

# Differential Impacts of Citrus Thrips Across Sweet Orange and Mandarin Species

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## Abstract

Several domesticated *Citrus* species are grown as major commercial crops in California. Despite this, farmers currently use a single set of management practices, originally created for sweet oranges (*Citrus sinensis* (L.) Osbeck [Sapindales: Rutaceae]), for both sweet oranges and all mandarin species. Mandarins, primarily *Citrus reticulata* Blanco, *Citrus clementina* hort. ex Tanaka, and *Citrus unshiu* Marcovitch, comprise almost 25% of California citrus acreage, and little work has been done to assess host–pest interactions for these species. Citrus thrips (*Scirtothrips citri* Moulton [Thysanoptera: Thripidae]) are one of the main pests in California citrus and are major targets for early spring, “petal fall” insecticide applications. We used mixed species citrus blocks to test the influence of *Citrus* species, including *C. sinensis*, *C. reticulata*, *C. clementina*, and *C. unshiu*, on 1) citrus thrips densities following petal fall; 2) citrus thrips-induced scarring on both the calyx and stylar ends of fruit; and 3) fruit deformation. *Citrus sinensis* and *C. unshiu* had relatively high citrus thrips densities and scarring levels, whereas *C. reticulata* had lower densities of citrus thrips and scarring levels. The age structure of citrus thrips populations also varied across *Citrus* species. Fruit deformity associated with citrus thrips scarring was found on all *Citrus* species examined. Scarring on the stylar-end of fruit, a previously largely ignored location of citrus thrips scarring, was found to be common in *C. reticulata*. It is clear from our work that species-specific management guidelines for citrus thrips are needed in sweet oranges and mandarins.

**Key words:** thrips, mandarin, integrated, pest, management

Commercial citrus is composed of several domesticated species of varying relatedness with a long and complex phylogenetic history (Wu et al. 2018). Despite this phylogenetic diversity, sweet oranges, *Citrus sinensis* (L.) Osbeck (Sapindales: Rutaceae) and mandarins, which together comprise the majority of commercial citrus grown in California, are currently managed with a single set of integrated pest management (IPM) guidelines originally created for sweet oranges (UC ANR 2012, 2015). However, mandarins, primarily *Citrus reticulata* Blanco, *Citrus clementina* hort. ex Tanaka, and *Citrus unshiu* Marcovitch, now comprise almost 25% of California citrus acreage and make up the majority of new plantings (CDFA 2018). Differences between host–plant species often have a large impact on host–pest interactions, and the citrus guidelines developed for sweet oranges may be inadequate for the diversity of California citrus crops (Bernays and Chapman 2007).

Citrus thrips, *Scirtothrips citri* [Moulton], is one of the main pests of California citrus, also infesting blueberries, grapes,

pomegranates, almonds, and other crops (Morse 1995, Haviland et al. 2009). Citrus thrips nymphs feed by piercing single cells with a modified stylet and extracting the contents. Only nymphal thrips are currently thought to cause citrus fruit scarring and recommended monitoring methods focus only on counting first and second instars (UCANR 2012). Citrus thrips are highly thigmotactic (preferring tight spaces) and may feed under the calyx of young fruit, creating a characteristic ring-shaped scar surrounding the calyx; the scar expanding as the fruit grows (Supp Fig. 1 [online only]; Horton 1918). Although calyx-end ring scarring is the only fruit damage reported in California citrus IPM guidelines, it is possible that citrus thrips cause other types of damage to citrus fruit as well (UC ANR 2012, UC ANR 2015). Fruit deformity, for instance, is a common consequence of thrips herbivory on a wide array of developing fruits and vegetables (Lewis 1997). Despite this, only a few studies focusing on navel oranges (the most commonly grown grouping within *C. sinensis*) have reported casual observations of fruit deformity caused by citrus thrips, and no attempt has been made to quantify the frequency or

extent of deformity beyond navel oranges (Horton 1918, McGregor 1944). Scarring caused by citrus thrips on the stylar-end of the fruit has also been observed to occur on navel oranges, but this has not been quantified (Tanigoshi 1991, Mukhopadhyay 2004). Although citrus thrips rind scarring and deformation are thought to be solely aesthetic, because California citrus is destined for fresh markets and exports, citrus thrips damage can result in the downgrading of the fruit at the packinghouse and monetary losses for farmers (Horton 1918, Ferguson and Grafton-Cardwell 2014).

Effective IPM guidelines and accurate treatment thresholds for citrus thrips are especially important as citrus thrips populations quickly develop resistance to pesticides. California populations of citrus thrips have evolved resistance against all classes of pesticides used for their control historically (Morse and Brawner 1986, Immargaju et al. 1989, Morse 1995, Khan and Morse 1998), and resistance is currently emerging to the widely used compounds spinosad and spinetoram (Morse and Grafton-Cardwell 2012). Economic thresholds and IPM guidelines for citrus thrips currently exist only for sweet oranges, *C. sinensis*, and no research has assessed the suitability of these guidelines for mandarin species (UC ANR 2012, UC ANR 2015). Furthermore, the current lack of understanding of mandarin–pest interactions, as well as the lack of established economic thresholds for *Citrus* species other than *C. sinensis*, may be promoting unnecessary pesticide applications, thereby accelerating the evolution of pesticide resistance.

An analysis of observational data gathered from 202 grove-years of commercial citrus production in California's San Joaquin Valley suggested that citrus thrips densities differed across *Citrus* species, with *C. reticulata* exhibiting substantially lower citrus thrips densities as well as decreased susceptibility to citrus thrips scarring (Cass et al., unpublished data). The current work builds on these earlier findings. Specifically, our objectives were to use mixed species research blocks to test the influence of *Citrus* species, including *C. sinensis*, *C. reticulata*, *C. clementina*, and *C. unshiu*, on 1) citrus thrips densities during the 2 mo following petal fall, when fruit are thought to be vulnerable to scarring; 2) the distribution of citrus thrips scarring across both the calyx and stylar ends of fruit, observed at harvest; and 3) citrus thrips-induced fruit deformation. Finally, we used the relationship between citrus thrips densities during the 2 mo following petal-fall and the resulting incidence of scarring on mature fruit to assess the possibility that different *Citrus* species vary in their susceptibility to scarring.

## Methods

Our study was conducted in four mixed species citrus research blocks at the University of California Lindcove Research and Extension Center (LREC) in Petal Fall District 1 of Tulare County, CA, during the 2018 growing season. In each of the four blocks, different *Citrus* species and cultivars were grown in a fully interspersed spatial array, creating a common-garden setting (see Supp Fig. 2 [online only] for a map of the study blocks). Trees used in the experiments were not pruned, and no pesticide treatments were applied during the 2018 calendar year. We monitored citrus thrips densities and fruit scarring on 48 trees: 12 trees each of *C. clementina*, *C. reticulata*, *C. sinensis*, and *C. unshiu* across the four mixed species citrus blocks (see Supp Table 1 [online only] for a list of the cultivars represented within each *Citrus* species). We later excluded one *C. reticulata* tree from our analyses, as all fruit on the tree abscised during maturation.

## Thrips Density Monitoring

We monitored thrips densities weekly from 2 May to 28 June 2018, covering 1 to 9 week(s) after petal fall. The Tulare County Agricultural Commissioner declared petal fall for District 1 on 24 April 2018. Petal fall is defined as the date when 75% of petals have fallen from the north side of the citrus tree and is designated as the date when pesticide treatments for early-season citrus pests may begin. We monitored thrips densities on experimental trees in a defined order, which we reversed weekly. All monitoring took place weekly between 0630 and 1530 h. On each tree, we collected thrips from 20 chest-high fruit selected from around the exterior of the tree canopy. If 20 fruit were not present, we collected from all fruit on the tree. We did not remove fruit from the tree after collection; and each week we collected from a new, but not necessarily unique, set of fruit. We collected all thrips present on the 20 chosen fruit at each weekly inspection via an aspirator fitted to a single 32-mm plastic vial. Collected thrips were preserved by filling the vials with 70% ethanol. Thrips were subsequently identified to species and life stage under a dissecting microscope following Hoddle et al. (2012).

## Fruit Scarring

We evaluated the surveyed trees for citrus thrips fruit scarring on 10 December 2018, shortly prior to harvest. We blindly (i.e., without regard to the potential presence of scarring) selected 50 chest-high fruit from around the exterior of the canopy and quantified citrus thrips scarring damage on each fruit. If 50 fruit were not present, we inspected all fruit on the tree. We assessed scarring on both the calyx-end and stylar-end of the fruit. Citrus thrips scarring was differentiated from wind scarring by citrus thrips scarring's circular nature extending around the circumference of the fruit (Broughton 2018). Each end of the fruit was categorized as having either no scarring, light scarring, or heavy scarring, following the UC ANR photographic guide to citrus fruit scarring (Grafton-Cardwell et al. 2003). Light scarring was defined as an aggregation of UC ANR citrus thrips scarring levels 1 and 2 (Supp Fig. 1 [online only], top) and heavy scarring as an aggregation of scarring levels 3 and 4 (Supp Fig. 1 [online only], bottom).

## Fruit Deformity

On 18 December 2018, we assessed the hypothesis that citrus thrips scarring causes fruit deformity. A single observer searched each of our 47 experimental trees for fruit with heavy citrus thrips scarring extending to the side of the fruit until 10 min had elapsed or five fruit had been found on the tree. Fruit shape was ignored when selecting fruit and only the presence of heavy citrus thrips scarring was used as a selection criterion. Fruit that had grown touching other fruit or tree limbs were excluded, as this is a common but separate cause of fruit deformity. The heavily scarred fruit were removed from the trees and evaluated in the laboratory. We 1) estimated the percentage of the fruit's surface scarred by citrus thrips feeding; 2) recorded whether the fruit appeared to be obviously misshapen (i.e., asymmetrical); and 3) measured two semiperimeters, the first starting from the calyx and ending at the stylar-end, traversing the site of heaviest scarring, and the second on the opposite side of the fruit (regardless of scarring found there). As a measure of asymmetry, we calculated the ratio of the scarred semiperimeter distance to the opposite side semiperimeter distance. Symmetrical fruit were expected to produce a ratio near 1.0, whereas if citrus thrips scarring inhibited normal fruit expansion, we expected ratios less than 1.0.

## Statistical Analyses

The statistical analysis and plotting were performed in R (R Core Team, 2017) using the packages geepack (Yan 2002, Yan and Fine 2004, Højsgaard et al. 2006), lsmeans (Lenth 2016), lme4 (Bates et al. 2015), plyr (Wickham 2011), DescTools (Signorell et al. 2018), ggplot2 (Wickham 2016), and cowplot (Wilke 2019).

## Thrips Densities

To account for the repeated measures design of the survey, we constructed a generalized estimating equation (GEE; Liang and Zeger 1986) examining the effects of *Citrus* species on season-long citrus thrips densities. The model used *tree* as the unit of replication measured repeatedly across time, included fixed effects for block number (1–4) and sampling date, assumed a Poisson error distribution for the count data, and used the 1-time step autoregressive correlation structure for citrus thrips counts across time (full model: *citrus thrips counts per tree* ~ *Citrus species* + *block* + *date*, family = Poisson, id = *tree*, correlation structure = ar1). We omitted trees with fewer than 20 fruit from this analysis. We computed post hoc pairwise contrasts across *Citrus* species with a Tukey HSD. Next, by pooling data across weeks 1–9, we also compared the proportions of citrus thrips that were in the nymphal stage across *Citrus* species, using a generalized linear mixed model (GLMM) followed by a post hoc Tukey HSD. The model included *block* as a random effect and assumed a binomial distribution (full model: *number of nymphs/total number of citrus thrips* ~ *Citrus species* + (1|*block*), family = binomial).

## Thrips Scarring and Fruit Susceptibility

To determine whether the proportion of fruit with citrus thrips scarring (aggregation of heavy and light scarring located anywhere on the fruit) varied across species, we conducted a GLMM followed by a post hoc Tukey HSD. The model included *block* as a random effect and assumed a binomial distribution (full model: *number of fruit with scarring on tree/number of fruit examined on tree* ~ *Citrus species* + (1|*block*), family = binomial). The same analysis was also performed with only heavy citrus thrips scarring. To evaluate the possibility that *Citrus* species vary in their susceptibility to citrus thrips scarring, we performed a multiple linear regression of the proportion of fruit scarred on each tree as a function of the average nymphal and adult citrus thrips densities across weeks 1–9 after petal fall (full model: *percentage of fruit scarred per tree* ~ *number of nymphal citrus thrips per tree averaged across season* + *number of adult citrus thrips per tree averaged across season* + *Citrus species*). Nymphal and adult citrus thrips counts were not strongly correlated to one another (Generalized Variance Inflation Factor,  $\text{GVIF}^{1/(2 \cdot \text{df})} = 1.29$  and 1.51, respectively; Fox and Monette 1992). We extracted the residuals to test the possibility that different *Citrus* species might have more or less scarring than expected after correcting for observed citrus thrips densities. This was followed by a two-sided one-sample *t*-test to calculate if the residuals of each *Citrus* species were significantly different from 0.

## Calyx-End and Styler-End Scarring

To test the hypothesis that styler-end scarring is caused by citrus thrips, we first ran a GLMM followed by a post hoc Tukey HSD to assess the degree to which styler-end scarring and calyx-end scarring were correlated (full model: *presence of styler-end scar* ~ *presence of calyx-end scar* + (1|*Citrus species*) + (1|*block*), family = binomial). We also ran a GLMM followed by a post hoc Tukey HSD to assess 1) the distribution of styler-end and calyx-end scarring (full model:

*number of fruit with styler (or calyx) scarring per tree/number of fruit per tree* ~ *Citrus species* + (1|*block*), family = binomial) and 2) the proportion of scarring occurring on the styler-end (styler-end scarring as a proportion of all citrus thrips scarring incurred) across the four *Citrus* species (full model: *number of styler-end scars observed/number of citrus thrips scars observed* ~ *Citrus species* + (1|*block*), family = binomial).

## Deformity

We ran an ANOVA followed by a post hoc Tukey HSD to compare deformity between *Citrus* species. We then ran a one-sided one-sample *t*-test to compare the ratio of semiperimeters lengths to 1.0 for each *Citrus* species to test for citrus thrips generated fruit deformation (i.e., asymmetry). We used the same one-sided one-sample *t*-test to ask if citrus thrips scarred fruit, judged by a human observer to be deformed, did, in fact, have semiperimeter ratios less than 1.0.

## Results

### Thrips Densities

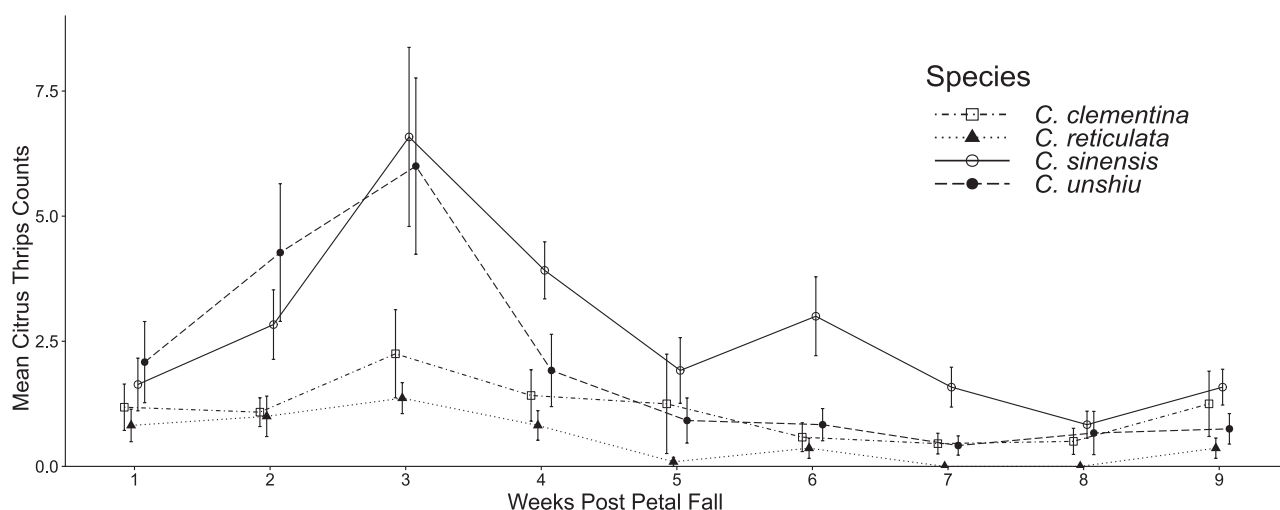
*Citrus* species differed significantly in the mean densities of citrus thrips found on their fruit during weeks 1–9 after petal fall (Fig. 1; Supp Table 2 [online only]). *Citrus reticulata* hosted the lowest citrus thrips densities throughout the sampling period ( $P < 0.05$ ), with the highest densities observed on *C. unshiu* and *C. sinensis* (Supp Table 3 [online only]). The age structure of citrus thrips populations also varied significantly across *Citrus* species. *Citrus sinensis* had a significantly higher proportion of adults within its thrips populations than did either *C. clementina* ( $P < 0.0001$ ) or *C. unshiu* (Fig. 2,  $P < 0.0001$ ; Supp Table 4 [online only]). *Citrus clementina* had a significantly lower proportion of adults when compared with all other *Citrus* species surveyed ( $P < 0.05$ ).

### Thrips Scarring and Fruit Susceptibility

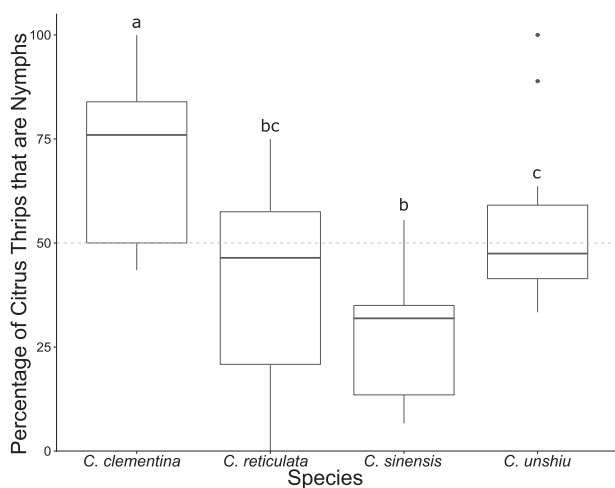
Citrus thrips scarring of fruit, scored at harvest, varied significantly across *Citrus* species (Supp Table 5 [online only]). *Citrus reticulata* had the lowest scarring at harvest, with the highest scarring found on *C. sinensis* and *C. unshiu* (Fig. 3; Supp Table 6 [online only]). These same results were observed when only heavy scarring was analyzed. We found both nymphal and adult citrus thrips counts to be significant predictors of the percentage of scarred fruit in a multiple regression ( $P = 0.02$  and  $P = 0.007$ , respectively; adjusted  $R^2 = 0.53$ ;  $N = 47$ ; Supp Table 7 [online only]). *Citrus* species was not a significant term in the model, indicating that *Citrus* species did not differ in their susceptibility or resistance to thrips scarring, given the observed densities of thrips. No species was found to have mean residual values significantly different from 0 (data not shown).

### Calyx-End and Styler-End Scarring

Calyx-end scarring varied across species (Supp Table 8 [online only]): *Citrus reticulata* had significantly less calyx-end scarring when compared with *C. sinensis* ( $P < 0.0001$ ), *C. unshiu* ( $P < 0.0001$ ), and *C. clementina* ( $P = 0.0002$ ). Styler-end scarring was positively correlated with calyx-end scarring ( $P < 0.0001$ ; Supp Table 9 [online only]). In every species surveyed, the probability of styler-end scarring on fruit was significantly greater when calyx-end scarring was present (Fig. 4). Styler-end scarring was evenly distributed across species (Supp Table 10 [online only]); however, the ratio of styler-end scarring to calyx-end scarring was widely different across species



**Fig. 1.** Mean  $\pm$  1 SE number of citrus thrips per 20 fruit surveyed after petal fall, plotted by *Citrus* species. Counts are averaged across all trees surveyed within a species. A slight horizontal jitter has been added so that error bars do not overlap; all species were sampled at the same time points.

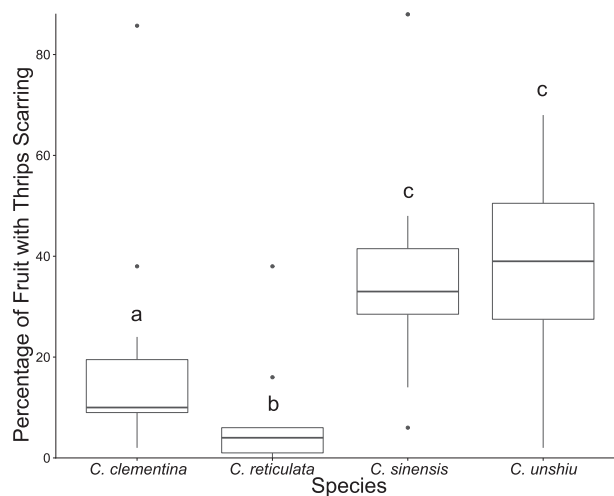


**Fig. 2.** Percentage of citrus thrips collected that were in a nymphal stage, plotted by *Citrus* species. Letters indicate statistical differences at  $P < 0.05$ . For this and all subsequent box plots, thick horizontal lines indicate means, with lower and upper hinges at first and third quartiles. Upper (and lower) whiskers extend to the largest (and smallest) value within 1.5 times the interquartile range from the hinge. Data points beyond the whiskers are plotted individually as outliers.

(Fig. 5; Supp Table 11 [online only]). *Citrus sinensis* and *C. unshiu* had a low proportion of scarring occurring on the stylar-end, whereas *C. reticulata* and *C. clementina* had a greater proportion of stylar-end scarring.

### Deformity

Thrips scarring produced similar levels of fruit asymmetry in all the *Citrus* species studied here, with significant departures from symmetry observed in all species except for *C. clementina* (Fig. 6). The magnitude of the asymmetry did not vary significantly across species ( $F = 1.5$ ;  $df = 3, 143$ ;  $P = 0.22$ ). Our measure of fruit asymmetry was in agreement with fruit that we judged, through informal visual inspection, to be deformed: fruit judged to be either slightly deformed or heavily deformed had a semiperimeter ratio less than

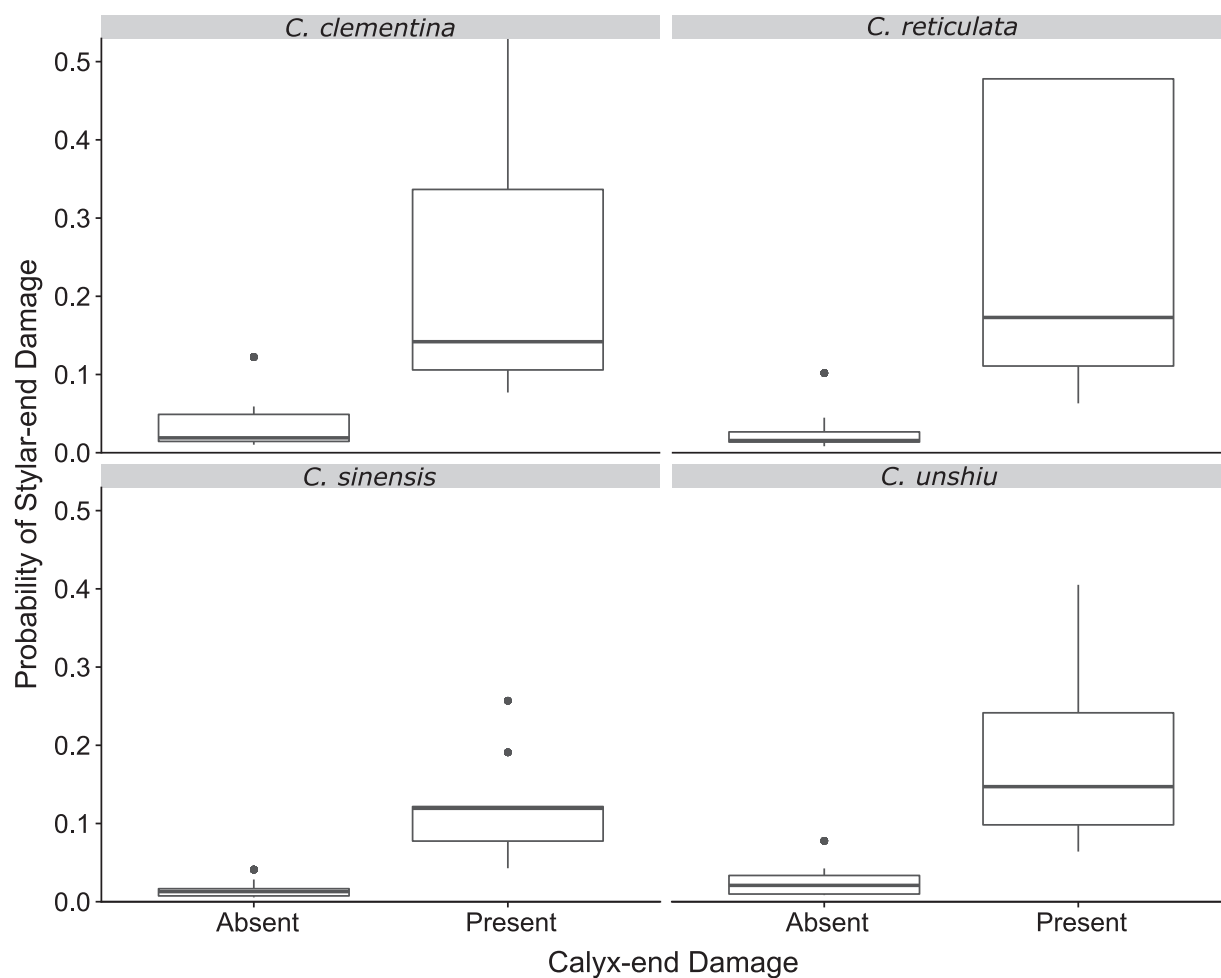


**Fig. 3.** Percentage of fruit with light or heavy citrus thrips scarring anywhere on the fruit at harvest, plotted by *Citrus* species. Letters indicate statistical differences at  $P < 0.05$ .

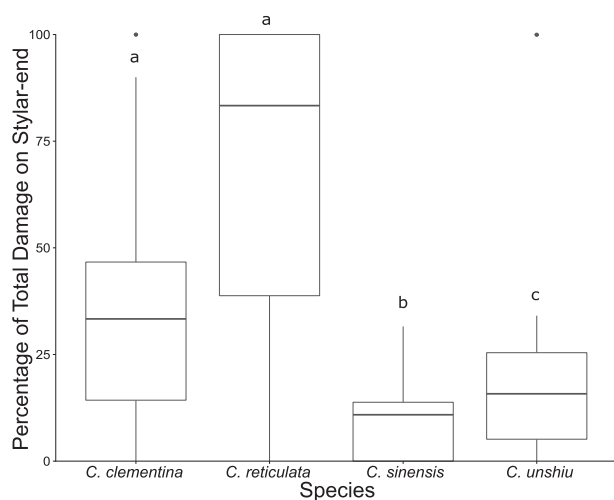
1.0 ( $t = -5.88$ ;  $df = 43$ ;  $P < 0.0001$ ;  $t = -4.23$ ;  $df = 69$ ;  $P < 0.0001$ , respectively), whereas fruit judged to be free of deformation had semiperimeter ratios not significantly less than 1.0 ( $t = 0.34$ ;  $df = 35$ ;  $P = 0.63$ ).

### Discussion

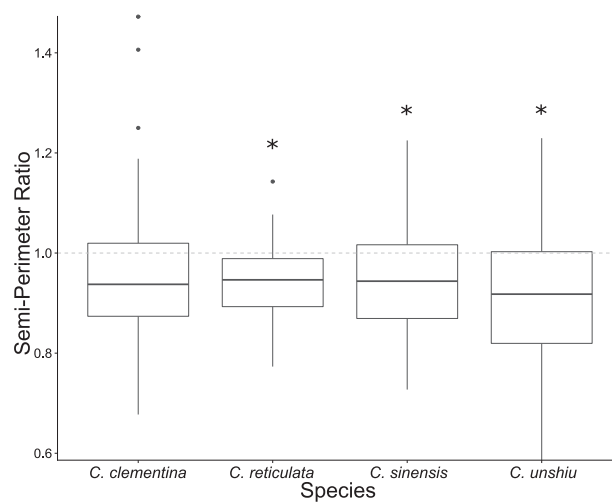
Our mixed species block experiments have revealed that different *Citrus* species interact with citrus thrips in different ways: species differ in 1) the densities of citrus thrips populations that they host; 2) their levels of citrus thrips scarring at harvest; and 3) the location of the scarring generated. In contrast, *Citrus* species exhibited a similar propensity to grow asymmetrically in response to scarring, resulting in deformed fruit. *Citrus sinensis* and *C. unshiu* are similar in both density of citrus thrips and subsequent scarring levels, whereas *C. reticulata* hosts lower densities of citrus thrips and has less citrus thrips scarring at harvest. Additionally, the location of scarring on *C. reticulata* is quite different, with the majority of



**Fig. 4.** Probability of a fruit having stylar-end scarring for fruit with versus without calyx-end scarring, plotted by *Citrus* species. In every *Citrus* species, the probability of stylar-end scarring is significantly greater when calyx-end scarring is present ( $P < 0.0001$ ).



**Fig. 5.** Percentage of the total scarring damage produced by citrus thrips on fruit that is found on the stylar-end, plotted across *Citrus* species. Letters indicate statistical differences at  $P < 0.05$ .



**Fig. 6.** Fruit asymmetry in thrips-damaged fruit, measured as the ratio of the scarred semi-perimeter divided by the opposite-side semi-perimeter, plotted by *Citrus* species. Ratios were compared with the expectation of symmetrical fruit (i.e., ratio = 1.0). \* $P < 0.05$ .



scarring occurring on the styler-end of the fruit, contrary to all other species tested.

### Thrips Densities

We found significant differences in citrus thrips densities across the studied *Citrus* species, with *C. reticulata* having lower citrus thrips densities than both *C. sinensis* and *C. unshiu*. The observed differences in densities could be due to female citrus thrips' preference for *C. sinensis* and *C. unshiu* as an oviposition site, greater mortality or lower fecundity on *C. reticulata*, or a combination of these processes. It is also possible that natural enemies might have different influences on citrus thrips populations on different *Citrus* species host plants. Further research will be needed to distinguish between these possibilities. *Citrus sinensis* was found to have the highest ratio of adult to nymphal citrus thrips out of the *Citrus* species surveyed. Our finding that adults make up the majority of citrus thrips on *C. sinensis*, coupled with adult thrips densities being a significant predictor of fruit scarring levels, suggests that adults may be causing scarring on *C. sinensis* fruit. This, however, is not direct evidence that adult citrus thrips are causing significant fruit scarring, and further work needs to be done to experimentally test this correlation and to assess to what degree adults scar *C. sinensis* fruit.

### Thrips Scarring and Fruit Susceptibility

Consistent with the observed differences in citrus thrips densities, we found that overall citrus thrips scarring at harvest was significantly lower in *C. reticulata* and *C. clementina* compared with *C. sinensis* and *C. unshiu*. The difference in scarring appears to be explained largely by the lower densities of citrus thrips, as no species showed a difference in susceptibility to citrus thrips scarring.

### Stylar-End Scarring and Fruit Deformation

Our study demonstrates the presence of two previously seldom-reported forms of citrus thrips damage in California citrus, namely,

stylar-end scarring, and fruit deformation. Stylar-end scarring was found to be highly correlated with calyx-end scarring, with stylar-end scarring significantly more likely to occur on a particular fruit if calyx-end scarring was also present. Stylar-end scarring was found to be relatively common, occurring on about 6% of all fruit sampled. It has likely not been widely reported because 1) stylar-end scarring exhibits different morphology than “standard” citrus thrips calyx-end scarring, often being deeper-set and smoother than calyx-end scarring (Fig. 7), and 2) because stylar-end scarring is a comparatively minor occurrence on *C. sinensis* compared with the frequency of calyx-end scarring. In *C. reticulata*, however, stylar-end scarring is more common than calyx-end scarring. It is possible that due to the deviance from “standard” citrus thrips damage morphology, as well as its occurrence primarily on the comparatively less-studied *C. reticulata*, stylar-end thrips damage is being misdiagnosed by pest control advisors as noncitrus thrips damage. This could be resulting in improper treatment for a nondamaging pest as well as lack of treatment for citrus thrips. We hypothesize that stylar-end scarring is likely occurring before or near petal fall, when the style is still attached to the fruit, creating a space in which thigmotactic citrus thrips may prefer to feed. If this proves to be the correct interpretation, stylar-end scarring would be especially problematic, because pesticide applications before petal fall are restricted to protect pollinators that are active during the bloom. More work is needed to better understand the timing of stylar-end scarring and what steps could be taken to prevent it. We also observed that citrus thrips side scarring is strongly correlated to a limited expansion of the developing fruit, and consequently, unequal growth and the eventual deformation of the mature fruit. Asymmetrical fruit were readily recognizable through informal visual inspection of the fruit, suggesting that asymmetry might be important in consumer preferences for different fruit.

Our work suggests that commercial *Citrus* mandarin species should no longer be viewed as a single crop with the same susceptibility to citrus thrips as *C. sinensis* when considering how best to manage citrus thrips, and that new scouting practices may need to be developed. The exception for this is *C. unshiu*, which has similar



**Fig. 7.** Citrus thrips scarring on the stylar-end of fruit. Photos a, b, and d are of scarring on *C. clementina*, photo c is of scarring on *C. reticulata*. Photos b and d are examples of citrus thrips scarring that is deeper and less “scabby” than the more common scarring morphology in photos a and c.

citrus thrips densities and levels of scarring as *C. sinensis*, and can likely be treated under the same management practices as *C. sinensis*. *Citrus reticulata*, however, has significantly lower citrus thrips densities and fruit scarring and therefore will require fewer pesticide treatments. The same pattern of reduced citrus thrips densities and scarring on *C. reticulata* was observed in a large observational data set collected in commercial citrus blocks (Cass et al., unpublished data), suggesting that the results of our experiments are likely to be relevant to citrus thrips management across commercial orange and mandarin production in California's San Joaquin Valley.

## Supplementary Data

Supplementary data are available at *Journal of Economic Entomology* online.

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