

NEW PERSPECTIVES IN POLLINATION BIOLOGY: FLORAL FRAGRANCES

A day in the life of a linalool molecule: Chemical communication in a plant-pollinator system.

Part 1: Linalool biosynthesis in flowering plants

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Abstract

The monoterpene alcohol, linalool, is present in the floral fragrance of diverse plant families and is attractive to a broad spectrum of pollinators, herbivores and parasitoids. Floral emission of linalool has evolved *de novo* in the fragrant, moth-pollinated annual *Clarkia breweri* (Gray) Greene (Onagraceae) through a combination of up-regulation and ectopic expression of its biosynthetic enzyme, linalool synthase (LIS), in conjunction with allometric size increases in all floral organs. Linalool synthase activity and linalool emissions are 1000-fold lower in a sibling species, *C. concinna* (Fischer & Meyer) Greene, that is diurnally pollinated. Linalool synthase expression is spatially and temporally regulated during *C. breweri* flower development, immediately precedes free linalool emission and is absent from nonfloral tissues. Its activity is highest in the style, but most of the linalool product appears to be converted to the pyranoid and furanoid linalool oxides. The LIS structural gene is a member of the terpene synthase gene family, sharing sequence identity with two discrete classes, represented by limonene synthase (LMS) and copalyl pyrophosphate synthase (CPS). Genetic crosses between *C. breweri* and *C. concinna* indicate that strong linalool emission segregates as a dominant mendelian trait, whereas the inheritance of linalool oxide formation is more complex, suggesting epistatic biosynthetic pathway interactions. We discuss areas for future research, including comparative studies of linalool biosynthesis in different plant families, entrainment of linalool emission to nocturnal circadian rhythms and the induction of vegetative linalool as an indirect herbivore defense.

Keywords: *Clarkia breweri*, floral scent, hawkmoths, head space, gas chromatography–mass spectrometry, monoterpenoids, Onagraceae, terpene synthase.

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Introduction

Flowering plants use diverse, multifunctional biosynthetic pathways to produce a broad spectrum of low molecular weight, volatile organic compounds (>700 described structures), which collectively impart characteristic fragrances to floral and vegetative tissues (see reviews by Williams 1983; Croteau & Karp 1991; Knudsen *et al.* 1993; Dudareva *et al.* 1999). Most of these metabolic pathways are ancient, having provided the earliest land

plants and their vascular descendants with a pharmacopoeia of UV-screening pigments, growth substances, signal transductants, essential amino acids, membrane lipids, allelopathic agents, fungal elicitors and lignin (Borg-Karlson *et al.* 1985; Pellmyr & Thien 1986; Metcalf 1987; Bergström 1991; Lichtenhaler *et al.* 1997). The appropriation of volatile secondary metabolites as pollinator attractants is thought to represent one of the signal events in the evolutionary proliferation of the angiosperms (Crepet 1983; Robacker *et al.* 1988; Pellmyr *et al.* 1991). Although botanists historically attempted to classify floral odors by their organoleptic qualities, chemical affinities and pollinator associations (Sprengel 1793;

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Delpino 1874; Kerner 1895; Knuth 1898; Vogel 1954; van der Pijl 1961), progress in understanding floral scent as a natural phenomenon remained elusive until relatively recently due to a lack of appropriate analytical methods. The application of gas chromatography–mass spectrometry (GC-MS) to the identification of volatiles trapped from the floral headspace, combined with advances in volatile trapping technology, has provided a basis for sensitive, reproducible analyses of floral scent chemistry (Bergström *et al.* 1980; Williams 1983; Kaiser 1991; Heath & Manukian 1994; Agelopoulos & Pickett 1998; Raguso & Pellmyr 1998).

As a result, there is a growing literature characterizing the floral scent chemistry of many flowering plant species, exploring spatial and temporal scent variation within flowers (Bergström *et al.* 1995; Schiestl *et al.* 1997), circadian rhythms in fragrance emission (Altenburger & Matile 1988; Hills 1989; Loughrin *et al.* 1991), differences in scent chemistry between lineages of related species (Thien *et al.* 1975; Whitten & Williams 1992; Dobson *et al.* 1997) and the role of fragrance in pollinator attraction (Metcalf 1987; Gottsberger & Silberbauer-Gottsberger 1991; Dobson 1994; Hossaert-McKey *et al.* 1994). Nevertheless, floral scent research remains largely descriptive, with pivotal unresolved questions ranging from the molecular control of biosynthesis to the selective forces exerted by discriminating pollinators, widespread methodological variance between studies, no standardized graphical methods for comparing differences in scent chemistry and few attempts to vertically integrate discoveries across levels of biological organization.

In this review, we explore the current state of floral scent research in microcosm, by following the fate of a representative scent compound, linalool, from its biosynthesis and metabolism within floral tissues to its emission from floral organs. Our review is divided into two sections. The first part introduces linalool by presenting a synopsis of its organic synthesis and chemical properties and surveying the breadth of its occurrence in flowering plants and other organisms. The second part describes events in the natural biosynthesis of linalool, drawing upon biochemical and molecular studies in a model plant species, *Clarkia breweri* (Gray) Greene (Onagraceae), whose powerful floral scent is rich in linalool and, in conjunction with other floral traits, arose as part of an evolutionary transition from a scentless, bee-pollinated ancestry to pollination by nocturnal moths (MacSwain *et al.* 1973; Raguso 1995; Raguso & Pichersky 1995). Whenever possible we focus on mechanism, evaluating the degree to which our findings are applicable to other systems and suggesting avenues for future research. The fate of linalool molecules once they are emitted from flowers will be addressed in a separate paper, with an emphasis on olfactory detection by nectar-foraging insects.

What is linalool?

Organic synthesis of linalool

Linalool (3,7-dimethyl-1,6-octadien-3-ol) is an acyclic monoterpene alcohol with a sweet, pleasant fragrance that occurs widely among diverse monocot and dicot families and is one of the most frequently encountered floral scent compounds (Knudsen *et al.* 1993). Linalool is prized by the flavor and fragrance industry as a component of bergamot and lavender essential oils and numerous commercial perfumes (Hanneguelle *et al.* 1992; Ohloff 1994). Because of the chiral properties of its hydroxylated third carbon, linalool occurs in two enantiomeric forms; (*R*)-linalool [$>80\%$ in ho oil (*Cinnamomum camphora*; Lauraceae) and rosewood oil] and (*S*)-linalool in coriander oil and many floral extracts (Bauer *et al.* 1990). Traditionally, linalool was obtained from α - or β -pinene (isolated from turpentine) or other terpenoids via a series of redox transformations (see Landolt *et al.* 1994). Most modern syntheses begin with 2-methyl-2-hepten-6-one and proceed via base-catalyzed ethynylation with acetylene to dehydrolinalool, yielding linalool through hydrogenation of the triple bond in the presence of a palladium–carbon catalyst (Boelens 1982; Bauer *et al.* 1990; Fig. 1). Alternative routes include a Grignard reaction between 2-methyl-2-hepten-6-one and vinyl halide (Brud & Danevskii 1971) and synthesis from prenyl phenyl sulfone through reaction with isoprene oxide and desulfurization with lithium in ethylamine (Bauer *et al.* 1990).

The importance of linalool in perfumery and the industrial preparation of vitamins A and E has inspired a large body of literature devoted to its organic synthesis and the conditions under which it is transformed to other commercially valuable terpenoid alcohols, acetates and oxides (Godtfredsen *et al.* 1977; Banthorpe *et al.* 1978a; Baxter *et al.* 1978; Boelens 1982; Cori *et al.* 1986). Linalool is unstable under acidic conditions, rearranging to geraniol, nerol and α -terpineol in various ratios depending upon the specific enantiomer, pH and reaction temperature used (Godtfredsen *et al.* 1977; Baxter *et al.* 1978). The conversion of linalool, via oxidation with peracetic acid, to

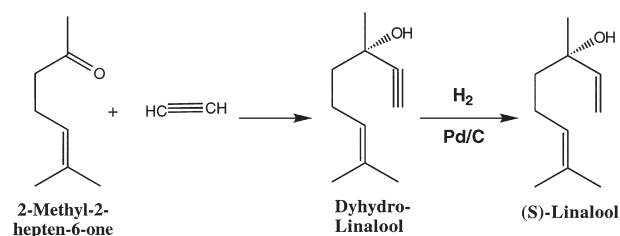


Fig. 1 Organic synthesis of linalool from 2-methyl-2-hepten-6-one via base-catalyzed ethynylation in the presence of a palladium catalyst. After Boelens 1982.

its pyranoid and furanoid oxides is of particular interest, because of their prominence as flavor components of papaya (*Carica papaya*, Caricaceae; Schreier & Winterhalter 1986; Flath *et al.* 1990), grapes (and wines; *Vitis viniflora*, Vitaceae; Williams *et al.* 1980; Strauss *et al.* 1986) and tea leaves, as is reflected in the 'tea index', calculated as the ratio of linalool and its oxides to the combination of linaloic and geraniolic compounds (Guo *et al.* 1994; Morita *et al.* 1994). Finally, the linalool oxides are structurally and biogenically related to an important class of fragrance and flavor compounds in perfumery and enology, the lilac aldehydes (Wakayama & Namba 1974; Winterhalter *et al.* 1986).

Natural distribution and pollinator affinities

Linalool, along with the acyclic sesquiterpene nerolidol, certain aromatic esters and the nitrogenous indole and oximes, is a component of the 'white floral olfactory image' described by Kaiser (1991, 1993) and confirmed by numerous surveys (Knudsen & Tollsten 1993; Dobson *et al.* 1997; Miyake *et al.* 1998; Raguso 1999) as nearly universal fragrance constituents of white, night-blooming, moth-pollinated flowers worldwide. Familiar examples of such plants are the evening primroses (*Oenothera* sp., Onagraceae; Kawano *et al.* 1995), nocturnal tobaccos (*Nicotiana* spp., Solanaceae; Loughrin *et al.* 1990), wild ginger (*Hedychium* spp., Zingiberaceae; Omata *et al.* 1991a; Knudsen & Tollsten 1993), long-spurred orchids (*Angraecum*, *Aerangis* and *Platanthera* spp., Orchidaceae; Kaiser 1993; Tollsten & Bergström 1993) and jasmines (*Jasminum* spp., Oleaceae; Watanabe *et al.* 1993).

However, linalool is not restricted to moth-pollinated flowers and occurs widely in many diurnal flowers pollinated by bees (Pham-Delègue *et al.* 1990; Olesen & Knudsen 1994; Borg-Karlson *et al.* 1996), beetles (Thien *et al.* 1975) and butterflies (Honda *et al.* 1998; see Appendix I, Fig. 2). Interestingly, linalool appears to play, at most, a minor role in the exclusively scent-driven interactions between euglossine bees and their orchids (e.g. *Catasetum*, *Cynoches*, *Gongora* and *Stanhopea*; Dodson *et al.* 1969; Gregg 1983; Williams & Whitten 1983; Whitten & Williams 1992) and is either absent or a minor component in fragrances attractive to bats (Knudsen & Tollsten 1995; Bestmann *et al.* 1997) and flies (Kaiser 1993; but see Borg-Karlson *et al.* 1994; Skubatz *et al.* 1996). In addition, linalool is present in free and bound forms in many non-floral tissues, including roots (*Zingiber officinale*, Zingiberaceae; Wu *et al.* 1990), bark (*Sassafras albidum*, Lauraceae; Budavari 1989), vegetation (*Mentha aquatica*, Lamiaceae; Murray & Lincoln 1970; *Umbellularia californica*, Lauraceae; Goralka & Langenheim 1996) and the pulp and rind of various fruits (*Carica papaya*, Caricaceae; Schreier & Winterhalter 1986; Schwab *et al.* 1989). Finally,

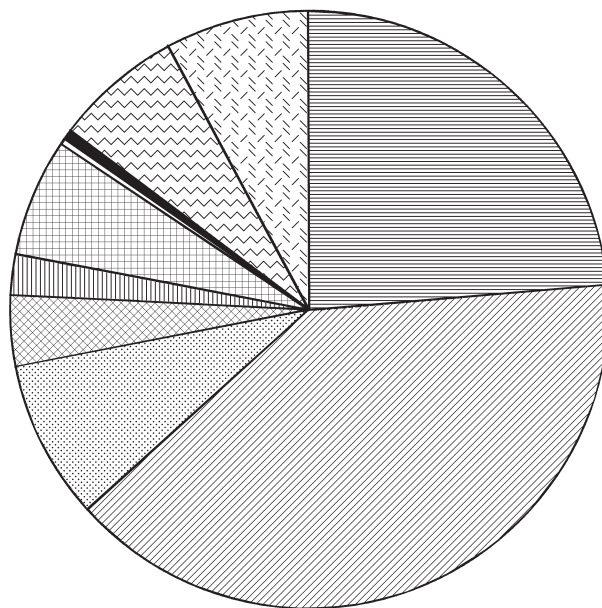


Fig. 2 Pollinator distribution for angiosperm and cycad species emitting linalool from reproductive organs (see Appendix I). Numbers reflect frequency of pollinator classes associated with linalool, as some plants have more than one pollinator class. (□) is given when pollinators are unknown. (▨) Bees and wasps, (▩) moths, (▧) orchid bees, (▦) butterflies, (▨) bats, (▩) flies, (▨) thrips, (■) hummingbirds, (▨) beetles.

linalool is emitted with significant quantities of other terpenoids by forests of junipers (Adams *et al.* 1983; Adams 1998), eucalyptus (Barton *et al.* 1989; Guenther *et al.* 1991) and Mediterranean oaks (Loreto *et al.* 1996). Linalool and other monoterpenes are also produced by diverse groups of ascomycete and basidiomycete fungi (Borg-Karlson *et al.* 1994; Breheret *et al.* 1997) and are important intrinsic semiochemicals for many species of insects, especially among the Hymenoptera and Lepidoptera (Komae *et al.* 1982; Aldrich *et al.* 1984, 1986; Borg-Karlson 1990; Heath *et al.* 1992b; Bestmann *et al.* 1993).

Linalool biosynthesis and emission in *Clarkia* flowers

Patterns of emission

Originally, we chose the genus *Clarkia* as a model system to investigate the phylogenetic novelty of fragrance in *C. breweri* and its correlation with an evolutionary pollinator shift, and to exploit its short generation times, tractability for genetic study and the wealth of genetic and systematic information available on this well-studied genus (Lewis & Lewis 1955; Gottlieb & Weeden 1979; Sytsma and Smith 1990). Our initial GC-MS analyses of *C. breweri* floral scent identified (s)-linalool and its pyranoid oxide, together with benzyl acetate, as the most abundant

volatiles emitted over the course of 4–6 days, with a peak in abundance during the first 36 h (Pichersky *et al.* 1994). The additional five to 12 floral volatiles identified in our analyses were aromatic esters and alcohols produced by the shikimate pathway: their biosynthesis in *C. breweri* is treated in detail elsewhere (Raguso & Pichersky 1995; Wang *et al.* 1997; Dudareva *et al.* 1998a,b; Wang & Pichersky 1998). Six- and 12-h scent collection periods over a time course of 5 days revealed that there were no marked quantitative or qualitative differences in diurnal versus nocturnal emissions, unlike the pronounced circadian rhythmicity of linalool emission in many species of night-blooming plants (Matile & Altenburger 1988; Kaiser 1991; Loughrin *et al.* 1991; Miyake *et al.* 1998). Scent analyses from modified *C. breweri* flowers identified autonomous emissions of linalool by all floral organs, in amounts roughly proportional to their relative masses, while linalool oxides were emitted exclusively by the pistil (Fig. 3a). Surprisingly, we also detected trace levels of linalool, linalool oxides, (*E*)- β -ocimene and a series of cyclic terpenoids from the smaller, 'scentless' flowers of *C. concinna*, the closest relative of *C. breweri*, at emission levels 250-fold lower per unit floral mass than was observed for *C. breweri* (Raguso & Pichersky 1995). In *C. concinna*, linalool, its oxides and all other volatiles were emitted solely from pistil tissues (Fig. 3b). Thus, the combination of a four-fold difference in floral mass and the extension of scent production to petal tissues accounts for

some, but not all of the disparity in linalool emissions between *C. breweri* and *C. concinna*.

Enzymatic activity and tissue-specific expression

In higher plants, monoterpenoids, such as linalool, are derived from isopentenyl pyrophosphate via the universal isoprenoid intermediate, geranyl pyrophosphate (GPP), through a class of membrane-bound enzymes called monoterpene synthases (Colby *et al.* 1993; Chappell 1995; McGarvey & Croteau 1995; Bohlmann *et al.* 1998). Linalool synthase (LIS), the biosynthetic enzyme that produces (*s*)-linalool from GPP, was characterized from *C. breweri* floral tissues with an enzyme assay using [³H]-labeled GPP and was purified to homogeneity from stigmatic tissue (Pichersky *et al.* 1994, 1995). In *C. breweri*, LIS functions as a monomer and, like other monoterpene synthases, requires a Mn²⁺ or Mg²⁺ cofactor (Pichersky *et al.* 1995; Fig. 4).

By using the LIS enzyme assay, combined with western blots using LIS-specific antibodies, we were able to measure the spatial and temporal patterns of linalool biosynthesis in *Clarkia* flowers. Consistent with emission data, LIS protein and enzyme activity are present in all *C. breweri* non-green flower parts and absent from vegetative tissues, with peaks in protein concentration and activity during the first day of anthesis, 1 day before the maximum emission of linalool and its oxides are observed

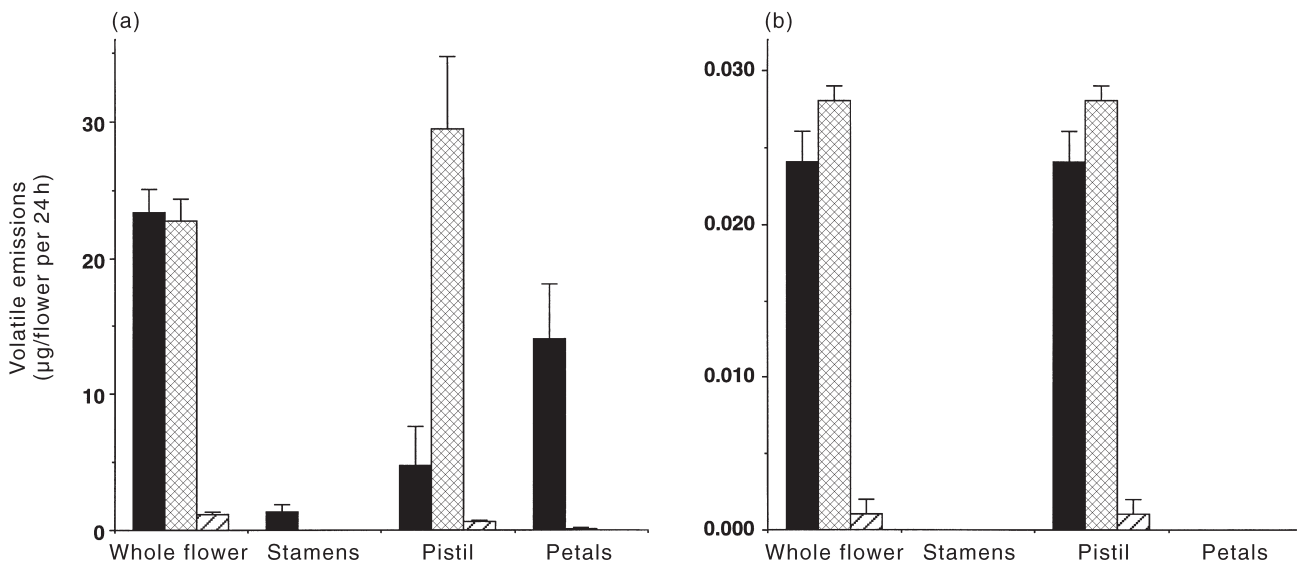


Fig. 3 Organ-specific volatile emissions ($\mu\text{g}/\text{flower per 24 h}$) from flowers of (a) *Clarkia breweri* and (b) *C. concinna*. (Onagraceae). Flower organs were removed selectively by forceps, leaving the hypanthium, sepals and one additional floral organ attached to the living plant. Intact flowers on the same plants were used as controls. Note the absence of linalool in petals of *C. concinna* and the 1000-fold difference in magnitude of floral emissions between species. (■) Linalool, (▨) pyranoid oxide, (▧) furanoid oxide. Data from Pichersky *et al.* (1994).

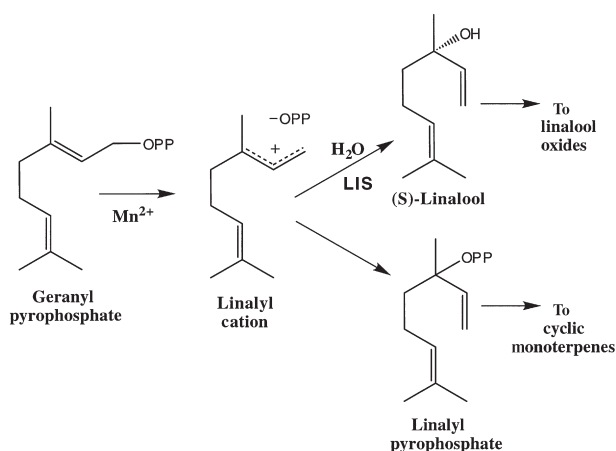


Fig. 4 Biosynthesis of (s)-linalool from geranyl pyrophosphate (GPP) via enzymatic catalysis in *Clarkia breweri*. LIS, linalool synthase. From Pichersky *et al.* (1995).

in petal and pistil tissues, respectively (Pichersky *et al.* 1994; Dudareva *et al.* 1996; Fig. 5). In contrast, LIS activity was detected only in the stigmatic tissue of *C. concinna*, at levels 33-fold lower per unit mass than those observed in *C. breweri* stigmata (Pichersky *et al.* 1994). Thus, the dramatic up-regulation of LIS, combined with allometric increases in floral dimensions and ectopic LIS expression within those expanded organs are the mechanisms responsible for the evolutionary amplification of monoterpene floral emissions in *C. breweri*.

Linalool synthase enzyme activity per unit mass is greatest in the stigma and style (only 10% of total *C. breweri* floral mass), but in these tissues most of the linalool product appears to be converted to pyranoid and furanoid linalool oxides. The mechanism of this process has not yet been determined, but most likely involves cytochrome P450 hydroxylation via a 6,7 epoxy linalool intermediary (Winterhalter *et al.* 1986; Hallahan *et al.* 1992; Funk *et al.* 1994; Demyttenaere & Willemsen 1998) (Fig. 6). Interestingly, LIS protein concentration and enzyme activity diminish after the first day in petal tissues, but remain at peak levels for 3–4 days in stigma and style tissues, as does hexane-extractable linalool oxide, long after volatile emissions have diminished (Pichersky *et al.* 1994; Dudareva *et al.* 1996). These observations suggest an undetermined, non-synomonal function for the linalool oxides in the *Clarkia* style, potentially related to defense or pollen tube growth. Alternatively, P450 catalyzed linalool oxide formation is a universal mechanism for linalool catabolism or detoxification in insect guts (Yu 1987; Southwell *et al.* 1995), fruit musts (Bock *et al.* 1986) and soil fungi (Demyttenaere & Willemsen 1998). Perhaps linalool oxide formation in *Clarkia* pistils is a form of protection for germinating pollen tubes through local detoxification of linalool.

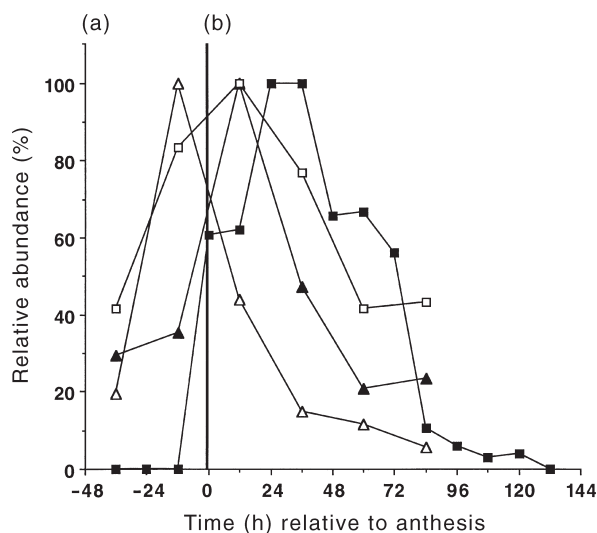


Fig. 5 Time course of linalool biosynthesis in petals of *Clarkia breweri* flowers from (a) buds 36 h before anthesis to (b) 5-day old (senescing) flowers. Data shown are relative amounts (% of the largest measurement) for each category. (■) Linalool emission, (□) linalool synthase (LIS) activity, (▲) LIS protein, (△) LIS mRNA. See Pichersky *et al.* (1994); Dudareva *et al.* (1996) for actual units and methods.

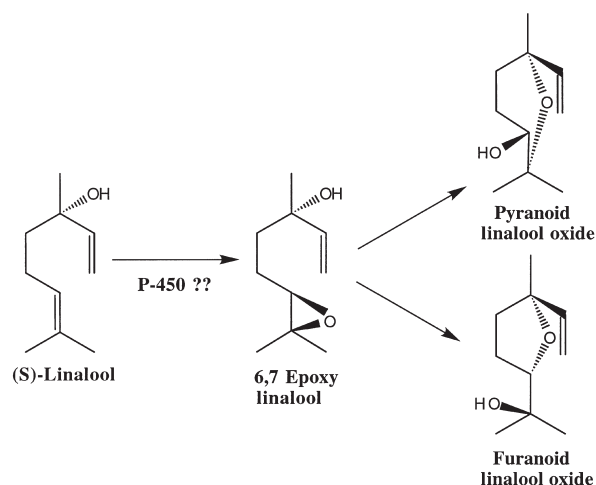


Fig. 6 Proposed pathway of linalool oxide production from (s)-linalool via 6,7 epoxy linalool in *Clarkia breweri*. From Pichersky *et al.* (1994).

Linalool synthase gene expression

The purification of LIS protein made it possible to isolate the LIS structural gene and LIS cDNA, using an initial probe fashioned from a partial amino acid sequence of LIS (Dudareva *et al.* 1996). The coding information consists of 870 codons and is interrupted by 11 introns. The LIS gene appears to have evolved from two types of terpene synthases as the direct result of a recombination event

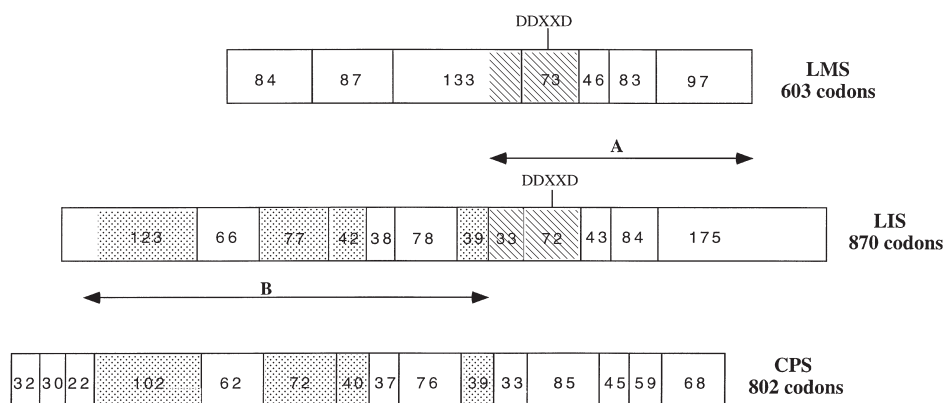


Fig. 7 Comparison of the gene structure of the full length *Clarkia concinna* linalool synthase gene (*LIS*) with genes encoding limonene synthase (*LMS*) from *Perilla frutescens* (Lamiaceae; Yuba *et al.* 1996) and copalyl diphosphate synthase (*CPS*) from *Arabidopsis thaliana* (Brassicaceae; Sun & Kamiya 1994). Arrow A indicates regions of similarity between *LIS* and *LMS*, with regions of high identity denoted by (▨). Arrow B indicates sequence similarity between *LIS* and *CPS*, with highest identity shown by (▩). The DDXXD-motif is conserved among all terpene synthases and is proposed to bind substrates and divalent metal cofactors. Modified from Cseke *et al.* 1998.

between the N-terminal coding region of a copalyl pyrophosphate synthase (*CPS*)-like gene and the C-terminal coding region of a limonene synthase (*LMS*)-like gene (Cseke *et al.* 1998) (Fig. 7). The second part of *LIS* includes the conserved DDXXD motif which is thought to constitute an important region of the enzymatic active site of many terpene synthases (Bohlmann *et al.* 1998). A comparison of promoter sequences between the *C. breweri* and *C. concinna* *LIS* genes identified sequence differences associated with transcription initiation sites (TATA and CAATT boxes) in the *C. concinna* *LIS* promoter (Cseke *et al.* 1998). Whether these small insertions are responsible for the distinct *LIS* expression patterns of the two *Clarkia* species remains to be tested experimentally. The *LIS* genes have now been isolated from *Oenothera arizonica* (Munz) Wagner (Onagraceae) and *Arabidopsis thaliana* L. (Brassicaceae), although no information on their expression in these species is available (Cseke *et al.* 1998). While the night-blooming, moth-pollinated flowers of *O. arizonica* emit copious amounts of linalool (R. A. Raguso, unpublished data, 1995), the flowers of *A. thaliana* are small and scentless; thus, *LIS* and linalool biosynthesis in *Arabidopsis* must serve a different function, perhaps related to anti-herbivore defense, as in maize and other plants (Turlings & Tumlinson 1992) or use as a substrate for the biosynthesis of other terpenoid compounds (Banthorpe *et al.* 1978b).

During *C. breweri* flower development, expression of the *LIS* gene is temporally and spatially regulated. *Linalool synthase* mRNA transcripts accumulate in floral tissues during the final days of bud maturation, anticipating by 1 day the peak concentration of *LIS* protein and by 2 days the peak emission of linalool (Fig. 5). *In situ* hybridization identified uniformly high concentrations of *LIS* mRNA in

petal epidermal cells, but elsewhere expression was limited to the transmitting tissues of the style (Dudareva *et al.* 1996). The relative abundance and time course of *LIS* transcripts in *C. breweri* and *C. concinna* floral organs is completely consistent with patterns of *LIS* protein accumulation and enzyme activity (Dudareva *et al.* 1996). The data summarized in Fig. 5 indicate that linalool biosynthesis is regulated at the nucleic acid level in *C. breweri*, that enzyme activity is directly proportional to *LIS* protein concentration without any discernible effects of post-translational modification, and that linalool is synthesized *de novo* within floral tissues and is emitted shortly thereafter.

Genetic control of linalool and linalool oxide emissions

The genetic inheritance of linalool and linalool oxide emission was examined by crossing inbred lines of *C. breweri* and *C. concinna* and producing F_1 , F_2 and backcross ($F_1 \times C. concinna$) interspecific hybrids. Floral scent was collected and analyzed under conditions such that volatiles from *C. concinna* were below the threshold of detection (1 ng/flower per 12 h) and were scored as 'absent'. Linalool and its oxides were present in all 37 F_1 individuals at emission rates intermediate with respect to parental phenotypes, but less than half of that of *C. breweri* (Raguso 1995). Linalool was detected in the floral headspace of 101 of 145 F_2 plants and 13 of 20 backcross individuals, supporting the hypothesis of simple mendelian dominance (Table 1). Multiple linear regression revealed that log-normal variation in the amount of linalool emitted per floral mass among F_2 plants was not significantly correlated with quantitative variation in any floral morphological character ($R^2=0.05$, $F_8=3.38$,

Table 1 *Clarkia breweri* × *C. concinna*: Segregation patterns of linalool and linalool oxides

Scent compounds	Phenotypic ratios	<i>C. breweri</i>	<i>C. concinna</i>	F ₁	F ₂	F ₁ × <i>C. concinna</i> backcross
(s)-Linalool	Observed	10/10	0/6	37/37	101/145	13/20
	Expected	10/10	0/6	37/37	109/145	10/20
	H ₀ one gene, dominant			χ^2 (1 d.f.) = P =	2.36 0.15	1.80 0.20
Pyranoid linalool oxide	Observed	10/10	0/6	37/37	108/145	20/20
	Expected	10/10	0/6	37/37	109/145	10/20
	H ₀ one gene, dominant			χ^2 (1 d.f.) = P =	0.04 0.80	20.0 <0.001
Furanoid linalool oxide	Observed	10/10	0/6	37/37	86/145	13/20
	Expected	10/10	0/6	37/37	109/145	10/20
	H ₀ one gene, dominant			χ^2 (1 DF) = P =	19.55 <0.005	1.80 0.20
	Expected	10/10	0/6	37/37	82/145	5/20
	H ₁ two gene, complementary epistasis			χ^2 (1 DF) = P =	0.45 0.50	12.8 <0.005

$P=0.81$). In contrast, quantitative variation in pyranoid linalool oxide emission was significantly associated with floral morphological variation ($R^2=0.22$, $F_8=1.97$, $P=0.002$) and was positively and significantly correlated with the length of the style, its site of emission in both *Clarkia* species (Raguso 1995).

For the pyranoid and furanoid linalool oxides, the F₂ segregation patterns did not depart significantly from 3:1 (single gene, dominant) and 9:7 (two genes, epistatic) ratios, respectively, but backcross data were not consistent with these hypotheses (Table 1). Assuming that the F₂ data are correct, the phenotypic segregation of linalool- and pyranoid linalool oxide-producing individuals differed significantly from the expectations of independent assortment, with a recombination frequency of 0.186 (Table 2). Interestingly, some F₂ individuals produced one or both of the linalool oxides without detectable levels of linalool, a pattern occasionally observed in other flowering plants (see Appendix I). The most likely explanation is that segregation of parental levels of GPP and alleles of LIS and the putative P450 linalool epoxidase in the F₂ produced a few individuals in which LIS was not expressed in petals, but small pools of linalool in the pistil were completely converted to linalool oxides.

It is tempting to conclude that the up-regulated LIS allele from *C. breweri* is dominant to the low activity LIS allele from *C. concinna* in interspecific hybrids, but it is clear from our data that other, unidentified factors also contribute to quantitative variation in linalool emission in hybrid *Clarkia* flowers. Additional studies incorporating direct comparison of LIS activity and linalool emission

Table 2 *Clarkia breweri* and *C. concinna*: phenotypic ratios in F₂ hybrids and test for linkage

Phenotypic categories	Null expected ratios	Observed (3 d.f.)	χ^2	P
(s)-Linalool and PLO	H ₀ : non-linkage of two dominant mendelian genes			
Linalool/PLO	81.5	96	41.90	<0.005
Linalool/-	27.2	12		(Reject H ₀)
-/PLO	27.2	15		Rf = 0.186
-/-	9.1	22		

PLO, pyranoid linalool oxide; Rf, recombinant frequency.

from hybrid plants, a larger backcross generation and controls for the segregation of pollen infertility will be required to better understand the genetics of this system. Previously, the only other genetic analysis of linalool production was performed by Murray and Lincoln (1970), using inbred lines of the tetraploid mint *Mentha citrata* (= *aquatica*). These authors defined a dominant allele *I* that was associated with the accumulation of linalool and linalyl acetate, and the absence of limonene and other cyclic monoterpenoids characteristic of mint oils (summarized by Hefendehl & Murray 1976). The cyclization of GPP to limonene and cyclic mint ketones related to menthone occurs through a linalyl pyrophosphate (LPP) intermediary (Suga *et al.* 1986; McGarvey & Croteau 1995), leading Croteau and Gershenzon (1994) to suggest that plants with the dominant *II* or *li* genotypes produce an enzyme catalyzing an abortive cyclization product,

allowing pools of linalool to accumulate, while the recessive *ii* genotype promotes cyclic monoterpenoid biosynthesis via LPP and the cyclic α -terpinyl cation. Given these observations, the *I* gene is unlikely to encode a linalool synthase function homologous to *C. breweri* LIS (Croteau & Gershenzon 1994).

Anatomy of linalool biosynthesis and secretion

The landmark survey by Vogel (1963) established the widespread occurrence of specialized, morphologically diverse scent glands (osmophores) in flowering plants. Subsequent studies have utilized histology and light and electron microscopy to characterize the anatomy and ultrastructure of osmophore tissues from a variety of fragrant orchids (Williams 1983; Stern *et al.* 1987; Curry *et al.* 1991). Using scanning electron microscopy, we found no unusual glandular structures that would increase surface area or otherwise enhance volatilization from the petals of *C. breweri* (Fig. 8). Linalool and the aromatic compounds appear to volatilize diffusely from the epidermal cell surfaces. In contrast, the entire pistil of *C. breweri* functions as an osmophore or scent gland, emitting substantial amounts of linalool oxides in spatial and chemical contrast to the rest of the flower. Potential explanations for this phenomenon include: (i) the style is an olfactory or contact-chemoreceptive nectar guide for insects (Lex 1954; Adey 1983); (ii) linalool oxides are secreted into nectar as gustatory stimulants for pollinators (Dobson 1994); or (iii) as antimicrobial prophylaxis (Lawton *et al.* 1993); or (iv) linalool oxides participate at some level in pollen tube germination and growth through the transmitting tissues of the style, perhaps indirectly, as products of a detoxification process that reduces potential allelopathic effects of linalool on pollen tube growth (e.g. Hamilton-Kemp *et al.* 1991).

Relatively little is known about the intracellular trafficking of volatile substances from their point of synthesis to their eventual emission in floral tissues of most angiosperms, including *Clarkia*. Recent studies have provided evidence for independent, compartmentalized biosynthesis of monoterpenes and sesquiterpenes, the former in plastids (Gleizes *et al.* 1983; review by Kleinig 1989) via the D-glyceraldehyde-3-phosphate/pyruvate (Rohmer) pathway (Lichtenthaler *et al.* 1997) and the latter in the cytosol through the distinct mevalonate pathway (Cheniclet & Carde 1985; Lichtenthaler *et al.* 1997). Mettall *et al.* (1988) documented the biosynthesis of linalool and other monoterpenes in chromoplasts isolated from the coronas of *Narcissus pseudonarcissus* (Amaryllidaceae) flowers and Loreto *et al.* (1996) presented evidence suggesting that foliar linalool is synthesized in non-photosynthetic plastids in leaves of *Quercus ilex* (Fagaceae). Kleinig (1989) proposed that monoterpenoids

are transported to the cytosol for further modification (e.g. hydroxylation) through the action of cytochrome P450 oxidases bound to the endoplasmic reticulum, but there are few direct studies localizing these reactions, and we have not yet explored the cellular details of linalool oxide biosynthesis in *Clarkia* pistils.

Unlike vegetative tissues, there are relatively few floral model systems in which the mechanisms of volatile production and emission can be compared, and some of the best studied cases represent plant lineages in which floral morphology is greatly modified (Vogel 1963). For example, the odoriferous appendix (sterile spadix) of the *Sauromatum guttatum* (Araceae) inflorescence produces a broad array of nitrogenous, aliphatic, phenolic and terpenoid scent compounds (including linalool and other monoterpenes), but lacks chromoplasts and leucoplasts (Skubatz *et al.* 1995, 1996). Starch-filled amyloplasts are abundant in these tissues and are implicated as the major energy source for scent biosynthesis in aroids and other thermogenic flowers (Vogel 1963), but evidence for monoterpene biosynthesis in amyloplasts is equivocal (see Curry 1987). While the sesquiterpenes copaene and caryophyllene are transported from the rough endoplasmic reticulum (rER) to the cell surface through channels formed from the fusion of the rER to the plasma membrane in the *Sauromatum* appendix (Skubatz *et al.* 1996), it is unclear whether these mechanisms are applicable to other volatile classes, including monoterpenes.

Linalyl glycosides and the precursor paradox

What happens to linalool when it is not emitted from flowers? Linalool is present in a bound, glycosidic form in many plant tissues as a conjugate of β -D-glucose or disaccharides containing this sugar (Watanabe *et al.* 1993; Guo *et al.* 1994; Moon *et al.* 1994). Conjugation of terpenes and phenolics is a ubiquitous metabolic strategy in plants, conferring detoxification, functional group protection (e.g. salicylic acid; León *et al.* 1993; Yalpani *et al.* 1993) and hydrophilic properties to the aglycones, facilitating vacuolar storage or transport via phloem to other tissues for storage, catabolism or synthesis of more complex compounds (Strauss *et al.* 1986; Ackermann *et al.* 1989; Funk *et al.* 1992; McGarvey & Croteau 1995). In particular, some iridoid defense compounds appear to be derived from 10-hydroxy-geraniol and other glycosidic monoterpenoid precursors (Ackermann *et al.* 1989; review by Bowers 1991). Monoterpene glycosides are important flavor precursors in fruits, as diverse aglycones are released during fruit ripening through the activity of various glycosidase enzymes (Gunata *et al.* 1985; Schreiber & Winterhalter 1986; Schwab *et al.* 1989; Buttery *et al.* 1990; Suárez *et al.* 1991; Marlatt *et al.* 1992). The observation that large quantities of monoterpene glycosides accumulate in maturing

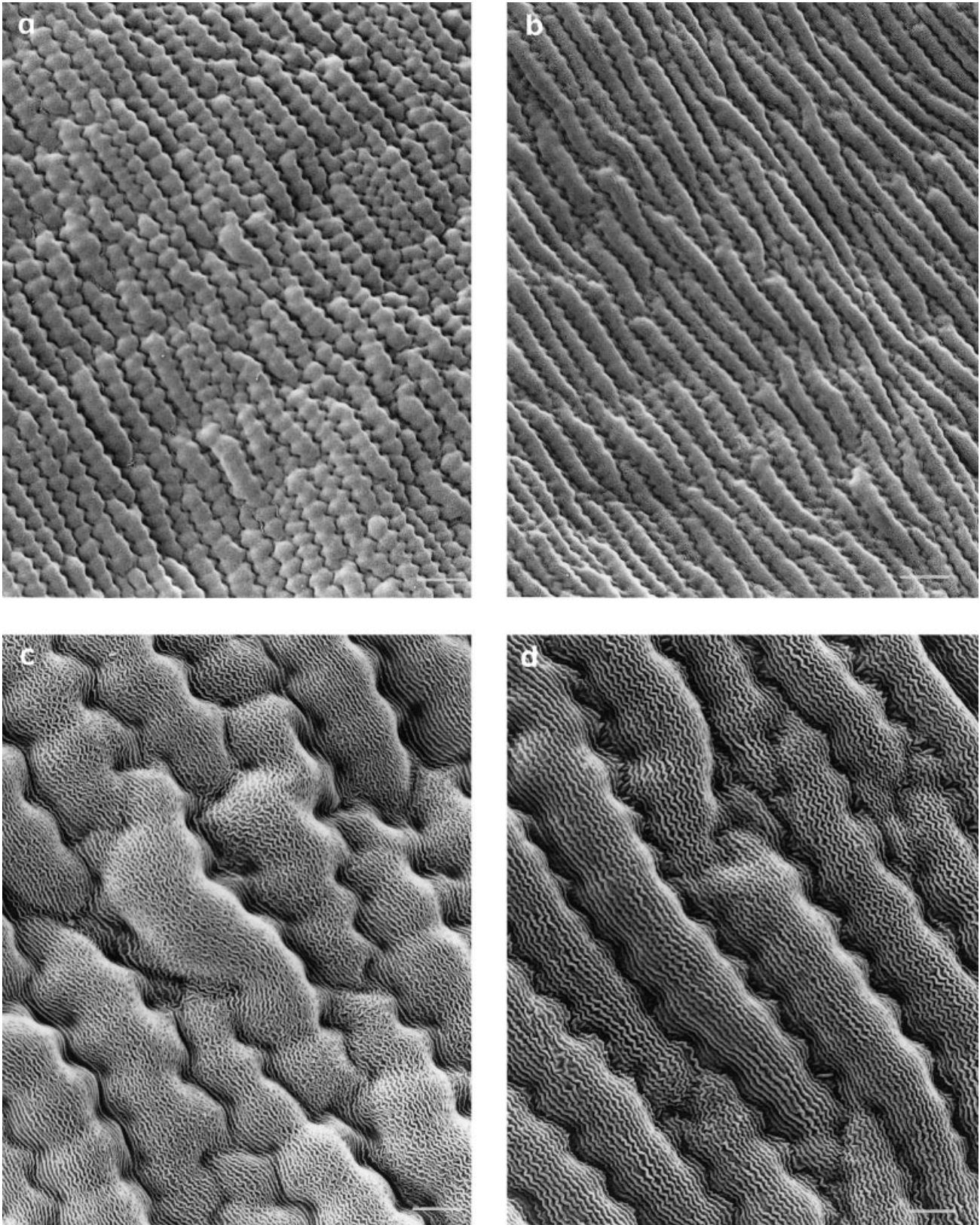


Fig. 8 Scanning electron microscopic comparison of petal surfaces from (a,c) *Clarkia breweri* and (b,d) *C. concinna* showing conspicuous absence of osmophores, papillate or rugose glandular tissue. (a,b) Original magnification $\times 150$, bar = 65 μm ; (c,d) original magnification $\times 600$, bar = 16 μm . From Raguso (1995).

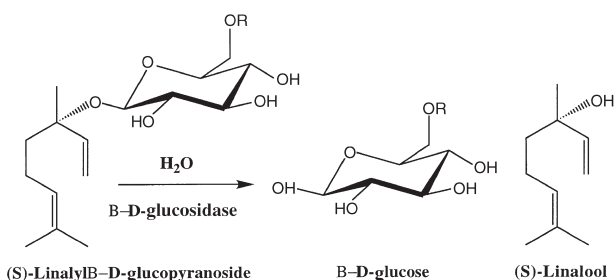


Fig. 9 Liberation of free linalool from a linalyl glycoside containing β-D-glucose, via enzymatic cleavage. Possible R-groups include arabinose, xylose, malonate or simply a proton (in β-D-glucoside). Modified from Watanabe *et al.* (1994).

rosebuds (Francis & Allcock 1969), combined with mevalonate-labeling assays that show rapid turnover of free and bound monoterpenols in rose petals (Francis & O'Connell 1969), generated the hypothesis that aroma glycosides are obligate precursors to floral scents, through their synthesis in green tissues, transport to developing buds and enzymatic liberation of free aglycones in opening flowers (Pogorelskaya *et al.* 1980; Watanabe *et al.* 1993; Fig. 9). (Note: we now know that monoterpenes are derived from pyruvic acid, not mevalonic acid; Lichtenthaler *et al.* 1997).

For the obligate precursor hypothesis to be supported *sensu strictu*, glycoside concentrations should peak in buds prior to anthesis in quantities comparable to those of subsequently emitted free volatiles and should decrease later as floral emissions cease. Most importantly, the activity of glycosidase enzymes, not biosynthetic enzymes, should mirror the time course and intensity of floral emissions. Our own pilot studies of fragrance glycosides in *Clarkia breweri* do not support an obligate precursor relationship between linalyl glycosides and free linalool emissions (R. A. Raguso, J. Wang and E. Pichersky, unpublished data, 1994). In flowers of *C. breweri*, the time course and concentration of linalyl glycosides are insufficient to explain emission levels; the temporal patterns of LIS transcription, translation and enzyme activity are more consistent with the hypothesis of *in situ* linalool biosynthesis and emission. The presence of low concentrations (5 μg/g fresh mass) of linalyl glycosides in *C. breweri* leaves (R. A. Raguso, J. Wang and E. Pichersky, unpublished data, 1994), despite the fact that LIS gene expression, LIS protein accumulation, enzyme activity and linalool emission are absent from leaves and roots (Pichersky *et al.* 1994, 1995; Raguso & Pichersky 1995; Dudareva *et al.* 1996), supports the alternative hypothesis that glycoside formation in flowers is a form of packaging of excess linalool for transport to other tissues.

The available evidence from other systems highlights additional shortcomings of the glycoside precursor

hypothesis. First, aroma glycosides are not universal. Watanabe *et al.* (1993) identified abundant terpenoid and phenolic glycosides in buds and flowers of *Gardenia jasminoides* (Rubiaceae), *Jasminum sambac* and *J. polyanthum* (Oleaceae), but did not detect similar conjugates in *Osmanthus fragrans* (Oleaceae), despite the presence of free volatiles (geraniol, β-damascenone) that have glycosides in other species (Mookherjee *et al.* 1990; Straubinger *et al.* 1997). Second, the quantitation of glycoside concentrations based on the efficiency of enzymatic cleavage is problematic, given the unexpected differences in specificity among five β-D-glucoside-cleaving enzymes for monoterpenol aglycones documented by Ackermann *et al.* (1989) and Watanabe *et al.* (1993). If glycosidase enzymes do not hydrolyze diverse fragrance glycosides with comparable efficiency, there would be no metabolic economy of this mechanism over *de novo* biosynthesis of odorants in floral tissues. Third, temporal changes in glycoside concentration and odor emissions often do not match. In the original rose study, Francis and Allcock (1969) observed a dramatic increase in free and bound monoterpene concentration 3 days after anthesis, but the expected large pools of monoterpene β-D-glucosides were not detected in unopened rosebuds. Phenylpropanoid glycoside levels do increase sharply during bud maturation in *Nicotiana sylvestris* and *N. suaveolens* (Solanaceae), but continue to increase after anthesis, independent of striking circadian rhythms in scent emissions (Loughrin *et al.* 1991, 1992). Finally, Ackermann *et al.* (1989) demonstrated uridine diphosphate-dependent glucosyl transferase activity toward free linalool and geraniol, but not toward GPP, suggesting that glycoside formation cannot precede the biosynthesis of free linalool. This conclusion is intuitive if linalool and other monoterpenes are synthesized within floral plastids and excreted through the plasma membranes of epidermal cells, as they appear to be in *Clarkia* and *Narcissus*. There is no requirement for a hydrophilic carrier molecule in such a hydrophobic environment.

While the available data do not support the obligacy of glycosides as floral scent precursors, they do not eliminate the possibility that this mechanism may contribute to natural fragrance production in some species. Although alternative functions for fragrance glycosides and their hydrolytic enzymes have not been widely explored in the flower glycoside literature, the same or similar glycosides in vegetation may function in plant defense against herbivore attack (Mattiacci *et al.* 1995). Given the mass harvesting and homogenization of cut flowers in these studies, floral processes involving glycosides that are limited to specific organs or tissues probably would not be detected. For example, the nectars of many fragrant, night-blooming flowers contain fragrance compounds in solution, where they are thought to

provide antimicrobial or antifungal protection for pollinator rewards (Knobloch *et al.* 1989; Lawton *et al.* 1993) and gustatory cues for pollinators (Metcalf 1987; Dobson 1994). It is possible that fragrance glycosides are transported via phloem to nectaries for this purpose. Perhaps the mechanism of floral fragrance production via glycosidic precursors might better apply to 1-day flowers with explosive, nocturnal anthesis, as is suggested by the results of Watanabe *et al.* (1993) with *Jasminum* and *Gardenia*, and would be predicted for species of *Datura* and *Oenothera*. Another alternative is that plants with fragrant, animal-dispersed fruits might sequester floral glycosides for later use in fruit ripening. One system in which these alternative hypotheses could easily be tested with a combination of enzymatic and precursor-labeling approaches is *Carica papaya* (Caricaceae), in which linalool and its oxides appear to be volatile attractants in both flowers (Knudsen & Tollsten 1993) and fruits (Schreier & Winterhalter 1986; Winterhalter *et al.* 1986; Flath *et al.* 1990).

Epilogue: Metabolism of linalool by soil microbes

What happens to free linalool in abscised flowers, fruits and vegetation that is not volatilized by the plant? Monoterpenes are generally toxic to microbes, impairing numerous functions of biological membranes (Knobloch *et al.* 1989; Lawton *et al.* 1993; Weidenhamer *et al.* 1993; Lee *et al.* 1998) and are difficult for bacteria to metabolize (Cantwell *et al.* 1978). However, several species of soil bacteria utilize linalool and other monoterpenes as carbon sources, including *Pseudomonas fluorescens* (Vandenbergh & Cole 1986), *P. citronellolis*, *P. incognita* (Seubert 1959; Devi & Bhattacharyya 1977; Madyastha *et al.* 1977; Renganathan & Madyastha 1983), *P. aeruginosa* and *P. putida* (de Smet *et al.* 1989). The capacity to metabolize linalool is conferred by a transposable plasmid with a structural gene encoding a cytochrome P450 hydroxylase. This function adds a second hydroxyl group to carbon 8 or 10 of linalool, after which a series of oxidation steps yields linalool-8-carboxylic acid and CO₂ through perillic acid (de Smet *et al.* 1989; Fig. 10). The plasmid-borne P450 function is substrate specific, such that bacterial strains that metabolize geraniol, nerol or citronellol cannot oxidize linalool, and can be acquired through bacterial conjugation (de Smet *et al.* 1989). These systems have been studied in the context of anthropogenically contaminated soils (e.g. citrus or turpentine processing plants), but would be relevant to the microbial catabolism of linalool introduced to natural soils via dehisced or decomposing plant tissues. Linalool is also toxic to many fungi, with the notable exceptions of the grape must *Botrytus cinerea* (Bock *et al.* 1986) and the soil fungus *Aspergillus niger*

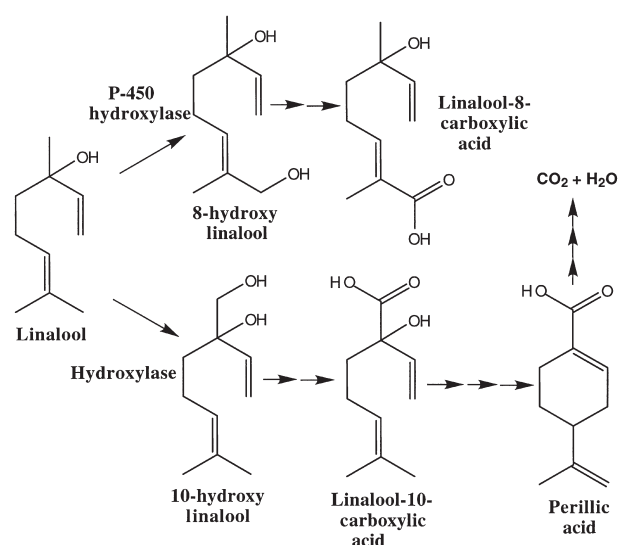


Fig. 10 Catabolism of linalool to CO₂ via perillic acid by *Pseudomonas* soil bacterium, using a P450 hydroxylase located on a transferable plasmid. Modified from DeSmet *et al.* 1989.

(Demyttenaere & Willems 1998). *Aspergillus niger* converts (R)-linalool to isomeric mixtures of its pyranoid and furanoid oxides and similarly transforms rose oxide and other monoterpenes to less toxic hydrocarbons for further catabolism (Miyazawa *et al.* 1995).

Synopsis and prospectus

We have learned much about the molecular, biochemical and physiological mechanisms of scent production from the *Clarkia* model system and have laid the groundwork for comparative studies in other plants. However, significant aspects of linalool biosynthesis and emission in *C. breweri* remain unclear, including petal epidermal cell ultrastructure and the excretory pathway of linalool, the tissue-specific control of linalool oxide biosynthesis in the pistil, the interaction between modifier genes, substrate pools, biosynthetic enzymes and environmental factors in genetic studies and the catabolism of bound linalool. Furthermore, certain important aspects of floral scent biology, such as circadian rhythms of scent emission, cannot be addressed in the *Clarkia* system and are better suited to a transformable model system showing such rhythms (e.g. *Nicotiana* or *Petunia*). Our biochemical and physiological studies of benzenoid and phenylpropanoid volatiles in *C. breweri* flowers suggest that these scent compounds also are produced and emitted *in situ* from petal tissues, albeit via different pathways (Wang *et al.* 1997; Dudareva *et al.* 1998a,b; Wang & Pichersky 1998). Similar investigations are now being extended to other model species, including snapdragon (*Antirrhinum majus*, Scrophulariaceae). Below we highlight three areas of particular interest for future study.

Linalool synthase expression in different tissues and organs

We have described species-specific differences in spatial (petal *vs* pistil) regulation of LIS expression in *Clarkia breweri* and *C. concinna*. A logical next step would be to explore the functional role of LIS promoter sequence variation on both qualitative and quantitative interspecific differences in LIS expression. Flower organ-specific scent production is widespread in many plant families and has important behavioral implications for insect orientation, particularly in bee-pollinated systems (Vogel 1963; Adey 1983; D'Arcy *et al.* 1990; Dobson *et al.* 1990; Knudsen & Tollsten 1991; Armbruster 1992; Lunau 1992; Bergström *et al.* 1995). It would be worth investigating whether floral tissue-specific transcription factors, such as those encoded by MADS-box floral homeotic genes (Mandel *et al.* 1992; Tsuchimoto *et al.* 1993), are involved in limiting LIS expression to the inner whorl (pistil) of the developing flower bud. Finally, it is unclear whether the entrainment of linalool emission to nocturnal circadian rhythms in *Hoya carnosa* and *Stephanotis floribunda* (Asclepiadaceae; Altenburger & Matile 1988; Matile & Altenburger 1988) and *Lonicera japonica* (Caprifoliaceae; Miyake *et al.* 1998) involve regulation at the transcriptional, translational or post-translational levels (Dudareva *et al.* 1999), and which physiological mechanisms couple LIS gene expression to photoperiod.

Herbivore-induced linalool biosynthesis in vegetative tissues

Recent studies have focused on the induced biosynthesis of linalool and other volatiles in the vegetation of maize and cotton in response to feeding damage by a generalist moth caterpillar, *Spodoptera exigua* (Noctuidae; Turlings & Tumlinson 1992; Loughrin *et al.* 1994). While mechanical damage results in the release of cyclic mono- and sesquiterpenes and lipoxygenase-derived aliphatic 'green leaf volatiles', *de novo* biosynthesis and emission of acyclic terpenoids, including linalool, ocimene, homoterpenes and some sesquiterpenes, is systemically induced through the action of an L-glutamine/linolenic acid-derived elicitor (volicitin) introduced to the wound through the saliva of the caterpillar (Röse *et al.* 1996; Alborn *et al.* 1997; Paré & Tumlinson 1997). Volicitin shows biochemical similarities to intermediates in the jasmonate wound signal cascade (Alborn *et al.* 1997; Creelman & Mullet 1997), which is a widespread plant response to herbivore wounding and is often coupled to synthesis of plant defense compounds (Farmer & Ryan 1990, 1992; Pearce *et al.* 1991; Wasternack & Parthier 1997). The acyclic volatile blend, including linalool, is attractive to parasitic wasps that use these volatiles and frass odors

to find *Spodoptera* caterpillars from a distance (Eller *et al.* 1988; Turlings *et al.* 1990, 1991, 1995; Röse *et al.* 1998). Incredibly, other herbivores may also be attracted to these induced emissions (Loughrin *et al.* 1995). Comparable mechanisms probably govern volatile linalool and methyl salicylate emission and the recruitment of predacious spider mites to wound damage by herbivorous mites in lima bean (Dicke *et al.* 1990). Similarly, in tobacco the same group of acyclic volatiles, including linalool, is induced exclusively through herbivory by *Manduca sexta* (Sphingidae) caterpillars through the jasmonate wound-response pathway (Baldwin 1999). These patterns suggest that the expression of a LIS-like gene in the vegetation of these plants should be inducible by systemin, a polypeptide signal molecule that triggers systemic induction of the jasmonate cascade in response to herbivory (Pearce *et al.* 1991; Farmer & Ryan 1992). Physiological and molecular studies of LIS expression in wounded vegetation or after application of volicitin, methyl jasmonate, systemin or other octadecanoid signal transductants would provide a valuable contribution to our understanding of induced plant defenses in tritrophic systems.

Chirality and homoplasy in linalool biosynthesis

We have reviewed the biosynthesis of (S)-linalool in *Clarkia* flowers, but many plants also produce (R)-linalool. Molecular and biochemical studies of the cyclic monoterpene limonene have revealed three surprising results: (i) distinct, enantiospecific limonene synthase enzymes are responsible for the biosynthesis of (S)- and (R)-limonene in caraway and spearmint, respectively (Gershenzon *et al.* 1989; Pyun *et al.* 1993; Bouwmeester *et al.* 1998); (ii) spearmint LMS (and some other terpene synthases) catalyze the synthesis of minor products (myrcene, α -pinene and β -pinene) in addition to the major product, 4S(-)-limonene, from GPP (Colby *et al.* 1993); and (iii) coding sequences of structural genes encoding the LMS function in gymnosperms (Pinaceae) and angiosperms (Lamiaceae) are not monophyletic: the LMS sequences from fir (*Abies grandis*) are more similar to other gymnosperm diterpene and sesquiterpene synthases than to angiosperm LMS (Yuba *et al.* 1996; Bohlmann *et al.* 1997, 1998).

The first result predicts that an (R)-LIS should be found in *Cinnamomum camphora* and other plants producing (R)-linalool, but the third result warns that it may not necessarily bear close sequence similarity or a common ancestry with *Clarkia* LIS. The second result, which has disturbing implications for genetic analysis of terpenoid production in any plant, suggests that linalool and other terpenoids may be produced not only as major products of their biosynthetic enzymes, but also as by-products of other enzymatic reactions. Investigations of the biosyn-

thesis of geraniol and nerol, which are structural isomers of linalool, should provide more information about alternative or minor biosynthetic routes to linalool production. Finally, the ubiquitous distribution of linalool among monocots and dicots suggests that there has been ample opportunity for the independent evolution of LIS-like enzymes, especially when the strongly scented, night-blooming condition is repeatedly gained and lost within and among plant families. In the Onagraceae, for example, linalool production is associated with hawkmoth pollination in genera related to *Clarkia*, such as *Oenothera* (Kawano *et al.* 1995; Miyake *et al.* 1998; Raguso 1999) and *Calylophus* (Raguso 1999). The phylogenetic mapping of fragrance chemistry and pollinator affinities in these genera, combined with comparative biochemical and molecular studies is currently underway, with the expressed goal of exploring the repeated evolution of floral scent as a component of mating systems and reproductive strategies in the Onagraceae. The potential for homoplasious evolution of linalool synthase-like functions should be even greater when comparisons are extended to include more distantly related linalool-producing organisms, such as the cycad *Zamia furfuracea* (Pellmyr *et al.* 1990), the blewit mushroom (*Lepista nuda*, Tricholomataceae; Breheret *et al.* 1997) and the Asian honeybee (*Apis cerana*, Apidae; Matsuyama *et al.* 1997).

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Appendix I.

Natural occurrence of linalool in the fragrance of flowering plants

Family	Species	Anthesis/pollinators	Reference
Alliaceae	<i>Allium schoenoprasum</i>	Day/bees?	Nilsson (1983b)
Amaryllidaceae	<i>Crinum asiaticum</i> *	Night/moths	Miyake <i>et al.</i> (1998)
	<i>Hippeastrum calyptratrum</i>	Night/bats	Bestmann <i>et al.</i> (1997)
	<i>Hymenocallis sonorensis</i>	Night/moths	Raguso (1999)
	<i>Narcissus assoanus</i>	Day/moths, bees	Dobson <i>et al.</i> (1997)
	<i>N. bugei</i>	Day/bees, flies, beetles	Dobson <i>et al.</i> (1997)
	<i>N. gaditanus</i>	Day/moths, bees	Dobson <i>et al.</i> (1997)
	<i>N. jonquilla</i>	Day/moths, bees	Joulain (1993)*; Dobson <i>et al.</i> (1997)
Annonaceae	<i>N. papyraceus</i>	Day/moths, bees, flies	Dobson <i>et al.</i> (1997)
	<i>N. serotinus</i> *	Day/moths, flies	Dobson <i>et al.</i> (1997)
	<i>Cananga odorata</i>	Day/beetles?	Ma <i>et al.</i> (1988)
Apiaceae	<i>Angelica archangelica</i> *	Day/bees, flies	Tollsten <i>et al.</i> (1994)

Appendix I. Continued

Family	Species	Anthesis/pollinators	Reference	
Apocynaceae	<i>Tabernaemontana amygdalifolia</i>	Night/moths	Knudsen & Tollsten (1993)	
	<i>Telosiphonia brachysiphon</i>	Night/moths	Raguso (1999)	
	<i>T. nacapulensis</i>	Night/moths	Raguso (1999)	
	<i>Plumeria alba</i>	Night/moths [§]	Knudsen & Tollsten (1993)	
	<i>P. rubra</i> *, [‡]	Night/moths [§]	Omata <i>et al.</i> (1991b)	
Araceae	<i>Anthurium fragrantissimum</i>	Day/?	Kuanprasert <i>et al.</i> (1998)	
	<i>A. lindenianum</i>	Day/?	Kuanprasert <i>et al.</i> (1998)	
	<i>Peltandra virginica</i>	Day/flies	Patt <i>et al.</i> (1995)	
	<i>Sauromatum guttatum</i>	Day/flies, beetles	Skubatz <i>et al.</i> (1996)	
Asclepiadaceae	<i>Stephanotis floribunda</i>	Night/moths, bees?	Altenburger & Matile (1988, 1990)	
	<i>Hoya carnosa</i>	Night/?	Surburg <i>et al.</i> (1993)	
Asteraceae	<i>Cichorium intybus</i> *	Day/bees	Dobson (1991)	
	<i>Leodontum alpinum</i>	Day/bees, flies	Erhardt (1993)	
	<i>Senecio articulatus</i> *	Day/flies	Kite & Smith (1997)	
Bombacaceae	<i>Ceiba trischistandra</i> *	Night/bats	Knudsen & Tollsten (1995)	
	<i>Ochroma pyramidalis</i>	Night/bats	Knudsen & Tollsten (1995)	
Brassicaceae	<i>Brassica napus</i>	Day/bees	Jakobsen <i>et al.</i> (1994); Blight <i>et al.</i> (1997)	
	<i>Erysimum X allionii</i>	Day/bees, butterflies?	Surburg <i>et al.</i> (1993)	
	<i>Hesperis matronalis</i>	Night, day/butterflies, moths	Nielsen <i>et al.</i> (1995)	
Cactaceae	<i>Dolicothele longimamma</i>	Day/bees?	Kaiser & Nussbaumer (1990)	
	<i>Rebutia marsoneri</i>	Day/bees?	Kaiser & Nussbaumer (1990)	
	<i>Selenicereus hamatus</i>	Night/moths	Kaiser (1991)	
	<i>Weberocereus biolleyi</i>	Night/bats	Bestmann <i>et al.</i> (1997)	
	<i>W. tunilla</i>	Night/bats	Bestmann <i>et al.</i> (1997)	
Calycanthaceae	<i>Chimonanthus praecox</i>	Day/beetles	Zheng <i>et al.</i> (1990) [‡]	
Capparidaceae	<i>Cleome anomala</i>	Night/bats	Knudsen & Tollsten (1995)	
Caprifoliaceae	<i>Lonicera americana</i>	Night/moths	Mookherjee <i>et al.</i> (1990)	
	<i>L. japonica</i>	Night/moths	Schlotzhauer <i>et al.</i> 1996 [‡] ; Miyake <i>et al.</i> (1998)	
	<i>Sambucus nigra</i> *	Day/bees, flies	Joulain (1987) [‡]	
Caricaceae	<i>Carica papaya</i> *	Night/moths, bees [§]	Knudsen & Tollsten (1993)	
Caryophyllaceae	<i>Silene maritima</i> *	Night/moths, bees?	Knudsen & Tollsten (1993)	
Combretaceae	<i>Quisqualis indica</i>	Night/moths	Raguso & Weiss, unpublished (1997)	
Cucurbitaceae	<i>Trichosanthes kirilowii</i>	Night/moths	Miyake <i>et al.</i> (1998)	
Fabaceae	<i>Albizia julibrissin</i> *	Night/moths	Li <i>et al.</i> (1988a) [‡] ; Miyake <i>et al.</i> (1998)	
	<i>Anthyllus vulneraria</i>	Day/bees	Nilsson (1983b)	
	<i>Brownepopsis disepala</i>	Night/bats, moths	Knudsen & Kitgaard (1998)	
	<i>Lupinus polyphyllus</i>	Day/bees	Dobson <i>et al.</i> (1996)	
	<i>Medicago sativa</i>	Day/bees	Loper (1972) Henning & Teuber (1992)	
		<i>Robinia pseudacacia</i>	Day/bees	Joulain (1986) [‡]
		<i>Wistaria sinensis</i>	Day/bees	Joulain (1986) [‡]
	Fagaceae	<i>Castanea creata</i> *	Day/bees, flies	Yamaguchi & Shibamoto (1980) [‡]
	Fumariaceae	<i>Corydalis cava</i>	Day/bees	Olesen & Knudsen (1994)
	Hydrangeaceae	<i>Philadelphus coronarius</i> *	Day/bees	Joulain (1986, 1987) [‡]
Iridaceae	<i>Freesia hybrida</i> *	Day/?	Harada & Mihara (1984) [‡] ; Mookherjee <i>et al.</i> (1990)	
Liliaceae	<i>Convallaria majalis</i> *	Day/	Kaiser (1991)	
	<i>Fritillaria meleagris</i> *	Day/bees, flies	Hedström (1983)	
	<i>Hyacinthus orientalis</i>	Day/?	Kaiser & Lamparsky (1977)	
	<i>Lilium candidum</i>	Day/?	Joulain (1986) [‡]	

Appendix I. *Continued*

Family	Species	Anthesis/pollinators	Reference
Lecythidaceae	<i>Couroupita guianensis</i> *	Day/bees	Knudsen & Mori (1996)
	<i>Corythophora amapaensis</i>	Day/bees	Knudsen & Mori (1996)
	<i>Couratari stellata</i>	Day/euglossine bees	Knudsen & Mori (1996)
	<i>Eschweilera coriacea</i>	Day/euglossine bees	Knudsen & Mori (1996)
	<i>Gustavia longifolia</i>	Day/bees	Knudsen & Mori (1996)
	<i>G. serrata</i>	Day/bees	Knudsen & Mori (1996)
	<i>Lecythis persistens</i>	Day/bees	Knudsen & Mori (1996)
	<i>L. pisonis</i>	Day/bees	Knudsen & Mori (1996)
Magnoliaceae	<i>Magnolia grandiflora</i>	Day/beetles, bees	Azuma <i>et al.</i> (1997)
	<i>M. heptapetala</i> *	Day/beetles, bees	Azuma <i>et al.</i> (1997)
	<i>M. hypoleuca</i> *	Day/beetles, bees	Azuma <i>et al.</i> (1997)
	<i>M. praecocissima</i> *	Day/beetles, bees	Azuma <i>et al.</i> (1997)
	<i>M. pyramidata</i>	Day/beetles, bees	Azuma <i>et al.</i> (1997)
	<i>M. tamaulipana</i>	Day/beetles, bees	Azuma <i>et al.</i> (1997)
	<i>M. tripetala</i>	Day/beetles, bees	Thien <i>et al.</i> (1975)
	<i>Michaelia compressa</i>	Day/beetles, bees	Azuma <i>et al.</i> (1997)
Moraceae	<i>Liriodendron chinensis</i> †	Day/beetles, bees	Azuma <i>et al.</i> (1997)
	<i>Ficus carica</i> *	Day/wasps	Gibernau <i>et al.</i> (1997)
Nelumbonaceae	<i>Nelumbo nucifera</i>	Day/bees, beetles	Omata <i>et al.</i> (1991c)
	<i>N. pentapetala</i>	Day/bees, beetles	Omata <i>et al.</i> (1991c)
Oleaceae	<i>Jasminum polyanthum</i>	Night/moths	Christensen <i>et al.</i> (1997)
	<i>J. grandiflora</i>	Night/moths	Mookherjee <i>et al.</i> (1990); Joulain (1993); Moon <i>et al.</i> (1994)
	<i>J. sambac</i> *	Night/moths?	Bu <i>et al.</i> (1987a); Joulain (1993); Watanabe <i>et al.</i> (1993)
	<i>Ligustrum</i> sp.	Day/bees, butterflies	Joulain (1987)†
	<i>L. japonica</i>	Day/bees, butterflies	Honda <i>et al.</i> (1998)
Onagraceae	<i>Osmanthus fragrans</i>	Day, night/?	Mookherjee <i>et al.</i> (1990), Watanabe <i>et al.</i> (1993)
	<i>Calylophus toumeyii</i>	Night/moths	Raguso (1999)
	<i>Clarkia breweri</i> *	Day, night/ moths, hummingbirds	Raguso & Pichersky (1995)
	<i>C. concinna</i> *	Day/bees, flies, butterflies	Raguso & Pichersky (1995)
	<i>Oenothera arizonica</i>	Night/moths	Raguso, unpublished (1995)
	<i>O. biennis</i>	Night/moths, bees	Kawano <i>et al.</i> (1995)
	<i>O. caespitosa</i>	Night/moths	Raguso (1999)
	<i>O. elata</i>	Night/moths, bees	Raguso (1999)
	<i>O. glazioviana</i>	Night/moths	Kawano <i>et al.</i> (1995)
	<i>O. harringtonii</i>	Night/moths, bees?	Raguso, unpublished (1998)
Orchidaceae	<i>O. odorata</i> *	Night/moths	Zheng <i>et al.</i> (1989)†
	<i>O. stricta</i>	Night/moths	Miyake <i>et al.</i> (1998)
	<i>Aerangis appendiculata</i> *	Night/moths	Kaiser (1993)
	<i>A. biloba</i>	Night/moths	Kaiser (1993)
	<i>A. brachycarpa</i>	Night/moths	Kaiser (1993)
	<i>A. confusa</i>	Night/moths	Kaiser (1993)
	<i>A. distincta</i>	Night/moths	Kaiser (1993)
	<i>A. fastuosa</i> *	Night/moths	Kaiser (1993)
	<i>A. kirki</i>	Night/moths	Kaiser (1993)
	<i>A. kotschyana</i>	Night/moths	Kaiser (1993)
	<i>A. somaliensis</i>	Night/moths	Kaiser (1993)
	<i>Aeranthus grandiflora</i> *	Night/?	Kaiser (1993)
	<i>Aerides fieldingii</i>	Day/bees	Kaiser (1993)
	<i>A. lawrenceae</i>	Day/bees	Kaiser (1993)
<i>Angraecum aporoides</i> *	Night/moths?	Kaiser (1993)	
<i>A. bosseri</i> *	Night/moths	Kaiser (1993)	

Appendix I. Continued

Family	Species	Anthesis/pollinators	Reference
	<i>A. eichlerianum</i> *	Night/moths	Kaiser (1993)
	<i>A. sesquipedale</i> *	Night/moths	Kaiser (1993)
	<i>Bifrenaria thyranthina</i>	Day/euglossine bees	Gerlach & Schill (1991)
	<i>Brassavola acaulis</i>	Night/moths [§]	Hills <i>et al.</i> (1968)
	<i>B. digbyana</i>	Night/moths [§]	Kaiser (1993)
	<i>B. glauca</i>	Night/moths [§]	Kaiser (1993)
	<i>B. nodosa</i>	Night/moths [§]	Kaiser (1993)
	<i>B. tuberculata</i>	Night/moths [§]	Kaiser (1993)
	<i>Brassia verucosat</i>	Day/?	Kaiser (1993)
	<i>Bulbophyllum lobbit</i> *	Day/?	Kaiser (1993)
	<i>Catasetum aff. barbatum</i>	Day/euglossine bees	Hills <i>et al.</i> (1968)
	<i>C. fimbriatum</i>	Day/euglossine bees	Hills <i>et al.</i> (1968)
	<i>C. russelianum</i>	Day/euglossine bees	Hills <i>et al.</i> (1972)
	<i>C. tenebrosum</i>	Day/euglossine bees	Hills <i>et al.</i> (1972)
	<i>C. warczewitzii</i>	Day/euglossine bees	Hills <i>et al.</i> (1972)
	<i>Cattleya araguaiensis</i>	Day/bees	Kaiser (1993)
	<i>C. dowiana</i>	Day/bees	Kaiser (1993)
	<i>C. labiata</i>	Day/bees	Kaiser (1993)
	<i>C. lawrenceana</i>	Day/bees	Kaiser (1993)
	<i>C. leopoldi</i>	Day/bees	Kaiser (1993)
	<i>C. maxima</i>	Day/bees	Kaiser (1993)
	<i>C. percivaliana</i>	Day/bees	Kaiser (1993)
	<i>C. porphyroglossa</i>	Day/bees	Kaiser (1993)
	<i>C. schilleriana</i> *	Day/bees	Kaiser (1993)
	<i>Chaubardiella hirtzii</i>	Day/euglossine bees	Gerlach & Schill (1991)
	<i>Chondrorhyncha lendyana</i>	Day/?	Kaiser (1993)
	<i>Cirrhaea dependens</i>	Day/?	Kaiser (1993)
	<i>Cirrhopetalum robustum</i>	Day/flies	Kaiser (1993)
	<i>Cochleanthes aromatica</i> *	Day/euglossine bees	Gerlach & Schill (1991)
	<i>C. discolor</i>	Day/euglossine bees	Kaiser (1993)
	<i>C. marginata</i>	Day/euglossine bees	Kaiser (1993)
	<i>Coelogyne zurowetzii</i> *	Day/?	Kaiser (1993)
	<i>Constantia cipoensis</i>	Night/bees	Kaiser (1993)
	<i>Coryanthes vieirae</i>	Day/euglossine bees	Kaiser (1993)
	<i>Cynoches densiflorum</i>	Day/euglossine bees	Gregg (1983)
	<i>C. diana</i>	Day/euglossine bees	Gregg (1983)
	<i>C. stenodactylon</i>	Day/euglossine bees	Gregg (1983)
	<i>Cymbidium pumilum</i> *	Day/bees [§]	Sasaki <i>et al.</i> (1991) [†]
	<i>C. goeringii</i>	Day/bees	Kaiser (1993)
	<i>C. floribundum</i> *	Day/bees [§]	Matsuyama <i>et al.</i> (1997)
	<i>Cypripedium calceolus</i>	Day/bees [§]	Bergström <i>et al.</i> (1992)
	<i>C. candidum</i>	Day/bees [§]	Barkman <i>et al.</i> (1997)
	<i>C. kentuckiense</i>	Day/bees [§]	Barkman <i>et al.</i> (1997)
	<i>C. parviflorum</i> *	Day/bees [§]	Barkman <i>et al.</i> (1997)
	<i>Dendrobium anosmum</i>	Day/bees	Kaiser (1993)
	<i>D. beckleri</i>	Day/bees	Kaiser (1993)
	<i>D. brymerianum</i>	Day/bees	Kaiser (1993)
	<i>D. carniferum</i> *	Day/bees	Kaiser (1993)
	<i>D. chrysotoxum</i>	Day/bees	Kaiser (1993)
	<i>D. delacourii</i>	Day/bees	Kaiser (1993)
	<i>D. lichenastrum</i>	Day/bees	Kaiser (1993)
	<i>D. moniliforme</i>	Night/moths?	Kaiser (1993)
	<i>D. monophyllum</i> *	Day/bees	Kaiser (1993)
	<i>D. pugioniforme</i>	Day/bees	Kaiser (1993)
	<i>D. trigonopes</i>	Day/butterflies?	Kaiser (1993)
	<i>D. unicum</i>	Day/butterflies?	Kaiser (1993)
	<i>D. virgineum</i>	Day/moths?	Kaiser (1993)

Appendix I. *Continued*

Family	Species	Anthesis/pollinators	Reference
	<i>D. williamsii</i>	Day/bees	Kaiser (1993)
	<i>Dendrochilum cobbianum</i> *	Day/bees	Kaiser (1993)
	<i>Diaphanathe pellucida</i>	Day/?	Kaiser (1993)
	<i>Encyclia adenocarpa</i>	Day/bees	Kaiser (1993)
	<i>E. fragrans</i>	Day/bees	Kaiser (1993)
	<i>E. glumacea</i>	Day/?	Kaiser (1993)
	<i>Epidendrum ciliare</i> *	Night/moths [§]	Kaiser (1993); Knudsen & Tollsten (1993);
	<i>E. lacertinum</i>	Day/? [§]	Kaiser (1993)
	<i>E. nocturnum</i>	Night/moths [§]	Kaiser (1993)
	<i>Epigyneium lonii</i>	Day/?	Kaiser (1993)
	<i>Eria hyacinthoides</i>	Day/?	Kaiser (1993)
	<i>Gongora armeniaca</i>	Day/euglossine bees	Kaiser (1993)
	<i>G. cassidea</i>	Day/euglossine bees	Kaiser (1993)
	<i>G. galeata</i>	Day/euglossine bees	Gerlach & Schill (1991)
	<i>G. grossa</i>	Day/euglossine bees	Gerlach & Schill (1991)
	<i>G. quinquenervis</i>	Day/euglossine bees	Hills <i>et al.</i> (1968)
	<i>Gymnadenia conopea</i>	Day/butterflies?	Kaiser (1993)
	<i>Himantoglossum hircinum</i>	Day/?	Kaiser (1993)
	<i>Huntleya meleagris</i>	Day/bees?	Kaiser (1993)
	<i>Laelia albida</i>	Day/?	Kaiser (1993)
	<i>L. perinii</i>	Day/?	Kaiser (1993)
	<i>Liparis viridiflora</i>	Day/beetles, flies	Kaiser (1993)
	<i>Listera ovata</i> *	Day/wasps, beetles, flies	Nilsson (1981)
	<i>Lycaste aromatica</i>	Day/bees?	Kaiser (1993)
	<i>L. cruenta</i>	Day/bees?	Kaiser (1993)
	<i>Masdaevalia estradae</i>	Day/flies	Kaiser (1993)
	<i>M. trichas</i>	Day/flies, beetles	Kaiser (1993)
	<i>Maxillaria picta</i>	Day/bees	Kaiser (1993)
	<i>M. tenuifolia</i>	Day/bees	Kaiser (1993)
	<i>M. variabilis</i>	Day/bees	Kaiser (1993)
	<i>Miltonia regnellii</i>	Day/bees	Kaiser (1993)
	<i>M. schroederiana</i> *	Day/bees	Kaiser (1993)
	<i>M. spectabilis</i>	Day/bees	Kaiser (1993)
	<i>M. phalaeopsis</i>	Day/bees	Kaiser (1993)
	<i>Neofinetia falcata</i>	Night/moths	Kaiser (1993)
	<i>Nigritella nigra</i>	Day/moths	Kaiser (1993)
	<i>Odontoglossum cirrhosea</i> *	Day/bees	Kaiser (1993)
	<i>O. constrictum</i>	Day/bees	Kaiser (1993)
	<i>O. pulchellum</i>	Day/bees	Kaiser (1993)
	<i>Oncidium longipes</i>	Day/bees	Kaiser (1993)
	<i>O. ornithorhynchum</i> *	Day/bees	Kaiser (1993)
	<i>O. sarcodes</i> *	Day/bees	Kaiser (1993)
	<i>O. tigrinum</i>	Day/bees	Kaiser (1993)
	<i>Ophrys sphecodes</i>	Day/bees [§]	Borg-Karlsön & Groth (1986)
	<i>O. splendida</i> *	Day/bees [§]	Borg-Karlsön & Groth (1986)
	<i>O. insectifera</i>	Day/bees [§]	Borg-Karlsön (1990)
	<i>O. aimoninii</i>	Day/bees [§]	Borg-Karlsön (1990)
	<i>O. aveyronensis</i>	Day/bees [§]	Borg-Karlsön (1990)
	<i>O. ferrum-equinum</i>	Day/bees [§]	Borg-Karlsön (1990)
	<i>Orchis mascula</i> *	Day/bees [§]	Nilsson (1983a)
	<i>O. morio</i>	Day/bees [§]	Nilsson (1983b)
	<i>Paphinia grandiflora</i>	Day/euglossine bees	Gerlach & Schill (1991)
	<i>Pescatorea corina</i>	Day/bees	Kaiser (1993)
	<i>P. dayana</i> *	Day/bees	Kaiser (1993)
	<i>Phalaeopsis violacea</i> *	Day/bees	Kaiser (1993)
	<i>Platanthera bifolia</i> *	Night/moths	Tollsten & Bergström (1993)

Appendix I. Continued

Family	Species	Anthesis/pollinators	Reference
	<i>P. chlorantha</i>	Night/moths	Kaiser (1993)
	<i>P. stricta</i>	Night/moths, flies	Patt <i>et al.</i> (1988)
	<i>Plectrelminthus caudatus</i>	Night/moths	Kaiser (1993)
	<i>Polycynis gratiosa</i>	Day/euglossine bees	Gerlach & Schill (1991)
	<i>Polystachya campyloglossa</i>	Day/?	Kaiser (1993)
	<i>P. fallax</i>	Day/bees	Kaiser (1993)
	<i>Rangaeris amaniensis</i>	Night/moths	Kaiser (1993)
	<i>Rhynchostylis coelestis</i>	Day/bees	Kaiser (1993)
	<i>Rodriguezia refracta</i>	Day/?	Kaiser (1993)
	<i>Stanhopea anfracta</i>	Day/euglossine bees	Whitten & Williams (1992)
	<i>S. annulata</i>	Day/euglossine bees	Hills <i>et al.</i> (1968)
	<i>S. connata</i>	Day/euglossine bees	Whitten & Williams (1992)
	<i>S. martiana</i>	Day/euglossine bees	Whitten & Williams (1992)
	<i>S. oculata</i>	Day/euglossine bees	Whitten & Williams (1992), Kaiser (1993)
	<i>S. peruviana</i>	Day/euglossine bees	Whitten & Williams (1992)
	<i>S. tigrina</i>	Day/euglossine bees	Kaiser (1993)
	<i>Trichocentrum tigrinum</i>	Day/bees	Kaiser (1993)
	<i>Trichoglottis philippiensis</i>	Day/?	Kaiser (1993)
	<i>Trixospermum arachnites</i>	Day/?	Kaiser (1993)
	<i>Vanda denisoniana</i>	Day/bees	Kaiser (1993)
	<i>V. tessellata</i>	Day/bees	Kaiser (1993)
	<i>Zygopetalum crinitum</i>	Day/bees	Kaiser (1993)
Paeoniaceae	<i>Peonia albiflora</i> *	Day/beetles, bees?	Kumar & Motto (1986) [‡]
Pittosporaceae	<i>Pittosporum tobira</i>	Day/butterflies, bees	Joulain (1986) [‡]
Polemoniaceae	<i>Linanthus dichotomus</i>	Night/moths [§]	Raguso, unpublished (1994)
	<i>Phlox bryoides</i> *	Day/bees, butterflies	Raguso & Roy (1998)
	<i>P. paniculata</i>	Day/butterflies	Surburg <i>et al.</i> (1993)
Primulaceae	<i>Primula veris</i>	Day/bees	Nilsson (1980)
Ranunculaceae	<i>Actaea rubra</i> *	Day/beetles, bees	Pellmyr <i>et al.</i> (1987)
	<i>A. asiatica</i> *	Day/?	Pellmyr <i>et al.</i> (1987)
	<i>A. pachypoda</i>	Day/beetles, bees	Pellmyr <i>et al.</i> (1987)
	<i>A. silvestris</i> *	Day/bees, flies	Pellmyr <i>et al.</i> (1987)
	<i>A. spicata</i>	Day/beetles	Pellmyr <i>et al.</i> (1987)
	<i>Cimicifuga simplex</i>	Day/butterflies	Groth <i>et al.</i> (1987)
	<i>Ranunculus acris</i> *	Day/bees, flies	Bergström <i>et al.</i> (1995)
Rosaceae	<i>Crataegus monogyna</i>	Day/bees, flies	Robertson <i>et al.</i> (1993)
	<i>Malus × Domestica</i>	Day/bees	Loughrin <i>et al.</i> (1990); Buchbauer <i>et al.</i> (1993) [‡]
	<i>Rosa chinensis</i>	Day/bees	Bu <i>et al.</i> (1987b)
	<i>Rubus idaeus</i>	Day/bees	Robertson <i>et al.</i> (1993)
Rubiaceae	<i>Hillia parasitica</i>	Night/moths	Knudsen & Tollsten (1993)
	<i>Coussarea</i> sp.	Night/moths	Knudsen & Tollsten (1993)
	<i>Gardenia jasminoides</i>	Night/moths, bees?	Tsuneya <i>et al.</i> (1979) [‡] ; Joulain (1993) [‡] ; Watanabe <i>et al.</i> (1993, 1994)
	<i>G. tahitiensis</i>	Night/moths?	Joulain (1993) [‡]
Rutaceae	<i>Citrus aurantium</i>	Day/bees	Toyoda <i>et al.</i> (1993)
	<i>C. depressa</i>	Day/bees	Loper (1972)
	<i>C. grandis</i>	Day/bees	Toyoda <i>et al.</i> (1993)
	<i>C. iyo</i>	Day/bees	Toyoda <i>et al.</i> (1993)
	<i>C. kawachinensis</i>	Day/bees	Toyoda <i>et al.</i> (1993)
	<i>C. limon</i>	Day/bees	Toyoda <i>et al.</i> (1993)
	<i>C. medica</i>	Day/bees	Altenburger & Matile (1988)

Appendix I. *Continued*

Family	Species	Anthesis/pollinators	Reference
	<i>C. natsudaidai</i>	Day/bees	Toyoda <i>et al.</i> (1993)
	<i>C. sinensis</i>	Day/bees	Toyoda <i>et al.</i> (1993)
	<i>C. sulcata</i>	Day/bees	Toyoda <i>et al.</i> (1993)
	<i>C. tachibana</i>	Day/bees	Toyoda <i>et al.</i> (1993)
	<i>C. unshui</i>	Day/bees	Toyoda <i>et al.</i> (1993)
Salicaceae	<i>Salix caprea</i>	Day/bees	Tollsten & Knudsen (1992)
	<i>S. cinerea</i>	Day/bees	Tollsten & Knudsen (1992)
	<i>S. repens</i>	Day/bees	Tollsten & Knudsen (1992)
Saxifragaceae	<i>Ribes nigrum</i> †	Day/bees	Hansted <i>et al.</i> (1994)
Simaroubaceae	<i>Ailanthus glandulosa</i>	Day, night/bee, fly?	Joullain (1987)
Solanaceae	<i>Brugmanssia suaveolens</i>	Night/moths, bats?	Knudsen, Tollsten (1993)
	<i>Cestrum nocturnum</i>	Night/moths	Li <i>et al.</i> (1988b)†
	<i>Datura wrightii</i>	Night/moths, bees	Raguso (1999)
	<i>Nicotiana sylvestris</i>	Night/moths	Loughrin <i>et al.</i> (1990)
	<i>N. tabacum</i>	Night, day/???	Loughrin <i>et al.</i> (1990)
	<i>N. tomentosiformis</i>		Loughrin <i>et al.</i> (1990)
Sterculiaceae	<i>Theobroma cacao</i>	Day/flies	Erickson <i>et al.</i> (1987)‡
Theaceae	<i>Camellia japonica</i> *	Day/bees	Omata <i>et al.</i> (1989)
Theophrastaceae	<i>Theophrasta americana</i>	Day/flies	Knudsen & Ståhl (1994)
	<i>Jacquinea keyensis</i>	Day/?	Knudsen & Ståhl (1994)
	<i>J. macrocarpa</i>	Day/hummingbirds	Knudsen & Ståhl (1994)
	<i>J. sprucei</i>	Day/?	Knudsen & Ståhl (1994)
Thymelaceae	<i>Daphne mezereum</i> *	Day/bees	Borg-Karlson <i>et al.</i> (1996)
Verbenaceae	<i>Clerodendrum trichotomum</i>	Night/moths	Miyake <i>et al.</i> (1998)
	<i>Lantana camara</i> *	Day/butterflies	Raguso & Weiss, unpublished (1997)
	<i>L. montevidensis</i> *	Day/butterflies	Raguso & Weiss, unpublished (1997)
Winteraceae	<i>Belliolum</i> sp.	Day/beetles, thrips	Pellmyr <i>et al.</i> (1990)
	<i>Zygogynum baillionii</i>	Day/moths	Thien <i>et al.</i> (1985)
	<i>Z. bicolor</i>	Day/moths	Thien <i>et al.</i> (1985)
Zingiberaceae	<i>Hedychium coronaria</i> *	Night/moths	Knudsen, Tollsten (1993)
Cydales	<i>Encephalartos altensteinii</i>	Day/beetles	Pellmyr <i>et al.</i> (1990)
	<i>Macrozamia moorei</i>	Day/beetles	Pellmyr <i>et al.</i> (1990)
	<i>Zamia furfuracea</i>	Day/beetles	Pellmyr <i>et al.</i> (1990)

*Also contains linalool oxides. †Only contains linalool oxides. ‡Steam or vacuum distillation was used. §Deceptive flower. ¶Presence of compounds inferred by behavior assay.