moree 2021	1.26bc	1.29a	1.26c	1.29ab	0.046	0.026
Wee Waa 2021	1.18b	1.25a	1.26a	1.25a	0.008	0.042
	Strength					
Warren 2019	32.34a	31.47ab	30.88b	31.06b	0.049	1.06
Whitton 2020	31.29a	30.10bc	31.07ab	29.45c	0.003	0.99
Wee Waa 2021	29.03c	32.23ab	31.74b	34.04a	0.007	2.01
	Micronaire					
Whitton 2019	5.38 a	5.01a	5.16a	4.60b	0.009	0.40
Cecil Plains 2020	4.87a	4.34b	4.35b	4.28b	0.019	0.35
Warren 2020	3.80a	3.94a	3.75a	3.19b	0.039	0.51
Whitton 2020	3.56a	3.31a	3.29a	2.83b	0.001	0.28
Cecil Plains 2021	4.65a	4.63a	4.68a	4.35b	0.037	0.23
Wee Waa 2021	4.60a	4.33ab	4.31ab	3.88b	0.042	0.46
Leeton (site 2) 2021	4.68a	4.45b	4.35bc	4.23c	0.005	0.20

Note: Within an experiment, treatment means with the same letter are not significantly different.

Abbreviations: LSD, least significant difference; S, sympodia.
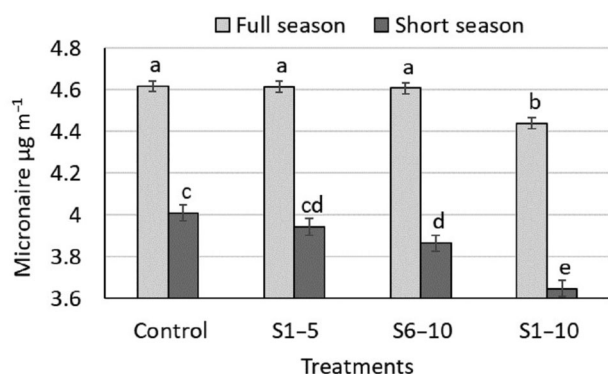
FIGURE 1 The relationship between environment (full and shorter season) and damage treatments for fiber micronaire µg in.$^{-1}$ measured for picked lint (Fprob = 0.007). Bars denote treatment means and bars with the same letter are not significantly different (least significant difference [LSD] = 0.09). Error bars denote ± SE.

with a nonsignificant environment × experiment × damage treatment interaction ($p = 0.22$), hence the data were explored across seasons. Micronaire was lower in the shorter season environments and more sensitive to later (S6–10) or more extensive (S1–10) damage treatments compared to full season environments (Figure 1).

Compared with the control, the S1–5 treatment only caused a significant ($p ≤ 0.05$) delay in attaining 60% of bolls open by 1.5–3.9 days at six experiment sites (Table 5). This increased to 21 and 23 experiments being delayed ($p < 0.05$) by 2.0–8.3 and 4.4–11.5 days for the S6–10 and S1–10, respectively, compared with the control (Table 5).

Final biomass was only affected by damage ($p ≤ 0.05$) in four of the 20 core experiments, while the boll proportion of final biomass was significantly different ($p ≤ 0.05$) in six experiments (Table 6). In these instances, total biomass generally increased, while the proportion of bolls decreased in response to later or more extreme damage (Table 6).

The total fruiting sites and bolls produced could be described by environment × damage treatment ($p < 0.001$ for both), as the nested term of experiment within environments, and its interaction with damage treatment was not significant. Total fruiting site number in the control did not vary between full and shorter season environments, but increased in response to later or more severe damage with experiments in shorter season environments, producing greater numbers than full season environments (Figure 2). This trend did not directly translate into an increasing number of bolls across treatments at maturity in full season environments, with no meaningful change for boll number occurring (Figure 3). Short season environments retained significantly higher numbers of bolls, but lacked a stepped commensurate increase in numbers with the damage treatments. The damaged treatments were not significantly different to each other, and S6–10 was not significantly different from the control (Figure 3). Boll size was mostly unaffected by the damage treatments with no differences ($p > 0.05$) in 25 of the 29 experiments. All damage treatments caused a reduction in boll size at Whitton in 2021, while impact was limited to only the S1–10 treatment at the three remaining experiment sites (Table 7).

TABLE 5 Time 60% boll opening (DAS) for experimental sites where significant damage treatments differences occurred (Fprob ≤ 0.05).

Location and year	Control	S1–5	S6–10	S1–10	Fprob	LSD
2018						
Goondiwindi	138.4c	140.9b	142.2b	149.3a	0.000	2.34
2019						
Emerald	161.6c	163.3bc	165.5ab	167.1a	0.011	2.96
Dalby	176.6c	179.7b	184.7ab	185.7a	0.000	2.27
Brookstead	173.4c	175.4bc	176.6b	180.9a	0.000	2.34
Goondiwindi	168.3b	169.3b	172.6a	173.7a	0.000	1.67
Whitton	199.2bc	201.0bc	202.9ab	204.0a	0.012	2.63
2020						
Comet	207.0b	208.9b	213.1a	215.5a	0.002	3.61
Norwin	177.6d	180.9c	185.9b	188.0a	0.000	2.00
Cecil Plains	189.1c	190.6c	195.9b	198.1a	0.000	1.87
Goondiwindi	188.6c	189.6c	191.5ab	193.0a	0.016	2.55
Warren	192.2c	193.5c	195.8ab	197.2a	0.044	3.58
Trangie	190.8c	191.5c	194.7b	197.8a	0.001	2.86
Whitton	209.1c	212.6c	212.3b	220.6a	0.000	2.52
2021						
Comet	175.2c	178.4c	178.6b	184.0a	0.001	3.10
Cecil Plains	195.0c	196.4c	200.7b	206.4a	0.000	3.65
Brookstead	203.0b	203.6b	208.3a	209.7a	0.008	3.88
St. George	182.3c	182.0c	185.8b	188.7a	0.000	2.37
Moree	162.6b	166.2b	167.8a	170.3a	0.043	5.05
Wee Waa	187.0c	190.8b	191.2b	195.3a	0.000	2.05
Trangie	172.2bc	171.6c	174.8b	180.0a	0.000	2.85
Whitton	200.9b	204.7b	205.1a	207.4a	0.006	2.99
Leeton (site 1)	204.6c	206.1b	206.6b	209.5a	0.001	1.72
Leeton (site 2)	197.5b	201.4a	203.4a	204.1a	0.003	3.01

Note: The 2020 Brookstead experiment could not be routinely maturity picked due to site access constraints and therefore was not included in this analysis. Within an experiment, treatment means for damage treatments with the same letter are not significantly different.

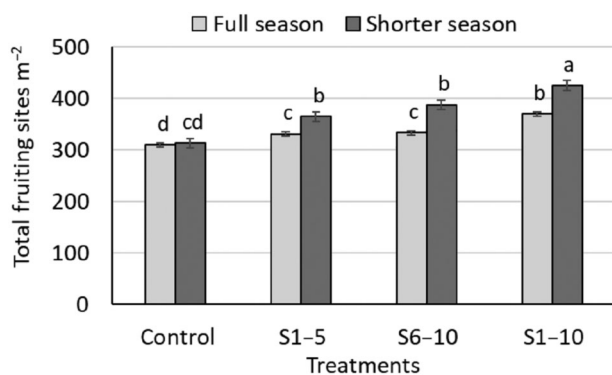Abbreviations: LSD, least significant difference; S, sympodia.

FIGURE 2 The relationship between environment (full and shorter season) and treatments for the total number of fruiting sites produced by crop maturity (Fprob < 0.001). Bars denote treatment means and bars with the same letter are not significantly different (least significant difference [LSD] = 18.5). Error bars denote ± SE.
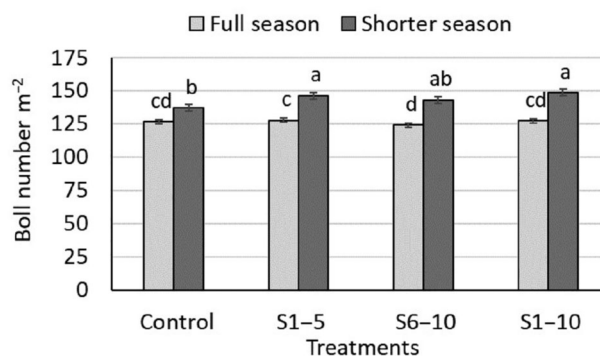

FIGURE 3 The relationship between environment (full and shorter season) and treatments for the total number of pickable bolls at crop maturity (Fprob < 0.001). Bars denote treatment means and bars with the same letter are not significantly different (least significant difference [LSD] = 5.92). Error bars denote ± SE.

TABLE 6 Mean final total biomass and relative proportion of bolls (vs. stem and leaf) for the damage treatments at the core experiment sites where biomass samples were taken.

Location and year	Final total biomass (g m^{-2})					Proportion of final biomass as bolls (%)				
	Control	S1–5	S6–10	S1–10	LSD	Control	S1–5	S6–10	S1–10	LSD
2018										
Goondiwindi	1118c	1195bc	1280b	1436a	139.11	57.9	57.7	58.4	56.5	1.78
2019										
Brookstead	1484	1455	1469	1673	260.69	55.0a	54.6a	50.8b	49.1b	2.39
Goondiwindi	1592bc	1547c	1778ab	1838a	189.45	57.1a	55.7ab	51.8bc	48.2c	4.34
2020										
Whitton	1177	1367	1230	1256	414.88	64.2a	56.5b	57.9b	49.4c	4.14
2021										
Comet	1723	2012	1862	1727	224.60	57.3a	57.9a	53.3b	49.0c	3.08
Cecil Plains	1457b	1497b	1578b	1764a	179.53	65.7a	61.3b	60.5b	52.3c	2.95
Brookstead	1571c	1883ab	1664bc	2053a	264.72	52.9	52.5	49.2	48.3	5.03
Leeton (site 2)	1669	1650	1757	1739	154.92	53.5a	52.1ab	50.7bc	49.1c	2.82

Note: Only the results from experiments with significant overall treatment effects (Fprob ≤ 0.05), for either trait, are shown. Within an experiment, treatment means for damage treatments with the same letter are not significantly different.
Abbreviations: LSD, least significant difference; S, sympodia.

TABLE 7 Mean boll size at experimental sites where significant damage treatment differences occurred (Fprob ≤ 0.05).

Location and year	Control	S1–5	S6–10	S1–10	Fprob	LSD
	Grams seed cotton/boll					
Leeton 2020	4.7a	4.7a	4.5ab	4.3b	0.039	0.32
Cecil Plains 2021	5.2a	5.3a	5.1a	4.7b	0.008	0.29
Whitton 2021	4.6a	4.3b	4.3b	3.7c	0.039	0.32
Leeton (site 2) 2021	5.4a	5.2a	5.3a	5.0b	0.001	0.23

Note: Within an experiment, treatment means with the same letter are not significantly different.
Abbreviations: LSD, least significant difference; S, sympodia.

None of the interactions were significant ($p > 0.05$) for final boll retention, which was highest ($p < 0.001$) for the control and decreased across damage treatments (Figure 4).

The spatial distribution of bolls and their size across the canopy was measured in 22 of the 30 experiments. An analysis comparing experiments, damage treatments, and the six canopy sections for both measures produced a complex three-way ($p < 0.001$) interaction that was difficult to meaningfully interpret. As the comparison between the S1–5 treatment that simulated pre-flowering square loss with the control was of most interest from a commercial pest management perspective, the analysis was re-run comparing just these two damage treatments. These analyses also produced a highly significant three-way interaction ($p < 0.001$). However, exploring the interaction within each canopy section showed meaningful trends for boll number, demonstrating the impact of fruit loss toward compensatory boll set (Figure 5).

The number of bolls in canopy section 1 was always higher for the control treatment compared to the S1–5 damage treatment and significantly so for 19 of 22 experiments (Table 8; Figure 5), and is explained by boll removal during damage implementation (Table 2). The retention of first position bolls on the subsequent next five sympodia (canopy section 2) was largely the same for the control and S1–5 treatment (Table 8). A general trend for increased boll retention in canopy sections 3 and 4 was apparent for the S1–5 treatment across most experiments (Figure 5) despite significance being limited to three experiments for canopy section 3, and two experiments for canopy section 4, and being reduced for canopy section 3 in one experiment (Table 8). Notably, the number of bolls retained on outer positions across the sympodia generally trended higher across nearly all experiments (Figure 5), with 10 out of 22 being significantly higher for S1–5 ($p < 0.001$). This trend was less evident across experiments for bolls borne on monopodia branches (Figure 5) but where significant dif-

TABLE 8 The number of experimental sites where significant differences occurred (Fprob ≤ 0.05) between the control and the S1–5 treatment in each canopy section for the number of harvestable bolls retained and boll size.

	Canopy section					
Treatments	**1**	**2**	**3**	**4**	**Outer bolls**	**Monopodia bolls**
	Boll number					
Control > S1–5 ($p < 0.001$)	19	1	1	0	0	0
Control < S1–5 ($p < 0.001$)	0	1	3	2	10	4
Control and S1–5 ($p > 0.05$)	3	20	18	20	12	18
Total experiments	22	22	22	22	22	22
	Boll size					
Control > S1–5 ($p < 0.001$)	5	0	1	3	0	1
Control < S1–5 ($p < 0.001$)	2	0	1	0	1	3
Control and S1–5 ($p > 0.05$)	13	22	20	11	21	18
Total experiments	20	22	22	14	22	22

Note: Not all experiments had bolls present at canopy section 4. Canopy sections 1–4 consist of first position bolls on sympodia 1–5, 6–10, 11–15, and ≥16 respectively. Outer bolls consist of all second, third, or fourth position bolls present across all sympodia and monopodia bolls were those borne on monopodial branches.
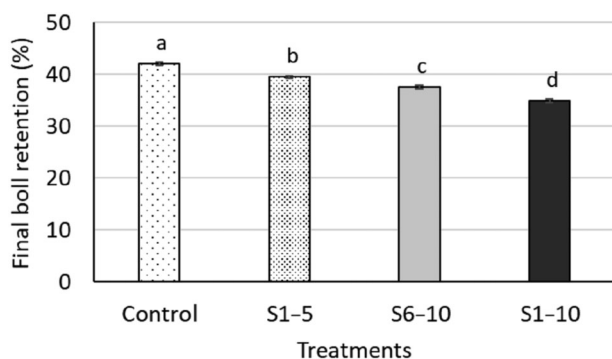
FIGURE 4 The number of bolls retained divided by total fruiting sites (%) across all experiments. All treatments are significantly different (Fprob < 0.001). Bars denote treatment means and bars with the same letter are not significantly different (least significant difference [LSD] 0.621). Error bars denote ± SE.

ferences occurred in four experiments, monopodial bolls were higher for the S1–5 treatment compared to the undamaged control (Figure 5; Table 8).

Boll size was less instructive with differences between the control and S1–5 when compared for the six canopy sections across experiments being largely nonsignificant with no consistent trends favoring either treatment where differences occurred (Table 8).

4 | DISCUSSION

The study sites were high yielding with the undamaged control treatment ranging from 1823 to 3316 kg lint ha^{-1} and mean of 2721 kg ha^{-1} (Table 3), exceeding the most recent Australian average (Conaty & Constable, 2020). Despite square removal from designated treatment sympodia being much more extensive than typical insect damage and reducing boll retention (Figure 4), subsequent impact at these high-yield levels was limited. Of most interest was the simulation of severe early-season square loss from the first five sympodia (S1–5) prior to flowering. Many crop managers control pest insects during this crop phase, intent on preserving yield potential (Sequeira, 2019; Whitehouse, 2011). In overall terms, extensive pre-flowering square loss did not negatively impact lint yield. The significant loss in one experiment was countered by gains in three experiments and no significant differences in the remaining 25 experiments (Table 3). The experiments where a significantly higher yield occurred due to the damage treatments can be explained by mature boll loss from the bottom sympodia in the control plots due to rainfall-induced boll rot during early dehiscence (Batson, 2001). The S1–5 treatment avoided this weather-related damage as subsequent compensatory bolls were set higher up or at more distal sympodia positions in the canopy (Figure 5) where the microclimate is less conducive to boll rot disease (Srivastava et al., 2010) and explains the relative yield difference. The near complete compensation for pre-flowering square loss in our experiments concurs with the findings of other studies where similar levels of pre-flowering damage were applied (Bednarz & Roberts, 2001; Herbert et al., 2006; Kerns et al., 2016; Lei & Gaff, 2003; Wilson et al., 2009) and suggests that cotton compensatory processes remain effective despite continued advancement of lint yield. Additionally, these results were achieved in shorter and full season environments, across multiple seasons, and under commercial conditions without any crop management intervention that might encourage compensation.

Square loss impact increased when either a similar quantum of damage was applied during early flowering (treatment S6–10) or as a second damage event (treatment S1–10),
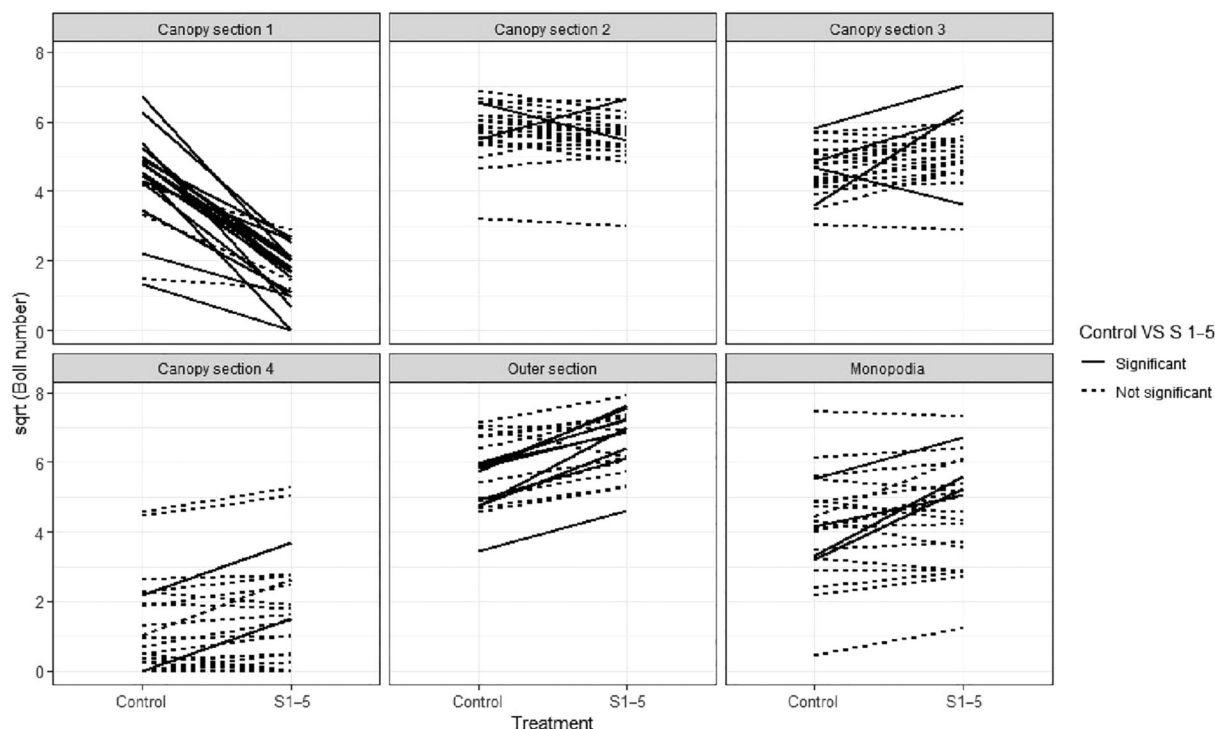
FIGURE 5 The sqrt of the number of bolls present in each canopy section for the undamaged control and the S1–5 early-season square removal treatment across 22 experimental sites. A solid line depicts where the control is significantly different to S1–5. Canopy sections 1–4 represent first branch position bolls on sympodia 1–5, 6–10, 11–15, and ≥16, respectively. Outer section represents second, third, or fourth branch position bolls across all sympodia. Monopodia represent bolls borne on monopodial branches. sqrt, square root.

although full compensation still occurred at 20 of 29 picked experiments for the severely damaged S1–10 treatment (Table 3), providing a compelling demonstration of compensation capacity at very high-yield levels. Notably, the additional fruiting sites and bolls produced as part of the compensatory process (Figures 2 and 3) were achieved within the time frame that the surrounding commercial field area (representative of the control plots) was defoliated for harvest preparation. Interestingly, the increase in total fruiting sites in response to square loss was more exaggerated in shorter season environments (Figure 2) and translated into more bolls, which did not occur in long season environments (Figure 3). This "overcompensation" did not increase yield, which is possibly explained by the interaction between climate-related resources impacting assimilate supply mid-season when fruiting sites were initiated and subsequent conditions late season as bolls are matured (Grundy et al., 2020; Sadras, 1995). The summer solstice coincides early flowering for full and shorter season crops grown in temperate Australia, which synchronizes increasing boll demand for assimilate (Guinn, 1985; Mauney et al., 1978) with conditions that are conducive for peak supply. The higher daily solar radiation during the solstice, followed by a quicker decrease in both radiation and temperature, compared to locations experiencing a full season (23–30° S), might clarify why the over-compensation pattern observed in shorter season locations (30–36° S) did not result

in proportionately increasing boll number across the damage treatments, as shown in Figures 2 and 3, or yield (Table 3).

From a market perspective, lint quality was largely unchanged by square loss, particularly when it occurred pre-flowering. Micronaire was responsive to square removal (Table 4) with more pronounced reductions in shorter season environments and when damage occurred during early flowering (Figure 1). Micronaire is an indirect measure of fiber fineness and maturity, with premium cotton being within a range of 3.8–4.5 µg in.$^{-1}$ (Luo et al., 2016) and penalties incurred for fiber outside of 3.5–4.9 µg in.$^{-1}$ (Bange et al., 2009). Temperature is one of the most important environmental factors impacting micronaire during boll development with sustained high temperatures increasing micronaire and lower temperatures reducing it (Braunack et al., 2012; Reddy et al., 1999). The delay in boll opening (Table 5), influenced by altered age structure as compensatory bolls were set in more distal sympodia positions (Table 8; Figure 5), explains the reducing micronaire trend, especially in shorter growing season environments (Figure 1) that have cooler early-autumn conditions. The impact of reduced micronaire on lint market quality would depend on mid-season conditions. In our experiments, micronaire reduction was detrimental at Whitton in 2020, with the damage treatments falling below 3.5 µg in.$^{-1}$ (Table 4) that would attract a price discount. However, the impact of decreasing micronaire following square loss on lint

marketability is weather dependent, as the same location in the previous year (Whitton location [2019]) produced lint with micronaire well above 5.0 μg in.$^{-1}$ and only the S1–10 treatment reduced it enough to fall within the market preference range at 4.6 μg in.$^{-1}$ (Table 4). As mid-season environmental conditions are difficult to predict when early-season squares are lost, implementing early-season insect management with the aim of preserving lint quality would appear unreliable.

Harvest delays of 6 or more days are concerning for cotton growers (Wilson et al., 2003) and can motivate early-season pest management. In our study, treatment plots were picked just prior to the harvest of the commercial fields in which they were situated, which disallowed harvest delay. Maturity picking was used to understand treatment impact on the time to 60% boll opening, which is one method for determining the time for defoliant and harvest aid application (Faircloth et al., 2004; Siebert & Stewart, 2006). Only minor boll opening delay was associated with pre-flowering square loss, which increased for later or more severe square loss (Table 5). Despite delays in early boll opening in the damage treatments, a higher percentage of bolls opened over a shorter period from mid-boll opening onward, limiting treatment impact on maturity and yield. This is similar to what has occurred in other cotton square loss studies (Mann et al., 1997; Stewart et al., 2001) and explains why minor delays to 60% boll opening, particularly for pre-flowering square removal, had little impact on yield despite fewer open bolls at the commencement of defoliation, with remaining unopened bolls being mostly mature. In comparison, in the nine experiments where yield of the S1–10 treatment was significantly reduced, five of these were significantly less mature at the commencement of defoliation (Table 5), which may partly explain lower yield with immature bolls being potentially abscised due to ethephon application (Kittock et al., 1973; Reddy, 1995).

Increases in biomass from square loss were skewed toward the most damaging treatment S1–10 and where boll proportion was altered, the trend was for decreased boll versus vegetative components (Table 6). This reflected the increase of total fruiting sites produced as retention decreased in response to delayed and more severe square removal (Figures 2 and 4), with fruit loss creating surplus assimilate (Mauney, 1986) and enabling continued growth and site initiation. This compensatory process following pre-flowering square loss increased retention of first position bolls in the upper canopy (sympodia 10–15) and distal sympodia sites (Figure 5; Table 8) where bolls might typically be shed due to demand from earlier set bolls (Mauney, 1986; Stewart et al., 2001). In comparison to boll production occurring via growth of additional sympodia ≥16 from the mainstem terminal, the compensatory boll set via the elongation of existing sympodia that occurred simultaneously was time efficient and explains the limited maturity, lint yield, and quality effects. Boll size remained the same between treatments at the majority of experiments

(Table 7) and across canopy sections when the control and S1–5 were compared, indicating increased boll size was not a primary compensation mechanism. This concurs with Bednarz and Roberts (2001) and Stewart et al. (2001) who found that compensation primarily occurred through subsequent boll production rather than increased boll size.

Our results at very high-yield levels were consistent with a range of previous studies (Kerns et al., 2016; Lei & Gaff, 2003; Mann et al., 1997; Stewart et al., 2001; Wilson et al., 2003) and support two compensatory hypotheses advanced by others (Bednarz & Roberts, 2001; Sadras, 1995). First, in response to square loss, reproductive structures that may have otherwise physiologically shed from more distal sympodial positions are instead retained, and second, additional fruiting sites may be produced. Consistent with Bednarz and Roberts (2001), there was little evidence in our study for a third compensatory mechanism suggested by Sadras (1995) for increased boll size. The first two mechanisms explain the compensation of yield with limited impacts on lint quality and crop maturity. However, adverse effects were observed when squares were removed after flowering had begun, particularly when this damage compounded pre-flowering square loss. With the potential for yield reduction to increase with ongoing fruit loss as flowering advanced, further research into the effect of square and boll loss throughout flowering could provide valuable insight for the limitations of yield compensation.

Our study suggests that pre-flowering pesticide use to prevent mirid-related square loss is unlikely to provide yield benefits, and that the third of sprays reportedly applied to below threshold populations (Sequeira, 2019) are inconsequential. Instead, crop protection inputs would be better focused from just prior to and following commencement of flowering.

5 | CONCLUSION

Despite the very high potential yield of Bollgard 3 cultivars grown in Australia, crop maturity, lint yield, and quality were not materially affected by pre-flowering square loss, with impacts becoming more significant when square loss occurred after the commencement of flowering or where pre-flowering loss was compounded by additional square loss during early flowering. The compensation of lost fruiting sites was rapid, enabled by increased retention of first position bolls on upper canopy sympodia and production of additional bolls on existing sympodia at more distal positions, avoiding the need to produce additional mainstem nodes that take additional development time. The compensation of pre-flowering square loss occurred without any crop management intervention. Crop managers should be confident to reduce pesticide usage prior to flowering, which may produce a range of ancillary benefits.

If pre-flowering square loss does occur, a focus on maintaining retention from flowering onwards should enable timely compensation.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

ORCID
Paul R. Grundy https://orcid.org/0000-0002-0889-7663

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