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Floral traits and functional role of whorls in pollinator attraction of *Magnolia grandiflora* L.

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Abstract

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Species within the primitive genus *Magnolia* may often produce specialized floral traits and behaviour to grab the attention of potential pollinators from their surroundings. These reproductive traits in plants undergo various selection pressures and frequently bring forth variations to adapt to the new habitat that may result in speciation. We have aimed to understand the floral traits, the functional role of floral parts, and the variable response of visitors in *Magnolia grandiflora* belonging to an ancient order Magnoliales. Our observations reveal that the floral traits of *M. grandiflora* resemble those of basal angiosperms, conforming to the primitive existence of the genus *Magnolia*. The inconsistency in floral form reflected that *M. grandiflora* has been experiencing various selection pressures from biotic and abiotic factors. Inconsistency in floral equations and diagrams reflect the structural variability in flowers, which can directly impact pollination and reproductive output. SEM images of pollen grains reveal that the pollen grains were monocolpate and boat-shaped in structure. GC-MS analysis showed that VOCs in stigmatic exudation of the flower were largely composed of terpene hydrocarbons such as Perthenine, β-Elemene, β-Caryophyllene, α-Humulene, Bicyclogermacrene, Germacrene A and D, etc. Beyond pollinators attraction, VOCs play a major role in repelling unwanted visitors and in improving the defensive mechanisms in *Magnolia*. Beetles, bees, and flies were found to be the active pollinators and the behaviour of bees indicates that bees were trying to replace the role of beetles in pollinating *M. grandiflora*. In summary, floral whorls were diversely functionalized to ensure maximum reproduction in *M. grandiflora*.

Keywords

dianthesis, floral traits, pollination, protogyny, SEM, VOCs

Introduction

Floral traits are important determinants of fitness, which is the result of long-term interaction with the pollinators and the local environment (Khanduri, 2022; 2023). Floral structure is generally conserved with four main organ types (sepals, petals, stamens, and carpel); however, the variation on this theme is breathtaking. The types of variations include abortion of organs, radial versus bilateral symmetry, whorled or spiral phyllotaxis, dramatic variations in the colour, arrangement, number or size of floral organs, or even evolution of extra floral organs (Becker

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et al., 2011, Khanduri et al., 2019a).The diversity in angiosperms is partially due to the evolution of a great variety of floral phenotypes, which enhanced the pollination success in plants. A pollinator's ability to detect a flower depends on many factors, especially those connected with a floral display, associated with flower numbers and features, type and height of inflorescences (Firmage and Cole, 1988; Huda and Wilcock, 2008), flower structure and colour (Trunschke et al., 2017), presence or absence of pigment patterns (Hansen et al., 2012), shape and size of the flower, and size of pigment patterns (Medel et al., 2003; Khanduri, 2022), symmetry of the flower including orientation (Citerne et al., 2010; Khanduri et al., 2021), amount of pollen and nectar as a floral reward (Alm et al., 1990; Perret et al., 2001; Kromer et al., 2008, Khanduri, 2022; 2023), among many other floral traits. Apart from offering nutritional rewards and using visual stimuli, flowers emit volatile organic compounds (VOCs) to attract pollinators and stimulate reproductive outcrossing.

Floral volatile organic compounds (VOCs) are important compounds derived from flowers. Floral volatiles are key floral traits that mediate flower–visitor interactions by attracting pollinators, structuring flower–visitor communities, and defending against plant and flower antagonists (Junker et al., 2010; Galen et al., 2011; Schiestl et al., 2014; Junker and Parachnowitsch, 2015). They also have other adaptive roles such as repellents (Borg-Karlson et al., 1993; Kessler et al., 2008; Paulus and Gack, 1990) and physiological protectors against abiotic stresses (Knudsen et al., 2006; Dudareva et al., 2013). VOCs are generally lipophilic and have low molecular weights and high melting points. VOCs have diverse chemical structures and are mainly classified into terpenoids, phenylpropanoids, and fatty acid derivates (Negre-Zakharov et al., 2009). VOCs produced by the female reproductive organs of the flower may have greater importance as they take part in a major role of attracting pollinators, repelling pollen scavengers or robbers, and defending against various forms of microbial pathogens.

M. grandiflora (Magnoliaceae) commonly known as the southern magnolia or bull bay is a medium-sized evergreen tree native from the Southeastern of the US, mostly cultivated over East Asia, Central America, and North America. *M. grandiflora* occurs within the relatively ancient order Magnoliales. Being a primitive plant among angiosperms, the flowers of *Magnolia* are considered as a theoretical starting point for understanding of the evolution of angiosperms (Cronquist, 1981). *Magnolia* species have also attracted a great deal of attention from evolutionary biologists and biogeographers (Qiu et al., 1995). In particular, *Magnolia* is one of approximately 65 plant genera common to both eastern Asia and eastern North America (Wen, 1999). Largely due to their attractive flowers, these plants are widely appreciated as ornamental trees and shrubs.

There is no main flush of flowering in *M. grandiflora*, instead the flowers open intermittently throughout summer and its fruit or seed set is low, and seedlings are rarely found in the wild. Flowers of the focal tree have an unusual structural specialization as large flowers with an elongated receptacle, on which numerous stamens and carpels are arranged spirally. The female reproductive organ is covered with a sticky, viscous, and shiny substance referred to as the stigmatic exudates. The flowers give off a slightly fruity aroma that intensifies throughout the day. *M. grandiflora* encourages cross-pollination, with its flowers designed to attract beetles for this purpose. Interestingly, honeybees also play a significant role in pollinating *M. grandiflora* flowers (Sukumaran et al., 2020, Thien, 1974; Yasukawa et al., 1992; Allain et al., 1999). This species is categorized as Least Concern on the IUCN Red List (Cicuzza et al., 2007). However, the population of *M. granidiflora* has likely been declining in the wild due to extremely small population size, forest fires, habitat destruction, and limited fruit and seed sets. The purpose of this study was to (i) investigate the floral traits and structure and compare its distinct functional role in attracting pollinators and reproduction of *M. grandiflora*, (ii) identify the volatile organic compounds in stigmatic exudates before and after anthesis and their relative importance.

Material and methods

Study site

The investigation was carried out in an isolated tree of *Magnolia grandiflora*, which was located at the College of Forestry, V.C.S.G. Uttarakhand University Horticulture and Forestry, Ranichauri, Tehri Garhwal (Latitude 30º18" N, Longitude 78º24" E, altitude 1,800–2,000 m amsl), Uttarakhand, India. The study was conducted from June to October in two successive years 2015 and 2016. During the study period, the mean monthly rainfall was 10.47 mm; the average relative humidity was between 76 and 91.6%. Maximum monthly means of daily temperature ranged from 22.38 (July 2015) to 23.42 °C (August 2016) and the corresponding minimum was from 17.75 (July 2016) to 17.26 °C (August 2016). July and August are the peak rainy season in the study area.

Floral traits and development

Floral traits and development were observed in 20 selected flowers of *Magnolia grandiflora*. Flower buds were tagged from the bud initiation. The development of the flower was observed daily, and every stage was recorded. Floral traits such as colour, shape, size, phyllotaxy, symmetry, and numbers were tabulated. Tepals were classified into upper, middle, and lower positions, and their sizes were measured. Dianthesis (each flower opened twice) was recorded in *M. grandiflora* (Sukumaran et al., 2020). Anthesis was observed frequently at regular intervals of the day and correlated with the time, temperature, and humidity of the day. Furthermore, traits of the flower have been enlisted by close observation and derived floral formulae and floral diagrams. The structure of anther, pollen, and stigmatic surfaces were examined using scanning electron micros copy (SEM). The specimens used for SEM were fixed in 2% (v/v) glutaraldehyde in 0.1 mol L^{-1} cacodylate buffer, pH of 7.2, and subjected to a dehydration series to 100% ethanol. Further, the specimens were critical-point dried through carbon dioxide using a critical point drier, mounted on aluminum stubs, and sputter-coated with gold, then observed with SEM at 15 kV (KHANDURI et al., 2019b).

Pollen production

Pollen production per flower was assessed by the noon loop method (KHANDURI and SUKUMARAN, 2019). Mean pollen production within a flower was determined by using the following formula. Fp = A × P, where Fp is the total pollen grains production per flower, A is the average number of anthers per flower and P is the average number of pollen grains per anther.

Stigma receptivity and VOCs composition

The stigmatic receptivity was also tested on flowers with the application of hydrogen peroxide solution *in-vivo* at various time intervals of the day from the first day of flower opening until the end of receptivity. Hydrogen peroxide was poured over the stigma, bubbling indicating peroxide activity and stigma receptivity (CARRINGTON et al., 2003). Stigmatic ingredients in samples were analysed to identify VOCs by Gas Chromatography-Mass Spectrometer technique (GC-MS). Two samples of stigmatic extracts were prepared by immersing stigmas in 10 ml acetone solution which were collected at different blooming periods [Sample 1(MG 1): before the 1st flower opening, Sample 2 (MG 2): immediately after 2nd flower opening]. Each sample was dissolved in CH_2Cl_2 to give a 1% w/v solution. The non-polar extracts of *M. grandiflora* were subjected to gas chromatographic-mass spectral analysis on a Varian 4000 Model GC-MS system. The GC capillary column was 30.0 m × 0.33 mm and, the film thickness was 0.25 μm). The carrier gas was helium and a flow rate of 1 mL^{-1} min^{-1}. The 2 μL injections using a splitless injection technique were used. The injection and MSD temperature was kept at 280 °C. GC oven temperature was initially maintained at 60 °C, held for 5 min, and increased at the rate of 3° C min^{-1} up to 280 °C; EIMS, electron energy, 70 eV. Identification of oil components was achieved based on their retention indices and by comparison of their mass spectral fragmentation patterns with the existing database.

Flower visitors and pollinators

Pollinator observations were carried out on four consecutive days in 2015 and 2016, between 07:00–16:00 hours in different flowers. Insects visiting the flowers were observed for their target of visit in the floral whorls, their numbers, and time spent by a particular visitor per flower. The behaviour of the insects visiting the flower was monitored to determine how they affect pollination. Insects were regarded as pollinators when they made direct physical contact with the functional reproductive structures of the flower. On the other hand, flower visitors that landed on accessory whorls but did not make physical contact with both dehisced anthers and stigma were considered as foragers. The types of insects and their behaviour inside the flower were recorded with the help of a videotape. Data pertaining to insect visitors were recorded on an average of three hours immediately after the first and second day of the flower opening. Video recording data along with field observations were used to ascertain the possibility of visitors likely to be the pollinators. The insects were captured using an insect trapping net (Sweep net) and polythene bags. Unfamiliar insects were collected and identified by specialists.

Statistical analysis

Means ± Standard deviation were calculated for all the observed parameters under study. The coefficient of variation (CV) values of floral parts (tepals, stamens, and cone size) was estimated to examine the variability in floral size within the flowers. One-way ANOVA was performed to assess the variability in the percentage composition of chemicals in stigmatic exudates before and after anthesis with duration from anthesis as a fixed effect (independent factor).

Results

Floral traits and development

The flowers of *M. grandiflora* were large creamy white, cup-shaped, hermaphrodite, actinomorphic, hypogynous, solitary, and borne terminally. Accessory floral whorls (calyx and corolla) were not distinguishable. The flower buds were covered with three fused sepal-like structures called calyptra or spathaceous bracts, which abscised 4–5 days prior to the flower opening. These were hairy, soil red in colour. Flower bud initiation commenced in the last week of June in both study years and the calyptras started to shed after 19–20 days. As these envelopes open, the tightly closed pale green perianth (undifferentiated calyx and corolla) becomes visible. First flower opening was observed at an interval of 23 to 24 days (i.e. third week of July) from the floral bud initiation. The average size of the opened flowers was 23.2 ± 1.5 cm. Tepals (9–12) were free, glossy silvery-whitish under part, deciduous, either trimerous or tetramerous and could be divided into three distinct classes: upper, middle, and lower. The length of the tepals varies from 9.1 to 11.5 cm, with a coefficient of variation (CV) ranging from 4.36% to 7.18% (from lower to upper), while base width ranged from 3.7 to 8.3 cm, with a CV of 9.40% to 18.79% (from middle to upper).

Essential whorls grow into an elongated axis called a torus or androgynophore. In androecium, stamen consists of anther and filament, however, the filament is attached throughout the whole length of the back of the anther (adnate). The mean number of stamens was 331 ± 6, and the length was 1.99 ± 0.16 cm (CV: 8.39%), spiral, apostemonous, whitish, three-veined containing four microsporangia, and dehisce longitudinally. Gynoecium, apocarpous, carpals mean number was 65 ± 2, they were spirally coiffed over the torus of 6.52 ± 4 cm long (CV: 5.98 %). The variation in size of floral whorls is detailed in Table 1. The ovary was superior, unilocular, having two ovules per carpel, ovule anatropous and with marginal placentation. Stigmas whitish, curved, with a good quantity of viscous exudates. The derived floral formula, and diagram of *M. grandiflora* are presented in Fig. 1.

M. grandiflora demonstrated an asynchronous flowering habit and dianthesis (each flower opened twice) pattern. The flower buds were opened on two successive days in a protogynous rhythm. During the first (pistillate) opening, the stigma was exposed and receptive. Anther dehiscence follows the second (staminate) opening. The peak period of anthesis was recorded in the morning between 07:00 h and 08:00 h of the day. The peak time of flower closing was observed between 14:00 and 16:00 h of the day (Table 2). The duration of flower opening varied highly depending on temperature, humidity, and rainfall of the day. We found that anther dehiscence started immediately after the second day of anthesis, which lasted around 5–6 hours (14.00 to 15.00 h of the day).

Table 1. Variability in means size of various floral parts of *Magnolia grandiflora,* CV= Coefficient of Variation of individual plant means

Flower part	Range	Mean	CV (%)
Stamen	1.7–2.2	1.99	8.39
Cone	6–7.1	6.52	5.98
Upper petal (L)	9.1–11.6	10.16	7.18
Middle petal (L)	10.9–13.1	11.9	5.71
Lower petal (L)	10.3–11.5	11.0	4.36
Upper petal (W)	3.7–6.2	5.08	18.79
Middle petal (W)	6.4–8.3	7.4	9.40
Lower petal (W)	4.4–7.1	6.18	14.40

L, Length; W, Weigth.

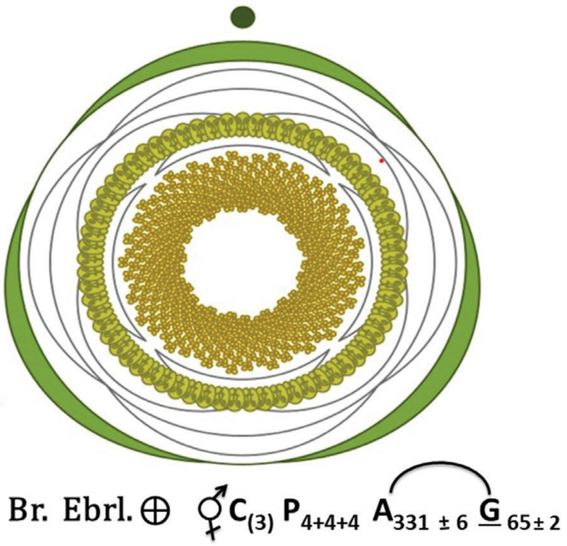


Fig. 1. Derived floral formula and diagram of *Magnolia grandiflora*. Br.: Bracteate Ebrl.: Ebracteolate; ⊕: Actinomorphic, ⚥: Bisexual flower, C(3): three bracts, P: Periyanth consist of 12 tepals arranged spirally in three whorls, A: androecium contains an average of 331 stamens spirally arranged below the torus, G: gynoecium consists of an average of 65 free carpels and ovary superior, ●: Flower terminal.

Stigma receptivity and composition of exudates

In the female phase, stigmas become fleshy, and greenish, having an ample amount of whitish starch-like substrate over the curved surface, whereas in the male phase, stigmas become yellow and produce liquefied exudates (Fig. 2A, B). The peroxide test of stigma receptivity *in-vivo* produced active bubbling immediately after the pistillate opening, indicating stigma receptivity. However, the bubbling was also noticed day after anthesis at 15.00 hours (Fig. 2C), conforming existence of stigma receptivity during the entire staminate phase. Stigmas displayed noticeable bubbling in the initial two days of flowering, then gradually diminished. Stigma became hard, dry, and blackish at the end of the third day of anthesis showing the termination of receptivity (Fig. 2E). Pollen grains were found to be germinating on the stigmatic surface (Fig. 2D). SEM studies revealed that the style and stigma united to form a curved structure (Fig. 2F). Curved stigmas created maximum surface area and received more pollen grains (Figs. 3D, E). The obtained Chromatogram is presented in Figs 4 A and B. The list of identified volatile compounds (VOCs) together with their formulae and structures produced from stigmatic exudates of *M. grandiflora* are presented in Table 3. The analysis of VOCs from the samples reveals that female whorl of the flowers in *M. grandiflora* emit mainly terpene hydrocarbons such as Perthenine (31%–62%), β-Elemene (9%–15%), β-Caryophyllene (2%–3%), Germacrene-A (8%–14%), Germacrene-D (5%–9%), α-Humulene (1.8%–6.3%), Bicyclogermacrene (1.2%–1.8%). Unfortunately, we were not able to identify chemicals 8 and 9 in Table 3, thus their

Table 2. Dianthesis behaviour in *Magnolia grandiflora* in relation to mean temperature and humidity of the day

Flower number	Pistilate (1st day) flower opening time	Flower closing time	Mean day temperature (°C)	Mean day humidity (%)	Staminate (2nd day) flower opening time
1	07:00–08:00	15:00–16:00	24.0	85	07:00-08:00
2	06:00–08:00	15:00–16:00	23.2	79	07:00-08:00
3	07:00–09:00	10:00–11:00	18	100	07:00-09:00
4	07:00–09:00	12:00–14:00	23.2	76	07:00-08:00
5	07:00–09:00	14:00–16:00	24.9	82	07:00-08:00

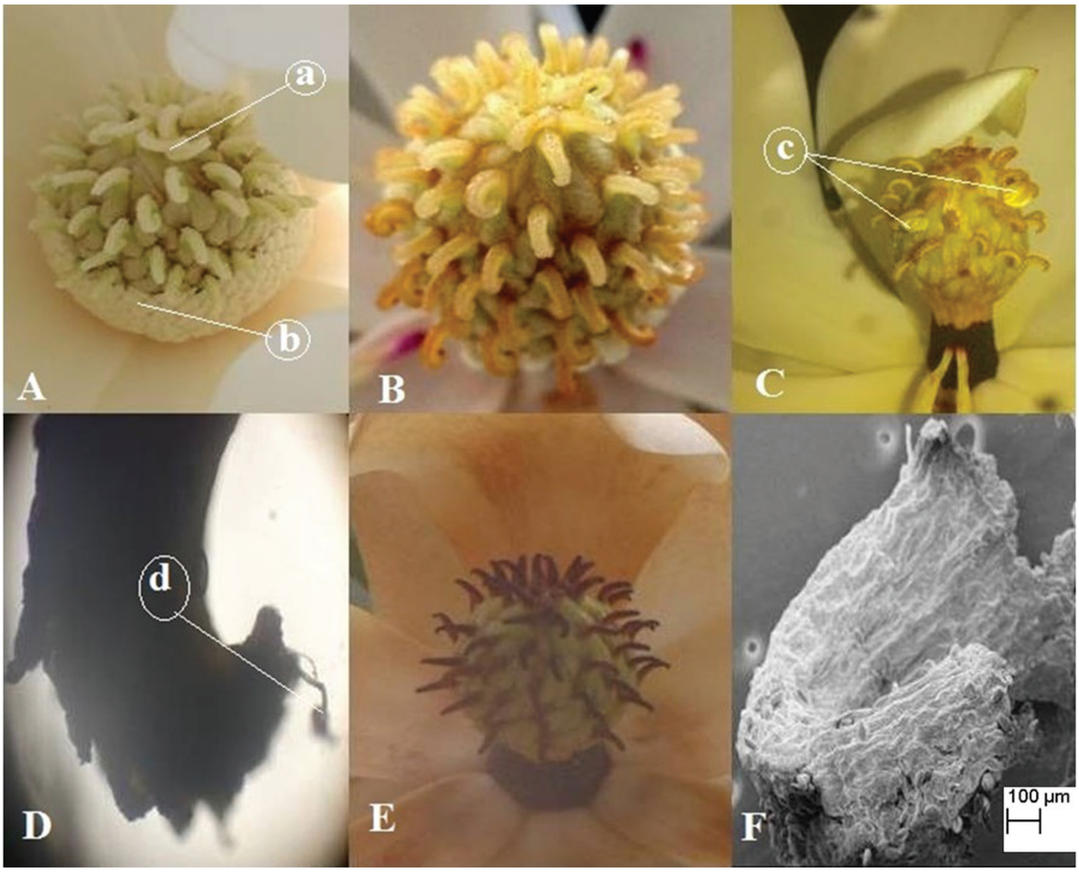


Fig. 2. A–F. Stages of stigmatic receptivity in *Magnolia grandiflora*. A. Visual aspect of stigma after pistillate opening (0 DAA, 08.00 hours) (a: curved stigmatic surface with amble odourless viscous exudates, b: undehisced anthers positioned below the carpel). B. High rich of liquefied substance over the stigma instantly after the staminate opening (01 DAA, 09.00 hours). C. Hydrogen peroxide text under *in-vivo* (01 DAA, 15.00 hours) (c: Occurrence of bubbles over the stigma). D. Structure of stigma after second flower opening through the compound microscopic view (d: Germination of pollen grains on the curved surface of stigma). E. Two days after the staminate opening and termination of receptivity (3rd DAA, 08.00 hours). F. SEM view of the curved section of a stigma. (DAA: Days After Anthesis).

structures remain unknown. Moreover, there were no significant differences among the percentage composition of the chemical constituents obtained from the two samples (Fc = 0.0742, $F_{0.05}$ (1, 18) p = 0.7884).

Pollen morphometrics

The mean number of counted pollen grains per anther was 15,229 ± 858 (N:10) and pollen grains per flower were 5,152,289 ± 285,094 (N:10). Morphological analysis of anther and pollen grains under SEM revealed that anthers were three veined, equipped with four microsporangia (Fig. 3A). Innermost layers were not distinguishable in the traverse section of the anther (Fig. 3B, C). Pollen grains were monocolpate, heteropolar, bilaterally symmetric, and boat-shaped in structure (Fig. 3F).

Flower visitors

Insects belonging to the orders Hymenoptera, Diptera, Coleoptera, Thysanoptera, and Araneae were observed visiting the flowers of *M. grandiflora* during the four days of observations. The number, abundance, foraging behaviour of insect visitors, and functional role of floral whorls are listed in Table 4. In 2015 and 2016, a total of 1,408 and 1,153 floral visitors were documented, with varying number of insects visiting each flower, including thrips (0–170), flower beetle (4–10), bees (3–5), flies (0–1), and spiders (1–2 per flower). Bees (*Apis melifera*), flower beetles, and flies were found to be the pollinators as they had direct physical contact with both stamen and carpel whereas spiders and thrips might be foragers mostly observed on tepals. On the first day of flower opening, bees were seen visiting from the morning, whereas beetles and thrips were observed between 14.00 and 16.00 h of the day at the time of the flowers began to close. The flowers received most visitors subsequently on the second flower opening, which was concomitant with anther dehiscence at 09:00–12:00 h. Moreover, a major part of the visitors was observed over the accessory whorl (tepals). It was observed that in the early hours of 2nd opening, tepals form a cup-shaped structure with an entrance through which bees and flies move frequently and make contact with the reproductive whorls (androecium and gynoecium). Flies usually settled on torus, basking in the sunshine or feeding on the stigmatic secretion, but they rarely collected

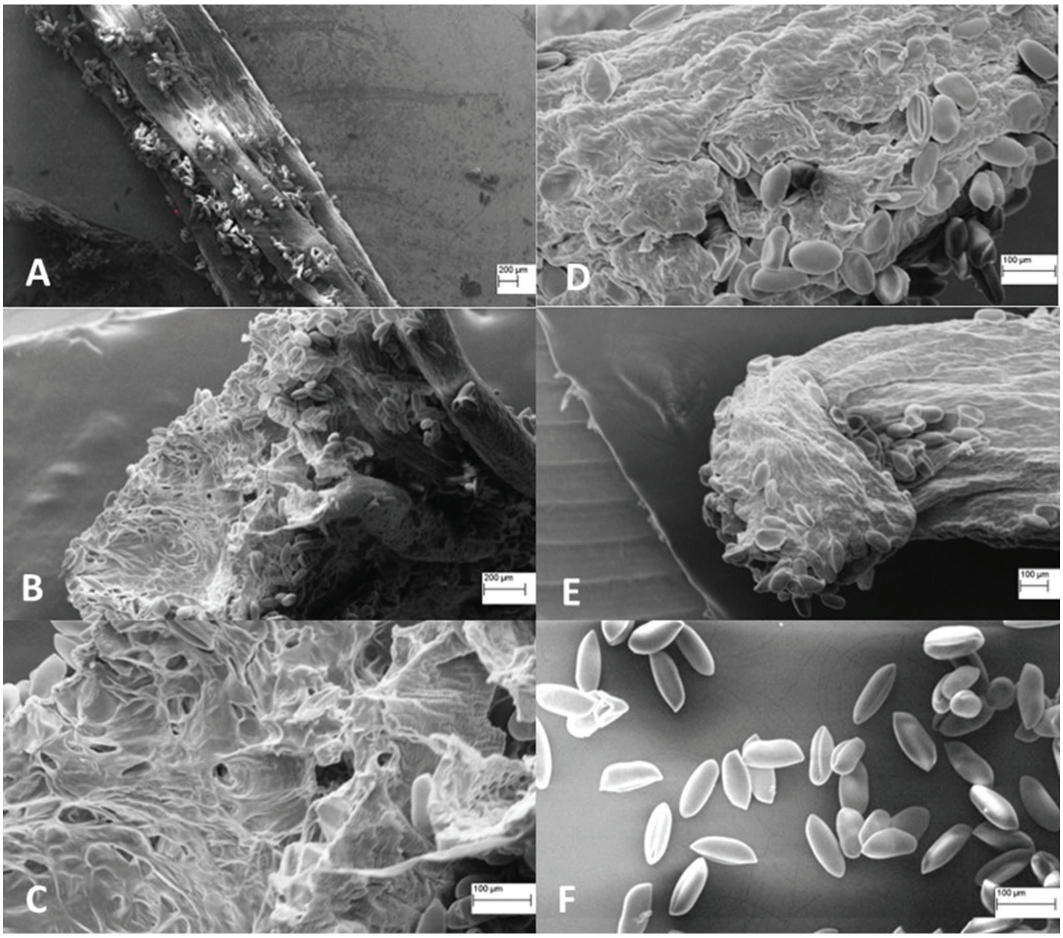


Fig. 3. Microscopic photographs of pollen and stigma in *M. grandiflora*. (A) Scanning Electron Micrograph of longitudinal section of dehisced anther, (B–C) transverse section of anther under SEM, (D–E) adherence of pollen grains over the stigma under SEM view (F) enlarged view of monocolpate pollen grains.

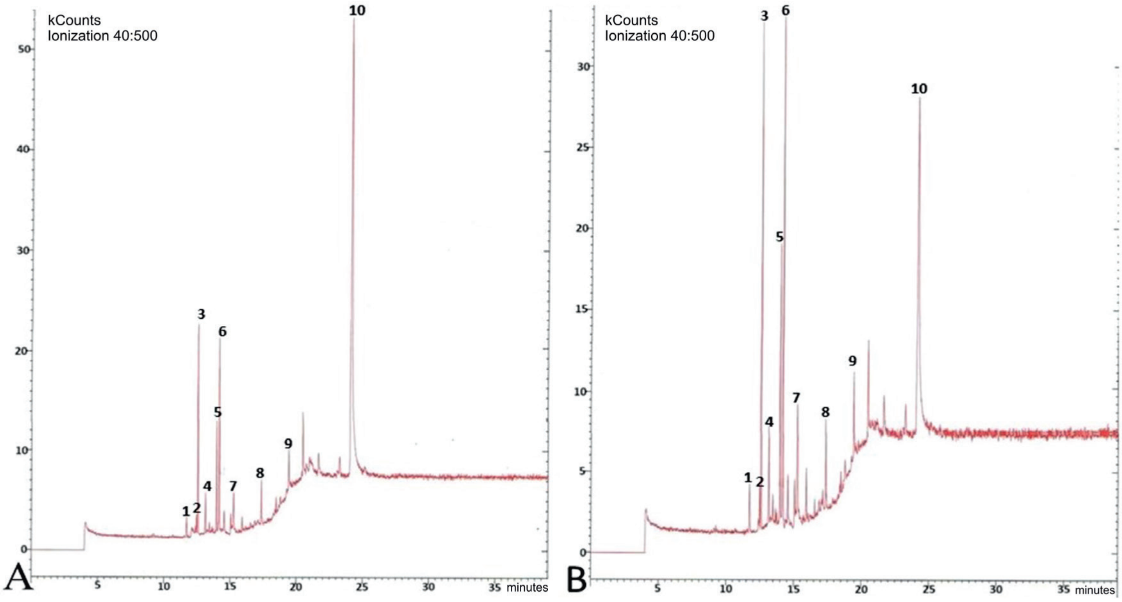
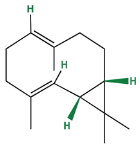
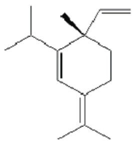
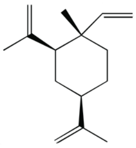
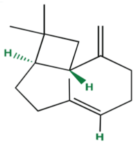
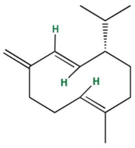
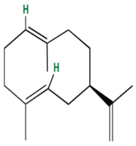
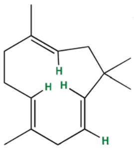
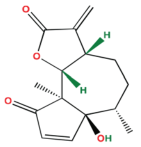


Fig. 4. A–B. Chromatogram obtained during the analysis of volatile organic compounds in stigmatic exudation of *Magnolia grandiflora*. A: MG-1 (Sample 1), B: MG-2 (Sample 2). The numbers in the chromatogram correspond to the numbers of identified compounds in MG-1 and MG-2 in Table 3. (A: Scan Range: 1–2642 Time Range: 0.00–38.98 min, B: Scan Range: 1–2641 Time Range: 0.00–38.98 min).

Table 3. List of VOCs molecular formulae, chemical structure identified in stigmatic exudation of *M. grandiflora* flowers

1	Name	Bicyclogermacrene		2	Name	α-Elemene	
	MF	$C_{15}H_{24}$			MF	$C_{15}H_{24}$	
	RT	11.7			RT	12.46	
	MG 1 area %	1.24			MG 1 area %	0.88	
	MG 2 area %	1.80			MG 2 area %	1.18	
3	Name	β-Elemene		4	Name	β-Caryophyllene	
	MF	$C_{15}H_{24}$			MF	$C_{15}H_{24}$	
	RT	12.58			RT	13.16	
	MG 1 area %	9.62			MG 1 area %	2.17	
	MG 2 area %	15.35			MG 2 area %	3.25	
5	Name	Germacrene-D		6	Name	Germacrene-A	
	MF	$C_{15}H_{24}$			MF	$C_{15}H_{24}$	
	RT	13.99			RT	14.19	
	MG 1 area %	5.00			MG 1 area %	8.57	
	MG 2 area %	8.99			MG 2 area %	14.19	
7	Name	α-Humulene		8	Name	Unidentified	
	MF	$C_{15}H_{24}$			MF	$C_{15}H_{24}$	
	RT	15.28			RT	17.37	
	MG 1 area %	1.87			MG 1 area %	1.72	
	MG 2 area %	6.34			MG 2 area %	14.19	
9	Name	Unidentified		10	Name	Perthenine	
	MF	$C_{15}H_{24}$			MF	$C_{15}H_{20}O_3$	
	RT	19.45			RT	24.15	
	MG 1 area %	1.68			MG 1 area %	62.40	
	MG 2 area %	2.74			MG 2 area %	30.92	

RT – Retention time, MF – Molecular formulae, MG-1 – Sample 1 and MG-2 – Sample 2.

pollen. Bees collected pollen from the dropped anthers resting on the tepals and sometimes assisting the plant to get dropped over the tepals. Bees habitually search for fresh pollens from anthers, pack pollens into their hind legs, and throw it down over the stigma by cleaning themselves. Beetle was found crawling over the dehisced anthers on the tepals, and torus and sucking exudates from the stigma. Thrips were seldom observed in contact with essential whorls that had crowded over the accessory tepals. It performs a creeping movement over the petals and consumes the nutritive tissues on it. Spiders mostly waited for prey and damaged the tepals, but did not touch any of the essential whorls.

Discussion

Our results demonstrated that floral traits of *M. grandiflora* have substantial importance in its fitness as they have not only attracted potential pollinators but also assisted pollinators in fertilizing the ovules and ensured the supply of rewards. It was highlighted that insects from five orders were found to be visiting the floral whorls in *M. grandiflora* out of which only three visitors (flower beetle, bees, and flies) were frequently found in making contact with the essential whorls of the flower. Contact of insect visitors with the floral reproductive organs provides a better understanding of the potential pollinators of the focal plant. GC-MS analyses have shown that the female reproductive parts of the flowers emit VOCs, which are thought to be crucial for deterring unwanted visitors. VOCs provide direct protections, both by inhibiting or repelling aggressors (Lo et al., 2024).

Floral traits and development

The flower of *M. grandiflora* is undoubtedly one of the classical examples of understanding the diversification of angiosperms. Our research indicates that the floral traits in *M. grandiflora* are consistent with those of basal angiosperms, conforming primitive origins of the genus *Magnolia*. Primitive flowers are often large, creamy white, actinomorphic, solitary, undifferentiated perianth, born terminally and numerous floral parts arranged spirally on an elongated axis (Arber and Parkin, 1907). The apocarpous gynoecium with a con-duplicate carpel and marginal placentation was taken as the most primitive condition among angiosperms (Canright, 1952; Ueda, 1986; Thorne, 1996; Xu and Rudall, 2006). In addition, pollen morphological analysis through SEM also strongly supports that the *M. grandiflora* is primitive among angiosperms. Boat-shaped and monocolpate pollen grains indicate the primitive nature of the order Magnolidae (Perveen, 2000: Takhtajan, 1969). We observed that the flowers open in

Table 4. List of insects visited, floral attributes and their functional role in *Magnolia grandiflora*

Floral whorls	Attributes	Insects visited					Functional role
		Name	Family	Range	TV 2015	TV 2016	
Bract	Colour: Soil red						Protection in the early developmental stages of flower buds
	Odour: Nil						
	Number: 3 fused	0	0	0	0	0	
	Size: 3–6 cm						
	Life span: 17–20 days						
	Pubescence: Present						
Tepals	Colour: Creamy white	Flower beetle^{P}	Coleoptera	4–10	186	167	Pollinator attractant Breeding site for insect
	Odour: Lemon scent	*Apis melifera*^{P}	Hymenoptera	3–5	98	76	Saucer to collect dehisced anther & pollen
	Number: 9–12	Thripidae^{F}	Thysanoptera	0–170	1,102	886	Food tissues to pollinator
	Size: L: 9–12 cm, W: 3–6 cm	Fly^{P}	Diptera	0	13	14	Thermal protection
	Life span: 27–30 days	Spider^{F}	Araneae	1–2	9	10	Provide shelter to visitors.
	Pubescence: Nil						
Stamens	Colour: White to pink	Flower beetle^{P}	Coleoptera	4–10	186	167	Source of male gamete
	Odour: Lemon scent	*Apis melifera*^{P}	Hymenoptera	3–5	98	76	Supply pollen as rewards to pollinators
	Number: 331–338	Thripidae^{F}	Thysanoptera	0–170	1,102	886	
	Size: L = 1.7–2.2 cm	Fly^{P}	Diptera	1	13	14	
	Life span: 2 days	Spider^{F}	Araneae	0	9	10	
	Pubescence: Nil						
Carpel with torus	Colour: Green to red	Flower beetle^{P}	Coleoptera	4–10	186	167	Production of VOCs Attracting specific pollinators
	Odour: Lemon scent	*Apis melifera*^{P}	Hymenoptera	3–5	98	76	Producing viscous exudates
	Number: 331–338	Thripidae^{F}	Thysanoptera	0–15	1,102	886	Production of anti-microbial & repellents
	Size: 6.5–6.8 cm L	Fly^{P}	Diptera	1	13	14	
	Life span: 85–80 days	Spider^{F}	Araneae	0	9	10	
	Pubescence: Nil						

TV: Total visits, P – Pollinator, F – Foragers visits.

a protogynous flowering cycle beginning in the morning of the first day with the female phase and continuing in the morning of the second day with the male phase, being protogyny the ancestral condition in angiosperms (Endress, 2010).

Floral equations and diagrams would be extremely beneficial to understand the number of parts of a flower, their arrangements, and the relation they share. In the flowers of *M. grandiflora*, we have found inconsistency in the number of tepals, stamens and carpels. The abnormalities in the number of floral whorls may directly affect the structure and pollination output. It seems that flowers of *M. grandiflora* have been subjected to various selection pressures to stabilize their reproductive structure and it has high adaptive value. Levin (2000) reported that the intra-specific inconstancy of floral formula has evolutionary potential if a particular deviation exhibits adaptive value and it might become favoured by selection. Variation within the perianth whorls may affect overall flower structure and pollination. Further, the abnormalities in the reproductive whorls might affect total reproductive output and male and female fitness (Byerley, 2006).

Volatile organic compounds and their role

Interestingly, in addition to the reproductive function, the female reproductive part of the flowers emits VOCs, which play a major role in deterring unwanted visitors including pathogens and pests rather than attracting pollinators in *M. grandiflora*. We found that more than 90% of VOCs in stigmatic exudates were largely composed of terpene hydrocarbons. Among the compounds identified in this study, Parthenina sesquiterpene was reported to be highly repellent to various insect, pest, and plant pathogens such as moths (Sharma and Joshy, 1977; Datta and Saxena, 1997), migratory grasshoppers (Picmanet al.,1981); mosquitos (Arnason et al., 1985); and to inhibit the sporangial germination and zoospore motility in various plant pathogens (Gupta et al., 2016). Germacrenes are now widely known to have high antimicrobial properties against a variety of microorganism strains (Di Sotto et al., 2017), β-caryophyllene serves as a defence against pathogens that invade floral tissues (Huang et al., 2012). The role of β-caryophyllene in plants is directly connected to plant defence and attraction. β-caryophyllene exerts a pivotal role in the survival and evolution of higher plants and contributes to the unique aroma of essential oils extracted from numerous species (Tetali, 2019). Moreover, Zhang (2018) reported that β-caryophyllene and β-elemene play a signalling role in attracting pollinators, especially honeybees. Furthermore, we have found no significant differences between the percentage composition of VOCs in the stigmatic exudates before and after anthesis, which indicates strong evidence of floral defence against pathogens.

Floral traits and visitors

Observations on the focal tree showed that at least five insect species visited the flowers of *M. grandiflora*, out of which three species (bees, flies, and beetles) made direct physical contact with both (male & female) reproductive parts of the flower, the remaining two visitors (thrips, spiders) are ineffective or illegitimate. Hymenopterans were the active pollinators of *M. grandiflora*. Bees appear to be replacing the role of beetles in pollination of *M. grandiflora*. Observations indicate that bees visit both the pistillate and staminate phases of the flowers. Several features of bees, i.e. (i) dispersing the dehisced anthers from the torus, (ii) collection of pollen grains actively, (iii) collection of pollen from the dropped anthers over the petals, (iv) frequent back-and-forth movements in the search for new anthers within the flower (v) a higher visitation frequency and (vi) secretion of favourable volatile organic compounds (β-caryophyllene and β-elemene) for bees in *M. grandiflora* helps in resulting pollination. This establishes bees as a primary pollinator in *M. grandiflora*. Previous studies also reported that honeybees play a significant role in pollination of *M. grandiflora* (Sukumaran et al., 2020; Losada, 2014; Allain et al., 1999; Yasukawa et al., 1992).

Flowers shape, size, colour, number, arrangement, tepal size, synchronism in flowering, and flower opening are considered as non-rewarding traits of pollinator attractions. Large size of the flowers likely makes them easily attractive to pollinators and the large flowers are more quickly located by bees (Tsujimoto and Ishii, 2017). Bees have often been shown to prefer large flowers, which typically contain a greater reward (Galen and Newport, 1987; Elle and Carney, 2003). Flowers of *M. grandiflora* opened sporadically with a brief break, which might be a strategy to increase the visitation rate of available pollinators within the limited compactable time to assure reproductive success. We presumed that asynchronous flowering may be an indication of the high cost of its reproduction and pollinator limitation.

The influence of accessory whorls in plant-pollinator interactions is less understood. Flowers of *M. grandiflora* usually produce very large tepals with large surface area and provide a landing pad to halt pollinators. Non-hovering pollinators require landing swabs on the flower so that they can rest and feed pollen and stigmatic exudates by making active contact to pollen and stigmas of the flower. Beetles were found to be not as agile in flight as other flying insects. The stamens tend to fall into the bowl-shaped perianth and pollen is taken from there by the pollinators (Heiser, 1962; Thien, 1974; Gibbs et al., 1977). Thus, tepals play an important role in collecting the abscised anthers and pollen, which is improving the accessibility of the pollen, especially to the beetles. Lloyd and Webb (1986) reported that the protogyny is common together with wind, beetle, fly, and thrips pollination, especially in refuge, trap, and brood blossoms. In addition, stamens abscise early in the male phase, before pollens were transferred to pollinators. The previous studies conducted on various genera and species of *Magnolia* suggests that the Coleopterans are considered as primary pollinators (Faegri and Van Der Pijl, 1979; Thien, 1974; Gibbs et al., 1977; Allain et al., 1999; Losada, 2014) and many species of Magnoliaceae are adapted for beetle pollination (Dieringer and Espinosa, 1994; Gottsberger et al., 2012) owing to various floral characteristics, viz. protogyny, bowl-like shape, emitting strong odour, and petals closing at night. Contrary to this, our research reveals that the honeybees are most effective pollinators and have been acting as primary pollinators in *M. grandiflora*, even though beetles perform pollination. The high pollen production in the flowers of *M. grandiflora* would more attract honeybees, offering extra pollination advantages. Moreover, we observed that tepals of *M. grandiflora* are functionalized to supply food tissues, warmth, shelter, and brood sites to the visitors, and appeared to play a relatively important role in the pollination biology of *M. grandiflora*.

Conclusion

Recent advances in our understanding of floral morphological traits underpinning plant–pollinator interactions have been occurring in multiple ways. We have focussed on the floral traits, the functional role of VOCs emitted from the stigmatic exudates, and floral visitors in *M. grandiflora*. The results indicate that beyond pollinator attraction, floral whorls are diversely functionalised for ensuring reproductive success. Further, physical contact with the functional reproductive parts of the flower within the compatible time is necessary to transfer the pollen grains effectively in biotic pollination. Floral traits of *M. grandiflora* are specifically suited to beetle pollination, although honeybees seem to be replacing the role of beetles in pollinating *M. grandiflora*. The study exposed that inconstancy in floral traits indicating that the *M. grandiflora* would be experiencing various degrees of selection pressure in its natural habitat.

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