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SHORT COMMUNICATION

Mating still disrupted: Future elevated CO_2 concentrations are likely to not interfere with *Lobesia botrana* and *Eupoecilia ambiguella* mating disruption in vineyards in the near future

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ABSTRACT

The successful, area-wide application of the mating disruption (MD) technique, an insect sex pheromone-based biotechnological pest control method, against the European grapevine moth *Lobesia botrana* and the European grape berry moth *Eupoecilia ambiguella*, has led to drastic reductions in insecticide application in vineyards. However, since insect pheromone perception and emission can be affected by abiotic conditions, the future success of MD may be affected by climate change. At the same time, politics and society are calling for drastic and sustainable reductions in pesticide application, making highly specific, efficient, and environmentally friendly pest control techniques like MD more important than ever. To anticipate whether climate change factors will interfere with the MD of *L. botrana* and *E. ambiguella* in vineyards, we conducted field experiments in the Geisenheim VineyardFACE (Free-Air Carbon dioxide Enrichment) facility. The insects were raised at ambient or elevated temperatures in the lab and male moths were released in cages installed in the VineyardFACE facility. Trap recapture rates obtained by pheromone lures or female moths under elevated or ambient CO_2 in areas with and without MD were evaluated. Our results did not indicate a reduced efficacy of *L. botrana* or *E. ambiguella* MD at elevated CO_2 concentrations, irrespective of the temperature the moths were raised under. From a practical point of view—and especially from an ecological one—our results are good news. They indicate that MD will not be negatively affected by future elevated CO_2 concentrations.

KEYWORDS: RAK, (E,Z)-7,9-dodecadien-1-yl acetate, FACE facility, IPM, viticulture, Lepidoptera, Tortricidae

INTRODUCTION

Mating disruption (MD) is a biotechnological pest control method from the integrated pest management (IPM) toolbox, based on the area-wide application of insect sex pheromones in the field to prevent males from locating females and, hence, prevent reproduction (Cardé, 2021). Unlike many synthetic chemical pesticides, this highly species-specific method is user-friendly and non-toxic for humans and other non-target species (Lucchi *et al*., 2018; Witzgall *et al*., 2010).

In Central European viticulture, MD is currently applied against two Lepidopteran pest species, the European grapevine moth, *Lobesia botrana* Denis & Schiffermüller 1775 and the European grape berry moth, *Eupoecilia ambiguella* Hübner 1796 (both Lepidoptera: Tortricidae). These are serious pests in European vineyards, with *L. botrana* exhibiting a large invasive potential worldwide (Gutierrez *et al*., 2012; Ioriatti *et al*., 2011). Uncontrolled, both species can inflict substantial economic damage on table and wine grapes (Ioriatti *et al*., 2011; Moschos, 2006). Traditionally, grapevine or grape berry moth control would consist of two to three applications of insecticides, which can, in many cases, be completely replaced by MD (Lucchi and Benelli, 2018), illustrating the technique's tremendous potential for sustainable and efficient pest control. Since the first results on MD against *L. botrana* were published in 1977 (Roehrich *et al*., 1977), its application has been refined and successfully established in vineyards around the world (Ioriatti *et al*., 2011). In the European Union, MD was applied on approximately 300,000 hectares of vineyards in 2019 (Benelli *et al*., 2019).

Pheromones are messenger compounds that mediate communication between individuals of the same species. Female *L. botrana* and *E. ambiguella* moths produce a pheromone blend in their abdominal gland that they release during their "calling behaviour" to attract males (Ioriatti *et al*., 2011). The male moth antennae and their finely tuned olfactory system perceive these pheromone blends and are able to distinguish single molecules over great distances. Upon perception, the olfactory signals are translated into behaviour, and the male moths follow the pheromone plume towards the source to find suitable mates. A sophisticated olfactory system and stimuli like sex pheromones are key elements in the survival and reproduction of insects (Leal, 2013). Commercially available pheromone dispensers used for MD of these two species contain the main active components of the respective sex pheromone blends: (*Z*)-9-dodecen-1-yl acetate for *L. botrana* and (*E*,*Z*)-7,9-dodecadien-1-yl acetate for *E. ambiguella*.

Temperature, atmospheric ozone, and CO_2 concentration are central impact factors of climate change (IPCC, 2021). These abiotic factors can affect insect pheromonal communication by altering their production, emission, signal dispersal, perception, and/or behavioural response, potentially reducing male attraction (Boullis *et al*., 2016; Choi *et al*., 2018; Groot and Zizzari, 2019). Accordingly, pheromone-mediated communication between insects is vulnerable to climate change (Boullis *et al*., 2016; Groot and Zizzari, 2019). However, the effect of elevated CO_2 concentration on pest control has received less attention in climate change research than, for instance, elevated temperature. Especially studies under realistic conditions are rare. While studying the impact under realistic conditions is not trivial, the Geisenheim VineyardFACE (Free-Air Carbon dioxide Enrichment) facility offers such an opportunity. It is installed in a vineyard where two grapevine cultivars, 'Riesling' and 'Cabernet-Sauvignon', are cultivated under ambient (ca. 411 ppm) and elevated (ca. 508 ppm) CO_2 concentrations. The elevated concentration represents a near future scenario, expected in 2050 or earlier (Ciais *et al*., 2013)

Considering the ambitious and important goals of the European Green Deal and the decreasing number of insecticides available, it is crucial to ensure that environmentally friendly pest control techniques like MD will be working reliably under future climatic conditions. Therefore, using the Geisenheim VineyardFACE facility, we investigated the following hypotheses:

1) Elevated CO_2 concentration affects male *L. botrana* and *E. ambiguella* pheromone perception leading to reduced attraction towards pheromone sources.

2) Development under elevated temperature affects male *L. botrana* pheromone perception and/or female pheromone production, leading to reduced male attraction towards pheromone sources.

MATERIAL AND METHODS

1. Geisenheim VineyardFACE facility

The Geisenheim VineyardFACE facility was established in 2011 at Geisenheim University, Germany (49°59′N, 7°57′E; 96 m above sea level) and consists of six ring-frame structures, each with an inner diameter of 12 m. Three rings are under elevated CO_2 (eCO_2, ca. 508 ppm) and three under ambient CO_2 (aCO_2, ca. 411 ppm) concentration. Each ring contains seven rows of grapevine *Vitis vinifera* L. 'Riesling' and 'Cabernet-Sauvignon' plants, with a total of 32 grapevine plants per variety in each ring. For a detailed description of the Geisenheim VineyardFACE facility, see publications by Reineke and Selim (2019) and Wohlfahrt *et al*. (2018). The vineyard is managed according to the principles of good agricultural practice and integrated pest management in viticulture. Recapture experiments were conducted in 2020 from May 18–27th and June 26th–July 7th (*L. botrana* and *E. ambiguella*). In 2021, experiments were conducted from July 28th–August 23rd (*L. botrana*). During these experimental periods, grapevine plants were in the developmental stages BBCH 55-57, BBCH 73-77, and BBCH 75-81 after Lorenz *et al*. (1995). Weather conditions and CO_2 concentrations during the experimental periods are shown in Supplementary Table 1.

2. Insects

The *L. botrana* and *E. ambiguella* colonies were maintained at Geisenheim University, Geisenheim, Germany, and

TABLE 1. Thermal conditions (°C) of the two daily fluctuating temperature regimes: the current ('ambient') and the future regime ('elevated'). Temperatures are based on the publication of Iltis *et al.* (2018). The elevated regime represents modelled temperatures for 2081–2100 in Dijon, Burgundy, France. Relative humidity was 65 %, and light intensity was 650 lx.

time of day (h)	light	temperature	
		ambient	elevated
7–11	on	18	22.9
11–15	on	22	27.8
15–19	on	25	30.5
19–23	on	23	28.3
23–3	off	19	24.2
3–7	off	16	21.4

regularly supplemented with additional genotypes either collected in local vineyards or received from other laboratory strains outside Geisenheim. Larvae were cultured in groups in plastic boxes (20 × 15 cm and 9 cm high) in an insect rearing room (24 ± 1 °C; 40 ± 12 % relative humidity; light/dark photoperiod: 16:8 h) and were fed ad libitum with a modified semi-synthetic diet according to the general-purpose diet of Singh and Moore (1985). Pieces of corrugated cardboard were offered for pupation. Pupae were then removed from the crevices, sexed under a binocular (LeicaR, EZR4 W), and stored individually in small plastic containers. They were inspected daily to monitor adult emergence. To test hypothesis 2, the effect of temperature during rearing was studied with *L. botrana*, comparing two daily fluctuating thermal regimes designed to simulate current ('ambient') and predicted future ('elevated') thermal conditions. Temperatures of the climate chambers (Memmert HCP 240 Humidity Chamber, 241 L; 115 VAC) were based on the publication of Iltis *et al.* (2018) for comparability purposes. Both thermal regimes were composed of six segments, each lasting 4 h, 65 % relative humidity, and a light/dark photoperiod of 16:8 h (650 lx; for details, please see Table 1).

3. Field experiments

To assess the success of MD field experiments were performed using a modified cage method (Hoffmann and Doye, 2017). Four nylon mesh cages (Figure 1; BugDorm NHBS, Bonn, Germany) with a size of 47.5 × 47.5 × 93 cm and a mesh size of 650 µm were installed in each elevated and ambient ring of the FACE facility (Figure 2) as well as in two external control vineyards, one with and one without MD. In the second year, experiments were performed only in the non-disrupted external control vineyard. In all FACE rings and in the disrupted vineyards, RAK® 1+2 dispensers containing the sex pheromone components (Z)-9-dodecen-1-yl acetate and (E,Z)-7,9-dodecadien-1-yl acetate (BASF, Ludwigshafen, Germany) were distributed along rows with a density of 500 dispensers per hectare. For the recapture experiments in the field, we used ten male moths and one synthetic pheromone lure in a delta trap (first year, 2020; Temmen, Hattersheim, Germany) or ten male moths and two females in a small metal cage (second year, 2021; traps with glue; Figure 1) per BugDorm. Moths used for the experiments were 24–72 h old. Two days after release, the numbers of trap-captured and non-captured males were counted.

In the first year, all tested moths were raised in the insect-rearing room under constant temperature. In the second year, half of the moths had been raised under ambient and the other half under elevated temperature, as described in Table 1. For an overview of the tested treatments in both years, see Table 2. In the first year, twelve replicates per treatment and moth species were obtained for the first-generation flight period, and 29–33 replicates for the second-generation flight period. In the second year, ten replicates per treatment were obtained for the second-generation flight period.

4. Statistics

The impact of elevated atmospheric CO_2 concentration on the efficacy of mating disruption in the different areas was evaluated using one-factorial generalized linear models (GLM) of the binomial family with logit-link. For multiple comparisons of means, Tukey contrasts (general linear hypotheses and multiple comparisons: glht, multcomp package) (Hothorn *et al*., 2008) were used. The interaction between temperature and CO_2 was evaluated using two-factorial GLM of the binomial family with logit-link and glht with Tukey contrasts for multiple comparisons of means. All evaluations were done using R version 4.1.1 (RStudioTeam, 2020), adopting a significance level of $\alpha = 0.05$.

RESULTS

1. Recapture rates with synthetic pheromone sources

Using synthetic pheromone lures, recapture rates of *L. botrana* and *E. ambiguella*, respectively, did not differ significantly between elevated and ambient atmospheric CO_2 concentrations in the VineyardFACE facility (Figure 3). During the first-generation flight period, the highest recapture

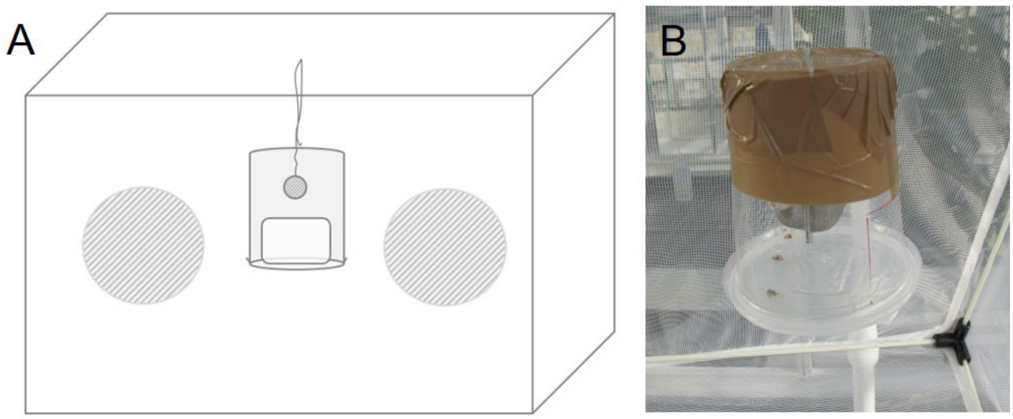

FIGURE 1. Experimental device in the second year, using female moths as pheromone sources.

The BugDorm (A) includes a glue trap under two female *L. botrana* moths that were placed in a small metal cage, as displayed in photo (B). The hatched circles indicate sleeve openings in the BugDorm. Figure by Anna Rummel, photo by Mirjam Hauck.

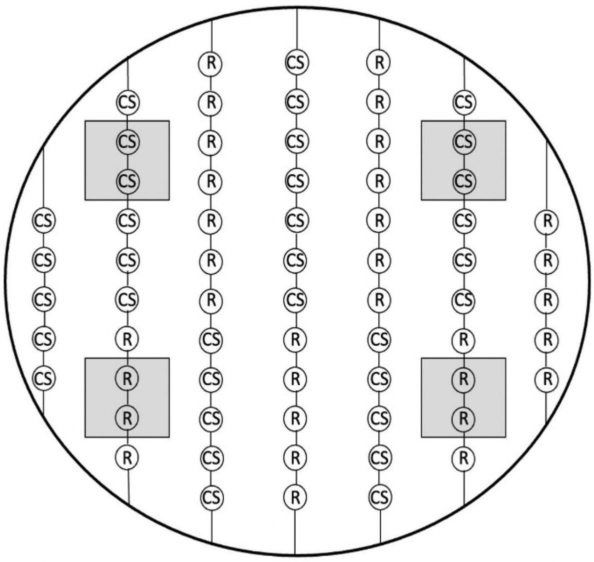

FIGURE 2. Experimental setup in the VineyardFACE facility.

Grapevine plants of the cultivars 'Riesling' (R) and 'Cabernet-Sauvignon' (CS) are planted in rows inside the ring structure. The VineyardFACE facility comprises six such ring structures, three with ambient CO_2 concentration, three with elevated CO_2 concentration (20 % higher). The grey squares indicate the position of the four BugDorms in the recapture experiments. Figure by Anna Rummel.

rates of males were obtained in areas without mating disruption ('external control_MD-'; Figure 3; A: $\chi^2_3 = 57.5$, $p < 0.0001$, B: $\chi^2_3 = 40.4$, $p < 0.0001$). They were significantly higher than the recapture rates in the MD-treated VineyardFACE facility and the external control_MD+. Recapture rates did not differ significantly between the MD-treated VineyardFACE facility and the external control_MD+. During the second-generation flight periods highest recapture rates of males were obtained in areas without mating disruption ('external control_MD-'; Figure 3 C: $\chi^2_3 = 29.7$, $p < 0.0001$), D: $\chi^2_3 = 51.2$, p < 0.0001). They were significantly higher than the recapture rates in the MD-treated VineyardFACE facility but not than those obtained in the external control_MD+. Regarding both *E. ambiguella* and *L. botrana*, recapture rates were not significantly different between the MD-treated ('external control_MD+') and not treated ('external control_MD-';) external control areas.

2. Recapture rates with female moths as pheromone sources

Using females as pheromone sources, recapture rates of *L. botrana* did not differ significantly between elevated and ambient atmospheric CO_2 concentrations in the VineyardFACE facility – independent of the temperature the moths were reared at (Figure 4; temperature: $\chi^2_1 = 0$, $p = 1$; CO_2: $\chi^2_2 = 50.4$, p < 0.0001; CO_2 * temperature: $\chi^2_2 = 8.7$, p = 0.01). The highest recapture rates were obtained in the non-disrupted external control area (external control_ MD-). The difference in recapture rates between the eCO_2

TABLE 2. Overview of the experimental setup in the field experiments. aCO_2: ambient CO_2 concentration (ca. 411 ppm), eCO_2: elevated CO_2 concentration (ca. 508 ppm), MD: mating disruption. FACE: Free-Air Carbon dioxide Enrichment facility. External control: vineyard without FACE and with (MD+) or without (MD-) MD.

Year	Flight period	Treatment	Pheromone source	Moth species	CO_2 concentration	MD applied	Temperature during moth development
2020	1st generation	aCO_2	synthetic lures	*L. botrana*	ambient (FACE)	yes	standard
		eCO_2			elevated (FACE)	yes	
		external control_MD+			ambient	yes	
		external control_MD-			ambient	no	
		aCO_2	synthetic lures	*E. ambiguella*	ambient (FACE)	yes	standard
		eCO_2			elevated (FACE)	yes	
		external control_MD+			ambient	yes	
		external control_MD-			ambient	no	
	2nd generation	aCO_2	synthetic lures	*L. botrana*	ambient (FACE)	yes	standard
		eCO_2			elevated (FACE)	yes	
		external control_MD+			ambient	yes	
		external control_MD-			ambient	no	
		aCO_2	synthetic lures	*E. ambiguella*	ambient (FACE)	yes	standard
		eCO_2			elevated (FACE)	yes	
		external control_MD+			ambient	yes	
		external control_MD-			ambient	no	
2021	2nd generation	aCO_2	female moths	*L. botrana*	ambient (FACE)	yes	standard
		eCO_2			elevated (FACE)	yes	
		external control_MD-			ambient	no	
		aCO_2	female moths		ambient (FACE)	yes	elevated
		eCO_2			elevated (FACE)	yes	
		external control_MD-			ambient	no	

VineyardFACE rings and the non-disrupted external control area is only approaching significance among moths from the standard temperature regime (p = 0.05, z = 2.80; Figure 4).

DISCUSSION

Our results showed that the attraction of male *L. botrana* and *E. ambiguella* moths to the respective female sex pheromone was not impaired by elevated atmospheric CO_2 concentration. Furthermore, the attraction of male *L. botrana* moths towards the sex pheromone was not reduced when insects developed under elevated temperatures. We can neither confirm our hypotheses 1 nor 2. The obtained results did not provide any indication for reduced efficacy of future *L. botrana* and *E. ambiguella* mating disruption in vineyards due to elevated CO_2 concentration.

In contrast, Choi *et al*. (2018) did find a decreasing male response to female pheromones under elevated CO_2 concentrations when studying another Lepidopteran species, the cotton bollworm *Helicoverpa armigera*. While the observed effects may, of course, be species-specific, the differences in results may also be due to the higher CO_2 concentration the authors used in their study (up to 1000 ppm). Furthermore, the authors observed an increased production of female pheromones under elevated CO_2, potentially offsetting the decreased response in males. In the present study, we did not investigate the male response or female pheromone production in lab experiments. However, an increased female pheromone production may well compensate for a decreased male pheromone sensitivity (Choi *et al*., 2018) and result in no discernable net effect of elevated CO_2 concentrations on trap catches in the field.

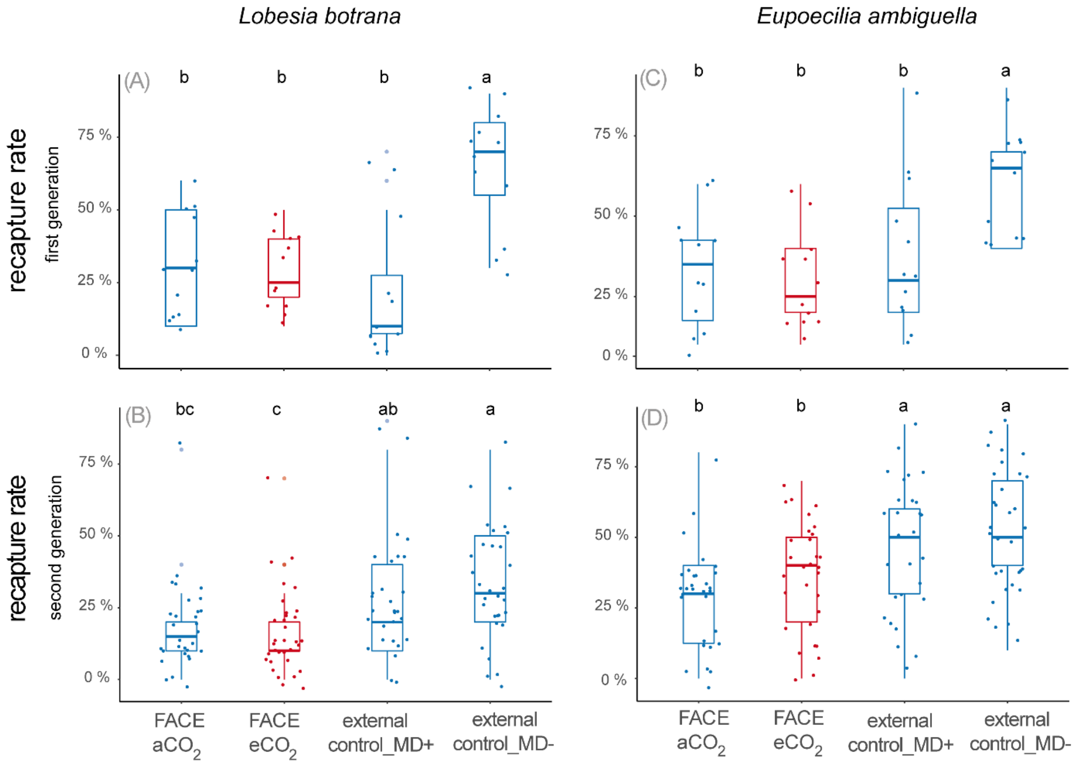

FIGURE 3. Recapture rates of male *L. botrana* (A, B) and *E. ambiguella* (C, D) in traps baited with synthetic pheromone lures during the first (A, C) and second (B, D) flight periods, respectively.

Recapture rates were assessed under ambient and elevated CO_2 concentration in the VineyardFACE facility under mating disruption and two external control areas under ambient CO_2, with ('control_MD+') and without ('control_MD-') mating disruption. Identical letters indicate that values did not differ significantly.

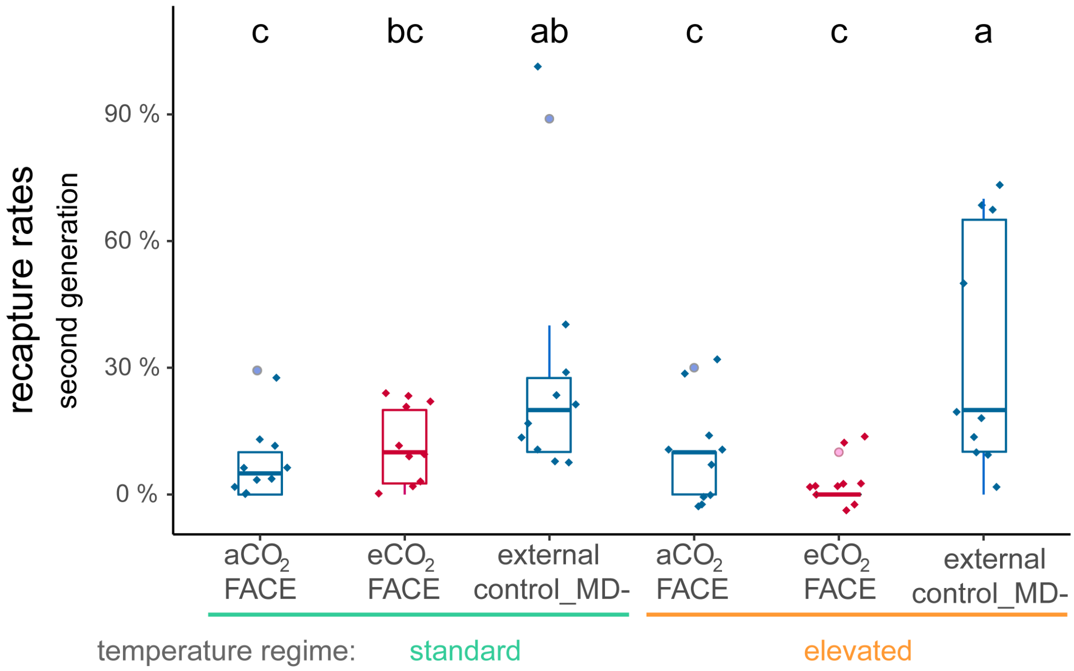

FIGURE 4. Recapture rates of male *L. botrana* in traps baited with female moths.

Both male and female moths were reared at two different temperature regimes. Recapture rates were assessed under ambient and elevated CO_2 concentration in the VineyardFACE facility under mating disruption and one external control area under ambient CO_2, without mating disruption (external control_MD-). Identical letters indicate that values did not differ significantly.

Recapture rates of both *L. botrana* and *E. ambiguella* during the first-generation flight period are comparable to those reported by Hoffmann and Doye (2017). It is interesting that recapture rates were very low in the eCO_2 VineyardFACE rings among moths from the elevated temperature regime. This might hint towards an interactive effect of CO_2 and temperature on male pheromone perception and/or female pheromone production. Since both males and females were reared under the same conditions, any effect could affect one or both genders. More detailed studies are necessary to determine if there is a biologically relevant impact behind this observation or if it is just natural variability. Recapture rates during the second-generation flight period showed more variance than those during the first-generation flight period. The flight period of the second generation is longer than that of the first one, and, therefore, the probability of unfavourable conditions, e.g., lower temperatures during dusk or dawn when the moths are most active, is higher. Since insects are ectotherms, their flight activity is influenced by temperature (Nation Sr, 2016), and variable temperatures can lead to variable recapture rates. Relative humidity can also influence recapture rates (Doye, 2006) and may have contributed to the different, sometimes rather low, recapture rates in our flight experiments. As a matter of fact, precipitation amounts were different during our experimental periods in May, late June, and late August (Table S1), probably also influencing recapture rates.

Unlike female moths, synthetic pheromone lures constantly emit active compounds at high concentrations. Female calling behaviour is more complex, influenced by abiotic conditions, and the emitted concentrations are lower than those from synthetic lures. However, this did not lead to apparent differences between our two experimental settings, using either females or a synthetic pheromone source. Generally, we have to bear in mind that the moths we studied came from an inbred laboratory colony, and wild populations may respond differently in some aspects.

Apart from the studied direct impact of climate change factors on the insect, they may be influenced indirectly as changing abiotic conditions can alter the host plant's nutritional quality and/or plant defence levels, possibly triggering bottom-up effects on higher trophic levels like herbivores and/or natural enemies (Han *et al*., 2019; Reineke and Thiéry, 2016). More experiments are necessary to investigate these complex interactions. Using the VineyardFACE facility, however, we were able to not only conduct our experiments under almost realistic abiotic conditions, incorporating weather variability during the respective generations' flight periods. We could moreover include potential indirect effects of elevated CO_2, mediated by potentially changed emissions of plant volatile organic compounds (VOCs). Plant VOC emission can be affected by abiotic impact factors such as CO_2 (Becker *et al*., 2015), and background odour composition can, in turn, affect moth olfactory orientation (Knudsen *et al*., 2017).

CONCLUSION

From a practical point of view—and especially from an ecological one—our results are good news. They indicate that MD will not be negatively affected by future elevated CO_2 concentrations. Furthermore, we did not detect a negative impact of elevated temperature. We have to keep in mind, though, that we did not study the immediate impact of elevated temperature during pheromone perception, only the effect during development before the perception events. Technically, experiments on the interactive effects of climate change factors are very challenging. Nevertheless, investigating these interactions is crucial to realistically anticipate the overall impact of climate change on MD to secure its future use as a sustainable pest management method.

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AUTHOR CONTRIBUTIONS

ARe, JGr, ARu, and CB designed the experiments. CB and ARu conducted the experiments and gathered the data. CB, ARu, and ARe evaluated the data. CB, JGa, JGr, ARu, and ARe wrote the manuscript. All authors read and approved the manuscript.

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