

Impact of Temperature on Floral Scent Production and Bee Pollination

Karthik R*

PhD Scholar, Department of Entomology, CSK HPKV, Palampur

*Corresponding Author E-mail: karthikramappa@gmail.com

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ABSTRACT

Floral scent, composed of volatile organic compounds (VOCs) including terpenoids, benzenoids, and phenylpropanoids, plays a critical role in mediating plant-pollinator interactions. Rising global temperatures due to climate change are increasingly disrupting both the biosynthesis and emission of these floral volatiles and the olfactory capabilities of bee pollinators. This review examines the biochemical pathways underlying floral scent production, the temperature-dependent nature of VOC emission, and the physiological and behavioral consequences for bee pollinators. Research demonstrates that floral terpene emissions follow a bell-shaped temperature response curve, peaking between 25–30°C and declining at higher temperatures, with species-specific variations in sensitivity. Elevated temperatures alter both the quantity and qualitative composition of floral scent bouquets, impairing the chemical signals that bees rely upon for flower recognition. Simultaneously, heat stress reduces bee antennal olfactory sensitivity by up to 80%, further compromising pollination efficiency. This dual disruption of chemical communication threatens biodiversity, ecosystem stability, and global food security. Understanding these interactions is essential for developing adaptive strategies to mitigate the impacts of climate change on pollination services.

Keywords: *Floral scent; Volatile organic compounds; Temperature; Bee pollination.*

INTRODUCTION

Pollination is a fundamental ecological process that underpins the reproductive success of approximately 87.5% of all flowering plant species worldwide (Ollerton et al., 2011). Among the diverse array of pollinators, bees (Hymenoptera: Apoidea) represent the most ecologically and economically significant group, contributing to the pollination of over one-third of global food crop production (Klein et al., 2007). The intricate relationship

between flowering plants and their bee pollinators is mediated through a sophisticated system of sensory signals, among which floral scent occupies a position of paramount importance (Raguso, 2008). Floral volatile organic compounds (VOCs) serve as long-range chemical signals that enable pollinators to locate, identify, and discriminate among floral resources, thereby facilitating efficient foraging and cross-pollination (Wright & Schiestl, 2009).

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Floral scent bouquets are complex mixtures of low molecular weight, high vapor pressure compounds that are biosynthesized through three major metabolic pathways: the methylerythritol phosphate (MEP) pathway for terpenoids, the shikimate/phenylpropanoid pathway for benzenoids and phenylpropanoids, and the lipoxygenase (LOX) pathway for fatty acid derivatives (Muhlemann et al., 2014). The emission of these volatiles is influenced by a multitude of endogenous and exogenous factors, including developmental stage, circadian rhythms, light intensity, humidity, and temperature (Farré-Armengol et al., 2020).

Temperature, in particular, exerts a profound influence on floral VOC dynamics through dual mechanisms: first, by affecting the physicochemical properties of volatile compounds such as volatility, solubility, and diffusivity; and second, by modulating plant physiological processes including enzyme activity, gene expression, and stomatal regulation that govern VOC biosynthesis and release (Niinemets et al., 2004). In the context of accelerating global climate change, with projected mean temperature increases of 1.5–5°C by the end of this century (IPCC, 2021), understanding the thermal sensitivity of floral scent production and its downstream effects on pollinator behavior has become a matter of critical scientific and agricultural concern.

This review comprehensively examines the current state of knowledge regarding: (i) the biochemistry of floral scent biosynthesis, (ii) the effects of temperature on floral VOC emission patterns, (iii) the impact of thermal stress on bee olfactory physiology and foraging behavior, and (iv) the broader implications for plant-pollinator mutualism, agricultural productivity, and ecosystem resilience under climate change scenarios.

2. Biochemistry of Floral Scent Production

2.1 Major Classes of Floral Volatile Organic Compounds

Floral scent bouquets comprise a diverse array of volatile organic compounds that can be classified into three principal biochemical categories based on their biosynthetic origins (Knudsen et al., 2006). Terpenoids constitute

the largest and most structurally diverse class, encompassing monoterpenes (C10) such as linalool, β -ocimene, and limonene, as well as sesquiterpenes (C15) including β -caryophyllene and (E,E)- α -farnesene. These compounds are synthesized via the plastidial methylerythritol phosphate (MEP) pathway and the cytosolic mevalonate (MVA) pathway through the action of terpene synthase (TPS) enzymes (Tholl, 2006).

Benzenoids and phenylpropanoids represent the second most diverse group of floral volatiles and include compounds such as benzaldehyde, methyl benzoate, eugenol, and *p*-anisaldehyde. These are derived from the shikimate pathway through phenylalanine as a central precursor, with phenylalanine ammonia lyase (PAL) serving as the gateway enzyme to the phenylpropanoid pathway (Li et al., 2024). Fatty acid derivatives, including green leaf volatiles and methyl jasmonate, are produced through the lipoxygenase (LOX) pathway and contribute to both scent profiles and herbivore defense signaling (Dudareva et al., 2013).

2.2 Regulation of Floral Scent Biosynthesis

The biosynthesis of floral volatiles is tightly regulated at the transcriptional level by a network of transcription factors. In *Petunia hybrida*, the R2R3-MYB transcription factor ODORANT1 (ODO1) activates the expression of key genes in the shikimate and phenylpropanoid pathways, including EPSPS and PAL (Verdonk et al., 2005). Additional regulators, including EMISSION OF BENZENOIDS I and II (EOBI and EOBI), form a hierarchical regulatory cascade that governs benzenoid/phenylpropanoid production (Spitzer-Rimon et al., 2012). These transcription factors exhibit diurnal rhythmicity, coordinating scent emission with pollinator activity patterns, as exemplified by nocturnal emission in moth-pollinated species and diurnal emission in bee-pollinated flowers (Li et al., 2024). Environmental factors, including temperature and light, influence this regulatory network, with heat shock factor HSF19 directly upregulating PAL expression under thermal stress conditions (Li et al., 2024).

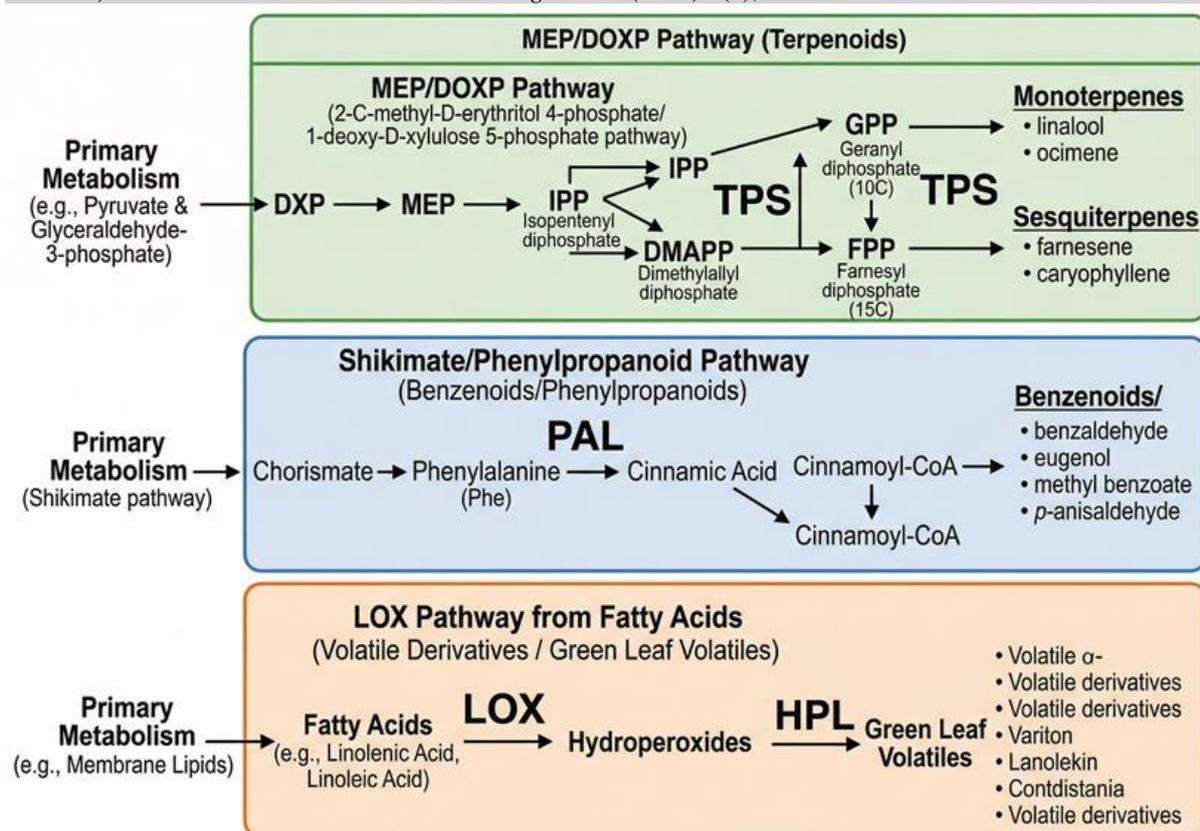


Figure 1: Biosynthetic Pathways of Floral Volatile Organic Compounds (VOCs)

3. Temperature Effects on Floral Scent Emission

3.1 Temperature-Response Curves of Floral VOC Emission

The relationship between temperature and floral volatile emission follows a characteristic bell-shaped response curve, with emission rates increasing from low temperatures to an optimum and declining at supraoptimal temperatures (Farré-Armengol et al., 2014). This pattern reflects the combined effects of temperature on enzyme kinetics, substrate availability, compound volatility, and membrane permeability. In a comprehensive study of seven Mediterranean plant species, Farré-Armengol et al. (2014) demonstrated that floral terpene emissions peaked between 25–35°C, depending on the species, with subsequent declines at higher temperatures due to enzyme denaturation and substrate depletion.

The magnitude of temperature-induced changes is substantial. Under the warmest IPCC projections predicting a maximum increase of 5°C in mean temperatures for Mediterranean climates, models predicted increases in floral terpene emission rates of 0.34–9.1-fold, depending on species (Farré-Armengol et al., 2014). However, species with the lowest baseline emission rates exhibited the highest relative increases, indicating differential vulnerability across the plant community. In *Osmanthus fragrans*, the treatment of 32°C resulted in lower numbers of chemical volatile compounds compared to the optimal 19°C, while temperatures below 15°C also reduced compound diversity (Xin et al., 2017). Similarly, in *Jasminum auriculatum*, floral volatile emission was highest at 25–30°C air temperature regimes, with correlated changes in enzyme activities and gene expression patterns (Bera et al., 2021).

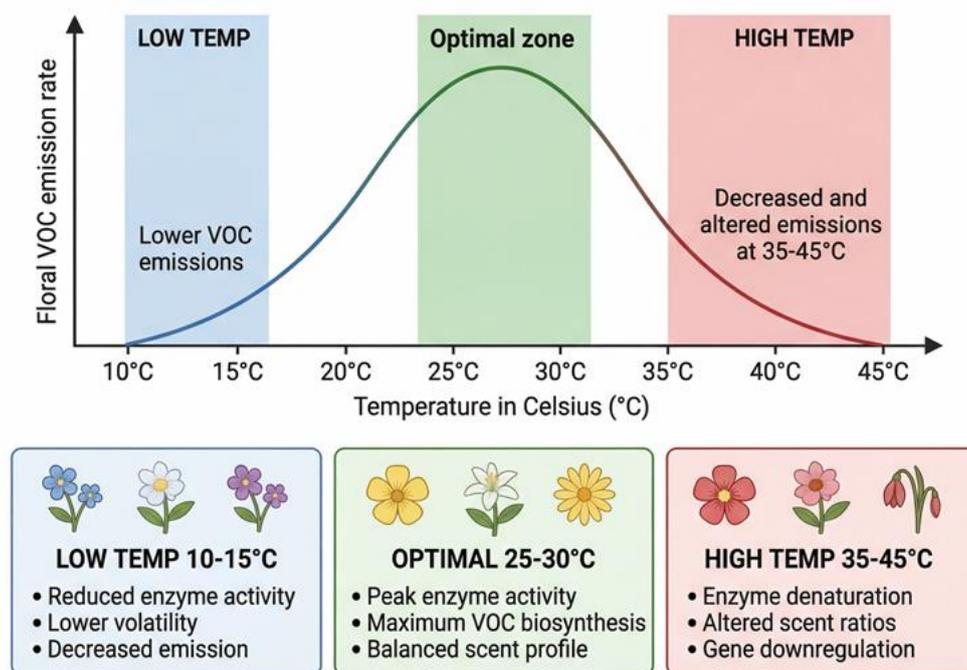


Figure 2: Temperature-Dependent Response Curve of Floral Volatile Emissions

3.2 Qualitative Changes in Floral Scent Composition

Beyond quantitative effects, temperature elevation induces compound-specific responses that fundamentally alter the qualitative composition of floral scent bouquets. Different volatile compounds within a floral blend respond differently to temperature increases due to variations in their physicochemical properties, biosynthetic regulation, and thermal stability (Niinemets & Reichstein, 2002). This differential sensitivity disrupts the characteristic compound ratios that constitute species-specific floral scent signatures, potentially impairing the ability of specialist pollinators to recognize their host plants (Farré-Armengol et al., 2014).

A striking demonstration of this phenomenon was reported by Cordeiro and Dötterl (2023a) in strawberry (*Fragaria × ananassa*), where a global warming scenario of +5°C completely abolished floral scent emission. Under optimum conditions (day 23°C/night 13°C), strawberry flowers emitted 10.45 ng of scent per flower per hour, dominated by *p*-anisaldehyde (81.9%), along with seven other compounds including benzyl alcohol, methyl salicylate, and (E,E)- α -farnesene. Under the warmer scenario (day

28°C/night 18°C), no detectable scent was emitted, representing a complete loss of the olfactory floral signal.

In buckwheat (*Fagopyrum esculentum*), increased temperatures resulted in threefold less floral scent emission and a qualitatively different composition, with key compounds such as linalool and indole disappearing entirely, while 2- and 3-methylbutanoic acid remained dominant at both temperature regimes (Cordeiro & Dötterl, 2023b). Notably, oilseed rape (*Brassica napus*) demonstrated remarkable thermal resilience, maintaining stable scent emission dominated by *p*-anisaldehyde and linalool across temperature treatments, highlighting species-specific sensitivity to thermal stress (Cordeiro & Dötterl, 2023b).

In *Petunia × hybrida*, increasing ambient temperature leads to a decrease in phenylpropanoid-based floral scent production, attributed to the downregulation of scent-related structural genes and the upregulation of negative regulators of scent biosynthesis (Xin et al., 2017). These findings collectively demonstrate that elevated temperatures can both reduce overall emission rates and fundamentally alter the informational content of floral scent signals.

4. Impact on Bee Olfactory Physiology and Foraging Behavior

4.1 Bee Olfactory System and Thermal Sensitivity

Bees possess a highly sophisticated olfactory system localized primarily in their antennae, which serve as the principal sensory organs for detecting floral VOCs. The antennal flagellum bears thousands of olfactory sensilla, predominantly pore plate sensilla in honeybees (*Apis mellifera*), which are distributed over the last eight sub-segments of the worker's antennae (Esslen & Kaissling, 1976). These sensilla house olfactory receptor neurons (ORNs) that bind volatile molecules and transduce chemical information into neural signals processed by the antennal lobes and mushroom bodies of the brain (Sandoz, 2011).

Recent research has revealed that heat stress severely compromises bee olfactory function. Pérez Ortega (2024) reported on a study in which exposure of bumble bees (*Bombus pascuorum* and *B. terrestris*) to simulated heat wave conditions (40°C for approximately 3 hours) reduced antennal electrophysiological responses to floral scent compounds (ocimene, geraniol, nonanal) by up to 80%. Critically, these olfactory impairments did not recover even after 24 hours of rest at cooler temperatures, indicating potentially long-lasting or permanent damage to sensory neurons. Wild *B. pascuorum* exhibited lower resilience than commercial *B. terrestris*, and female worker bees, which are the primary foragers, were more susceptible than males.

4.2 Temperature Effects on Bee Foraging Behavior

Elevated ambient temperatures profoundly alter bee foraging dynamics through multiple interacting mechanisms. Studies on *Bombus terrestris* demonstrated that at 32°C compared to 24°C, flower visitation time decreased while visitation rate and flight speed increased, consistent with the reduction in flight metabolic rate at higher temperatures (Marriott et al., 2024). However, the number of foraging

trips per worker decreased at elevated temperatures, suggesting that despite reduced energetic costs of flight, sustained foraging at high temperatures induces physiological stress.

Colony-level consequences are equally significant. Colonies of *Bombus impatiens* maintained at constant 35°C exhibited increased thermoregulatory fanning behavior but failed to maintain optimal nest temperatures (30–33°C), resulting in increased colony abandonment and reduced offspring production (Parsons et al., 2024). This trade-off between thermoregulation and foraging effort under thermal stress has direct implications for colony fitness and population sustainability.

Furthermore, flower temperature itself influences pollinator preferences. Apland and Koski (2025) demonstrated through field manipulations that when air temperature exceeded 30°C, pollinators preferentially visited cooler flowers, while at cool air temperatures, flies spent more time in warmer flowers. These findings underscore the complex, context-dependent nature of temperature effects on pollinator behavior and floral selection.

5. Dual Disruption of Plant-Pollinator Chemical Communication

The convergence of temperature effects on both floral scent production and bee olfactory perception creates a compounding “dual disruption” of chemical communication between plants and their pollinators. On the plant side, elevated temperatures alter the quantity, composition, and temporal patterns of floral VOC emission, degrading the quality of the chemical signal available to pollinators (Farré-Armengol et al., 2014). On the pollinator side, heat stress impairs the sensory apparatus responsible for detecting and processing these signals (Pérez Ortega, 2024). The net result is a progressive breakdown in the fidelity of chemical communication that has been fine-tuned through millions of years of coevolution.

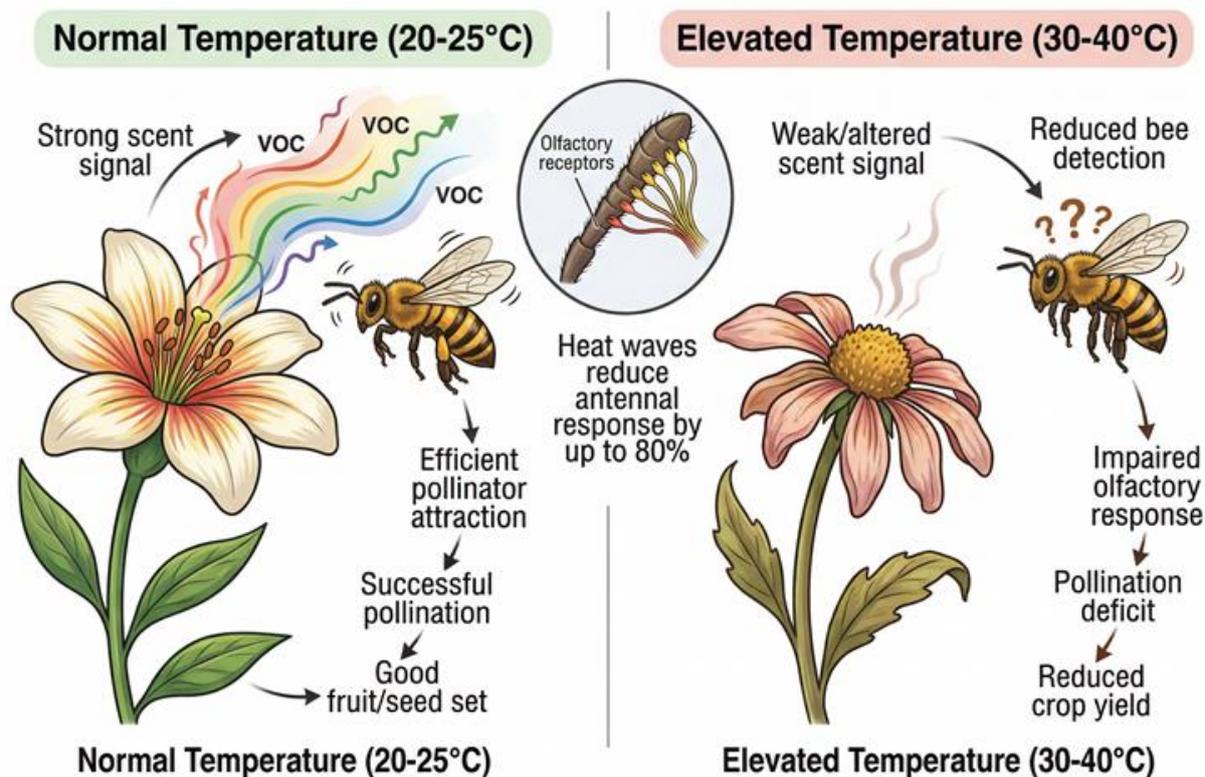


Figure 3: Disruption of Chemical Communication Between Flowers and Bee Pollinators Under Elevated Temperature

This dual disruption is further compounded by phenological shifts driven by climate change. As warming advances flowering times, temporal mismatches between flower availability and pollinator emergence can reduce the overlap between mutualistic partners (Burkle & Runyon, 2017). When combined with altered scent signals and impaired olfactory detection, these phenological shifts create a multi-layered threat to pollination efficiency.

The agricultural implications are substantial. Bee-pollinated crops including strawberry, buckwheat, almonds, and numerous fruits and vegetables face potential yield losses as warming disrupts the chemical signaling essential for efficient pollination. Cordeiro and Dötterl (2023a) noted that the complete loss of floral scent in strawberry under a +5°C warming scenario could significantly reduce pollinator attraction, given that visual cues alone are less effective for

long-range flower detection. The differential sensitivity of crop species to thermal stress—with some species like oilseed rape showing resilience while others like buckwheat and strawberry are highly vulnerable—necessitates species-specific assessments of climate change impacts on pollination services (Cordeiro & Dötterl, 2023b).

Climate change also threatens wild pollinator populations. Bumble bees, adapted to cooler climates, are particularly vulnerable to warming temperatures (U.S. Fish and Wildlife Service, 2023). Temperature has been identified as the single largest climate variable affecting bumble bee occupancy, with heat waves decimating both bee populations and the native floral communities they depend upon. The synergistic effects of habitat loss, pesticide exposure, disease, and climate change create a compounding crisis for pollinator conservation globally (UC Davis, 2022).

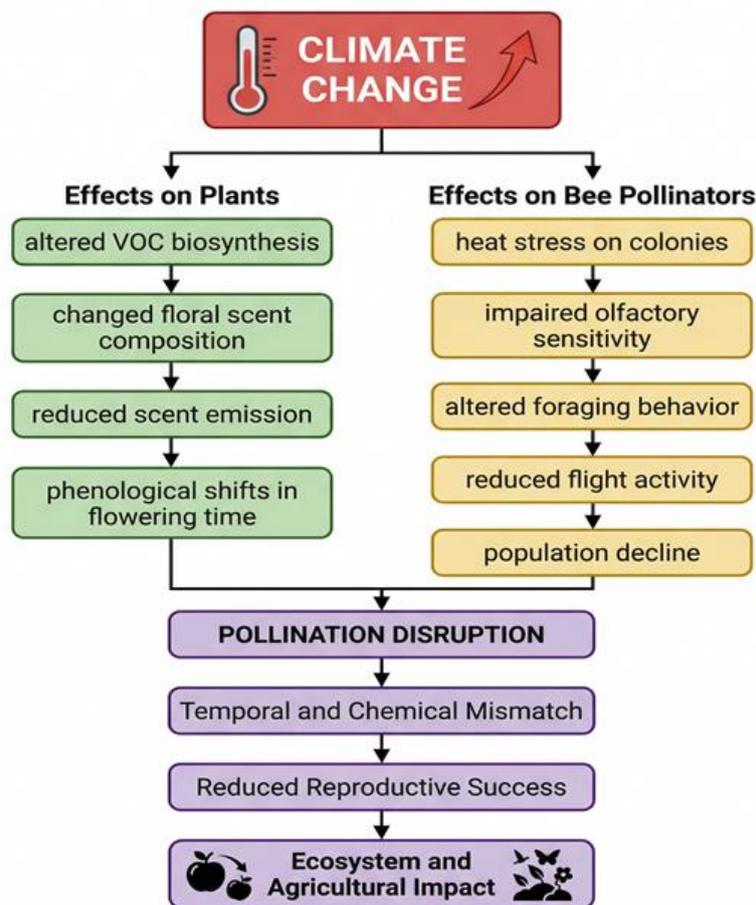


Figure 4: Cascading Effects of Climate Change on Plant-Pollinator Chemical Communication

6. Mitigation Strategies and Future Research Directions

Addressing the impacts of temperature on floral scent and bee pollination requires an integrated approach spanning molecular biology, ecology, agriculture, and conservation. Several key strategies and research priorities emerge from the current literature.

First, breeding and genetic engineering approaches offer potential for developing thermally resilient crop varieties that maintain robust floral scent emission under elevated temperatures. Understanding the molecular basis of species-specific thermal resilience, as demonstrated by oilseed rape's stable scent emission across temperature treatments (Cordeiro & Dötterl, 2023b), could inform the identification of heat-tolerant alleles and regulatory elements that can be introgressed into thermally sensitive crops.

Second, landscape-level conservation strategies should prioritize the maintenance

and restoration of diverse floral resources and pollinator habitat. Climate-smart planting schemes that incorporate species with complementary thermal tolerances can buffer pollination networks against temperature-induced disruptions. Microclimate management through shading structures, windbreaks, and water features in agricultural settings may help maintain conditions favorable for both floral scent emission and pollinator foraging.

Third, further research is needed to elucidate the molecular mechanisms underlying temperature-induced changes in floral scent biosynthesis. While transcription factors such as ODO1, EOBI, and EOBI have been characterized in model species, the molecular basis of thermal sensitivity in these regulatory networks remains poorly understood (Li et al., 2024). The role of heat shock factors, such as HSF19, in modulating scent gene expression under thermal stress warrants further investigation.

Fourth, long-term field studies are essential to quantify the realized impacts of progressive warming on plant-pollinator interactions in natural and agricultural ecosystems. Laboratory and controlled-environment studies, while valuable for mechanistic understanding, cannot fully capture the complexity of real-world interactions involving multiple stressors, behavioral plasticity, and community-level dynamics.

CONCLUSION

The relationship between temperature, floral scent production, and bee pollination represents one of the most consequential yet under-examined dimensions of climate change biology. This review has demonstrated that floral volatile emissions follow temperature-dependent response curves, with optimal emission typically occurring between 25–30°C and significant quantitative and qualitative alterations occurring at both suboptimal and supraoptimal temperatures. The compound-specific nature of these temperature responses means that warming not only increases or decreases total emission rates but fundamentally alters the chemical identity of floral scent bouquets, potentially disrupting species-specific recognition signals.

Simultaneously, heat stress severely impairs bee olfactory sensitivity, with heat wave exposure reducing antennal responses by up to 80% and causing potentially irreversible damage to sensory neurons. This dual disruption of chemical communication—weakened signals from plants and degraded reception by pollinators—threatens the integrity of plant-pollinator mutualisms that sustain both natural ecosystems and agricultural production systems.

The differential vulnerability of plant species to thermal disruption of scent signaling highlights the need for species-specific risk assessments and targeted mitigation strategies. Future research should prioritize the molecular mechanisms of thermal sensitivity in scent biosynthesis pathways, the development of heat-resilient crop varieties, and the

implementation of landscape-level strategies that buffer pollination networks against the cascading effects of climate change. Given that approximately one-third of global food production depends on bee pollination, safeguarding the chemical dialogue between flowers and their pollinators is essential for food security and ecological resilience in a warming world.

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Author Contribution:

All authors have participated in critically revising of the entire manuscript and approval of the final manuscript.

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