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Article

Thermotolerance in a spider mite: implications in disinfestation treatment

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Abstract

Tetranychus ludeni Zacher is a European spider mite species and an important invasive pest in horticulture. We investigated the effects of hot air on its survival and reproduction, providing knowledge for development of disinfestation programs using heat. We tested how each life stage responded to heat treatments of five air temperatures (45 to 57°C) and five exposure durations (three to 15 hours). We showed that no eggs hatched after exposed to 45°C for ≥ 15 hours, 48°C for ≥ 12 hours, or 51°C for three hours; no adults survived 51°C or 54°C for ≥12 hours or 57°C for ≥ six hours, and heat tolerance of other life stages fell in between. Higher temperature and longer exposure time also reduced developmental success and fecundity. These findings suggest that we may be able to eradicate the mites of all stages using one hot air treatment at 57°C for six hours or two treatments at 51°C for three hours at a 10-day interval to kill all eggs in the first treatment and those laid by survived adults in the second. The eradication strategy using hot air of 51–57°C may be more suitable for treating plant residues on exported/imported machinery, farm equipment and containers because it may have negative impact on fresh postharvest products. With the knowledge that exposure to 45°C substantially reduced the mites' fecundity, particularly when the younger stages were treated, we suggest that heat treatment of fresh postharvest products with 45°C could still greatly reduce the quarantine risk of this pest.

Key words: Acari, disinfestation, heat treatment, invasive pest, Tetranychidae

Introduction

Heat treatment has been widely used as a non-chemical disinfestation measure for postharvest crops (e.g., Cowley *et al.* 1992; Waddell *et al.* 1993; Jessup *et al.* 1998; Jacobi *et al*. 2001; Macana & Baik 2018). In invertebrates, particularly insects and mites, response to high temperature and exposure duration varies among species (Bertelsmeier *et al*. 2015; Gray 2017; Kingsolver *et al*. 2021) as well as among life stages within species (Heather *et al*. 2002; Kingsolver *et al*. 2011; Gotoh *et al*. 2013; Chiu *et al*. 2014; Hsu *et al*. 2018; Yao *et al*. 2019). Therefore, the effectiveness of heat disinfestation treatment should be determined by temperature, treatment duration (Dentener *et al*. 1997; Lurie *et al*. 1998; Finkelman *et al*. 2006; Hara 2013) and life stages treated (Heard *et al*. 1992; Heather *et al*. 2002; Gotoh *et al*. 2013; Hsu *et al*. 2018). However, heat tolerance benchmarks have not yet been established for most pest species.

Tetranychus ludeni Zacher (Acari: Tetranychidae) is a European spider mite species but has invaded many regions, including Africa, America, Asia, and Oceania (CABI 2020; Zhou *et al*. 2021),

and become an important pest of many crop species globally (Zhang 2003; Kaimal & Ramani 2011). However, some countries still require disinfestation treatment of postharvest products for *T. ludeni*. For example, Korea bans *T. ludeni*-infested fruit and vegetables (MPI 2019). Several workers have tested the effectiveness of heat treatment to disinfest the spider mite *T. urticae* Koch on postharvest products, showing promising outcome (Waddell & Birtles 1992; Waddell *et al*. 1993; Gotoh *et al*. 2013). However, thermotolerance has yet to be established for *T. ludeni*. It is also unknown how high temperature could affect its reproduction.

In the present study, we investigated how each life stage responded to high temperature exposure in *T. ludeni*. We exposed all life stages to five temperatures for five durations and recorded their mortality rates, and developmental success and reproductive fitness of survived individuals. Information presented here is essential for development of heat disinfestation programs for this important pest. It may also provide knowledge for future evaluation of its invasion potential in relation to heat waves caused by climate change.

Materials and Methods

Experimental mite preparation

We collected *T. ludeni* adults from *Passiflora mollissima* (Kunth) (Malpighiales: Passifloraceae) in Palmerston North, New Zealand, in 2017. A breeding colony from these adults was established and maintained on 20 potted kidney bean plants *Phaseolus vulgaris* L. (Fabales: Fabaceae) in the Entomology and IPM Laboratory of Massey University, New Zealand. We replaced ten oldest plants with new ones every two weeks by cutting the infested leaves of old plants and placing them on the top of new ones. The mite colony was maintained, and experimental mites prepared at 25 ± 1°C and 50 ~ 70% RH with a photoperiod of 16L:8D hours.

We randomly collected 20 adult females and four adult males from the colony and transferred them onto a bean leaf disc (3 cm × 3 cm) positioned upside down on a water-saturated cotton pad in a Petri dish (5.5 cm diameter × 1.0 cm height). The adults were allowed to stay on the leaf disc for 24 hours and then removed. The larvae were transferred to a new leaf disc of the same size immediately after the eggs laid by these adults hatched. We reared them at 25°C for 1, 4, 6 and 8 days to obtain larvae, protonymphs, deutonymphs and female adults, respectively, for experiment. In total, we set up 800 such leaf discs. To obtain adult males, we randomly collected 20 female deutonymphs from the colony, placed them on a leaf disc as above and allowed the newly emerged virgin females to lay eggs for 24 hours. The newly hatched larvae were then transferred to a new leaf disc and allowed to develop to adult males for the experiments.

Heat-dependent mortality rate in each life stage

To determine heat-dependent mortality rate of mites of each life stage, we treated eggs, larvae, protonymphs, deutonymphs, virgin adult males and females with five temperatures (45, 48, 51, 54 and 57°C) for five heat durations (3, 6, 9, 12 and 15 hours), resulting in a total of 150 treatments (6 life stages × 5 temperatures × 5 durations). There were 20 replicates for each treatment. For each replicate, 10 individuals were introduced onto a bean leaf disc (3 cm × 3 cm) on a water-saturated cotton pad in a Petri dish (5.5 cm diameter × 1.0 cm height) and then the dish was transferred into an incubator (Series Five, Contherm Scientific Company, New Zealand) with a treatment temperature. Immediately after treatment, we moved the Petri dishes to 25°C, and transferred all life stages except eggs onto new leaf discs in Petri dishes as above. Eggs that did not hatch in 10 days and individuals of other life stages that had no sign of movement 48 hours after treatment were considered as dead.

Effect of heat treatment on immature development to adult stage

To determine the probability of immature mites surviving heat-treatment to develop to adulthood, we randomly took up to 20 individuals that survived from each treatment of the above experiment and reared them individually at 25ºC on leaf discs as above. The leaf discs were replaced with new ones every 4 days and the total number of adults that emerged from these juveniles was recorded. However, if no juveniles survived in some treatments, we did not follow their development.

Effect of Heat Treatment on Reproduction

To determine how heat treatment affected reproduction, we individually transferred up to 20 females that were heat-treated during the adult stage and 20 newly emerged females that developed from each heat-treated immature stage in the above experiment onto leaf discs and reared them at 25 on leaf discs as above. The mortality of females was monitored daily and leaf discs were replaced with new ones once every 4 days if they were still alive. The total number of eggs laid by each female was recorded. However, if no individuals survived in some treatments, we did not follow their reproduction in those treatments.

Statistical Analysis

All data analyses were performed using SAS software (SAS 9.4, SAS Institute Inc., Cary, NC). We analyzed the mortality rate (%) of different life stages using a generalized linear mixed model (GLIMMIX procedure) with temperature, exposure duration and their interactions as the fixed factors and replicate as a random effect followed by a Binomial distribution and a Logit link function for the model. A Tukey-Kramer test was used to compare the difference in the mortality rate between temperatures of a given duration and between durations of a given temperature within each life stage. The same method was used to compare the difference in overall mortality rate between life stages. The proportions of individuals that developed to adult stage after being treated at different temperatures for various durations were analyzed using a likelihood ratio test in a logistic regression model (GENMOD procedure) with a Binomial distribution and a Logit function used to the model and the CONTRAST statement for multiple comparisons. The generalized linear mixed model (GLIMMIX procedure) with a Poisson distribution and a Log link function was applied to determine the combined effect of temperature and duration on the number of eggs laid, followed by a Tukey-Kramer test for multiple comparisons.

Results

Heat-dependent mortality rate in each life stage

In each life stage, temperature and exposure duration significantly interacted ($F_{16,456}$ = 4.26 ~ 14.10, P < 0.0001), with higher temperature ($F_{4,76}$ = 8.26 ~ 136.64, P < 0.0001) and longer exposure ($F_{4,76}$ = 26.96 ~ 162.94, P < 0.0001) causing significantly higher mortality (Table 1). At any treatment duration no eggs hatched when temperature was 51°C or higher, and all life stages died at 57°C of any treatment duration except about 10% of adult females and 1% of deutonymphs which survived 57°C for 3 hours (Table 1). Our results also show that younger life stages, particularly eggs, were significantly more susceptible to heat treatment [overall mean (± SE) mortality rate (%) = 93.1 ± 0.9 for egg, 83.1 ± 0.9 for larva, 75.9 ± 1.1 for protonymph, 75.4 ± 1.1 for deutonymph, 71.8 ± 1.5 for adult male and 62.7 ± 1.7 for adult female; $F_{5,2975}$ = 529.33, P < 0.0001] (Table 1).

TABLE 1. Mean (± SE) mortality rates (%) of different life stages of *Tetranychus ludeni* after treatment at different temperatures for various durations*

Life stage	Duration	Temperature (ºC)					$F_{4,76}$	P
	(hours)	45	48	51	54	57		
Adult female	3	11.5 (±3.2) D d	14.0 (±2.7) D d	25.0 (±5.6) D c	42.5 (±5.2) C b	89.0 (±3.5) B a	123.90	< 0.0001
	6	13.0 (±3.2) D d	14.0 (±3.1) D d	47.0 (±4.8) C c	85.5 (±4.3) B b	100 A a	162.94	< 0.0001
	9	21.5 (±3.4) C c	23.5 (±4.0) C c	54.5 (±4.4) B b	100 A a	100 A a	143.12	< 0.0001
	12	34.0 (±3.7) B c	61.5 (±6.3) B b	100 A a	100 A a	100 A a	129.14	< 0.0001
	15	47.0 (±3.8) A c	85.5 (±4.2) A b	100 A a	100 A a	100 A a	98.55	< 0.0001
	$F_{4,76}$	42.08	136.64	114.95	109.68	12.99		
	P	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001		
Adult male	3	15.5 (±2.8) D e	29.5 (±3.7) D d	68.0 (±6.0) C c	86.5 (±5.3) C b	100 A a	147.17	< 0.0001
	6	15.0 (±3.9) D e	36.5 (±4.9) C d	81.0 (±3.2) B c	90.0 (±4.2) C b	100 A a	156.14	< 0.0001
	9	27.5 (±3.4) C e	37.5 (±3.2) C d	85.0 (±2.9) B c	94.5 (±3.1) B b	100 A a	145.79	< 0.0001
	12	44.5 (±4.4) B b	49.0 (±6.2) B b	100 A a	100 A a	100 A a	118.12	< 0.0001
	15	54.5 (±6.1) A c	79.5 (±4.3) A b	100 A a	100 A a	100 A a	80.03	< 0.0001
	$F_{4,76}$	52.45	54.25	40.01	13.91	0		
	P	< 0.0001	< 0.0001	< 0.0001	< 0.0001	1		
Deutonymph	3	40.5 (±4.0) D c	43.5 (±5.8) D c	56.5 (±2.0) C b	59.0 (±3.6) B b	99.0 (±0.9) A a	54.92	< 0.0001
	6	52.0 (±4.8) C c	53.0 (±3.9) C bc	59.5 (±2.3) C b	64.5 (±4.9) B b	100 A a	40.46	< 0.0001
	9	54.0 (±4.1) BCd	67.0 (±3.3) B c	85.0 (±4.4) B b	96.5 (±1.8) A a	100 A a	66.22	< 0.0001
	12	59.0 (±3.0) B d	72.5 (±4.1) ABc	88.5 (±2.7) B b	95.5 (±1.5) A a	100 A a	55.57	< 0.0001
	15	68.5 (±2.7) A d	76.5 (±4.1) A c	94.0 (±1.8) A b	100 A a	100 A a	47.20	< 0.0001
	$F_{4,76}$	16.6	29.66	53.4	72.59	0.16		
	P	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0.9572		
Protonymph	3	38.0 (±2.8) C c	40.5 (±4.3) Dbc	44.0 (±3.9) D bc	45.5 (±3.5) C b	100 A a	54.52	< 0.0001
	6	47.5 (±4.9) C e	60.5 (±3.9) C d	76.5 (±3.6) C c	82.0 (±3.4) B b	100 A a	57.21	< 0.0001
	9	54.5 (±4.7) B e	62.0 (±4.2) C d	78.0 (±3.8) BCc	91.0 (±2.8) A b	100 A a	56.79	< 0.0001
	12	61.5 (±4.0) B e	76.5 (±3.6) B d	82.5 (±2.9) B c	89.5 (±3.1) A b	100 A a	38.33	< 0.0001
	15	81.5 (±2.8) A b	86.5 (±3.1) A b	100 A a	100 A a	100 A a	26.96	< 0.0001
	$F_{4,76}$	38.6	46.2	61.98	78.47	0		
	P	< 0.0001	< 0.0001	< 0.0001	< 0.0001	1		
Larva	3	51.5 (±6.1) C b	56.0 (±3.8) D b	58.0 (±4.2) D b	90.0 (±3.1) B a	100 A a	64.92	< 0.0001
	6	62.5 (±4.0) B c	64.0 (±3.7) C c	78.0 (±3.0) C b	93.0 (±2.2) B a	100 A a	47.34	< 0.0001
	9	64.5 (±3.9) B c	71.0 (±2.7) B c	89.5 (±2.6) B b	96.5 (±1.3) A a	100 A a	49.63	< 0.0001
	12	76.5 (±3.5) A b	76.5 (±3.3) B b	95.0 (±1.4) A a	100 A a	100 A a	37.46	< 0.0001
	15	75.5 (±2.9) A c	82.5 (±3.6) A b	98.5 (±0.8) A a	99.5 (±0.5) A a	100 A a	36.74	< 0.0001
	$F_{4,76}$	17.27	17.99	54.22	8.26	0		
	P	< 0.0001	< 0.0001	< 0.0001	< 0.0001	1		
Egg	3	32.0 (±6.8) D c	67.0 (±4.8) B b	100 A a	100 A a	100 A a	128.52	< 0.0001
	6	60.0 (±7.4) C c	95.0 (±2.2) A b	100 A a	100 A a	100 A a	75.79	< 0.0001
	9	76.5 (±5.0) B b	98.0 (±0.9) A a	100 A a	100 A a	100 A a	38.31	< 0.0001
	12	99.0 (±1.0) A a	100 A a	100 A a	100 A a	100 A a	0.16	0.9572
	15	100 A a	100 A a	100 A a	100 A a	100 A a	0	1
	$F_{4,76}$	107.95	55.57	0	0	0		
	P	< 0.0001	< 0.0001	1	1	1		

* Mortality rate with the same small letters in rows or the same capital letters in columns within each life stage are not significantly different ($P > 0.05$)

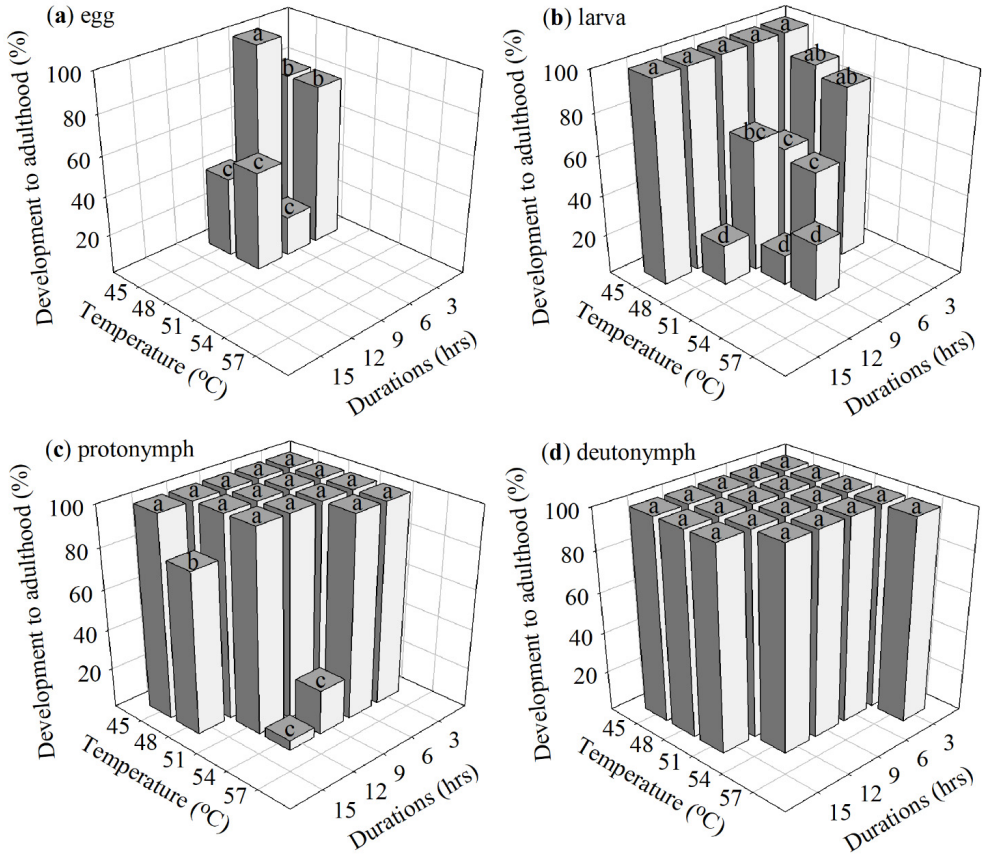

FIGURE 1. Proportion of immatures surviving heat treatment that developed to adult stage in *T. ludeni.* For each life stage, columns with the same letters are not significantly different ($P > 0.05$).

Effect of heat treatment on immature development to adult stage

We show that increasing treatment temperature and exposure duration significantly reduced the probability of immatures to develop to adulthood (x_5^2 = 34.71, P < 0.0001 for egg; x_{12}^2 = 136.25, P < 0.0001 for larva; x_{17}^2 = 180.34, P < 0.0001 for protonymph; x_{19}^2 = 0, P = 1 for deutonymph) (Figure 1). These findings also indicate that older immatures were significantly more likely to complete development across treatments (x_3^2 = 158.64, P < 0.0001) (Figure 1).

Effect of heat treatment on reproduction

Females that resulted from eggs treated at > 48°C (Figure 2a) or larvae treated at > 51°C for any duration (Figure 2b) did not lay any eggs. Those that developed from other treated life stages laid significantly fewer eggs with the increase of temperature and exposure duration ($F_{14,271}$ = 45.48, P < 0.0001 for protonymph; $F_{16,310}$ = 26.68, P < 0.0001 for deutonymph; $F_{13,266}$ = 54.32, P < 0.0001 for adult female) (Figure 2c–e).

Discussion

Here we reported the responses of *T. ludeni* to air temperatures ranged from 45 to 57°C for three to 15 hours. We showed that higher temperature and longer exposure caused higher mortality to all life stages, but younger life stages were more sensitive to heat than older ones, with adults being most

tolerant and eggs most susceptible (Table 1). All adults died after exposure to 51°C or 54°C for 12 hours or 57°C for ≥ six hours, while no eggs survived 45°C for ≥ 15 hours, 48°C for ≥ 12 hours, or ≥ 51°C for any duration. We also demonstrate that higher temperature and longer exposure time reduced the probability of heat-treated juveniles to successfully develop to adulthood, but older immatures were more likely to complete development across treatments (Figure 1). Females that developed from heat-treated eggs or larvae laid only a few eggs and those from other treated life stages laid fewer eggs with increasing temperature and exposure time (Figure 2).

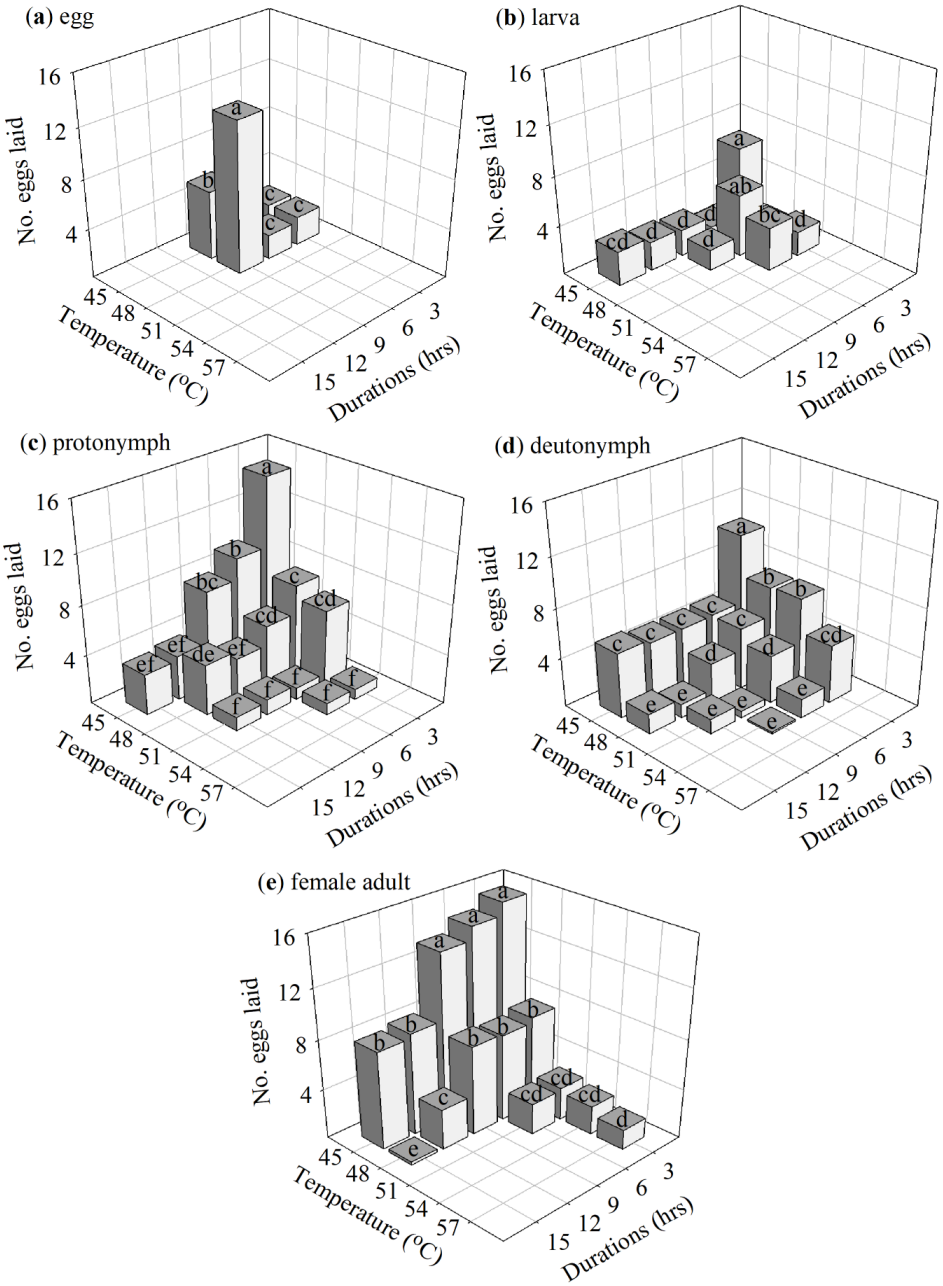

FIGURE 2. Mean number of eggs laid by *T. ludeni* females after their or their juvenile stages' exposure to different temperatures for various durations. For each life stage, columns with the same letters are not significantly different ($P > 0.05$).

Heat treatment has been used or trialled for killing insects (e.g., Cowley *et al*. 1992; Dentener *et al*. 1997; Jessup *et al*. 1998; Jacobi *et al*. 2001; Hara 2013; Macana & Baik 2018) and mites (Waddell & Birtles 1992; Waddell *et al*. 1993; Gotoh *et al*. 2013) on postharvest products. In *T. ludeni*, the egg stage was the least tolerant to air heat with all eggs killed at 51C within three hours (Table 1). Because all life stages may be present at the same time due to short life cycle and overlapping generations (Adango *et al*. 2006; Ristyadi *et al*. 2019) and some individuals of life stages other than eggs may survive this temperature (Table 1), two treatments of 51C for three hours at a 10-day interval can fully disinfest products with all eggs being killed in the first treatment and those laid by survived individuals destroyed in the second. Alternatively, we can eradicate the mites of all stages using one treatment of 57°C for about six hours.

However, the full disinfestation strategy using hot air of 51–57°C may be more suitable for treating plant residues on exported/imported machinery, farm equipment and containers because it may have negative impact on fresh postharvest products. With the knowledge that exposure to 45C for a few hours substantially reduced the mites' fecundity, particularly when the younger stages were treated, we suggest that heat treatment of fresh postharvest products with 45°C could still considerably reduce the quarantine risk of this pest. Moreover, Auger *et al*. (2003) report that wettable sulphur can kill all stages of *T. urticae* at the air temperature of 35C. We thus predict that air temperature much lower than 45°C for shorter than three hours can achieve complete disinfestation for *T. ludeni* if a chemical like wettable sulphur is also used. Further investigation into possible combinations of chemical and heat treatments for this pest would provide valuable information for exporters.

In conclusion, we demonstrate that heat shock tolerance is stage-dependent in *T. ludeni* with eggs being the most vulnerable and adults the most tolerant. Heat shock also reduces developmental success and fecundity. We may fully disinfest plant residues on machinery, equipment and containers using two treatments of 51°C for three hours at a 10-day interval or one treatment of 57°C for about six hours, and substantially reduce quarantine risk by treating fresh products with 45°C for a few hours. This study provides important knowledge for development of hot air disinfestation programs of this invasive pest. Information presented here may offer a reference for future evaluation of its invasion potential in relation to heat waves caused by climate change.

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