Thermal Death Kinetics of Mediterranean, Malaysian, Melon, and Oriental Fruit Fly (Diptera: Tephritidae) Eggs and Third Instars

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ABSTRACT The late-aged egg and third-instar life stages of laboratory-reared Malaysian fruit fly, *Bactrocera latifrons* (Hendel); Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann); melon fly, *B. cucurbitae* Coquillett; and oriental fruit fly, *B. dorsalis* (Hendel), (Diptera: Tephritidae); and the third instars of wild Mediterranean fruit fly were exposed to thermal treatments. A heating block system was used to determine the thermal death kinetics of the four fruit fly species. Treatments consisted of heating the fruit fly life stages to 44, 46, 48, and 50°C and holding for different times ranging from 0 to 120 min depending on the thermal mortality response and time required to obtain 100% mortality for each species and life stage. The 0.5-order kinetic model had the best fit to the survival ratio for all the treatment temperatures and was used to predict lethal times. The thermal death time (TDT) curves showed a tolerance order of Mediterranean fruit fly eggs ≤ third instars at 44, 46, and 50°C, third instars ≤ eggs at 48°C, and wild third instars < the laboratory-reared third instars. Comparison between Mediterranean fruit fly third instar thermotolerance from Hawaii and Israel showed that Israel Mediterranean fruit fly was more thermotolerant. A comparison of minimum treatment times at a given temperature required to obtain 100% mortality of laboratory-reared Malaysian, Mediterranean (Hawaii and Israel strains), melon, Mexican, and oriental fruit fly eggs or third instars and wild Mediterranean fruit fly (Hawaii strain) eggs or third instars showed that oriental fruit fly was the most thermotolerant among the third instars, and the difference in heat tolerance between third instars and eggs was negligible at 50°C.

KEY WORDS fruit fly, heating block system, heat treatments, thermal death, quarantine

Fruite flies (Diptera: Tephritidae) include many species that are major pests in almost all fruit-growing areas worldwide. Fruit flies are among the most economically important insect pests because they attack fruit commercially grown for local consumption or export, and they are capable of moving beyond their native range to become quickly established in new geographical areas. Both domestic and foreign quarantine restrictions, including prescribed quarantine treatments, have been legislated to limit the spread of economically important fruit flies (White and Elson-Harris 1992). Four fruit fly species of major quarantine importance are found in Hawaii: Malaysian fruit fly, *Bactrocera latifrons* (Hendel); Mediterranean fruit fly, *Ceratitis capitata* (Wiedemann); melon fly, *B. cucurbitae;* and oriental fruit fly, *B. dorsalis* (Hendel). Most fruits and vegetables cannot be exported from Hawaii without quarantine treatment to eliminate potential egg or larval infestations of one or more of the four species.

Numerous quarantine heat treatments have been developed for the export of tropical fruits from Hawaii, such as vapor heat and forced hot air treatments for papaya (APHIS 2002b, c) and hot water immersion treatments for litchi and longan (APHIS 2002a), to kill potential fruit fly egg or larval infestations. However, the temperature and treatment times required to kill fruit fly eggs or larvae is very close to the thermal tolerances of the treated fruit (Chan et al. 1996), and injury in the form of surface damage, incomplete ripening, increased postharvest decay, and reduced shelf life are known to occur (Paull and McDonald 1994). Vapor heat, forced hot air, and hot water immersion treatments rely on heat conduction to transfer thermal energy from the fruit surface to the fruit interior. Because the resulting temperature gradient inside the fruit is directly influenced by fruit size, with larger fruit heating at a slower rate, a more uniform and rapid heating method is needed to minimize thermal damage to fruit (Wang et al. 2001b). The application of radio frequency (RF) has shown potential as a uniform and rapid thermal treatment against insect pests (Andreuccetti et al. 1994; Hallman and Sharp 1994; Nelson 1996; Tang et al. 2000; Wang et al. 2001a, 2002c, 2007a, b).

The treatment times and temperatures used in commercial heat treatments are determined first by testing the different fruit fly egg and larval stages in vitro to determine the thermal exposure necessary

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to kill them and by testing fruits infested with a sufficient population of the most heat-tolerant species and life stage(s) to develop adequate data required by the regulatory agencies of importing countries to meet quarantine security levels (Gazit et al. 2004). To facilitate the development of or to optimize quarantine heat treatments, including RF, information on the relative thermotolerances of the life stages is needed for the target fruit fly species at temperatures within the range of those that will control the insects. Identifying the most heat-tolerant species and life stage(s) helps to exclude less heat-tolerant species and life stages in treatment efficacy testing, thus significantly reducing the overall number of tests required to establish treatment parameters.

From the original work by Armstrong (1982) tol the work by Gazit et al. (2004), the approach used to determine the most heat-tolerant fruit fly species and life stage(s) was by direct hot water immersion of the insects (Foliaki and Armstrong 1997, Heather et al. 1997, Jang 1986, Jang et al. 1999, Sales et al. 1997, Waddell et al. 1997). However, anomalies occurred whereby direct hot water immersion indicated that Mediterranean, melon, and oriental third instars were the most thermotolerant stage (Jang 1991), but in situ tests with infested fruit indicated that late-aged eggs were the most thermotolerant stage (Armstrong et al. 1995) for the same fruit fly species. Later hot water immersion tests by Jang et al. (1999) determined that the late-aged egg stage was more thermotolerant than third instars. Heat reduces the level of dissolved oxygen in water, which may have contributed to increased mortality found in fruit fly eggs (Moss and Jang 1991) and larvae (Hansen and Sharp 1998). Consequently, by altering the level of dissolved oxygen, hot water immersions may cause anomalies when determining the relative thermotolerance of fruit fly life stages. Therefore, a more optimum approach for determining thermotolerance of fruit fly life stages would be a heating method that allowed test insects free access to air.

A unique experimental heating block system (HBS) has been developed and used for testing responses of insects to high temperatures (Ikediala et al. 2000; Wang et al. 2002a, b; Johnson et al. 2003). The HBS is able to heat insects directly and uniformly. The HBS can be programmed to simulate the heating rate of the interior of fruit when subjected to different heating methods, such as hot air, hot water, and RF treatments. Thermal mortality data developed with the HBS have been validated in efficacy tests on fresh fruits or nuts infested with target insect pests, including apples (Wang et al. 2006), cherries (Feng et al. 2004, Hansen et al. 2004), and walnuts (Wang et al. 2001a, c, 2007a, b; Mitcham et al. 2004). Data from these studies also were used successfully to develop thermal death kinetic models for codling moth, *Cydia pomonella* L. (Lepidoptera: Tortricidae) (Wang et al. 2002a), Indianmeal moth, *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae) (Johnson et al. 2003); navel orangeworm, *Amyelois transitella* (Walker) (Lepidoptera: Pyralidae) (Wang et al. 2002b); Mediterranean fruit fly (Gazit et al. 2004); red flour beetle, *Tribolium castaneum* (Herbst) (Coleoptera: Tenebrionidae) (Johnson et al. 2004); and Mexican fruit fly, *Anastrepha ludens* (Loew) (Diptera: Tephritidae) (Hallman et al. 2005).

We report the results of tests with the HBS: 1) to determine the relative thermotolerances of Malaysian fruit fly, Mediterranean fruit fly, melon fly, and oriental fruit fly; 2) to develop thermal death kinetic models for the egg and larval instars; and 3) to determine the most heat-tolerant species and life stage(s).

Materials and Methods

Test Insects. Malaysian fruit flies, Mediterranean fruit flies, melon flies, and oriental fruit flies used in our studies were obtained from the USDA–ARS U.S. Pacific Basin Agricultural Research Center rearing facility in Honolulu, HI. Mediterranean fruit flies, melon flies, and oriental fruit flies were reared as described by Vargas and Carey (1989). Malaysian fruit flies were reared as described by Vargas and Mitchell (1987). Fruit flies were shipped to Hilo, HI, in the pupal stage. After eclosion, ≈10,000 adults (50 ± 5% females) of each species were kept in separate 14.3-m^3 screen cages and fed water, sugar, and protein hydrolysate until sexually mature (11 ± 1 d). Eggs (16 ± 1 h old) were collected in eggs deposition tubes as described by Vargas and Carey (1989). Eggs not used in thermotolerance tests were reared on larval diet (Vargas and Carey 1989) at ambient (22 ± 2°C) temperatures until they were third instars. Therefore, the eggs and third instars used in each successive thermotolerance test replication were from the same cohort. Wild Mediterranean fruit flies were from Jerusalem cherries, *Solanum pseudocapsium* L., collected from Hawaii Volcanoes National Park, HI, and reared to adults using the same procedures as stated above.

HBS and Thermotolerance Tests. The HBS was built by the Department of Biological Systems Engineering at Washington State University, Pullman (Wang et al. 2005), and was similar to the system described by Gazit et al. (2004). Two hundred eggs were placed with a fine-tipped brush on moistened filter paper (1.5 by 1.5 cm), or 200 naked third instars were removed from larval diet by flotation and counted into small plastic cups (Armstrong et al. 1995). The eggs or larvae were placed directly on the heating surface of the bottom of the HBS (Gazit et al. 2004). The top of the HBS was positioned to enclose the eggs or larvae in the heating chamber, and the HBS was heated for selected time and temperature combinations (Gazit et al. 2004). Control insects were placed in the unheated block for the longest exposure time for each temperature–time combination.

Treated or control eggs were placed in petri dishes (25 cm diameter) lined with black filter paper moistened with distilled water and held at ambient (23 ± 2°C) temperature for 1 wk, after which time obser-

vations were made to count hatched (live) and unhatched (dead) eggs (Armstrong et al. 1995).

Treated or control (200) third instars were placed on larval diet in small trays as described by Armstrong et al. (1995), and the trays were held individually in plastic containers with sand on the bottom to facilitate pupation (Armstrong et al. 1995). Treated and control third instars were held at ambient (23 ± 2°C) temperature until pupation was complete, at which time the pupae (survivors) were counted.

Treatment Design and Statistical Analysis. For the two developmental stages of Mediterranean fruit fly, oriental fruit fly, and melon fly together with the third instars of Malaysian fruit fly, the four temperature set points we selected based on preliminary tests were 44, 46, 48, and 50°C. For the eggs of Malaysian fruit fly, the four temperature set points we selected based on preliminary tests were 44, 46, 49, and 50°C. Five to six exposure times were selected to provide a wide range of mortality levels, including 100%. Before each treatment, the HBS was preheated to 25°C, bringing the insects to a constant initial temperature. The heating rate (5°C/min) to obtain the set point temperatures was the same as described by Gazit et al. (2004).

Mortality rates for eggs were determined by subtracting the number of unhatched eggs from the initial number of eggs in each treatment replication, and mortality rates for third instars were determined by subtracting the number of pupae from the initial number of larvae in each treatment replication. Natural mortality in the controls was adjusted for treated insects using Abbott's formula (Abbott 1925). The mean and SD values of the corrected data were calculated over three replications. These data were further used to establish thermal death kinetic models and to compare the heat tolerance between eggs and third instars. Corrected treatment mortality for eggs and third instars was compared for each temperature and time combination using the SAS *t*-test (TTEST) procedure (SAS Institute 1989). We used an arcsine transformation to normalize the data before analysis.

Thermal Death Kinetic Model. The kinetic model is similar to that previously used for codling moth (Wang et al. 2002a), Indianmeal moth (Johnson et al. 2003), and navel orangeworm (Wang et al. 2002b), and is based on the following equation:

$$\frac{d(N/N_0)}{dt} = -k(N/N_0)^n \qquad [1]$$

where k is the thermal death rate constant (1/min), n is the kinetic order of the reaction, and N_o and N are the initial and surviving numbers of insects, respectively. The integration form of equation 1 can be obtained for different reaction orders as follows:

$$\begin{aligned} \ln(N/N_0) &= -kt + c \quad (n = 1) \\ (N/N_0)^{1-n} &= -kt + c \quad (n \neq 1) \end{aligned} \qquad [2]$$

For each temperature, survival (N/N_0) was regressed against exposure time (t, min) according to equation 2 for the 0, 0.5, 1, 1.5, and 2 reaction orders. The reaction order is defined as the power to which its survival ratio in the rate equation is raised. The most suitable reaction order was determined by comparing the coefficients of determination (r^2) for all treatment temperatures. The lethal times of LT_{95}, LT_{99}, $LT_{99.83}$, and $LT_{99.9968}$ (probit 9) could be estimated by inputting one survivor out of 20, 100, 600, and 31,250 treated insects, respectively.

Activation Energy Calculation. The activation energy is defined as the energy that must be overcome in order for insect thermal death to occur and is useful in determining the sensitivity of insect mortality to changes in temperature. From the thermal-death-time (TDT) curve, which was developed by plotting for each temperature the minimum exposure time required to achieve 100% mortality of test insects on a semilog scale, the activation energy (E_a, J/mol) can be calculated according to Tang et al. (2000) as:

$$E_a = \frac{2.303RT_{\min}T_{\max}}{z} \qquad [3]$$

where R is universal gas constant (8.314 J/mol K), T_{min} and T_{max} are the minimum and maximum absolute temperatures (K) of a test range, respectively, and z is the negative inverse of the slope of the TDT curve (°C). From the k-T curve, developed by plotting log k versus the reciprocal of the absolute temperature ($1/T$), the k value follows an Arrhenius relationship (Tang et al. 2000):

$$k = k_{ref}e^{\frac{-E_a}{R}\left(\frac{1}{T}-\frac{1}{T_{ref}}\right)} \qquad [4]$$

where k_{ref} is the reference thermal death rate constant (1/min) at reference temperature (T_{ref}, K). Applying logarithms to both sides of equation 4, we derive the following:

$$\log k = \log A - E_a/(2.303*R*/T) \qquad [5]$$

E_a can be calculated from the slope of the experimentally developed k-T curve.

Results and Discussion

Determination of Thermal Death Kinetic Orders. Coefficients of determination (r^2) derived for each kinetic order model and treatment temperature for all tested fruit fly eggs and larvae are given in Tables 1 and 2, respectively. The 0.5-order model provided the best average fit over the four temperatures for survival ratio and exposure time among the four fruit fly species for both eggs (mean $r^2 = 0.966$; Table 1) and larvae (mean $r^2 = 0.924$; Table 2) compared with 0-, 1.0-, 1.5-, and 2.0-order models. The r^2 values in Table 1, compared with the r^2 values in Table 2, suggest the model prediction for eggs was better than for third instars.

The 0.5-order thermal death kinetic models at all treatment temperatures for the eggs and larvae of the four fruit fly species are given in Tables 3 and 4, respectively. The 0.5-order model was found to be the most applicable for a Mediterranean fruit fly strain in Israel (Gazit et al. 2004), codling moth (Wang et al.

Table 1. Coefficients of determination (r^2) from kinetic order (n) models for thermal mortality of laboratory-reared Malaysian, Mediterranean, melon, and oriental fruit fly eggs at four temperatures

Fruit fly species[a]	Temperature (°C)	$n = 0$	$n = 0.5$	$n = 1$	$n = 1.5$	$n = 2$
Malaysian	44	0.972	0.994	0.766	0.359	0.192
	46	0.949	0.951	0.792	0.522	0.404
	49	0.977	0.952	0.710	0.433	0.356
	50	0.937	0.961	0.879	0.686	0.629
Mediterranean	44	0.911	0.997	0.792	0.423	0.267
	46	0.823	0.932	0.933	0.845	0.783
	48	0.848	0.941	0.924	0.725	0.600
	50	0.883	0.980	0.911	0.655	0.561
Melon	44	0.917	0.969	0.825	0.533	0.446
	46	0.881	0.971	0.939	0.719	0.575
	48	0.862	0.982	0.913	0.701	0.635
	50	0.912	0.979	0.870	0.557	0.452
Oriental	44	0.866	0.987	0.875	0.545	0.390
	46	0.806	0.951	0.961	0.768	0.616
	48	0.941	0.968	0.973	0.824	0.652
	50	0.768	0.941	0.940	0.665	0.564
	Mean	0.891	0.966	0.875	0.623	0.508

[a] Laboratory reared.

Table 3. Thermal death kinetic parameters for the 0.5 kinetic model of laboratory-reared Malaysian, Mediterranean, melon, and oriental fruit fly eggs at four temperatures

Fruit fly species[a]	Temperature (°C)	Thermal death constants of $(N/N_0)^{0.5} = -kt + c$		
		k (±SEM)	c (±SEM)	r^2
Malaysian	44	0.0081 (0.0003)	1.0048 (0.0287)	0.994
	46	0.0347 (0.0040)	1.0712 (0.0934)	0.951
	49	0.3295 (0.0425)	1.0702 (0.0979)	0.952
	50	0.7060 (0.0826)	1.0796 (0.1009)	0.961
Mediterranean	44	0.0122 (0.0003)	0.9969 (0.0195)	0.997
	46	0.0429 (0.0058)	0.9905 (0.1193)	0.932
	48	0.1761 (0.0220)	0.9698 (0.1064)	0.941
	50	1.0016 (0.0827)	0.9669 (0.0656)	0.980
Melon	44	0.0214 (0.0019)	1.0946 (0.0808)	0.969
	46	0.0878 (0.0076)	0.9946 (0.0799)	0.971
	48	0.3187 (0.0249)	0.9445 (0.0600)	0.982
	50	2.0241 (0.1484)	1.0008 (0.0621)	0.979
Oriental	44	0.0133 (0.0008)	0.9060 (0.0425)	0.987
	46	0.0469 (0.0062)	0.8712 (0.0959)	0.951
	48	0.2463 (0.0319)	0.9401 (0.1007)	0.968
	50	0.9035 (0.1302)	0.8461 (0.0991)	0.941

[a] Laboratory reared.

2002a), Indian meal moth (Johnson et al. 2003), and navel orangeworm (Wang et al. 2002b). Therefore, the 0.5-order model was used for all further calculations in our study. The thermal death rate constant k increased with temperature. Under ideal conditions, the value of constant c in equation 2 should be equal to 1 because at time zero the survival number should be the same as the initial number of insects [i.e., $(N/N_0)^{0.5} = 1$ at $t = 0$]. In reality, however, the best-fitted curve may not pass this point as shown in Tables 3 and 4, which was also the case for the 0.5-order model constants developed by Gazit et al. (2004). The fitted regression lines based on the mortality data at each temperature are shown in Figs. 1 and 2 for eggs and third instars, respectively. The r^2 values in Tables 1 and 2 indicate better model predictions for the eggs of the four fruit fly species than for the third instars. The longest exposure times resulting in 100% mortality varied with species and life stages at the four temperatures (Figs. 1 and 2), and the data were used to develop the TDT curves for comparing the relative thermotolerance among the four fruit fly species.

Table 2. Coefficients of determination (r^2) from kinetic order (n) models for thermal mortality of wild Mediterranean and laboratory-reared Malaysian, Mediterranean, melon, and oriental fruit fly third instars at four temperatures

Fruit fly species	Temperature (°C)	$n = 0$	$n = 0.5$	$n = 1$	$n = 1.5$	$n = 2$
Malaysian[a]	44	0.907	0.978	0.879	0.577	0.422
	46	0.755	0.903	0.848	0.710	0.620
	48	0.816	0.940	0.965	0.705	0.520
	50	0.889	0.940	0.957	0.887	0.761
Mediterranean[a]	44	0.947	0.942	0.674	0.375	0.260
	46	0.905	0.980	0.915	0.537	0.379
	48	0.763	0.923	0.960	0.673	0.540
	50	0.728	0.903	0.989	0.842	0.703
Mediterranean[b]	44	0.756	0.931	0.964	0.744	0.583
	46	0.816	0.953	0.980	0.814	0.683
	48	0.967	0.967	0.786	0.520	0.430
	50	0.743	0.813	0.909	0.950	0.880
Melon[a]	44	0.984	0.942	0.668	0.385	0.317
	46	0.878	0.971	0.909	0.588	0.461
	48	0.714	0.821	0.945	0.936	0.848
	50	0.684	0.854	0.948	0.927	0.915
Oriental[a]	44	0.995	0.907	0.430	0.159	0.119
	46	0.737	0.884	0.802	0.471	0.369
	48	0.904	0.987	0.857	0.567	0.459
	50	0.868	0.938	0.955	0.829	0.784
	Mean	0.838	0.924	0.867	0.660	0.553

[a] Laboratory reared.
[b] Wild.

Table 4. Thermal death kinetic parameters for the 0.5 kinetic model for wild Mediterranean and laboratory-reared Malaysian, Mediterranean, melon, and oriental fruit fly third instars at four temperatures

Fruit fly species	Temperature (°C)	Thermal death constants of $(N/N_0)^{0.5} = -kt + c$		
		k (±SEM)	c (±SEM)	r^2
Malaysian[a]	44	0.0171 (0.0015)	0.9863 (0.0676)	0.978
	46	0.0482 (0.0079)	0.9014 (0.1235)	0.903
	48	0.2007 (0.0253)	0.9163 (0.1057)	0.940
	50	0.4731 (0.0689)	0.6687 (0.0830)	0.940
Mediterranean[a]	44	0.0065 (0.0008)	0.9636 (0.1016)	0.942
	46	0.0379 (0.0031)	0.9312 (0.0792)	0.980
	48	0.2393 (0.0400)	0.8849 (0.1265)	0.923
	50	0.6436 (0.1053)	0.8676 (0.1362)	0.903
Mediterranean[b]	44	0.0093 (0.0015)	0.6523 (0.0609)	0.931
	46	0.0350 (0.0055)	0.5341 (0.0368)	0.953
	48	0.4074 (0.0434)	1.0624 (0.0840)	0.967
	50	0.7054 (0.2389)	0.6383 (0.1767)	0.813
Melon[a]	44	0.0177 (0.0020)	1.1253 (0.0985)	0.942
	46	0.0678 (0.0059)	0.9760 (0.0739)	0.971
	48	0.1992 (0.0466)	0.8357 (0.1948)	0.821
	50	0.6410 (0.1324)	0.8276 (0.1713)	0.854
Oriental[a]	44	0.0056 (0.0008)	1.0443 (0.0996)	0.907
	46	0.0215 (0.0035)	0.9000 (0.1346)	0.884
	48	0.1980 (0.0113)	0.9910 (0.0471)	0.987
	50	0.5226 (0.0674)	1.0122 (0.1131)	0.938

[a] Laboratory reared.
[b] Wild.

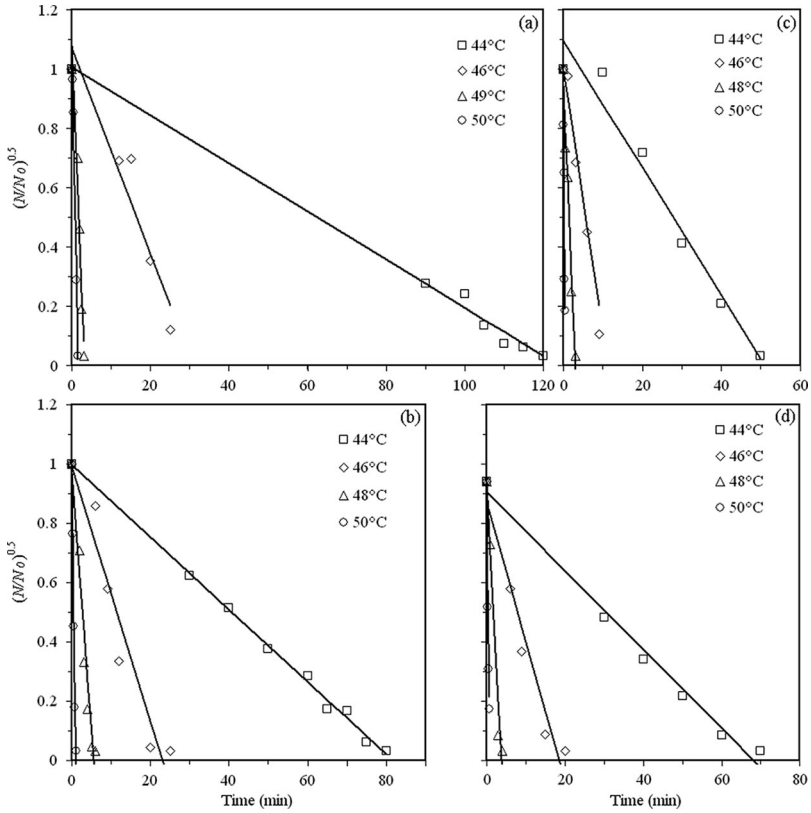

Fig. 1. Thermal mortality curves for laboratory-reared Malaysian (a), Mediterranean (b), melon (c), and oriental (d) fruit fly eggs at four temperatures using a 0.5-order kinetic model.

Relative Thermotolerance of Eggs and Third Instars. Tables 5 and 6 compare the lethal times between LT_{99} and $LT_{99.9968}$ (probit 9) at 95% CI obtained by the 0.5 kinetic model and with experimentally observed treatment times required to obtain 100% mortality for eggs and third instars of four fruit fly species. The observed exposure time for 100% mortality of 600 eggs or larvae in this study corresponded to the estimated lethal times to produce >99.83% mortality (to kill >599 of 600). The results showed that the predicted $LT_{99.83}$ was slightly less than the observed time to obtain complete kill of 600 eggs or larvae at temperatures above 46°C. These results are similar to those of Gazit et al. (2004), where the 0.5 kinetic model seemed to have slightly underestimated the lethal times for eggs and third instars at each temperature compared with the experimental values obtained in treatments using the HBS. The lethal times of experimental data and predicted values were not much different at 48 and 50°C, especially for practical considerations in applying actual heat treatments for insect control. Lethal times increased with increasing predicted sample sizes (e.g., from 300 to 32,000). However, the differences between $LT_{99.83}$ and $LT_{99.9968}$ decreased at higher temperatures (Tables 5 and 6).

TDT Curves and Activation Energy. TDT curves (Fig. 3) show that melon fly was the least heat-tolerant and Malaysian fruit fly was the most heat-tolerant among the eggs of the four fruit fly species. The slopes for the eggs of all fruit fly species were similar, which resulted in similar z values (e.g., 3.1, 3.2, 3.0, and 3.2°C for Malaysian, Mediterranean, melon, and oriental fruit flies, respectively). That is, the eggs of all fruit fly species have similar sensitivity to temperature increase. Oriental fruit fly third instars were the most heat tolerant among the four fruit fly species (Fig. 4). The reciprocal of the slopes resulted in z values of 3.7, 3.0, 3.9, and 3.1°C for third-instar Malaysian, Mediterranean, melon, and oriental fruit flies, respectively.

Table 7 compares the activation energies for the eggs and third instars of the four fruit fly species estimated by both the TDT curve and the k-T curve (Figs. 5 and 6) methods. The differences in activation energies between TDT and k-T curves were small (<1.8%) for eggs but large (≈9.3%) for third instars. The activation energies for eggs of the four fruit fly species were similar, as reflected in the parallel TDT curves in Fig. 3. Conversely, the activation energies for third instars varied widely as indicated by the greatly different slopes of their TDT curves shown in Fig. 4. In particular, the activation energy for Malaysian and melon fruit fly third instars were distinctively different from those for Mediterranean and oriental fruit fly third instars (Table 7; Fig. 6). Activation energy is important to the development of heat treatments because the

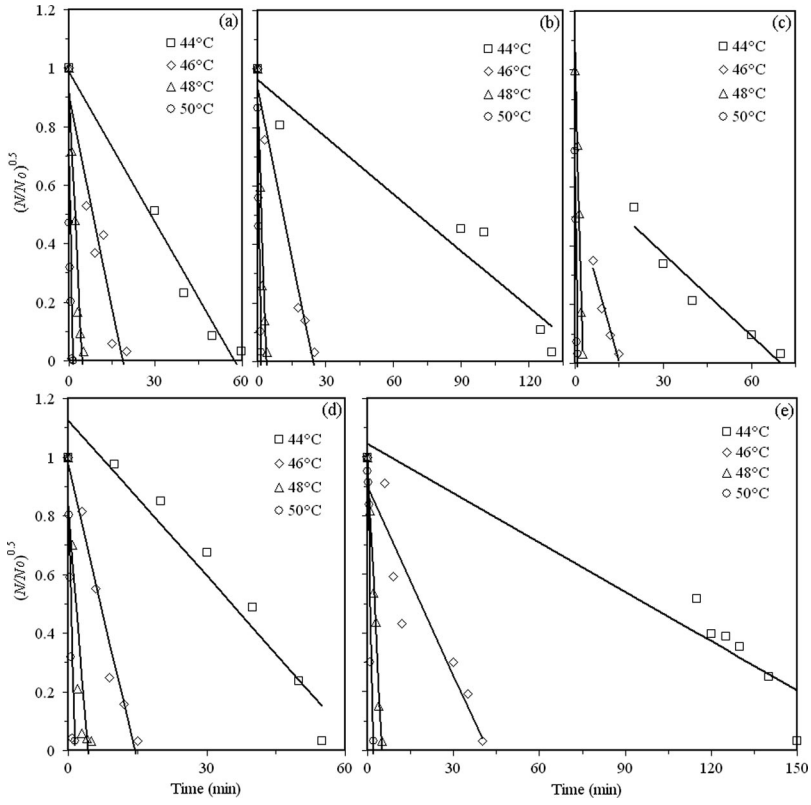

Fig. 2. Thermal mortality curves for Malaysian (a), laboratory (b) or wild (c) Mediterranean, melon (d), and oriental (e) fruit fly third instars at four temperatures using a 0.5-order kinetic model.

higher the activation energy, the more sensitive the target insect is to temperature change.

Table 8 summarizes the minimum observed treatment times required to obtain 100% mortality for 600 each of laboratory-reared Malaysian, Mediterranean (Hawaii and Israel strains), melon, Mexican, and oriental fruit fly eggs or third instars and wild Mediterranean fruit fly (Hawaii strain) eggs or third instars. The oriental fruit fly was the most heat tolerant among the third-instars. The difference of heat tolerance be-

Table 5. Comparison of lethal times (min) obtained by the 0.5 kinetic model and observed exposure to achieve 100% mortality for laboratory-reared Malaysian, Mediterranean, melon, and oriental fruit fly eggs at four temperatures

Fruit fly species[a]	Temperautre (°C)	Minimum time observed for 100% mortality	0.5-order kinetic model							
			LT_{95}	95% CI	LT_{99}	95% CI	$LT_{99.83}$	95% CI	$LT_{99.9968}$[b]	95% CI
Malaysian	44	120	96.4	93.0–99.9	111.7	107.9–115.5	119.0	114.9–123.2	123.4	119.0–127.7
	46	30	24.4	20.7–28.2	28.0	23.5–32.4	29.7	24.8–34.5	30.7	25.6–35.8
	49	3	2.6	2.1–3.1	2.9	2.3–3.6	3.1	2.5–3.8	3.2	2.5–3.9
	50	1.5	1.2	0.9–1.5	1.4	1.1–1.7	1.5	1.1–1.8	1.5	1.1–1.9
Mediterranean	44	80	63.4	62.0–64.8	73.5	71.8–75.2	78.4	76.5–80.2	81.2	79.3–83.2
	46	25	17.9	14.2–21.5	20.8	16.4–25.1	22.1	17.5–26.8	23.0	18.1–27.8
	48	6	4.2	3.5–5.0	4.9	4.1–5.8	5.3	4.4–6.2	5.5	4.5–6.4
	50	1	0.7	0.6–0.9	0.9	0.7–1.0	0.9	0.8–1.1	1.0	0.8–1.1
Melon	44	50	40.7	35.0–46.4	46.5	39.8–53.2	49.2	42.0–56.5	50.9	43.3–58.4
	46	12	8.8	7.5–10.1	10.2	8.6–11.7	10.9	9.2–12.5	11.3	9.5–13.0
	48	3	2.3	1.9–2.6	2.6	2.2–3.1	2.8	2.4–3.3	2.9	2.5–3.4
	50	0.5	0.4	0.3–0.5	0.4	0.3–0.5	0.5	0.4–0.6	0.5	0.4–0.6
Oriental	44	70	51.3	47.4–55.2	60.6	56.0–65.2	65.1	59.9–70.2	67.7	62.3–73.1
	46	20	13.8	10.6–17.0	16.4	12.6–20.3	17.7	13.5–21.9	18.5	14.1–22.9
	48	4	2.9	1.9–3.9	3.4	2.3–4.6	3.7	2.4–4.9	3.8	2.5–5.1
	50	1	0.7	0.5–0.9	0.8	0.6–1.0	0.9	0.7–1.1	0.9	0.7–1.2

[a] Laboratory reared.

[b] Probit 9 level of quarantine security (Baker, A.C. 1939. The basis for treatment of products where fruit flies are involved as a condition for entry into the United States. U.S. Department of Agriculture Circular No. 551).

Table 6. Comparison of lethal times (min) obtained by the 0.5 kinetic model and observed exposure to achieve 100% mortality for wild Mediterranean and laboratory-reared Malaysian, Mediterranean, melon, and oriental fruit fly third-instars at four temperatures

Fruit fly species	Temperature (°C)	Minimum time observed for 100% mortality	0.5-order kinetic model							
			LT_{95}	95% CI	LT_{99}	95% CI	$LT_{99.83}$	95% CI	$LT_{99.9968}$[a]	95% CI
Malaysian[b]	44	60	44.6	38.6–50.6	51.8	44.8–58.9	55.3	47.7–62.9	57.3	49.3–65.4
	46	20	14.1	10.9–17.2	16.6	12.8–20.4	17.9	13.7–22.0	18.6	14.2–22.9
	48	5	3.5	2.8–4.1	4.1	3.3–4.8	4.4	3.5–5.2	4.5	3.7–5.4
	50	1.5	0.9	0.7–1.2	1.2	0.9–1.5	1.3	0.9–1.7	1.4	1.0–1.8
Mediterranean[b]	44	130	113.8	92.5–135.2	132.9	107.4–158.4	141.9	114.2–169.7	147.4	118.2–176.5
	46	25	18.7	15.7–21.6	21.9	18.5–25.3	23.5	19.8–27.2	24.4	20.6–28.3
	48	4	2.8	1.9–3.6	3.3	2.3–4.2	3.5	2.5–4.6	3.7	2.6–4.8
	50	1.5	1.0	0.7–1.3	1.2	0.8–1.5	1.3	0.9–1.7	1.3	0.9–1.7
Mediterranean[c]	44	70	46.1	37.1–55.1	59.4	47.9–70.8	65.8	52.3–79.3	69.5	54.7–84.4
	46	15	8.9	6.4–11.3	12.4	9.9–14.9	14.1	10.9–17.3	15.1	11.4–18.8
	48	2.5	2.1	1.7–2.4	2.4	1.9–2.8	2.5	2.0–3.0	2.6	2.1–3.1
	50	1.0	0.6	0.1–1.1	0.8	0.1–1.4	0.8	0.2–1.5	0.9	0.2–1.6
Melon[b]	44	55	50.9	43.1–58.8	57.9	48.6–67.3	61.3	51.2–71.4	63.3	52.7–73.8
	46	15	11.1	9.6–12.6	12.9	11.2–14.7	13.8	11.9–15.7	14.3	12.3–16.3
	48	5	3.1	2.0–4.1	3.7	2.5–4.9	4.0	2.7–5.3	4.2	2.8–5.5
	50	1.5	0.9	0.6–1.3	1.1	0.7–1.5	1.2	0.8–1.7	1.3	0.8–1.7
Oriental[b]	44	150	146.6	126.3–166.8	168.6	143.4–193.8	179.2	151.2–207.2	185.5	155.8–215.2
	46	40	31.5	24.1–38.8	37.2	28.4–46.0	40.0	30.3–49.6	41.6	31.5–51.7
	48	5	3.9	3.5–4.2	4.5	4.1–4.9	4.8	4.3–5.2	5.0	4.5–5.4
	50	2	1.5	1.1–1.9	1.7	1.3–2.2	1.9	1.4–2.3	1.9	1.4–2.4

[a] Probit 9 level of quarantine security (Baker, A.C. 1939. The basis for treatment of products where fruit flies are involved as a condition for entry into the United States. US Department of Agriculture Circular No. 551).
[b] Laboratory reared.
[c] Wild.

tween third instar and eggs became negligible for those four flies at 50°C. Compared with other fruit flies from the literature (Gazit et al. 2004, Hallman et al. 2005), the reported thermotolerance for third-instar Mediterranean fruit flies in Israel was higher than the four fruit flies in this research. This may have been caused by different experimental conditions and genetic differences. In practical protocol development, the treatments at 48 or 50°C for 7 or 2 min, respectively, are effective in controlling all life stages of the fruit flies in tropical fruits. Table 8 and Fig. 7 show that the laboratory-reared Mediterranean fruit fly third instar was more heat tolerant than wild larvae, indicating that the thermal treatments developed based on the laboratory-reared Mediterranean fruit fly should be effective against the wild Mediterranean fruit fly in Hawaii.

There are numerous studies reported in the literature on using hot water immersion to determine the relative thermal tolerances for the eggs and larvae of different fruit fly species. Overall, these studies yielded variable results when identifying the most thermotolerant life stage(s), showing (1) late-aged eggs generally equal to first instars in thermal tolerance, (2) late-aged eggs and first instars more thermotolerant than nonfeeding third instars, or (3) nonfeeding third instars more thermotolerant than late-aged eggs and first instars (Jang 1986, 1991, Sharp and Chew 1987, Foliaki and Armstrong 1997, Heather

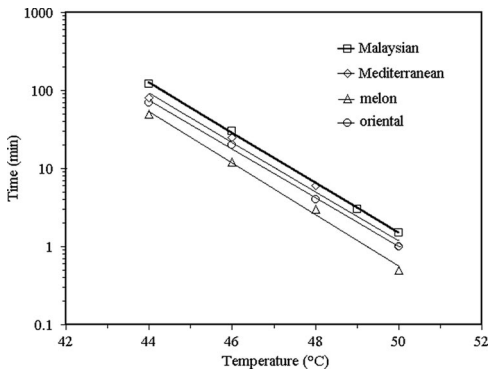

Fig. 3. Minimum time-temperature combinations to obtain 100% mortality of 600 laboratory-reared Malaysian, Mediterranean, melon, or oriental fruit fly eggs.

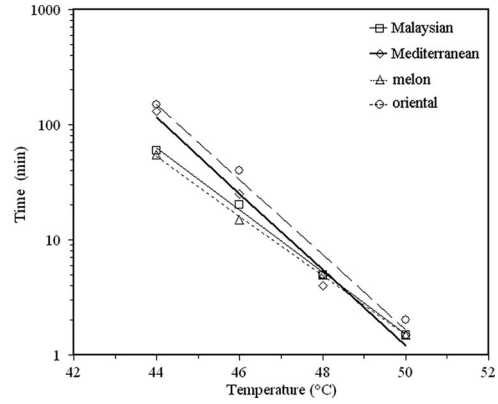

Fig. 4. Minimum time-temperature combinations to obtain 100% mortality of 600 Malaysian, Mediterranean, melon, and oriental fruit fly third instars.

Table 7. Activation energy for laboratory-reared Malaysian, Mediterranean, melon, and oriental fruit fly eggs and third instars

Fruit fly species	Activation energy (kJ/mol)			
	TDT curve		*k-T* curve	
	Eggs	Third instars	Eggs	Third instars
Malaysian	627.9	530.4	635.1	485.3
Melon	647.8	507.1	636.3	504.9
Mediterranean	621.1	647.6	623.4	666.4
Oriental	611.7	641.3	609.9	674.6

et al. 1997, Sales et al. 1997, Tora Vueti et al. 1997, Waddell et al. 1997, Hansen and Sharp 1998, Jang et al. 1999, Gazit et al. 2004, Hallman et al. 2005). The first heat tolerance studies with fruit flies reported by Armstrong (1982) compared only temperatures and exposure times that resulted in 100% mortality of Mediterranean, melon, or oriental fruit fly eggs and larvae. Although the immersion times used in the study did not provide adequate data from which to determine relative heat tolerances between eggs and larvae, the results did show a heat tolerance trend between fruit fly species with Mediterranean fruit fly ≥ melon fly ≥ oriental fruit fly (Armstrong 1982). The first in-depth studies to determine the relative thermotolerance between Mediterranean, melon, and oriental fruit fly eggs and larvae conducted by Jang (1991) reported that third instars were more thermotolerant than either late-aged eggs or first instars. Jang et al. (1999) further refined the data analyses used to determine thermotolerance in studies with Malaysian fruit fly and found the late-aged eggs and first instars for this species were more thermotolerant than third instars. Using the newer data analyses, Jang et al. (1999) revisited the original data for Mediterranean, melon, and oriental fruit flies (Jang 1986, 1991) and determined that the thermal tolerance for the life stages of these three species more closely resembled that of Malaysian fruit fly, with the late-aged eggs and first instars more thermo-tolerant than third instars. Additionally,

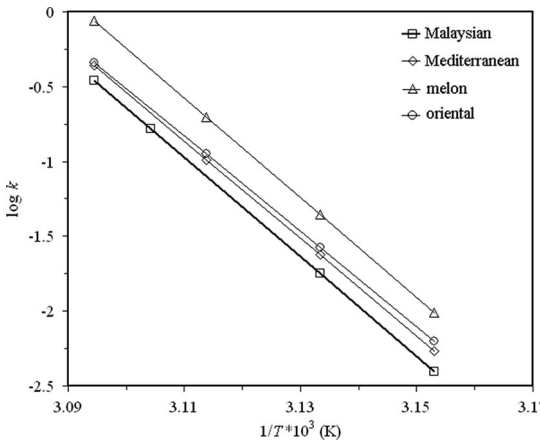

Fig. 5. Arrhenius plot for temperature effects on thermal death rate constant for laboratory-reared Malaysian, Mediterranean, melon, and oriental fruit fly eggs.

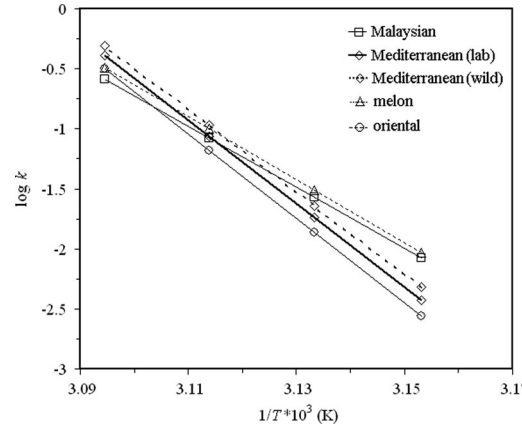

Fig. 6. Arrhenius plot for temperature effects on thermal death rate constant for laboratory-reared Malaysian, laboratory-reared or wild Mediterranean, and laboratory-reared melon and oriental fruit fly third instars.

in situ tests using papaya infested with eggs or larvae located at the same distance from the surface of the fruit found Mediterranean, melon, and oriental fruit fly eggs and first instars survived the same heat treatments that killed all third instars (Armstrong et al. 1995).

Most arguments supporting possible causes for the lack of a unifying thermotolerance hierarchy among tephritid fruit flies tend to identify potential issues with experimental design, materials, and methods. Jang et al. (1999) cautioned against extrapolating the results of hot water immersion thermotolerance tests to expected in situ results and identified most of the potential causes for variations in thermal tolerance hierarchies among and between fruit fly genera. Specifically, Jang et al. (1999) listed biotic and abiotic factors that influence thermotolerance, including prior thermal history (Meats 1987, Jang 1992, Hallman and Sharp 1994, Beckett and Evans 1997), age and metabolic stress (Moss and Jang 1991), density effects (Hansen and Sharp 1997), and the composition of the growth and treatment media (Hallman 1996, Hansen 1996). The HBS, experimental design, and data analyses we used were identical to Gazit et al. (2004). However, Gazit et al. (2004) found Mediterranean fruit fly third instars (Israel strain) more thermotolerant than eggs, whereas we also found Mediterranean fruit fly (both wild and laboratory-reared Hawaii strains) third instars were more thermotolerant than late-aged eggs at 44, 46, and 50°C (Table 8). The cause for this anomaly cannot be explained. Table 8 also shows that the thermotolerance variability between life stages for all species tested using the HBS narrows with increased temperature, which also was found by Foliaki and Armstrong (1997), Jang (1986), Jang et al. (1999), Sales et al. (1997), Tora Vueti et al. (1997), and Waddell et al. (1997) for the fruit fly species they tested using hot water immersion. Moreover, for many economic species of *Bactrocera* in the Pacific Basin, the late-aged egg stage and first instar seem equivalent

Table 8. Comparison of observed minimum times (min) to obtain 100% mortality for Malaysian, Mediterranean (Hawaii and Israel strains), melon, Mexican, and oriental fruit fly eggs[a] or third instars at four temperatures

Temperature (°C)	Fruit fly species and life stages											
	Mediterranean (Hawaii)			Melon		Malaysian		Oriental		Mediterranean (Israel[b])		Mexican[c]
	Egg	Laboratory third instar	Wild third instar	Egg	Third instar	Egg	Third instar	Egg	Third instar	Egg	Third instar	Third instar
44	80	130	70	50	55	120	60	70	150	—	—	100
46	25	25	15	12	15	30	20	20	40	25	60	25
48	6	4	2.5	3	5	7[d]	5[d]	4	5	5	15	6
50	1.0	1.5	1.0	0.5	1.5	1.5	1.5	1	2	3	4	2

[a] Laboratory reared.
[b] Data for Israel strain of Mediterranean fruit fly from Gazit at al. (2004); no data available for 44°C.
[c] Mexican fruit fly data from Hallman et al. (2005).
[d] Data estimated from the thermal death curve.

in thermotolerance and more tolerant to heat than third instars, including *B. cucurbitae*, *B. dorsalis*, *B. latifrons*, *B. melanotus* (Coquillett), *B. passiflorae* (Froggatt), *B. tryoni* (Froggatt), *B. xanthodes* (Broun), (Armstrong et al. 1995, Waddell et al. 1996, 1997, Sales et al. 1997, Tora Vueti et al. 1997, Jang et al. 1999), and for *B. facialis* (Coquillett) at temperatures ≤47°C (Foliaki and Armstrong 1997).

Regardless of anomalies in thermotolerance between life stages found among *Anastrepha*, *Bactrocera* and *Ceratitis* species, thermotolerance studies have played an important role in developing hot water immersion, vapor heat, and forced hot air quarantine treatments for a variety of exported fruits and vegetables in international trade (Armstrong and Mangan 2007). Thermotolerance testing will retain an essential role in identifying the most heat tolerant fruit fly species and life stage(s) to accelerate quarantine heat treatment development and facilitate confirmatory testing of candidate treatments. We concur with Jang et al. (1999) that a fruit fly thermotolerance database covering all tephritid species of economic importance is needed and that the data should be developed by standardized experimental design, methods, and statistical analyses.

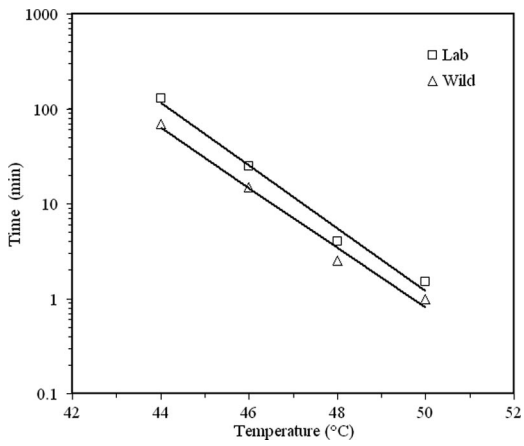

Fig. 7. Minimum time-temperature combinations for 100% mortality of 600 laboratory and wild Mediterranean fruit fly third instars.

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