More lessons from linalool: insights gained from a ubiquitous floral volatile

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Abstract

Linalool (3,7-dimethyl-1,6-octadien-3-ol) is a common floral volatile with two distinct enantiomers and related metabolites involved in the full spectrum of plant-pollinator interactions. Recent studies reveal a complex interplay between pollinator attraction and plant defense mediated by linalool and its derivatives, from the smallest (*Arabidopsis*, *Mitella*) to the largest (*Datura*) flowers studied. Accordingly, fig wasps, fungus gnats and moths of all sizes show remarkable electrophysiological, neural and behavioral sensitivity to different enantiomers and quantitative ratios of linalool in floral bouquets. The diverse functions of linalool, ranging from toxin to long distance pollinator attractant are discussed in the broader context of floral volatile ecology and evolution.

Introduction

Scent remains the least understood dimension of floral phenotype, given the spatiotemporal dynamism of volatile emissions, the chemical toolkit and lexicon needed to characterize their

composition, and the challenges of pinpointing their often scale- or context-dependent functions. Over 1700 volatile organic compounds (VOCs) have been identified from floral headspace [1], and more are discovered each year as researchers cast broader phylogenetic nets into the sea of [phytochemical](#) diversity [2,3]. In the face of such complexity, it is noteworthy that a small subset of VOCs (e.g. benzaldehyde, β -caryophyllene, limonene, methyl salicylate) is over-represented in floral scents, present in 50-70% of all species studied to date [1] and encompassing a multitude of ecological functions [4,5]. Here I focus on a ubiquitous and multifunctional VOC, the monoterpene alcohol known as linalool (3,7-dimethyl-1,6-octadien-3-ol), building on an earlier review that dealt primarily with biosynthetic details [6]. Although linalool is a fascinating compound in its own right, here I treat it as a placeholder for common floral VOCs, by which to highlight recent advances and opportunities for further growth towards an integrated understanding of the biology of floral scent.

I. Which linalool? A pair of enantiomers and their many derivatives

In a chemical context, “linalool” is a misleading name because it implies a single compound where, in fact, there are two enantiomers, (*R*)-(-)- and (*S*)-(+)-linalool, due to the hydroxyl bearing stereocenter at C-3 of 3,7-dimethyl-1,6-octadien-3-ol. The available evidence supports the semantic treatment of these enantiomers as separate entities, as they are chemically, biosynthetically, electrophysiologically and behaviorally distinct. The genes responsible for their production are members of the terpene synthase (*tps*) gene family, along with nearly all structural genes responsible for the biosynthesis of monoterpenoids [in the tissues of higher plants](#) [7,8]. However, *tps* sequences responsible for the biosynthesis of (*R*)-(-)- and (*S*)-(+)-linalool,

respectively, do not cluster closely with each other, and thus represent multiple examples of convergent or parallel molecular evolution within a large multigene family across the angiosperms [9]. For example, in *Arabidopsis thaliana*, two enantiospecific enzymes (TPS10 and TPS14) produce (*R*)-(-)- and (*S*)-(+)-linalool, respectively, as their major products [10]. Linalool synthases often differ in spatial and temporal aspects of their expression, with LeMTS1 producing (*R*)-(-)-linalool in leaf trichomes of tomato (induced by spider mite herbivory) [9] and LIS producing (*S*)-(+)-linalool constitutively in flower petals of *Clarkia breweri* [6].

The double bonds and C-3 hydroxyl group that characterize the linalool skeleton make it vulnerable to further modification, including derivatization to the well-characterized furanoid and pyranoid linalool oxides common to wines, floral scents and papaya fruit [11,12]. Of these, the furanoid linalool oxides may give rise to 16 possible stereoisomeric aldehydes and alcohols, collectively known as “lilac compounds”, owing to their discovery in the floral scent of *Syringa vulgaris* [13; see 52]. Lilac compounds attract specific functional groups of pollinators, such as noctuid moths [14,15] and long tongued fungus gnats [16] in different floral contexts. Accordingly, these compounds have drawn the attention of pollination biologists, because in well-studied plant lineages such as *Platanthera* orchids, *Silene* and *Mitella*, lilac compounds mediate ecologically specialized pollination systems by attracting specific pollinator classes (Figure 1A).

However, lilac compounds do not function only as pollinator attractants. In the tiny, self-pollinating flowers of *A. thaliana*, lilac compounds contribute to an array of volatile and non-volatile linalool metabolites. Both enantiomers of linalool (synthesized in plastids) are oxidized by two cytochrome P450 enzymes (CYP71B31 and CYP76C3, located in the endoplasmic reticulum) into several isomers of hydroxy- and epoxylinalool, some of which are converted to

non-volatile conjugates [10]. Subsequent experiments revealed another p450 (CYP76C1) with high expression in floral tissues and the capacity to progressively oxidize the C-8 position of linalool to alcohol, aldehyde and acid forms, and (presumably through a furanoid intermediate) to lilac alcohols and aldehydes [17]. Why would an autogamous plant invest in such complex metabolism of a common floral VOC? Null mutants of *cyp76c1* show no inherent fitness costs (e.g. seed reduction) in the lab, so the authors suspected a defensive function against floral predators in nature. Choice bioassays using these mutants as well as synthetic VOCs revealed that thrips, generalist (*Spodoptera littoralis*) and specialist (*Plutella xylostella*) moth larvae all are attracted to linalool, but are repelled either by lilac compounds or by hydroxylinalools (Figure 1E, D). Thus, linalool metabolism in *A. thaliana* flowers is more germane to floral defense than to pollinator attraction (Fig. 1).

II. Mixed messages: floral signals and cues in a whole-plant context

The previous section ended with the caveat that floral volatile evolution can be driven by natural enemies as well as by pollinator-mediated selection [18]. Recent studies have revealed complex selective pressures on specific floral VOCs due to the interplay between pollinators and florivores, which would not have been appreciated without experimental manipulation of specific compounds in field settings [19,20,21]. Because linalool is nearly ubiquitous in flowers, it has been thought to function primarily as a pollinator attractant (Figure 1B), particularly in night-blooming flowers pollinated by hawkmoths [22,23], which are attracted even to low dosages of linalool in VOC blends [24]. However, [hawkmoth larvae \(hornworms\)](#) are [herbivores](#), and female *Manduca sexta*, *M. quinquemaculata* and *Hyles lineata* moths frequently intersperse oviposition with nectar feeding when host plants [provide](#) floral nectar [25,26,27].

How might plants navigate a fitness landscape in which their primary or most effective pollinator may also be a destructive herbivore? Some plants stagger flowering and leaf flush, apparently in response to similar selective pressures [28], but this [ecological](#) strategy is not always an option. The herbivorous pollinator paradox has been addressed in a series of studies on the interactions between female *M. sexta* moths and *Datura wrightii*, their primary host plant and nectar source in the Sonoran Desert of North America [29]. Flowers of *D. wrightii* emit a complex VOC bouquet that includes small amounts of (*R*)-(-)- and (*S*)-(+)-linalool [30], which (along with other compounds) stimulate feeding by flower-naïve *M. sexta* [24]. Feeding responses to linalool are not enantioselective, but females lay more eggs in the presence of the (*S*)-(+)-enantiomer and fewer when (*R*)-(-)-linalool is present [30]. This result is consistent with the finding that adult *M. sexta* lay fewer eggs on tomato plants that emit (*R*)-(-)-linalool in a bouquet of VOCs released by leaf trichomes after damage by larval *M. sexta* [9,31].

As with *Arabidopsis* (see above), one benefit of model systems is the increased availability of background information to guide interpretation of ecological or behavioral results. Because *M. sexta* is a model system for the study of insect olfaction, a large body of neurophysiological studies provides context for understanding host choice by these moths (e.g. [32]). Earlier work on the neural organization of the *M. sexta* antennal lobes (AL) revealed a pair of unique glomeruli in female ALs, one of which receives inputs exclusively when antennae are stimulated with linalool [33]. Further studies revealed enantioselective responses of projection neurons (PNs) innervating adjacent female-specific glomeruli to (*R*)-(-)- and (*S*)-(+)-linalool, which is not observed in general odorant-encoding glomeruli also found in male ALs [34]. These patterns suggest that feeding and oviposition are mediated by two separate neural channels in female *M. sexta*, the former via sexually isomorphic AL processing of racemic linalool and the latter

through potentially inhibitory interactions between female-specific, enantioselective AL glomeruli [30]. This is precisely the kind of sensory/cognitive bias that flowering plants so adroitly manipulate in their ecological interactions with insect mutualists and antagonists [35], and likely explains why flowers of *D. wrightii* emit such low doses of (S)-(+)-linalool [24].

Recent studies have documented female-specific responses to (S)-(+)-linalool in the silk moth *Bombyx mori* [36] and enantio-specific responses (greater sensitivity to (R)-(-)-linalool) in the noctuid moth *Mamestra brassicae* [37], moths whose phylogenetic and ecological affinities differ markedly from those of *M. sexta*. These findings, along with the homologous nature of the olfactory receptor neurons that selectively respond to linalool [38], suggest a much broader relevance for this plant volatile and the selective pressures driving its perception by insect herbivores. Indeed, herbivory often induces systemic emission of linalool and other volatile terpenes (e.g. (E)- β -ocimene, (E)- β -caryophyllene) in different plants [rev. by 39,40], in which linalool emissions may reduce further herbivory by inhibiting further oviposition [41] or by attracting natural enemies of the herbivores [42]. Although a detailed treatment of herbivore-induced plant volatiles is well beyond the scope of this review, it is worth considering the many parallels between plant-pollinator and plant-herbivore interactions mediated by VOCs [43].

III. Volatile versatility: from conventional signals to secret handshakes

Two emerging themes in the study of chemical ecology are (a) that most secondary compounds have multiple and context-dependent functions, and (b) that many infochemicals appear to originate as deadly toxins which, through co-evolutionary processes, [come to be utilized as](#) signals and cues [by](#) organisms that [evolve tolerance of them](#) [44]. The available

evidence suggests that these themes are equally relevant to the ecology and evolution of floral VOCs. At high dosages, linalool can be auto-toxic to plant cells. Attempts to engineer the over-production of (S)-(+)-linalool in petunia flowers [45] and tomato fruits [46] resulted in the formation of linalool conjugates and 8-OH-linalool (see *Arabidopsis*, above), respectively. Linalool (in essential oils) is a potent control agent against the parasite responsible for Leishmaniasis [47] and *Candida* yeasts [48], and is among the most repellent floral VOCs in bioassays performed with two common ant species (*Camponotus floridanus* and *Lasius fuliginosus*) that opportunistically rob floral nectar [49; Figure 1C]. Junker and Blüthgen [50] expanded such assays to a large panel of floral scents, individual VOCs and a full spectrum of flower-visiting insects. The results of these assays led them to propose that obligate flower-visiting insects have evolved the ability to tolerate floral VOCs, in many cases utilizing them as attractants, whereas facultative flower visitors remain vulnerable to their toxicity, and are repelled by them.

What kind of information can linalool convey to obligate flower-visiting insects? One recent study demonstrated that variation in floral scent was significantly associated with seed fitness in a day-blooming, bee pollinated plant, *Penstemon digitalis*, identifying (S)-(+)-linalool as the target of phenotypic selection [51]. Further analyses identified the nectar spur as the source of this VOC [52], suggesting that (S)-(+)-linalool might function as an honest indicator of the presence of nectar, or might enhance floral constancy by pollinators, or might protect nectar from microbial infestation. Floral constancy is likely to result from a learned association of the consistent relationship between nectar availability and linalool, either as a scent or a flavor. If the bees that pollinate *P. digitalis* do not innately prefer (S)-(+)-linalool, then this VOC would

constitute a conventional honest signal, in the sense that bees could be conditioned on any perceivable, non-toxic volatile that accurately predicts nectar profitability [53].

In contrast, the obligate relationship between figs and fig wasps precludes such a relationship, as female fig wasps depart their natal fig with pollen loads and perish within the first receptive fig that they pollinate. Both fig and wasp lineages are hyper-diverse, and species-specific chemical signals have long been implicated as the key links to maintaining the specificity of their interactions [54]. To date, all fig species studied have been found to produce complex VOC blends dominated by monoterpene and sesquiterpene hydrocarbons, many of which have one or more stereocenters [55]. Studies focused on a tropical Asian species, *Ficus hispida*, revealed that its pollinator wasp, *Ceratosolen solmsi* is highly attracted to a 20:1 ratio of (*S*)-(+)-linalool : (–)-β-pinene, but does not respond either to (*R*)-(–)-linalool or to other monoterpenes individually [56]. Thus, two common floral VOCs, in specific ratios of specific enantiomers, can mediate the most intimate of plant-pollinator interactions. However, these interactions do not occur in an ecological vacuum, and third parties often eavesdrop on such interactions. In a related fig species (*Ficus racemosa*), predatory ants (e.g. *Oecophylla smaragdina*) can learn to associate the VOCs of receptive figs with fig wasps as prey, whereas *Myrmicaria brunnea* ants, patrolling the same branches for honeydew, show no responses to fig volatiles [57].

Conclusions

Intensified study of floral volatiles has revealed a nuanced landscape of context-dependent interactions, in which critical details of chemical structure and function mediate ecological

pattern and process. Given the multifunctional nature of linalool and the conflicting selective pressures brought to bear by floral mutualists and antagonists in response to its emission from flowers, this VOC would seem ideally suited to studies of geographic variation in phenotypic selection [58], in accordance with predictions of the Geographic Mosaic Theory of Coevolution, which outlines scenarios in which coevolutionary interactions should differ in the strength and direction of selection [59]. However, it should be clear from this review that linalool is not a special case, and we should expect most widespread floral volatiles to demonstrate a similar diversity of biological functions (see [4, 20]). Finally, the discoveries reviewed here reveal how collaborative efforts between fields as disparate as plant molecular biology, insect neurophysiology and pollination ecology promise to unveil exciting new questions (e.g. [60]) as the study of floral volatiles enters the next phase of its evolution.

References and Recommended Reading

Papers of particular interest, published within the period of review, have been highlighted as

*Of special interest

** Of outstanding interest

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**This study answered one trivial question (why don't *Spodoptera* moths behave in wind tunnels?) and one profound one (what are the neural correlates of behavioral shifts from nectar foraging to host plant selection in mated females?), using calcium imaging and single sensillum recording to track AL and antennal responses to linalool and lilac compounds emitted by lilac flowers.

Figure 1: Schematic diagram of floral filters mediated by linalool metabolism, represented here by conversion of (*R*)-(-)-linalool (right of the blue arrow) to lilac aldehydes and alcohols (left of the blue arrow). Blue arrows represent biosynthetic transformation, green arrows indicate attraction and red piston-ended lines indicate repellence. A: attraction of specialized pollinators (noctuid moths, long tongued fungus gnats – and repellence of short tongued gnats) by lilac compounds [14,16], B: attraction of generalized pollinators (bees, butterflies) by linalool [42], C: (hypothesized) exclusion of ants [42] and yeasts [40] by linalool solved in nectar, D, E: repellence of facultative visitors to *Arabidopsis thaliana* flowers by lilac compounds and attraction of same by linalool [17]. F: decreasing dependence upon pollinators to effect reproductive success, from a nectar-bearing allogamous flower on the left (e.g. *Silene latifolia* [15]) to an unrewarding autogamous flower on the right (e.g. *A. thaliana* [17]). Visitor images

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