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Historical and projected interactions between climate change and insect voltinism in a multivoltine species

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Abstract

Climate change can cause major changes to the dynamics of individual species and to those communities in which they interact. One effect of increasing temperatures is on insect voltinism, with the logical assumption that increases in surface temperatures would permit multivoltine species to increase the number of generations per year. Though insect development is primarily driven by temperature, most multivoltine insect species rely on photoperiodic cues, which do not change from year-to-year or in response to climate warming, to initiate diapause. Thus, the relationship between climate change and voltinism could be complex. We use a phenology model for grape berry moth, *Paralobesia viteana* (Clemens), which incorporates temperature-dependent development and diapause termination, and photoperiod-dependent diapause induction, to explore historical patterns in year-to-year voltinism fluctuations. We then extend this model to predict voltinism under varying scenarios of climate change to show the importance of both the quality and quantity of accumulated heat units. We also illustrate that increases in mean surface temperatures $>2\,^{\circ}$C can have dramatic effects on insect voltinism by causing a shift in the ovipositional period that currently is subject to diapause-inducing photoperiods.

Keywords: climate change, diapause, insect population dynamics, phenology, photoperiod, seasonality, voltinism

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Introduction

Climate change has the potential to induce significant changes to ecosystems at the level of individual species, communities, and regional landscapes. Among many taxa, much attention has been given to the fact that increases in temperature can cause an expansion of species' distributional ranges and an increase in outbreak intensity (Parmesan *et al*., 1999; Walther *et al*., 2002; Logan *et al*., 2003; Thuiller, 2004). There has also been considerable interest in understanding the effect of climate change on seasonality, particularly so for poikilothermic species (Porter *et al*., 1991; Masters *et al*., 1998; Bale *et al*., 2002; Walther *et al*., 2002). The logical assumption is that increases in temperature permit more rapid rates of development, with the consequence that multivoltine insects may be capable of increasing the number of generations per year. Past work has highlighted this consequence, mainly by examining the direct effects of increases in temperature relative to thermal constants and minimum developmental temperature thresholds (Yamamura & Kiritani, 1998; Kiritani, 2006) that are characteristic in poikilothermic development (e.g. Wagner *et al*., 1984a, b).

However, insect seasonality in multivoltine species can be complex, and although temperature is the primary driver of development, photoperiodic cues are often the primary driver of diapause induction (Tauber & Tauber, 1976; Denlinger, 2002). Insect developmental rates can vary with fluctuations in annual temperatures, but responses to photoperiod, which changes with precision every year (de Wilde, 1962), do not. Compounding the complexity is the considerable variability in rates of development (Sharpe & DeMichele, 1977) and in the response to photoperiodic cues that induce diapause (Danks, 1987; Bradford & Roff, 1993; Gomi, 1997) within a population.

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Though it is intuitive that increases in temperature would cause an increase in insect voltinism, the nonlinear and dynamic interaction between temperature and photoperiod makes it challenging to quantify precisely the effect of climate change. Although it would be infeasible to generate a description of the effect of climate change for each species given the tremendous diversity among species and in the abiotic conditions and ecological communities in which they interact (Bale *et al*., 2002), precisely quantifying such a relationship between climate change and voltinism for a representative insect species could still provide a conceptual framework for how these specific changes may manifest themselves in other species. We show that, using the grape berry moth, *Paralobesia viteana* (Clemens), as a model system, and report that subtle changes in climate can have, and likely did have, pronounced effects in its year-to-year voltinism.

The grape berry moth is native to eastern North America where it feeds on wild *Vitis* (also native to eastern North America) and cultivated *Vitis* spp. (not necessarily native to North America). Adults emerge from overwintering pupae in spring, mate, and females oviposit on buds, flower clusters, or fruit. Larvae burrow into the fruit and feed, and then exit the berry to pupate by rolling leaves or in the bark of the grapevine. Like most multivoltine insects, its development (Tobin *et al*., 2001) and diapause termination (Tobin *et al*., 2002) are driven by temperature, while its diapause initiation is driven by photoperiod (Nagarkatti *et al*., 2001). Based upon the interaction between temperature and photoperiod, there are generally two–three generations a year in the Great Lakes region of North America. Depending on the photoperiod at which eggs are exposed, larvae will either develop into diapausing pupae, or continue their development to the adult stage (Nagarkatti *et al*., 2001). Thus, a general predictor of its voltinism is the number of degree-days that accumulate before the postsummer solstice photoperiod at which oviposited eggs develop exclusively into diapausing pupae (Tobin *et al*., 2003). In this paper, we used a model of grape berry moth phenology (Tobin *et al*., 2003) to explore past effects of climate on year-to-year voltinism, and then extend this model to examine how changes in mean surface temperatures would affect voltinism.

Materials and methods

Model development

The phenology model was initialized using male moth counts from pheromone-baited traps to characterize the first generation of moth flight, defined as the emergence of adults from overwintering pupae. We supplemented previously published trap catch data from 1996 to 1998 that were used in the development of a phenology model for grape berry moth (Tobin *et al*., 2003) with unpublished data between 1998 and 1999. Traps were generally checked every 1–4 days. In all years, six traps were placed in vineyards located at the Lake Erie Regional Grape Research and Extension Center in North East, Pennsylvania [42.2°N, 79.9°W, 222 m a.s.l. (MSL)]. In 1998, three traps were also each placed in three additional vineyards in North East, PA; Westfield, NY (42.3°N, 79.6°W, 190 MSL); Portland, NY (42.4°N, 79.5°W, 240 MSL); Fredonia, NY (42.4°N, 79.3°W, 230 MSL); and Irving, NY (42.6°N, 79.1°W, 184 MSL). Weather data were obtained from a weather station at Lake Erie Regional Grape Research and Extension Center, or from the closest weather station available from the National Climatic Data Center (2007).

For each location and year, daily maximum and minimum temperatures were used to estimate daily degree-day accumulations from January 1 based upon a minimum base temperature threshold of 8.4 °C (Tobin *et al*., 2001) and a modified sine-wave method (Allen, 1976). Using trap catch data within the first 650 degree-days, which generally captures first generation moth flight (Tobin *et al*., 2003), we used an exponential model to fit the proportion of moths (P_m) over accumulated degree-days (DD),

$$P_m = \exp(-\exp(-r\mathrm{DD} + b)), \quad (1)$$

in which r and b are the rate of increase and lag, respectively (Brown & Mayer, 1988). A total of 6514 moths across all years and trap locations were used to develop this model. Nonlinear convergence was based on the Marquardt algorithm (Marquardt, 1963) in R (R Development Core Team, 2007). This function was used to estimate peak of first generation flight (Fig. 1), which was then used to initialize a model of grape berry moth seasonality (cf. Tobin *et al*., 2003) that combines first generation moth flight, preovipositional thermal requirements (Luciani, 1987), temperature-dependent development (Tobin *et al*., 2001), and diapause initiation (Nagarkatti *et al*., 2001). The premise is that grape berry voltinism is driven by the degree-days that accumulate prior to diapause-inducing photoperiods.

Historical model predictions

We obtained historical daily surface maximum and minimum temperature data from the National Climatic Data Center (2007) for (1) Erie, PA (42.1°N, 80.1°W, 210 MSL), 1926–2005; (2) Cornell University's Research Farm, Geneva, NY (42.9°N, 77.0°W, 180 MSL), 1914–2005; and (3) Holland, MI (42.8°N, 86.1°W, 186 MSL), 1909–2005. We conducted our analyses within these

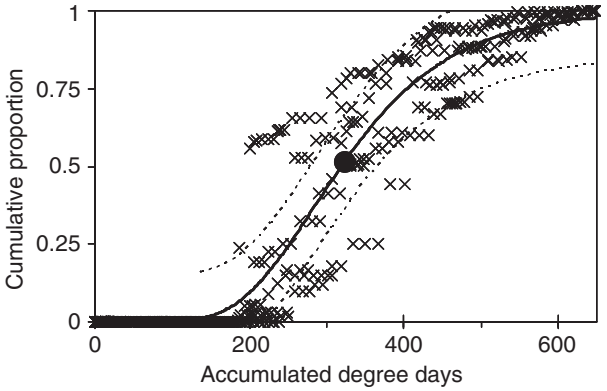

Fig. 1 Cumulative proportion of first generation males trapped in pheromone-baited traps, 1996–1999, over accumulated degree-days from January 1. Based upon the nonlinear model, peak of first generation flight (i.e. cumulative proportion of 0.5, represented by the closed circle) was initialized at 320 degree-days (base 8.4 °C).

latitudes due to the potential of clinal geographic variation in diapause-inducing photoperiods (Danks, 1987; Gomi, 1997). Each location still provided a different set of potential interactions between temperature and photoperiod during the course of the active season for the grape berry moth and its hosts within its native distribution (Fig. 2). For each location and year, we estimated daily degree-days from January 1 using 8.4 °C as the minimum base threshold and the modified sine wave method, from which we could determine the calendar day of peak oviposition by the second and third generation (in grape berry moth, eggs eventually develop into either adults or diapausing pupae depending on photoperiod, Nagarkatti *et al*., 2001). At each location, these dates were then related to the respective photoperiod to determine year-to-year voltinism. For example, in a given year, if peak oviposition by the second generation of adults occurred at a photoperiod at which half of the eggs would develop into diapausing pupae rather than adults, we considered this year to have 2.5 generations. This general rule-of-thumb allowed us to examine historical year-to-year variability in voltinism.

To measure the feasibility of this approach in predicting historical voltinism, we measured, for each location, the correlation between yearly mean temperatures during the growing season (March–October) and the number of generations predicted by our model. Because of potential bias due to autocorrelated data, we first measured the autocorrelation in each location's time series of mean temperatures data using the partial autocorrelation function (PACF). Autocorrelated time series were then prewhitened through the use of an autoregressive model with the appropriate order based upon the PACF.

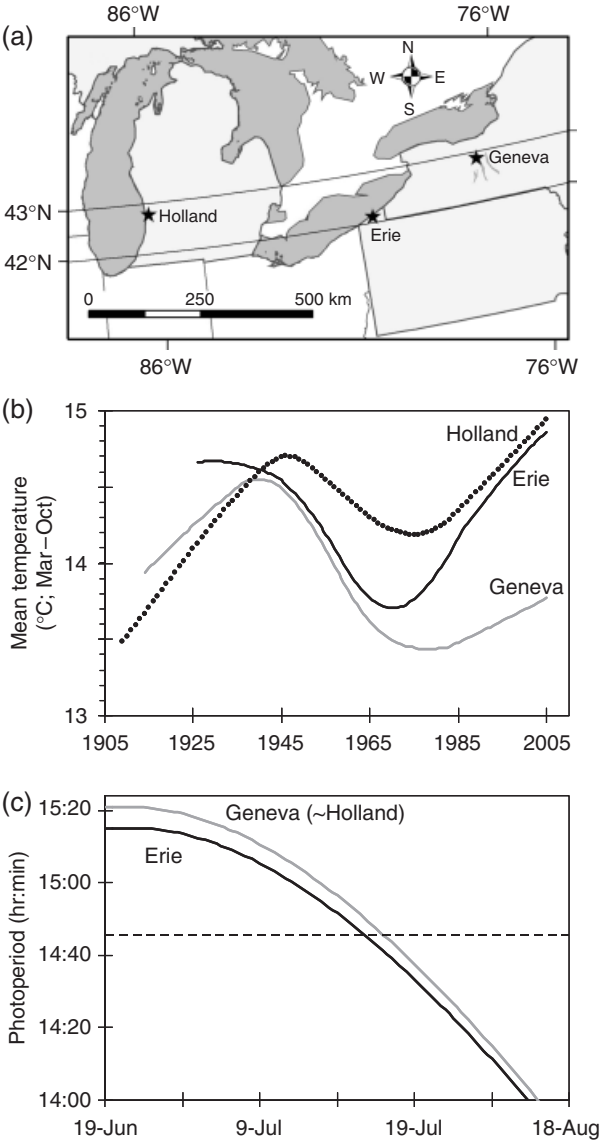

Fig. 2 (a) Locations used in analyses. (b) Mean temperature trends using locally weighted nonparametric regression. (c) Post-summer solstice photoperiods (Geneva serves as a surrogate for Holland). The dashed line represents the photoperiod at which half of oviposited eggs develop into diapausing pupae.

The residuals were obtained and the lack of autocorrelation in the residuals was verified with the PACF. Residuals were then used to calculate Pearson's correlation coefficient. All analyses were conducted in R (R Development Core Team, 2007).

Forecasting voltinism under climate change

We used temperature data from 1996 to 2005 from Erie, Geneva, and Holland to calculate each location's mean

daily maximum and minimum temperatures over the 10-year period as a surrogate for recent climatic trends. We then modified each day's maximum or minimum temperature by adding or subtracting 0.5–5 °C, in increments of 0.5 °C, to reflect both climate warming and cooling trends, respectively. Using these modified temperatures, we then estimated daily degree-day accumulations, from which we then estimated the number of generations (as described above) under these different scenarios of climate change. We then related recent warming trends in Erie, Geneva, and Holland to this forecast of voltinism under these different scenarios.

Results and discussion

The relationship between historical weather data and voltinism in the grape berry moth is presented in Fig. 3. This relationship illustrates the considerable variability in year-to-year seasonality, which is supported by past observations (Gleissner & Worthley, 1941; Gleissner, 1943; Taschenberg, 1945; Biever & Hostetter, 1989; Hoffman *et al.*, 1992). Temperatures during the growing season were significantly positively correlated with the predicted number of generations at each location (Erie: $\rho = 0.65$, df = 79, $P < 0.001$; Geneva: $\rho = 0.74$, df = 91, $P < 0.001$; Holland: $\rho = 0.72$, df = 96, $P < 0.001$). However, although warmer years do generally, and intuitively, correspond with more generations, the relationship is fairly complex. The number of generations predicted in each year over the accumulated degree-days is shown in Fig. 4, and highlights that it is not strictly the quantity of degree-days that accumulate during the course of the year, but rather, the quantity at the right time. Indeed, the relationship between voltinism and accumulated degree-days is much stronger when only those degree-days that accumulate prior to August 3, which is the date at which day length at the study latitudes induces 90% of oviposited eggs to develop into diapausing pupae rather than adults (Nagarkatti *et al.*, 2001), are considered (Fig. 4b).

One factor that could add to this complexity is the concept of upper developmental thresholds, which were not used in this analysis. In the case of grape berry moth, developmental rate under laboratory conditions begins to decrease slightly at constant temperatures between 30 and 32 °C, and mortality rates increase when larvae are exposed to constant temperatures $\geq$34 °C (Tobin *et al.*, 2001), which is typical for many temperate insect species (e.g. Wagner *et al.*, 1984a). In the historical weather data used in this analysis, <0.6% of daily maximum temperatures exceeded 34 °C, and when they did, do so for only a few hours of the day; thus, it is probably unlikely that developmental rates would significantly decrease with continual warming trends.

Diapause for many multivoltine insects is triggered by short or shortening photoperiods following the summer solstice (Lees, 1955). For a temperate species like the grape berry moth, diapause is initiated as early as 2–3 weeks following the summer solstice (Nagarkatti *et al.*, 2001). Warmer summer days, especially if they occur after the trigger for diapause initiation, thus will have little effect on voltinism in the absence of evolutionary change in the responses to photoperiodic cues that mediate diapause induction. However, milder winters and particularly, warmer spring temperatures

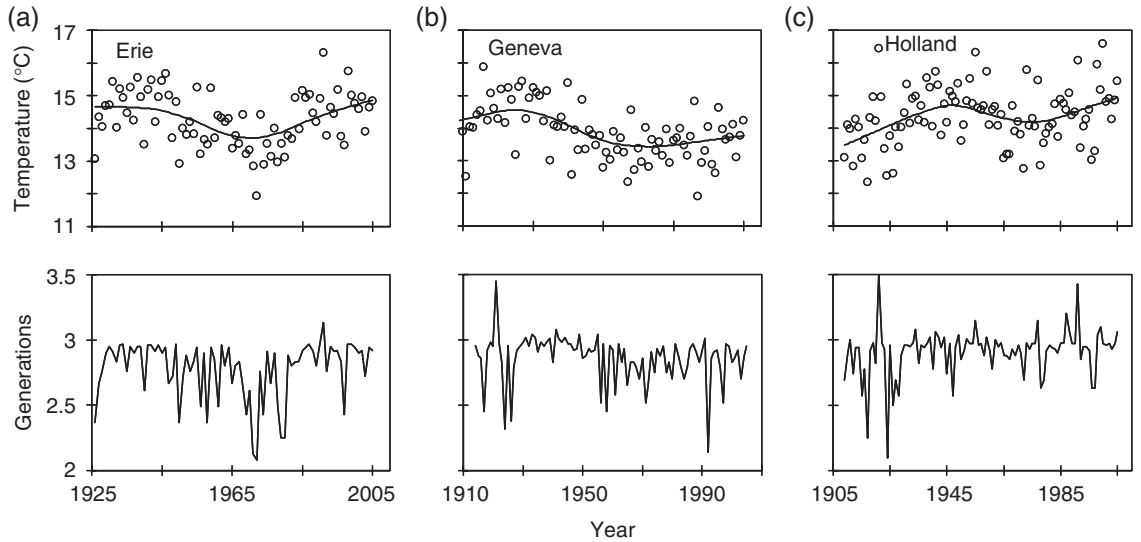

Fig. 3 Yearly mean observed temperatures (top row, with trends from Fig. 2b shown) and the estimated number of generations per year (bottom row).

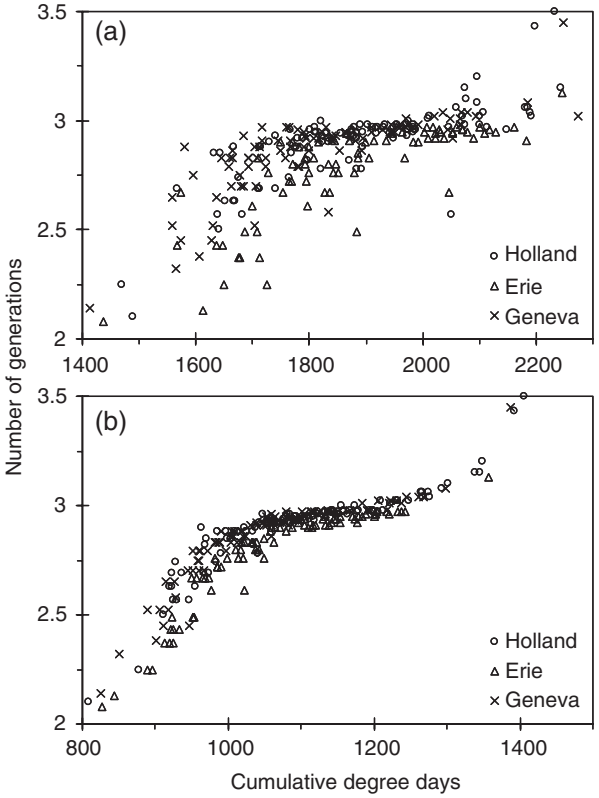

Fig. 4 The estimated number of generations per year based upon (a) the total yearly degree-day accumulation and (b) the degree-day accumulation from January 1 to August 3 (the day at which 90% of oviposited eggs developed into diapausing pupae instead of adults, Nagarkatti *et al*., 2001).

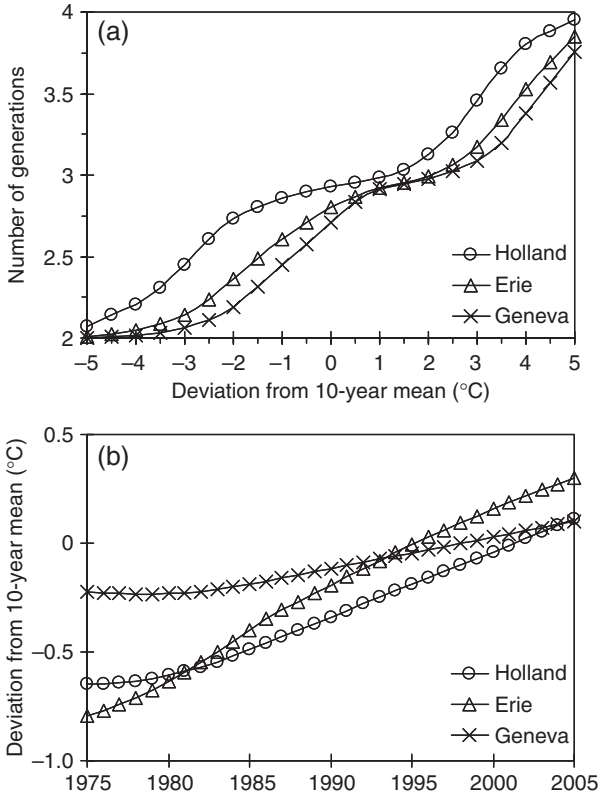

Fig. 5 (a) Forecasted number of generations under climate change scenarios based upon a 10-year mean (1996–2005). (b) Location-specific deviations in the 10-year mean (1996–2005) over the course of the recent warming trend illustrated in Fig. 2b.

would have pronounced effects because first generation adults would emerge from overwintering pupae sooner than in the past; therefore, oviposition by subsequent generations would more likely occur prior to the photoperiod at which diapause is always induced.

The complex relationship between both expected cooling and warming trends, and voltinism, is shown in Fig. 5a. Voltinism of grape berry moth is fairly static through the historical temperature series, generally oscillating between 2.5 and three generations per year (Fig. 3). However, more abrupt and nonlinear changes in voltinism would occur when mean temperatures increase by 2 °C or more (Fig. 5a) due to the nonlinear changes in photoperiod and in the gradient of photoperiodic change (Fig. 2c). Around the summer solstice, there are very little changes in photoperiods from day-to-day, but day length changes more rapidly as the midpoint between the solstice and equinox is approached. Thus, increases in mean temperature that are <2 °C above normal have proportionally less effect on voltinism than >2 °C (Fig. 5a) because the former is insufficient to shift the timing of oviposition from photoperiods that induce diapause. Conversely, years in which temperatures are <2 °C below normal have more pronounced effects on voltinism than for those that are >2 °C below normal. Again, this relationship is largely due to the fact that in each location, oviposition by the second generation is generally currently occurring (July to early August) during photoperiods at which some-to-most individuals enter diapause (Nagarkatti *et al*., 2001). However, heating trends of 2 °C or more above recent mean temperatures is sufficient to shift this distribution so that oviposition occurs in advance of diapausing-inducing photoperiods (Fig. 6). Earlier work in other multivoltine insect species have likewise suggested the likelihood of additional generations when temperatures increase >2 °C (Yamamura & Kiritani, 1998; Musolin, 2007).

Considering the considerable diversity in life-history strategies, different species of insects will likely respond to climate change in different ways (Bale *et al*., 2002). Many multivoltine species that do initiate diapause, such as the grape berry moth, may undergo as many generations as temperature and photoperiod conditions

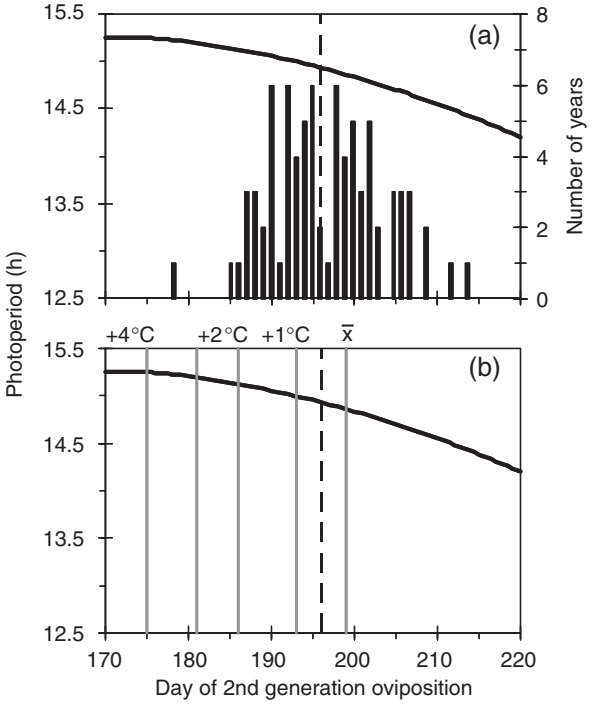

Fig. 6 (a) Histogram of the calendar day of 50% oviposition by second generation grape berry moth in Erie, PA, 1926–2005. The thick curve represents corresponding photoperiod, and the dashed vertical line represents (as a reference) the onset of diapause-inducing photoperiods (cf. Nagarkatti *et al.*, 2001). Note how in at least half of the years, peak oviposition is subject to diapause-inducing conditions. (b) Estimated midpoint of oviposition based upon a 10-year mean in weather (1996–2005), and projected midpoints when assuming a 1, 2, or 4 °C increase. Note the shift of the timing of second generation oviposition, particularly at >2 °C.

will allow, assuming that there is an available food source. Such a response has important ecological and economic ramifications. For example, grape berry moth eggs can be exposed to diapause-inducing daylengths in July (Nagarkatti *et al.*, 2001), while commercial harvests of grapes within the latitudes of this study do not occur until September–October. Increases in temperature, particularly >2 °C (Fig. 5a), shifts the timing of second generation oviposition (Fig. 6), and increases the risk of a late summer generation with a direct economic impact. Moreover, although the photoperiodic threshold for diapause induction is not temperature-dependent and should not change, there could be the possibility of genetically based phenological adaptation in grape berry moth as a result of climate change (van Asch *et al.*, 2007).

Anecdotally, the timing of second generation oviposition could be already in the process of shifting. In recent years, grape growers from this region have reported (to G. L. and M. C. S.) increases in late summer populations that in the past have been lower in density. Historically, more eggs may have been induced to develop into diapausing pupae instead of initiating another generation of fruit-feeding larvae. Unfortunately, robust temporal data on grape berry moth seasonality are not available to allow for a comprehensive assessment of this potential shift in the timing of oviposition. However, we can relate the expected number of generations when temperatures deviate from a 10-year mean (Fig. 5a) to temperature trends over the most recent warming period (1975–2005, Fig. 2b) in each of our study locations. This relationship is shown in Fig. 5b, and reveals that in each location, recent temperature increases could have resulted in an increase in grape berry moth voltinism.

Our analyses that quantify the interactions between climate change and voltinism, when likewise considering the role of photoperiod, enhance prior work (Yamamura & Kiritani, 1998; Kiritani, 2006). Future work could extend this study from population to individual levels and explore how changes in voltinism in response to climate change affect population abundance. Global mean temperatures are increasing, and increase of 1.5–2.5 °C above current surface temperatures will likely impact ecosystems to include increases in species geographic ranges, outbreak intensity, risk of extinction, and decreases in biodiversity (e.g. Bale *et al.*, 2002; Walther *et al.*, 2002; Logan *et al.*, 2003). Based upon this study, the number of annual generations in multivoltine insect species is also likely to increase, and such increases can greatly exacerbate the negative ecological and economical costs of insect pest species.

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