

RESEARCH



Phenology-based recommendations for control of the litchi fruit borer (*Conopomorpha sinensis* Bradley, Lepidoptera)

Tai-Chuan Wang^{1,2} , JenYu Chang^{1,3*} , and Jer-Way Chang¹

Abstract

The litchi fruit borer (*Conopomorpha sinensis* Bradley) is a major pest threatening litchi (*Litchi chinensis* Sonn.) production by causing substantial fruit infestation and drop. Although pesticides are widely used, optimal application timing is debated due to imprecise descriptions of fruitlet stages and limited knowledge of pest behaviour in orchards. To address this, we aligned fruitlet development with litchi fruit borer behaviour to identify ideal pest-control timing that balances control intensity while maintaining productivity. Oviposition increased sharply during mid-development in both pesticide-treated and pesticide-free trees. Fruit abscission and fruitlet infestation rates were similar during this period, indicating that physiological factors largely determine early abscission despite borer attacks. Subsequently, pesticide-free trees exhibited higher infestation. During late development, 75–100% of shed fruitlets were damaged by the borer, suggesting the pest is the dominant factor in late fruit drop. Further analysis showed that fruit weight is the principal factor correlated with oviposition, while meteorological factors modulate the occurrence of damage. Using a fruit length of approximately 20 mm as a phenology-based indicator optimizes the timing of pesticide application. Furthermore, because insecticides primarily reduce post-oviposition survival rather than deterring oviposition itself, targeting this specific developmental stage is crucial for effectively preventing late-stage fruit loss.

Significance of the Study

1. What is already known on this subject?

Litchi fruit borer (*Conopomorpha sinensis* Bradley) is a major pest that causes substantial pre-harvest fruit drop and yield loss in litchi production. Currently, growers primarily rely on calendar-based pesticide applications, which often fail to align with the fruit's physiological susceptibility, leading to ineffective control, unnecessary chemical use and an increased risk of pesticide resistance.

2. What are the new findings?

Our high-frequency field monitoring combined with robust modelling identified a precise phenology-based indicator for pest control. We found that the borer predominantly causes late-stage fruit drop, whereas early-stage drop is mainly physiological. A fruitlet length of approximately 20 mm provides a practical early-warning reference for optimizing chemical interventions. Furthermore, applied insecticides were shown to primarily reduce post-oviposition survival (acting as ovicides or targeting young larvae) rather than deterring adult oviposition.

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3. What are the expected impacts on horticulture?

These findings provide orchard managers with a simple, actionable visual metric (20 mm fruitlet length) to optimize the timing of pesticide applications. This approach effectively eliminates wasted early-season sprays, promotes targeted chemical selection based on ovicidal activity and supports the development of more sustainable integrated pest management strategies for litchi and potentially other tropical fruit tree crops.

Keywords: subtropical fruit tree, insecticides, pest, infestation, oviposition

Introduction

Litchi (*Litchi chinensis* Sonn., Sapindaceae) is an important subtropical fruit crop valued culturally and economically. It has been revered as a royal tribute in China since the Han Dynasty, about 2000 years ago Hong (2020). Today, the fruit is grown in more than 20 countries in subtropical regions (Zhao *et al.*, 2020) and produces about 3.5 million tonnes annually, according to estimates (Mitra and Pan, 2020). However, litchi production incurs substantial losses due to the litchi fruit borer (*Conopomorpha sinensis*), which is widely distributed across East and South Asia and is a major pest of litchi and longan (Srivastava *et al.*, 2016; Li *et al.*, 2018). The litchi fruit borer completes multiple generations during the fruit development of litchi. Under field conditions, egg, larval and pupal periods range from 3–7, 7–11 and 7–13 days, respectively, resulting in a full life cycle of about 30–40 days (Hung *et al.*, 2002; Siraj *et al.*, 2023). Females lay eggs on fresh pericarp (approximately 80–160 eggs per female), and hatched larvae bore into fruit, causing premature drop and severe damage (Xie *et al.*, 2005; Siraj *et al.*, 2023). Consequently, orchard management targets this pest to protect yield and quality (Wang *et al.*, 2019).

Pesticides remain the primary method for controlling the litchi fruit borer (Wang *et al.*, 2022). Alternative approaches, such as fruit bagging, can reduce infestation but incur high labour costs (Debnath and Mitra, 2008; Wang *et al.*, 2019). In Taiwan, extension recommendations typically advise growers to begin insecticide applications 10–20 days after flowering ends and to reapply at 7–10-day intervals to disrupt the pest life cycle (Wang *et al.*, 2019; Chen *et al.*, 2022). However, calendar-based guidance is imprecise because phenology varies with environmental and physiological conditions (Chang *et al.*, 2015; Lee and Chang, 2019). Moreover, litchi experiences massive fruitlet drop in the first 2 months after female bloom due to competition for assimilates, embryogenesis and seed development (Stern *et al.*, 1995; Chang and Lin, 2008). The efficiency and effectiveness of early pesticide input need to be carefully assessed. A phenology-based timing tied to observable fruitlet developmental stages would therefore provide clearer, actionable guidance for growers. In this study, we examine oviposition and infestation timing relative to fruitlet development and identify key phenological and meteorological drivers of oviposition to inform targeted pest control.

Methods

FIELD MANIPULATION

To better understand the ecology of litchi fruit borer infestation, how pesticides interrupt pest damage and to effectively manage practical pest inputs, two pesticide-reduction field trials were performed in this study. The trial was conducted on 30-year-old 'Hak Ip' litchi trees at the agricultural experiment station (Latitude 23°29'05" N, Longitude 120°28'27" E, Altitude 77 m) in 2014 and 2015. In 2014, 18 'Hak Ip' trees were assigned to three regimes, which were separated by buffer rows of litchi trees to prevent

spray drift during chemical applications. Trees in two regimes, the pesticide-reduced treatment and the conventional treatment (positive control), were sprayed with 50% fenthion EC (1000× diluted, approximately 350 g a.i./ha; Sinon Corporation, Taiwan). Trees in the third regime were sprayed with water, serving as a pesticide-free control.

In 2014, trees in the pesticide-reduced regime were sprayed with the insecticide four times during fruit bearing on April 29, May 14, May 29 and June 10. For the conventional treatment, which followed the guidance of the domestic Plant Protection Manual, insecticide was initially scheduled for five applications at 10-day intervals (April 29, May 9, May 19, May 29 and June 10). However, an additional resupply was performed on May 14 in the conventional treatment due to heavy rainfall (47.5 mm) on May 13.

In 2015, the three regimes were arranged in the same orchard, separated by buffer rows, with five trees selected per regime. The conventional and pesticide-reduced treatments were applied using 2.4% deltamethrin SC (1500× diluted, approximately 18 g a.i./ha; Bayer, Germany). The conventional pesticide application was performed five times on April 22, May 1, May 12, May 22 and June 1. The pesticide-reduced treatment skipped the initial application and was performed four times, starting on May 1, following the exact corresponding dates of the conventional treatment. The remaining pesticide-free regime was sprayed with water on the same dates when chemical management was conducted. All fruit in the orchard was harvested on June 20, 2014, and June 11, 2015.

MONITORING THE LITCHI FRUIT GROWTH AND ABSCISSION PATTERNS, PEST OVIPOSITION AND INFESTATION BEHAVIOURS

A total of 26 and 31 panicles were labelled at full female bloom on each examined tree in 2014 and 2015, respectively. The number of fruits on six labelled panicles was investigated weekly after full female bloom (AFFB). The weekly relative fruit abscission rate (rFAR) was calculated according to the formula described by Chang *et al.* (2015). Ten fruitlets were randomly collected weekly from the remaining 20 (in 2014) or 25 (in 2015) labelled panicles on the left side of each tree in both years to measure fruit length, biomass, pest oviposition and infestation. Oviposition was observed under a stereomicroscope (Leica S8 APO).

The infestation rate of shed fruit was monitored weekly using three lattice baskets (48.5 × 38.3 × 12.5 cm) placed under the canopy of each tree starting three weeks AFFB. The quantity of shed fruit and the extent of pest infestation were subsequently calculated.

STATISTICAL ANALYSIS

Comparisons among field treatment groups (presence/absence of pesticide, infestation and damage metrics) were performed using R version 4.5.0 (R Core Team, Vienna, Austria). Percentage data, including relative fruit abscission rate, fruit retention rate (the ratio of final fruit number to that at week 1 AFFB), oviposition rate

and infestation rate, were arcsine-transformed before analysis to improve normality and homogeneity of variance. Transformed data were analysed using linear models, and post hoc pairwise comparisons were conducted using Fisher's least significant difference (LSD) test at $\alpha = 0.05$. We report sample sizes, test statistics and *P*-values for all tests; figures and percentages presented in the main text are presented as back-transformed means ($\pm$ SE) for ease of interpretation.

THRESHOLD ANALYSIS OF LITCHI FRUIT BORER OVIPOSITION

To identify the fruit-length threshold for oviposition, we fitted a hinge threshold regression between fruit length and oviposition rate for each treatment-by-year combination. The breakpoint was selected by grid search at 0.2-mm intervals within the 10th–90th percentile range of fruit length, and the value minimizing residual sum of squares was retained. Uncertainty was assessed by non-parametric bootstrap resampling (500 iterations). For each bootstrap sample, the breakpoint and fitted values were re-estimated, and 95% confidence intervals were obtained from the 2.5th and 97.5th percentiles of the bootstrap predictions. The lower confidence limit was constrained to be no less than zero. All analyses were performed in R.

RELATIONSHIPS BETWEEN FRUIT SIZE AND FRUIT WEIGHT

Fruit data from the control (pesticide-free) regime were analysed for 2014 and 2015. To examine the relationship between fruit length and fruit weight, fruit weight was log-transformed and an exponential regression model was fitted separately by year. The relationship was expressed as $fw = a \times \exp(b \times fl)$, where *fw* is fruit weight and *fl* is fruit length. After model fitting, R^2 and the *P*-value for the fruit length term were calculated for each year to evaluate model fit and statistical significance. These analyses were also performed in R.

IDENTIFICATION OF FACTORS INFLUENCING LITCHI FRUIT BORER OVIPOSITION

Field survey records from control (pesticide-free) regimes in 2014 and 2015 were merged with daily meteorological observations from the local weather station (<https://agr.cwa.gov.tw/>; site: G2L020). Observations were restricted to instances where both fruit weight and egg presence were recorded. From the daily series, we computed biologically informed rolling-window predictors for 1, 3 and 7 days: cumulative precipitation, and within-window minimum, mean and maximum temperatures, mean relative humidity and mean air pressure.

Candidate predictors comprised the full set of generated windowed features. Variable selection and hyperparameter tuning were performed using LASSO logistic regression (Tibshirani, 1996), implemented via the *LogisticRegressionCV* class in the scikit-learn library (Pedregosa et al., 2011). The model was configured with an L1 penalty and the SAGA solver to handle the non-smooth optimization required for sparse feature selection (using 10 candidate *C* values, 5-fold internal cross-validation and 5000 iterations). Fruit weight (*fw*) was specified a priori as a management-relevant covariate because it may serve as a key phenological indicator for the timing of pest control interventions; it was thus forced into the selected set regardless of the LASSO shrinkage. Variables retained by LASSO were examined for multicollinearity, and an iterative variance inflation factor (VIF) reduction procedure (threshold VIF = 10) (O'Brien, 2007) was

applied to remove highly collinear predictors while preserving the forced *fw* term.

All continuous predictors retained after VIF reduction were standardised (mean = 0, SD = 1). The final explanatory model was a generalized linear model (binomial family, logit link) fitted with heteroskedasticity-consistent HC3 standard errors to obtain robust confidence intervals for parameter estimates (MacKinnon and White, 1985). Results are reported as odds ratios (OR) per one standard deviation change with 95% confidence intervals. As a predictive complement, permutation importance (50 repetitions) was computed from a Random Forest classifier using the area under the receiver operating characteristic curve (ROC-AUC) as the scoring metric. This provided an alternative valuation of variable importance based on predictive performance (Breiman, 2001).

Results

Fruit retention is the primary objective of litchi production. Three fruit abscission peaks exist in all treatments during 'Hak Ip' fruit development (Fig. 1). These patterns were initially similar but different in the end. All the examined trees suffered a massive loss of fruitlets before the 5-week AFFB, ranging from 83.6% to 89.3% in 2014 and from 86.8% to 91.9% in 2015. After that, 46.7% to 50.4% and 27.6% to 43.3% of the left fruitlets dropped in the following month of each year. Notably, during the final month before harvest, the fruit abscission rate rose dramatically in 2014, especially in trees without pesticide treatment (Fig. 1A), representing a much lower fruit retention rate (0.98%) compared with those in pesticide applied regimes (conventional: 5.57%, pesticide-reduced: 3.59%; without significant difference between the two treatments) (Table 1). The ascent also occurred in pesticide-free treatment, reaching 75.2% in the last week in 2015 (Fig. 1B), with only 1.12% fruit retention rate. Apart from that, fruit drop remained slight in trees sprayed with 2.4% deltamethrin SC in that year, resulting in 8.61% and 7.90% in the conventional and pesticide-reduced treatment (Table 1).

To determine the relationships between pest infestation and fruit abscission, the shed fruitlets were sampled and checked whether litchi fruit borers damaged them. The quantity of shed fruit showed similar patterns among conventional, pesticide-reduced and pesticide-free trees each year, with a maximum before 4-week AFFB and a minimum at 8- to 9-week AFFB. Afterwards, the number of shed fruit went up again in the last month before harvest (Fig. 2). Regarding the infestation rate, there were no shed fruits preyed upon by litchi fruit borers at first until 4- or 5-week AFFB. At the same time, the proportion of pest-damaged fruits then significantly increased over the following weeks and reached a majority after 9-week AFFB. Over the last 3 weeks, the infestation rate in sampled fruitlets ranged from 75.0% to 100.0% (Fig. 2).

This study also surveyed litchi fruit borer infestation and oviposition behaviour on fruitlets. The pest infestation was observed around 6-week AFFB and increased sharply in the regimes without using pesticides, ending at 82.6% in 2014 and 90.0% in 2015 (Fig. 3). Both conventional and pesticide-reduced treatments had milder growth, especially on the previous one, during the fruit development as well, ending with 15.0% and 38.3% in 2014 and 10.0% and 18.0% in 2015, respectively (Fig. 3). In contrast to infestation, differences in the number of eggs laid among treatments were not significant (Fig. 4). Given fruit size was strongly and consistently related to fruit weight ($P < 0.0001$;

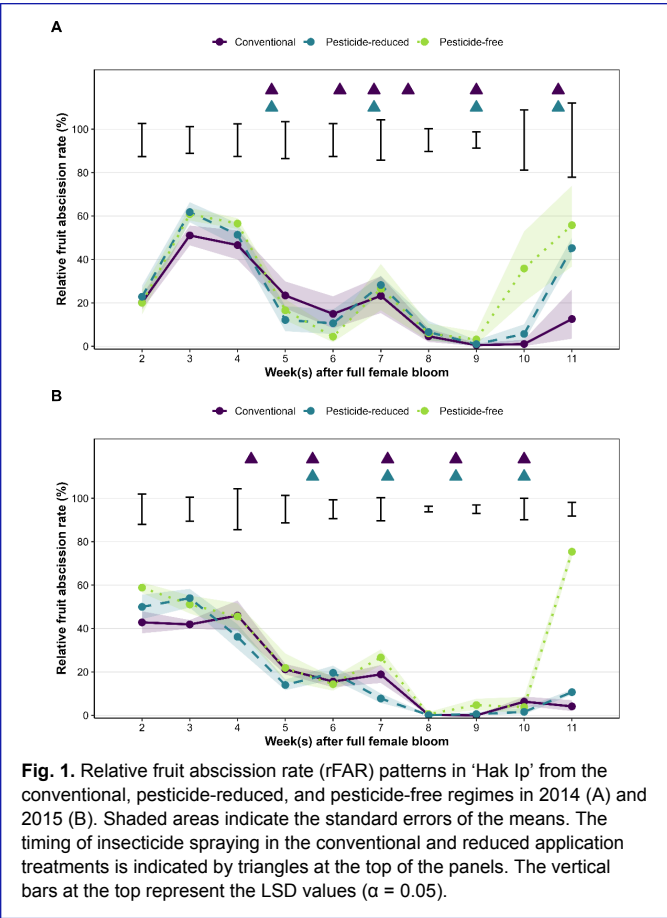


Table 1. Fruit number per panicle and final fruit retention rate under distinct pesticide management strategies evaluated in two independent trials (2014 and 2015).

Treatment	Fruit number per panicle		Fruit retention rate (%)
	1 week AFFB	11 week AFFB	
2014 (50% fenthion EC)			
Conventional	37.90 ± 6.91	2.35 ± 0.82	5.57 a
Pesticide-reduced	42.15 ± 4.10	1.42 ± 0.35	3.59 a
Pesticide-free	40.32 ± 3.92	0.35 ± 0.08	0.98 b
2015 (2.4% deltamethrin SC)			
Conventional	73.16 ± 10.39	5.76 ± 0.79	8.61 a
Pesticide-reduced	74.62 ± 6.88	5.62 ± 0.77	7.90 a
Pesticide-free	67.28 ± 2.36	0.74 ± 0.14	1.12 b

Data are expressed as mean ± standard error (SE). AFFB: after full female bloom. Statistical comparisons were performed exclusively among treatments within the same year. Different lowercase letters in the same column indicate significant differences according to Fisher's LSD test ($P < 0.05$). Note that the pesticide-reduced schemes differed between the two independent trials (see Materials and Methods for details). Linked Footnotes

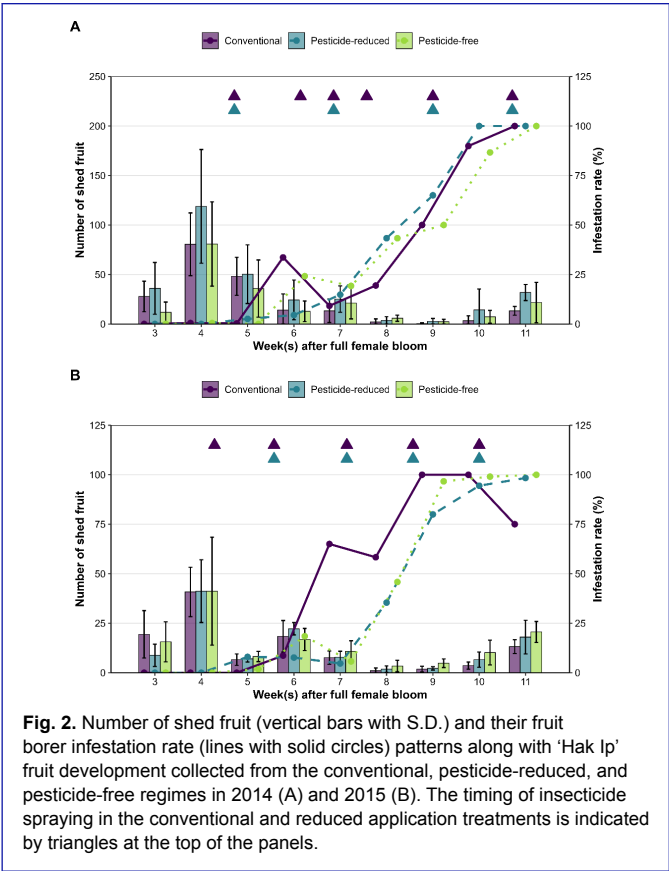


Fig. 2. Number of shed fruit (vertical bars with S.D.) and their fruit borer infestation rate (lines with solid circles) patterns along with 'Hak Ip' fruit development collected from the conventional, pesticide-reduced, and pesticide-free regimes in 2014 (A) and 2015 (B). The timing of insecticide spraying in the conventional and reduced application treatments is indicated by triangles at the top of the panels.

Fig. S1), fruit length was used as a proxy for assessing the onset of litchi fruit borer oviposition. Based on the threshold models, the onset of litchi fruit borer oviposition exhibited considerable interannual variation. In 2014, oviposition initiated when fruit length reached approximately 16.9–19.1 mm (3–5 weeks AFFB). However, in 2015, the critical fruit size for oviposition was notably larger, shifting to between 26.0 and 30.9 mm (Fig. 5). The oviposition rate reached and fluctuated from 95.0% to 100.0% after 8-week AFFB in 2014. It also showed a gradual upward trend in 2015. That year, the oviposition rate peaked at 10-week AFFB, then decreased in the next week, ranging from 38.0% to 60.0% on the fruit (Fig. 4).

Multiple factors may drive the probability of litchi fruit borer oviposition during fruit development. The LASSO selection procedure identified a parsimonious subset of six primary predictors from the initial meteorological candidate pool. These included standardized 3-day maximum temperature, standardized 1- and 3-day minimum temperatures, standardized 7-day mean relative humidity, and standardized 3-day mean air pressure, alongside the forced covariate, standardized fruit weight. The generalized linear model (GLM) was fitted using 877 observations from the 4–11 weeks after full female bloom in 2014 and 2015, yielding a pseudo R^2 of 0.52. Analysis revealed a highly significant association between the survey year and oviposition probability ($P < 0.001$). Using 2014 as the reference year, the standardized odds ratio (OR) for 2015 was 0.22, indicating a substantial reduction in the background pest level for the second study year.

Among the meteorological predictors, the 3-day maximum temperature exerted the strongest influence on the probability of egg presence ($P < 0.001$, OR = 4.979; Table S1). This was

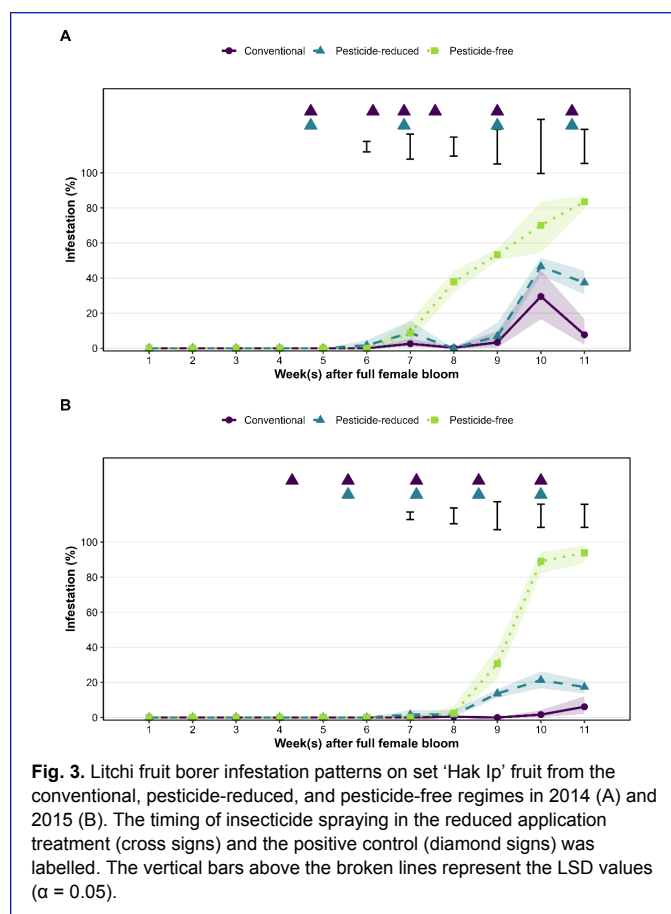


Fig. 3. Litchi fruit borer infestation patterns on set 'Hak Ip' fruit from the conventional, pesticide-reduced, and pesticide-free regimes in 2014 (A) and 2015 (B). The timing of insecticide spraying in the reduced application treatment (cross signs) and the positive control (diamond signs) was labelled. The vertical bars above the broken lines represent the LSD values ($\alpha = 0.05$).

followed by the 7-day mean relative humidity ($P < 0.001$, OR = 3.908; Table S1), and host phenology, represented by fruit weight, was also a significant positive predictor ($P = 0.004$, OR = 1.677; Table S1). Conversely, the 3-day mean air pressure was significantly and negatively correlated with infestation ($P = 0.006$, OR = 0.302; Table S1). Two additional predictors, the 1-day and 3 day minimum temperatures, were retained in the model through the selection process but did not reach statistical significance ($P = 0.122$ and $P = 0.255$, respectively).

To evaluate the robustness of each factor's contribution to model performance, we used a random forest classifier with permutation importance analysis. Fruit weight served as the primary baseline predictor, accounting for 86.8% of the relative predictive importance (AUC decrease = 0.0979; Fig. 6). This result highlights its role as the primary baseline for predicting pest presence. Relative importance scores for the remaining meteorological predictors ranged from 0.49% to 6.88% (Fig. 6). Specifically, mean air pressure over 3 days yielded a relative importance of 6.88% (AUC decrease = 0.0078), followed by 3-day maximum temperature (2.49%, AUC decrease = 0.0028) and 7-day mean relative humidity (1.32%, AUC decrease = 0.0015).

Discussion

The fruit abscission behaviour in 'Hak Ip' (Fig. 1) was similar to that of other litchi cultivars (Stern *et al.*, 1995; Stern and Gazit, 1999; Chang *et al.*, 2015). There was no significant difference in rFAR patterns between trees sprayed with pesticide and those not sprayed before the 9-week AFFB. The dramatic rise in rFAR occurred later across all treatments, especially in the

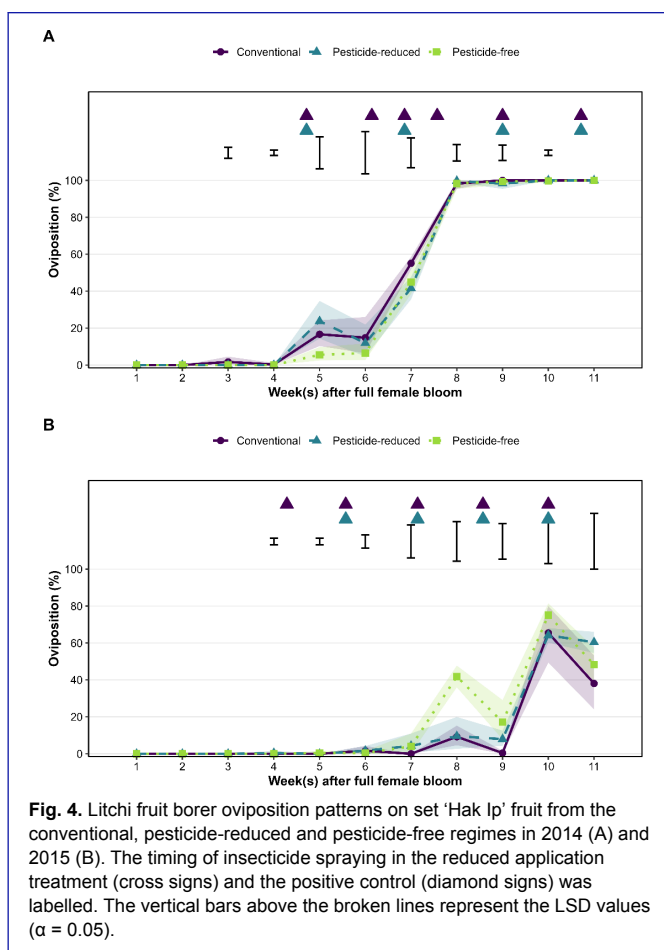
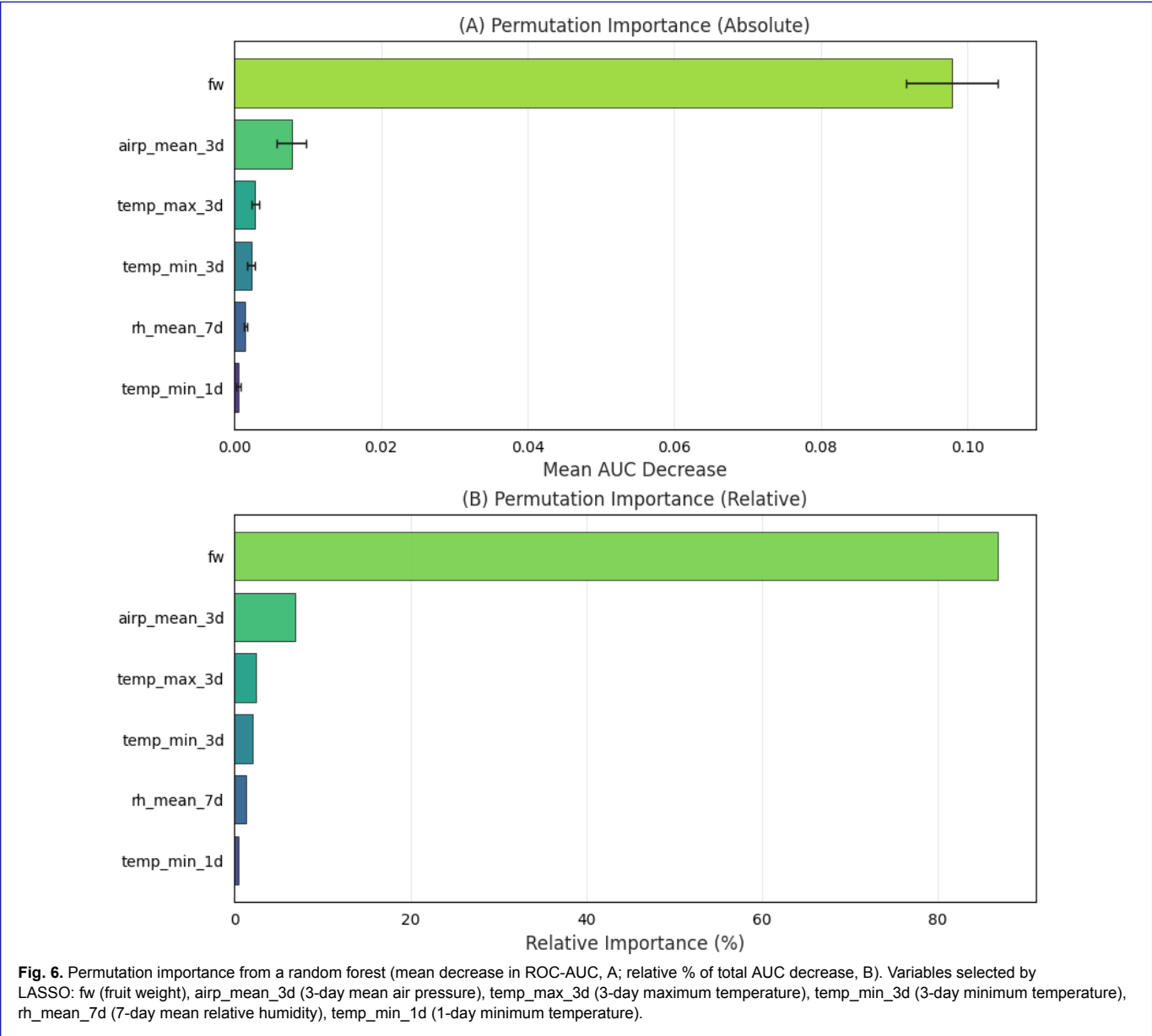
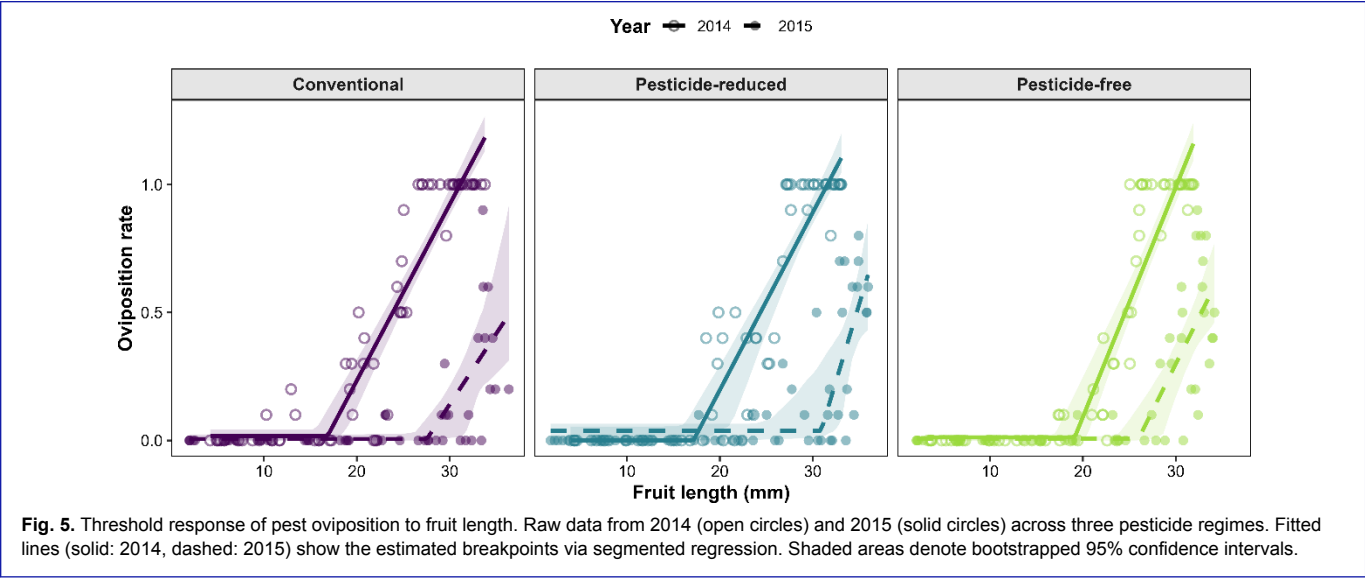


Fig. 4. Litchi fruit borer oviposition patterns on set 'Hak Ip' fruit from the conventional, pesticide-reduced and pesticide-free regimes in 2014 (A) and 2015 (B). The timing of insecticide spraying in the reduced application treatment (cross signs) and the positive control (diamond signs) was labelled. The vertical bars above the broken lines represent the LSD values ($\alpha = 0.05$).

pesticide-free control, which experienced a massive fruit drop just before harvest, resulting in low yield (Fig. 1; Table 1). This implied that the pest infestation primarily contributed to fruit abscission during the last month of litchi fruit development.

The ground investigation in the trials strongly supported the viewpoint. During the first and second fruit abscission waves, less than 50% of dropped fruitlets were infected by litchi fruit borers (Fig. 2). In general, fruit abscission at the early and middle stages of litchi fruit abscission is mainly affected by physiological factors such as pollination and fertilization (Degani *et al.*, 1995; Stern *et al.*, 1996; Froneman *et al.*, 2012), assimilate allocation and competition (Roe *et al.*, 1997; Chang and Lin, 2008). The existence ratio of litchi fruit borer quickly increased along with fruit development (Fig. 3). Most of the dropped fruit had been infected with the pest since 9-week AFFB (Fig. 2). In other words, litchi fruit borer carries out most fruit abscission in the late stage of 'Hak Ip' fruit development in the trials. Effective pest management for litchi fruit borers is crucial to maintaining fruit quantity and quality during the final month before harvest.

Egg-laying timing seems to be a good indicator for controlling the damage of litchi fruit borers. Recent studies have also highlighted the importance of phenology-guided interventions, noting that *C. sinensis* population peaks often coincide with specific fruit developmental stages (Zuo *et al.*, 2025). Based on the field survey, oviposition of the litchi fruit borer began around 4-week AFFB, with 1–2 weeks earlier than infestation was detected (Figs. 3 and 4), which aligned with previous studies (Hung *et al.*, 2002;



Siraj *et al.*, 2023). These phenomena led to the idea that chemical or physical protection against litchi fruit borers can be implemented just after the 4-week AFFB period, which is reasonable (Wang *et al.*, 2019). Interestingly, in the pesticide-reduced regime, we bypassed the first round of pesticide spraying, as it was performed under conventional management, and the adjustment did not lead to significant yield loss. Therefore, the results suggested that activities of litchi fruit borers may be tolerable until 5-week AFFB, when the fruitlet size reaches about 20 mm.

Our segmented regression analysis (Fig. 5) further supports the use of fruit size as a reference. The model estimated the onset of oviposition at fruit lengths of approximately 16.9–19.1 mm in 2014. Although pests delayed substantial oviposition in 2015 until the fruits had enlarged to 26.0–30.9 mm, reflecting the immediate modifying effects of short-term weather anomalies or specific microclimatic conditions on the phenological baseline, approximately, the 20-mm mark may provide a safe and observable threshold for early warning.

The insecticide mode of action is an important consideration for practical pest management. Application of 50% fenthion EC controlled the infestation rate of litchi fruit borer larvae in both conventional (15.0%) and reduced (38.3%) application procedures. The short half-life of fenthion led to rapid decreases in pest mortality in the field (Hung and Hwang, 1995; Minelli *et al.*, 1996). Therefore, the fruit cannot be fully protected when the chemical is applied at a ca. 10-day interval. On the other hand, fenthion kills eggs and adults of the litchi fruit borer, but it weakens larvae and pupae (Hung and Hwang, 1995). Differential patterns in oviposition and infestation rates suggested that fenthion acted to prevent egg hatching rather than to reduce oviposition behaviour. Nevertheless, despite its practical effectiveness in the field, fenthion has been withdrawn or restricted in several countries because of its high avian toxicity (McKenzie *et al.*, 1996), secondary poisoning risk to non-target birds (Hunt *et al.*, 1991), aquatic ecological risk (Wang *et al.*, 1989; Wnag and Tucker, 1990) and concerns over residues and occupational exposure.

In the other trial, the synthetic pyrethroid 2.4% deltamethrin SC, can quickly knock down pests by paralyzing their nervous system (Laufer *et al.*, 1984). Deltamethrin also represses the pupation of the litchi fruit borer and has excellent mortality on the pupa (Hung and Hwang, 1995). These functions make the pesticide effective in controlling the litchi fruit borer and increasing the economic output of 'Hak Ip' fruit production. Interestingly, deltamethrin did not reduce the oviposition rate or the number of eggs per fruit, suggesting that the chemical affected egg development and had potential ovicidal effects on pests (Ho and Goh, 1984). In this context, insecticides with ovicidal activity may represent a feasible management strategy. Consistent with this idea, acetamiprid has been reported to show strong ovicidal activity against Lepidoptera pests on fruit trees (Yamada *et al.*, 1999), and it has also been reported to perform well against litchi fruit borer infestations in the field (Chen *et al.*, 2022). These present findings highlight the insecticide mode of action rather than product-specific superiority.

Predicting the litchi fruit borer infestation requires a hierarchical understanding of host phenology and meteorological drivers. While Bhat *et al.* (2025) reported general field correlations between pest occurrence and minimum temperature or rainfall, our high-resolution GLM identifies 3-day maximum temperature and 7-day mean humidity as the primary acute triggers in our study region. These findings bridge the gap between the laboratory-based physiological limits reported by Li *et al.*

(2013), who identified an optimal oviposition temperature of about 25°C, and field dynamics. Moreover, the random forest analysis elucidates a dual-layered mechanism governing pest oviposition: although meteorological drivers exhibit stronger marginal effects (as reflected by ORs) in the GLM, fruit weight dominates variable importance in the random forest (approximately 90%, Fig. 6).

This hierarchical host–phenology mechanism aligns with observations from other systems. For example, Myers *et al.* (2006) reported that eggs of the oriental fruit moth (*Grapholita molesta*) concentrated on shoots early in the season but shifted to fruit later in the season, and Polavarapu *et al.* (2004) found delayed plum curculio (*Conotrachelus nenuphar*) infestation on late-season 'Elliott' blueberries relative to earlier cultivars. Kamala Jayanthi and Verghese (2011) thus recommend using explicit developmental stages as practical decision rules for orchard pest control. Our results are consistent with that principle: fruit phenology (indexed by weight or length) provides an observable baseline of susceptibility, and short-term weather anomalies act as immediate triggers on top of that baseline. Because fruit weight and length are strongly correlated in 'Hak Ip' (Fig. S1), fruit length, an easy field measurement, can serve as a practical proxy for phenological susceptibility in management decisions.

Overall, the litchi fruit borer can cause substantial economic losses when not effectively managed. Oviposition begins about 4 weeks after full female bloom, and pest abundance increases rapidly as fruit develops, leading to severe preharvest fruit loss. Although conventional management relies on multiple pesticide applications, our results indicate that pest infestation contributes less to physiological fruit drop than to the early fruit-development stage. The present results suggest that pesticide application at about 5 weeks after full female bloom, when the fruitlet is approximately 20 mm in length, may provide a practical approach for litchi fruit borer management. In addition, oviposition behaviour was not reduced by pesticide use, suggesting that insecticides with ovicidal activity may be an important component of litchi fruit borer management.

CONFLICT OF INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

ETHICS STATEMENT

The authors confirm that the research meets any required ethical guidelines, including adherence to the legal requirements of the study country.

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AUTHOR CONTRIBUTIONS

Tai-Chuan Wang (funding acquisition [lead], conceptualization [equal], investigation [lead], methodology [equal], project administration [equal], writing – original draft [lead], writing—review and editing [equal]), JenYu Chang (conceptualization [equal], data curation [lead], investigation [lead], methodology

[equal], project administration [supporting], writing – review and editing [equal]), Jer-Way Chang (project administration [lead], supervision [lead], writing—review and editing [supporting]).

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SUPPLEMENTARY DATA

The supplementary material is available in the online version of this article.

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DATA AVAILABILITY

Data will be made available upon request.

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