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SPECIAL ISSUE: PLANT REPRODUCTION IN A CHANGING GLOBAL ENVIRONMENT

Effects of experimental warming on floral scent, display and rewards in two subalpine herbs

Carrie Wu[1,2], John M. Powers[2,3], David Z. Hopp[2,4] and Diane R. Campbell[2,3,*]

[1]Department of Biology, University of Richmond, Richmond, VA, USA, [2]Rocky Mountain Biological Laboratory, Crested Butte, CO, USA, [3]Department of Ecology and Evolutionary Biology, University of California, Irvine, CA, USA, and [4]Department of Natural and Environmental Sciences, Western Colorado University, Gunnison, CO, USA
[*]For correspondence. E-mail drcampbe@uci.edu

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• **Background and Aims** Floral volatiles, visual traits and rewards mediate attraction and defence in plant–pollinator and plant–herbivore interactions, but these floral traits might be altered by global warming through direct effects of temperature or longer-term impacts on plant resources. We examined the effect of warming on floral and leaf volatile emissions, floral morphology, plant height, nectar production, and oviposition by seed predators.
• **Methods** We used open-top chambers that warmed plants in the field by +2–3 °C on average (+6–11 °C increase in daily maxima) for 2–4 weeks across 1–3 years at three sites in Colorado, USA. Volatiles were sampled from two closely related species of subalpine *Ipomopsis* with different pollinators: *Ipomopsis aggregata* ssp. *aggregata*, visited mainly by hummingbirds, and *Ipomopsis tenuituba* ssp. *tenuituba*, often visited by hawkmoths.
• **Key Results** Although warming had no detected effects on leaf volatiles, the daytime floral volatiles of both *I. aggregata* and *I. tenuituba* responded in subtle ways to warming, with impacts that depended on the species, site and year. In addition to the long-term effect of warming, temperature at the time of sampling independently affected the floral volatile emissions of *I. aggregata* during the day and *I. tenuituba* at night. Warming had little effect on floral morphology for either species and it had no effect on nectar concentration, maximum inflorescence height or flower redness in *I. aggregata*. However, warming increased nectar production in *I. aggregata* by 41 %, a response that would attract more hummingbird visits, and it reduced oviposition by fly seed predators by ≥72 %.
• **Conclusions** Our results suggest that floral traits can show different levels of plasticity to temperature changes in subalpine environments, with potential effects on animal behaviours that help or hinder plant reproduction. They also illustrate the need for more long-term field warming studies, as shown by responses of floral volatiles in different ways to weeks of warming vs. temperature at the time of sampling.

Key words: Experimental warming, floral morphology, floral scent, *Ipomopsis aggregata* ssp. *aggregata*, *Ipomopsis tenuituba* ssp. *tenuituba*, nectar, phenotypic plasticity, seed predation, volatile organic compound.

INTRODUCTION

Climate change is projected to increase average global surface temperature by 1.5 °C or more in the next several decades, even for low greenhouse gas emissions scenarios (Pörtner *et al.*, 2022). These increased temperatures have the potential to disrupt plant–pollinator interactions in a variety of ways, including stress damage to flowers (Inouye, 2008), changes in flowering phenology (Hegland *et al.*, 2009; CaraDonna *et al.*, 2014) that might decouple flowering and pollinator availability and changes to traits of individual flowers (Scaven and Rafferty, 2013; Descamps *et al.*, 2018). Pollinators make behavioural choices in response to floral traits, which, in turn, can affect both natural selection on those traits (reviewed by Harder and Johnson, 2009) and resource acquisition by the pollinators (Junker *et al.*, 2013). Additionally, some floral traits can also influence oviposition by predispersal seed predators (Brody, 1992; Campbell *et al.*, 2002) or floral herbivores (Sletvold *et al.*, 2015), hence warming-induced changes in these traits could impact seed predation.

One floral trait that is crucial to pollinator choice is floral scent (Majetic *et al.*, 2009; Kessler *et al.*, 2013; Byers *et al.*, 2014; Bischoff *et al.*, 2015). Flowers emit volatile organic compounds (VOCs), of which >1700 have been identified (Knudsen *et al.*, 2006), in combinations that produce characteristic scents. Despite their importance to plant–pollinator interactions (Raguso, 2008; Kantsa *et al.*, 2019; de Manincor *et al.*, 2022), little is known about how emission rates of floral VOCs respond to temperature in nature (Yuan *et al.*, 2009). Instead, studies of how plant VOCs respond to temperature have largely focused on emissions by leaves or whole plants (e.g. Guenther *et al.*, 1993; Feng *et al.*, 2019). Although studies of ≥22 species have found quantitative effects on floral volatiles in response to increasing temperature (Hansted *et al.*, 1994; Jakobsen and Olsen, 1994; Sagae *et al.*, 2008; Hu *et al.*, 2013; Farré-Armengol *et al.*, 2014, 2015; Cheng *et al.*, 2016; Zeng *et al.*, 2019; Barman and Mitra, 2021), those studies have been limited to short-term responses to a constant elevated temperature (ranging from 10 min to 7 days; Supplementary Data Table S1), with the exception of a study on *Petunia* in which the plant was exposed to differing

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day and night temperatures over a 1-month period (Cna'ani *et al.*, 2015). More complex temperature profiles that occur in nature might have different or more nuanced effects on emission of floral volatiles or effects that differ over short- and long-term temporal scales.

At very short (hourly) temporal scales, temperature at the time of emission could affect volatility of individual VOCs or rates of diffusion (Sagae *et al.*, 2008; Farré-Armengol *et al.*, 2013). For leaves, emission rates of VOCs are affected by diffusion at the leaf–air boundary formed at the stomatal opening (Niinemets *et al.*, 2004). Short-term responses of floral VOCs are likely to be more complex, because there is no single organ necessarily responsible for their emission. Floral VOCs can be emitted by any part of the flower, including the nectar (Raguso, 2004). Rates of compound synthesis typically increase with temperature up to the point of maximum synthase enzymatic activity and decline as those enzymes denature (Guenther *et al.*, 1993; Farré-Armengol *et al.*, 2015). Transcriptional changes of the plant in response to temperature change might also impact VOC emissions by altering the expression of synthase genes (Barman and Mitra, 2021).

At longer temporal scales (weeks to years), warming could influence resource acquisition by the plant, given that effects of elevated temperature on plant productivity are common (Wu *et al.*, 2011), and thereby affect the size of individual flowers that develop (Descamps *et al.*, 2018, 2021). Although emission rate seems likely to increase with flower size, demonstrated correlations between the size of individual flowers or parts of flowers and scent emission are rare (Zu and Schiestl, 2017; Campbell *et al.*, 2022*a*).

Elevated temperatures can also impact flower colour by slowing the production of anthocyanin pigments on the scale of days (reviewed by Zhao and Tao, 2015), and these changes in pigmentation could potentially affect pollinator attraction (Dudash *et al.*, 2011; Bergamo *et al.*, 2016).

We focused on a model subalpine plant species, *Ipomopsis aggregata* spp. *aggregata* (Polemoniaceae), and its congener, *I. tenuituba* ssp. *tenuituba*, to test impacts of temperature on expression of floral volatiles and other floral traits in the field. Both VOCs and the other measured traits, including corolla size, corolla colour and nectar production, influence pollinator visitation, pollination success or seed production in *Ipomopsis* (Campbell *et al.*, 1991, 1996, 2022*b*; Mitchell, 1993; Meléndez-Ackerman and Campbell, 1998; Bischoff *et al.*, 2015). Differences between these two species in floral morphology and VOCs also contribute to specialization of hummingbird vs. hawkmoth pollinators (Aldridge and Campbell, 2007; Bischoff *et al.*, 2015). Thus, any impacts of temperature on these traits have the potential to alter pollinator-mediated selection and reproductive isolation. In addition, oviposition by flies that act as predispersal seed predators is correlated with corolla size (Campbell *et al.*, 2002). Using open-top chambers (OTCs) in the field (Marion *et al.*, 1997), we examined effects of increased temperature at two temporal scales: temperature at the time of VOC measurement (hereafter, 'short-term effects') and cumulative effects over 2–4 weeks of warming (hereafter, 'long-term effects'). We asked the following questions:

1. How does emission of floral and leaf volatiles respond to temperature at two temporal scales?
2. Does warming affect inflorescence height, flower number, corolla size, nectar production and concentration, corolla colour or seed set?
3. Does warming affect the rate of oviposition on flowers and fruit damage by predispersal seed predators (Diptera: Anthomyiidae)?

MATERIALS AND METHODS

Study species

The closely related congeners *Ipomopsis aggregata* ssp. *aggregata* (Pursh) V. Grant and *I. tenuituba* ssp. *tenuituba* (Rydb.) V. Grant are distributed throughout western North America and sometimes form natural hybrids in sympatry (Grant and Wilken, 1988; Aldridge, 2005). Individuals of both *Ipomopsis* species are monocarpic perennials that typically germinate in the summer after seed production and spend 2–12+ years as a basal rosette, after which they flower during a single summer, set seed and die (Campbell *et al.*, 2008). Plants typically produce a single flowering inflorescence unless browsed, which can result in multiple inflorescences from one leaf rosette or from multiple leaf rosettes owing to browsing in an earlier year (Brody *et al.*, 2007). In both species, individual flowers remain open during both the day and night for several days before senescing.

Differences in flower colour, shape and scent contribute to pollinator-mediated reproductive isolation between the species. *Ipomopsis aggregata* is most commonly visited by hummingbirds (94 % of pollinator visits near our sites; Price *et al.*, 2005). Hummingbirds (*Selasphorus platycercus* and *Selasphorus rufus*) prefer the wider-tubed, red flowers of *I. aggregata* (Campbell *et al.*, 1997; Meléndez-Ackerman and Campbell, 1998; Campbell, 2004; Bischoff *et al.*, 2015). In contrast, hawkmoths (*Hyles lineata*) prefer indole-scented, narrow *I. tenuituba* flowers, and at night they also prefer white rather than red flowers (Campbell *et al.*, 1997; Bischoff *et al.*, 2015), leading to frequent visitation of that plant species at some sites (Aldridge and Campbell, 2007).

Predispersal seed predation from flies (*Delia* sp., Anthomyiidae) is common in both species, with 10–30 % of *I. aggregata* fruits attacked near our sites (Campbell *et al.*, 2002; Brody *et al.*, 2008; Brody and Irwin, 2012; Price *et al.*, 2021). Female flies deposit a single egg per flower between the sepals and corolla, and the larva typically consumes all of the seeds in the developing fruit before exiting as a pupa (Brody, 1997). Flies oviposit on elongated buds and open flowers (Brody and Mitchell, 1997).

Study sites

Warming studies were conducted using OTCs at three dry subalpine meadow sites in Gunnison National Forest, CO, USA, where natural *Ipomopsis* plants are abundant but hybrids do not occur (Supplementary Data Fig. S1). The two *I. aggregata* sites were located near the Rocky Mountain Biological Laboratory (RMBL). In 2018 ($n = 5$), 2019 ($n = 5$) and 2021 ($n = 9$), OTCs were placed in the Gothic Natural Area (GNA), 4.7 km north of

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RMBL on the west side of County Road 317. In 2021 ($n = 12$), OTCs were also placed in Maxfield Meadow, 1.0 km south of RMBL. In 2019 ($n = 5$) and 2021 ($n = 9$), OTCs were placed in an *I. tenuituba* site near Spring Creek (SC), located 0.5 km south-east of Mosca Campground at the junction of County Roads 744 and 748 (Bischoff *et al*., 2015). Chambers were located haphazardly within each site and typically enclosed two to five *Ipomopsis* plants with elongating inflorescences that were tagged for measurement. Flowering plants used for ambient control comparisons were tagged within 2 m of each OTC (typically, two to four plants outside each OTC). Chambers were deployed on 25 June–6 July of each year, before flower buds had elongated, meaning that warming would impact the entirety of floral development for flowers that were subsequently measured. Plants were warmed only during their flowering year, because manipulation of temperature over the long vegetative lifespan before the year of flowering was impractical.

Open-top chamber design

Temperatures were manipulated in the field using hexagonal OTCs with sloping sides, constructed from SUNTUF corrugated polycarbonate panelling (Palram Americas, Kutztown, PA, USA; following Marion *et al.*, 1997) and cable ties. Each OTC had a base diameter of 1.0 m, top opening diameter of 0.5 m and height of 0.5 m and was secured to the ground with landscape staples. On the south-facing side of each OTC, a 15-cm-wide by 5-cm-tall opening was cut halfway up the panel to increase ventilation. In the centre of each OTC, a data logger (HOBO Pendant Temperature/Light Data Logger, Onset Computer Corporation, Bourne, MA, USA) was mounted on a wooden dowel 30 cm above the ground to record air temperatures at typical *Ipomopsis* inflorescence height every 15 min. An 8 cm section of white PVC pipe with 48 mm outer diameter served as a ventilated radiation shield for each data logger. An additional data logger was located within 1–2 m of each OTC, adjacent to an *Ipomopsis* plant. Data loggers were placed at 65 of the 90 possible locations in the experiment ($n = 45$ OTC and 45 control areas), owing to a limited number of loggers.

To analyse floral volatiles as a function of temperature at each site for the OTC and ambient treatments separately, the mean temperature was calculated from all data loggers from each treatment for every hour when volatiles were sampled. To characterize the impact of OTCs on soil moisture, volumetric water content was measured adjacent to flowering plants at the time of volatile sampling (18 dates, with the exception of *I. tenuituba* at night in 2019) and throughout the study at one to five points both inside and outside each OTC (11 dates) using a 12 cm probe (HydroSense II, Campbell Scientific, Logan, UT, USA). The OTCs remained in the field for 27–54 days until measurements ended (Supplementary Data Fig. S2).

Volatile sampling

Volatile organic compounds were sampled in the field from flowers or leaves using dynamic headspace sampling and analysed at RMBL with thermal desorption–gas chromatography–mass spectrometry (TD-GC-MS; for methods, see Campbell *et al.*, 2019). A single flower or leaf was bagged to allow scent accumulation for 30 min before pumping the volatiles through a scent trap for 15 min, yielding a total sampling time of 45 min. Floral sampling occurred during the day from 09:00 to 15:00 h for both *Ipomopsis* species (203 samples from 153 *I. aggregata* plants and 92 samples from 61 *I. tenuituba* plants). Because the floral scent of *I. tenuituba* changes at night, consistent with visitation by nocturnal hawkmoths (Bischoff *et al.*, 2014), flowers of that species were also sampled from 20:00 to 23:00 h (83 samples from 58 plants). In 2018 and 2019, flowers were sampled 20–27 days after OTC deployment, whereas in 2021 plants were sampled at two time points (after 13–16 days and again after 27–31 days) to observe any changes over time. Similar numbers of warmed and control plants were sampled on each date. In 2019, volatiles from one leaf per plant were sampled 13–27 days after OTC deployment from a subset of 18 *I. aggregata* plants and 17 *I. tenuituba* plants. At least one air control was taken per sampling date at each site (76 air samples in total).

Volatile compound identification, filtering and quantification followed Campbell *et al.* (2019). Volatiles were quantified in the Shimadzu Postrun software by integrating their base peak and confirming the presence of two reference ions. Filtering was performed in the *bouquet* R package (Eisen *et al.*, 2022) separately for flowers and leaves. To be included in further analyses, a compound had to be present in 10 % of samples of either species (or 25 % of all leaf samples), have a maximum peak area of ≥1 million counts, and its mean in floral samples had to exceed three times the mean in air controls (Campbell *et al.*, 2019). Although it did not meet the last criterion, we also included indole in our analyses, because that volatile was detected in a prior study of *I. tenuituba* (Bischoff *et al.*, 2014). To account for background noise, in each year the 80th percentile of the amount of indole in air controls was subtracted from amounts in samples, and negative values were set to zero. Quantification used a dilution series of seven standards (α-pinene, β-caryophyllene, farnesol, hexenol, indole, linalool and methyl salicylate), with each compound quantified using the standard of the same compound class. This yielded a filtered dataset of emission rates per flower per hour for each floral sample. Emission rates were square-root transformed before analysis.

To assess the plastic response of volatile emission rates, we used canonical analysis of principal coordinates (CAP; Anderson and Willis, 2003) with Bray–Curtis distances, as implemented in the *capscale* function of the R package *vegan* (Oksanen *et al.*, 2022). This constrained ordination method is suited to discovery of multivariate patterns among predefined predictors. We used a permutation test (*anova.cca* function) to test the marginal effect of each term when possible (models without an interaction) or, when not possible, the sequential effect of each term. Site was included in models with *I. aggregata*. Because random effects are not possible in *capscale*, the two repeated measures of each plant in 2021 are treated as independent in ordinations.

The amount of OTC warming varied daily and hourly with incoming solar radiation and between sites with different microclimates (see Results; Supplementary Data Fig. S3), which led us to measure and analyse sampling temperature separately from treatment effects. For each species and time (day or night), we analysed responses of floral volatile emissions to warming at

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two time scales in the same CAP model: (1) the short-term effect of mean temperature in each treatment at the time of sampling, which varies hourly and among sampling dates; and (2) the long-term effect of the OTC treatment, which might also include accumulated effects on plant resources and floral development over the course of the experiment (2–4 weeks). To determine whether the effect of OTC treatment changed with time (e.g. exacerbation or a decrease owing to plant acclimation), in a second CAP model we compared emissions between the two 2021 time points by examining effects of treatment, time point and their interaction. Because OTCs also affected soil moisture, we ran a third model that assessed the impact of both soil moisture at the time of sampling and sampling temperature. This model was run for daytime emissions with both species together and for *I. tenuituba* at night when soil moisture data were available in 2021. To characterize the differences in *I. tenuituba* floral emissions between day and night, we ran a CAP model with treatment, year, time of day and the interaction of year and time of day. For the leaf volatiles, we used a CAP model with the factors of treatment and species (the interaction was not significant).

To analyse effects of warming treatment on total emissions within each species and time of day, we used a linear mixed model with the factors of year, site and treatment, without interactions (*lmer* function of the R package *lme4*). To examine univariate effects on individual volatiles and total emissions within each species, site, time of day and year, we analysed emissions as a function of either sampling temperature or treatment using linear models (*lm* function in R). To facilitate interpretation of the effects of each of these variables (e.g. in terms of change in emissions per change in temperature), we did not combine both variables in the same linear model.

Floral size, rewards, seed predation and reproductive success

In addition to volatiles, in 2021 we measured several traits that have been demonstrated to influence pollinator visitation, pollination success or seed production in *Ipomopsis*: corolla size (Campbell *et al.*, 1991, 1996, 2022*b*), nectar production (Mitchell, 1993) and corolla colour (Meléndez-Ackerman and Campbell, 1998; Bischoff *et al.*, 2015). Corolla length and width were measured as indicators of flower size using dial callipers (Campbell, 1989) 7–31 days after OTC deployment on one to five flowers per plant for 126 *I. aggregata* plants (both sites) and 31 *I. tenuituba* plants, for a total of 275 flowers. An additional 110 *I. aggregata* flowers were measured for length only on the same plants, using the same pair of callipers.

Several additional floral traits, fly oviposition and damage, and reproductive success were measured on *I. aggregata* plants at Maxfield Meadow in 2021 (measurements were not feasible at the farther sites). Nectar production rate and concentration were assessed by excluding pollinators from elongated unopened flower buds for 48 h with a bent plastic straw (51 plants, 12 and 19 days after OTC deployment, one or two flowers per plant in total; Mitchell, 1993). Nectar volume was quantified with microcapillary tubes and sucrose concentration with a hand-held refractometer (Campbell *et al.*, 1991). Corolla colour was measured with a reflectance spectrometer to calculate a redness index that describes relative reflectance in red vs. green wavelengths (46 plants, 19 and 31 days after OTC deployment, one or two flowers per plant in total; Campbell and Powers, 2015).

To estimate the incidence of fly oviposition on *I. aggregata* at Maxfield Meadow, each week we counted the number of fly eggs laid under the sepals on all open flowers and elongated buds (61 plants, 2 days before and 5–39 days after OTC deployment). The tallest inflorescence height was also recorded weekly to estimate the maximum floral display height over the season, although browsing by deer occasionally reduces this height.

To estimate reproductive success, for 62 plants at Maxfield Meadow we measured fruit and seed production, along with seed predator damage, by collecting fruits immediately before dehiscence and calyces from flowers that failed to make a fruit (i.e. aborted). Collections were conducted weekly over the entire fruiting period (dates are given in Supplementary Data Fig. S2). Seed production in undehisced fruits was counted directly, whereas seed production by fruits that had already dehisced and dispersed seeds was estimated as the average number of seeds per intact fruit for that plant. Fruits filled with frass, indicating predation by a fly larva, generally had no viable seeds. Seed predator damage was calculated as the proportion of non-aborted fruits with fly frass (10 % of fruits) or eaten by a caterpillar (2 % of fruits). The number of flowers per plant was the total of damaged and intact fruits, aborted flowers and flowers collected early for trait measurement. The number of seeds per flower was calculated for each plant as the estimated number of seeds divided by the number of flowers.

To detect changes in floral traits, reproductive success and fly attack with warming, we ran linear mixed models for each trait and site, with the main effect of treatment and a random effect of plant for traits with repeated measures of the same plant. Given that the number of flowers and oviposition rate (fly eggs per flower) were measured weekly, for those responses we also included date and the interaction between date and treatment in the model, and we did not include data before treatments started. ANOVAs used the Satterthwaite correction for degrees of freedom, as implemented in the R package *lmerTest* (Kuznetsova *et al.*, 2017), for models constructed in *lme4* (Bates *et al.*, 2015).

RESULTS

Open-top chamber efficacy

Over the period of deployment, the OTCs raised the mean hourly air temperature measured 30 cm above the soil by +2.8 °C in 2018, +2.4–2.7 °C in 2019 and +1.7–2.2 °C in 2021 (Supplementary Data Fig. S3). By capturing solar radiation, OTCs produced the largest warming effect at noon and almost no effect at night. The average temperature difference between OTCs and controls during volatile sampling was +5.3 ± 2.5 °C during the day and +1.0 ± 0.4 °C at night (mean ± s.d.). OTC warming was greater on hot days: OTCs increased daily maximum temperatures by +2.5 °C when the ambient maximum was 20 °C, but for days with ambient maxima of 40 °C, warming increased to +7.5–11.3 °C, depending on the site and year. The average increase in maximum daily temperature was +10.7 °C in 2018, +8.8–8.9 °C in 2019 and + 6.1–6.9 °C in 2021, depending on the site.

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The OTCs decreased soil moisture measured at the focal plant or in general by −2.3 ± 1.7 % volumetric water content (mean ± s.d. across all dates measured), with the effect depending on the site and date. The drying effect was greatest on days with high soil moisture and diminished at <5 % volumetric water content (Supplementary Data Fig. S4).

Warming effects on floral volatiles

In this experiment, *I. aggregata* and *I. tenuituba* flowers produced a similar set of floral volatiles to those reported previously (Irwin and Dorsett, 2002; Bischoff *et al.*, 2014; Campbell *et al.*, 2019). The volatile blend for *I. aggregata* during the day was dominated by α-pinene (53 % on average), followed by minor amounts (5–8 %) of (*E*)-hex-3-en-1-ol, (*E*)-β-ocimene and (*Z*)-β-ocimene, with 21 other volatiles contributing ≤5 % to the blend. For *I. aggregata* during the day, volatile emissions responded not only to the sampling temperature ($P = 0.002$), but also to the warming treatment in a way that was not explained fully by sampling temperature ($P = 0.027$; Table 1A). Volatile emissions also differed by year and between the two sites (CAP; Table 1A; Fig. 1). However, total volatile emissions did not change with warming overall (Supplementary Data Table S2; Fig. S5).

The volatile blend for *I. tenuituba* during the day was also dominated by α-pinene (54 % on average), followed by minor amounts (5–7 %) of (*E*)-hex-3-en-1-ol and β-myrcene, with 21 other volatiles contributing ≤5 % to the blend. The volatiles with the largest increases in emissions from day to night averaged across treatments were (*E*)-β-ocimene (82-fold) and α-farnesene (31-fold), whereas emissions decreased the most at night for 3-methylbutanal oxime (9-fold decrease) and (*E*)-hex-3-en-1-ol (7-fold decrease; time effect in CAP, $P = 0.001$). During the day, volatile emissions responded significantly to the warming treatment ($P = 0.023$), but not independently from sampling temperature, and differed by year (CAP; Table 1B; Fig. 2). At night, *I. tenuituba* volatile emissions responded to sampling temperature ($P = 0.011$), but not independently from the warming treatment, and differed by year (Table 1C; Fig. 3). The CAP models explained from 8 to 15 % of the inertia, depending on the species and time of day. Total *I. tenuituba* volatile emissions did not change overall with the warming treatment during the day or night (Supplementary Data Fig. S5; Table S2), nor did levels of indole ($P = 0.45$ for day and $P = 0.32$ for night).

Long-term effects of the warming treatment on emissions of individual volatiles and total emissions varied by site and year (Fig. 4B; Supplementary Data Fig. S5). The warming treatment increased the emissions of (*E*)-hex-2-enal by 191–347 % in *I. aggregata* during the day in 2021 and by 240 % in *I. tenuituba* at night in 2019. For *I. tenuituba* in 2021, the warming treatment increased daytime (*E*)-β-ocimene emissions by 164 % and decreased linalool emissions by 72 %. Other effects were not statistically significant ($P > 0.05$).

The short-term effects of sampling temperature on volatile emissions also varied by site and year (Fig. 4A; Supplementary Data Fig. S6). The largest effects of sampling temperature (>15 % change per °C) were an increase in β-caryophyllene of 23 % per °C in *I. aggregata* at GNA in 2021 and decreases of 17–18 % per °C in α-pinene and pseudoionone in *I. aggregata* at Maxfield Meadow in 2021. Total daytime volatiles decreased 10 % per °C in *I. aggregata* at Maxfield Meadow in 2021 and increased 5 % per °C in *I. tenuituba* in 2021 ($P < 0.03$). Across all volatiles, the effect of sampling temperature and the effect of treatment (calculated for each species and time) were correlated only for *I. tenuituba* during the day ($r = 0.48$, $P = 0.016$), but not for that species at night ($r = –0.20$, $P = 0.34$) or for *I. aggregata* during the day ($r = 0.25$, $P = 0.21$).

In 2021, daytime volatile emission rates across both species shifted between the two time points after OTC deployment (e.g. α-pinene emissions increased 34 % in *I. tenuituba* and 93–347 % in *I. aggregata* across 2 weeks, depending on the site), but there was no detected interaction between time point and warming treatment (Supplementary Data Table S3A). For *I. tenuituba* at night in 2021, there was also no significant interaction between time point and warming treatment (Supplementary Data Table S3B).

In a model that also included sampling temperature, soil moisture did not alter daytime emissions of floral volatiles in

TABLE 1. *Effect of warming on* Ipomopsis aggregata *and* Ipomopsis tenuituba *floral and leaf volatile emissions, based on canonical analysis of principal coordinates. Separate analyses were conducted for daytime* I. aggregata *floral volatiles (A), daytime (B) and night-time (C)* I. tenuituba *floral volatiles, and leaf volatiles for both species (D). The number of samples and the percentage of the total inertia explained by the predictors are included for each analysis. Predictors with significant effects are indicated in bold.*

Parameter	d.f.	*F*	*P*-value
(A) ***I. aggregata flowers***, day			
Year	2	5.5	**0.001**
Temperature	1	3.5	**0.002**
Treatment	1	2.1	**0.027**
Site	1	2.6	**0.004**
15 % explained			$n = 196$
(B) ***I. tenuituba flowers***, day			
Year	1	2.2	**0.024**
Temperature	1	1.5	0.125
Treatment	1	2.1	**0.023**
8 % explained			$n = 92$
(C) ***I. tenuituba flowers***, night			
Year	1	6.5	**0.001**
Temperature	1	2.5	**0.011**
Treatment	1	0.9	0.468
13 % explained			$n = 83$
(D) Leaves, day			
Species	1	3.2	**0.012**
Treatment	1	1.0	0.412
13 % explained			$n = 35$

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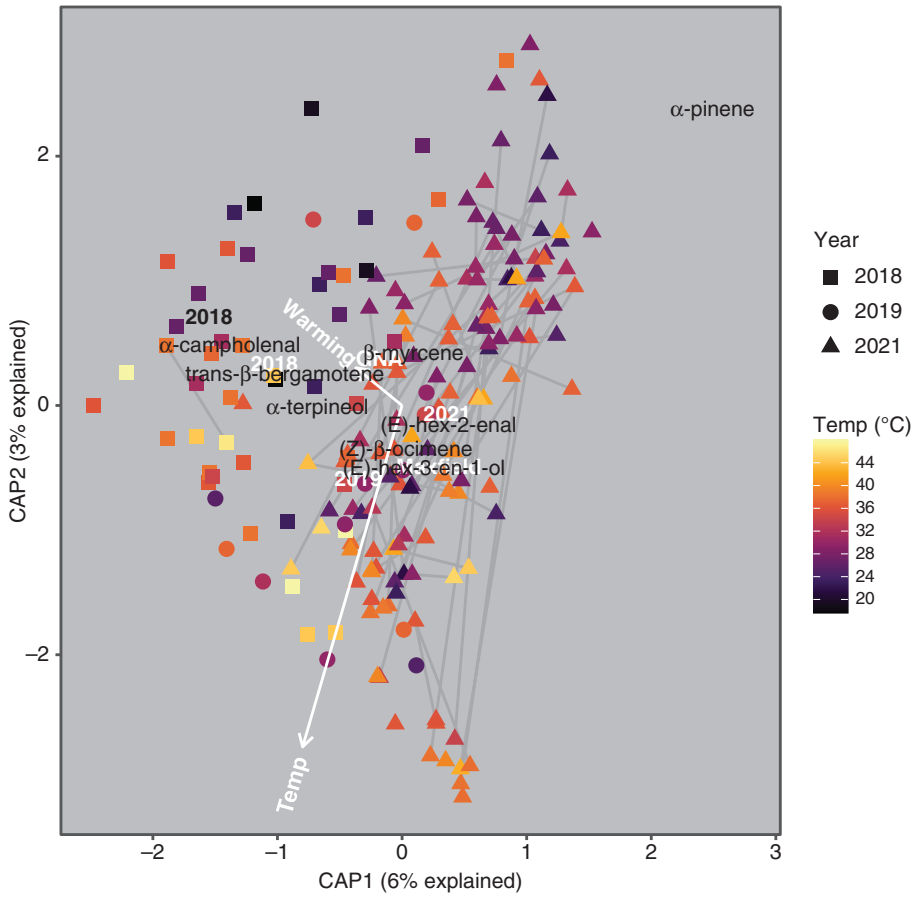


FIG. 1. Effect of warming on floral volatile emissions of *Ipomopsis aggregata* during the day. Ordination shows the results of a canonical analysis of principal coordinates (CAP) with warming treatment, sampling temperature, site and year as predictors. Points represent samples of one to three flowers per plant, coloured by sampling temperature, with samples from the same plant connected with lines. The centroids of each group are indicated with white labels. The arrows show the direction of increase in sampling temperature and the effect of the warming treatment. Compound names are positioned in the direction in which they increase from the origin.

both species or nighttime floral volatiles of *I. tenuituba* in 2021 (Supplementary Data Table S3B).

Warming effects on leaf volatiles

We detected 17 volatiles in *I. aggregata* and *I. tenuituba* leaf samples that met the filtering criteria, including three sesquiterpenes, two monoterpene derivatives and 12 aliphatic compounds (Supplementary Data Table S4). The average leaf volatile blend across both species was composed of α-pinene (33 %), the green-leaf volatiles (*E*)-hex-3-en-1-ol (32 %), [(*E*)-hex-3-enyl] acetate (11 %) and (*E*)-hex-2-enal (8 %), with the remaining volatiles each representing <3 % of the blend. The two species differed in emission rates of several volatiles (Supplementary Data Fig. S7; Table S4), but there was no detected effect of warming on emission rates (CAP; Table 1D) or total volatiles (Supplementary Data Table S2).

Effects of warming on floral display, rewards, reproductive success and seed predation

In 2021 across both sites, warmed *I. aggregata* plants produced corollas that were 4 % longer ($P = 0.035$; results for all trait analyses are given in Supplementary Data Table S2), but corolla width was unaffected ($P = 0.47$; Fig. 5). Warmed *I. tenuituba* plants produced corollas that were 10 % narrower ($P = 0.048$), but warming had no effect on corolla length ($P = 0.69$). At Maxfield Meadow in 2021, warming increased *I. aggregata* nectar production by 41 % ($P = 0.032$) but had no effect on nectar concentration, maximum inflorescence height or flower redness (all $P > 0.40$; Fig. 6). Although the combined number of open flowers and elongated buds across 5 weeks was unaffected by warming ($P = 0.27$; interaction between treatment and week, $P = 0.95$), fly eggs per flower decreased on warmed plants ($P = 0.023$), and the effect of warming changed through the summer (interaction between treatment and week, $P = 0.005$). Although fly oviposition was similar on plants chosen for the warming treatment 2 days before OTC deployment, the number of fly eggs per flower was 72 % less on warmed plants 5 days after OTC deployment and dropped to near zero the following week, 3 weeks earlier than control plants (Fig. 7).

For *I. aggregata* at Maxfield Meadow in 2021, warming had no detected effect on the total number of flowers, the proportion of aborted fruits, the number of non-aborted fruits, the estimated number of total seeds, the estimated number of seeds

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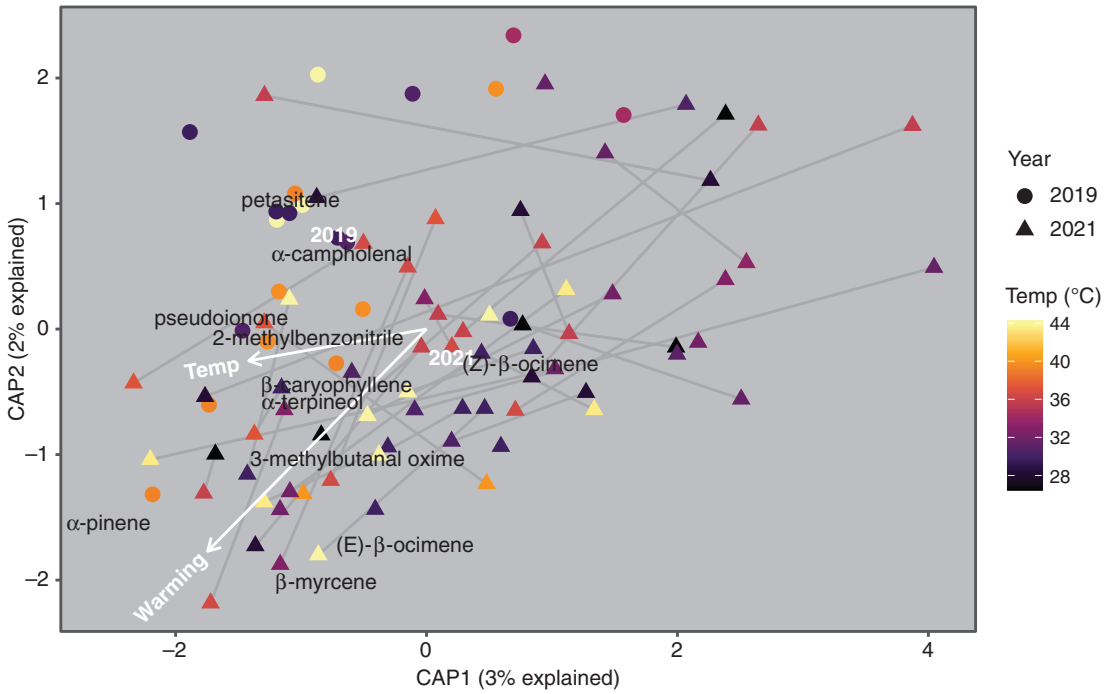


FIG. 2. Effect of warming on floral volatile emissions of *Ipomopsis tenuituba* during the day. Ordination shows the results of a canonical analysis of principal coordinates (CAP) with warming treatment, sampling temperature and year as predictors. Points represent samples of one to three flowers per plant, coloured by sampling temperature, with samples from the same plant connected with lines. The centroids of each group are indicated with white labels. The arrows show the direction of increase in sampling temperature and the effect of the warming treatment. Compound names are positioned in the direction in which they increase from the origin.

per flower or the number of seeds per fruit ($n = 62$, all $P > 0.45$; Fig. 8). Warming did not significantly alter the proportion of non-aborted fruits that were damaged by fly larvae ($P = 0.29$), which averaged 12 % and ranged from 0 to 33 % in control plants and from 0 to 60 % in warmed plants.

DISCUSSION

Rapid warming of the atmosphere by anthropogenic carbon emissions is likely to disrupt ecosystems not only through direct effects on plant and animal survival, but also by modifying interactions among species. Visual and olfactory floral traits that mediate mutualistic or antagonistic interactions with animals and herbivores might be altered by warming temperatures on either short or long time scales. In a subalpine habitat, we observed both short-term (temperature at the time of sampling) and long-term (weeks) impacts of experimental warming by +2–3 °C on floral volatiles, in addition to long-term effects on flower size and nectar rewards in *Ipomopsis*. This trait plasticity might have influenced a decline in seed predator oviposition but ultimately did not significantly affect reproductive output during the time frame of this study.

Floral volatile plasticity to short- and long-term warming

Responses of plant volatiles to environmental stressors depend on many physiological processes, including nutrient and carbon acquisition, gene regulation, activation of synthesis enzymes, transport out of the cell, volatilization from the surface and diffusion through the air (Sagae *et al.*, 2008; Farré-Armengol *et al.*, 2013; Barman and Mitra, 2021). By exposing plants to elevated daytime temperatures for 2–4 weeks and measuring volatiles at temperatures influenced both by short-term natural weather fluctuations and by long-term experimental passive warming, our experiment tested the immediate and cumulative effects of warming on these processes in field conditions. In *I. aggregata*, we saw independent changes in floral volatile emissions at these two time scales that were orthogonal (Fig. 1), with each having an effect on a different set of volatiles (Fig. 4). Not only were there cumulative effects of warming on plant resources or on regulation of volatiles, but these effects differed from the immediate responses to increased temperature, which are typically the focus of experimental studies (Supplementary Data Table S1). In *I. tenuituba*, daytime volatiles were affected only by long-term warming, and nighttime volatiles were affected only by sampling temperature (Table 1), indicating that response time scales can differ even within a species.

Responses of volatiles to environmental change are often species specific (Farré-Armengol *et al.*, 2014; Burkle and Runyon, 2017), and here we show that this is true even within the same genus. The only volatile compound that showed a similar response to the warming treatment across the two *Ipomopsis* species was the green-leaf volatile (*E*)-hex-2-enal, whose emissions increased 3- to 4-fold both in *I. aggregata* during 2021 and in *I. tenuituba* at night during 2019. Similar spikes in green-leaf volatiles with heat stress have been observed in leaf emissions (Jardine *et al.*, 2015), and it is possible that a common mechanism is involved. In contrast, responses of other

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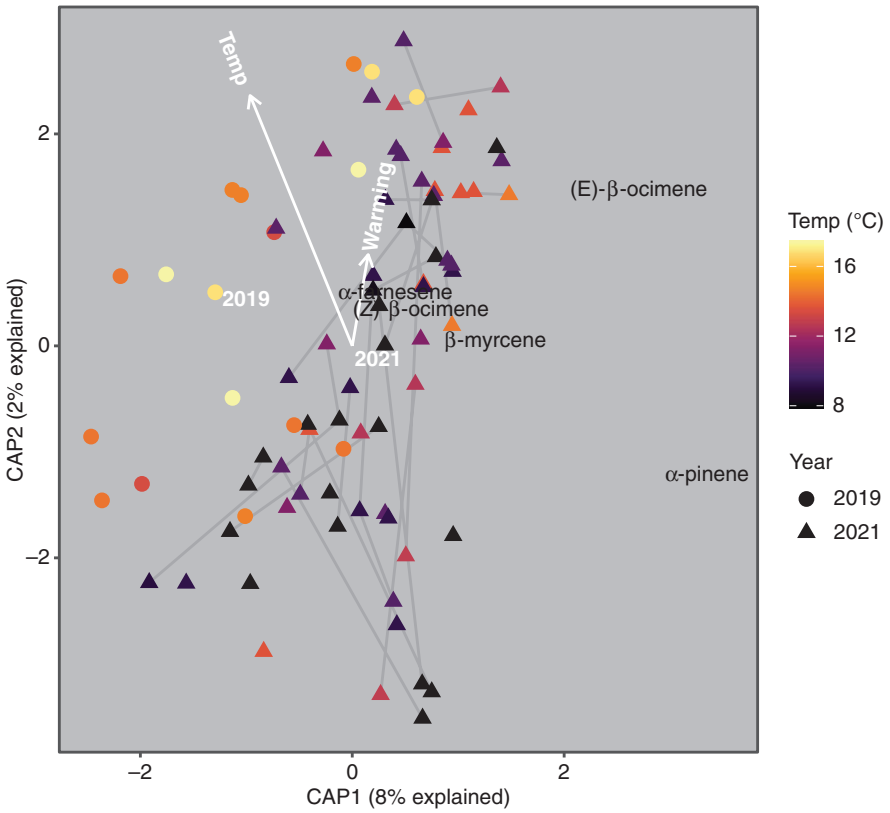


FIG. 3. Effect of warming on floral volatile emissions of *Ipomopsis tenuituba* at night. Ordination shows the results of a canonical analysis of principal coordinates (CAP) with warming treatment, sampling temperature and year as predictors. Points represent samples of one to three flowers per plant, coloured by sampling temperature, with samples from the same plant connected by lines. The centroids of each group are indicated with white labels. The arrows show the direction of increase in sampling temperature and the effect of the warming treatment. Compound names are positioned in the direction in which they increase from the origin.

volatiles were idiosyncratic and subtle, both between species and between the two *I. aggregata* sites (Fig. 4). Similar patterns have been observed both in cultivated plants (Zeng *et al.*, 2019) and in several common species in a Mediterranean shrubland (Farré-Armengol *et al.*, 2014), such that different volatile compounds within a given species often showed differing responses to warming.

Long-term shifts in *Ipomopsis* volatile emissions might have consequences for pollinator attraction and defence against herbivores and pathogens. *Ipomopsis tenuituba* daytime floral emissions of (*E*)-β-ocimene increased 2.6 times with warming in 2021 and showed a similar but non-significant increase in 2019. This compound is a common attractant for a wide range of pollinators that is found as a floral volatile in 71 % of angiosperm families (Knudsen *et al.*, 2006) and is also thought to play a role as an antioxidant owing to its high reactivity, increasing thermotolerance (Jardine *et al.*, 2017). Interestingly, emissions of this compound were also 82 times greater at night than in the day for this species, representing 37 % of the nighttime blend averaged across treatments. Temporal regulation of (*E*)-β-ocimene could have evolved to attract night-flying hawkmoths, because *Hyles lineata* can detect this compound (Raguso *et al.*, 1996). With increasing climate warming, floral scent advertisement might increase during the day, which is outside the typical activity period of these crepuscular pollinators. Conversely, nighttime linalool emissions decreased 72 % in warmed *I. tenuituba* in 2021, which, based on its functions in other species, could weaken pollinator attraction or defence against insect herbivores (Zhang *et al.*, 2023).

Effects of temperature on volatiles at hourly or daily scales could also alter communication and defence in ways that affect plant fitness. β-Caryophyllene, which increased in emissions with sampling temperature in *I. aggregata* at GNA in 2021, is a common floral volatile that, in other taxa, defends against bacterial pathogens and serves as both a direct and indirect defence from insect herbivores (Huang *et al.*, 2012). The dominant floral compound in both species, α-pinene, decreased in emissions with increased temperature in *I. aggregata* at Maxfield Meadow in 2021. Given that higher values of α-pinene increase seed production and the trait is also under stabilizing selection owing to changes in pollination (Campbell *et al.*, 2022*b*), this decrease could diminish female reproductive success.

Although warming had strong short- or long-term effects on some floral volatiles, many did not vary across the warming treatments (Fig. 4), which could indicate that their production or emission is buffered from heat stress or that they respond to unmeasured variables, as suggested by the large amount of unexplained variation. Leaf volatiles of both *Ipomopsis* species also showed no detectable response to warming after 23–27 days (Table 1D), in contrast to many studies that show strong effects in the short term (e.g. Jardine *et al.*, 2015). Such differing responses to warming duration illustrate the need for caution

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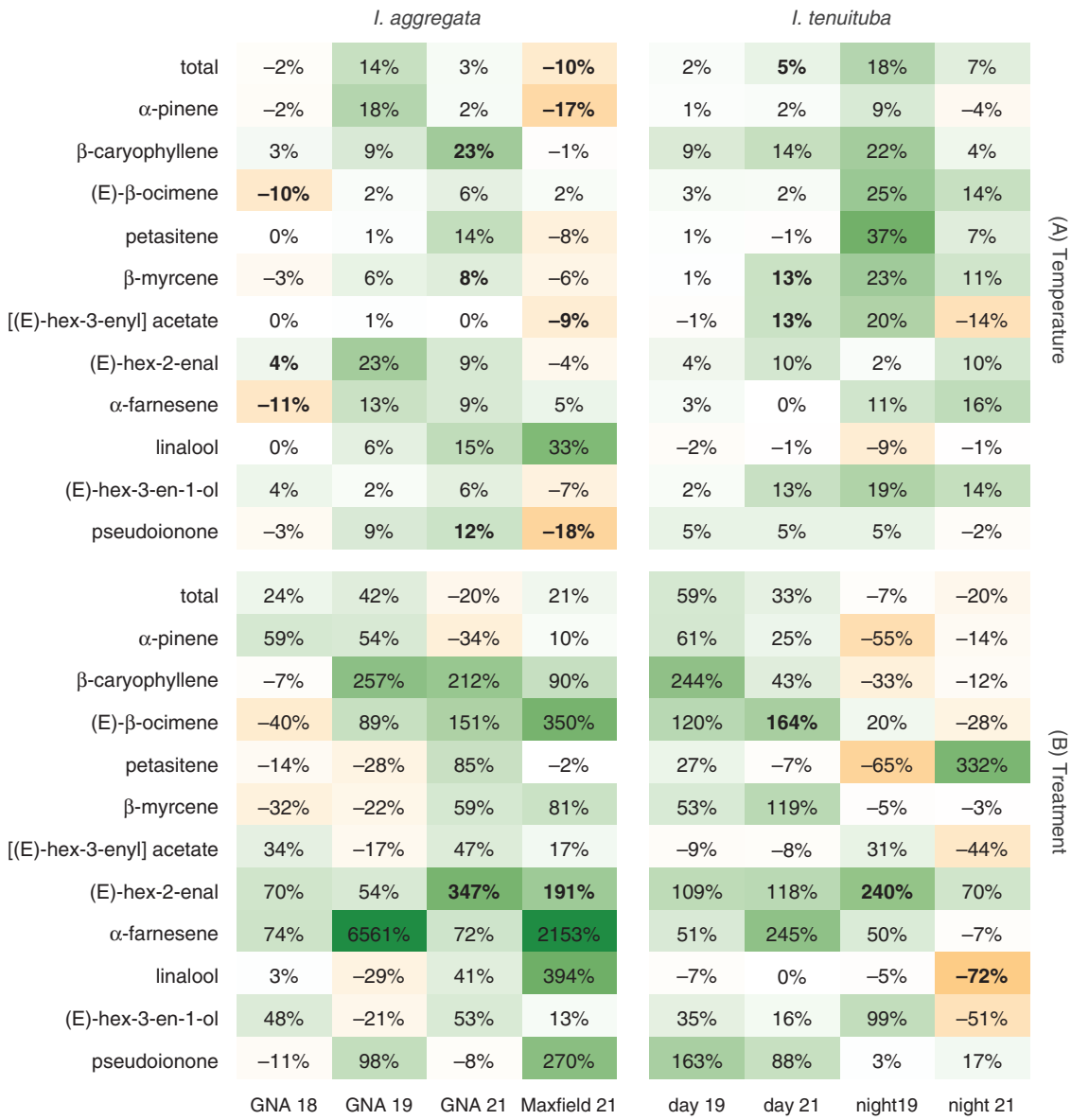


FIG. 4. Warming effects on total and individual floral volatile emissions from *Ipomopsis aggregata* at the Gothic Natural Area or Maxfield Meadow and *Ipomopsis tenuituba* at Spring Creek, across 3 years. The 11 most commonly detected volatiles (>18 % of samples) are presented in descending order of prevalence. Volatile emissions that increased with warming are highlighted in green, and those that decreased are shown in orange. Bold text indicates statistically significant effects ($P < 0.05$). (A) Effects of sampling temperature (averaged hourly within treatment), showing the percentage change relative to the mean per degree Celsius increase in temperature. (B) Effects of the warming treatment, showing the percentage change in emissions in the open-top chambers relative to the ambient control plants.

when basing predictions solely on the short-term experiments typically conducted and also when extrapolating from OTC manipulations, which might not capture the complexities, such as higher nighttime temperatures, that plants are experiencing in natural warming conditions.

In addition to warming temperatures, climate change is affecting precipitation patterns in alpine ecosystems (Seager *et al.*, 2013). Although a drydown experiment with *I. aggregata* in a screenhouse found non-linear effects of soil moisture on emissions of some volatiles, including α-pinene and α-farnesene (Campbell *et al.*, 2019), we did not detect an effect of soil moisture on floral emissions in a model that also included sampling temperature (Supplementary Data Table S3). However, in our study the soil moisture and temperature were not independent or controlled separately, and the current OTC design probably had non-trivial impacts on soil drying both by increasing evapotranspiration in the warmed chamber and by diverting some precipitation. Further studies that tease apart these two factors might uncover additional independent and/or interactive effects on floral traits.

Floral morphology and rewards respond to warming

In addition to scent, flowers can attract pollinators using specific visual cues and rewards, some of which were impacted slightly by warming in this experiment. Although other

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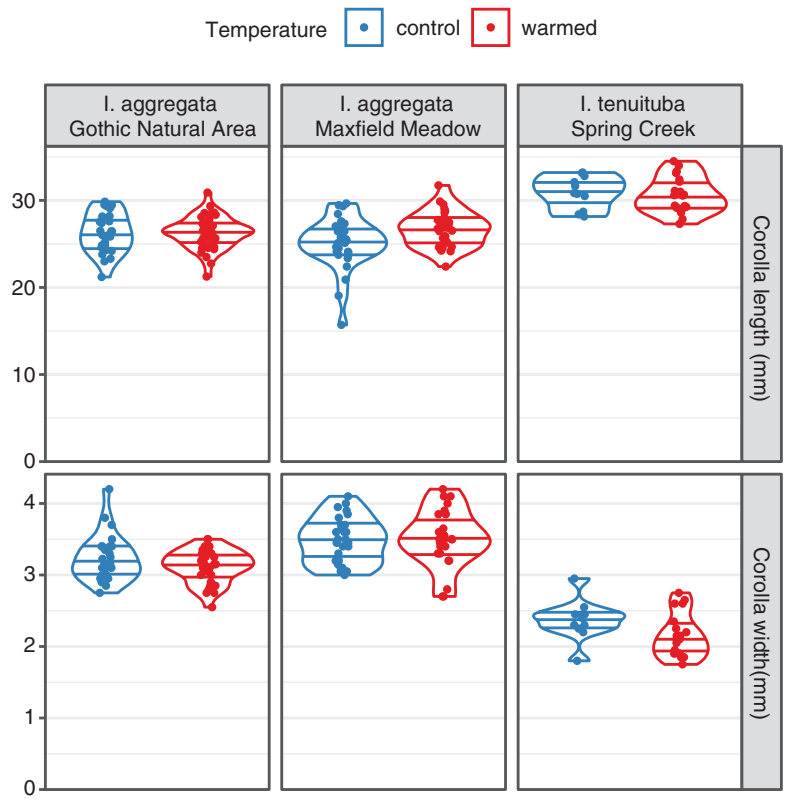


FIG. 5. The effect of warming on *Ipomopsis aggregata* and *Ipomopsis tenuituba* corolla length and width at each site in 2021. Points indicate the mean value for each plant if multiple measurements were taken (one to three flowers per plant). The density estimates for each treatment are broken by lines indicating the median and 25th and 75th percentiles.

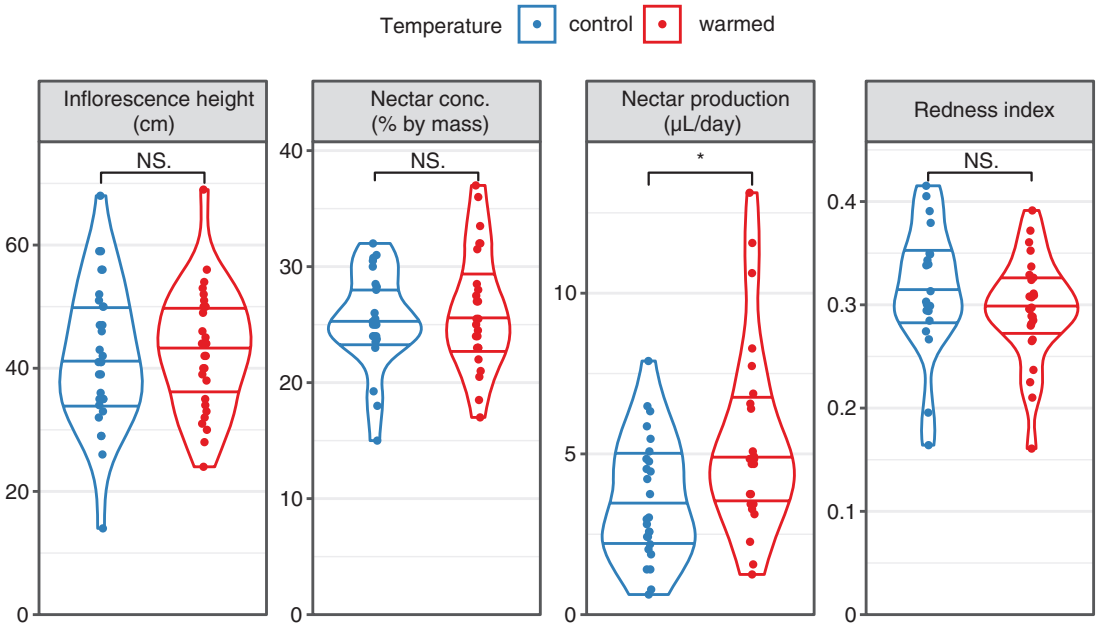


FIG. 6. The effect of warming on *Ipomopsis aggregata* floral traits at Maxfield Meadow in 2021. Points indicate the mean value for each plant if multiple measurements were taken (one to three flowers per plant). The density estimates for each treatment are broken by lines indicating the median and 25th and 75th percentiles. Brackets indicate the significance of the effect for each trait based on a linear mixed model (N.S. for not significant; $*P < 0.05$).

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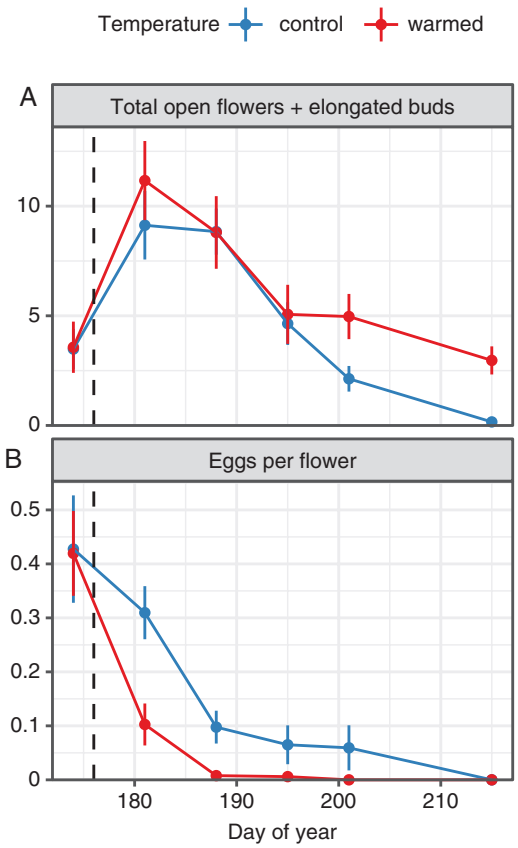


FIG. 7. Changes in flowering (A) and fly oviposition (B) on *Ipomopsis aggregata* in each treatment at Maxfield Meadow throughout the duration of the study. Points show means (±s.e.m.) for each date. The vertical line indicates the date when open-top chambers were deployed. Fly oviposition was estimated as the number of fly eggs per open flower or elongated bud.

floral systems have generally shown flower size shrinking with increasing temperatures (Descamps *et al.*, 2018, 2021; Wiszniewski *et al.*, 2022) or drought (Villarreal and Freeman, 1990; Campbell and Wendlandt, 2013; Kuppler *et al.*, 2021), we observed little or no change in corolla length and width in either species. Only *I. aggregata* showed a 4 % increase in corolla length with warming treatment, consistent with a 7 % increase in corolla length for *I. longiflora* when grown at 30 vs. 20 °C in a growth chamber (although length decreased again at 35 °C in that study; Villarreal and Freeman, 1990). The mechanism of this plasticity is unknown, but the slightly longer corolla tubes could lead to a higher visitation rate from hummingbird pollinators (Campbell *et al.*, 1991), which was not measured in this experiment. All other aspects of floral display measured in our study, including inflorescence height, corolla redness, the number of open flowers, and the total flowers produced over the season, were not significantly affected by warming. This suggests that the visual floral advertisement might be maintained in this species despite increases in temperature, unlike the reduced size and bumblebee attraction observed with warming of *Borago* (Descamps *et al.*, 2018, 2021).

Daytime warming increased nectar production by 41 % in *I. aggregata*. Nectar production in this species increases on sunny days compared with overcast days (Pleasants, 1983), is generally lower at night, and peaks between 15:00 and 17:00 h when it is warm (Brown and Kodric-Brown, 1979; Supplementary Data Fig. S3). Our results suggest that this higher nectar production during sunny days and warm times could be attributable, at least in part, to higher temperatures. Although leaf-level photosynthesis in *I. aggregata* increases from 15 °C to the optimal temperature for photosynthesis at 22 °C (Wu and Campbell, 2006), the photosynthetic rate gradually declines above that temperature; therefore, higher carbon assimilation is unlikely to explain the increased nectar production in OTCs. Alternatively, higher enzymatic activities in other aspects of nectar production might be driving the observed increase in production.

Warmer temperatures might be expected to increase nectar evaporation and result in a smaller volume of more concentrated nectar, but we found that nectar sugar concentration was unaffected by the warming treatment. This might be attributable, in part, to the OTCs blocking the wind experienced by plants inside the chambers, thereby reducing the higher evaporation rates produced by warmer temperatures. A long corolla tube could also reduce evaporation (Villarreal and Freeman, 1990), although the small increase in length with warming is unlikely to explain the large observed increase in nectar volume.

The additional nectar rewards offered by warmed plants could potentially have positive effects on male reproductive success if there is increased visitation by hummingbird pollinators that respond to this cue. In a previous study, increased nectar production in *I. aggregata* flowers was associated with increased visitation by hummingbirds and pollen dispersal to neighbours, but did not impact female reproduction (Mitchell, 1993). Consistent with this result, we observed no effect of warming on *I. aggregata* female reproductive output, including total seeds, seeds per flower, seeds per fruit or fruit abortion, despite increased nectar rewards with warming. There are, however, several other possible explanations for that lack of concordance. Effects on other traits (such as reduced α-pinene) could have had negative effects that offset the benefit of higher nectar rewards. Alternatively, it is possible that the OTCs visually or physically impeded pollinator visitation, counteracting the attractiveness of larger rewards. Furthermore, the tests for effects on seed production could have had low statistical power, given that we obtained results only from the 62 plants at one site in a single year.

Impacts of warming on seed predators

In addition to mediating pollination mutualisms, floral traits can impact the attraction or deterrence of antagonists such as seed predators (Campbell *et al.*, 2022*b*), such that responses of these traits to warming might alter plant defence and reproductive success. Despite observing no negative effects of temperature on visual floral display traits that might attract flies, fly oviposition on *I. aggregata* flowers was heavily reduced starting 5 days after OTC deployment and continuing for 5 weeks. Changes in floral volatile emissions with temperature might have altered attractiveness to flies, although most volatiles did not increase significantly at this site and year (Maxfield Meadow in 2021; Fig. 4). Alternatively, OTCs might have deterred flies with elevated air or flower temperatures, visually obscured plants from flies or physically restricted flight

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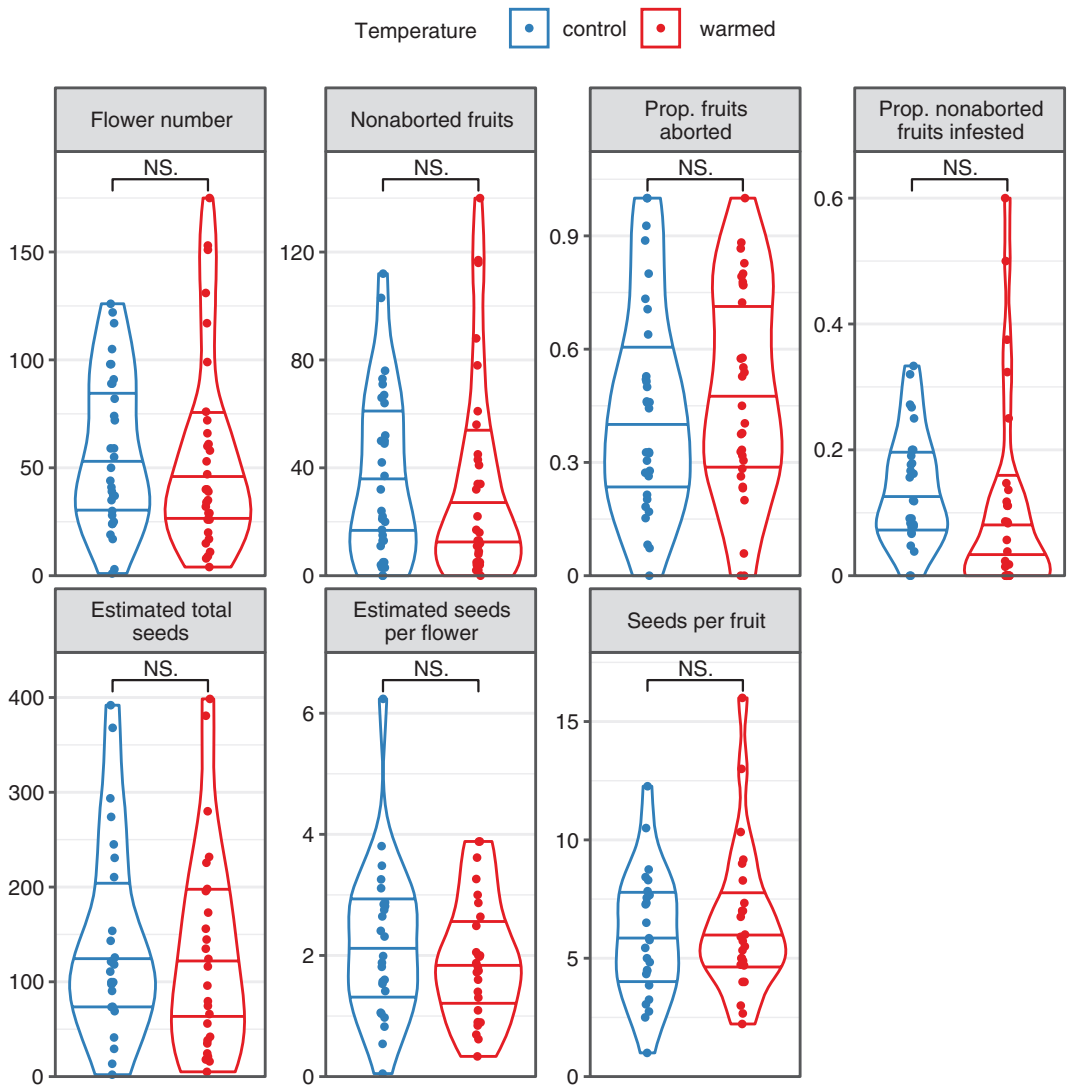


FIG. 8. The effect of warming on traits related to *Ipomopsis aggregata* reproduction at Maxfield Meadow in 2021. The density estimates for each treatment are broken by lines indicating the median and 25th and 75th percentiles. Brackets indicate the significance of the effect for each trait based on a linear mixed model (N.S. for not significant; $*P < 0.05$).

trajectories. Nonetheless, we caution that even if flies do show a preference for ovipositing on unwarmed plants, any future warming of the region resulting from climate change will probably not allow flies to oviposit selectively if all plants in a given region are impacted by elevated temperatures to some extent (Burkle and Runyon, 2017).

Unlike fly oviposition, the proportion of fly-damaged fruits at the end of the season was not significantly affected by the OTC treatment (Fig. 8). Given that the highest rate of oviposition was observed before OTC deployment, it is possible that most fly eggs had already been laid when the warming treatment began. Alternatively, low fly oviposition on warmed plants could result in similar levels of fruit damage if resistance or tolerance of the plant to seed predation were compromised in warmed plants. Finally, measurement bias might also contribute to this discrepancy, if OTCs obstruct the ability of observers to locate fly eggs on plants. In a multi-year study, fruit damage by flies was higher in plants with lower combined α- and β-pinene emissions (β = 0.05; Campbell *et al.*, 2022*b*), but the predicted reduction of fly damage following reduced α-pinene emissions with increasing temperature at this site (Fig. 4) was not observed in our study.

Conclusions

We have shown that floral volatiles and other traits can vary in complex patterns, even among closely related species, in response to elevated temperatures in the field across different temporal scales. The passive warming chamber approach adopted in this experiment highlights both advantages and limitations for simulating future climate trends, in comparison to growth chamber studies (Marion *et al.*, 1997). A realistic and dynamic abiotic environment that includes variation in temperature, wind, precipitation, solar radiation and soil moisture allows conclusions from this field experiment to apply to existing natural environments that also include

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pollinators and herbivores. Nonetheless, because passive heating occurred only during the day (see also Marion *et al.*, 1997), future studies should also examine the effects of elevated nighttime temperatures that are expected with climate change. Within the limitations of OTCs, an important message from our work is the need for more long-term field warming studies, beyond the more common approach of manipulating temperature for only a few hours or days, as shown by the independent and different responses of volatiles on these two time scales.

SUPPLEMENTARY DATA

Supplementary data are available at *Annals of Botany* online and consist of the following.

Table S1: summary of temperature manipulation studies. Table S2: effects of warming on all traits, including sample sizes. Table S3: effects of length of treatment and soil moisture on floral volatiles. Table S4: leaf volatile emissions. Fig. S1: locations of sites. Fig. S2: timing of measurements relative to open-top chamber (OTC) deployment. Fig. S3: hourly air temperatures in and out of open-top chambers (OTCs). Fig. S4: soil moisture in and out of open-top chambers (OTCs). Fig. S5: warming effects on floral volatile emissions. Fig. S6: effects of sampling temperature on floral volatile emissions. Fig. S7: effect of warming on leaf volatile emissions.

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DATA AVAILABILITY

All data and scripts are available at https://github.com/jmpowers/ipomopsis-temp.

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