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Author(s): V. M. Walton, A. J. Dreves, L. B. Coop, G. V. Jones, and P. A. Skinkis
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Developmental Parameters and Seasonal Phenology of *Calepitrimerus vitis* (Acari: Eriophyidae) in Wine Grapes of Western Oregon

V. M. WALTON,[1,2] A. J. DREVES,[3] L. B. COOP,[4] G. V. JONES,[5] AND P. A. SKINKIS[1]

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ABSTRACT Developmental parameters of protogyne *Calepitrimerus vitis* (Nalepa) (Acari: Eriophyidae) were determined at 12, 15, 17, 22, 25, 28, 31, and 34°C to better understand seasonal activity, population growth, and ultimately more effectively manage pest mites in wine grapes. Net reproductive rate (R_o) was greater than zero at all temperatures with the maximum R_o (9.72) at 25°C. The lowest estimated R_o (0.001) occurred at 34°C. There was a gradual decrease in mean generation time (T) as temperatures increased from 17 to 31°C. The shortest and longest generation time was recorded at 31°C (T = 5.5 d) and 17°C (T = 17.5 d). Rates of natural increase were lowest at 17°C (0.035) and increased with increasing temperatures, respectively. The peak rate of natural increase value (0.141) was at 25°C. Estimations for minimum and maximum developmental thresholds were 10.51 and 39.19°C, respectively, while the optimum developmental temperature was 26.9°C. The thermal constant for egg to adult development was estimated at 87.7DD. The highest fecundity was observed at 25°C. These parameters indicated that mites begin feeding at the onset of shoot growth when tissue is most susceptible in spring. Historical weather data showed that vines are in this susceptible growth stage for longer periods in the cool Willamette Valley compared with warmer Umpqua and Applegate/Rogue Valley regions. Estimation of degree-days indicated when deutogyne mites move to overwintering refuge sites. Degree-day accumulations indicated up to 14 generations per growing season.

KEY WORDS *Calepitrimerus vitis*, grapevine rust mite, degree-days, protogyne, developmental parameters

The grapevine rust mite, *Calepitrimerus vitis* (Nalepa 1905) (Acari: Eriophyidae), has a free-living (vagrant) lifestyle during the growing season. Rust mites are usually found on leaves and young shoot surfaces, while it is a refuge seeking mite when it overwinters as a specialized female (deutogyne) protected in the buds and in the rytidoma crevices (Duffner 1999). It is believed that these mites cause economic damage and extensive crop losses to vines in other countries and in United States (Pacific Northwest) vineyards (Walton et al. 2007). Surviving overwintering deutogyne *C. vitis* populations cause damage most likely during the early springtime. In Oregon, nine mites per bud in spring were associated with leaf and shoot distortions, retarded growth in emerging green tissue, and crop losses (Hluchy and Pospisil 1992, Bernard et al. 2005, Walton et al. 2007), and symptoms are described as short shoot syndrome. Bud break failure along with yield losses was correlated with *C. vitis* infestations in California (Smith and Stafford 1948), South Africa (Dennill 1986), and Australia (Whiting and Strawhorn 1997). Carmona (1973) found that winter buds infested with *C. vitis* can lead to scarification and tissue necrosis. It is suspected that early feeding of deutogyne mites on slowly developing vine tissues within buds cause mite-associated damage symptoms (Bernard et al. 2005, Walton et al. 2007). Early season developing tissue is known to be more susceptible to damage (Trumble et al. 1993, Strauss and Agrawal 1999) compared with older tissue that has completed cell division. It is known that eriophyid mite feeding on young tissues may cause hypersensitive responses (toxemias or distorted growth in developing tissues), accompanied by production of pathogenesis-related proteins, which may result in mite death (Bronner et al. 1991, de Lillo and Monfreda 2004, Monfreda and Spagnuolo 2005, Monfreda and de Lillo 2006). Research conducted on vines to simulate damage caused by leaf-feeding insects at early and late stages of seasonal development show that early insect-induced grapevine injury causes more profound damage and decreased carbon assimilation compared with late season insect feeding (Mercader and Isaacs 2003). Newly planted and establishing vineyards have been found to be especially susceptible to pest insects (Mercader and Isaacs 2003) and eriophyid mite damage (Duso and de Lillo 1996), but no reasons were

[1] Department of Horticulture, Oregon State University, Corvallis, OR 97331.
[2] Corresponding author, e-mail: waltonv@hort.oregonstate.edu.
[3] Department of Crop and Soil Science, Oregon State University, Corvallis, OR 97331.
[4] Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331.
[5] Department of Environmental Studies, Southern Oregon University, Ashland, OR 97520.

given to explain this phenomenon. The possible lack of within-vine shading in new plantings may result in higher temperatures and more sensitive tissue. In addition, the lack of ability to retain adequate moisture levels or uptake of nutrients could stress the plant and increase susceptibility to pest damage. It is believed that differences in tissue development rates and temperature may influence vine susceptibility to mite feeding, however this theory has not been illustrated.

Mite populations are known to increase to high levels during the growing season, but the relationship between temperature and population increase has not been described. It is known that when temperature and daylength begin to decrease during late summer and early fall, deutogynes are found at high levels on leaf and shoot surfaces (Oldfield and Newell 1973, Duffner 1999). Grape growers observe leaf bronzing because of mite feeding on the epidermal surface of leaves, however large *C. vitis* populations (up to 10,000 mites) on leaves often result in bronzing that appear after feeding (Perez-Moreno and Moraza-Zorilla 1998, Duffner 1999, Bernard et al. 2005, Walton et al. 2007). These bronzing symptoms are not known to cause economic damage, but mites may move to protected overwintering sites during this period which may make control efforts less efficient. Development parameters have been estimated for pear and citrus rust mite development, feeding, and movement onto exposed plant tissue (Hobza and Jeppson 1974, Easterbrook 1978, Bergh 1992, Bergh and Judd 1993, Bergh 1994, Allen et al. 1995). Mite development at different temperatures has been determined for *C. vitis* in Germany (Duffner 1999), but was not correlated with grapevine tissue susceptibility. Despite successful mite rearing at different temperatures, no developmental parameters were estimated in work done by Duffner (1999). For these reasons, this study will determine developmental parameters for *C. vitis* in Oregon correlated with grapevine growth stages to better understand the biology, movement and connection to grapevine damage. This information will help wine grape producers accurately time mite treatments to the vulnerable stage of this species.

Materials and Methods

Late spring populations of *C. vitis* protogynes were collected on heavily infested vine leaves in a commercial Pinot Noir vineyard (45°14′54′′N; 123°04′28′′W; alt. 150 m) at Dundee, OR, from 7 to 11 May 2007 and brought back to the OSU laboratory for rearing. Mite-infested leaves were lightly rubbed on potted vine plants to facilitate mite transfer onto new host plants. Cultures of *C. vitis* were reared on 1-yr-old own-rooted Pinot Noir vines in a growth medium (Sungro Metro Perennial Mix IV, Bellevue, WA) in 3.8 liter pots. Vine plants were grown under conditions of 14:10 h (L:D) and 23°C (±5°C) day and night temperatures from the initial collection date to 30 September 2007. These mite colonies were used to inoculate freshly cut leaf disks containing petioles. Each leaf disk containing a petiole was placed with its adaxial surface on sterile seed germination paper (Anchor Paper Company, St. Paul, MN) and positioned on top of cut sterile sponges surrounded by a water moat within covered petri dishes. The petri dishes were covered to keep humidity at adequate levels and minimize air movement that could possibly dislodge mites from leaf surfaces. The petiole of each leaf disk was inserted into a moist sponge that allowed adequate translocation of water into leaf tissues during the experimental period.

Temperature-Dependent Development, Fecundity, and Oviposition. The effect of eight constant rearing temperatures on protogyne *C. vitis* development time was determined at 12, 15, 17, 22, 25, 28, 31, and 34°C (±1°C). Mites were placed in growth chambers with a photoperiod of 16:8 h (L:D). Fifty rest phase two (RP II) (Duffner 1999) *C. vitis* were transferred onto each of six leaf disks (300 total RP II per temperature) using a camel hair brush containing a single hair and mites were allowed to oviposit for 24 h. One egg was transferred in situ on a piece of leaf onto each of forty leaf disks. Leaf disks were inspected every 24 h and the developmental stage was determined by quantifying relative size and number of molts. When visible, exuviae were removed after each molt during evaluation. Nonovipositing individuals were assumed to be males and sexed if no egg laying occurred during adulthood. Fecundity was subsequently determined by summing the total number of eggs laid by each female to mortality. In some cases, larvae were found on leaf disks only containing adult females. It was assumed that these larvae were from eggs that hatched undetected and these numbers were included to calculate female fecundity.

Population Parameter Determination. The following population modeling parameters were used: L_x, the proportion of individuals alive on day X (age of mites in days), and M_x the mean number of female progeny produced on day X, were determined for the duration of the life span of each *C. vitis.* The net reproductive rate (R_o) was determined using,

$$\sum_{x=1}^{t} L_x M_x,$$

where t = time in days. The mean generation time (T) (Price 1997) was calculated using,

$$T = \frac{\sum L_x M_x X}{\sum L_x M_x}.$$

These values were subsequently used to obtain an initial estimate of the intrinsic rate of natural increase (r_m), and net reproductive rate (R_o) (Price 1997).

Developmental and Reproductive Parameters and Thresholds. The lower threshold temperature for development was determined using linear regression (Statistica 7.1, StatSoft Inc. 2005) on our data as well as data from Duffner (1999). The regression equation $y = ax + b$ describes the rate of development regressing $1/t$ on temperature for *C. vitis* and then solving the regression equation for $1/t = 0$, where t = time in days.

The thermal constant (k) from birth to adult, in required degree-days (DD), was calculated using $k = 1/a$ (Liu and Meng 1999). In instances where the rate of development decreased at temperatures higher than the optimum temperature, nonlinear model estimation was used to estimate optimum and upper thresholds for development of *C. vitis* by entering the user specified regression function (Briere et al. 1999). The reciprocal of developmental T was fitted on temperature (°C) (Briere et al. 1999) using,

$$r(T) = nT(T - T_L)(T_U - T)^{1/m}.$$

Here $r(T)$ is the rate of development at temperature T; T_U is the upper developmental temperature threshold; T_L is the lower developmental temperature threshold, and m and n are empirical constants. The optimum temperature T_{opt} was estimated by using a derivative of this model by entering the user-defined parameters. The effect of temperature on oviposition was described by the function (Briere et al. 1999),

$$o(T) = nT(T - T_L)(T_U - T)^{1/m},$$

where $o(T)$ is the mean female oviposition at temperature T; T_U the upper threshold where oviposition took place; T_L the lower threshold temperature for oviposition, and m and n are empirical constants.

The bud break stage (Meier 2001) were recorded in eight vineyards in the northern Willamette Valley (44°26′ - 45° 32′N; 122°28′ - 123° 32′W), 10 vineyards in the Umpqua Valley (43°12′ - 43° 34′N; 123°16′ - 123° 32′W) and nine vineyards in the Rogue/Applegate Valleys (42°08′ - 42° 27′N; 122°35′ - 123° 16′W) during 2007 and 2008. Principle growth stage 0 (PGS 0), including wooly bud until before bud break, is the period when grapevine tissues are most susceptible to feeding damage by eriophyid mites. Wooly bud stage is the growth stage described as when bud swelling occurs and brown wool is clearly visible, but precedes bud break. The onset of wooly stage was recorded when 25% of buds developed to this stage, and wooly stage when 50% of vines were in this stage. Bud break was recorded when green tips were clearly visible and when a minimum of 50% of vines exhibited this stage. These growth stages were determined by observing buds on twenty randomly spaced vines within each block. In our phenology graphs, the number of DD for grapevines was estimated starting on 1 January during each year, using 10.56°C as the lower threshold and a single sine curve calculation (Moncur et al. 1989, Failla et al. 2004). The number of DD was estimated for each location using publicly available calculators and temperature data (http://uspest.org/cgi-bin/ddmodel.pl).

Mite-Days in Three Grape Growing Regions During 2007 and 2008. Damage caused by phytophagous pests is a function of their pest numbers, feeding time and plant surface area. Insect numbers and feeding duration are quantified as 'insect-days' (Ruppel 1983) and herein referred to as 'mite-days'. During grapevine dormancy, rust mites inhabit outer bud scales, areas under bark, and crevices. Tissue expansion and development of the bud (onset of wooly stage) results in movement of mites onto susceptible tissues within the bud, and the number of mite-days were estimated from the onset of wooly bud to 50% bud break in each grape-growing region during 2007 and 2008. Mite-days were calculated using,

$$\text{Mite-days} = (X_{i+1} - X_1)[(Y_i + Y_{i+1})/2],$$

where X_i and X_{i+1} are adjacent points of time and Y_i and Y_{i+1} are corresponding points of mite numbers. Previous work shows that mean mite numbers between 2 and 25 deutogynes per bud may cause significant economic damage (Carmona 1973, Baillod and Guignard 1986). In our calculations, we assume nine mites per bud as these population levels resulted in severe damage in the northern Willamette Valley. There is no population change expected because of low r_m values during this period and for this reason Y_i and Y_{i+1} has the same value.

Statewide Mapping of DD Accumulation for Grapevines and *C. vitis*. To identify long-term weather trends across Oregon vineyard regions, a statewide distribution map of cumulative daily heat summation, DD was estimated for grapevines for 2007 and 2008. Heat summation was estimated starting on 1 January and ending on 24 April using historical 30-yr average climate temperature data. This time period was selected based on timing of bud-break across all of Oregon's grape-growing regions. Heat summation values for *C. vitis* were calculated using the minimum threshold of *C. vitis* (10.51°C) estimated from Duffner's (1999) daily development data.

Map estimates of DD were produced using the online degree-day mapping calculator (Coop 2007) that uses publicly available weather data and PRISM climate maps (Daly et al. 2002). The system uses climatologically aided interpolation (Willmott and Robeson 1995) by means of the following steps: (1) The user enters temperature thresholds, calculation method, the range of dates for calculation, mapping options, and then instructs the program to do calculations; (2) The Web/GIS server receives user inputs and starts a GIS session in GRASS (Neteler and Mitasova 2008); (3) The GIS calculates PRISM-only based degree-days using PRISM monthly average maximum and minimum temperature GIS raster maplayer; (4) All site data from public weather networks (e.g., AGRIMET and SNOTEL) are processed using a site-only degree-day calculator; (5) The most accurate site-based degree-days are then subtracted from the PRISM-only degree-day estimates at the same locations as sites; (6) These differences are then spatially interpolated into a grid using inverse distance weighted interpolation; (7) This grid is then added as a correction layer to the PRISM-only maplayer to produce the CAI-corrected map; and (8) Additional reference layers, such as grape-growing regions and reference landmarks, are added and the map is converted to a graphic format.

Validation of Seasonal DD for *C. vitis* Populations in the Field. To validate developmental thresholds from our laboratory trials, we recorded *C. vitis* population levels on leaves in a 0.5 ha 3-yr-old Pinot Noir

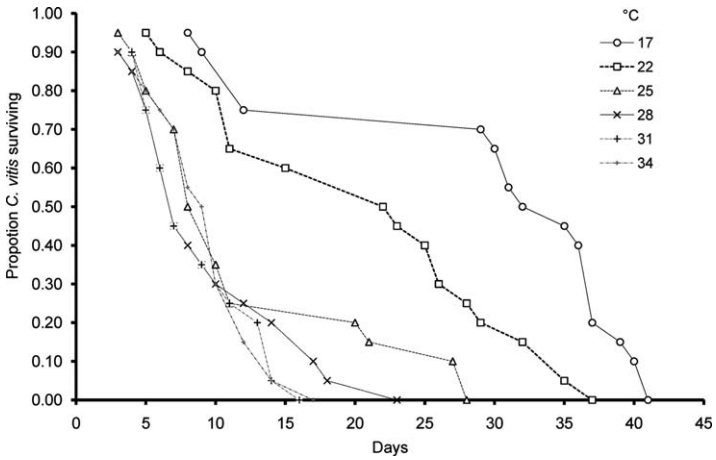

Fig. 1. Proportion surviving *C. vitis* individuals on days at six constant temperatures.

vineyard block located in the Willamette Valley, OR (45°14′54″ N; 123°04′28″ W, alt. 150 m). Leaf samples were taken every 2 wk starting early May and continued until the end of September during the 2007 and 2008 season. Forty-eight average-sized, mid shoot leaves (10–15 cm in length) were systematically collected from cane-pruned vines in each of four rows. Leaves were taken to the laboratory in cooled boxes to minimize mite movement and 15 mm diameter leaf disks cut at the petiole and mites counted using a stereo microscope. Accumulated DD for *C. vitis* were calculated using a single-sine model (Zalom et al. 1983). The number of generations were calculated based on the thermal constant of 87.7DD for *C. vitis* estimated from this study. Estimations of DD started on 1 January each season and accumulated until the end of November.

Results

Temperature-Dependent Development, Fecundity, and Oviposition. Eggs produced by protogyne *C. vitis* did not survive at 12°C. Mortality of eggs at this temperature was 100% after 3 wk. At 15°C, few individuals developed and only 23% of the eggs hatched. After the eggs hatched no further development was recorded as the remainder of larvae died. Rearing and complete development was successful at all other temperatures studied (Fig. 1). At 31 and 34°C, 100% mortality occurred after completion of the full life cycle at 17 and 16 d, respectively. Individuals survived for longer periods at the lower constant temperature (17°C), with 100% mortality of initial individuals occurring at 41 d. Mortality at 17°C followed a type I survivorship curve with relatively low mortality during the early life stages. At 22°C higher mortality rates were found, displaying a type II survival curve. Comparatively higher mortality was found at 25, 28, 31, and 34°C, all following a type III curve (Table 1).

Development time at each life stage was temperature dependent for the protogynes. There was a decrease in developmental time from egg to the adult stage in the temperature range from 17 to 34°C (Table 1). Increased time (2.1 d >31°C) was needed for development at 34°C. There was a three-fold decrease of longevity of mites between lowest to highest temperatures (Table 1). Less time was spent in the adult stage at higher temperatures (3.7 d at 34°C, compared with 20.7 d at 17°C). Sexing of mites in our studies showed similar ratios at all temperatures. The mean male to female ratio was 1:2.3. Low fecundities (<1 egg per day) were found at the lower and upper extreme temperatures (17 and 35°C, respectively; Table 1) for the deutogynes.

Population Parameter Determination. The parameter values calculated in this study were empirical

Table 1. Developmental times in days ± SEM (*N*) at each developmental stage and female fecundity of *C. vitis* on Pinot noir grapevine leaf disks at six constant temperatures

Developmental stage	Average developmental times in days at constant temp (°C)					
	17	22	25	28	31	34
Egg	6.6 ± 0.35 (40)	4.3 ± 0.5 (40)	3.3 ± 0.4 (40)	2.1 ± 0.2 (40)	2.1 ± 0.2 (40)	2.4 ± 0.3 (40)
Larva	2.1 ± 0.22 (40)	2.0 ± 0.2 (40)	1.2 ± 0.2 (40)	1.2 ± 0.2 (40)	1.2 ± 0.2 (40)	2.2 ± 0.4 (40)
RPI	1.9 ± 0.2 (40)	1.8 ± 0.1 (40)	1.6 ± 0.2 (40)	1.4 ± 0.1 (40)	1.3 ± 0.2 (40)	1.7 ± 0.3 (37)
Nymph	2.5 ± 0.3 (31)	1.9 ± 0.3 (29)	1.3 ± 0.2 (31)	0.9 ± 0.2 (30)	0.8 ± 0.2 (27)	1.1 ± 0.2 (28)
RPII	1.9 ± 0.21 (31)	1.5 ± 0.2 (29)	1.5 ± 0.2 (30)	1.3 ± 0.2 (24)	1.2 ± 0.2 (25)	1.3 ± 0.2 (25)
Adult	20.7 ± 1.5 (31)	17.2 ± 1.2 (24)	16.0 ± 1.4 (21)	10.4 ± 0.6 (20)	6.8 ± 0.8 (22)	3.7 ± 0.4 (19)
Egg to Adult	14.9 ± 0.8 (31)	11.2 ± 0.8 (24)	8.8 ± 1.0 (22)	6.1 ± 0.7 (20)	6.6 ± 0.6 (22)	8.7 ± 1.3 (19)
Egg to Mortality	35.5 ± 1.0 (31)	28.6 ± 1.5 (24)	24.8 ± 1.8 (21)	17.5 ± 1.5 (20)	13.3 ± 0.8 (22)	12.3 ± 1.9 (19)
Fecundity	0.2 ± 0.1 (28)	9.6 ± 1.4 (25)	26.1 ± 3.8 (20)	7.0 ± 1.4 (26)	1.8 ± 0.1 (21)	0.6 ± 0.2 (24)

Table 2. Developmental and reproductive parameters for *C. vitis* on Pinot noir grapevine leaf disks at six different temperatures (net reproduction rate = R_o; mean generation time = T; intrinsic rate of increase = r_m)

Temperature °C	Developmental and reproductive parameters		
	R_o	T	r_m
17	0.54	17.5	0.035
22	4.38	13.5	0.109
25	9.72	10.5	0.141
28	1.34	5.5	0.112
31	0.54	5.5	0.112
34	0.001	7.5	0

(Price 1997) and for this reason these values were not compared statistically. There were clear trends in the change of these values and these were directly related to temperature (Table 2).

The R_o. R_o was greater than zero at all temperatures, indicating positive population growth (Table 2). The maximum R_o (9.72) for *C. vitis* were estimated at 25°C. The lowest estimated R_o (0.001) occurred at 34°C.

Mean T. The *T*-values estimated for each temperature are given in Table 2. Mean generation time, *T*, decreased gradually with increasing temperatures from 17 to 31°C. The longest generation time, 17.5 d, was estimated at 17°C, with values decreasing to the shortest generation time at 5.5 d at 28 and 31°C. At 34°C this value increased to 7.5 d.

Intrinsic r_m. The estimated values at each experimental temperature are given in Table 2. All r_m values were positive at temperatures ranging between 17 and 31°C, indicating positive population growth in these cases. The lowest estimation of r_m was 0.035 at 17°C. The low r_m value at 17°C indicates virtually no population growth at this temperature. The peak r_m value was 0.141 at 25°C, the average temperature typically found during May to August in the northern Willamette Valley. The r_m values decreased at temperatures higher than 25°C to 0.112 at 28 and 31°C, the temperature typically found during the middle to late summer. At 34°C, the r_m value was zero indicating neither growth nor decline in populations related to temperature.

Developmental and Reproductive Parameters and Thresholds. The linear regression used to describe the minimum temperature using the lower four temperatures (17, 22, 25, 28°C) was $y = 0.0114x - 0.1619$ ($R^2 = 0.98$; $F = 120.52$; df = 1, 2; $P = 0.008$) (Fig. 2). The estimated minimum and maximum threshold temperatures for development of *C. vitis* were 10.51 (linear equation, estimated with the use of additional data from Duffner 1999) and 39.19°C (nonlinear equation), respectively, while the optimum developmental temperature was 26.93°C (Fig. 2). The nonlinear function (Briere et al. 1999) describing maximum and optimum developmental temperatures was $y = (0.000000339)*(x-39.19)*(15.01-x)^{(1/0.21)}$ ($R^2 = 0.97$; $F = 63.15$; df = 1, 4; $P = 0.015$). The thermal constant was estimated at 87.7°C DD.

Fecundity (F). No egg production was found at 15°C. The lowest fecundity (0.2 ± 0.1 eggs per female) was recorded at 17°C. Female fecundity increased with increasing temperatures to a maximum of 26.1 eggs per female at 25°C (Table 1). At higher temperatures a decrease of fecundity was found. These data were fitted by the nonlinear function (Briere et al. 1999). The fit was good and female fecundity was described by the function: $y = 0.64-6(x-16.36)) * ((33.81)-x)^{(1/0.53524)})$ ($R^2 = 0.75$; $F = 18.5$; df = 1, 4; $P = 0.03$; Fig. 3). The estimates for the lower and upper threshold for oviposition were 16.4 and 33.8°C, respectively and the optimal temperature was estimated to be 26.5°C.

Mite-Days in Three Grape Growing Regions During 2007 and 2008. Accumulation of DD lagged during 2008 in comparison with 2007 in all three grape production regions because of a cool spring (Table 3; Fig. 4). These differences in DD accumulation were

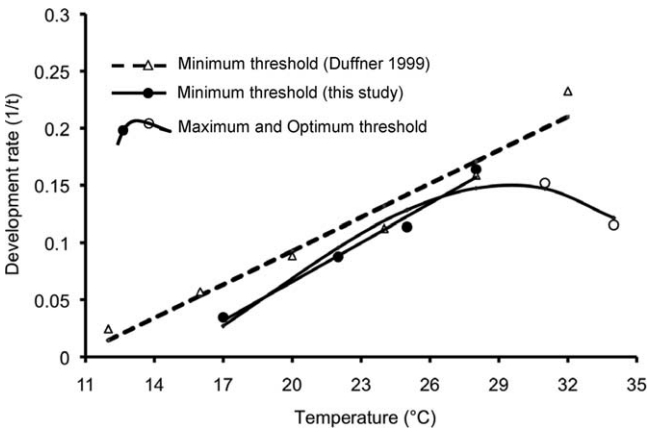

Fig. 2. *C. vitis* development rate from day 0 (egg deposition) to adults on temperature. A nonlinear function was fitted (data used was all circles) to obtain optimum and maximum developmental thresholds. Linear regression was done (solid line) on the lower four trialed temperatures (solid circles) to determine the minimum threshold for development but this value was unrealistically high. For this reason a linear function (dotted line) was regressed on data from Duffner 1999 (triangles) to obtain a more realistic minimum developmental threshold.

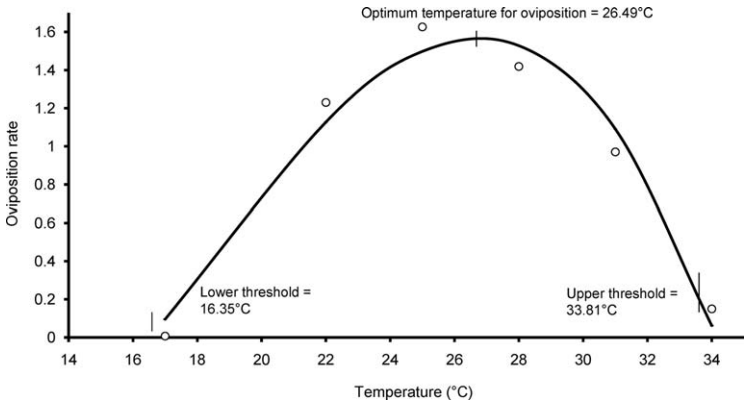

Fig. 3. *C. vitis* oviposition rates (eggs per day per female) at six constant temperatures (17, 22, 25, 28, 31, 34°C).

visible when looking at growth stage development of grape vines in all areas. The onset of wooly bud was 10 d later in 2008 compared with 2007 in the northern Willamette Valley. In 2007, the accumulation of DD on 3 April was two times more than in 2008. In 2008, the low value indicated slower tissue development during that year. By 10 April (bud break), DD accumulations were 96 in 2007 and 78 in 2008 again showing slightly cooler conditions the latter year.

The 2007 and 2008, spring DD accumulation calculated for the early grapevine growth stages in both the Umpqua and Rogue/Applegate regions were higher than those in the northern Willamette Valley. However, growth (DD) in 2007 still lagged behind in year 2008 (Table 3). There was an increase of DD for *C. vitis* development corresponding with principle growth stage 0 (PGS 0) (Meier 2001) in all three wine grape regions (Table 3; Fig. 4) indicating increased mite feeding activity during this growth stage. During 2007 and 2008, vines were in PGS 0 for shorter periods of time in the southern region vineyards (Umpqua and Rogue/Applegate) compared with the northern vineyards (northern Willamette Valley; Table 3). The number of mite-days in the northern Willamette Valley was also higher (35–177 mite days in the 2 yr).

Statewide Mapping of DD Accumulation for Grapevines and *C. vitis*. To visualize heat accumulation for grapevines and mites, maps were generated using a base temperature of 10.56°C. The DD accumulation early in the season for grapevines showed higher DD values in southern grape-growing areas during 1 January to 24 April for 2007 and 2008 (Fig. 5). Lower thermal availability was estimated in the northern Willamette Valley (Fig. 5). Tissue collections during 1 January through 30 April in 2007 and 2008 showed that vines in the northern Willamette Valley were in less advanced growth stages compared with the southern regions.

Validation of Seasonal DD for *C. vitis* Populations in the Field. Based on DD calculations for the northern Willamette Valley, data from our laboratory trials suggest that *C. vitis* can complete up to 14 generations (2007; Fig. 6) within a season. Calculation was started on 1 January and ended on 31 December. Rust mites were first found on leaves on 7 May 2007 and ≈1 wk later on 13 May in 2008 (≈10 cm shoot length, PGS 10; Meier 2001). During both years, there was a gradual increase in mite populations on leaves until mid July to late August, after which mite population numbers started to decrease. Accumulation of DD for *C. vitis* were relatively slow

Table 3. Estimated mite-days and total no. of days, date, and degree-days for grapevine growth and mite development in principal growth stage 0 (PGS 0) during 2007 and 2008 in three grape–growing regions in Oregon

Oregon grape–growing regions	Year	Vine growth stages, date and degree-days[a]			Mite development, degree-days[a]			Feeding duration	
		Onset wooly bud	50% wooly bud	50% bud break	Onset wooly bud	50% wooly bud	50% bud break	Total days[b]	Mite-days[c]
Northern Willamette Valley	2007	25 Mar 65	03 Apr 73	10 Apr 96	14.8	16.6	31.1	17	151
	2008	05 Apr 28	11 Apr 33	7 May 78	1.9	4.2	28.2	32	293
Umpqua Valley	2007	29 Mar 96	03 Apr 106	09 Apr 134	4.2	25.4	37.4	11	98
	2008	01 Apr 50	12 Apr 73	22 Apr 86	4.2	7.9	16.6	20	205
Rogue/Applegate Valley	2007	12 Apr 133	17 Apr 139	25 Apr 148	38.9	39	40.4	13	116
	2008	18 Apr 97	21 Apr 97	30 Apr 122	20.9	20.9	28.9	12	116

[a] Degree-days were estimated for grapevines and mites using lower thresholds of 10.56 and 10.51°C, respectively, and a single sine curve calculation starting 1 Jan.

[b] Total days were computed by taking a summation of individual mite-days.

[c] Mite-days were calculated using: (Xi +1 - X1) [(Yi + Yi + 1)/2], where Xi and Xi + 1 are adjacent points of time and Yi and Yi + 1 are the corresponding points of mite numbers. A pop of nine mites per bud at which damage is seen was used.

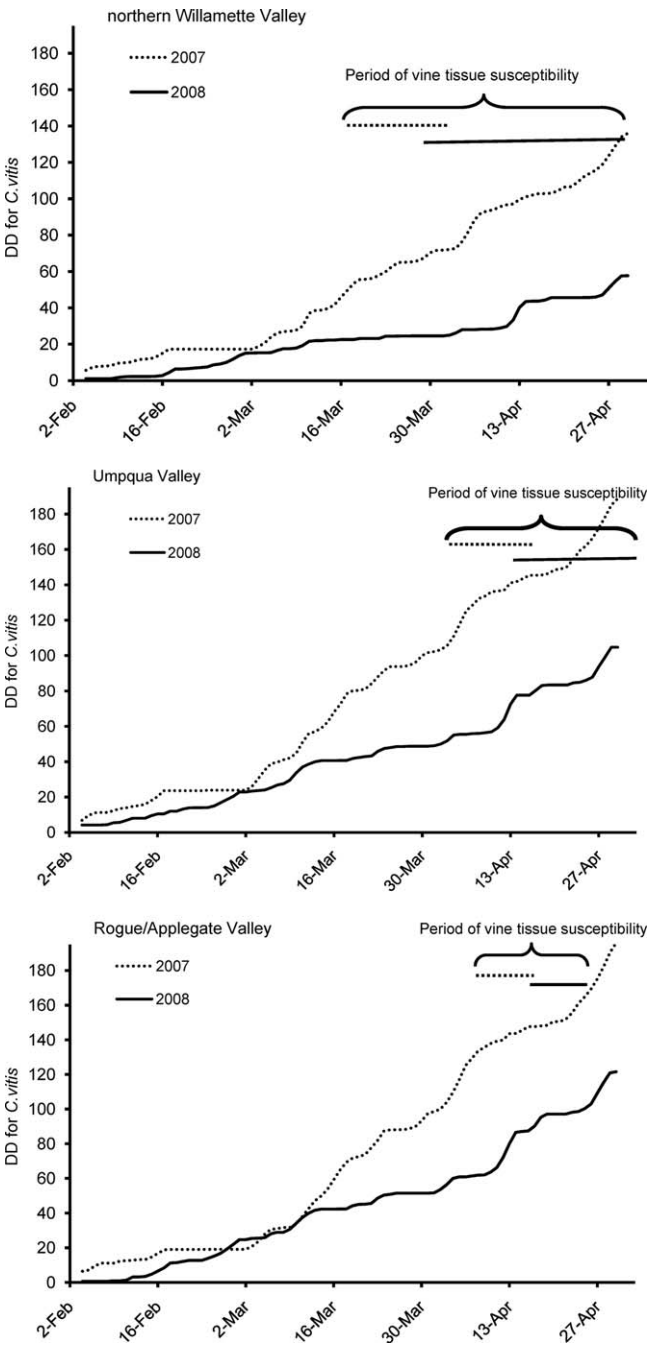

Fig. 4. Cumulative degree-days of *C. vitis* in three grape growing regions in Oregon during 2007 and 2008. Susceptible mite-feeding periods are indicated by dotted (2007) and solid (2008) lines.

until the beginning of July during both years after which multiple, closely spaced generations were found until the end of August (Fig. 6). During September and October in both years we estimated that generations were less closely spaced. Mite populations continued to decrease on leaf surfaces during this period. Double-sided sticky tapes showed their movement to overwintering sites during the middle to late summer (V.M.W., unpublished data).

Discussion

C. vitis developmental rate determined by Duffner (1999) was 40.9 ± 2.4 d at 12°C. Egg to adult devel-

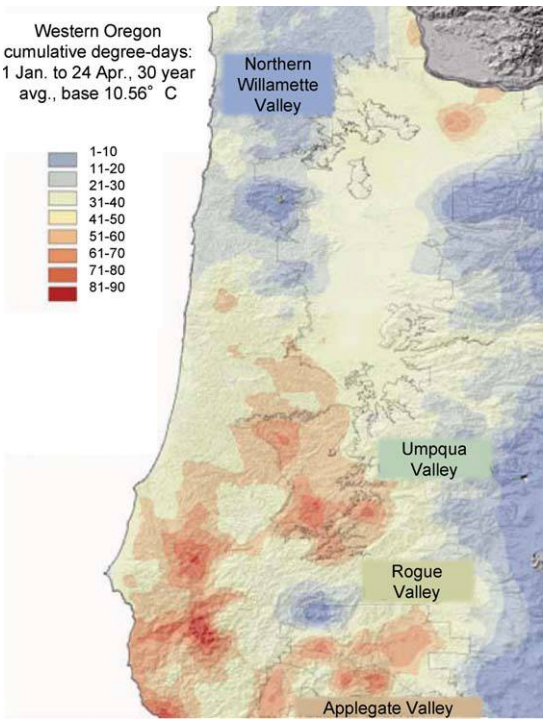

Fig. 5. Accumulated degree-days (DD) for grapevines, using 30-yr temperature averages. A 10.56°C minimum threshold was used and degree-days were accumulated starting on 1 January to 24 April.

opment at 16°C in this study was 17.5 ± 1.2 d compared with 14.9 ± 0.8 d at 17°C found in our study. The remaining developmental periods from egg to adult was comparable to our study and is 11.3 ± 1.7 (20°C), 8.9 ± 1.4 (24°C), 6.3 ± 0.4 (28°C), and 4.3 ± 0.4 (32°C) days. Bergh (1994) found that protogyne pear rust mite, *Epitrimerus pyri* (Nalepa), eggs developed to adults in 15.4 d at 15–16°C and 9.4 d at 20–22°C which is very similar to our data. The sex ratios found in our study were similar to that found in Duffner (1999) and average fecundity levels of *C. vitis* at 24°C over a period of 8 d was 16.4 ± 0.33 eggs per female with the highest egg production at 25°C. For pear rust mite, the highest fecundity was 37 eggs per female but the temperature at which this occurred was not mentioned (Easterbrook 1978). Bergh (1994) reported 60 and 39.5 eggs at 20°C for *E. pyri* protogyne and deutogyne females, respectively. Additional recordings of eriophyid egg production ranged from 10 eggs (Skoracka and Kuczyn'ski 2004) to 51 eggs (Ansaloni and Perring 2004) by *Abacarus hystrix* (Nalepa) and *Aceria guerreronis* (Nalepa) (Acari: Eriophyidae), respectively.

Because published information was not available from Duffner (1999), developmental parameters of *C. vitis* values from this study were compared with those of citrus rust mite, *Phyllocoptruta oleivora* (Ashmead), where published developmental parameters were available (Hobza and Jeppson 1974, Allen et al. 1995). At 17°C the R_o was 0.78, these values gradually increased to a maximum of 3.44 at 23°C, and decreased to 0.11 at 33°C in the Allen et al. (1995) study. Our highest R_o values corresponded much closer to the values found in the Hobza and Jeppson (1974) study where the maximum R_o value was 9.97 at 25°C.

At 34°C the generation time increased to 7.5 d. This increase may be an indication of less optimal metabolic activity because of sub optimal high temperature. Allen et al. (1995) found mean generation times citrus rust mite were 20.8, 10.3, and 9.1 d at 17, 25, and 33°C. These values were similar to those found in this study.

At lower temperatures, 10.51°C (the minimum threshold for deutogyne *C. vitis* development estimated from Duffner [1999]), population growth (r_m) can be expected to be negligible. These low temperature ranges are typically found during the early part of spring season during PGS 0. The r_m values found in our study were higher than values found for citrus rust mite (Allen et al. 1995) with r_m values estimated to be 0.0119, 0.0971, and −0.2403 at 17, 25, and 33°C, respectively. Intrinsic rate of natural increase ranged from 0.2 for *A. hystrix* (Acari: Eriophyoidea)

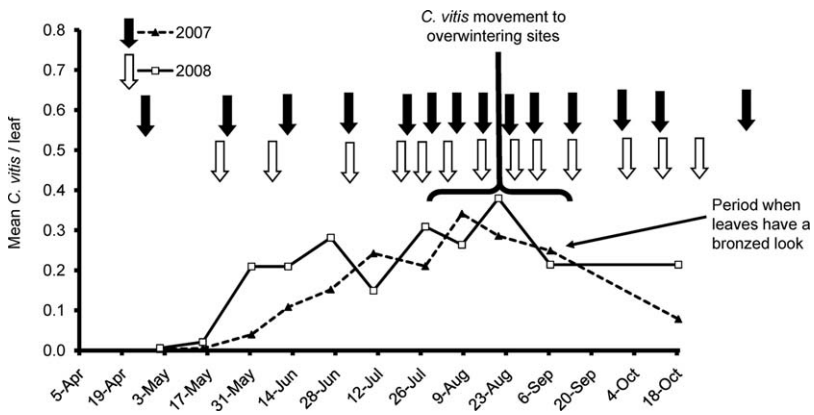

Fig. 6. Comparison of *C. vitis* population densities found on grapevine leaves at the northern Willamette Valley over two seasons. Generations were estimated using a thermal threshold of 87.7DD and each arrow represents one generation.

(Skoracka and Kuczynski 2004) to 0.35 for *Phyllocoptruta oleivora* (Ashmead) (Ebrahim 2000), which is higher than our estimates but our parameter estimates fall within the range reported by Sabelis and Bruin (1996) for vagrant eriophyoid mite species.

Duffner (1999) managed to rear protogyne *C. vitis* at 12°C which indicates this species can develop at temperatures below those found in this study. Bergh (1994) managed to rear deutogynes of pear rust mite at 10°C and fecundity of deutogynes at this temperature was 40.3. These data may help explain why we find egg laying below 12°C field temperatures during early season bud dissections in Oregon vineyards (V.M.W., unpublished data). In addition, we would expect mainly deutogynes to be present during the early part of the season.

Our minimum developmental threshold may therefore be considered unrealistically high, even for protogynes. Deutogyne longevity and oviposition was reported by Bergh (1994) at 10°C. Bergh (1994) reported that threshold base temperatures for development of eggs, nymphs and generations of *E. pyri* deutogynes were 2.2, 3.3, and 3.8°C, respectively. For this reason the function to describe the minimum threshold for development of protogyne *C. vitis* by Duffner (1999) is expected to be more realistic. This function is $y = 0.99978x - 0.102865$ ($R^2 = 0.95$; $F = 92$; df = 1, 4; $P = 0.0006$) with the minimum temperature threshold estimated at 10.51°C. Egg production of other species of vagrant eriophyoid mites ranged between 0–90 eggs per female (Sabelis and Bruin 1996). The fecundity of *C. vitis* therefore falls within this range.

Developmental data for protogyne *C. vitis* obtained under controlled laboratory conditions indicate high potential for population increase, with up to fourteen generations estimated to occur per growing season. Furthermore, the results indicate that *C. vitis* is well adapted for the environmental conditions found in Oregon vineyards. High numbers of mites found on leaves during the growing season is supported by developmental parameters.

Bud break and subsequent grapevine tissue development are directly related to temperature (McIntyre et al. 1982, Moncur et al. 1989). This valuable information can help predict the onset of the wooly stage and the movement of deutogynes, the two main periods of mite exposure. The work by Bergh and Judd (1993) indicate that the majority of pear rust mite deutogynes migrate during the late dormant period, and this is when pesticide applications were recommended to kill the majority of mite populations. Growers can optimize late-dormant and in-season treatments when vine tissue and mites are most susceptible. The area-wide vine DD map displays the importance of temperature and the effect on vines and mite feeding potential.

It is believed that optimal mite control is dependent on two factors. First, pest mite populations must come in contact with pesticides and this is enabled when bud tissue becomes less tightly packed during the wooly bud stage allowing for movement of mites out of the bud area and pesticides into these areas. Second, mite activity and movement to exposed plant parts start to take place during early spring. Treatments targeted at exposed and active pest mite populations should result in lower in-season establishment and targeted sprays mid season should decrease potential overwintering populations (Bergh and Judd 1993). The damage done by the existing mite populations early season, however, will not be completely avoided in some cases. This work together with previous efforts indicates that the early part of the growing season (PGS 0) is when vines are susceptible to damage caused by overwintering *C. vitis* deutogynes. Action during this period may be problematic because of sub-optimal spraying conditions including low temperatures, wet conditions (making sprays and vineyard access difficult), impenetrability of pesticides and little to no movement of mites to exposed feeding sites. For these reasons, growers have reported inconsistent control efficacy using phenology-timed pesticide applications during this period also reported by Bergh and Judd (1993). One way to overcome these limitations is to time a pesticide spray in an attempt to maximize efficiency and control by, treating mites during the season before mites start moving to overwintering refuges.

Long-term heat accumulation maps of vineyard regions indicate that when vines are in PGS0 for prolonged periods of time, they are more susceptible to early season damage by *C. vitis.* Grape-growing areas where heat accumulation during the early part of the season is slow, such as the northern Willamette Valley have recorded up to 80% losses because of mite feeding. Here, in-season mite population levels on leaves increase gradually until the beginning of July. The population peak of *C. vitis* on leaves were during the first half of August. Mite populations start to decrease on vine leaves during the second half of August until after harvest in October. Estimation of population development using our model shows closely spaced generations and high potential for population growth. Unpublished data (V.M.W.) collected from sticky traps in middle August to early October indicate high levels of mite movement to overwintering sites. Growers are often tempted to act during this period as this is when visible signs of leaf infestation, such as bronzed leaves, are clearly visible. However, these sprays are futile as most of the mite populations have already moved to protected overwintering sites by the time bronzing occurs (Westigard 1969, 1975, Easterbrook 1978, Manson and Oldfield 1996). By the time bronzing is observed, large portions of mite populations already moved to protected overwintering sites, reducing their exposure to pesticides. It is believed that this work contributes to a better understanding of mite-related short shoot syndrome experienced in cool climate grape growing areas and periods of mite susceptibility to treatments.

More information is needed on the impact and potential of biological control agents that may mitigate population explosions of pest mites. Work is needed on the impact of commonly used pesticides on key

beneficial organisms to enhance conservation biological control. Optimal timing and efficacy of treatments for control of *C. vitis* pest populations in the field needs to be validated and refined.

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