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Effects of photoperiod and relative humidity on diapause termination and post-winter development of *Rhagoletis cerasi* pupae

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Abstract

The European cherry fruit fly, *Rhagoletis cerasi* (Diptera: Tephritidae), is a univoltine species that undergoes obligatory summer–winter diapause at pupal stage in the soil (2–5 cm) beneath host trees. To study the effects of photoperiod and humidity on diapause termination and post-winter developmental duration of *R. cerasi*, pupae collected from Dossenheim (Germany) were exposed to different photoperiod or relative humidity regimes during a chilling period ranging from 2 to 8.5 months. Specifically, pupae were exposed to four photoperiod regimes: (a) light conditions (24L:00D), (b) dark conditions (00L:24D), (c) short photoperiod (08L:16D) and (d) long photoperiod (16L:08D), as well as to three relative humidity regimes: (a) low (40% RH), (b) medium (60% RH) and (c) high (70–80% RH). Data revealed that relative humidity is not a significant predictor of diapause termination, but it affects the post-winter developmental period. Higher relative humidity promotes post-winter pupae development. On the other hand, photoperiod significantly affected both diapause termination and post-winter development of *R. cerasi* pupae. Light conditions (24L:00D) accelerate adult emergence, particularly for females. Regardless of the photoperiod (24L:00D, 00L:24D, 08L:16D), rates of adult emergence were high (>75%) for chilling intervals longer than 6.5 months. Nonetheless, exposure to a long day photoperiod (16L:08D), during chilling, dramatically reduced the proportion of adult emergence following 6 months exposure to chilling. Our findings broaden the understanding of factors regulating diapause responses in European cherry fruit fly, local adaptation and synchronization of adult emergence with the ripening period of major hosts.

Introduction

Diapause is one of the primary mechanisms whereby herbivorous insects synchronize their life cycles with specific phases of host plants (Tauber *et al.*, 1986; Denlinger, 2002). Photoperiod, temperature and moisture/humidity strongly affect the physiological processes that take place throughout the different diapause and post-diapause stages of insects (Koštál, 2006). For example, photoperiodism (e.g. exposure to short days of autumn) is most commonly reported in diapause induction and maintenance (Tauber *et al.*, 1986; Masaki, 1999). For the insects of the temperate zone, exposure to low temperatures (0–10°C) is typically a prerequisite for diapause termination (Saulich and Musolin, 2012). Then, high temperatures accelerate post-diapause developmental rates and promote synchronization of adult emergence (Stålhandske *et al.*, 2015; Moraiti *et al.*, 2017). Populations from ecologically different habitats have shown differential responses to environmental factors (particularly temperature and photoperiod) for terminating diapause and/or concluding post-diapause development (Moraiti *et al.*, 2014, 2017; Stålhandske *et al.*, 2014).

Photoperiod is acknowledged to provide the most accurate information for the timing of seasonal events in insect life cycles, particularly for species at high latitudes where autumn temperatures are highly variable (Bradshaw and Holzapfel, 2007; Śniegula and Johansson, 2010; Saunders, 2014). It 'triggers' facultative diapause responses well before conditions become unfavourable for survival and/or reproduction (Tauber and Tauber, 1976). The diapause-inducing photoperiod is also likely to influence the diapause intensity in many insect species, given that longer scotophases found to induce more intense diapause compared with shorter scotophases (Koštál and Hodek, 1997; Nakamura and Numata, 2000; Wang *et al.*, 2014). Post-diapause development can also be affected by photoperiod (Wang *et al.*, 2014; Liu *et al.*, 2017), even though exceptions exist (Terao *et al.*, 2012; Cheng *et al.*, 2017).

Geographic variation of photoperiodic responses in diapause induction, diapause intensity and/or post-diapause development is common among populations inhabiting different latitudes or among individuals of the same species, based either on genetic factors or on plastic responses (Śniegula and Johansson, 2010; Chen *et al*., 2013; Zeng *et al*., 2013; Wang *et al*., 2014; Lindestad *et al*., 2019). It is important to point out that photoperiod and temperature are usually interacting in inducing, maintaining and/or terminating diapause (Wang *et al*., 2009; Chen *et al*., 2014; Norling, 2018).

Compared to both temperature and photoperiod, the role of moisture in diapause developmental processes is less understood (Tauber *et al*., 1998; Hodek, 2003). In general, moisture is likely to act as a token stimulus that induces, maintains or terminates diapause (Okuda, 1990; Tauber *et al*., 1998). Nonetheless, moisture is rarely expected to serve as a cue for diapause induction because of spatial and temporal variability in its occurrence (Tauber *et al*., 1998). However, moisture remains an important factor that triggers resumption of development at the end of dormancy stimulating adult emergence in many insects (Hodek, 2003; Jin *et al*., 2016; Socías *et al*., 2016). For example, the larvae of the wheat blossom midges, *Contarinia tritici* and *Sitodiplosis mosellana* (Diptera: Cecidomyiidae), need high soil moisture or rainy conditions for pupation after the temperature-regulated diapause development (Cheng *et al*., 2017). The decreased rate of adult eclosion under dry soil conditions has been attributed to the ability of dry soil to act as a mechanical barrier preventing adult emergence (Weston and Desurmont, 2008; Johnson *et al*., 2010). Recently, inadequate soil moisture was found to promote prolonged diapause in already diapausing individuals of *S. mosellana* (Cheng *et al*., 2017). On the other hand, exposure to excessive moisture can be detrimental for the resumption of post-diapause development as well (Jin *et al*., 2016). Regardless of the amount of precipitation, the timing of rainfall and the persistence of moist soil may regulate diapause processes of insects, given that diapausing stages may only be sensitive to soil moisture for a short period and different soil textures have various water-retention capacities (Ma *et al*., 2017). A combined effect of moisture with temperature on post-diapause development rates has also been reported for *Apolygus lucorum* (Hemiptera: Miridae) (Jin *et al*., 2016), *S. mosellana* (Cheng *et al*., 2017) and *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae) (Tauber *et al*., 1994).

The European cherry fruit fly, *Rhagoletis cerasi* (Linnaeus) (Diptera: Tephritidae), is a highly destructive pest of cherries (*Prunus* spp.) (Rosaceae), in Europe and temperate regions of Russia and Asia, and has recently been detected in North America (White and Elson-Harris, 1992; Daniel and Grunder, 2012; Barringer, 2018). It is an univoltine species that undergoes obligatory winter diapause at the pupal stage in order to synchronize its flight period with the short seasonal period for oviposition in suitable fruits at a local scale (Boller and Prokopy, 1976; Daniel and Wyss, 2009; Daniel and Grunder, 2012). Under field conditions, diapause termination usually takes place from the middle to the end of winter, and then pupae remain in post-diapause quiescence until temperature increases above 5°C, which is known to promote pupae development and adult emergence (Baker and Miller, 1978; Papanastasiou *et al*., 2011). The patterns of *R. cerasi* adult emergence under field conditions differ among populations from ecologically different habitats due to geographical variation in diapause termination and post-diapause developmental rates (Papanastasiou *et al*., 2011; Moraiti *et al*., 2014, 2017; Moraiti and Papadopoulos, 2017). Even though patterns of local host fruiting are reliable predictors of the adaptive response of *R. cerasi* pupae to winter temperatures for diapause termination, they cannot explain the geographical variation in post-winter developmental rates of *R. cerasi* (Moraiti *et al*., 2014, 2017). Interestingly, inter-annual (temporal) climatic variability results in two types of long life cycles within *R. cerasi* populations, expressed either as prolonged dormancy due to insufficient chilling (higher chilling temperatures and shorter chilling periods) or as a second, successive, facultative cycle of dormancy driven by an extended exposure to chilling (Vallo *et al*., 1976; Moraiti *et al*., 2014). Thus, *R. cerasi* has evolved a complex dormancy strategy based on a combination of local adaptation and diversified bet-hedging strategies for ensuring population survival and reproduction at ecologically different habitats (Moraiti and Papadopoulos, 2017).

The roles of temperature and geographic origin in diapause termination and post-diapause development of *R. cerasi* pupae have been thoroughly studied (Baker and Miller, 1978; Papanastasiou *et al*., 2011; Moraiti *et al*., 2014, 2017; Moraiti and Papadopoulos, 2017); however, the impact of moisture and photoperiod on pupal diapause and post-diapause development is less explored. In this study, we investigated the effects of relative humidity and photoperiod on both diapause termination and post-diapause development of *R. cerasi* pupae that were exposed to various chilling regimes until adult emergence. Taking into account that *R. cerasi* pupae overwinter underneath host plants in a soil depth ranged usually from 2 to 5 cm based on soil type (Daniel and Grunder, 2012) and that adult emergence is reduced in extremely wet environments and/or wet clay soils (Boller, 1966), we examined the hypothesis that relative humidity but not photoperiod is a significant predictor of both diapause termination and post-diapause developmental duration of *R. cerasi* pupae. Photoperiod is not expected to have an impact on diapause traits because soil can act as a physical barrier for light, even though soils in the field have many cracks and pores in the surface made by plant roots and soil invertebrates, and those openings are likely to allow some light to come through (Gustin and Schumacher, 1989). Sexual differences in post-diapause developmental time were also assessed.

Materials and methods

We used *R. cerasi* pupae that were recovered from infested sweet cherries collected from an orchard in 2010 located at the experimental field of JKI in Dossenheim in the north part of Baden-Württemberg state, Germany, situated in the upper Rhine valley. This region falls under the 'humid, warm temperate' climate (Cfb) of the Köppen and Geiger climate classification: oceanic with warm summers and mild winters, with rainfall distributed throughout the year (Kottek *et al*., 2006; Peel *et al*., 2007). Flowering of cherry cultivars usually takes place during April, and the fruit ripening period lasts from beginning of June to the middle of July. In 2007–2010, mean spring temperatures ranged from 8 to 16°C with mean precipitation levels from 35 to 100 mm per month. In 2018, the shortest and longest day in Dossenheim was 8:08 h (start of winter, 22 December) and 16:14 h (start of summer, 21 June). Fruits were placed in plastic boxes with a grid bottom over a layer of dry sand (1 cm thick) allowing mature larvae to pupate at ambient temperature in a rain-protected hall. Pupae were sieved out of the sand twice per week or weekly and stored at room temperature for up to 2.5 months. Then pupae were put in transparent colourless 1.5 ml reaction vials (100 pupae per vial)

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with holes in the lid and cotton wool between pupae and lid. Light could reach the pupae as the vials were transparent and colourless and humidity could reach the pupae as the lid had holes. Pupae were assigned to the treatments at 4 ± 1°C.

Effect of photoperiod on diapause termination and post-winter development

To determine whether photoperiod is a significant predictor of diapause termination and post-winter development, *R. cerasi* pupae were exposed to different photoperiod conditions during the chilling period. Specifically, pupae were exposed to continuous light (24L:00D) and dark (00L:24D) conditions as well as to short- (08L:16D) and long-day photoperiod (16L:08D). Newly formed pupae collected in Dossenheim and stored as described above and finally put into vials ($n = 100$ pupae per vial) before being transferred to a cool chamber (4 ± 1°C, 75–80% RH) for a period ranging from 2 to 8.5 months. In total, 5600 pupae in 56 Eppendorf units were used for this experiment (4 treatments × 14 periods × 100 pupae). To achieve different photoperiod conditions, pupae were put in dark grey plastic boxes (60 × 40 × 34 cm, with two small openings, 3 × 14 cm each, at the top part of opposite sides), wherein a Neon lamp (Radium NL 85W/865, cool day light, spectralux plus; resulting in ∼1000 lux at the position where the pupae were stored) and a ventilator to prevent heat up were had been installed. The light periods where regulated by timers. In case of dark conditions (00L:24D), pupae were put in an open box in the cool chamber. Every 15 days, one sample of 100 pupae from each treatment was transferred back to a climate chamber (25 ± 1°C during the light period of 16 h and 18 ± 1°C during the dark period of 8 h, 70 ± 5% RH,) until adult emergence was completed. Upon emergence, adults were sexed and counted for each treatment.

Effect of relative humidity on diapause termination and post-winter development

R. cerasi pupae were exposed to low (4041.7 ± 0.9%), medium (58.3 ± 0.9%) and high (75.6 ± 10% RH) relative humidity conditions during a chilling period ranging from 2 to 8.5 months to assess the effects of humidity on diapause. For this purpose, newly formed pupae from the same population in Dossenheim, stored as described above and finally put into vials ($n = 100$ pupae per vial) were placed at 4 ± 1°C (with a photoperiod of 00L:24D) for the mentioned chilling periods. In total, 4200 pupae in 42 vials were used for this experiment (3 treatments × 14 periods × 100 pupae). Low and medium humidity regimes were achieved in an exsiccator with $MgCl_2$ and $Mg(NO_3)_2$, respectively. The standard humidity in the cool chamber was 75.6 ± 10% RH. Every 15 days, one sample of 100 pupae from each treatment was transferred back to a climate chamber (25 ± 1°C during the light period of 16 h and 18 ± 1°C, 70 ± 5% RH) until adult emergence was completed. Upon emergence, adults were sexed and counted in each treatment.

To estimate the duration of post-winter developmental period, time was recorded from the end of the chilling period to adult emergence (Stålhandske *et al.*, 2015; Moraiti *et al.*, 2017). The post-diapause development of *R. cerasi* pupae is likely to begin during exposure to chilling and thus an overlapping with the diapause termination phase may occur (AliNiazee, 1988), particularly when chilling include exposure to temperatures ≥5°C (Baker and Miller, 1978). Taking into account that the main criterion for both diapause termination and post-winter development of *R. cerasi* pupae in each photoperiod and relative humidity treatment is the number of emerging adults, it is of outmost importance to be capable of distinguishing environmental effects on diapause termination from those on post-chilling development. To this end, we assumed that the peak of adult emergence (>60% of pupae gave adults) is a milestone for diapause termination. In this sense, pupae of each treatment maintained in cold for a long enough period (minimum 2 months and maximum 8.5 months) for a proportion >60% of pupae to yield adults were used for assessing photoperiod and relative humidity effects on the duration of post-winter developmental period (for details see Moraiti *et al.*, 2017).

Statistical analyses

Binary logistic regression analysis was used to assess the effects of chilling period, relative humidity and photoperiod on adult emergence. The Cox proportional hazard model was used to assess the effects of: (1) photoperiod, (2) relative humidity and (3) sex on the duration of post-winter developmental period of *R. cerasi* pupae. Significant factors were entered in a multifactorial Cox regression model using a forward stepwise procedure for model selection. All statistical analyses were performed using SPSS 22.0 (IBM Corp., Armonk, NY, USA).

Results

Effect of photoperiod on diapause termination and post-winter development

Diapause termination

Peak of adult emergence after chilling (>60% of pupae yielded adults) was recorded at (i) 4 months in 24L:00D and 08L:16D, and (ii) 4.5 months in 00L:24D and 16L:08D (fig. 1). Thereafter, adult emergence rates remained high (close to 80%) for all treatments, excluding 16L:08D where emergence rates fluctuated a great deal. Binary logistic regression revealed that photoperiod, chilling period and the interaction of photoperiod by chilling period were significant predictors of adult emergence (table 1).

Post-winter developmental time

For males, the average duration of post-winter developmental period of pupae that were exposed to short photoperiod (08L:16D), long photoperiod (16L:08D), light conditions (24L:00D) and dark conditions (00L:24D) during chilling ranged (a) from 20 ± 0.3 to 42 ± 2.2 days, (b) from 18 ± 0.3 to 38 ± 2.1 days, (c) from 19 ± 0.3 to 39 ± 0.8 days and (d) from 21 ± 0.2 to 36 ± 2.3 days, respectively. For females, the average duration of post-winter developmental period of pupae that were exposed to short photoperiod (08L:16D), long photoperiod (16L:08D), light conditions (24L:00D) and dark conditions (00L:24D) ranged (a) from 19 ± 0.3 to 35 ± 1.9 days, (b) from 18 ± 0.3 to 34 ± 1.1 days, (c) from 19 ± 0.5 days to 36 ± 2.8 days and (d) from 20 ± 0.2 to 37 ± 1.4 days, respectively (Supplementary Material, tables S1–S4, fig. S1).

Post-winter developmental time was the shortest for pupae that give adults (both males and females) upon peak of adult emergence after chilling under light conditions (for a period ranging from 2 to 8.5 months). Males emerged from pupae that remained in 08L:16D during chilling had the longest post-winter developmental time. On the other hand, long photoperiod conditions during chilling resulted in an extended post-winter

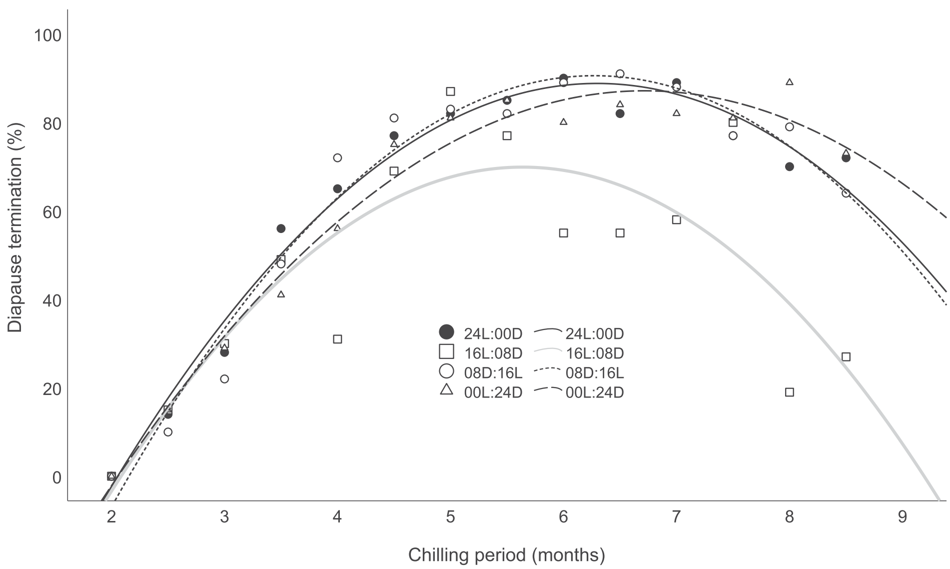

Figure 1. Diapause termination of *R. cerasi* pupae from Dossenheim population (Germany) after chilling for a period ranged from 2 to 8.5 months. During chilling period, pupae were exposed to: (a) continuous light (24L:00D) ($y = -1.2335x^2 + 23.67x - 24.736$, $R^2 = 0.9745$), (b) dark conditions (00L:24D) ($y = -1.004x^2 + 20.945x - 22.077$, $R^2 = 0.9743$), (c) short photoperiod (08L:16D) ($y = -1.3352x^2 + 25.487x - 31.066$, $R^2 = 0.9665$) and (d) long photoperiod (16L:08D) ($y = -1.3839x^2 + 22.904x - 24.877$, $R^2 = 0.7134$).

Table 1. Variables of the binary logistic regression analysis exploring the effects of photoperiod and chilling period on diapause termination of *R. cerasi* pupae from Dossenheim population (Germany) after chilling for a period ranging from 2 to 8.5 months

Source of variation	β	SE	Exp (*B*)	*P*
Photoperiod				$P < 0.001$
24L:00D	0.493	0.252	1.638	$P = 0.051$
16L:08D	1.443	0.240	4.231	$P < 0.001$
08L:16D	0.303	0.255	1.354	$P = 0.235$
Chilling period	0.605	0.036	1.830	$P < 0.001$
Chilling period × photoperiod				$P < 0.001$
Chilling period × 24L:00D	−0.091	0.050	0.913	$P = 0.068$
Chilling period × 16L:08D	−0.429	0.046	0.651	$P < 0.001$
Chilling period × 08L:16D	−0.052	0.051	0.950	$P = 0.308$

Throughout chilling period, pupae were exposed to continuous light (24L:00D) and dark (00L:24D) conditions as well as to short (08L:16D) and long (16L:08D) photoperiod regimes. Dark conditions form the baseline.

Table 2. Post-winter development (days ± SE) of *R. cerasi* males and females from Dossenheim population (Germany)

	Post-winter development (days)			
	Males		Females	
Photoperiod	*N*	Mean ± SE	*N*	Mean ± SE
24L:00D	404	21.7 ± 0.2	385	20.5 ± 0.2
		(15, 39)		(12, 41)
16L:08D	177	22.3 ± 0.4	136	21.7 ± 0.4
		(15, 40)		(15, 33)
08L:16D	383	22.4 ± 0.2	423	21.3 ± 0.2
		(17, 47)		(15, 42)
00L:24D	385	22.0 ± 0.2	345	21.1 ± 0.2
		(17, 38)		(15, 33)

We used lots of pupae that yielded >60% adult (second period pupae) maintained at 4 ± 1°C for various time intervals before being transferred to room temperature for adult emergence. Throughout chilling period, pupae were exposed to continuous light (24L:00D) and dark (00L:24D) conditions as well as to short (08L:16D) and long (16L:08D) photoperiod regimes. The range is given in parenthesis.

developmental time for females (table 2). For all treatments no adults emerged after chilling for a period of only 2 months and females emerged earlier than males. Cox regression analysis revealed that both photoperiod and sex were significant predictors of post-winter development of *R. cerasi* pupae (table 3).

Effect of relative humidity on diapause termination and post-winter development

Diapause termination

After chilling emergence rates reached high levels (>60%) for (i) pupae that remained under medium and high relative humidity for 4 months, and (ii) pupae exposed to low relative humidity for 4.5 months (fig. 2). Binary logistic regression analyses revealed that only chilling period ($\chi^2 = 718.540$, df = 2, $P < 0.001$) was a significant predictor of the proportion of pupae giving adults, as opposed to relative humidity ($\chi^2 = 0.514$, df = 2, $P = 0.773$).

Table 3. Variables of the Cox regression model exploring the effects of photoperiod and sex on the duration of the post-winter development of *R. cerasi* pupae from Dossenheim population (Germany)

Source of variation	β	SE	Exp (*B*)	*P*
Photoperiod				$P = 0.013$
24L:00D	0.067	0.052	1.069	$P = 0.193$
16L:08D	−0.105	0.068	0.900	$P = 0.121$
08L:16D	−0.074	0.051	0.928	$P = 0.149$
Sex	0.225	0.039	1.253	$P < 0.001$

We used lots of pupae that yielded >60% adult (second period pupae) which maintained at 4 ± 1°C for various time intervals before being transferred to a climate chamber for adult emergence. Throughout chilling period, pupae were exposed to continuous light (24L:00D) and dark (00L:24D) conditions as well as to short (08L:16D) and long (16L:08D) photoperiod regimes. Dark conditions and males form the baseline.

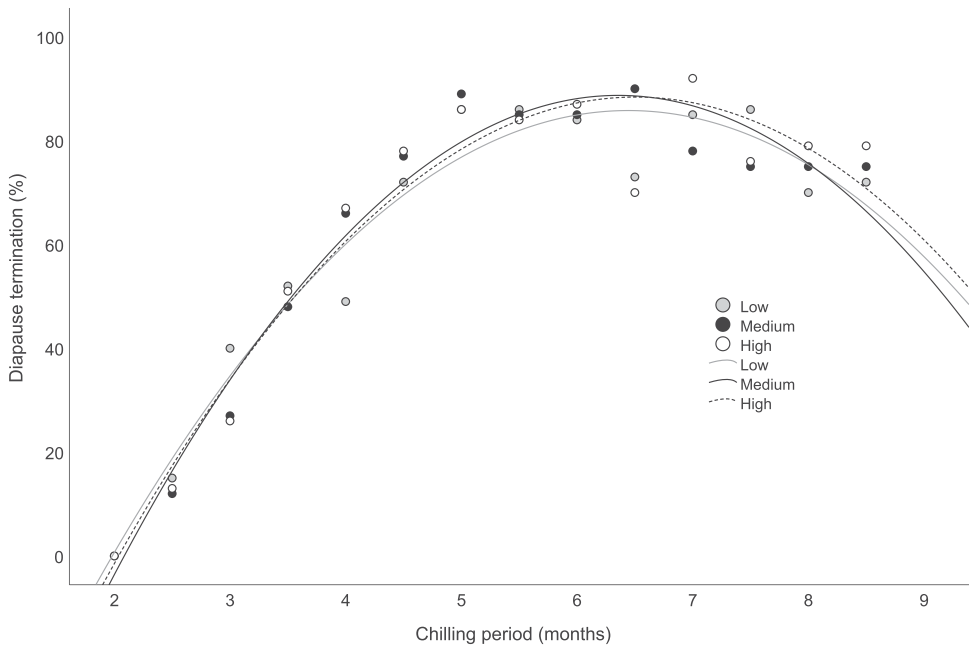

Figure 2. Diapause termination of *R. cerasi* pupae from Dossenheim population (Germany) after chilling for a period ranged from 2 to 8.5 months. During chilling period, pupae were exposed to: (a) low relative humidity ($y = -1.0776x^2 + 21.311x - 19.566$, $R^2 = 0.9474$), (b) medium relative humidity ($y = -1.2157x^2 + 23.62x - 26.011$, $R^2 = 0.9624$) and (c) high relative humidity ($y = 1.1065x^2 + 22.157x - 22.533$, $R^2 = 0.9349$).

Post-winter developmental time

For males, the average duration of post-winter developmental period of pupae that were exposed to low, medium and high relative humidity during chilling ranged (a) from 22 ± 0.3 to 39 ± 1.5 days, (b) from 21 ± 0.3 to 41 ± 0.9 days and (c) from 21 ± 0.2 to 39 ± 1.9 days, respectively. For females, the average duration of post-winter developmental period of pupae that were exposed to low, medium and high relative humidity during chilling ranged (a) from 20 ± 0.3 to 38 ± 2.2 days, (b) from 20 ± 0.2 to 37 ± 1.6 days and (c) from 20 ± 0.2 to 35 ± 0.9 days, respectively. For all treatments, no adults emerged after chilling for a period of only 2 months (Supplementary Material, tables S5–S7, fig. S2).

After the peak of adult emergence (60%), high relative humidity during chilling stimulated the fastest post-winter developmental time for both males and females (≈22 days). However, the post-winter developmental period for females and males remained short under low relative humidity conditions (40% RH) as well (table 4). In general, females emerged earlier than males. However, sex differences in post-winter developmental time were limited for adults emerged from pupae that were exposed to high relative humidity during chilling. Cox regression revealed that both relative humidity and sex were significant predictors of post-winter development of *R. cerasi* pupae (table 5).

Table 4. Post-winter development (days ± SE) of *R. cerasi* males and females from Dossenheim population (Germany)

	Post-winter development (days)			
	Males		Females	
Photoperiod	*N*	Mean ± SE	*N*	Mean ± SE
Low humidity	345	23.2 ± 0.2	369	21.7 ± 0.2
		(1736)		(15, 34)
Medium humidity	398	23.3 ± 0.2	397	22.4 ± 0.2
		(18, 37)		(17, 36)
High humidity	323	22.0 ± 0.2	408	21.5 ± 0.2
		(18, 36)		(16, 36)

We used lots of pupae that yielded >60% adult (second period pupae) maintained at 4 ± 1°C for various time intervals before being transferred to a climate chamber for adult emergence. Throughout chilling period, pupae were exposed to low, medium and high relative humidity conditions.

Discussion

Our data revealed that the response of the *R. cerasi* pupae to photoperiod and relative humidity for concluding obligatory dormancy schedules differs between diapause termination and quiescence post chilling development. Together with chilling duration (under high humidity), photoperiod regulates diapause termination of *R. cerasi* pupae. On the other hand, different relative humidity regimes had no effect on diapause termination rates as revealed by adult emergence rates. Specifically, pupae from Dossenheim require at least 4–4.5 months under chilling in order to reach peak adult emergence rates (>60% of pupae to give adults), regardless of the photoperiod or relative humidity regime. On the other hand, post-winter developmental rates of pupae that were incubated at (optimum) high temperatures were affected by both relative humidity and photoperiod. High relative humidity or light conditions (24L:00D) were found to accelerate post-winter development of *R. cerasi* pupae, regardless of sex. Additionally, post-winter development of females remains short under medium relative humidity. Regardless of the photoperiod or humidity treatment, females completed post-winter development faster and thus emerged earlier than males. This result is in line with previous studies on *R. cerasi* populations (Baker and Miller, 1978; Moraiti et al., 2017).

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Table 5. Variables of the Cox regression model exploring the effects of relative humidity and sex on the duration of the post-winter development of *R. cerasi* pupae from Dossenheim population (Germany)

Source of variation	β	SE	Exp (B)	*P*
Relative humidity				$P < 0.001$
Low	−0.167	0.053	0.846	$P = 0.002$
Medium	−0.269	0.052	0.764	$P < 0.001$
Sex	0.243	0.043	1.275	$P < 0.001$

We used lots of pupae that yielded >60% adult (second period pupae) which maintained at 4 ± 1°C for various time intervals before being transferred to a climate chamber for adult emergence. Throughout chilling period, pupae were exposed to low, medium and high relative humidity conditions. Males that remain in high humidity form the baseline.

Photoperiod effects on diapause traits

Low temperature (winter chilling) is frequently the most important environmental signal for diapause termination in insects of the temperate zone (Tauber *et al*., 1986; Zhou *et al*., 2016). For *R. cerasi*, temperatures ranging from 3 to 10°C have proven to be optimal for pupae diapause termination. Populations from warmer habitats respond adaptively to higher temperatures within the above range. The optimum chilling period for diapause termination of *R. cerasi* pupae is population-specific in order to ensure timely adult emergence with host fruit availability at a local scale (Moraiti *et al*., 2014). For sweet cherry cultivars chilling requirements for overcoming endodormancy are specific for each genotype and therefore determine geographic distribution of sweet cherry cultivars. For example, the earlier-flowering cultivars are those with the lowest chilling requirements and are expected to be cultivated in warmer areas (Fadón *et al*., 2007; Castède *et al*., 2014). Additionally, a minimum cold period (winter chill) is required before spring heat (forcing) can become effective (Heide, 2008; Kaufmann and Blanke, 2019). In line with chilling requirements of sweet cherry trees, *R. cerasi* pupae regardless of the other stimuli (photoperiod, humidity) did not yield adults after chilling for only 2 months at optimal low temperatures.

Besides chilling, our results revealed that the interaction between the photoperiod and chilling duration (at optimum low temperatures for diapause termination) was also a significant predictor for diapause termination of *R. cerasi* pupae. Pupae that terminated diapause under long photoperiod conditions exhibited a declining trend in adult emergence rates after the peak of diapause termination. Even though, in the current study, we did not examine the status of the remaining pupae (dead or overlaying pupae that enter prolonged dormancy), our previous study on diapause patterns of Dossenheim pupae revealed that the numbers of overlaying pupae increase after 6.2 months under similar chilling conditions while emergence rates decline (Moraiti *et al*., 2014). Recently, long photoperiod and continuous illumination under warm conditions at the pupal stage found to extend the dormancy period and increased the proportion of overlaying *Rhagoletis pomonella* pupae from late-fruiting hawthorn Mexican populations (Rull *et al*., 2019*a*), despite the fact that previous studies with North American *R. pomonella* populations found the larval but not the pupal as the sensitive stage to photoperiod (Prokopy, 1968). Indeed, North American *R. pomonella* larvae exposed to continuous light and high temperatures become 100% nondormant (Prokopy, 1968). Given that *R. cerasi* pupae undergo an obligatory diapause and thus photoperiod has no effect on diapause induction, diapause intensity was not expected to be affected by photoperiod, which is usually reported in species following a photoperiod-inducing facultative diapause (Tauber and Tauber, 1972; Nakamura and Numata, 2000). Whenever diapause termination is regulated by both low temperature and photoperiod, photoperiodic responses to diapause termination can be highly temperature dependent. This suggests that low temperatures remain the key factor for terminating diapause while long daylength has a valid role only in promoting the uniform diapause termination of individuals in a population (Liu *et al*., 2017). In addition, diapause response to both photoperiod and temperature is likely to be genetically different among geographical isolated populations that are located at different latitudes. For example, diapause termination of the multivoltine moth *Helicoverpa armigera* (Lepidoptera: Noctuidae) is highly sensitive to photoperiod in northern populations and temperature dependent in southern populations (Chen *et al*., 2013). However, Filchak *et al*. (2001) found no effect of photoperiod on the genetics of *R. pomonella*. Further studies involving populations from different, distant, geographic areas are required to fully elucidate photoperiodic responses of *R. cerasi* pupae for diapause termination.

Photoperiod is a significant predictor of post-diapause developmental rates of many insects, including *Dendrolimus punctatus* (Lepidoptera: Lasiocampidae) (Zeng *et al*., 2013), *Cydia pomonella* (Lepidoptera: Tortricidae) (Liu *et al*., 2017) and *Laodelphax striatellus* (Hemiptera: Delphacidae) (Wang *et al*., 2014). In most cases, long daylength has a valid role in promoting the uniform diapause termination of individuals in a population. However, in our study, light conditions, as opposed to long daylength, seem to accelerate emergence of *R. cerasi* adults. Regarding other temperate *Rhagoletis* species, photoperiod, to the best of our knowledge, remain an unexplored factor regarding post-diapause development but other environmental factors, such as latitude and pre-chill duration, have been found to affect the post-diapause development. Specifically, an increased pre-chilling period at room temperature resulted in increased thermal requirement of *Rhagoletis completa* pupae (Emery and Mills, 2019*a*), while latitude is suggested to have a negative effect on the thermal requirements of both *Rhagoletis mendax* and *R. pomonella* (Dambroski and Feder, 2007) as well as *R. completa* pupae (Emery and Mills, 2019*a*).

Relative humidity effects on diapause traits

For tephritids pupating in the soil, substrate moisture may influence pupae survival and emergence. Even though humid environments are known to increase survival of *R. cerasi* and *R. pomonella* pupae (Wakie *et al*., 2018; Rull *et al*., 2019*b*), our results revealed that humidity had no influence on diapause termination of *R. cerasi* pupae. Response to substrate moisture has been found to be highly variable within *Rhagoletis*. For instance, *Rhagoletis indifferens* seems to be tolerant to a wide range of soil moisture regimes since adult emergence rates were found to be high (≥60%) under both dry and moist conditions (Yee, 2013). On the other hand, dry soil and medium to low relative humidity (≤60%) prevented the emergence of adults of the apple maggot fly, *R. pomonella* (Trottier and Townshend, 1979), while 80 and 100% RH resulted in 81 and 70% emergence, respectively (Neilson, 1964). For the walnut husk maggot fly, *Rhagoletis suavis*, 40% RH resulted in 15% adult emergence, whereas those of 90 and 100% resulted in 50–60% adult emergence (Beck, 1932). Considering the above findings, it seems that a species-specific response of *Rhagoletis* pupae to humidity regimes for yielding adults exists.

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On the other hand, our results reveal that relative humidity affects the post-winter development of *R. cerasi* pupae. Specifically, high relative humidity accelerates post-winter developmental rates of pupae for both sexes. High relative humidity is suggested to benefit adult insect emergence by reducing the risk of desiccation of soft-bodied adults (Yee, 2013). In addition, emergence of *R. cerasi* adults often starts after a rainy period which increases soil penetration (Wiesmann, 1933). Rainfall and soil moisture were found to reduce the thermal requirements of pupae of *R. pomonella* (Smith and Jones, 1991), which is less tolerant of low relative humidity than pupae of *R. indifferens* (Yee, 2013). Even though rainfall during months preceding the first adult emergence can accelerate the timing of *R. indifferens* adult emergence (Song *et al.*, 2003), flies can also emerge earlier when pupae are located in a relatively dry soil as long as relative humidity is high. This implies that relative humidity rather than soil moisture is the key factor regulating adult emergence rates in this species (Yee, 2013). Additional field studies revealed that *R. completa* adult emergence, in walnut orchards in California, was neither affected by spring nor by winter precipitation levels (Emery and Mills, 2019*b*). It seems therefore that soil humidity that is not always related to the precipitation level and/or soil moisture can serve as a reliable predictor of the post-diapause development of *Rhagoletis* sp. Indeed, recent studies revealed that humidity at 5 cm beneath the surface of both bare and grass-covered soils (where most *Rhagoletis* pupate) remained >60%, including summers, regardless of the irrigation status (Yee and Chapman, 2018). Thus, soil humidity remains sufficiently high even under low soil moisture conditions that are likely to be met in rainfed orchards during spring and summer.

Overall, our results revealed that *R. cerasi* pupae responds positively to high humidity for concluding post-winter development but the diapause termination processes remained unaffected. Previous studies confirmed that temperature is a significant predictor of both diapause termination and post-diapause development of *R. cerasi* pupae (Moraiti *et al.*, 2014; Moraiti and Papadopoulos, 2017). Temporal variability of soil temperatures regulates diapause processes of *R. cerasi* pupae that overwinter within 5 cm of the soil surface, beneath host plants. However, moisture reduces the temporal variability of soil temperatures, which is expected to vary under both high temperature and low humidity conditions due to increased vapour pressure deficit (VPD) (Ashcroft and Gollan, 2013). As a result, substantial fluctuation in soil temperatures is likely to take place in warm periods of the year that coincide with the post-diapause development period of *R. cerasi* pupae (Zhang *et al.*, 2016). On the contrary, in winter when diapause termination is progressing, VPD remains low, and soil temperature fluctuations are buffered. In addition, rainfall reduces the spatial variability in soil moisture (Buttafuoco and Castrignanò, 2005) leading to temperature patterns that are determined largely by elevation (Ashcroft and Gollan, 2012). It is therefore plausible to suggest that humidity has an impact on post-diapause development of *R. cerasi* pupae through regulating spring soil temperatures fluctuations, as opposed to diapause termination that is mainly driven by spatial variability of chilling temperatures.

Conclusions

In sum, our data show that diapause termination of *R. cerasi* pupae is affected by low temperature treatments and photoperiod, whereas both relative humidity and photoperiod regimes have an impact on post-winter developmental time of both sexes, regardless of the high temperatures that prevail during this last part of pupae development. Our results underscore the need to thoroughly address the geographical variation in the response of different diapause stages to combinations of environmental factors such as temperature, photoperiod and relative humidity in order to determine plastic and adaptive dormancy responses in *R. cerasi*. An in-depth understanding of the impact of environmental factors on diapause development processes of *R. cerasi* pupae from populations located at ecologically and latitudinally different habitats will enable better prediction of population dynamics, and consequently more efficient pest management, especially under the projected changes in temperature and precipitation levels due to climate warming.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0007485320000073.

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