Can Plants Coordinate Flowering?

A Literature Review and A Pilot Study Evaluating *Collinsia heterophylla* as a Model for VOC-Mediated Reproductive Strategies.

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Can Plants Coordinate Flowering? A Literature Review and A Pilot Study Evaluating *Collinsia heterophylla* as a Model for VOC-Mediated Reproductive Strategies.

Kan växter samordna blomningen? En litteraturöversikt och en pilotstudie där Collinsia heterophylla utvärderas som modell för VOC-medierade reproduktionsstrategier.

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Abstract

The role of volatile organic compounds (VOCs) in plant-plant communication has garnered increasing interest. An understudied aspect is that regarding their potential influence on reproductive timing. This study explores, in literature, whether floral VOCs emitted by flowering individuals can alter the phenology or reproductive strategies of neighbouring conspecifics.

Through a synthesis of empirical studies and reviews, this paper discusses the mixed evidence surrounding VOC-mediated flowering synchronisation. It also explores broader theoretical contexts, such as cue reliability, kin recognition, stigma receptivity, microbial modulation of floral VOCs, and the ecological complexity of signal interpretation. While conclusive evidence for intentional synchronisation remains lacking this study proposes further research incorporating genetic relatedness, environmental stress, and microbial influences to deepen our understanding of floral VOCs in plant communication and evolution.

A pilot study is also performed, where *Collinsia heterophylla* was evaluated for its suitability in future research on VOC-influenced flowering. While it demonstrated some advantageous traits, being an annual, wild species capable of growing and flowering under the experimental conditions, it is also a mixed-mating species which flowers indeterminately, which may limit its usefulness in such studies.

Keywords: Collinsia heterophylla, floral VOCs, flowering synchronisation, plant-plant communication, reproductive strategies

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Abbreviations

Abbreviation	Description
VOC(s)	Volatile Organic Compounds(s)
HIPV(s)	Herbivore Induced Plant Volatile(s)

1. Introduction

The idea that plants are capable of cognition or behaviour has long been met with scepticism, largely due to the absence of a central nervous system. However, a growing body of research challenges this traditional perspective, suggesting that plants can perceive, process, and respond to environmental information in ways that are adaptive and often rapid relative to their life cycle, and this warrants a discussion regarding behaviour and cognition (Karban, 2008, Segundo-Ortin & Calvo, 2021).

Karban (2008) defines plant behaviour as non-random, flexible responses to environmental cues that affect fitness. These include foraging strategies, morphological changes, defence activation, and modulation of reproduction. Such responses are context-dependent, vary between individuals, and may even reflect memory, where past experiences shape future reactions. Plants can process complex, reliable cues to anticipate conditions and adjust accordingly.

Karban (2008) also draws parallels between plant and animal reproductive behaviours. For example, plants may increase nectar rewards under herbivory threat, switch to self-pollination when pollinators are scarce, or re-flower if fertilization fails. Hermaphroditic species may even shift functional gender depending on resource availability. These examples highlight plants' ability to adjust reproductive strategies to environmental conditions.

Segundo-Ortin and Calvo (2021) extend this framework by proposing that plants possess forms of "ecological cognition," challenging the idea that cognition is exclusive to animals. They define it as the ability to perceive, process, and respond adaptively to environmental information, involving context-sensitive behaviour, information integration, and even memory. Plants can combine multiple stimuli, including volatile organic compounds (VOCs), electrical activity, acoustic cues, and light gradients, into coordinated physiological responses. This enables them to sense their surroundings and interact with pollinators, herbivores, competitors, microbes, and even kin. While not conscious in the human sense, such processing appears to enhance survival and reproduction.

Plant communication, especially through volatile organic compounds (VOCs), is an expanding field that challenges traditional assumptions about plant behaviour and cognition. One emerging hypothesis suggests that floral volatiles may play a role not only in pollinator attraction but also in coordinating reproductive timing, potentially leading to synchronised flowering among conspecifics (Caruso & Parachnowitsch, 2016). Understanding the mechanisms and ecological implications of such coordination has relevance beyond our understanding of ecology and evolution of flowering plants. In Agri- and horticulture, synchronised flowering could influence crop yield stability through improved pollen transfer, seed production, and the maintenance of genetic diversity. However, limitations exist. Plants operate without intention in the human or animal sense, and distinguishing between active signalling and passive cueing remains a conceptual and empirical challenge which largely remains to be studied.

Experimental approaches to studying plant–plant volatile communication often rely on airflow to ensure that any observed responses are attributable solely to airborne cues. In a setup by Ninkovic et al. (2013), purified air is first passed through an activated charcoal filter to remove background volatiles before entering a sealed chamber containing the VOC-emitting plants (emitters). As the air flows across the donors, it becomes enriched with their volatiles and is then directed into a separate chamber housing the receiver plants. A unidirectional flow prevents feedback and ensures that volatile transfer occurs only from donor to receiver, while physical separation eliminates the possibility of tactile contact, shared soil, or root exudates influencing the outcome. The receiver chamber's outlet vents air either through adsorbent traps for chemical analysis or directly out of the system, with a constant flow rate maintained to avoid heat or humidity accumulation. Such designs provide a controlled means of investigating how volatile organic compounds, including floral scents, may mediate interactions between plants and potentially influence their development, physiology, or ecological relationships.

This study reviews literature on whether floral volatile organic compounds (VOCs) emitted by flowering plants can influence the flowering phenology or reproductive strategies of neighbouring conspecifics.

Additionally, a small pilot test examined whether *Collinsia heterophylla* could serve as a model species for investigating VOC-mediated flowering synchronisation, using growth in the controlled airflow chambers, designed by Ninkovic et al. (2013), as a proof-of-concept for future experiments.

Rather than focusing in depth on the chemical composition or biosynthetic pathways of VOCs, the emphasis is placed on the biological, ecological, and evolutionary implications of such plant–plant interactions.

2. Literature Study

2.1 Research Questions

This review asks whether plants can in fact respond to floral VOCs by altering their flowering time or other reproductive traits. It further inquiries under what ecological conditions VOC-mediated flowering could be adaptive. Another central question is how floral VOCs should be understood conceptually as signals, cues, or instances of eavesdropping and to what extent such communication may be complicated or disrupted by factors such as microbial interactions or species-specific life histories.

2.2 Method

Relevant literature was identified primarily through keyword searches using Google Scholar, with "flower synchronisation" as the initial search term. Additional articles were sourced through recommendations and direct contributions from the project supervisors, Åsa Lankinen and Velemir Ninkovic.

2.3 Volatile Organic Compounds (VOCs)

One of the mechanisms through with plants interact with their environment and each other is the emission and reception of Volatile Organic Compounds (VOCs) (eg. Karban, 2008, Bouwmeester et al. 2019, Segundo-Ortin & Calvo, 2021). These are chemical signals consisting of compounds with low molecular weight and low vapor pressure (Caruso & Parachnowitsch, 2016) which can relay ecologically meaningful information (Segundo-Ortin & Calvo, 2021). They are emitted by plants from a variety of tissues, including leaves, stems, flowers, and fruits (Caruso & Parachnowitsch, 2016).

These chemical signals mediate a range of interactions, including pollinator attraction, herbivore and pathogen defence, microbial recruitment, and inter-plant signalling (e.g. Karban, 2008, Bouwmeester et al. 2019, Segundo-Ortin & Calvo, 2021). Plant to plant communication (also plant-microbe communication) is within very short distances while plant-insect communication VOCs can travel up to multiple hundred meters (Bouwmeester et al. 2019). These VOC emissions form an ecological language that contributes to plant fitness and survival.

2.3.1 Pollinator attraction

One of the most extensively studied roles of VOCs is their interaction with pollinators. Attracting specific pollinator species can enhance plant fitness by improving the efficiency of pollen transfer and increasing outcrossing rates in flowering plants (Caruso & Parachnowitsch, 2016; Bouwmeester et al. 2019). It is previously well known that flowers use their morphology and colour to communicate visually to target specific pollinator species or group of pollinating insects (Bouwmeester et al. 2019, Rebolleda-Gómez & Wood 2019). An even more precise way to target the ideal pollinators are through floral scent, consisting of floral volatile blends which through coevolution with insects' neurons elicit response from the preferred pollinators to promote the mutualistic interaction (Bouwmeester et al. 2019). A VOC blend has the potential to be more specific in its communication with pollinators than just morphology and colour alone (Bouwmeester et al. 2019). Plants also use VOC blends to attract pollinators by mimicking non-floral attractions, like insects mating partners or oviposition sites (Bouwmeester et al. 2019). This exploitation is costly for the insect's fitness to put energy and effort towards a plant mimic instead of its real target (Bouwmeester et al. 2019).

2.3.2 HIPVs and defence

Another major role VOCs play is in response to herbivore damage. One of the biggest threats that plants face is herbivory and being consumed, commonly by insects. As a defence mechanism, many plants produce secondary metabolites such as nicotine in tobacco or glucosinolates in Brassica (Brosset et al. 2023), which function as chemical deterrents against herbivores. When a plants experience herbivory, often through tissue damage, they emit VOCs known as Herbivore Induced Plant Volatiles (HIPVs), often consisting of green leaf volatiles (Caruso & Parachnowitsch 2016) and can function either to deter herbivorous insects and/or to recruit biological control agents by attracting natural enemies of the herbivores (Bouwmeester et al. 2019, Segundo-Ortin & Calvo 2021, Brosset et al. 2023). Predators, parasites and parasitoids of these herbivores have been shown to react to HIPVs and are attracted to the plant and their prey upon it (Bouwmeester et al. 2019). For certain natural enemies of the herbivores, HIPVs are their only way to locate their prey (Bouwmeester et al. 2019).

HIPVs are also a well-studied aspect of plant–plant communication. While early research in this area faced significant scepticism, it is now increasingly accepted (Caruso & Parachnowitsch 2016). Studies on HIPVs role in plant-plant communications have established that plants exposed to these compounds show an increased defence and/or priming to increase defences (Caruso & Parachnowitsch 2016, Segundo-Ortin & Calvo 2021). Many studies have found that neighbouring plants may eavesdrop on these VOCs and prime their own defences even if they themselves have not taken damage yet (Brosset et al. 2023). Exposure to herbivory lowers the plant's leaf areas available for energy production, or other majorly important organs like flowers and/or seeds can get damaged which have a devastating effect on the plant's overall fitness. But relocating resources to defence instead of growth and/or reproduction is also costly if done unnecessarily (Brosset et al. 2023). Therefore, it is known that priming defences is not the only way in which plants respond to perceived HIPVs, other responses found have been to increase photosynthesis, numbers of flowers or accelerate flowering in an anticipation and compensation of herbivore induced damages (Brosset et al. 2023). Producing more flowers earlier in response to HIPVs may represent a strategy known as reproductive escape, aimed at avoiding herbivory that threatens the reproductive event. Although it is unclear whether seeds and offspring produced following HIPV-induced flowering have the same quality and fitness as those from naturally timed flowering, this strategy may still offer an advantage over missing a reproductive opportunity entirely (Brosset et al. 2023).

For example, in a recent study, Brosset et al. (2023) found that *Brassica rapa oleifera* var. Cordelia plants exposed to herbivore-induced VOCs from neighbouring individuals flowered significantly earlier and produced more flowers than unexposed controls. These plants also showed an increase in photosynthetic activity, despite not experiencing any herbivory themselves. The authors interpret these responses as a form of anticipatory resource reallocation, possibly reflecting a reproductive escape strategy where early flowering helps avoiding damage during periods of elevated biotic stress. Plants exposed to herbivory emitted significantly more VOCs than the rest, and released higher levels of several specific VOCs, but only for 48h. The controls showed no difference in total volatile emissions. This suggests that VOCs may serve as environmental forecasting tools, allowing plants to optimize reproductive timing in response to ecological cues.

2.3.3 Microbe communication

Like plant–insect communication, plant–microbe interactions also involve VOCs in a similar way; pathogenic microbes can stimulate VOC production in plants, which in turn induces defensive responses against the pathogens in both plant and its eavesdropping neighbours (Bouwmeester et al. 2019). Liu and Brettell (2019) describe how plants under biotic stress, such as herbivory or pathogen attack, can release root- or leaf-derived volatiles that recruit beneficial soil microbes. These microbes enhance the plant's resistance and may also improve the microbial environment for neighbouring plants, a strategy known as “calling for help.” This mechanism is similar to plant–insect interactions, where the VOCs attract natural enemies of herbivores. In addition to defence, the recruitment of beneficial microorganisms through VOCs or root exudates can aid in nutrient uptake and bolster plant immunity, helping plants adapt to environmental stresses and maintain overall fitness. Although Bouwmeester et al. (2019) states in their review that this communication is much more complex; plants VOCs can be influenced by the microbes or other agents and instead make plant and neighbours more susceptible to herbivory or pathogens. Further complicating these interactions, microbes can infest nectar and other floral tissues, modifying the floral VOC blend by enhancing or suppressing specific compounds, which alters the scent bouquet and consequently affects pollinator attraction (Bouwmeester et al. 2019, Rebolleda-Gómez & Wood, 2019). Microbes can influence plant attractiveness to pollinators, affecting pollen transfer, reproductive success, and potentially ecosystem composition (Rebolleda-Gómez & Wood, 2019). They can also emit VOCs that plants perceive, triggering responses such as altered growth, adding further complexity to these interactions (Bouwmeester et al. 2019).

2.4 Signalling, cues, eavesdroppers and deception

To understand plants communication within their ecosystems it is important to understand different kinds of information transfers. Rebolleda-Gómez and Wood (2019), emphasize in their review that the primary difference lies in the intentionality of the emitter, which becomes especially challenging to determine in plants compared to animals. One way to try and gauge the intention is to study the fitness implication of information transfer, albeit this is not always an easy task either (Rebolleda-Gómez & Wood, 2019). An overview of the main categories of information transfer, including their intentionality, costs, and benefits to emitters and receivers, is provided in Table 1.

‘Signals’ have evolved to relay information to an intended recipient which in turn reacts to the signal, leading to increased fitness for the emitter, and most often the receiver too. Signals are also often identified to be costly to produce but their compounds remain stable. ‘Cues’ on the other hand, are incidental by-products of physiological processes, that can still provide valuable information to a receiver, although they are not emitted with communicative intent and are often less energetically costly nor as stable as signalling compounds (Rebolleda-Gómez & Wood, 2019).

According to Rebolleda-Gómez and Wood (2019), determining whether plant-released volatiles are signals or cues is challenging, as many of these compounds also function as hormones for internal plant signalling, which may be their primary role. This overlap complicates interpretations of their ecological function. Obtaining empirical evidence is further hindered by the fact that most laboratory experiments use VOC concentrations higher than those typically occurring in nature. To identify potential signalling VOCs, the authors suggest focusing on compounds that exhibit qualities such as high concentrations and extended release periods, as these traits might suggest adaptation for communication.

Eavesdropping is the interceptions of signals by unintended receivers (Rebolleda-Gómez & Wood, 2019). Despite the name it is not limited to auditory signals, it could be of any type, olfactory, electrical, chemical or vibrational (Rebolleda-Gómez & Wood, 2019). All signals or cues can be eavesdropped on, which commonly, but not necessarily, come with a fitness loss to the emitter (competition, predators, parasites etc) (Rebolleda-Gómez & Wood, 2019). This poses an evolutionary conflict; the fitness benefit from a successful transmitted signal or the risk of fitness cost from getting eavesdropped on. A straightforward example that Rebolleda-Gómez and Wood (2019) presents is the big and colourful visual flower display and chemical floral volatiles which has clear fitness benefits for both plant and insect, but which can be eavesdropped upon by herbivores. Rebolleda-Gómez and Wood (2019) argues that herbivores would put a higher selective pressure on flowers than pollinators selection pressure, at least in most cases.

Other examples Rebolleda-Gómez and Wood (2019) give on eavesdropping are as discussed above, plants which react to HIPVs released by neighbours and as a response increase their own resistance. It has also been shown that parasitic plants eavesdrop on VOCs to locate their ideal host (Rebolleda-Gómez & Wood, 2019). Plants can also themselves eavesdrop on the presence of parasites in their biotic environment to anticipate attacks (Rebolleda-Gómez & Wood, 2019).

The view of plant communication gets even murkier when considering dishonest and manipulative signals meant to deceive receivers (Rebolleda-Gómez & Wood, 2019). This is usually understood as a clear fitness benefit for the signaller and at a clear cost to the receiver (Rebolleda-Gómez & Wood, 2019). A common example of this is deceptive flowers which lure pollinators without providing a reward in form of nectar or similar (Rebolleda-Gómez & Wood, 2019). It is believed that the evolutionary pressure of honest signals often outweighs the dishonest ones through a positive mutual coevolution (Rebolleda-Gómez & Wood, 2019). Rebolleda-Gómez and Wood (2019) pose the question of what happens if dishonest signals get eavesdropped on which remains to be studied.

Table 1. Overview of types of information transfer in communication, based on intentionality, associated costs and benefits to emitters and receivers. Categories follow definitions by Rebolleda-Gómez & Wood (2019), distinguishing signals, cues, eavesdropping, and manipulative/dishonest signalling

Type	**Intentionality**	**Cost to emitter**	**Benefit to emitter**	**Benefit to Receiver**
Signal	Intentional	High (Costly to produce)	High (Attracts pollinators, mutualists ets.)	Low to high (can help guide appropriate behaviour, e.g. nectar foraging)
Cue	Unintended (byproduct etc.)	Low	None or incidental	Varies (may still extract valuable information)
Eavesdropping	Unintended receiver	High risk (e.g. if exploited)	None	High (e.g. host/prey localisation, avoid herbivory)
Manipulative/ Dishonest	Intentional deception	Varies (Deceptive investment)	High (e.g. deceptive pollination)	Low (fitness loss for receiver misled by false information)

2.5 Flower synchronisation

2.5.1 Hypothesis

Caruso and Parachnowitsch published 2016 a hypothesis that floral VOCs are used by plants as social cues regarding neighbours' reproductive state. They propose that plants might use this scented information to gauge conspecifics patch density and/or competition and respond by adjusting traits such as nectar production, flower size and/or flowering time to optimize fitness. Caruso and Parachnowitsch (2016) suggest that perception of floral volatiles might be an understudied yet significant aspect of plant communication and adaptation since it might affect fitness directly through pollination and mating. They mean that since plants already react to other types of VOCs with changes in their phenotype, like increased defences, it would not be impossible for floral VOCs to elicit reproductive phenotype changes. They argue that floral volatiles are likely perceivable by plants, as chemical ecologists hypothesize, because their chemical composition is similar to herbivore-induced plant volatiles (HIPVs), which are known to be detectable by plants. Similarly, they cite evidence from reproductive biology suggesting that female plants in gynodioecious species, such as *Lobelia siphilitica*, adjust their flower-opening rate according to the frequency of neighbouring hermaphrodites. This adjustment is likely mediated by floral volatiles, as studies have ruled out other potential mechanisms for perceiving this information.

Since all parts of plants emit VOCs, Caruso and Parachnowitsch (2016) speculate, similarly to Rebolleda-Gómez & Wood (2019) that what decides the likelihood of that the VOCs are used as signals or cues are dependent on two factors, the concentration of the specific VOCs (blends) in the air surrounding the plants, and the duration of VOC release. The more and for longer time the likelier it is that the VOC can be perceived by another organism and Caruso and Parachnowitsch (2016) point to floral volatiles being emitted at higher rates than leaf volatiles and are therefore more likely able to be perceived by other plants. They also argue for the nuanced and stage specific role of floral volatiles; a bud got a different VOC blend than an open flower, an unpollinated flower got a different VOC blend than a pollinated one. Over 1700 different VOC compounds have been identified as floral volatiles among angiosperms with variation in concentration and makeup between species, which is more diverse than VOCs emitted from leaf or stems (Caruso & Parachnowitsch, 2016).

Caruso and Parachnowitsch (2016) defines the mating environment as "environmental factors that affect plant reproduction", which can include conspecific plants that act as mates, pollinators and heterospecific plants that influence pollination (through competition or facilitation). For instance, the proportion of pollinated to unpollinated flowers can serve as an indirect indication of pollinator availability and activity within a given ecosystem. They argue that since the information of floral volatiles mostly convey mating information it is likely that perceived information therefor results in changes in floral and reproduction traits, probably on traits with a relatively short lag time for the adaptive plasticity to remain advantageous to plant fitness. Caruso and Parachnowitsch (2016) gives examples of such traits: the rate of flower opening, since it affects pollination and can open within just a few minutes (as seen by other environmental factors like temperature or light availability). Accelerating flower opening could be advantageous in the presence of a competitor, more open flowers would result in a bigger floral display to attract pollinators. Likewise nectar production could be altered by perception of a competitor, an increase in nectar production would attract more pollinators. The floral volatile production itself could be another trait which could be changed at the presence of a competitor since it too would attract more pollinators (Caruso & Parachnowitsch, 2016).

Since getting things wrong in communication is costly for fitness (Segundo-Ortin and Calvo 2021, Brosset et al. 2023), reliable signalling is essential for neighbouring plants to respond appropriately to VOCs in the context of the mating environment (Caruso & Parachnowitsch, 2016). Caruso and Parachnowitsch (2016) mean that under three conditions it is more likely for the cues to be accurate; (1) in high plant densities, means closer neighbours which gives a higher chance for the VOCs to reach them. (2) higher temperatures have been shown to enhance floral volatile emissions, raising their atmospheric concentration and thereby improving the likelihood of detection by neighbouring plants, and (3) plants with highly specific floral volatiles also increase the reliability of the information.

Caruso and Parachnowitsch (2016) paper only presented a hypothesis, but they give suggestions on methods to empirically test it. They propose three experimental approaches: (1) testing whether a flowering plant responds to a co-flowering neighbour (regardless of cue type), (2) isolating the effect of floral volatiles specifically, and (3) synthetically manipulating VOC blends to identify which compounds elicit responses. Appropriate controls include both negative (no VOC exposure) and alternative VOC exposures (e.g., non-floral volatiles). These approaches can be implemented in both laboratory and field settings.

2.5.2 Studies on Plant Volatiles, Flowering and Kin Interactions

Brosset et al. (2023) HIPVs on Brassica rapa

To test whether volatile cues influence flowering phenology, Brosset et al. (2023) exposed *Brassica rapa oleifera* var. Cordelia to HIPVs from conspecifics attacked by *Plutella xylostella*, placing receiver plants 15 cm downwind in climate-controlled chambers. The study showed that *B. rapa* plants exposed to volatiles from herbivore damaged neighbours flowered earlier and produced more flowers compared to the control as well as the infested plants themselves. Receiver plants from undamaged emitters also flowered earlier (but did not produce more flowers) than the plants which did not receive any VOCs: This occurred despite attempts to avoid potential flower synchronization by selecting only plants that had neither flowers nor visible flower buds at the start of the experiment. The study found that both herbivory-exposed plants and those exposed to HIPVs initially had higher photosynthesis rates, which declined after three days. Brosset et al. (2023) attribute this decline to the onset of flowering They also showed that exposure to HIPVs did not influence the overall VOC emission rates neither before nor after the herbivore feeding.

Producing more flowers when the perceived herbivory threat is high is a known strategy called reproductive escape, to flower earlier before getting eaten (Brosset et al. 2023). Brosset et al. (2023) were surprised that even plants exposed to volatiles, but not herbivore induced, also flowered earlier. They discussed that it might be the higher concentration of VOCs in the air circulation that might cause the plants to anticipate competition and thus flower earlier to secure resources to reproduce although these plants did not show an increase in photosynthesis as the HIPV exposed plants had, raising the question of where the resources came from. Brosset et al. (2023) also asks the question of whether it matters what stage a plant is in for it to be influenced and respond to VOCs of different kinds.

Fricke et al. (2019) Floral volatiles on flower synchronisation in Brassica rapa

However, in a directly related study on *Brassica rapa* Maarssen, Fricke et al. (2019) tested the hypothesis proposed by Caruso and Parachnowitsch (2016), that floral volatiles can influence the phenology of not-yet-flowering conspecifics, but found no evidence of flowering synchronization. Their data suggest that, at least in short-lived annuals like *Brassica rapa* Maarssen, plants may not reliably respond to floral volatile cues from neighbours, or that such cues may not be ecologically relevant enough to drive phenological changes in this context.

B. rapa Maarssen is annual and relies on insect pollination for outcrossing since it is self-sterile. The flowering emitter plants where on average 14 days older than the conspecific receiver plants, which was not sufficient for synchronisation. It is unknown in what developmental stage flowering synchronization could be possible: time to first bud, duration of buds until flower opening or maybe flower duration.

Fricke et al. (2019) discuss if the fitness benefit from synchronized flowering is marginal enough that it is only a viable option under certain circumstances. As previously argued by Caruso and Parachnowitsch (2016) it might be advantageous regarding pollen transfer efficiency but at the same time it might cause competition for pollinator resources and then asynchronous flowering might be preferred (Fricke et al. 2019).

Similarly, the argument for synchronisation can be made regarding threats of herbivory, flowering together could lower the risks of florivores on individual flowers but evidence of escaping herbivores through asynchronous flowering has also been found. It is not known on what side of the argument *B. rapa* Maarssen falls. Fricke et al. (2019) makes the case that HIPVs could be more valuable as a signal to induce flowering even though it might cause flowering before the optimal timing for the individual regarding gathered resources and could reduce the overall seed quality. Signals and cues might only be beneficial when earlier than optimal flowering is essential to reproduce at all, e.g. when threatened with herbivory or other stressors (reproductive escape strategy).

Mass flowering plants show higher levels of synchronisation compared to constant flowering plants. This means that stronger effects of VOCs on flowering in conspecifics are to be expected in species with a shorter flower duration when synchronisation might play a bigger role to their fitness (Fricke et al. 2019). *B. rapa* Maarssens flowering period of 30-40 days (with some individual variation) might be substantial enough to overlap for effective outcrossing without communicated synchronization. And some plants use other environmental cues (e.g. heavy rain) to synchronise and in those cases, VOCs might be redundant as plant-plant communication.

It might be that the benefit from synchronization does not outweigh the costs of it. The distance in which VOCs would be in large enough concentrations to function in communication might not be large enough to reach outside the emitters own patch even though synchronisation with other patches would be more beneficial for gene flow.

Fricke et al. (2019) suggest that further studies should be made on other species, preferably those who only flower once before death to maximize the fitness benefits of flowering synchronization, especially if the flowering is known to be inducible by ethylene exposure. They suggest members of the bromeliad family, fitting these criteria.

Torices et al. (2018) Kin discrimination

Further supporting aspects of the hypothesis of flower synchronisation through communication is Torices et al. (2018) study on kin discrimination and how that relates to reproductive strategies. Pollinators are attracted by large flower displays, especially important when pollinators are few then larger flower displays can lead to more pollination. The study showed that the insect pollinated plant *Moricandia moricandioides* uses a “magnet effect” to attract pollinators to the whole flowering patch and not only to the own individual. This reproductive strategy only results in fitness benefits if the individuals in the patch are kin and share the same genes. Kinship's influence on altruism and mating behaviour is well understood in many animals. Some birds display more altruistic behaviour when with kin, and *Drosophila* fight less with kin over females, plants show kin recognition, behaving less aggressively in resource gathering (root growth) (Torices et al. 2018). The study showed that individuals grown in patches with related neighbours invested more resources into producing larger flower displays than those grown without kin, presumably to share the "magnet effect" with their relatives. Although the study could not show by which mode of communication was used to recognise kin in neighbours, some kind of signal or cue did affect the flowering phenology in individuals.

3. Pilot Study

3.1 Aim of study

This study presents an initial investigation into the suitability of *Collinsia heterophylla* as a model species for future research on flower synchronisation through volatile organic compound (VOC) communication. The primary goal was to determine whether the species can grow, flower, and complete its life cycle under the controlled conditions of the airflow chamber system designed by Ninkovic et al. (2013), which are intended for use in future experiments. Rather than testing for treatment effects, the study aimed to establish baseline information on growth performance, floral morphology, and nectar production, providing reference values and documenting the range of natural variation in these traits. Such baseline data are for identifying which traits are reliably measurable, estimating natural variability, and informing sample size requirements for detecting VOC-related effects in later experiments. As it may also be of interest to conduct herbivore-induced plant volatile (HIPV) studies with *C. heterophylla* in the future, a simple “acceptance test” was carried out using the green peach aphid (*Myzus persicae*) to assess the species’ suitability for insect-related assays.

3.2 Collinsia heterophylla

Collinsia heterophylla is native to California, annual, bee pollinated, mixed-mating species (Lankinen & Hydbom 2017, Larsson et al. 2021). This means they rely on pollinators for outcrossing but can also self-pollinate. It typically grows on drier north-facing slopes together with other co-flowering species; commonly *Allium, Artemisia, Castilleja, Clarkia, Delpjinium, Helanthus, Lupinus, Mumulus, Silene* despite risking competition for the pollinator resource (Larsson et al. 2021).

Both Lankinen and Hydbom (2017) and Larsson et al. (2021) showed that outcrossing success can be linked to floral traits such as flower size and colour or delayed self-fertilization (temporal separation of female and male organs). *C. heterophylla* has on average 50% outcrossing rate (range: 0.29-0.84) (Larsson et al. 2021). The usual pollinators of *C. heterophylla* are long-tongued bee species (e.g. Osmia, Bombus, Anthophora, Habropoda), as its bilabiate corolla and zygomorphic flowers possess a keel that must be pressed down by a relatively heavy insect, like a bee, for the pollen and stigma to become accessible (Larsson et al. 2021). The flowers are positioned in whorls on the flowering stem, and they flower indeterminate, bottom up, allowing a prolonged flowering period. The four anthers become reproductive and release pollen sequentially (about one per day) before the style elongates and the stigma becomes receptive. Pollinators can collect pollen from day 1-4 after flower opening (Larsson et al. 2021), increasing the chances for outcrossing while still allowing for self-fertilization (Lankinen & Hydbom, 2017).

Larsson et al. (2021) conducted a study on *C. heterophylla* and analysed the floral emissions. Approximately 13 ng of floral volatiles were collected per flower. They identified 26 volatile compounds distinct from flowers, mostly terpenoids such as β-myrcene, (Z)- and (E)-β-ocimene, and sesquiterpenes like (E)-α-bergamotene and β-sesquiphellandrene. These compounds are well established attractants for bees. Plants that use insect pollination can have a rich bouquet of floral volatiles although it has been shown that the insects in question react to specific compounds in the blend. Larsson et al. (2021) also noted a lack of humanly perceived floral scent.

Lankinen and Hydbom (2017) raise the conflict of stigma receptivity. Earlier receptivity helps ensure that the plant's pollen fertilizes the ovules first (benefiting the male function), while later receptivity gives the plant more time to acquire resources or better pollen, improving seed quantity and/or quality (benefiting female function) (see Table 2). Delayed stigma receptivity benefits the maternal reproduction by enhancing pollen competition (more pollen is collected on the stigma before its receptive, ensuring a fair start in the pollen tube race towards the ovules at the base of the pistil).

Table 2. Advantages and disadvantages to early and late stigma receptivity

Stigma receptivity	**Advantages**	**Disadvantages**
Early, benefit paternal	+ Secure paternity	- Suboptimal pollen quality
Late, benefit maternal	+ Optimized pollen quality + Successful fertilization + More gathered resources + More seeds	-Risk of missing reproductive chance

3.3 Research question

Is *Collinsia heterophylla* a suitable model species for future studies on flower synchronisation and herbivore-induced plant volatile (HIPV) communication in controlled airflow chamber systems? Suitability is here assessed through its ability to grow, flower, and complete its life cycle under controlled conditions, as well as through measurable traits reflecting vegetative growth (height, side shoots), reproductive investment (flower number, flower size, nectar volume). A further question is whether the green peach aphid accepts *C. heterophylla*, which would indicate its potential usefulness in future defence-related VOC studies.

3.4 Material and method

3.4.1 Plant material

C. heterophylla commercial seeds supplied from Plant World Seeds were planted shallowly in plant soil mixed with sand (2:1) and after 1-2 days in room temperature transferred to a cold room until the cotyledons were visible 10 days later before being moved to a greenhouse. 15 days later they were replanted, one plant per pot (0,45L), and moved to the controlled airflow chambers (figure 2) for about 8 weeks.

3.4.2 Controlled airflow chambers

The experimental setup made use of transparent, air-sealed plastic chambers designed to enable controlled transfer of VOCs. Each chamber features two openings: a larger one located lower on one side for air intake and watering access, and a smaller opening positioned on the opposite upper side to accommodate tubing.

An air pump could be connected to the tubing, drawing air through the larger opening, across an emitter plant inside the first chamber. As the air passed through, it collected volatile organic compounds (VOCs) released by the plant. The VOC-laden air then exited through the upper opening and could either be directed into a second chamber containing a receiver plant, or into a collection apparatus for further analysis.

Figure 1. Collinsia heterophylla in the controlled airflow chamber. The inlet and outlet of air are marked in red.

3.4.3 Evaluation

Once all six plants had begun flowering 8 weeks later, they were evaluated twice, three days apart. The plants and flowers were measured in five different ways to establish baseline morphological and floral trait data for *C. heterophylla* grown in the airflow setup.

Plant height

The distance from the soil to top of the terminal shoot when lightly pulled taut. Measured with a simple ruler with 0.5 cm accuracy.

Number of side shoots

The number of side shoots, which contained flowers, buds or signs of wilted flowers, were counted.

Number of flowers in terminal shoot

The number of individual flowers were counted in the terminal shoot, including buds and signs of wilted flowers.

Flower size

Three different measurements of flower size were taken (see figure 3).

1. The height of the banner (b)
2. The length of the keel (k)
3. The length of the corolla tube (t).

The ruler was placed as indicated by the red line in all three cases and measurements were taken with 0.1 cm accuracy with the help of magnifying glasses.

Three flowers per plant were measured. When possible, they were the same flowers that nectar was collected from (described below) and when that was not possible the flowers were semi randomly chosen, not taken from the same shoot.

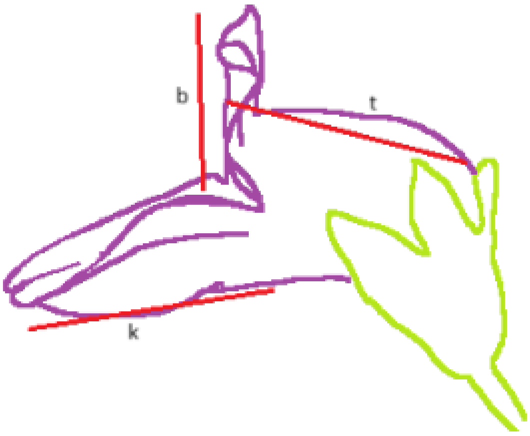

Figure 2. Illustrative drawing of a Collinsia heterophylla flower, bilabiate corolla, in profile. Three points of measurements are marked 1. The height of the banner (b) 2. The length of the keel (k) 3. The length of the corolla tube (t).

Nectar volume

Microcapillary glass tubes (1 µL capacity, 3.2 cm length) were inserted into the corolla tube of flowers in which all four stamens had dehisced. The length of the nectar-filled portion of the tube (X) was then measured with a ruler under a stereoscope. Given that the total tube length (3.2 cm) corresponds to 1 µL, the nectar volume (Y) was calculated as: $Y = \frac{Xcm}{3.2cm} * 1\mu L$.

3.4.4 Aphid acceptance test

Myzus persicae (green peach aphid), reared on *Brassica* species under controlled conditions, were placed in groups of ten in test tubes, which were then positioned at the base of young *C. heterophylla* seedlings, bearing only a few fully developed true leaves, inside closed containers (see Figure 3). After three hours, the number of aphids present on the plant itself was counted. This number was used to determine the acceptance rate, meaning the proportion of aphids that chose to settle on the plant compared to the total number introduced. The experiment was conducted with ten replicates.

Figure 3. Young Collinsia heterophylla plants (left) at start of aphid acceptance test. Aphids were places in the testing tube at the base of the plant. The ten replicates of the aphid acceptance test (right). Glass tubing ensuring no aphids escape.

3.5 Results

All plants survived and flowered in their controlled airflow modules.

3.5.1 Evaluation in the controlled airflow modules

Table 3. Average plant height, number of side shoots, number of flowers, flower size and nectar volume in the terminal shoot at the time of first and second measurement (three days apart) for plants grown in controlled airflow chambers. Bracketed numbers represent the standard deviation across all six plants.

	First point of measure, (SD)	Second point of measure, (SD)
Plant height (cm)	24.3 *(5.32)*	25.3 *(5.31)*
Number of side shoots	19.2 *(2.41)*	19.3 *(2.29)*

Number of flowers in terminal shoot	16.5 *(7.01)*	20.0 *(6.98)*
Flower size, banner (cm)	0.53 *(0.13)*	0.58 *(0.10)*
Flower size, keel (cm)	0.66 *(0.17)*	0.72 *(0.13)*
Flowe size corolla tube (cm)	0.52 *(0.10)*	0.54 *(0.06)*
Nectar volume (µL)	0.12 *(0.14)*	0.10 *(0.10)*

Plant height

The plants showed an average height of 24.3 ± 5.32 cm (mean ± SD) at first measure and grew on average 1cm to the second measure three days later.

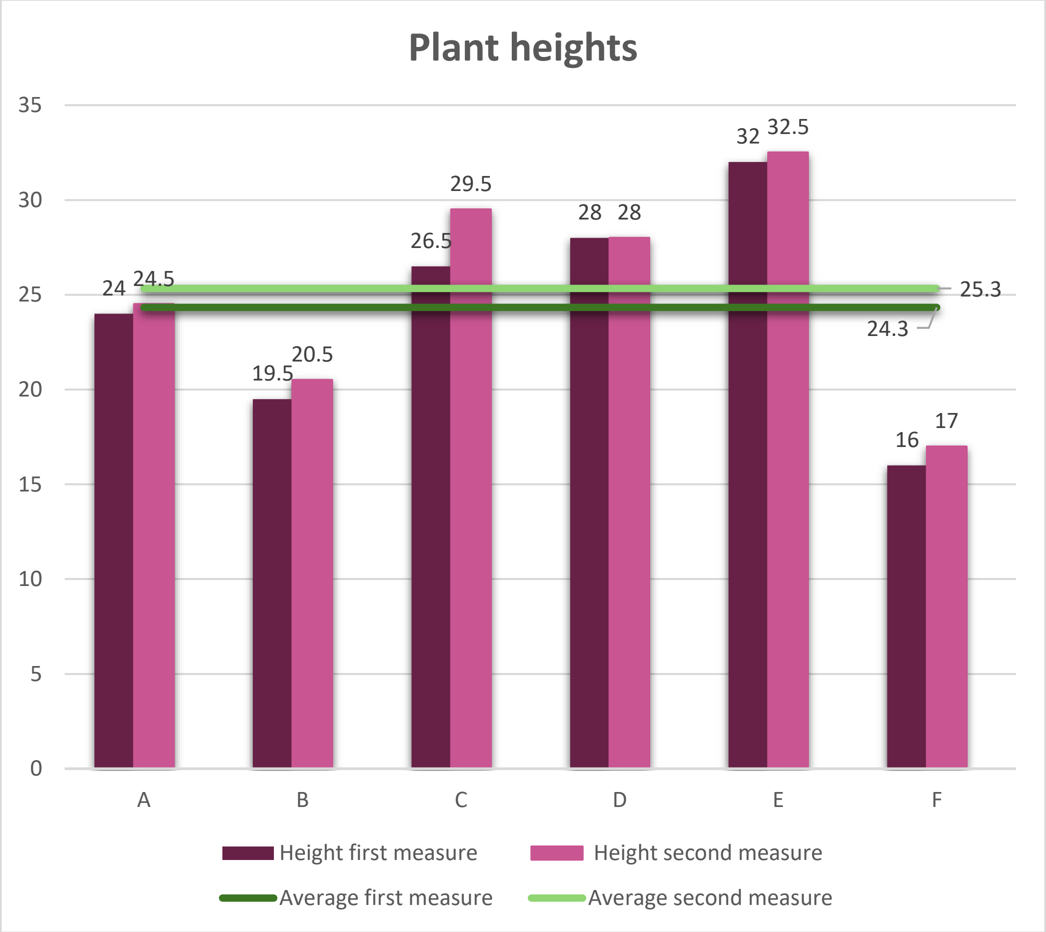

Figure 4. Graph showing the results of plant height of plants grown in controlled airflow modules, each column cluster representing one plant, the left column at first measure and second measure the right column. The lines showing the overall average at both times of measurement.

Number of side shoots

The plants showed an average number of side shoots of 19.2 ± 2.41 (mean ± SD). Only one plant grew a new shoot within three days, changing the overall average to 19.3.

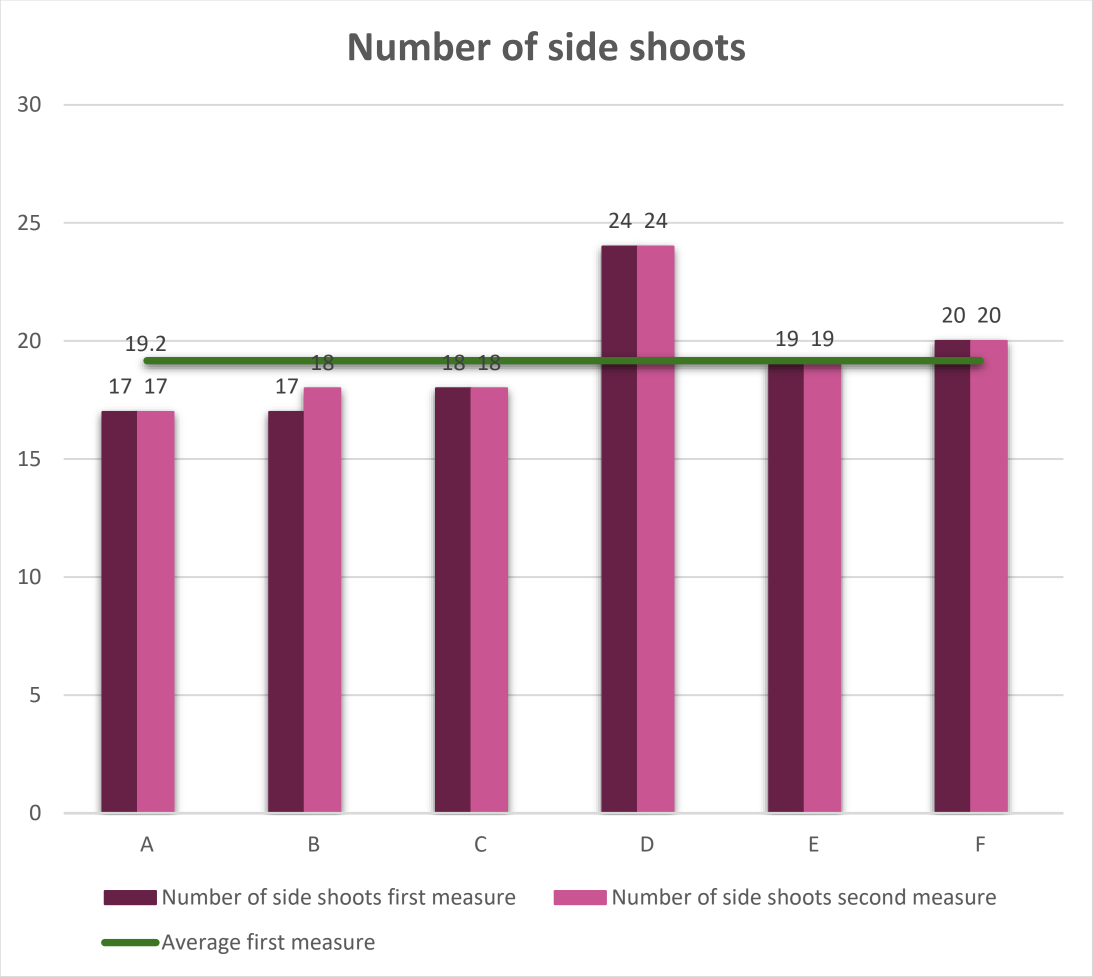

Figure 5. Graph showing the results of number of side shoots, each column cluster representing one plant, the left column at first measure and second measure the right column. The line showing the overall average.

Number of flowers in terminal shoot

The plants showed an average number of flowers of 16.5 ± 7.01 (mean ± SD) at first measure and grew on average 3.5 more to the second measure three days later totalling 20.0 ± 6.98

Figure 6. Graph showing the results of number of flowers in terminal shoot, each column cluster representing one plant, the left column at first measure and second measure the right column. The lines showing the overall average at both times of measurement.

Flower size

Average banner size increased slightly from 0.53 ± 0.13 cm (mean ± SD) at the first measurement to 0.58 cm at the second measurement. The keel size rising from 0.66 ± 0.17 cm (mean ± SD) to 0.72 cm between measurements. Corolla tube length remained stable, increasing only from 0.52 ± 0.10 cm (mean ± SD) to 0.54 cm. Overall, all three floral structures exhibited small increases in mean size between the two time points.

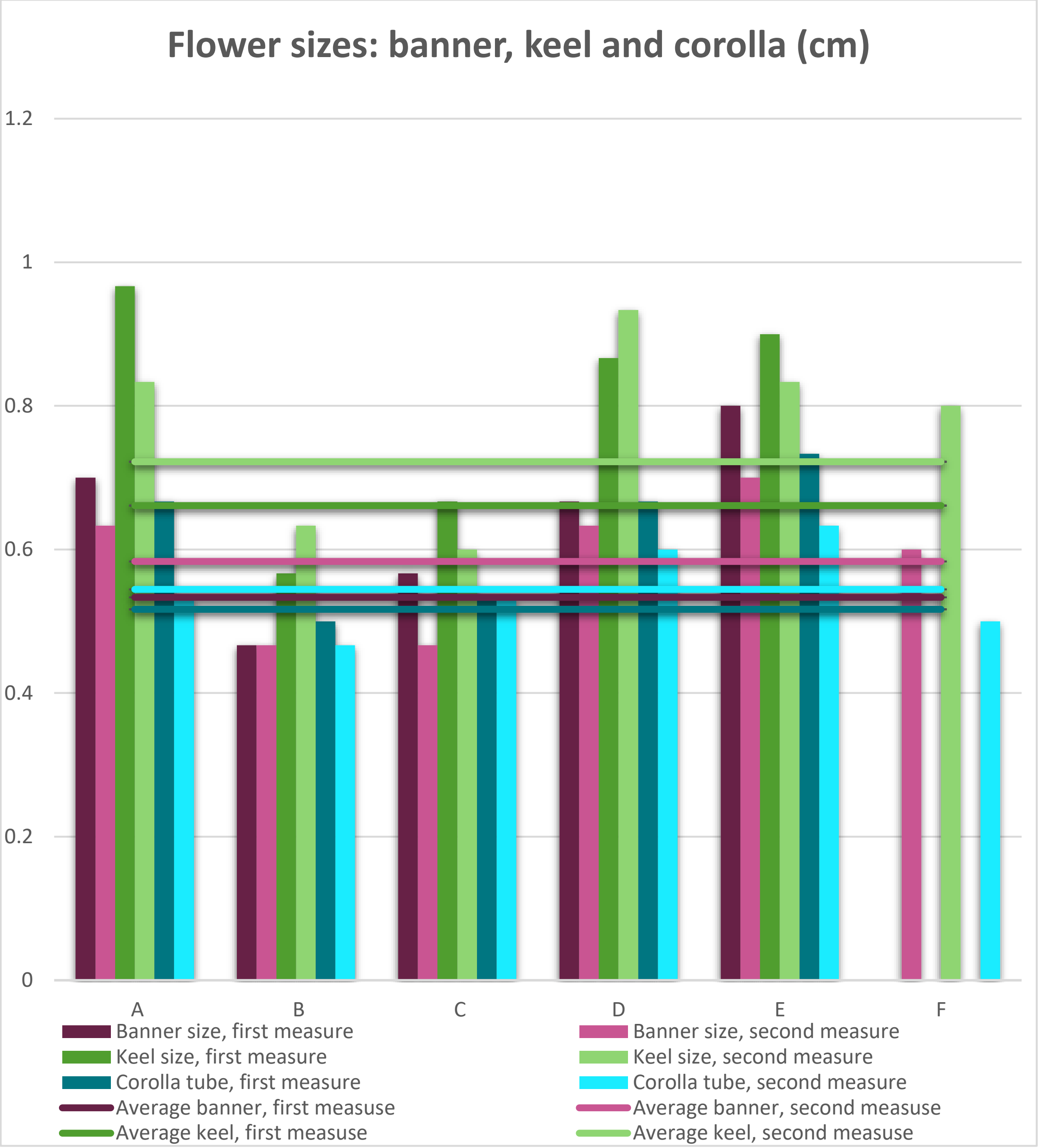

Figure 7. Flower size measurements (cm) of banner, keel, and corolla tube in Collinsia heterophylla for six individual plants (A–F). Each column cluster represents one plant, the left column in each colour pair (darker) shows the first measurement and the right column (lighter) shows the second measurement. Horizontal lines indicate the overall average size for each floral structure at each measurement time.

Nectar volume

Average nectar volume decreased slightly from 0.12 ± 0.14 µL (mean ± SD) at the first measurement to 0.10 µL at the second measurement. There were multiple times where no nectar was found on a plant.

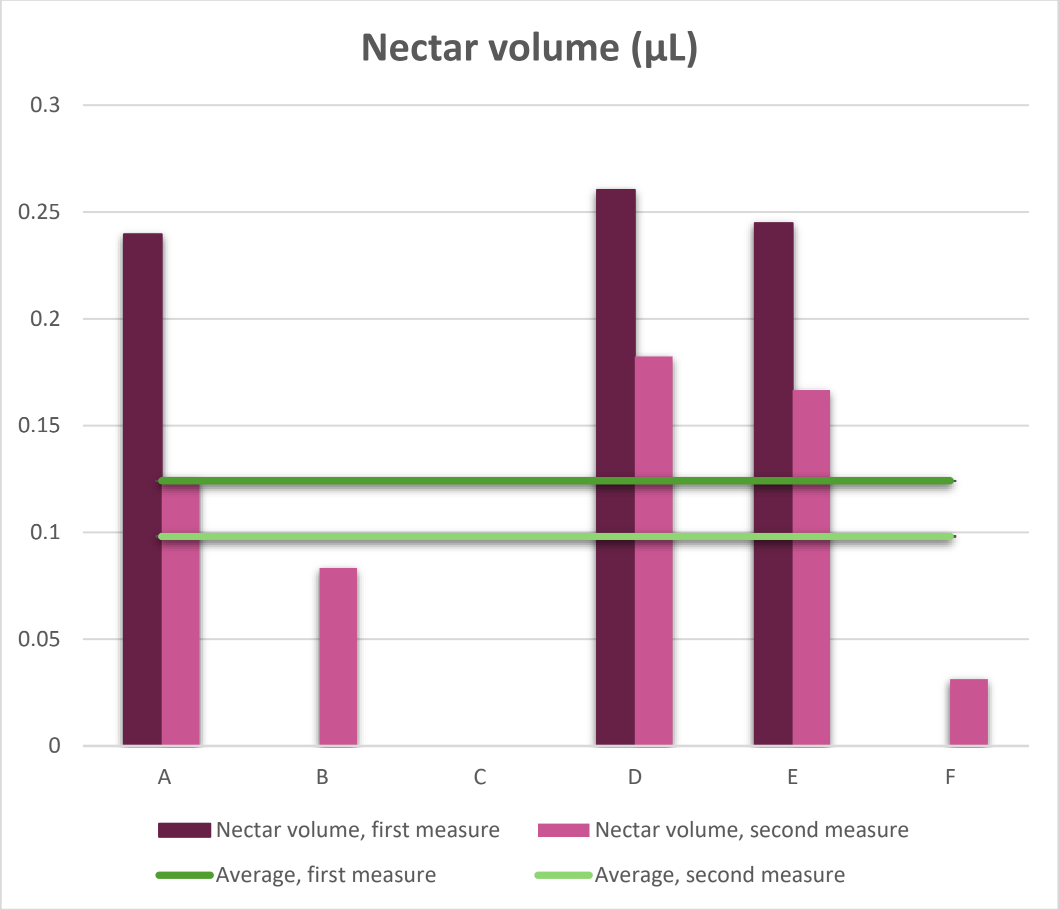

Figure 8. Graph showing the results of nectar volume, each column cluster representing one plant, the left column at first measure and second measure the right column. The lines showing the overall average at both times of measurement.

3.5.2 Aphid Acceptance test

On average, 5.80 ± 1.66 aphids (mean ± SD) accepted the plants, corresponding to an acceptance rate of 58.0 ± 16.6 % across the ten replicates.

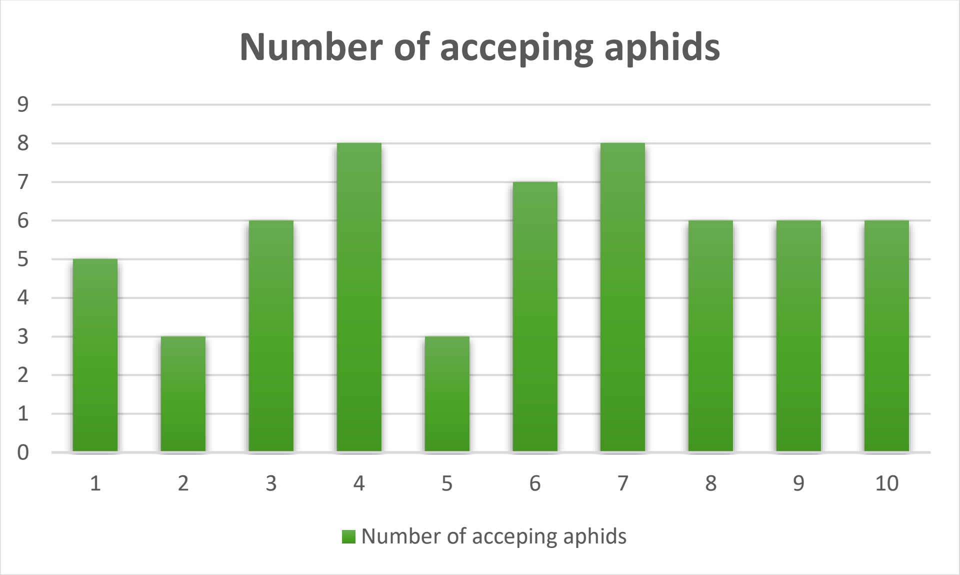

Figure 9. Graph showing the number of accepting aphids per each plant.

4. Discussion

4.1 VOC communicated flower synchronisation at large

The theory at large is interesting to discuss. Evolution in its core tends to streamline and maximise processes and strategies down to the tiniest details and in the growing field of plant-plant communication flowering synchronisation is a valid hypothesis although it lacks empirical evidence.

The two studies performed by Brosset et al. (2023) and Fricke et al. (2019) gives interesting yet not decisive evidence in either direction. Fricke et al. in a direct response to Caruso and Parachnowitschs theory (2016) did not find evidence of synchronisation in *B.rapa* Maarssen. They discuss if flower synchronisation could be species dependent since they have different life histories and reproduction strategies and perhaps the *B.rapa* did not meet the right qualities. But Brosset et al. (2023) found some evidence in their control group that floral volatiles, not influenced by herbivore attack did change the flowering timing in conspecifics in another *B.rapa* (*oleifera* var. Cordelia). This discrepancy raises questions about the generality and mechanisms of VOC-mediated flowering: What types of volatiles trigger flowering shifts? Do plants require stress-associated compounds, or can floral volatiles alone suffice? And how does life history (e.g. being a short-lived annual) influence sensitivity to reproductive cues?

Karban's (2008) discussion of cue reliability and response plasticity helps us interpret the variability in the experimental findings. He notes that for a volatile signal to drive consistent behavioural change, it must be reliable, ecologically informative, and predictively linked to an outcome of fitness relevance. This may help account for why *B. rapa* responded to herbivore-induced volatiles (HIPVs) with earlier flowering (Brosset et al. 2023), but not to floral volatiles alone (Fricke et al. 2019). HIPVS signal a time-sensitive threat, whereas floral volatiles in themselves might be less predictive of the reproductive environment, competition and mating success. However, Caruso and Parachnowitsch (2016) argue that the information in floral VOCs should provide relevant information to conspecifics, such as species, sex and developmental stage, all crucial information in the mating environment. The degree to which these cues are reliable and interpretable by conspecifics likely determines the strength and precision of the response. Greater cue reliability enables more finely tuned behavioural plasticity, reducing unnecessary energy expenditure and thereby offering potential fitness advantages.

Karban (2008) encourages researchers to treat VOC responses as part of a cost–benefit strategy. Emitting volatiles can be energetically expensive and expose the sender to eavesdroppers (e.g. herbivores), while responding to false or unreliable cues can lead to maladaptive timing or wasted resources. This reinforces the idea that plant–plant signalling through VOCs is context-sensitive and may be species-dependent.

Further broadening this discussion, other forms of VOC signalling between lifeforms have been shown to alter plant interactions beyond flowering. The rhizosphere, among the most complex ecosystems; Liu and Brettell (2019) argues that it would be weird if the organisms within did not communicate. Although distinct from flowering signals, this demonstrates that VOC responses often occur within a community context, where the actions of one individual shape the physiological or reproductive fate of others. Likewise, it would be weird if plants when flowering, the most crucial part of their lives did not communicate to optimize their fitness since we know they are able to communicate about other things, unless it is too costly and therefore not selected for.

4.1.1 Eavesdropping or intentional communication?

Caruso and Parachnowitsch (2016) refer to the potential for neighbouring plants to respond to floral volatiles as "eavesdropping" on "cues" and "signals". However, this terminology may warrant further scrutiny. If empirical evidence ultimately supports the hypothesis that plants use volatile organic compounds (VOCs) to synchronise their flowering with conspecifics, then the interaction may not be a case of unintended information interception. Instead, it could be argued that such responses reflect an evolved and intentional communication system where conspecifics are intended receivers. In this scenario, synchronised flowering could enhance outcrossing success, thereby increasing the fitness of both the signal emitter and the receiver, qualities typically associated with true signals rather than cues or eavesdropping.

Rebolleda-Gómez and Wood (2019) caution that discerning intentionality in plant communication is inherently difficult, given the absence of cognition in the animal sense. Still, distinguishing between cues and signals remains important for a deeper understanding of their evolution and ecology. One approach is to isolate and identify the specific VOCs or blends responsible for phenological plastic changes in neighbouring plants. If these compounds are found to serve primarily in plant-plant communication rather than for internal regulation or pollinator attraction, it would support their classification as evolved signals rather than incidental cues. Such findings would also call into question the use of the term "eavesdropping", as it would assume the receiving plant as the intended recipient of the information.

This leads to further questions about the ecological and evolutionary nature of these interactions. If the receiver's phenological changes, such as altered flowering time or floral display, benefit the emitter by increasing pollen transfer efficiency or reducing competition for pollinators, the interaction may resemble a form of cooperation. But even if the empirical evidence shows signs of increased desynchronisation this could also be considered a form of cooperation to avoid competition of resources such as pollinators.

Thus, the framing of these interactions depends not only on the behavioural outcomes involved but also on their fitness consequences for both emitter and receiver. Until these aspects are empirically clarified, caution should be exercised when applying terms such as "eavesdropping," which may not fully capture the complexity or potential intentionality of floral VOC-mediated communication.

4.1.2 Kin recognition and cooperative flowering strategies

Torices et al. (2018) found that individuals grown in kin groups produced larger floral displays compared to those grown with non-kin, suggesting a form of altruistic investment in reproductive effort that is consistent with kin selection theory. Although the study by Torices et al. did not identify the specific mechanisms underlying kin recognition, the observed phenotypic plasticity in floral investment suggests that some form of communication, potentially chemical cues such as volatile organic compounds (VOCs), may mediate kin discrimination. This aligns conceptually with Caruso and Parachnowitsch's (2016) proposal that floral volatiles can inform neighbouring plants about the reproductive environment and potentially elicit changes in flowering phenology.

Synchronized flowering within kin groups may thus represent an evolved cooperative strategy: if one plant is already attracting pollinators via floral display or scent, nearby kin may benefit from synchronizing their own flowering to exploit the increased pollinator traffic. Moreover, since VOC emissions are also involved in pollinator attraction, future research should explore if kin groups adjust both floral display and VOC emission in response to relatedness, since this would further support the role of communication in coordinating reproductive strategies.

However, this raises a broader question: how complex and context-specific are plant reproductive strategies? If plants can perceive pollinator availability or competition, could kin groups desynchronise flowering to promote outcrossing between patches and reduce inbreeding risk? Conversely, under low pollinator pressure, might related individuals prioritise synchronisation to enhance within-patch mating success? These questions highlight the need to consider kin recognition and ecological context when interpreting plant–plant communication and reproductive timing.

In future studies on floral synchronisation, it is advisable to document whether experimental individuals are genetically related, and if so, to what degree. Kinship may influence communication or synchronisation patterns, as plants could behave more cooperatively with relatives than with non-kin. If kin discrimination affects responses to VOCs, overlooking relatedness could lead to misinterpretation of plant behaviour. Including kinship as a factor could help clarify the role of plant–plant communication in reproductive timing.

4.1.3 Stigma receptivity

As Lankinen and Hydbom (2017) explain in their study the timing of stigma receptivity in flowering plants can determine the outcome of reproduction. Delayed receptivity is often thought to enhance the potential for receiving high-quality or genetically diverse pollen, thereby improving outcrossing rates. However, this strategy carries the inherent risk of missing fertilization altogether, especially under conditions of low pollinator availability or rapid floral senescence.

Given that floral VOCs convey information about the reproductive status of conspecifics (Caruso & Parachnowitsch, 2016), it is worth exploring whether the perception of such volatiles could influence the timing of stigma receptivity and, by extension, the outcome of sexual conflict over fertilization. For example, if a neighbouring plant emits volatiles associated with full floral maturity or high pollinator activity (Fricke et al, 2019), this could serve as a cue that optimal pollen is currently available, potentially prompting stigma receptivity in the receiver. Such cues might strengthen female control by delaying receptivity or increasing the selectivity of pollen screening mechanisms to favour genetically diverse or non-self-pollen.

It is conceivable that plants could use floral volatiles as an external source of information to navigate internal trade-offs between reproductive timing and resource allocation. Future studies should investigate whether floral VOCs not only attract pollinators but also modulate intra- and inter-plant sexual strategies, including the degree of female reproductive control over fertilization outcomes.

4.1.4 Microbial added complexity

Rebolleda-Gómez and Wood (2019) complicate the topic further. Their paper discusses the influence of microbial communities on plants and flowers. Flowers host diverse microbiota, including bacteria and yeasts, that colonize nectar, petals, and reproductive structures. These microorganisms are not passive residents; they can chemically modify the composition of volatile organic compounds (VOCs) emitted by flowers, thereby altering the olfactory signals intended for pollinators and potentially for neighbouring plants.

Such microbial influence can have ecological and reproductive consequences. Alterations to the VOC profile can either enhance or suppress specific floral scent components, thereby increasing or decreasing pollinator attraction. Since successful pollination is tightly linked to plant fitness, this microbial mediation indirectly impacts reproductive success, mating patterns, and pollen transfer efficiency. Given the potential role of floral VOCs in plant-plant communication, including the hypothesized coordination of flowering, microbial interference may have broader implications for population-level synchrony and reproductive timing.

The extent to which microbial-altered VOCs affect inter-plant signalling remains largely unexplored. However, if microbes suppress or exaggerate certain volatiles, neighbouring conspecifics may misinterpret the reproductive status or condition of the emitter. This could lead to desynchronized flowering or maladaptive shifts in stigma receptivity.

4.2 Collinsia heterophylla as model species

4.2.1 Pilot study

According to the result of this study *C. heterophylla* both survive and manage to flower and produce nectar in the controlled airflow chambers, intended to be used in future studies, and thus based solely on that is a valid candidate species to be used. But because of the individual variations noted, a larger replicate base is recommended in all treatments of future studies to get more accurate statistical results, as well as control groups included grown outside the modules.

Aphid Acceptance test

The result of the acceptance test of 58% was also regarded as positive, showing over half of the aphids were interested in the plant and can thus be used in potential future pest studies. Although, if relevant, other pests with higher acceptance rate of *Collinsia heterophylla* can surely be located.

4.2.2 Species qualities

Regarding *C. heterophyllas* usefulness as a model species for flower synchronisation using VOCs, arguments can be made both for and against. Being an annual increases the pressure for reproductive success within a single season, which may favour adaptations like synchronised flowering to maximise reproductive outcomes.

On the other hand, a quality that speaks against *C. heterophylla* as a suitable species is the indeterminate flowering. It prolongs the period when pollen can be transferred which lessens the need for synchronisation if individuals in a patch or nearby patches overlap each other sufficiently anyway. Especially if flower initiation can be triggered by other environmental factors that are similar enough withing a patch/between patches and thus synchronise the flowering inadvertently.

Other qualities like being a mixed mating species, where self-pollination is possible, decreases that pressure since it opens a window of possibilities where outcrossing isn't the only answer. And as *C. heterophylla* outcrossing rate of 50% (Larsson et al.2021) leads to a heavy reliant on self-pollination so less adaptation and resources must then be put towards outcrossing. The strategies described by Lankinen and Hydbom (2017) and Larsson et al. (2021), delayed stigma receptivity and enhanced pollinator attraction, may be sufficient to promote adequate outcrossing and maintain healthy gene flow in this species. Additional mechanisms might therefore be unnecessary if their energetic or fitness costs exceed the potential benefits gained by avoiding inbreeding depression. Especially since Fricke et al. in *Brassica rapa* Maarssen, a theoretically more suitable species because of its self-incompatibility, did not yield results in support of flower synchronization.

But, since Larsson et al. (2021) did find floral specific volatiles for pollinator attractions, how high would the cost be to eavesdrop on these signals for neighbouring plants and for them to respond in a way that ensures an overlap in the individuals flowering time. If the substances are already produced and the mechanisms are there for detection (Caruso & Parachnowitsch, 2016), could the benefits of eavesdropping and outcrossing be outweighed by the cost of the plastic changes?

Collinsia heterophylla is a wild, non-domesticated species, which makes it a useful subject for studying natural flowering behaviours such as synchronisation. Domesticated plants are often bred for traits like uniform flowering or reduced environmental sensitivity, which may unintentionally eliminate or mask natural communication mechanisms. Studying wild species could offer a clearer view of how plants might coordinate reproduction in their natural environment.

Collinsia heterophylla may present useful traits as a model species but cannot be regarded as an ideal candidate for investigating flowering synchronisation strategies. Their extended flowering period and capacity for multiple reproductive events reduce the evolutionary pressure for precise temporal coordination. Future studies would benefit from including species with a single, terminal flowering and reproductive episode, where the success of that single event is critical for gene transmission. As suggested by Fricke et al. (2019) a species from the Bromeliaceae family may offer a more suitable model under such criteria. preferably one with the shortest flowering and fertile period.

5. Conclusion

The hypothesis that floral VOCs mediate flowering synchronisation remains intriguing but lacks strong empirical support. Mixed results from previous studies suggest that such signalling may be species-specific and context dependent. Kin recognition, cue reliability, and the costs of emitting or responding to volatiles all shape whether synchronisation would be an adaptive strategy. Further complexity is introduced by microbial communities that can alter floral VOCs, potentially influencing both pollinator behaviour and inter-plant signalling. Future research should consider species traits, kinship, microbial interactions, and identify specific VOC compounds to clarify the ecological and evolutionary relevance of plant-plant communication.

This study demonstrates that *Collinsia heterophylla* can be used in controlled experimental setups, but its indeterminate flowering and reliance on mixed mating reduce its suitability as a model species for studying floral synchronisation via VOCs. However, its status as a wild, non-domesticated plant makes it valuable for exploring natural communication traits that may be absent in domesticated species.

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