The floral biology of the Magnoliaceae

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The family Magnoliaceae, a well defined group of trees or shrubs, is a component of the order Magnoliales (subclass Magnoliidae) distributed in temperate (four-fifths of the species) and tropical Asia from the Himalayas eastward to Japan and southeastward through the Malay Archipelago to the New Guinea area (see map, Takhtajan 1969; Law 1984). The remainder of the family is found in the Americas from temperate North America to Brazil, including the West Indies (Heywood 1978; Treseder 1978). Concepts of the reproductive biology of the family, however, are based primarily on studies of various species of *Magnolia* located in temperate regions of the world (Heiser 1962; Thien 1974; Yasukawa et al. 1992).

The interaction of insects with flowers as pollinators is considered to be one of the major factors in the success and diversification of flowering plants (Stebbins 1981; Baker & Hurd 1968; Crepet & Friis 1987; Regal 1977). Early pollination studies of *Magnolia* (in European gardens) found beetles to be pollinators (Delphino 1875). Since Coleoptera and magnolias constitute old groups of organisms, the flower of *Magnolia* became a model of pollination for the "earliest flowering plants" (Eyde 1975; Endress 1990). The "mess and spoil" principle of pollination was applied particularly to beetles tramping around in *Magnolia* flowers (Faegri & van der Pijl 1979). It was thought that "Higher pollinators, like bees, are ill at ease in these large blossoms which have no guide structures (like a small child in a big bed)", (Faegri & van der Pijl 1979). Recent findings in many areas of science have greatly modified earlier concepts of Magnoliaceae and other ancient plant taxa. The flower of extant Magnolias is now considered to be specialized and not a large, floppy reproductive structure devoid of ultraviolet (UV) patterns, movements, specialized food sources, fragrances, heat production, etc.

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Magnolia flowers

The family Magnoliaceae is characterized by the presence of bisexual flowers (except *Kmeria*), an androecium of numerous spirally arranged stamens and a gynoecium with usually numerous simple pistils (ovules 1–2) spirally arranged on an elongated axis (Lawrence 1951; Nooteboom 1993; Cronquist 1981). The flowers are protogynous, the dominant mode in extant primitive angiosperms. (Bernhardt & Thien 1987). The temporal isolation of the protogynous flowers may be a means whereby self-pollination is avoided in flowers that extrude or shed their pollen (Bernhardt & Thien 1987). In the extant Magnoliidae pollen is shed or extruded when the anthers dehisce (Vogel 1978) and most lack spatial isolation between anthers and stigmas due to the absence of slender styles and long staminal filaments (Bernhardt & Thien 1987). Protogyny probably represents an ancestral condition but should not necessarily be interpreted as having evolved as a response to beetle pollination.

Self-incompatibility is widespread within the Magnoliidae as many species bear wet stigmas and bicellular pollen (Heslop-Harrison & Shivanna 1977; Bernhardt & Thien 1987); self-incompatibility also occurs in species of *Magnolia*, although self-compatibility is common. Over a hundred *Magnolia* hybrids are in cultivation (Callaway 1994) yet few hybrids between the various species have been found in nature (Thien 1974).

The extant flowers of *Magnolia* vary greatly in size from just a few centimetres to approximately 40 cm across in *M. macrophylla*, one of the largest flowers in North America (Treseder 1978). Many large- and small-flowered Magnoliidae are present in the early fossil record (Friis & Crepet 1987; Crane, Friis & Pederson 1995; Crepet 1996). Individual flowers usually remain functional 2–4 days (Thien 1974) although environmental conditions may be a factor in the shortening or lengthening of floral functions (Heiser 1962). Individual flowers of *M. kobus* var. *borealis* in northern Japan function for nine days (Ishida 1996). Most species of *Magnolia* typically present a large number of flowers over a period of weeks or months.

The movements of petals and stigmas in *Magnolia* flowers were noted by Heiser (1962). Subsequently, Thien (1974) suggested the movement of petals to be an adaptation to encourage insects to enter and exit flowers at certain times, as in *Calycanthus* (Grant 1950). Closed petals preserve pollen, stigma secretions, etc. for beetles. Partially closed flowers were considered not to be traps for insects, particularly for beetles which are capable of entering or exiting via the smallest opening; in *M. grandiflora* bees try unsuccessfully to enter unopened flowers (Thien 1974). Movements of floral parts have also been noted in other Magnoliidae (Endress 1990), e.g. *Talauma* (Gibbs et al. 1977).

Visual Guides

Magnolia flowers range in colour from purple, pink, green, yellow, to white (Callaway 1994). White is a particularly common flower colour in species of *Magnolia* native to the southeastern United States.

The flowers of many Magnolia species display patterns in UV light which essentially act as "nectar" guides and as a general insect attractant (Silberglied 1979). The staminate flowers of *M. kobus*, *M. grandiflora* and many other species display UV patterns (Yasukawa et al. 1992; Burr & Barthlott 1993). Ultraviolet patterns are known to be particularly effective in attracting Hymenoptera (Kevan 1972). Ultraviolet patterns are also known to be present in flowers of other genera of Magnoliidae, i.e. *Liriodendron* (Utech & Kawano 1975). In *L. tulipifera* the orange spots at the base of the petals appear dark in UV light. Presumably the extrose stamens drop pollen on these areas which are coated with a liquid and insects pick up the pollen on their legs while landing and walking on the petals.

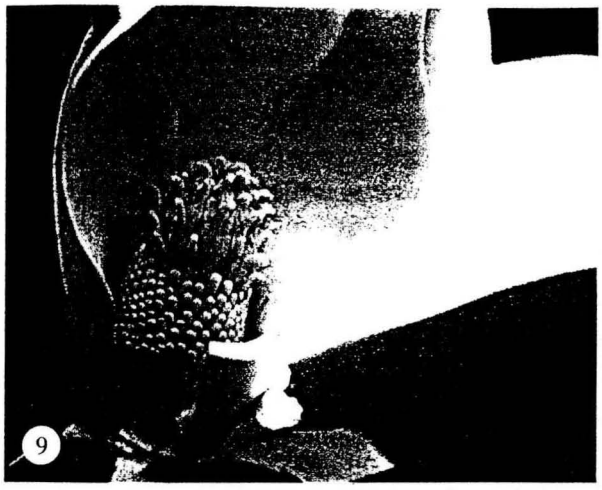
Fluorescence

In a limited survey of floral fluorescence, the flowers of *M. macrophylla*, *M. ashei*, *M. grandiflora*, *M. acuminata*, *M. virginiana*, *M. tripetala*, *M. pyramidata*, *Michelia* sp., and *Liriodendron tulipifera* were photographed in daylight and UV light (in darkness illuminated with a UV lamp; Thien et al. 1995). The UV light-illuminated flowers are clearly visible to the human eye even in semi-darkness. The flowers of *M. macrophylla*, *M. ashei*, *M. grandiflora*, *M. tripetala* and *M. virginiana* displayed fluorescence; other species mentioned above did not exhibit patterns. The flowers of *M. macrophylla* [**9–13**] and *M. ashei* displayed blue and red fluorescence patterns; *M. grandiflora* [**14–17**] a red strobilus, and blue petals with a white sheen; *M. tripetala* had distinctive two-toned stamens and also a white-blue sheen on petals [**21, 22**]; *M. virginiana* exhibited blue petals.

The female-phase flowers of *M. macrophylla* and *M. ashei* produce large "droplets" (>3 ml/flower) in the axil of the stigmas and strobilus (Thien et al. 1995) which contain no sugars and less than 1% dissolved solids. As the petals gradually open these droplets eventually burst and flow over the stigmas (except for the tips) and portions of the strobilus [**9**]. The secretions (at times) and floral tissue fluoresce a brilliant blue in UV light. On the following day the petals completely unfurl and the entire flower displays an intricate array of colours. The male phase commences when the anthers begin to dehisce and stigmas turn brown. The female and male stages are distinct yet share colour-patterns, e.g. the fluorescent tips of the stigmas resemble pollen and the fluid-coated portion of the stigmas are similar in colour to the adaxial surface of the stamens which may be interpreted as the female phase mimicing the male phase (Thien et al. 1995).

It should be noted that in all flowers (and twigs) of Magnoliaceae mentioned above the blue fluorescence occurs in the interior of the strobilus (particularly in the ovules) even if the exterior of the strobilus, stamens, petals, etc., *do not* fluoresce. In old strobili the fluorescence can be seen if you break off the old black stigmas [**16–19**]. The pollen of all species of *Magnolia* fluoresced in UV light.

The chemical that produces the blue fluorescence in the pedicels and twigs of *M. macrophylla* (and presumably in floral parts) has been tenatively identified by Stella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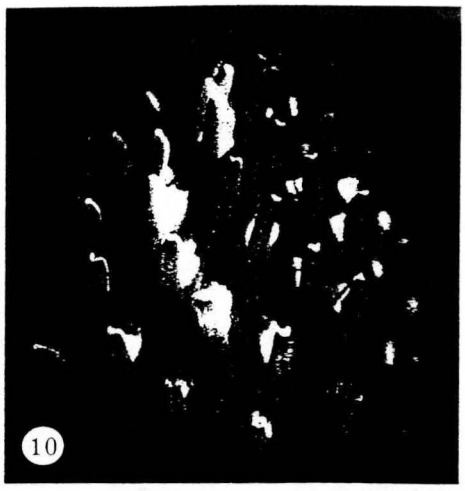
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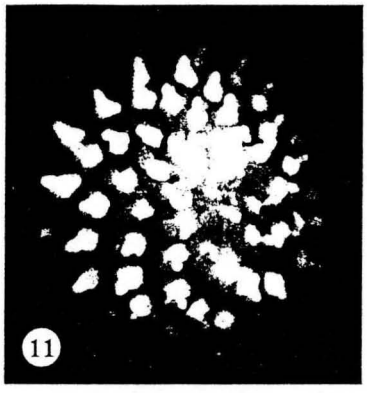
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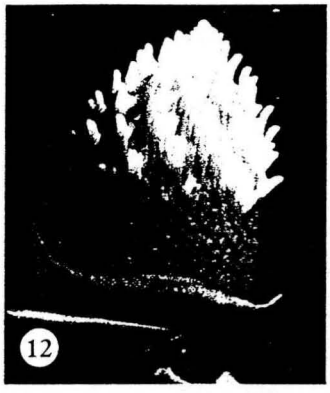
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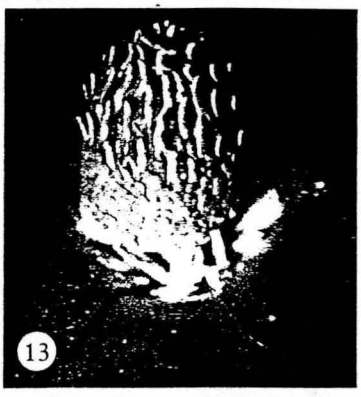
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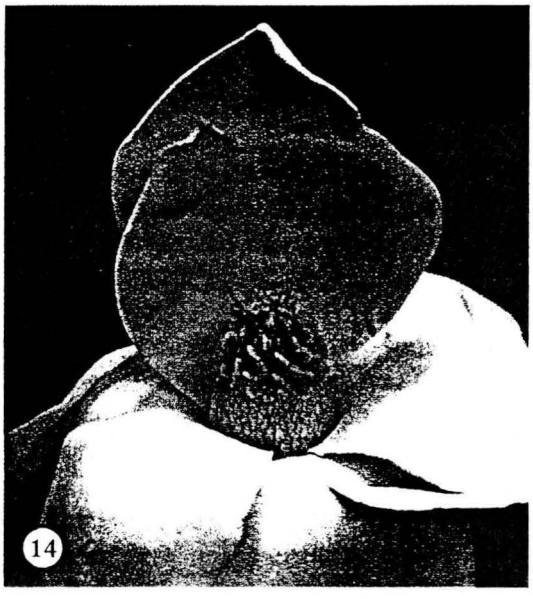
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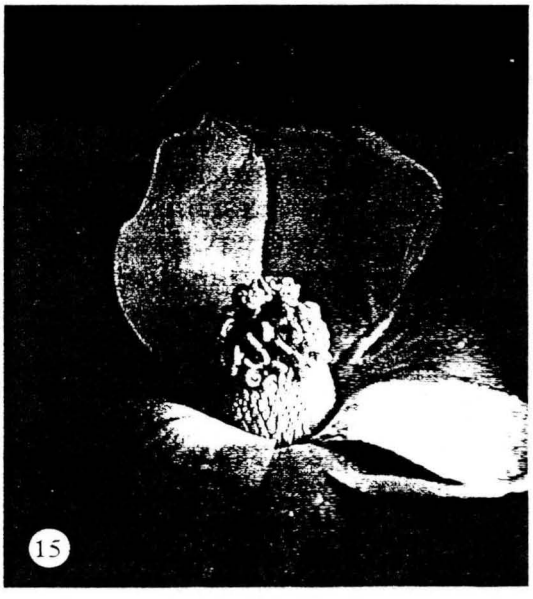
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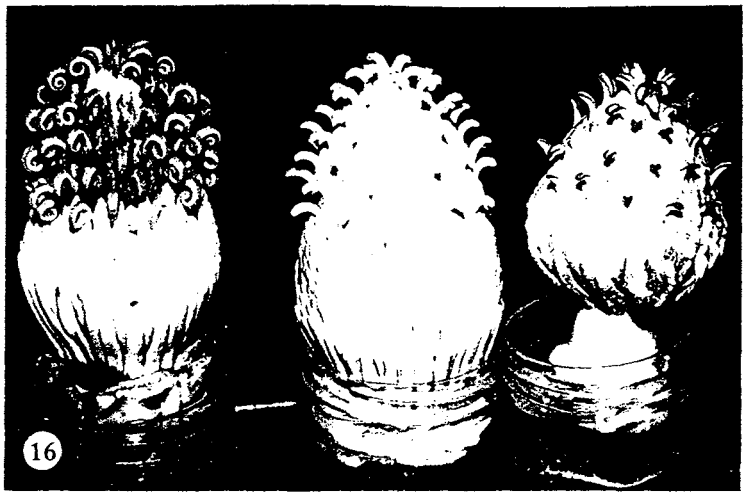


9. *Magnolia macrophylla*, female-phase flower showing strobilus stigma droplets and vase-like structure (some petals were removed). 10. *M. macrophylla*, female-phase flower photographed in UV light. The strobilus/stigma droplets are blue. 11. *M. macrophylla*, female phase photographed in UV light displaying the fluorescent droplets. 12. *M. macrophylla*, female phase photographed in UV light; petals removed to show droplets and complete strobilus. 13. *M. macrophylla*, early male phase photographed in UV light. The fluorescent tips of the stigmas resemble pollen grains; the stigmas and stamens are similar in colour (deception). 14-15. *M. grandiflora* (cultivated), photographed in daylight (female phase) and in UV light. Note the white sheen on the petals and deep red colour of the strobilus. 16. "Cones" of *M. grandiflora* (left), *M. macrophylla* and *M. ashei* photographed in daylight. 17. The same cones photographed in UV light. Note that the strobili of *M. macrophylla* and *M. ashei* are pink whereas the cone of *M. grandiflora* is deep red. 18-19. *M. macrophylla*, old strobilus photographed in daylight and in UV light. Note the blue fluorescence where the old black stigmas were broken.

Elakovich, using gas chromatography-mass spectrometry, as scopoletin (6-methoxy-7-hydroxy coumarin; unsaturated lactone; Goodwin & Taves 1950). The pleasant odour of new mown hay is due to coumarin (Harborne 1982). Scopoletin is a common constituent of many plants and is responsible for the blue fluorescence of oat roots (Andreae 1952). It has been observed in plants with certain viral diseases and in a protective zone of potato tubers infected by fungi. It also affects root growth, depending upon concentration (Goodwin & Taves 1950; Harborne 1982).

It is well known that many objects in nature, e.g. types of xylem (Radley & Grant 1954), when viewed only with UV light, display dramatic and intricate fluorescent patterns, which simply may have no biological significance. Many angiosperm families display fluorescent nectar (Thorp et al. 1975). Its adaptive value, however, is debated (Kevan 1976), because energy is taken from an impoverished portion of the insect visual spectrum (UV) and transformed to an already rich part of that spectrum. In addition, the contribution of fluoresced light to longer wavelengths may possibly be obscured by overall diffusion reflection against various backgrounds (Kevan 1976; Cruden 1972). In a series of training experiments with honey bees and the nectar of *Fremontodendron* (Sterculiaceae), however, honey bees responded positively to visual cues in the fluorescent nectar (Thorp, pers. comm.; odour of nectar not controlled in the experiment).

The blue-purple patterns presented by the flowers of *M. macrophylla* and *M. ashei* attract bees as well as beetles. Blue is considered bees' favourite colour (Lubbock 1881), but the role of bees in pollination of magnolias is controversial (Yasukawa et al. 1992). The oldest known fossil bee, *Trigona prisca*, is dated Late Cretaceous (Michener & Grimaldi 1988).

Food

The primary food for insect visitors to *Magnolia* flowers is pollen (Heiser 1962; Thien 1974; Yasukawa et al. 1992). In the protogynous phase the stamens slowly separate and some stamens dehisce; then the stamens detach and fall into the petals. As a result, the petals accrue large quantities of stamens containing pollen, spread over the petal surfaces (see review of beetles and floral rewards, Bernhardt 1966; Crowson 1981). This disarray of stamens and pollen attracts insects that crawl through the piles. The eating, mating, and crawling insects become coated with pollen. The percentage of free amino acids (over 30) contained in the pollen of some common *Magnolia* species is listed by Yasukawa et al. (1992) and is a significant source of nitrogen for insects.

The petals in some *Magnolia* species offer secretions (food) that are available in both female and male phases of the flower. In a study of Japanese magnolias, a large spectrum of Diptera (flies) was observed not only to eat the pollen, but also to suck petal secretions (colour photograph, Yasukawa et al. 1992).

In *M. schiedeana*, an endemic species in east-central Mexico closely associated with cloud forests, the starch-filled petals and stamens are eaten by *Cyclocephala*

jalapensis, an endemic dynastine scarab which also mates on the flowers (Dieringer & Espinosa 1994; Dieringer & Delgado 1994). Many species of *Magnolia*, however, apparently have chemical deterrents in floral parts which deter chewing insects, as Azuma et al. (1996) reported the presence of naphthalene (a constituent of moth-balls) in *Magnolia* floral parts.

In the female phase of some *Magnolia* species, petals, stigma and gynoecium secretions may also serve as food for insect visitors (Heiser 1962; Thien 1974; Yasukawa et al. 1992). As noted the large stigmatic drops in flowers of *M. macrophylla* and *M. ashei* are eaten by bees, beetles and other insects (Thien et al. 1995; Latimer 1994).

Pollination droplets secreted by ovules of female strobili of *Gnetum gnemon* (Gnetales) growing in Sarawak, Malaysia, were consumed by nectar-seeking moths of Pyralidae and Geometridae (Kato & Inoue 1994). These droplets contained sugar (3–13%) and it is thought that, since the angiosperms may have evolved from the Gnetales, unspecialized nectar-feeding insects may have been important to early pollination systems (Lloyd & Wells 1992). Our work with pollination droplets in *M. macrophylla* suggests other chemicals may be equally if not more important than sugars in these systems. A gas chromatograph-mass spectrometry analysis of the stigmatic droplets of *M. macrophylla* showed a wide variety of chemicals including Vitamin C and naphthalene as major constituents (but no appreciable amounts of sugar, *fide* Stella Elakovich).

Thermoregulating flowers: *M. tamaulipana*

The flowers of *Magnolia tamaulipana*, an endemic in the cloud forest, located in the UNESCO Biosphere Reserve, El Cielo, Tamaulipas, Mexico, produce significant amounts of heat above ambient temperature (Dieringer et al. 1998). The flowers open in the evening and throughout the night and the petals initially are held erect to form a floral chamber. In the population some plants produce fewer but larger flowers (statistically significant; Dieringer et al. 1998).

Floral and ambient temperatures were recorded using thermocouples inserted into the androphore of newly opened flowers, connected to a digital thermometer. The flowers emitted the most heat when they first opened and then gradually declined with time and the sexual phase. By the third day the floral temperatures did not differ from ambient temperature (Dieringer et al. 1998). Floral temperatures ranged from 9.3–1.0°C for the female phase and 5.0–0.2°C for the male phase (Dieringer et al. 1998). Other families of Magnoliidae are also thermogenic (Endress 1994) but this is the first report for Magnoliaceae.

A scarab, *Cyclocephala caelis*, and a Staphylinid, *Myrmecophalis sp.* accounted for respectively 52% and 46% of the insect visitors (Dieringer et al. 1997). The scarab beetles seemed to prefer plants with the large flowers and the numbers of beetles in the flowers correlated with high flower temperatures. In contrast, the Staphylinids were evenly distributed in all floral stages without correlation to any floral cues

20. Longitudinal section of a flowerbud of *M. grandiflora* photographed in UV light. The pollen is fluoresced yellow. 21. *M. tripetala* with some petals removed, photographed in UV light displaying the two-toned stamens and white sheen on petals. 22. Petals *M. tripetala* photographed in UV light showing white sheen in mid-portion of some petals.

(Dieringer et al. 1997). Recent studies with another species of scarab, *Cyclocephala lurida*, indicate adult males may have lost the ability to produce sex pheromones (Haynes & Potter 1995). Dieringer et al. (1997) maintain that the scarabs are endothermic and suggest the beetles may be utilizing floral odours to substitute for sex phermones. The floral fragrance of *M. tamaulipana* was analyzed by H. Azuma and comprised geranyl-methyl ether (80%), geraniol (3%) and limonene (3%) of both female and male phase flowers (Table 1).

The scarabs feed on the petals of *M. tamaulipana* which have higher protein and lipid values then sepals; however, the sepals had very high fibre values in comparsion to petals (Dieringer et al. 1997) which presumably encourages petal consumption.

Floral fragrances

Over 700 compounds in 441 taxa (60 families) have been identified in the floral scents of flowering plants (cross-listed by chemical and plant names, Knudsen et al. 1993). The Magnoliaceae is one of the few families of flowering plants in which the chemical composition of a relatively large number of species has been analyzed

Table 1. Floral volatiles of *Magnolia* and *Liriodendron*

Taxon	Major volatile compounds (% in total volatile)	Chemical class
Magnolia subg. Magnolia		
M. virginiana		
(in Louisiana)	Linalool (47%)	Monoterpene
	Methyl decanoate (16%)	Fatty acid ester
	Methyl dodecanoate (14%)	Fatty acid ester
(in Maryland)	2-Phenylethanol (53%)	Benzenoid
	Methyl phenylacetate (14%)	Benzenoid
	Verbenone (8%)	Monoterpene
M. grandiflora	Geraniol (20%)	Monoterpene
	trans-b-Ocimene (14%)	Monoterpene
	β-Myrcene (13%)	Monoterpene
M. tamaulipana	Geranyl methyl ether (85%)	Monoterpene
	Geraniol (3%)	Monoterpene
	Limonene (3%)	Monoterpene
M. pyramidata	Methyl octanoate (25%)	Fatty acid ester
	Limonene (16%)	Monoterpene
	Methyl tiglate (16%)	Branched-chain fatty acid ester
M. tripetala	Methyl benzoate (52%)	Benzenoid
	Acetophenone (36%)	Benzenoid
M. obovata (M. hypoleuca)	Methyl benzoate (55%)	Benzenoid
	1,2-Dimethoxybenzene (10%)	Benzenoid
	Isopentyl benzoate (10%)	Benzenoid
M. sieboldii ssp. japonica	Caryophyllene (65%)	Sesquiterpene
	α-Humulene (15%)	Sesquiterpene
Magnolia subg. Yulania		
M. acuminata	Pentadecane (94%)	Hydrocarbon
M. denudata (M. heptapeta)	Pentadecane (60%)	Hydrocarbon
	4,8-Dimethyl-1,3(E),7-nonatriene (29%)	Sesquiterpene
M. kobus (M. praecocissima)	Linalool oxides (66%)	Monoterpene
	Linalool (22%)	Monoterpene
M. stellata (M. tomentosa)	Methyl benzoate (100%)	Benzenoid
M. salicifolia	1,2-Dimethoxybenzene (65%)	Benzenoid
	Benzyl alcohol (17%)	Benzenoid
	Benzaldehyde (10%)	Benzenoid
Liriodendron		
L. tulipifera	Limonene (82%)	Monoterpene
	4,8-Dimethyl-1,3(E),7-nonatriene (15%)	Sesquiterpene

(Thien et al. 1975; Yasukawa et al. 1992; Knudsen et al. 1993; Kaiser 1991; Croteau & Karp 1991). For analysis techniques, history, and unusual chemicals in flowers see Kaiser (1991). It is assumed that floral fragrance is one of the major attractants for insect visitors to *Magnolia* flowers. Gottsberger (1977) suggested that the use of flowers as mating sites is common in beetle-pollinated Magnoliidae..It is proposed that insect pollination evolved primarily through the meshing of the sexual life cycles of phytophagous insects with flowers in which floral odours served as chemical cues for mating sites and food (Pellmyr & Thien 1986). In addition, these floral fragrances may have originated from chemicals serving as herbivore deterrents in leaves (Pellmyr & Thien 1986).

The floral fragrances of North American species of *Magnolia* and *Liriodendron* contain mostly methyl esters of fatty acids, aliphatic normal hydrocarbons, monoterpenes, sesquiterpenes, terpene derivatives, and compounds with benzene rings ranging in molecular weight from 94 to 242 (Table 1 and fig. 1). The methyl esters usually have fruity odours; terpenes, and aromatic compounds vary from sweet to spicy (Thien et al 1975). The normal hydrocarbons have slightly unpleasant odours. In *M. acuminata*, the floral fragrance consists exclusively of hydrocarbons and in *M. pyramidata* only of methyl esters of fatty acids (Thien et al. 1975).

Hydrocarbons are produced by flowers from fatty acids by decarboxylation and methy esters by methylation of fatty acids (Thien et al. 1975). The other major metabolic pathway for large lipid molecules is the incorporation of acetate via mevalonic acid into terpenes and steroids (Thien et al. 1975).

Some of the Asiatic Magnolia species have been analyzed (primarily Japanese species) and the flowers emitted various hydrocarbons, monoterpenes, sesquiterpenes, acetogenins, and phenylpropanoids in mixed combinations and quantities (Yasukawa et al. 1992; fig. 1). The floral components of Asiatic species of Magnoliaceae are derived from three different pathways: the mevalonate (terpenoids), the acetate-melonate (fatty acids and hydrocarbons) and the shikimate (benzenoid) pathways (phenyl-propanoids; Yasukawa et al. 1992).

Anti-herbivore chemicals in Magnoliaceae leaves and flowers

Secondary compounds in higher plants are involved in many adaptive structures and processes crucial to the life history and evolution of a species, i.e. protection against herbivores, flower colour, floral fragrances (pollination), co-evolution, etc. (Ehrlich & Raven 1964; McKey 1979). Leaf-injury may cause the release of volatile secondary compounds and increase the quantity of similar chemicals in undamaged leaves on a plant (Baldwin 1988). Inducible defence responses in plants can be activated locally and systemically by signalling molecules through the atmosphere to activate defence mechanisms in nearby plants (Farmer & Ryan 1990).

The leaf odours of damaged leaves and the floral fragrances of *Magnolia* and *Liriodendron* taxa native to or cultivated in Japan and the United States were analyzed using gas chromatography and mass spectrometry (Table 2; Azuma et al.

1997). The artificially damaged leaves (wire brush) released high amounts of 3(Z)-hexenyl acetate (one of the "green odours") in the early stages (0–2 hrs) of damage in several *Magnolia* species (fig. 2). Other volatiles such as 3(Z)-hexenol (a green odour), trans-B-ocimene, cis-B-ocimene (monoterpenes) and caryophyllene (sesquiterpene), etc., were also detected from these damaged leaves at early stages in relatively small amounts and are also common in floral volatiles of angiosperms (Knudsen et al. 1933). It should be noted that these volatiles were not detected in undamaged leaves. The damaged leaves also released 4,8-dimethyl-1,3(E),7-nonatriene in various patterns different from the green odours and other terpenes (fig. 2; Table 2; Azuma et al. 1997).

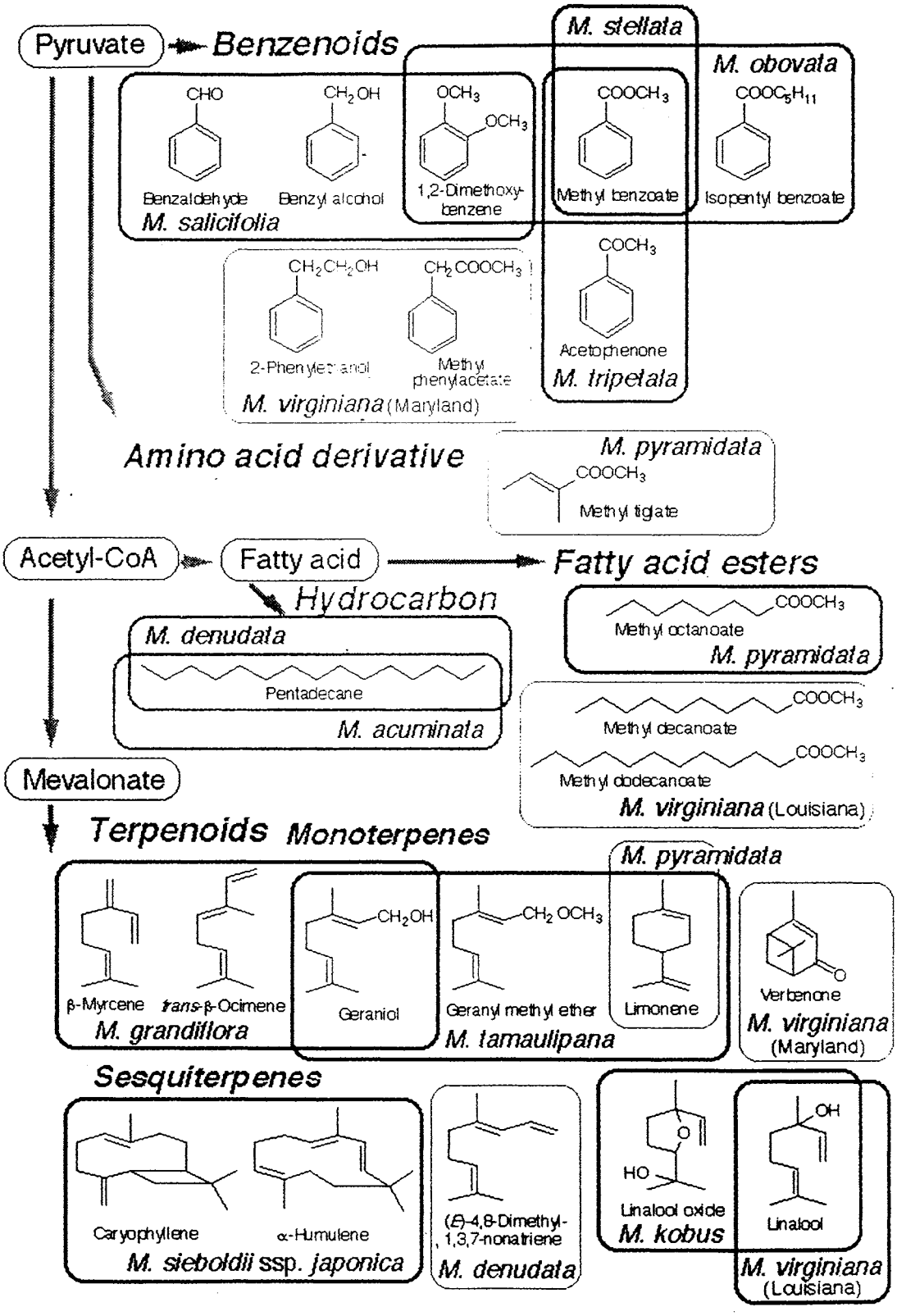
Analysis of the floral fragrances (flowers undamaged; Table 2) displayed a wide variety of chemicals also including 4,8-dimethyl-13(E),7-nonatriene, which in some species comprised up to 30% of the fragrance.

The attack of noctuid caterpillars on corn seedlings results in plant emission of nonatriene which attracts parasitoids which feed on the caterpillars (Turlings et al. 1990; Turlings & Tumlinson 1992). Exploitation of such chemical signals by predators to locate prey formed the basis for the hypothesis that plants may actively signal predators as a defense mechanism (Turlings et al. 1995; Price et al. 1980; Dicke & Sabelis 1988). Thus the production of nonatriene in agricultural plants is a novel plant-insect interaction involving active signaling by plants (first trophic level) via semiochemicals to predators (third trophic level) to control herbivores.

What is the role of nonatriene in the flowers and damaged leaves of Magnoliaceae? It should be noted that artifically damaged leaves of agricultural plants emit nonatriene, but in very low quantities. The saliva, faeces etc. of a caterpillar is needed to "enhance" emission of nonatriene (Turlings et al. 1993). No field or laboratory data are available as to the role of nonatriene in Magnoliaceae.

In species of *Magnolia* various chemicals appear to play different roles in different structures (but see Tucker 1977 for mechanical protection of leaves). Thus nonatriene, a putative anti-herbivore chemical in leaves, is also expressed as a major component of floral fragrance. Naphthalene is a common component of floral tissue in several species of *Magnolia* (particularly in Section *Yulania*; Azuma et al. 1996) yet in *M. macrophylla* and *M. ashei* it is present in pollination droplets and is eaten by insects (Thien et al. 1995; Latimer 1994).

Biochemical exaptations (preadaptations, Gould & Urba 1982) may be important in establishing new ecological relationships between plants and animals (Armbruster et al. 1997; Vogel, 1978). In *Dalechampia* vines (Euphorbiaceae) biochemical exaptation appears to have played major roles in defence and reward systems (Armbruster et al. 1997). The resin reward system in these vines appears to have originated as a defence and secondarily assumed a role in attracting pollinators (Armbruster et al. 1997).


Pyruvate
Benzenoids
M. stellata
M. obovata
CHO
CH2OH
OCH3
OCH3
COOCH3
COOC5H11
Benzaldehyde
Benzyl alcohol
1,2-Dimethoxy-benzene
Methyl benzoate
Isopentyl benzoate
M. salicifolia
CH2CH2OH
CH2COOCH3
COCH3
2-Phenylethanol
Methyl phenylacetate
Acetophenone
M. virginiana (Maryland)
M. tripetala
Amino acid derivative
M. pyramidata
COOCH3
Methyl tiglate
Acetyl-CoA
Fatty acid
Fatty acid esters
Hydrocarbon
M. denudata
Pentadecane
M. acuminata
COOCH3
Methyl octanoate
M. pyramidata
COOCH3
Methyl decanoate
COOCH3
Methyl dodecanoate
M. virginiana (Louisiana)
Mevalonate
Terpenoids
Monoterpenes
M. pyramidata
β-Myrcene
trans-β-Ocimene
M. grandiflora
CH2OH
Geraniol
CH2OCH3
Geranyl methyl ether
M. tamaulipana
Limonene
O
Verbenone
M. virginiana (Maryland)
Sesquiterpenes
Caryophyllene
α-Humulene
M. sieboldii ssp. japonica
(E)-4,8-Dimethyl-1,3,7-nonatriene
M. denudata
O
HO
Linalool oxide
M. kobus
OH
Linalool
M. virginiana (Louisiana)

Pollination

The hypothesis that beetles pollinated the early angiosperms was put forth by Diels (1916) and Grant (1950). It was Delphino (1875) who first observed pollination of *Magnolia* flowers by beetles, and subsequent workers noted these insects as the major pollinating agents (Prantl 1888; Dauman 1930; Heiser 1962; Baker & Hurd 1968; Faegri & van der Pijl 1979; Thien 1974). In recent years, Japanese biologists Kikuzawa & Mizui (1990), Yasukawa et al. (1992) and Ishida (1996) have studied the Asiatic species of magnolias. Yasukawa et al. (1992) studied eight Magnolia taxa in Japan and concluded that Diptera (flies), Hymenoptera (bees etc.), and Coleoptera (beetles) were all pollinators of *Magnolia*. It was noted that bees are important pollinators of some species of *Magnolia*.

Beetles

The finding of beetles in *Magnolia* flowers a century ago plus subsequent verification in other basal angiosperms established this mode of pollination as representative of the first angiosperms. Undoubtedly beetles are overall the primary pollinators of *Magnolia* and many other extant basal angiosperms (Gottsberger 1977; Grant 1950; Baker & Hurd 1968; Heiser 1962; Peigler 1988; Crepet & Friis 1987; Endress 1990). It is important to note, however, that a variety of other insect taxa, i.e. Diptera and Hymenoptera, are also primary pollinators of basal angiosperms including *Magnolia* (Thien 1980; Thien et al. 1985; Thien et al. 1983 Yasukawa et al. 1992; Chaw 1992; Crepet & Friis 1987; Endress 1990).

As pointed out by Labandeira & Sepkoski (1993) the familial diversity of insects is roughly a long-linear trend from the mid-Triassic through the early Cretaceous. They maintain the expansion of angiosperms did not, however, influence insect family diversification. Yet Coleoptera, Diptera, Hymenoptera (including bees) began expansion in the Triassic and Jurassic. Presumably a wide variety of insects visited the flowers of early angiosperms (Crepet 1993).

Beetle-pollinated flowers within the basal angiosperms tend to have strong floral odours and provide large quantities of pollen. In many taxa, particularly in the Annonaceae, Winteraceae and Calycanthaceae, beetles are present only in a relatively small number of flowers, but then in great quantities (Thien 1980; Grant 1950; Gottsberger 1989a, 1989b).

Fig. 1. Structure and distribution of major floral volatiles of eastern Asiatic and North American *Magnolia* (see also Table 1.). Eight sections of the genus are represented by the 12 species analyzed: Magnolia (*M. virginiana*), Rhytidospermum (*M. tripetala, M.* [*fraseri* subsp.] *pyramidata, M. obovata*), Oyama (*M. sieboldii* subsp. *japonica*), Theorhodon (*M. grandiflora, M. tamaulipana*), Yulania (*M. denudata*), Buergeria (*M. kobus, M. stellata, M. salicifolia*) and Tulipastrum (*M. acuminata*). For further details see Azuma et al. (1998). [The differentiation of *M. pyramidata* from the other members of sect. Rhytidospermum, and of the Maryland and Louisiana forms of *M. virginiana*, are noteworthy in view of discussion elsewhere in ths volume concerning the classification of these taxa. – Ed.]

In temperate species of *Magnolia* a wide variety of Coleoptera pollinate a given species (Heiser 1962; Thien 1974; Yasukawa et al. 1992; Peigler 1988; Latimer 1994). The insects crawl about, feeding on stigma and petal secretions, pollen and in some cases petals (Dieringer & Delgado 1994; Dieringer & Espinosa 1994; Yasukawa et al. 1992).

Knowledge of the pollination biology of tropical species of *Magnolia* throughout the world (one-fifth of the species) is almost completely lacking except for the fine

	Leaf[a]		Flower[b]	
	µg/12 hrs 100cm² leaf area		%/2 hrs/ 1–3 flowers	%(µg)/9 hrs/ flower
Taxa	Damaged	Undamaged	Detached[c]	Intact
Magnolia				
subg. Magnolia				
M. virginiana			–[d]	
M. virginiana[e]			2.5	
M. grandiflora[f]	2.48	–	0.5	
M. pyramidata			–	
M. tripetala			–	
M. obovata	1.74	–	–	
M. sieboldii				
subsp. japonica	–	–		–
subg. Yulania				
M. acuminata			0.1	
M. kobus	0.03	–	3.1	–
M. stellata	–	–	37.9	–
M. salicifolia	–	–	–	8.3 (0.48)
M. denudata[f]	–	–	51.8	28.9 (39 37)
Liriodendron				
L. tulipifera			14.7	

[a] Both damaged and undamaged leaves remained attached to branches during sampling.
[b] Floral organs were not damaged.
[c] Amounts of compounds compared with an internal standard were not examined.
[d] No characteristic ion indicating the compound was detected in GC-MS ion chromatogram.
[e] A cultivated plant at Tulane University was examined.
[f] Cultivated plants at Kyoto University were used.

Table 2. Distribution and amount (µg) of (E)-4,8-dimethyl-1,3,7-nonatriene in artificially damaged and undamaged leaf volatiles, and relative amount (mean %) in floral volatiles of *Magnolia* and *Liriodendron* taxa.

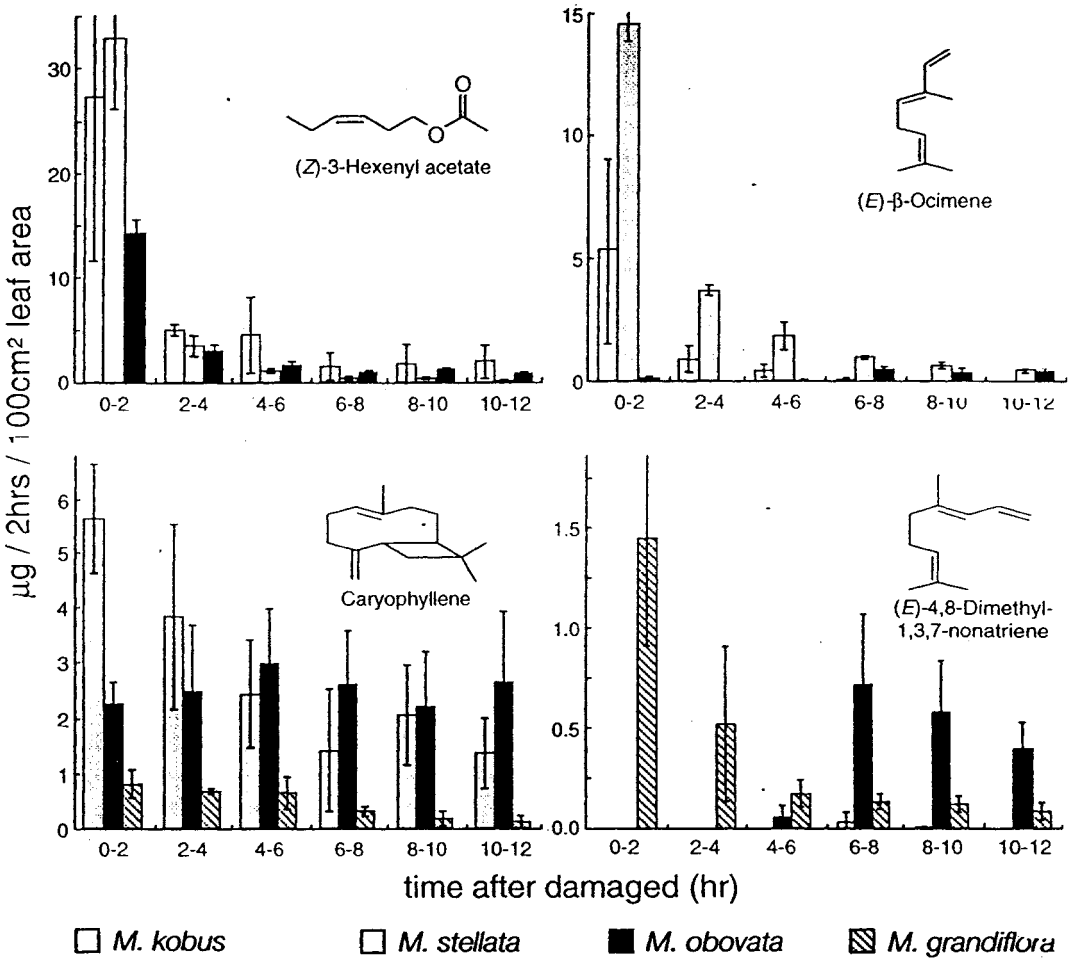


Fig. 2. Emissions of (Z)-3-hexenyl acetate, (E)-B-ocimene, caryophyllene and (E)-4,8-dimethyl-1,3,7-nonatriene from artificially damaged leaves of four *Magnolia* taxa over time. Data represents the mean of three samples.

studies of Dieringer & Espinosa (1994) on *M. schiedeana* and *M. tamaulipana* in Veracruz, Mexico. Other studies, by Howard (1968) on West Indian species of *Magnolia* (Diptera as pollinators?) and by Carvajal (1993) on *M. dealbata* (Coleoptera, Diptera and Hymenoptera) in Veracruz, are valuable observations but limited in scope.

In their study of *M. schiedeana*, a threatened species in the cloud forests of Veracruz, Dieringer & Delgado (1994) and Dieringer & Espinosa (1994) observed that the flowers produced a strong fruity fragrance and the inner petals formed a small cavity around the gynoecium and androphore. No nectar was produced. Early

each morning, pollinating beetles visited newly opened female- and male-phase flowers (Dieringer & Espinosa, 1994). Only two species visited the flowers, an unidentified species of *Stenagria* (Staphylinidae: Aleocharinae) and *Cyclocephala jalapensis* (Scarabaeidae: Dynastinae). Both are considered effective pollinators. The species of *Stenagria* was abundant (highest recorded, 68 insects in 6 flowers) whereas the *Cyclocephala* visited only open flowers (and sometimes chewed into buds and petals and ate stamens) and was never abundant (both visited female phase flowers; Dieringer & Espinosa 1994). *Talauma ovata* (in Brazil) is another dynastine scarab-pollinated taxon (Gibbs et al. 1977). The pollination of *M. schiedeana* appears to be more specialized in comparison to more temperate species of *Magnolia* in the low diversity of its pollinators and use of petals as a food source.

Bees

The role of bees in the pollination of *Magnolia* is controversial (Yasukawa et al. 1992). In his observations, Heiser (1962) observed honey bees (*Apis mellifera*) on the flowers of *M. tripetala*, honey bees and carpenter bees on *M. grandiflora*, and a *Xylocopa sp.* on *M. virginiana*. He discounted honey bees as pollinators of *M. virginiana* because they visited only fully open flowers at which time the stigmas were not receptive.

In a survey of insects on *Magnolia* (Thien 1974), honey bees were observed on flowers of *M. grandiflora*, *M. virginiana*, *M. macrophylla*, and *M. ashei* and *Xylocopa virginica* on flowers of *M. grandiflora*. Small green bees were observed on flowers of *M. ashei*.

The study of Yasukawa et al. (1992) on Japanese species of magnolias strongly implicated bees as pollinators. Nine species of bees were listed as pollinators: *Andrena watasei*, *Apis cerana*, *A. mellifera*, *Bombus ardens*, *B. diversus*, *B. ignitus*, *B. hypocrite*, *B. sp.* and *Lasioglossum spp.* In their discussion of the role of bees as pollinators of *Magnolia* it was noted that frequent visits were made to flowers in the male phase. It was observed that *Bombus* workers were not very effective pollinators. One of the most frequent visitors to the flowers of *M. kobus* var. *borealis* was *B. ignitus*, an important pollinator (Yasukawa et al. 1992). In *M. obovata*, another bumblebee, *B. diversus*, visited flowers in the female and male phases of the flowers and was also a pollinating agent. They concluded that bumblebees play a significant role in the pollination of *Magnolia* flowers.

In a study of pollination in *M. ashei* in the panhandle of Florida, Latimer (1994) also found bees to be important pollinators. The flowers of *M. ashei* are vase-shaped in the female phase and stand upright and at the commencement of the male phase open fully (Thien 1974; Latimer 1994). Latimer (1994) found a variety of beetles, thrips, and bees to be pollinators. The bees included *Lasioglossum reticulatum*, *Lasioglossum* sp., *Augochlora pura*, *Augochlora gemula*, *Xylocopa virginiana*, and *Apis mellifera*. Of these bees, over 100 *L. reticulatum* were observed on female-phase flowers and 25 in the male phase. The other bee species were also found on the

female-phase flowers but in lower proportions (Latimer 1994). The Halictid bees comprised 14% of all floral visitors; 41% of the bee visitations were to flowers in the female phase (Latimer 1994). Bees also displayed a temporal element in visitation with peak activity between 10:00 and 12:00 hrs, Central Standard Time (Latimer 1994). This activity correlated with the appearance of the sun above the horizon of the ravines in the panhandle of Florida. The Halictid bees were capable of quickly flying into and out of the vase-shaped female phase flowers and Latimer (1994) concluded that the bees might be "fooled" into visiting female-phase flowers (see mimicry discussed earlier in *M. macrophylla* and *M. ashei*) because after landing on the stigmas, etc., their wings become wet and they have to dry their wings to fly. The vertical surfaces of the female-phase flowers appear slippery and other insects often fall into the base of the flower. More than ten bees may be found in a single flower, all trying to exit. However, some seem to collect substances from surfaces around the stigma and move their abdomens in a manner similar to pollen-collecting activities (Latimer 1994).

It is apparent that bees play a significant role as pollinating agents in some species of *Magnolia*. Pollination of *Magnolia* flowers by bees is, however, controversial because pollen is the primary food (mainly on petals) in protogynous flowers and the bees do not seem to "fit the flower". The majority of insect-pollinated, extant angiosperms are pollinated at least in part by Apidae and it is important to recognize trends in the floral evolution of basal angiosperms (Bernhardt & Thien 1987). The pattern seems to suggest that bee-pollination is of polyphyletic origin in the basal angiosperms (Bernhardt & Thien 1987). It is suggested that possibly bee pollination evolved rapidly in recent times (Bernhardt & Thien 1987). The majority of the basal angiosperms appear to be pollinated by advanced, eusocial Apidae (Bernhardt & Thien 1987) and there are few reports of pollination of basal angiosperms by the most primitive bee family, the Colletidae (Bernhardt & Thien 1987).

Flies

Nineteen genera of Diptera were observed eating, collecting pollen, sucking petal surface secretions, etc., on the flowers of five Japanese species of *Magnolia* (Yasukawa et al. 1992). The Anthomyiidae and Syrphidae were particularly abundant and also used *Magnolia* flowers as mating sites (Yasukawa et al. 1992). Diptera were also noted by Heiser (1962) especially Syrphidae. The frequent visits of Diptera suggests some role in the pollination of *Magnolia* (Yasukawa et al. 1992).

The eight West Indian speces of *Magnolia* are unique in the world in that the stamens have a filamentous or setaceous tip (>10 mm) that embeds in the gynoecium (Howard 1948). The extension of the connective is a trend also present in *Aromadendron* and *Dugandiodendron* (Magnoliaceae), but the reduced tips do not embed in the gynoecium nor detach at the base as in the West Indian species (Vázquez-G. 1994). The setaceous tips embed in the gynoecium and when the buds open detach from the androphore and thus dangle on the gynoecium held by the

setaceous tip (Howard 1948). The stamens then apparently reverse in position and are held upside down, probably as the stamens dry; the tips curl upward. Eventually the tips snap and the stamens fall from the flowers. This is a major deviation in floral structure and function that places the male segments of the flower into the same position as the female counterpart.

What is apparently missing from the *Magnolia* pollination syndrome in the West Indian species is the litter of stamens and pollen that tends to accumulate in petal bases of temperate species. Howard (1948) does mention, however, that the petal-surfaces become coated with pollen. On theoretical grounds, perhaps, flies may indeed be pollinators as they tend to crawl rapidly on surfaces, etc. Is it possible the West Indian species are pollinated by flies? In a letter (to LBT, 12 November 1973), Howard reported that his daughter found two honey bees on the stamens, three flies similar to houseflies, and one large fly that collected secretions near the base of the petals. Unfortunately the forests of the West Indies are rapidly disappearing and on many islands magnolias now only inhabit very restricted habitats. No doubt the insect populations have also declined and study of these magnolias is urgently needed to gain reproductive information.

The flowers of extant temperate species of Magnoliaceae are very complex and are pollinated by a wide variety of insect taxa. Except for a few studies, little is known about the reproductive biology of the tropical species. What is particularly tragic is that so few of the tropical species are preserved in private or public botanical gardens.

References

ARMBRUSTER, W.S., HOWARD, J.J., CLAUSES, T.P., DEBEVEC, E.M., LOQUVAM, J.C., MATSUKI, M., CERENDOLO, B. & ANDEL, F. (1997). Do biochemical exaptations link evolution of plant defense and pollination systems? Historical hypotheses and experimental tests with *Dalechampia* vines. Amer. Nat. 149: 461–483.

ANDREAE, W.A. (1952). Effect of scopoletin on indoleacetic acid metabolism. Nature 170: 83–84.

AZUMA, H., TOYOTA, M., ASAKAWA, Y. & KAWANO, S. (1996). Naphthalene – a constituent of Magnolia flowers. Phytochemistry 42: 999–1004.

———, ———, ———, YAMAOKA, R., DIERINGER, G., GARCIA-FRANCO, J.G., THIEN, L.B. & KAWANO, S. (1998). Floral scents of *Magnolia* and allied genera (Magnoliaceae): chemical divergence and plant-insect interactions. Plant Species Biology 12: 69-83.

———, THIEN, L.B., TOYOTA, M., ASAKAWA, Y. & KAWANO, S. (1997). Distribution and differential expression of (E)-4,8-dimethyl-1,3,7-nonatriene in leaf and floral volatiles of *Magnolia* and *Liriodendron* taxa. J. Chem. Ecol. 23: 2467–2478.

BAKER, H.G. & HURD Jr, P.D. (1968). Intrafloral ecology. In: Smith, R.F. & Miller, T. E. (eds) Ann. Rev. Entomol. 13: 385–414.

BALDWIN, I.T. (1988). Short-term damage-induced increases in Tobacco alkaloids protect plants. Oecologic 75: 367–370.

BERNHARDT, P. (1996). Anther adaptation in animal pollination. In: D'Arcy, W.D. & Keating, R.C. (eds). The Anther: Form, Function, and Phylogeny, 192–220. Cambridge: Cambridge University Press.

—— & THIEN, L.B. (1987). Self-isolation and insect pollination in the primitive angiosperms. Pl. Syst. Evol. 156: 159–176.

BURR, B. & BARTHLOTT, W. (1993). Untersuchungen zur Ultraviolettreflexion von Angiospermenbluten. II. Magnoliidae, Ranunculidae, Hamamelididae, Caryophyllidae, Rosidae. Trop. Subtrop. Pflanzenwelt no. 87: 1–193.

CALLAWAY, D.J. (1994). The World of Magnolias. Portland, Oregon: Timber Press Inc.

CARVAJAL, L.G. (1993). Estúdio biológico de una especie forestal endémica (*Magnolia dealbata* Zucc.) Thesis. Universidad Autónoma de Nuevo León, Monterrey, México.

CHAW, S.M. (1992). Pollination, breeding syndromes, and systematics of *Trochodendon aralioides* Sieb. & Zucc. (Trochodendraceae), a relictual species in eastern Asia. Acad. Sin. Monogr. ser. 12: 63–77.

CRANE, R., FRIIS, E.M. & PEDERSON, K.R. (1995). The origin and early diversification of angiosperms. Nature 374: 27–33.

CREPET, W.L. (1996). Timing in the evolution of derived floral characters: Upper Cretaceous (Turonian) taxa with tricolpate and tricolpate-derived pollen. Rev. Palaeobot. Palynol. 90: 339–359.

—— & FRIIS, E.M. (1987). The evolution of insect pollination in angiosperms. In: Friis, E.M., Chaloner, W.G. & Crane, P.R. (eds), The origins of angiosperms and their biological consequences, 181–203. Cambridge: Cambridge University Press.

CRONQUIST, A. (1981). An integrated system of classification of flowering plants. New York: Columbia University Press.

CROTEAU, R. & KARP, F. (1991). Origin of natural odorants. In: Muller, P.M. & Lamparsky, D. (eds), Perfumes – Art, Science and Technology, 101–124. New York: Elsevier Applied Science.

CROWSON, R.A. (1981). The biology of Coleoptera. New York: Academic Press.

CRUDEN, R.W. (1972). Pollination biology of *Nemophila menziesii* (Hydrophyllaceae) with comments on the evolution of oligolectic bees. Evolution 26: 373–389.

DAUMAN, E. (1930). Das Blutennektarium von *Magnolia* und die Futterkorper in der Blute von *Calycanthus*. Planta 11: 106–116.

DIELS, L. (1916). Kaferblumen bei den Ranales und ihre Bedestung fur die Phylogenese der Angiospermen. Ber. Deutsch. Bot. Ges. 34: 758–774.

DELPINO, F. (1875). Ulteriori osservazioni e considerazioni sulla dicogamia nel regno vegetale. Milan.

DICKE, M. & SABELIS, M.W. (1988). How plants obtain predatory mites as bodyguards. Netherl. J. Zool.

DIERINGER, G. & ESPINOSA, J.E. (1994). Reproductive ecology of *Magnolia schiedeana* (Magnoliaceae): a threatened cloud forest tree species in Veracruz, Mexico. Bull. Torrey Bot. Club 121: 154–159.

—— & DELGADO, L. (1994). Notes on the biology of *Cyclocephala jalapensis* (Coleoptera: Scarabaeidae): An endemic of eastern Mexico. Southw. Entomol. 19: 309–311.

——, CABRERA-R., L., LARA, M., LOYA, L. & REYES-CASTILLO, P. (1998). Beetle pollination and floral thermogenicity in *Magnolia tamaulipana* (Magnoliaceae). International Journal of Plant Sciences (*in press*).

EHRLICH, P.R. & RAVEN, P.H. (1964). Butterflies and plants: a study in coevolution. Evolution 18: 576–608.

ENDRESS, P.K. (1990). Evolution of reproductive structures and functions in primitive angiosperms (Magnoliidae). Mem. New York Bot. Gard. 55: 5–34.

——, P.K. (1994). Diversity and evolutionary biology of tropical flowers. New York: Cambridge University Press.

EYDE, R.H. (1975). The foliar theory of the flower. Amer. Sci. 63: 430–437.

FARMER, E.E. & RYAN, C.A. (1990). Interplant communication: Airborne methyl jasmonate induces synthesis of proteinase inhibitors in plant leaves. Proc. Nat. Acad. Sci. 87: 7713–7716.

FRIIS, E.M. & CREPET, W.L. (1987). Time of appearance of floral features. In: Friis, E.M., Chaloner, W.G. & Crane. P.R. (eds). The origins of angiosperms and their biological consequences, 145–181. Cambridge: Cambridge University Press.

FAEGRI, K. & VAN DER PIJL, L. (1979). The principles of pollination ecology. New York: Pergamon Press.

GIBBS, P.R., SEMIR, J. & CRUZ, N.D. 1977. Floral biology of *Talauma ovata* St. Hil. (Magnoliaceae). Ciencia e Cultura 29: 1436–1441.

GOULD, S.J. & VRBA, E.S. (1982). Exaptation – a missing term in the science of form. Paleobiology 8: 4–15.

GOTTSBERGER, G. (1977). Some aspects of beetle pollination in the evolution of flowering plants. Pl. Syst. Evol. Suppl. 1: 211–226.

—— (1989a). Beetle pollination and flowering rhythm of *Annona* sp. (Annonaceae). Pl. Syst. Evol. 167: 165–187.

—— (1989b). Comments on flower evolution and beetles pollination in the genera *Annona* and *Rollinia* (Annonaceae). Pl. Syst. Evol. 167: 189–194.

GOODWIN, R.H. & TAVES, C. (1950). The effect of coumarin derivatives on the growth of avena roots. Amer. J. Bot. 37: 224–231.

GRANT, V. (1950). The pollination of *Calycanthus occidentalis*. Amer. J. Bot. 37: 294–297.

HARBORNE, J.B. (1982). Introduction to ecological biochemistry. New York: Academic Press.

HAYNES, K.F. & POTTER, D.A. (1995). Chemically mediated sexual attraction of male *Cyclocephala lurida* (Coleoptera: Scarabaeidae) and other scarabaeid beetles to immature stages Environmental Entomology 24: 1302–1306.

HEISER Jr, C.B. (1962). Some observations on pollination and compatibility in *Magnolia*. Proc. Indiana Acad. Sci. 72: 259–266.

HESLOP-HARRISON, Y. & SHIVANNA, K.R. (1977). The receptive surface of the angiosperm stigma. Ann. Missouri Bot. Gard. 41: 1233–1258.

HEYWOOD, V.H. (1978). Flowering plants of the world. New York: Mayflower Books, Inc.

HOWARD, R.A. (1948). The morphology and systematics of the West Indian Magnoliaceae. Bull. Torrey Bot. Club 75: 335–357.

ISHIDA, K. (1996). Beetle pollination of *Magnolia praecocissima* var. *borealis*. Plant Species Biology 11: 199–207.

KATO, M. & INOUE, T. (1994). Origin of insect pollination. Nature 368: 195.

KAISER, R. (1991). Trapping, investigation and reconstitution of flower scents, In: Müller, P.M. & Lamparsky, D. (eds), Perfumes – Art, Science and Technology, 213–250. New York: Elsevier Applied Science.

KEVAN, P.G. 1983. Floral colors through the insect eye: What they are and what they mean. In: Jones, C.E. & Little, R.J. (ed.), Handbook of Experimental Biology, 3–30. New York: Scientific and Academic Editions.

KIKUZAWA, K. & MIZUI, N. (1990). Flowering and fruiting phenology of *Magnolia hypoleuca*. Pl. Species Biol. 5: 255–261.

KNUDSEN, J.T., TOLLSTEN, L. & BERGSTROM, L.G. (1993). Floral scents – a checklist of volatile compounds isolated by head-space techniques. Phytochemistry 33: 253–280.

LABANDEIRA, C.C. & SEPKOSKI Jr, J.J. (1993). Insect diversity in the fosil record. Science 261: 310–315.

LATIMER, S.D. (1994). *Magnolia ashei* Weatherby (Magnoliaceae): Biology and Conservation of an Endangered Species. Pp. 190. Doctoral Dissertation, Tulane University, New Orleans.

LAW, Y.-W. (1984). A preliminary study on the taxonomy of the family Magnoliaceae. Acta Phytotax. Sin. 22: 89–108.

LAWRENCE, G.H.M. (1951). Taxonomy of vascular plants. The Macmillan Co., New York.

LLOYD, D.G. & WELLS, M.S. (1992). Reproductive biology of a primitive angiosperm, *Pseudowintera colorata* (Winteraceae), and the evolution of pollination systems in the Anthophyta. Pl. Syst. Evol. 181: 77–95.

LUBBOCK, J. (1881). Observations on ants, bees, and wasps. Part IX. Colours of flowers as an attraction to bees: experiments and considerations thereof. J. Linn. Soc. (Zool.) 16: 110–112.

MCKEY, D. (1979). The distribution of secondary compounds within plants. In: Rosenthal, G.A. & Janzen, D.H. (eds), Herbivores, 56–122. New York: Academic Press.

MICHENER, D.D. & GRIMALDI, D.A. (1988). A *Trigona* from Late Cretaceous amber of New Jersey (Hymenoptera: Apidae: Meliponinae). Amer. Mus. Nov. no. 2917: 1–12.

NOOTEBOOM, H.P. (1993). Magnoliaceae. In: Kubitzki, K. (ed), The Families and Genera of Vascular Plants 2: 391–401. Berlin, Heidelberg: Springer Verlag.

PEIGLER, R.S. (1988). A review of pollination of *Magnolia* by beetles, with a collecting survey made in the Carolinas. Magnolia 45: 1–8.

PELLMYR, O. & THIEN, L.B. (1986). Insect reproduction and floral fragrance: Keys to the evolution of angiosperms? Taxon 35: 76–85.

PRANTL, K. (1888). Magnoliaceae. In: Engler, A. & Prantl, K., Die Natürlichen Pflanzenfamilien 16: 14.

PRICE, P.W., BONTON, C.E., GROSS, P., MCPHERON, B.A., THOMPSON, J.N. & WEIS, A.A.E. (1980). Interactions among three trophic levels: Influence of plant interactions between herbivores and natural enemies. Ann. Rev. Ecol. Syst. 11: 41–65.

RADLEY, J.A. & GRANT, J. (1954). Fluorescence analysis in ultra-violet light. London: Chapman & Hall.

REGAL, P.J. (1977). Ecology and evolution of flowering plant dominance. Science 196: 622–629.

SILBERGLIED, R.E. (1979). Communication in the ultraviolet. In: Johnston, R.F., Frank, P. W., & Michener, C.D. (eds), Ann. Rev. Ecol. Syst., 373–399. Annual Reviews, Inc. Palo Alto, California.

STEBBINS, G.L. (1981). Why are there so many species of flowering plants? Bioscience 31: 573–577.

TAKHTAJAN, A. (1969). Flowering plants. Edinburgh.

THIEN, L.B. (1974). Floral biology of *Magnolia*. Amer. J. Bot. 61: 1037–1045.

——— (1980). Patterns of pollination in the primitive angiosperms. Biotropica 12: 1–14.

———, BERNHARDT, P., GIBBS, G.W., PELLMYR, O., BERGSTROM, G., GROTH, I. & MCPHERSON, G. (1985). The pollination of *Zygogynum* (Winteraceae) by a moth, *Sabatinca* (Micropterigidae): An ancient association? Science 227: 540–543.

———, HEIMERMANN, W.H. & HOLMAN, R.T. (1975). Floral odors and quantitative taxonomy of *Magnolia* and *Liriodendron*. Taxon 24: 557–568.

———, KAWAMO, S., LATIMER, S., DEVALL, M.S., ROSSO, S., AZUMA, H. & JOBES, D. (1995). Fluorescent *Magnolia* flowers. Pl. Species Biol. 10: 61–64.

———, WHITE, D.A. & YATSU, L.Y. (1983). The reproductive biology of a relict – *Illicium floridanum* Ellis. Amer. J. Bot. 70: 719–727.

THORP, R.W., BRIGGS, D.L., ESTES, J.R. & ERICKSON, E.H. (1975). Nectar fluorescence under ultraviolet irradiation. Science 189: 476–478.

TRESEDER, N.G. (1978). Magnolias. London, Boston: Faber & Faber.

TUCKER, S.C. (1977). Foliar sclerids in the Magnoliaceae. Bot. J. Linn. Soc. 75: 325–356.

TURLINGS, T.C.J., TUMLINSON, J.H. & LEWIS, W.J. (1990). Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. Proc. Nat. Acad. Sci. 250: 1251–1253.

———, LOUGHRIN, J.H., MCCALL, P.J., ROSE, U.S.R., LEWIS, W.J. & TUMLINSON, J.H. (1995). How caterpillar-damaged plants protect themselves by attracting parasitic wasps. Proc. Nat. Acad. Sci. 92: 4169–4174.

———, MCCALL, P.J., ALBORN, H.T. & TUMLINSON, J.H. (1993). An elicitor in caterpillar oral secretions that induces corn seedlings to emit chemical signals attractive to parasitic wasps. J. Chem. Ecol. 19: 411–425.

——— & TUMLINSON, J.H. (1992). Systemic release of chemical signals by herbivore-injured corn. Proc. Nat. Acad. Sci. 89: 8399–8402.

UTECH, F.H. & KAWANO, S. (1975). Spectral polymorphisms in angiosperm flowers determined by differential ultraviolet reflectance. Bot. Mag. (Tokyo) 88: 9–30.

VÁZQUEZ-G., J.A. (1994). Magnolia (Magnoliaceae) in Mexico and Central America: A synopsis. Brittonia 46: 1–23.

VOGEL, S. (1978). Evolutionary shifts from reward to deception in pollen flowers. In: Richards, A.J. (ed), The pollination of flowers by insects. Linn. Soc. Symposium 6. London: Academic Press.

YASUKAWA, S., KATO, H., YAMAOKA, R., TANAKA, H., ARAI, H. & KAWANO, S. (1992). Reproductive and pollination biology of *Magnolia* and its allied genera (Magnoliaceae)–1. Floral volatiles of several *Magnolia* and *Michelia* species and their roles in attracting insects. Pl. Species Biol. 7: 121–140.