

# Floral scents, leaf volatiles and thermogenic flowers in Magnoliaceae

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## Abstract

The role and chemical composition of floral scent in pollination systems of angiosperms has been largely ignored because of the difficulty in characterizing scent components. Magnoliaceae is one of the few plant families in which the floral scents of a large number of species have been analyzed. Within the family, floral scents of taxa are dominated by one chemical class of compounds (e.g. benzenoids or terpenoids etc.). Artificially damaged leaves emit a variety of chemicals, some of which also occur in the floral scents (e.g. 4,8-dimethyl-1,3(E),7-nonatriene, linalool etc.). Floral thermogenesis occurs in Magnoliaceae and enhances evaporation of floral scent (in *Magnolia tamaulipana* A. Vázquez, sp. nov.) and may serve as a direct energy reward to visiting insects. It is hypothesized that floral heat and scent may have been key components in the breeding systems of early angiosperms. Floral heat may have been a major resource for insects and one that could be provided by plants without evolution of elaborate morphological features. In this regard, fragrance signals not only food and mating sites, but also heat.

*Keywords:* 4,8-dimethyl-1,3(E),7-nonatriene, chemical signal, floral scent, linalool, Magnoliaceae, thermogenic flowers.

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## Introduction

One of the main contributions of Sprengel (1773) to pollination biology was the concept of mutual adaptation of flowers and pollinators (reviewed in Harborne 1993; Proctor *et al.* 1996). Fragrance is undoubtedly one of the chief attractants in a wide variety of insect–flower interactions (Knudsen *et al.* 1993) and it is hypothesized that floral scents played a role in the early evolution of pollination systems. Porsch (1950, 1954) maintained that pollen itself emitted a smell (the oldest flower scent) and pollen-specific volatile compounds were identified (Bergström *et al.* 1995; Dobson *et al.* 1996). Indeed, van der Pijl (1960) suggested that floral odor preceded color as a pollinator attractant and Pellmyr & Thien (1986) hypothesized that floral volatiles may have originated from secondary plant compounds that originally functioned as herbivore deterrents. Subsequently, these volatiles func-

tioned as chemical cues for insects signifying the availability of food, mating, etc. (Pellmyr & Thien 1986; Gottsberger 1988). The role and chemical composition of floral scent in pollination systems in most plant taxa; however, has been largely ignored because of the difficulty in characterizing (sampling and analyzing) the scent components (Bergström 1987).

Magnoliaceae is one of the few families of flowering plants in which the floral scents of a relatively large number of species has been chemically analyzed using modern techniques (Yasukawa *et al.* 1992; Azuma *et al.* 1997b; Thien *et al.* 1998). It is a well-defined group of shrubs or trees of approximately 200 species, distributed in temperate, subtropical and tropical regions of the world (Treseder 1978; Callaway 1994; Frodin & Govaerts 1996). Concepts of the reproductive biology of the family are based primarily on species of *Magnolia* in temperate regions of the world (Thien *et al.* 1998).

This paper presents an overview of floral fragrances and floral thermogenesis in Magnoliaceae and other basal angiosperms.

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### Chemistry of floral scents and leaf volatiles (Magnoliaceae)

Chemical analysis of floral scents of various Magnoliaceae taxa has been conducted mainly on species of *Magnolia* growing in temperate to subtropical regions of the world (Thien *et al.* 1975; Yasukawa *et al.* 1992). Recently, precise analysis of floral scents and leaf volatiles was conducted by Azuma *et al.* (1997a,b). The flowers of *Magnolia* and allied genera emit various classes of volatile compounds (i.e. terpenoids, benzenoids, fatty acid esters and hydrocarbons; Azuma *et al.* 1997b).

Generally, the chemical composition of floral scents in the family vary among the taxa but display characteristic scent profiles (Table 1). Although most species emit a number of volatile compounds, major portions of the floral scents of most taxa are dominated by one

chemical class of compounds, for example the monoterpenes, benzenoids or hydrocarbons etc. (Table 1). Most of these volatile compounds are also common components of the floral scents of other plant taxa (Knudsen *et al.* 1993).

Leaf volatiles of artificially damaged leaves of Magnoliaceae taxa consist of the three green odor volatiles (i.e. 3(Z)-hexenal, 3(Z)-hexenol and 3(Z)-hexenyl acetate) and terpenes such as  $\beta$ -myrcene, *cis*- $\beta$ -ocimene, *trans*- $\beta$ -ocimene, limonene, linalool, 4,8-dimethyl-1,3(E),7-nonatriene and caryophyllene (Azuma *et al.* 1997a). These chemical compounds are also common in the leaves of many higher plants. The evergreen leaves of *Magnolia grandiflora* L. are different in emitting several sesquiterpenes, e.g.  $\beta$ -elemene,  $\alpha$ -bisabolene, bicyclogermacrene, 4,8-dimethyl-1,3(E),7-nonatriene, caryophyllene and  $\gamma$ -cadinene (Azuma *et al.* 1997a).

**Table 1** Main components in floral scents of Magnoliaceae (summarized from Azuma *et al.* 1997b)

	Main compounds (% of total volatiles)	Chemical class
<i>Magnolia</i> L.		
<i>M. virginiana</i> L. (in Louisiana)	Linalool (47%)	Monoterpene
	Methyl decanoate (16%)	Fatty acid ester
(in Maryland)	2-Phenylethanol (53%)	Benzenoid
	Methyl phenylacetate (14%)	Benzenoid
<i>M. grandiflora</i> L.	Geraniol (20%)	Monoterpene
	<i>trans</i> - $\beta$ -Ocimene (14%)	Monoterpene
	$\beta$ -Myrcene (13%)	Monoterpene
<i>M. schiedeana</i> Schltr.*	Geranyl methyl ether (88%)	Monoterpene
<i>M. tamaulipana</i> Vázquez	Geranyl methyl ether (85%)	Monoterpene
<i>M. fraseri</i> Walt. var. <i>pyramidata</i> (Bartram) Pamp.	Methyl octanoate (25%)	Fatty acid ester
	Limonene (16%)	Monoterpene
<i>M. dealbata</i> Zucc.*	Methyl tiglate (16%)	Amino acid derivative
<i>M. tripetala</i> (L.) L.	$\beta$ -Phenethyl alcohol (78%)	Benzenoid
	Methyl benzoate (52%)	Benzenoid
	Acetophenone (36%)	Benzenoid
<i>M. obovata</i> Thunb.	Methyl benzoate (55%)	Benzenoid
	1,2-Dimethoxybenzene (10%)	Benzenoid
<i>M. sieboldii</i> K. Koch ssp. <i>japonica</i> K. Ueda	Caryophyllene (65%)	Sesquiterpene
<i>M. acuminata</i> (L.) L.	Pentadecane (94%)	Hydrocarbon
<i>M. denudata</i> Desr.	Pentadecane (60%)	Hydrocarbon
<i>M. kobus</i> DC.	Linalool oxide (39%)	Monoterpene
	Linalool (22%)	Monoterpene
<i>M. stellata</i> (Siebold & Zucc.) Maxim.	Methyl benzoate (100%)	Benzenoid
<i>M. salicifolia</i> (Siebold & Zucc.) Maxim.	1,2-Dimethoxybenzene (65%)	Benzenoid
<i>M. mexicana</i> * (= <i>Talauma mexicana</i> (DC.) G. Don)	$\alpha$ -Farnesene (66%)	Sesquiterpene
<i>Michelia</i> L.		
<i>Mi. compressa</i> (Maxim.) Sarg.	Methyl benzoate (94%)	Benzenoid
<i>Mi. figo</i> (Lour.) Spreng.	Isobutyl acetate (78%)	Amino acid derivative
<i>Liriodendron</i> L.		
<i>L. tulipifera</i> L.	Limonene (82%)	Monoterpene
<i>L. chinense</i> (Hemsl.) Sarg.	$\alpha$ -Farnesene (71%)	Sesquiterpene

\* Unpublished data.

The distribution of volatile compounds in the floral scents and damaged leaves of Magnoliaceae taxa are shown in Table 2. The flowers of Magnoliaceae emit many terpenoids, some of which, mainly terpenoids of hydrocarbon types, are also emitted from damaged leaves (Table 2). However, benzenoids, fatty acid derivatives, amino acid derivatives and N-containing compounds, which are widely distributed in the floral scents of Magnoliaceae taxa (Azuma *et al.* 1997b) and other flowering plants (Knudsen *et al.* 1993), are not emitted from the damaged leaves (Table 2).

Artificially damaged leaves of Magnoliaceae taxa emitted 17 different chemical compounds (depending on taxa analyzed) of which eight compounds occurred only in the leaves and nine compounds occurred in both leaves and flowers (Table 2). Interestingly, most of the compounds consisted of terpenoids of hydrocarbon types, while only linalool was an oxygenated terpenoid. It should be noted that the leaf volatiles (some of which occur in the flower) are herbivore-induced volatiles (i.e. 4,8-dimethyl-1,3(E),7-nonatriene, linalool,  $\beta$ -ocimenes etc.). These chemicals are emitted in relatively large amounts when the leaves are damaged and attract predators (parasitoids) or herbivores (Turlings *et al.* 1990, 1995; Turlings & Tumlinson 1992; Loughrin *et al.* 1994, 1995; Takabayashi *et al.* 1994a,b; Bolter *et al.* 1997). In an evolutionary sense, the initial property of floral scent chemistry may have been dominated by terpenoids in damaged leaves and, subsequently, flowers emitted oxygenated compounds (oxygenated monoterpenes, benzenoids and fatty acid esters) in specific pollinator interactions.

### Floral heat production in angiosperms

Floral thermogenesis in flowering plants was discovered by Lamarck in 1778, but occurs in only nine extant angiosperm families: Araceae, Arecaceae, Cyclanthaceae, Annonaceae, Aristolochiaceae, Nelumbonaceae, Nymphaeaceae, Magnoliaceae and Illiciaceae (Gottsberger 1989a,b; Schneider *et al.* 1990; Skubatz *et al.* 1990; Endress 1994; Seymour & Schultze-Motel 1996, 1997; Seymour *et al.* 1998; Dieringer *et al.* 1999). Heat-producing flowers in Magnoliaceae and Illiciaceae were only recently reported by Dieringer *et al.* (1999) for *Magnolia tamaulipana* Vázquez. This species is endemic to the United Nations Education, Scientific and Cultural Organization Biosphere Reserve, El Cielo, Tamaulipas, Mexico (Puig & Bracho 1987) and closely related to *M. schiedeana* Schltdl. and the Southern Magnolia, *M. grandiflora* L. (common in the southeastern United States). The cycads are the only other plant taxon with heat-producing reproductive structures (male and female cones; Skubatz *et al.* 1993).

The flowers of *M. tamaulipana* open in the evening around 18.00 h (female phase) and continue to open

throughout the night (Dieringer *et al.* 1999). Floral temperatures ranged from 1.0 to 9.3°C above ambient air temperature for female phase flowers and 0.2–5.0°C for male-phase flowers (Dieringer *et al.* 1999). Insect visits by *Cyclocephala caelestis* were five-fold more abundant during the evening compared to daytime the following day. Indeed, peak floral temperatures and numbers of beetles in flowers were correlated (Dieringer *et al.* 1999). Statistical analysis of *M. tamaulipana* flower size and insect visits indicated *C. caelestis* preferred trees with fewer, but larger, flowers. Dieringer *et al.* (1999) suggest that flowers with larger petals possess more surface area and thus dissipate more heat and more floral odor than flowers with smaller petals.

Gottsberger (1989b) suggested that floral thermogenicity, coupled with scarab beetle pollination in different plant families, represented parallel evolution. This conclusion was put forth before the discovery of floral thermogenicity in Magnoliaceae and Illiciaceae (Dieringer *et al.* 1999) and the publication of many plant relationships based on DNA (Soltis *et al.* 1997). Dieringer *et al.* (1999) note that all thermogenic families are located in the same clade in the *rbcL* cladogram of angiosperms (Chase *et al.* 1993), and that perhaps a gene or group of genes is functioning in these taxa to regulate heat production in the flowers. He suggests numerous other examples of floral thermogenicity will be discovered in other basal angiosperms.

Some thermogenic species of plants, *Nelumbo nucifera* Gaertn., *Philodendron selloum* Koch and *Symplocarpus foetidus* (L.) Nutt. (Seymour & Schultze-Motel 1996) regulate their temperatures via 'set-points' in reference to ambient temperature (Lamprecht *et al.* 1998; Seymour *et al.* 1998). *Nelumbo nucifera* regulates its temperature between 30 and 35°C in air temperatures varying between 10 and 30°C throughout a 2–4-day period (Seymour *et al.* 1998). Regulation occurs at the cellular level and can be triggered by changes in air temperature. The set-point in this species is 30°C and a progressive inhibition of heat production occurs as flower temperature rises from 30 to 36°C, and vice versa (Seymour & Schultze-Motel 1997; Seymour *et al.* 1998). Thus, flower temperatures can move up and down a temperature slope with inhibition of heat production above 30°C and heat production below 30°C, to maintain a relatively stable flower temperature in ambient temperatures between 10 and 45°C.

In comparison, *Philodendron selloum* maintains floral temperatures between 35 and 45°C (with inhibition of heat production between 37 and 46°C; Seymour *et al.* 1983). The flowers of the eastern skunk cabbage, *Symplocarpus foetidus*, maintain a flower temperature of approximately 24°C in an air temperature of 15°C (Seymour & Schultze-Motel 1997). Although all flowers have biochemical activity and heat is a by-product of this activity,

**Table 2** Distribution of volatile compounds in the floral scents and/or damaged leaf volatiles from Magnoliaceae summarized from Azuma *et al.*, 1997a,b)

Organ	Green odors	Sesquiterpene	Terpenoid Monoterpene (Hydrocarbon)	Terpenoid (Oxygenated)	Benzenoid	Fatty acid derivative	Amino acid derivative	N- compounds
Leaf	3(Z)-Hexenal	(Hydrocarbon-type)						
	3(Z)-Hexenol	$\beta$ -Elemene						
	3(Z)-Hexenyl acetate	$\gamma$ -Cadinene	p-Cymene					
		$\alpha$ -Bisabolene						
Leaf and flower		Caryophyllene						
		$\alpha$ -Humulene	$\beta$ -Myrcene					
		Bicyclogermacrene	Limonene					
		4,8-Dimethyl- 1,3(E),7-nonatriene	<i>trans</i> - $\beta$ - Ocimene					
Flower			<i>cis</i> - $\beta$ -Ocimene	Linalool				
		4,8-Dimethyl- 1,3(Z),7-nonatriene	Terpinolene	Linalool oxides	1,2-Dimethoxybenzene	Ethyl butanoate	Ethyl isobutanoate	Methyl nicotinate
		$\alpha$ -Farnesene (Oxygenated-type)	$\beta$ -Pinene	Nerol	Trimethoxybenzene	Methyl hexanoate	Isobutyl acetate	Isobutyl acetate
		Caryophyllene oxide	Sabinene	Geraniol	Benzaldehyde	Methyl hexenoate	Methyl 2-methyl- butanoate	Methyl 2-methyl- Indole
			$\beta$ -Phellandrene	Neral	Benzyl alcohol	Ethyl hexanoate		
				Geranial	Methyl benzoate	Methyl octanoate		
				Neryl methyl ether	Ethyl benzoate	Methyl decanoate		
				Geranyl methyl ether	Propyl benzoate	Methyl decenoate		
				Methyl nerylate	Isobutyl benzoate	Methyl dodecanoate		
				Methyl geranylate	Isopentyl benzoate	Methyl dodecenoate		
				Geranyl acetate	Methyl	Methyl tetradecanoate		
				$\alpha$ -Terpineol	2-hydroxybenzoate	Methyl tetradecanoate		
			Isopinocampnone	Isobutyl	Methyl hexadecanoate			
			Verbenone	2-hydroxybenzoate	Tridecane			
			Perillene	Isopentyl	Tetradecane			
				2-hydroxybenzoate	Tetradecene			
				Phenylacetaldehyde	Pentadecane			
				2-Phenylethanol	Pentadecene			
				Acetophenone	Heptadecene			
				Methyl phenylacetate	Heptadecadiene			
				2-Phenylethyl acetate				
				Anetole				
				Estragol				

thermogenic flowers produce large quantities of heat which function in the reproductive biology of the plant.

### Breeding system characteristics of thermogenic flowering plants

Plants with thermogenic flowers are protogynous, with heat production peaking with female (stigma) receptivity (Seymour & Schultze-Motel 1997). Protogyny is a characteristic of beetle-pollinated plants (Bertin & Newman 1993; Momose *et al.* 1998) and is almost an exclusive characteristic of the breeding systems of plants in the Magnoliidae (Endress 1990) and many of these families contain plants that produce strong floral fragrances, e.g. Magnoliaceae, Annonaceae, Aristolochiaceae etc. In a survey of 34 angiosperm families in the Magnoliidae (classification of Cronquist 1981), Endress (1990) noted a high preponderance of fly and beetle pollinators over other insect vectors.

Temperatures in many thermogenic flowers are in the range preferred by active beetles (Heinrich 1974; Bartholomew & Casey 1977; Heinrich & McClain 1986; Seymour & Schultze-Motel 1997). All endothermic increases of body temperature above ambient temperature by insects is the result of heat produced by active flight muscles (Heinrich 1974). Many beetles regulate their temperature by shivering, seeking sun or shade, flying and in some species, warming up rapidly before flight to minimize total energy expenditure (Bartholomew & Casey 1977; Chappell 1984; Heinrich & McClain 1986). Such elevated body temperatures in beetles are necessary to carry on many activities (e.g. competing for mates and food; Seymour & Schultze-Motel 1997).

Diptera generally have low body temperatures and do not thermoregulate in flight because of their small body size (Heinrich 1993). However, many species of flies live in cool temperate regions and are adapted to cold (Heinrich 1993). Diptera are also primary pollinators of many basal angiosperms (Endress 1990) including not only trap flowers (*Aristolochia* sp.) which function as egg-laying sites, but also the smaller flat flowers, such as those of *Illicium floridanum*, which attract a wide variety of flies (Thien *et al.* 1983). The discovery of floral heat production in *I. floridanum* (Dieringer *et al.* 1999) is surprising in that large amounts of energy must be produced to maintain elevated temperatures because the flowers are flat, only approximately 2.5 cm across and must, therefore, readily lose heat. The plants flower in early spring and air temperatures vary from 0 to 30°C. Typically, small flies alight on the flowers to take nectar secreted at the base of the petals. It was recently observed (D. White, personal communication), however, that on cold nights (air temperature below ≈ 10–15°C) the flowers attract many more insects than on warmer nights, suggesting that the

insects are seeking warm habitats in the community. In this scenario, floral fragrance may signal heat and food.

Explanations for heat production in flowers include protection of flowers from cold temperatures; stabilization of floral development; enhancement of evaporation of floral scent; added success in pollen germination; and, perhaps, an optimum temperature for pollen tube growth. In insect–plant relationships of heat-producing flowers (breeding systems), insects receive a direct energetic heat reward (Seymour & Schultze-Motel 1997) which enhances feeding, mating, conserving energy and maintaining thoracic temperature required to initiate flight.

Seymour & Schultze-Motel (1997) also note that thermogenic families of flowering plants appear only among ancient groups of seed plants (see above). They suggest beetle pollination coevolved with thermogenic flowers, floral fragrance (Pellmyr & Thien 1986) and protogyny as these characteristics match predilections of beetles searching for feeding places etc.

### Role of heat in early angiosperm evolution

The Magnoliidae (Cronquist 1981) contains the extant families of flowering plants considered to be basal by systematists (Chase *et al.* 1993; Soltis *et al.* 1997). The flowers of most of these plants are bisexual, protogynous, produce strong floral odors and the primary pollinators are flies and beetles (Endress 1990). Dieringer *et al.* (1999) and Seymour & Schultze-Motel (1997) suggest that floral thermogenicity is predominantly found in basal angiosperms.

Pellmyr & Thien (1986) suggested that in early angiosperms, floral odors functioned as chemical signals to insects for food and mating sites, with subsequent meshing of the sexual life cycle of insects and plants (leading to flower constancy). The fragrances of many basal angiosperms contain the damaged leaf volatiles which are also found in the leaves of plants (Thien *et al.* 1975; Turlings *et al.* 1990, 1995; Pellmyr *et al.* 1991; Turlings & Tumlinson 1992; Yasukawa *et al.* 1992; Knudsen *et al.* 1993; Loughrin *et al.* 1994, 1995; Takabayashi *et al.* 1994a,b; Azuma *et al.* 1997a,b; Bolter *et al.* 1997; Kawano *et al.* 1999). In early plants, some insects bypassed the deterrent effects and utilized them to identify hosts (Pellmyr & Thien 1986).

In the absence of floral color, specialized food bodies and nectaries in early flowers, heat and floral odors may have been key components of early angiosperm breeding systems. Heat should be considered a major resource for insects and one that could be provided by plants without evolution of elaborate morphological features. In this regard, fragrance could signal not only food and mating sites, but also heat (in early and extant basal angiosperms).

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