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Comparative influence of temperature on development and biological control of two common vineyard pests (Acari: Tetranychidae)

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ABSTRACT

We studied the effects of temperatures from 10 to 40 °C on development of the Pacific spider mite, *Tetranychus pacificus* (McGregor), and the Willamette spider mite, *Eotetranychus willamettei* McGregor (Acari: Tetranychidae), feeding on grape foliage. In addition, we investigated the influence of temperatures from 10 to 37 °C on development of the western predatory mite, *Galendromus occidentalis* (Nesbitt) (Acari: Phytoseiidae), feeding on *T. pacificus* and evaluated the suitability of *E. willamettei* as prey for the predatory mite at 28 °C. Using a non-linear development rate model we estimated that the lower threshold for development of the three mites lay around 10 °C. *T. pacificus* was the most heat-resistant, with its upper threshold for development at 40.3 °C, followed by *G. occidentalis* at 37.1 °C and *E. willamettei* at 31.0 °C. *T. pacificus* developed significantly more rapidly than *E. willamettei* above 22.8 °C, whereas *G. occidentalis* developed significantly faster than either spider mite from approximately 11 to 36 °C. *G. occidentalis* developed 5% faster when feeding on *E. willamettei* than *T. pacificus* at 28 °C. These results confirm field observations linking *E. willamettei* damage to cooler, coastal vineyards and early in the season in inland vineyards, and *T. pacificus* infestations to hot vineyards in inland and coastal areas. Although *T. pacificus* seems to be more heat tolerant than *G. occidentalis*, additional information on temperature effects on adult life history details of the two mites is needed to fully evaluate *G. occidentalis* performance at high temperatures.

1. Introduction

As ectotherms, arthropod pests and their natural enemies are greatly influenced by temperature, and the temperature tolerances and requirements may vary markedly between species (Bowler and Terblanche, 2008). Consequently, temperature plays a major role in determining the distribution and abundance of agricultural pests and the effectiveness of their natural enemies (Bale et al., 2002; Roy et al., 2002, 2003).

The Pacific spider mite, *Tetranychus pacificus* McGregor, and the Willamette spider mite, *Eotetranychus willamettei* (McGregor) (Acari: Tetranychidae), are important pests of grapes in the western US. Adult and immature spider mites feed by penetrating the plant tissue with their sharp stylets, leading to a loss of photosynthetic ability, leaf discoloration, and eventually leaf death (Tanigoshi et al. 2004). While both species of spider mites inflict significant damage by reducing grape fruit sugar content and yield (Welter et al., 1989a,b, 1991), *T. pacificus* is considered the most damaging of the two (Flaherty et al., 1992). The western predatory mite, *Galendromus occidentalis* (Nesbitt) (Acari: Phytoseiidae), is a dominant natural enemy of both spider mites in California vineyards (Hoy and Smilanick, 1981; Hanna and Wilson, 1991; Flaherty et al., 1992; Bentley et al., 2006; Stavrinides and Mills, 2009). Yet, in California alone, grape growers treat more than 100,000 ha annually with pesticides against the two spider mites at a cost of 20 million dollars (Anonymous, 2007).

T. pacificus and *E. willamettei* exhibit an interesting and generally distinct distribution in California vineyards with *T. pacificus* outbreaks more common in interior and some hotter coastal vineyards, whereas *E. willamettei* is more abundant in cooler, coastal vineyards or earlier in the season in interior vineyards (Bentley et al., 2006). While competition between the two spider mites in California vineyards has received particular attention in the past (e.g. Hougen-Eitzman and Karban, 1995; Hanna et al., 1997; Karban et al., 1997), no information exists on the effects of temperature on the development of the two species on grapes.

In addition to direct effects on arthropod pests, temperature may also have an indirect effect on the occurrence of outbreaks by influencing the effectiveness of natural enemies (Roy et al., 2003). *T. pacificus* outbreaks are more frequent during hot summer

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months, suggesting that high temperatures allow *T. pacificus* to escape control by *G. occidentalis*. Although the influence of temperature on the development of *G. occidentalis* on *T. pacificus* feeding on a variety of hosts has been studied before (Croft and McMurtry, 1972; Tanigoshi et al., 1975; Badii and McMurtry, 1984; Bruce-Oliver and Hoy, 1990), no studies have monitored its development on *T. pacificus* feeding on grapes at the full range of temperatures experienced in vineyards. Furthermore, although the type of prey may significantly affect the development of predatory mites (Escudero and Ferragut, 2005), there have been no previous studies on the suitability of *E. willamettei* as prey for *G. occidentalis*.

Our objective in this study was to identify the effects of temperature on the development of *T. pacificus* and *E. willamettei* to better understand the role of this pivotal climatic factor in shaping their distribution and likelihood of outbreaks in vineyards. In addition, we investigated the effect of temperature on development of *G. occidentalis* feeding on *T. pacificus* and evaluated the suitability of *E. willamettei* as prey at 28 °C.

2. Materials and methods

2.1. Experimental procedures

We studied the survivorship and immature development of *T. pacificus* and *E. willamettei* feeding on grape foliage, and of *G. occidentalis* feeding on *T. pacificus* at temperatures ranging from 10 to 34 °C (±1 °C – range of daily average) and a 16:8 h L:D photoperiod. In addition, we investigated the survivorship and immature development of *G. occidentalis* feeding on *E. willamettei* at 28 °C. To identify the upper threshold for development (T_L) for *T. pacificus* and *G. occidentalis* we exposed eggs at temperatures higher than 34 °C in 3 °C increments until we identified the temperature at which no eggs hatched. Since no *E. willamettei* eggs hatched at 34 °C ($n = 36$), we also exposed eggs at 31 °C to identify its upper threshold for development. Because of small variations in incubator temperatures, the actual mean temperatures used for each species were 9.9, 14.7, 22.4, 27.9, 34.0, 37.1 and 40.3 °C for *T. pacificus*; 9.9, 14.9, 22.4, 25.0, 27.9 and 31.0 °C for *E. willamettei*; 9.9, 14.9, 21.8, 28.3, 34.0 and 37.1 °C for *G. occidentalis* on *T. pacificus*; and 28.2 °C for *G. occidentalis* on *E. willamettei*.

T. pacificus and *E. willamettei* were collected from two separate vineyards of variety Zinfandel in the summer of 2005 in Lodi, California (*T. pacificus*: 38°11′9.26″N, 121°17′42.87″W; *E. willamettei*: 38°7′10.06″N, 121°11′46.08″W). The spider mites were cultured on Chardonnay grape plants at 28.3 ± 1.5 °C, 26.6 ± 10% RH for *E. willamettei* and 29.6 ± 1.5 °C, 25.0 ± 5% RH for *T. pacificus* with a 18:6 h L:D photoperiod. We obtained *G. occidentalis* from Sterling Insectaries (McFarland, CA) raised on two-spotted spider mite (*Tetranychus urticae* Koch). The female predatory mites were fed with *T. pacificus* at 28 °C for at least 24 h before collecting eggs for experiments.

Experiments were carried out using grape plants of clone Chardonnay 4 grafted on rootstock SO4, supplied by Duarte Nurseries, Inc. (Hughson, CA). The plants were kept in a greenhouse at the Insectary and Quarantine facility of UC Berkeley at an average daily temperature of 21.9 (18.6–28.9) °C and 58.2 (29.2–79.6)% RH. Supplemental lighting was provided to maintain a minimum of 14 h of light. The plants were fertilized twice a week with a standard fertilizer solution (13–3–14) (N–P–K) and one tablespoon of Osmocote 19–6–12 (3–4 month formulation, Sierra Chemical Company, Milpitas, CA) once every three months. The plants were sprayed biweekly with the botanical pesticide EcoTrol EC (Ecosmart Technologies, Alpharetta, GA) and the surfactant Silwet L-77 (Helena Chemical Company, Collierville, TN) at a rate of 1.32 ml/l of formulated product to prevent infestations by insects and mites. At least five days elapsed between spray application and use of leaves in experiments after rinsing with running water.

Development studies were carried out on individual 20 mm grape leaf disks placed with their lower surface facing up on top of seven 25 mm diameter filter papers moistened with distilled water in a small 25 × 13 mm (diameter × height) Petri dish. The lid of the Petri dish had a 5.5 mm hole with a mesh screen (50 × 50 μm openings, Small Parts, Inc., Hollywood, FL) glued on the inside of the lid using a non-toxic glue (ACE All-Purpose Adhesive – Product # 1147941, ACE Hardware, Berkeley, CA). Although not measured, the relative humidity within each Petri dish must have been high as the filter paper was kept continuously moist.

We collected mite eggs for experiments by transferring 20 female mites on a grape leaf disk and allowing them to oviposit for 12 h at temperatures up to 28 °C and 8 h at higher temperatures. Leaf disks used for *G. occidentalis* egg laying were infested with all stages of *T. pacificus* on bean leaves for 10 and 28 °C, and on grape leaves for all other temperatures. Eggs of *G. occidentalis* were transferred individually to grape leaf disks infested with an abundance of all stages of *T. pacificus* or *E. willamettei* depending on the experiment; observations for egg hatch for *T. pacificus* and *E. willamettei* were carried out with the eggs on the original leaf disk and individual larvae were transferred onto leaf disks after hatch. Observations for egg hatch and immature development were made every 48 h at 10 and 15 °C, every 24 h at 22 °C, every 12 h at 25 °C and 28 °C and every 8 h for higher temperatures. Life history stage changes were assumed to occur at the midpoint between two consecutive observations. Because *G. occidentalis* went through its quiescent stages within a single observation interval, we confirmed stage changes by the presence of an exuvium.

We replaced leaf disks for *T. pacificus* and *E. willamettei* as needed to ensure a fresh green color. For *G. occidentalis* we either supplied all stages of spider mites or replaced leaf disks with infested ones as needed to ensure an abundance of prey. Mites that escaped were included in calculations of survivorship up to the stage at which they escaped.

2.2. Immature survivorship

We compared immature survivorship from egg to adult between *T. pacificus, E. willamettei* and *G. occidentalis* feeding on *T. pacificus* at each temperature with a *G*-test using Yates correction for continuity (Zar, 1999). We also compared immature survivorship of *G. occidentalis* feeding either on *T. pacificus* or *E. willamettei* at 28 °C. *P*- values were corrected using the false discovery rate correction at the level of 0.05 (Benjamini and Hochberg, 1995) to account for multiple tests.

2.3. Development rates and thresholds

We modeled the development rate (d) of the three mites using the non-linear Briére 1 model (Briére et al., 1999):

$$d = a \times T \times (T - T_0) \times (T_L - T)^{1/2}$$

where T is temperature in degrees Celsius, a is a scale parameter, and T_0 and T_L are the lower and upper threshold temperatures for development, respectively. Development rate was calculated as the reciprocal of development time. The model was fitted to the data in SAS/STAT® software, Version 9.1 for Windows using the procedure NLIN with the Gauss–Newton algorithm (SAS Institute Inc., 2004). For each species, we fitted the model using development rate data from 15 °C up to its upper threshold, as determined from the observations on egg hatch (see above). We did not use the data at 10 °C to avoid biasing the model estimate for T_0, as no eggs hatched at this temperature. For each mite species, data for individual mites were fitted to the model as replicates.

We tested for differences in model parameters between males and females within each species following a hierarchical model comparison approach and the extra sums of squares test (Ratkowsky, 1983). We first fitted a full model to the data that included different parameters for females and males for each of the three mite species (18 parameters) and compared its fit to a model with common parameters for the two sexes for each species (9 parameters) using an *F*-test. Because the fit of the full model was significantly better that that of the reduced 9-parameter model, we proceeded by fitting separate models to data for each species and testing which parameters differed between males and females as outlined in Schabenberger (1999). Following a similar approach, we tested for differences in model parameters between females of each species by fitting a model to data from any two species at a time and testing which parameters differed.

We identified the temperature at which the development rate of females of each species became significantly different from each other by calculating the 95% lower and upper confidence bounds for the fitted Briére 1 model with the commands L95MEAN and U95MEAN in SAS/STAT 9.1 (Schabenberger, 1999). The confidence bounds give the 95% confidence interval for the prediction of the mean development rate of the population at any given temperature. The optimum temperature for development for each species was calculated using the formula provided by Briére et al. (1999).

We compared the development rate of *G. occidentalis* females feeding on either *T. pacificus* or *E. willamettei* at 28 °C with one-way ANOVA using the function aov in the **stats** package of R v.2.7.1 (R core development team, 2008). Similarly, we compared the development rate of *G. occidentalis* females and males feeding on *E. willamettei* at 28 °C with one-way ANOVA. Plots of the data showed no major departures from the assumptions of normality and variance homogeneity.

3. Results

3.1. Immature survivorship

None of the eggs of *T. pacificus* ($n = 50$), *E. willamettei* ($n = 75$) and *G. occidentalis* ($n = 50$) hatched after seven weeks at 10 °C. *E. willamettei* did not complete its development at 31.0 °C as 99.02% of eggs ($n = 102$) failed to hatch, and the one larva that hatched died soon after. None of the eggs ($n = 50$) of *T. pacificus* hatched at 40.3 °C. *T. pacificus* egg mortality was also high at 37.1 °C (92.76%, $n = 51$), and although we did not record development rate at this temperature, we observed that some *T. pacificus* individuals survived to the adult stage. None of the eggs ($n = 51$) of *G. occidentalis* hatched at 37.1 °C.

Immature survivorship increased with temperature up to 28 °C for both *T. pacificus* and *G. occidentalis*, whereas survivorship for *E. willamettei* showed no clear trend (Table 1). Immature survivorship for *T. pacificus* and *G. occidentalis* was similar between 15 and 28 °C, while that for *E. willamettei* was significantly lower (Table 1). At 34 °C only 30% of *T. pacificus* immatures survived to the adult stage whereas survivorship for *G. occidentalis* was significantly higher at around 70% (Table 1). Immature survivorship did not differ significantly ($G = 0.02$, $df = 1$, $P = 0.90$) for *G. occidentalis* feeding either on *E. willamettei* (95.56%, $n = 86$) or on *T. pacificus* (Table 1).

3.2. Development rates and thresholds

Tables 2–4 show the development times of the three mites at different temperatures and Table 5 shows the parameters of the Briére 1 model for males and females of each species. Model comparisons suggested that the Briére 1 model with different parameters for females and males within each species fitted the development rate data significantly better than the model with common parameters for the two sexes ($F_{9,\,807} = 2.94$, $P = 0.002$). Further comparisons between males and females within each species demonstrated that males of *T. pacificus* had a higher T_0 and a than females (Table 5). None of the model parameters differed significantly between females and males of either *E. willamettei* or *G. occidentalis* (Table 5). Comparisons among models for females showed that T_0 was similar for all three species, at around 10 °C, while a and T_L differed significantly (Table 5). *T. pacificus* had the highest T_L followed by *G. occidentalis* and *E. willamettei* (Table 5). The temperature at which the development rates of the three species became significantly different from each other was determined by comparing the overlap of the 95% confidence bounds for the fitted models for females. Non-overlapping 95% confidence bounds demonstrated that the development rate of *G. occidentalis* became significantly higher than that of *E. willamettei* and *T. pacificus* at 10.9 and 11.2 °C respectively (Fig. 1), and became significantly lower than that of *T. pacificus* at 36.4 °C. The development rate of *T. pacificus* females surpassed that of *E. willamettei* at 22.8 °C (Fig. 1). The optimum temperature for development was 33.4, 26.1 and 30.9 °C for *T. pacificus*, *E. willamettei* and *G. occidentalis* females respectively.

The development rate of female *G. occidentalis* feeding on *E. willamettei* at 28 °C [0.245 ± 0.004 (mean ± 1 SE), $n = 34$] was significantly greater ($F_{1,\,58} = 11.69$, $P = 0.001$) than that of females feeding on *T. pacificus* (Fig. 1). Additionally, the development rate of *G. occidentalis* females feeding on *E. willamettei* was significantly greater ($F_{1,\,75} = 14.03$, $P < 0.001$) than that of males (0.228 ± 0.003, $n = 43$).

4. Discussion

The results of this study show that under laboratory conditions immature survivorship was lower for *E. willamettei* than for *T. pacificus*, especially at 15 °C (Table 1), suggesting either an innate difference between the two spider mites or that grape is a better host for *T. pacificus*. Immature survivorship was also higher for *G. occidentalis* than for *T. pacificus* and *E. willamettei* at all temperatures (Table 1). In addition, there was no significant difference in immature survivorship for *G. occidentalis* feeding on either *T. pacificus* or *E. willamettei* at 28 °C.

T. pacificus and *E. willamettei* had a similar estimated T_0 of 10 °C (Table 5, Fig. 1). This estimate of T_0 for *E. willamettei* is within 3 °C of values reported for other *Eotetranychus* species (Bonato et al., 1990; Su Xugen et al., 1996; Lai and Lin, 2005), although some

Table 1
Percent immature survival (egg to adult) (mean ± 1 SE) at different temperatures for *T. pacificus*, *E. willamettei*, and *G. occidentalis* feeding on *T. pacificus*.[a]

Temperature	15 °C	22 °C	25 °C	28 °C	34 °C
T .pacificus	76.49 a [70]	89.28 a [84]	–	92.00 a [62]	30.18 b [35]
E. willamettei	30.76 b [58]	70.74 b [74]	42.28 [30]	62.73 b [33]	–
G. occidentalis	80.18 a [53]	94.30 a [49]	–	96.61 a [56]	72.65 a [34]

[a] Square brackets show number of individuals that survived to the adult stage. Means followed by different letters within each column are significantly different ($P < 0.05$, *G*-test).

Table 2
Time in days (mean ± 1 SE) to completion of successive developmental stages for female and male *T. pacificus* at different temperatures. Sample size in square brackets.

Temperature	Sex	Egg	Larva	Protonymph	Deutonymph	Egg to adult
15 °C	Females	13.85 ± 0.13	7.97 ± 0.30	5.91 ± 0.22	6.88 ± 0.20	34.61 ± 0.59 [66]
	Males	15.00 ± 0.00	8.00 ± 0.00	6.00 ± 1.15	5.33 ± 0.67	34.33 ± 0.67 [3]
22 °C	Females	5.15 ± 0.09	3.37 ± 0.13	2.98 ± 0.08	3.39 ± 0.07	14.89 ± 0.23 [51]
	Males	5.44 ± 0.07	3.42 ± 0.19	3.12 ± 0.14	3.18 ± 0.13	15.17 ± 0.39 [33]
28 °C	Females	3.56 ± 0.05	2.03 ± 0.06	1.67 ± 0.06	1.96 ± 0.06	9.21 ± 0.12 [28]
	Males	3.90 ± 0.05	1.73 ± 0.05	1.50 ± 0.09	1.82 ± 0.11	8.95 ± 0.18 [34]
34 °C	Females	2.58 ± 0.05	1.67 ± 0.11	1.23 ± 0.08	1.59 ± 0.08	7.06 ± 0.24 [29]
	Males	3.06 ± 0.20	1.56 ± 0.36	1.28 ± 0.16	1.61 ± 0.23	7.50 ± 0.69 [6]

Table 3
Time in days (mean ± 1 SE) to completion of successive developmental stages for female and male *E. willamettei* at different temperatures. Sample size in square brackets.

Temperature	Sex	Egg	Larva	Protonymph	Deutonymph	Egg to adult
15 °C	Females	13.55 ± 0.16	7.50 ± 0.22	5.30 ± 0.25	7.70 ± 0.24	34.05 ± 0.39 [40]
	Males	14.22 ± 0.29	7.11 ± 0.37	5.67 ± 0.40	6.78 ± 0.37	33.78 ± 0.74 [18]
22 °C	Females	5.66 ± 0.10	3.63 ± 0.12	2.98 ± 0.14	3.16 ± 0.09	15.43 ± 0.24 [43]
	Males	5.98 ± 0.11	3.29 ± 0.13	2.84 ± 0.20	3.00 ± 0.10	15.11 ± 0.25 [31]
25 °C	Females	4.77 ± 0.08	2.85 ± 0.10	2.17 ± 0.12	2.87 ± 0.11	12.66 ± 0.26 [23]
	Males	4.82 ± 0.23	2.43 ± 0.23	2.07 ± 0.13	2.43 ± 0.13	11.75 ± 0.48 [7]
28 °C	Females	4.38 ± 0.04	2.13 ± 0.08	1.80 ± 0.05	2.27 ± 0.09	10.58 ± 0.14 [27]
	Males	4.38 ± 0.20	2.13 ± 0.18	1.75 ± 0.26	2.15 ± 0.27	10.40 ± 0.66 [6]

Table 4
Time in days (mean ± 1 SE) to completion of successive developmental stages for female and male *G. occidentalis* feeding on either *T. pacificus* or *E. willamettei* at different temperatures. Sample size in square brackets.

Temperature	Sex	Egg	Larva	Protonymph	Deutonymph	Egg to adult
15 °C	Females	6.13 ± 0.18	3.63 ± 0.30	3.31 ± 0.17	3.88 ± 0.20	16.94 ± 0.40 [32]
	Males	6.88 ± 0.21	3.41 ± 0.23	3.41 ± 0.33	3.65 ± 0.19	17.35 ± 0.49 [17]
22 °C	Females	2.76 ± 0.09	1.39 ± 0.09	1.32 ± 0.09	1.48 ± 0.09	6.95 ± 0.12 [31]
	Males	3.06 ± 0.12	1.11 ± 0.08	1.44 ± 0.12	1.44 ± 0.12	7.06 ± 0.12 [18]
28 °C – feeding on *T. pacificus*	Females	1.96 ± 0.07	0.83 ± 0.05	0.81 ± 0.05	0.83 ± 0.05	4.42 ± 0.07 [26]
	Males	1.95 ± 0.06	0.83 ± 0.05	0.90 ± 0.07	0.90 ± 0.06	4.58 ± 0.08 [20]
28 °C – feeding on *E. willamettei*	Females	1.65 ± 0.05	0.82 ± 0.04	0.72 ± 0.04	0.93 ± 0.04	4.12 ± 0.06 [34]
	Males	1.81 ± 0.04	0.81 ± 0.04	0.83 ± 0.05	0.95 ± 0.05	4.40 ± 0.05 [43]
34 °C	Females	1.50 ± 0.02	0.97 ± 0.07	1.00 ± 0.07	1.00 ± 0.05	4.47 ± 0.13 [21]
	Males	1.58 ± 0.04	0.92 ± 0.04	1.06 ± 0.06	1.14 ± 0.08	4.69 ± 0.10 [12]

Table 5
Fitted model parameter values and their associated 95% confidence intervals, sample size (n) and the adjusted coefficient of multiple determination (R^2) for the Briére 1 model fitted to development rate data (egg to adult) for females or males of *T. pacificus*, *E. willamettei* and *G. occidentalis* feeding on *T. pacificus*.[a]

Model parameters	Scale parameter (a)	Lower development threshold – T_0 (°C)	Upper development threshold – T_L (°C)	n	R^2
Females					
T. pacificus	6.6×10^{-5} Cb (6.2×10^{-5} to 6.9×10^{-5})	10.0 Ab (9.3–10.7)	40.3 Aa (40.3–40.3)	206	0.94
E. willamettei	9.5×10^{-5} Ba (9.0×10^{-5} to 10.0×10^{-5})	10.5 Aa (9.9–11.2)	31.0 Ca (31.0–31.0)	201	0.95
G. occidentalis	14.7×10^{-5} Aa (14.1×10^{-5} to 15.4×10^{-5})	9.7 Aa (9.0–10.4)	37.1 Ba (37.1–37.1)	144	0.96
Males					
T. pacificus	7.4×10^{-5} a (6.7×10^{-5} to 8.1×10^{-5})	12.4 a (11.1–13.7)	40.3 a (40.3–40.3)	94	0.94
E. willamettei	9.1×10^{-5} a (8.3×10^{-5} to 10.0×10^{-5})	10.2 a (9.1–11.3)	31.0 a (31.0–31.0)	96	0.94
G. occidentalis	13.9×10^{-5} a (13.3×10^{-5} to 14.5×10^{-5})	9.4 a (8.7–10.1)	37.1 a (37.1–37.1)	84	0.98

[a] Fitted values followed by different letters are significantly different ($P < 0.05$). Uppercase letters compare model parameters between females of each mite species and lowercase letters between females and males within each mite species. Sample size for each species and sex are summed across temperatures from Tables 2–4, and added to the number of eggs observed at the upper threshold for development (see text for details) apportioned to each sex using progeny sex ratio estimates from the next lowest temperature from Stavrinides (2009).

studies provide estimates as low as 2 °C (Bonfour and Tanigoshi, 2001) and as high as 20 °C (Jackson et al., 1983). Similarly, the estimated T_0 for *T. pacificus* falls within 3 °C of values reported for other *Tetranychus* species (de Moraes and McMurtry, 1987; Tsai et al., 1989; Kim et al., 1993; Bonato, 1999; Bonfour and Tanigoshi, 2001; Roy et al., 2002; Gotoh et al., 2004a).

The estimated T_L for *T. pacificus* was almost 9 °C higher than that for *E. willamettei* (Table 5 and Fig. 1). *Tetranychus* species seem to be more heat tolerant than *Eotetranychus* species as most published T_L for *Tetranychus* are equal to or greater than 35 °C (Pande and Sharma, 1986; Bonfour and Tanigoshi, 2001; Roy et al., 2002; He et al., 2005; Liang et al., 2007), whereas for *Eotetranychus* most

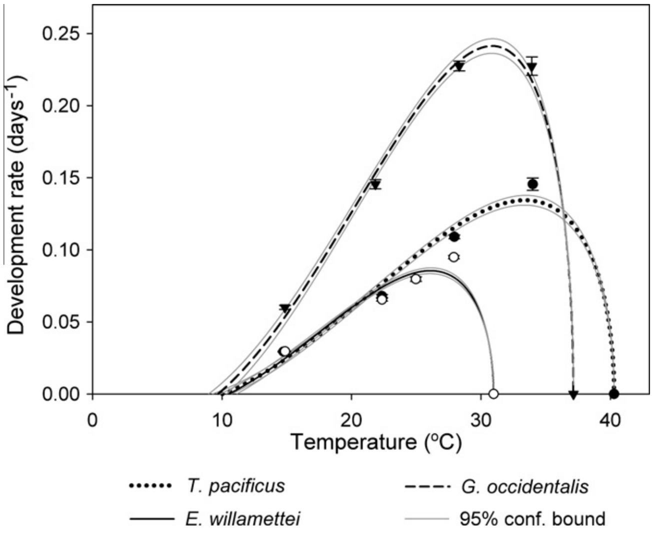

Fig. 1. Development rate from egg to adult (mean ± 1 SE) for female *T. pacificus* (solid circles), *E. willamettei* (open circles) and *G. occidentalis* (solid triangles) in relation to temperature. Fitted curves show predicted values and associated 95% confidence bounds for the Briére 1 model. Model parameters, sample size and associated statistics are provided in Table 5.

T_L fall below 35 °C (Jackson et al., 1983; Bonfour and Tanigoshi, 2001; Lai and Lin, 2005).

The estimated T_0 for *G. occidentalis* was similar to that for the two spider mites (Table 5, Fig. 1). In contrast, the T_L for the predatory mite was 37 °C, 6 °C higher than that for *E. willamettei*, but 3 °C lower than that for *T. pacificus*. The T_0 reported here for *G. occidentalis* lies within 1–2 °C of T_0 reported for many other phytoseiid mites (Broufas and Koveos, 2001; Gotoh et al., 2004b and references therein; Tsoukanas et al., 2006; Broufas et al., 2007; Kim et al., 2009). Similarly, the estimated T_L for *G. occidentalis* falls within 2 °C of that for other phytoseiid mites (Hamamura et al., 1976; Broufas and Koveos, 2001; Gotoh et al., 2004b; Tsoukanas et al., 2006; Broufas et al., 2007; Kim et al., 2009). It is important to note, however, that the choice of model used for development rate may affect the estimates of T_0 and T_L (e.g. Kim et al., 2009).

T. pacificus and *E. willamettei* developed at the same rate from 10 to 23 °C, with *T. pacificus* developing significantly faster at higher temperatures (Fig. 1). The faster development for *T. pacificus* above 23 °C together with its higher T_L than that of *E. willamettei* may be the reason for the higher abundance of *T. pacificus* than *E. willamettei* in hot inland and coastal vineyards (Bentley et al., 2006). The prevalence of *E. willamettei* in cooler vineyards and earlier in the season in hot vineyards may result from its ability to induce defenses in grape plants against *T. pacificus* (e.g. Hougen-Eitzman and Karban, 1995; Karban et al., 1997).

G. occidentalis achieved a higher development rate than *T. pacificus* from 11 to 36 °C (Fig. 1). However, *T. pacificus* had a higher estimated optimum temperature for development and T_L than *G. occidentalis* suggesting that hot conditions favor the former over the latter. Furthermore, the development rate of the predatory mite declined rapidly above 30.9 °C, its optimum temperature for development (Fig. 1, Table 5). The rapid decline in development rate for *G. occidentalis* may decrease its ability to effectively control *T. pacificus* at higher temperatures, and may explain the higher frequency of *T. pacificus* outbreaks during the hot part of the grape growing season (Bentley et al., 2006). It is important to note that only 7% of eggs of *T. pacificus* hatched at 37 °C, and if we select this temperature as the upper threshold for *T. pacificus* development the Briére 1 model predicts 31 and 37 °C as the optimum temperature for development and T_L for this mite respectively, which are similar to the values for *G. occidentalis* (Table 5). The possible similarity in T_L and optimum temperature for development between the two mites, suggests that information on adult life history details at different temperatures is needed to fully understand the impact of temperature on the ability of the predatory mite to control *T. pacificus*.

G. occidentalis developed significantly faster when feeding on *E. willamettei* than *T. pacificus* at 28 °C suggesting that the former is more suitable as prey. The higher T_L for *G. occidentalis* together with its faster development than *E. willamettei* (Fig. 1) suggest that higher temperatures are unlikely to limit the effectiveness of the predatory mite against this spider mite.

This study demonstrates that a sound knowledge of the effects of temperature on the survivorship and development of pests and their natural enemies can enhance our understanding of pest outbreaks. Our study shows that higher temperatures favor *T. pacificus* over the less damaging *E. willamettei*, but may also reduce the effectiveness of *G. occidentalis*. The higher temperature tolerance of *T. pacificus* than *E. willamettei* may contribute to the higher densities of the former on water stressed grape plants that have higher leaf temperatures than non water stressed plants (Stavrinides et al., 2010). Furthermore, temperature increases because of climate change (Jones, 2005; White et al., 2006) may explain why outbreaks by *T. pacificus* have become more common in recent years, even in parts of coastal California where *E. willamettei* used to be the prevalent species. Additional studies on the effects of other environmental factors, such as relative humidity (Mangini and Hain, 1991), on development of spider mites and their natural enemies can further increase our understanding of prey–predator interactions in vineyards and other cropping systems.

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References

Anonymous, 2007. Summary of Pesticide Use Report Data 2006 Indexed by Commodity. California Department of Pesticide Regulation, Sacramento, CA.

Badii, M.H., McMurtry, J.A., 1984. Life history of and life table parameters for *Phytoseiulus longipes* with comparative studies on *P. persimilis* and *Typhlodromus occidentalis*. Acarologia 25, 111–123.

Bale, J., Masters, G., Hodkinson, I., Awmack, C., Bezemer, T., Brown, V., Butterfield, J., Buse, A., Coulson, J., Farrar, J., Good, J., Harrington, R., Hartley, S., Jones, T., Lindroth, R., Press, M., Symrnioudis, I., Watt, A., Whittaker, J., 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Global Change Biology 8, 1–16.

Benjamini, Y., Hochberg, Y., 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of the Royal Statistical Society. Series B 57, 289–300.

Bentley, W.J., Varela, L.G., Zalom, F.G., Smith, R.J., Purcell, A.H., Phillips, P.A., Haviland, D.R., Daane, K.M., Battany, M.C., 2006. UC IPM Pest Management Guidelines: Grape – Insects and Mites. University of California Agriculture and Natural Resources, Oakland, CA. URL: http://www.ipm.ucdavis.edu/PMG/selectnewpest.grapes.html. Date accessed: February 10, 2009.

Bonato, O., Cotton, D., Kreiter, S., Gutierrez, J., 1990. Influence of temperature on the life history parameters of the yellow grapevine mite *Eotetranychus carpini* (Oudemans) (Acari: Tetranychidae). International Journal of Acarology 16, 241–245.

Bonato, O., 1999. The effect of temperature on life history parameters of Tetranychus evansi (Acari: Tetranychidae). Experimental and Applied Acarology 23, 11–19.

Bonfour, M., Tanigoshi, L.K., 2001. Effect of temperature on development and demographic parameters of *Tetranychus urticae* and *Eotetranychus carpini* borealis (Acari: Tetranychidae). Annals of the Entomological Society of America 94, 400–404.

Bowler, K., Terblanche, J.S., 2008. Insect thermal tolerance: what is the role of ontogeny, ageing and senescence? Biological Reviews 83, 339–355.

Briére, J.F., Pracros, P., Le Roux, A.Y., Pierre, J.S., 1999. A novel rate model of temperature-dependent development for arthropods. Environmental Entomology 28, 22–29.

Broufas, G.D., Koveos, D.S., 2001. Development, survival and reproduction of *Euseius finlandicus* (Acari: Phytoseiidae) at different constant temperatures. Experimental and Applied Acarology 25, 441–460.

Broufas, G.D., Pappas, M.L., Koveos, D.S., 2007. Development, survival, and reproduction of the predatory mite *Kampimodromus aberrans* (Acari: Phytoseiidae) at different constant temperatures. Environmental Entomology 36, 657–665.

Bruce-Oliver, S.J., Hoy, M.A., 1990. Effect of prey stage on life-table attributes of a genetically manipulated strain of *Metaseiulus occidentalis* (Acari: Phytoseiidae). Experimental and Applied Acarology 9, 201–217.

Croft, B.A., McMurtry, J.A., 1972. Comparative studies on four strains of *Typhlodromus occidentalis* Nesbitt (Acarina: Phytoseiidae). IV. Life history studies. Acarologia 13, 461–470.

De Moraes, G.J., McMurtry, J.A., 1987. Effect of temperature and sperm supply on the reproductive potential of *Tetranychus evansi* (Acari: Tetranychidae). Experimental and Applied Acarology 3, 95–108.

Escudero, L.A., Ferragut, F., 2005. Life-history of predatory mites *Neoseiulus californicus* and *Phytoseiulus persimilis* (Acari: Phytoseiidae) on four spider mite species as prey, with special reference to *Tetranychus evansi* (Acari: Tetranychidae). Biological Control 32, 378–384.

Flaherty, D.L., Wilson, L.T., Welter, S.C., Lynn, C.D., Hanna, R., 1992. Spider mites. In: Flaherty, D.L., Christensen, S.P., Lanini, W.T., Marois, J.J., Philips, P.A., Wilson, L.T. (Eds.), Grape Pest Management. University of California, Division of Agriculture and Natural Resources, Oakland, California, pp. 180–192.

Gotoh, T., Suwa, A., Kitashima, Y., Rezk, H.A., 2004a. Developmental and reproductive performance of *Tetranychus pueraricola* Ehara and Gotoh (Acari: Tetranychidae) at four constant temperatures. Applied Entomology and Zoology 39, 675–682.

Gotoh, T., Yamaguchi, K., Mori, K., 2004b. Effect of temperature on life history of the predatory mite *Amblyseius* (*Neoseiulus*) *californicus* (Acari: Phytoseiidae). Experimental and Applied Acarology 32, 15–30.

Hamamura, T., Shinkaji, N., Ashihara, W., 1976. The relationship between temperature and developmental period, and oviposition of *Phytoseiulus persimilis* Athias-Henriot (Acarina: Phytoseiidae). Bulletin of Fruit Tree Research Station, Japan E1, 117–125.

Hanna, R., Wilson, L.T., 1991. Prey preference by *Metaseiulus occidentalis* (Acari: Phytoseiidae) and the role of prey aggregation. Biological Control 1, 51–58.

Hanna, R., Wilson, L.T., Zalom, F.G., Flaherty, D.G., 1997. Effects of predation and competition on the population dynamics of *Tetranychus pacificus* on grapevines. Journal of Applied Ecology 34, 878–888.

He, L., Zhao, Z.M., Cao, X.F., Deng, X.P., Wang, J.J., 2005. Effect of temperature on development and fecundity of resistant *Tetranychus cinnabarinus* (Boiduval). Acta Entomologica Sinica 48, 203–207.

Hougen-Eitzman, D., Karban, R., 1995. Mechanisms of interspecific competition that result in successful control of Pacific mites following inoculations of Willamette mites on grapevines. Oecologia 103, 157–161.

Hoy, M.A., Smilanick, J.M., 1981. Non-random prey location by the phytoseiid predator *Metaseiulus occidentalis*: differential responses to several spider mite species. Entomologia Experimentalis et Applicata 29, 241–253.

Jackson, P.R., Hunter, P.E., Payne, J.A., 1983. Biology of the pecan leaf scorch mite *Eotetranychus hicoriae* (Acari: Tetranychidae). Environmental Entomology 12, 55–59.

Jones, G.V., 2005. Climate change in the 429 western United States grape growing 430 regions. In: Proceedings of the VII International Symposium on Rapevine Physiology and 431 Biotechnology. ISHS Acta Horticulturae, 689. Davis, CA, pp. 41–59.

Karban, R., English-Loeb, G., Hougen-Eitzman, D., 1997. Mite vaccinations for sustainable management of spider mites in vineyards. Ecological Applications 7, 183–193.

Kim, S.S., Paik, C.H., Kim, D.I., Park, J.D., Lee, S.C., 1993. Some ecological characteristics of tea red spider mite, *Tetranychus kanzawai* Kishida (Acarina, Tetranychidae). Korean Journal of Entomology 23, 261–266.

Kim, T., Ahn, J., Lee, J., 2009. Temperature-dependent developmental model of *Neoseiulus californicus* (McGregor) (Acari, Phytoseiidae). Journal of Applied Entomology 133, 284–291.

Lai, H.S., Lin, F.C., 2005. Development and population parameters of the Lewis spider mite, *Eotetranychus lewisi*, on poinsettia. Plant Protection Bulletin (Taichung) 47, 379–390.

Liang, Y., Zhou, Y.S., Liu, H.M., 2007. Effect of temperature on the population growth of *Tetranychus urticae* in laboratory. Chinese Bulletin of Entomology 44, 837–840.

Mangini, A.C., Hain, F.P., 1991. Vapor-pressure deficit differentially affects laboratory populations of *Metaseiulus occidentalis* and *Neoseiulus fallacis* (Acarina: Phytoseiidae) reared together. Environmental Entomology 20, 823–831.

Pande, Y.D., Sharma, B.L., 1986. Effect of food and temperature on the biology of red cucurbit mite *Tetranychus neocaledonicus* Andre (Acarina: Tetranychidae). Revista Brasileira de Biologia 46, 597–602.

R core development team, 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL: http://www.R-project.org.

Ratkowsky, D.A., 1983. Nonlinear Regression Modeling. Marcel Dekker Inc., New York.

Roy, M., Brodeur, J., Cloutier, C., 2002. Relationship between temperature and developmental rate of *Stethorus punctillum* (Coleoptera: Coccinellidae) and its prey *Tetranychus mcdanieli* (Acarina: Tetranychidae). Environmental Entomology 31, 177–187.

Roy, M., Brodeur, J., Cloutier, C., 2003. Effect of temperature on intrinsic rates of natural increase (r_m) of a coccinellid and its spider mite prey. BioControl 48, 57–72.

SAS Institute Inc., 2004. SAS/STAT® 9.1 User's Guide. SAS Institute Inc., Cary, NC.

Schabenberger, O., 1999. Nonlinear regression in SAS. UCLA: Academic Technology Services, Statistical Consulting Group. URL: http://www.ats.ucla.edu/stat/sas/library/SASNLin_os.htm. Date accessed: August 1, 2008.

Stavrinides, M.C., 2009. Biology, Ecology and Management of Spider Mites (Acari: Tetranychidae) in California Vineyards. Ph.D. dissertation, University of California, Berkeley, CA.

Stavrinides, M.C., Mills, N.J., 2009. Demographic effects of pesticides on biological control of Pacific spider mite (*Tetranychus pacificus*) by the western predatory mite (*Galendromus occidentalis*). Biological Control 48, 267–273.

Stavrinides, M.C., Daane, K.M., Lampinen, B.D., Mills, N.J., 2010. Plant water stress, leaf temperature and spider mite (Acari: Tetranychidae) outbreaks in California vineyards. Environmental Entomology 39, 1232–1241.

Su Xugen, Z.C., Liu, Y., Liang, H., Cui, Z., 1996. Studies on bionomics and effective accumulated temperature of *Eotetranychus populi* (Koch) (Acariformes: Tetranychidae). Acta Entomologica Sinica 39, 166–172.

Tanigoshi, L.K., Hoyt, S.C., Browne, R.W., Logan, J.A., 1975. Influence of temperature on population increase of *Metaseiulus occidentalis* (Acarina: Phytoseiidae). Annals of the Entomological Society of America 68, 979–986.

Tanigoshi, L.K., Martin, N.A., Osborne, L.S., Peña, J.E., 2004. Biological control of spider mites on ornamental crops. In: Heinz, K.M., Van Driesche, R.G., Parrella, M.P. (Eds.), Biocontrol in Protected Culture. Ball Publishing, Batavia, IL, pp. 185–199.

Tsai, S.M., Kung, K.S., Shih, C.I., 1989. The effect of temperature on life history and population parameters of kanzawa spider mite *Tetranychus kanzawai* Kishida (Acarina: Tetranychidae) on tea. Plant Protection Bulletin (Taichung) 31, 119–130.

Tsoukanas, V., Papadopoulos, C., Fantinou, A., Papadoulis, G., 2006. Temperature-dependent development and life table of *Iphiseius degenerans* (Acari: Phytoseiidae). Environmental Entomology 35, 212–218.

Welter, S.C., Farnham, D.S., McNally, P.S., Freeman, R., 1989a. Effect of Willamette mite and Pacific spider mite (Acari: Tetranychidae) on grape photosynthesis and stomatal conductance. Environmental Entomology 18, 953–957.

Welter, S.C., McNally, P.S., Farnham, D.S., 1989b. Effect of Willamette mite (Acari: Tetranychidae) on grape productivity and quality: a reappraisal. Environmental Entomology 18, 408–411.

Welter, S.C., Freeman, R., Farnham, D.S., 1991. Recovery of Zinfandel grapevines from feeding damage by Willamette spider mite (Acari: Tetranychidae) – implications for economic injury level studies in perennial crops. Environmental Entomology 20, 104–109.

White, M.A., Diffenbaugh, N.S., Jones, G.V., Pal, J.S., Giorgi, F., 2006. Extreme heat reduces and shifts United States premium wine production in the 21st century. Proceedings of the National Academy of Sciences of the United States of America 103, 11217–11222.

Zar, J.H., 1999. Biostatistical Analysis. Prentice-Hall, Inc., Upper Saddle River.