Leaf Volatile Compounds and Flower-Visiting Insects of Siraitia grosvenorii: Dioecious Differences and Their Ecological Impact Postprint

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Abstract

To elucidate the underlying causes of poor natural pollination in Siraitia grosvenorii, we performed a comparative analysis of flower-visiting insects and leaf volatile components between female and male plants. Flower-visiting insects were surveyed using a fixed-point and fixed-time method, while leaf volatile components were analyzed by GC-MS. The results demonstrated that 102 species of flower-visiting insects were observed on male plants, classified into 8 orders and 29 families, including pollinator groups such as Apidae, Satyridae, Noctuidae, and Sphingidae; conversely, 69 species were observed on female plants, classified into 7 orders and 16 families, with the aforementioned pollinator groups absent. Species richness, abundance, and Shannon-Wiener diversity of flower-visiting insects on male plants were significantly higher than those on female plants ($P < 0.05$). Jaccard similarity analysis indicated a moderate level of dissimilarity in flower-visiting insect communities between the sexes. In male leaves, 17 volatile components were identified, with terpenoids as the dominant compounds (67.31% of total content); whereas in female leaves, 12 volatile components were identified, with alkanes as the dominant compounds (44.27% of total content). Male plants exhibited a greater number of unique components, including 7 terpenoids and 3 esters (45.45% of total components); female plants possessed fewer unique components, comprising only 4 alkanes and 1 ester (22.72% of total component types). Jaccard similarity analysis demonstrated that volatile components between the sexes reached an overall moderate dissimilarity level, with terpenoids and esters showing extremely low similarity. Further analysis suggests that the significant differences in dominant volatile compounds and the substantial presence of unique components between male and female S. grosvenorii plants may have contributed to the observed differences in flower-visiting insect communities, consequently influencing the natural pollination process of S. grosvenorii.

Leaf Volatiles and Foraging Insects of Dioecious *Siraitia grosvenorii*: Sex Differences and Ecological Effects

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Abstract: To investigate the causes of poor natural pollination in *Siraitia grosvenorii*, we compared the foraging insect communities and leaf volatile compounds between female and male plants. Using fixed-point and timed surveys, we observed flower-visiting insects on both sexes, while GC-MS analysis was employed to characterize leaf volatiles. The results revealed 102 species of foraging insects on male plants, belonging to 8 orders and 29 families, including pollinator groups such as Apidae, Satyridae, Noctuidae, and Sphingidae. In contrast, 69 species were observed on female plants, belonging to 7 orders and 16 families, with none of the aforementioned pollinator groups present. Species richness, abundance, and Shannon-Wiener diversity of foraging insects were significantly higher on male plants ($P < 0.05$), with Jaccard similarity analysis indicating medium dissimilarity between sexes. Male leaves contained 17 volatile compounds, with terpenes as dominant components (67.31% of total content), whereas female leaves yielded 12 compounds dominated by alkanes (44.27%). Male plants possessed more unique compounds, including 7 terpenes and 3 esters (45.45% of total components), while females had fewer unique compounds: 4 alkanes and 1 ester (22.72% of total). Jaccard similarity analysis showed moderate overall dissimilarity in volatiles between sexes, with terpenes and esters being extremely dissimilar. Further analysis suggests that these differences in dominant and unique volatile compounds likely drive the significant divergence in foraging insect communities between sexes, thereby affecting natural pollination in *S. grosvenorii.*

Keywords: *Siraitia grosvenorii*, leaf volatiles, foraging insects, dioecious, plant-insect interactions

Siraitia grosvenorii is a dioecious perennial vine in the Cucurbitaceae family with traditional edible and medicinal value (Li and Zhang, 2000). As a medicinal herb, its fruit treats hypertension, tuberculosis, asthma, and acute or chronic bronchitis; in the food industry, mogroside extracts from the fruit are widely used in foods, dairy products, beverages, and health supplements, enjoying popularity in Europe and America with expanding export markets (Sun and Yang, 2018). To meet growing demand from pharmaceutical and food industries, *S.*

grosvenorii cultivation has rapidly expanded in recent years from traditional growing areas in Yongfu County, Guilin, to multiple counties and districts in Guilin, with promotion to Nanning, Liuzhou, Hezhou, and Hechi in Guangxi, contributing significantly to agricultural development (Sun and Yang, 2018). However, poor natural pollination severely constrains cultivation efficiency. During flowering, pollen from male plants is rarely transferred by natural insect vectors to female stigmas, resulting in low natural fruit set (Zhou et al., 1985; Jia et al., 2011). Consequently, artificial pollination is widely practiced to improve fruit set (Jia et al., 2011). With rising labor costs and declining rural populations, artificial pollination has become a major bottleneck for the sustainable development of *S. grosvenorii* cultivation. Therefore, investigating the causes of poor natural pollination and exploring solutions is critically important for the long-term stability of the industry. Observing and comparing flower-visiting insects on male and female plants constitutes a key step in this research.

Flower-visiting insects are those frequently active on flowering plants, including pollinators, herbivores, and natural enemies (Qin, 1985; Guan et al., 2005). Insect selection of host plants is influenced by multiple factors including chemical composition, morphological traits, and environmental conditions, with chemical recognition playing a dominant role (Groot et al., 1999; Qin and Wang, 2001; Rid et al., 2019). Numerous studies have demonstrated that flower-visiting insects identify plant chemical signals via chemoreceptors on their antennae, with these signals primarily composed of plant volatile compounds (Fraser et al., 2003; Wei et al., 2018). Plant volatiles are short-chain hydrocarbons and their derivatives produced during plant metabolism, including alkenes, alkanes, alcohols, aldehydes, ketones, esters, and organic acids (Ding and Guo, 1995). Different volatile compounds can have varying effects on flower-visiting insects –some may attract (Karpati et al., 2013), while others may defend or repel (Hu et al., 2019). Therefore, cross-comparing insect visitation patterns with plant volatile profiles often reveals the underlying causes of pollination failure (Wang, 2017; Friberg et al., 2019).

This study observed and quantified flower-visiting insects on male and female *S. grosvenorii* plants while identifying leaf volatile compounds. Through comparative analysis, we aimed to document differences in insect communities between sexes and examine their relationship with leaf volatiles, providing a foundation for understanding pollination deficiency in this crop.

1.1 Materials and Reagents

Experiments used seedlings of the *S. grosvenorii* cultivar “Dadi No. 2” purchased from Guilin Jifosi Siraitia Co., Ltd. Ethyl acetate was obtained from Guangdong Guanghua Technology Co., Ltd. Additional materials including absorbent cotton, insect pins, and specimen boxes were purchased from Guilin Bell Chemical Reagent Co., Ltd.

1.2 Equipment

- 50/30 m DVB/CAR/PDMS SPME fiber (Supelco, USA)
- 40 mL headspace vials (Agilent, USA)
- Headspace solid-phase microextraction device (Supelco, USA)
- HP-5MS quartz capillary column (Agilent, USA)
- Agilent 7890A gas chromatograph (Agilent, USA)
- Agilent 5975C mass spectrometer (Agilent, USA)
- DHP-9602 digital constant temperature oven (Shanghai Yiheng Scientific Instruments Co., Ltd.)

1.3 Experimental Methods

1.3.1 Planting In April 2018, *S. grosvenorii* seedlings were planted at the experimental site of Guangxi Institute of Botany, Guangxi Zhuang Autonomous Region and Chinese Academy of Sciences (Yanshan District, Guilin). Three experimental plots (L1, L2, L3) were established, each approximately 30 m^2 with ~10 m spacing between plots. Each plot contained 20 seedlings at a 1:1 female-to-male ratio, with normal irrigation and fertilization management.

1.3.2 Flower-Visiting Insect Observation In August, during peak flowering, three female and three male plants were randomly selected in each plot, tagged, and observed for flower-visiting insects using fixed-point, timed surveys. From 6:00 to 18:00 daily, insect species and individuals were recorded at 1-hour intervals, with photographs taken for identification over three consecutive days. On the fourth day, insect specimens were collected, killed with ethyl acetate, and prepared as vouchers. Classification was based on photographs and specimens, with difficult samples identified by entomology experts at Guangxi Institute of Botany.

1.3.3 Leaf Volatile Collection Concurrent with insect observations, three healthy, uniformly sized leaves without insect damage or disease spots were collected from each tagged plant. Petioles were quickly cut with medical scissors, and leaves were immediately placed in headspace vials to avoid mechanical damage. Samples were promptly delivered to the laboratory.

An activated 50/30 m DVB/CAR/PDMS SPME fiber was inserted into each vial, which was then placed in a 37°C constant temperature oven for 30 min extraction. The fiber was subsequently inserted into the GC-MS inlet for 5 min desorption before analysis. Blank air samples from empty vials were analyzed as controls using the same method.

1.3.4 GC-MS Analysis of Volatile Compounds Following Huang et al. (2015) with modifications:

GC conditions: HP-5MS quartz capillary column (30 m × 0.25 mm × 0.25 m); temperature program: initial 50°C, then increased at 5°C min ^{1} to 200°C;

injection volume 2 L, splitless; injector temperature 230°C; carrier gas: high-purity helium (99.999%) at 1.0 mL min ^{1}.

MS conditions: EI ionization at 70 eV; ion source temperature 230°C; interface temperature 280°C; quadrupole temperature 150°C; mass scan range m/z 35-450.

Qualitative analysis: Retention indices were calculated for each peak using retention times of C8-C40 n-alkanes under identical GC-MS conditions. Compounds were preliminarily identified using the NIST05a library, confirmed through manual spectral interpretation with literature references, and relative contents were calculated using ion current peak area normalization.

1.4 Data Analysis

Jaccard similarity coefficients (Zhao and Guo, 1990) were calculated to compare similarity in flower-visiting insect species and leaf volatile compounds between sexes:

Jaccard similarity coefficient (q):

$$q = \frac{c}{a+b-c}$$

where q is the similarity coefficient: $0 \quad q \quad 0.25$ indicates extreme dissimilarity; $0.25 < q \quad 0.50$ indicates medium dissimilarity; $0.50 < q \quad 0.75$ indicates medium similarity; and $0.75 < q \quad 1.00$ indicates high similarity. The variable c represents shared volatiles or insects between sexes, while a and b represent volatiles or insects unique to female and male plants, respectively.

Flower-visiting insect diversity was analyzed using richness index (R), abundance index (A), and Shannon-Wiener diversity index (H') (Xu, 1987; Ding, 1994):

Patrick richness index (R):

$$R = S$$

(where S is number of species)

Abundance index (A):

$$A = N$$

(where N is number of individuals)

Shannon-Wiener diversity index (H'):

$$H' = -\sum_{i=1}^{S} P_i \ln P_i$$

where $P_i = N_i/N$ is the proportion of individuals of species i, N_i is the number of individuals of species i, and N is the total number of individuals.

Two-way ANOVA was used to assess differences in volatile compound contents among plots for each sex, while t-tests analyzed differences in insect richness, abundance, and Shannon-Wiener diversity between sexes. Data were processed and analyzed using SPSS 17.0 and MS Office 2010.

2.1 Flower-Visiting Insect Species on Female and Male *S. grosvenorii*

A total of 115 insect species belonging to 8 orders and 31 families were recorded across all plots. Diptera exhibited the highest diversity with 9 families and 26 species, representing 29.03% of families and 22.61% of species in the community. Hemiptera ranked second (16.12% of families, 22.61% of species), followed by Lepidoptera (16.12% of families, 9.56% of species), Hymenoptera (12.09% of families, 13.04% of species), and Coleoptera (9.67% of families, 12.12% of species). These five orders accounted for 82.61% of all species.

On female plants, 69 flower-visiting insect species belonging to 7 orders and 16 families were observed. Dominant groups included Formicidae (Hymenoptera), Pentatomidae (Hemiptera), Chrysomelidae (Coleoptera), and Tephritidae (Diptera). Notably, important pollinator groups such as Apidae, Nymphalidae, Noctuidae, and Sphingidae were absent from female plants (Figure 1 [Figure 1: see original paper]). In contrast, male plants hosted 102 species across 8 orders and 29 families, with dominant groups including Tephritidae (Diptera), Formicidae (Hymenoptera), Pentatomidae (Hemiptera), and Chrysomelidae (Coleoptera). Unlike females, male plants attracted Apidae, Satyridae, Noctuidae, and Sphingidae, with Apidae showing relatively high frequency (3.78% of total insects) and other groups ranging from 0.75% to 1.13% (Figure 1).

2.2 Similarity of Flower-Visiting Insects Between Sexes

Across the three experimental plots, similarity patterns in flower-visiting insects between sexes were consistent (Table 1). At the order level, Jaccard similarity coefficients ranged from 0.75 to 0.82, indicating medium to high similarity, suggesting that insect communities were relatively similar at higher taxonomic levels. However, at the family level, coefficients decreased to 0.34–0.45, indicating medium dissimilarity and showing a clear decline in similarity as taxonomic resolution increased. At the species level, coefficients ranged from 0.35 to 0.41, also indicating medium dissimilarity (Table 1). Overall, flower-visiting insect communities diverged markedly at the family level, with further differentiation at the species level.

2.3 Species Diversity of Flower-Visiting Insects

While diversity indices (R, A, and H') varied somewhat among plots, differences between plots for the same sex were not significant ($P > 0.05$). Comparisons between sexes showed that across all three plots, male plants exhibited 71% higher species richness (R) ($P < 0.05$), 186% higher abundance (A), and 12.8% higher Shannon-Wiener diversity (H') ($P < 0.05$) than female plants (Table 2). These results demonstrate that male *S. grosvenorii* plants supported not only more diverse but also substantially more abundant flower-visiting insect communities.

2.4 Dominant and Unique Volatile Compounds in Female and Male Plants

GC-MS analysis identified 22 volatile compounds in leaf samples, categorized as terpenes, alkanes, aldehydes, esters, and amines (Table 3). Male leaves released 17 compounds, with terpenes as the dominant group (9 terpenes comprising 67.31% of total volatiles). Other components included esters (4 types, 29.4%), aldehydes (2 types, 2.97%), and amines (2 types, 0.3%). Female leaves released fewer compounds (12 total), with alkanes as the dominant group (4 alkanes comprising 44.27% of total volatiles). Other components included aldehydes (2 types, 27.05%), esters (2 types, 13.07%), terpenes (2 types, 11.19%), and amines (2 types, 4.41%). No significant differences were found among plots for either sex ($P > 0.05$).

Both sexes produced unique volatile compounds. Males had 10 unique compounds among the 22 identified (45.45%), concentrated in terpenes (7 of 9 terpenes, 77.77%) and esters (3 of 5 esters, 60.00%). Females had fewer unique compounds (5 of 22, 22.72%), primarily alkanes (all 4 alkane compounds were female-unique, 100% of alkanes) and one ester (cis-3-hexenyl acetate, 20% of esters).

2.5 Similarity of Leaf Volatile Components Between Sexes

Similarity analysis of overall and class-specific volatile compounds revealed identical values across all three plots because volatile profiles were identical among individuals of the same sex. The overall similarity coefficient was only 0.31, indicating medium dissimilarity ($0.25 < q \quad 0.50$) and low similarity between sexes (Table 4). Alkanes showed complete dissimilarity ($q = 0$), while terpenes and esters were extremely dissimilar ($q = 0.22$ and 0.20, respectively, within the $0 \quad q \quad 0.25$ range). Aldehydes and amines showed the highest similarity ($q = 1.00$), indicating identical compounds in both sexes. However, concentrations differed dramatically: aldehydes accounted for 27.05% of female volatiles but only 2.97% of male volatiles, while amines comprised 4.41% of female volatiles versus 0.30% of male volatiles (Table 3). Specifically, acetaldehyde content was significantly higher in females (26.33%) than males (2.36%) ($P < 0.01$), and

3,3' -iminobispropylamine was also significantly higher in females (4.21%) than males (0.12%) ($P < 0.01$).

Discussion

Insect pollination services critically contribute to crop production (Campbell et al., 2018; Fijen et al., 2018), and pollinator diversity decisively affects yield stability and quantity (Garibaldi et al., 2011; Sun et al., 2018; Woodcock et al., 2019). As an entomophilous plant, poor natural pollination in *S. grosvenorii* may result from insufficient pollinator diversity. This study documented 115 flower-visiting insect species across 8 orders and 31 families, with dominant groups from Diptera, Hemiptera, Lepidoptera, and Hymenoptera. Important pollinator resources included Calliphoridae (Diptera), Satyridae (Lepidoptera), Noctuidae (Lepidoptera), and Apidae (Hymenoptera). Compared with other economic plants, *S. grosvenorii* hosted relatively high insect diversity. For example, Zhong et al. (2014) recorded 60 species across 7 orders and 28 families on longan (*Dimocarpus longana*) in Hainan, with similar dominant groups but only 52% of the species richness found on *S. grosvenorii.* Studies on jujube (*Ziziphus jujuba*) in Shanxi (23 species, 4 orders, 12 families) and apricot (*Prunus armeniaca*) in Shandong (11 species, 6 orders, 8 families) also showed lower diversity (Wu et al., 2016; Gong et al., 2017). Notably, longan, jujube, and apricot exhibit normal natural pollination without reports of pollination failure or artificial pollination requirements. Despite high overall diversity on *S. grosvenorii*, significant differences between sexes may underlie its pollination problems.

Our results show low similarity in flower-visiting insects between sexes: female plants hosted 69 species from 7 orders and 16 families, while males supported higher diversity with 102 species from 8 orders and 29 families ($P < 0.05$). Crucially, nearly all pollinator groups—including Apidae, Satyridae, Noctuidae, and Sphingidae—occurred exclusively on male plants. This pattern prevents pollen transfer from males to females, likely limiting natural pollination.

For dioecious plants, flower-visiting insects often show strong male bias (Miljkovic et al., 2018). Cornelissen and Stiling (2005) found consistently higher insect diversity on male individuals across 33 dioecious species, though they did not specifically analyze pollinators. Rivkin et al. (2018) confirmed this bias across large geographic scales but noted it diminishes with increasing elevation. The prevailing explanation involves chemical defense: females may evolve stronger chemical defenses to protect seeds, deterring insects (Obeso, 2002; Tsuji and Sota, 2010). For example, leaf aldehydes can strongly repel flower-visiting insects (Guo et al., 2012). Our findings support this: female *S. grosvenorii* leaves released aldehydes at approximately 10× the concentration of males (Table 3), potentially explaining lower insect diversity on females.

Conversely, chemical attraction involves plants releasing specific volatiles to attract insects (Yan et al., 2003). Terpenes are common leaf volatiles (Du et al., 2018; Zhang et al., 2019; Zhou et al., 2019). Dobson (2006) demonstrated that herbivore-induced terpenes attract natural enemies for pest control, while monoterpenes such as -pinene, -pinene, myrcene, and camphene strongly attract beetles (Chénier and Philogène, 1989) and can also attract pollinators (Li et al., 2018). Male *S. grosvenorii* leaves emitted nine terpenes including -pinene, -pinene, myrcene, camphene, and limonene, while females produced only two terpenes at much lower concentrations. Males possessed seven unique terpenes among the nine identified (Table 3), likely contributing to their ability to attract diverse pollinators. However, volatile effects can be complex: Andrews et al. (2007) found that some pumpkin volatiles attract both pollinators and herbivores, while others selectively attract only one group.

In summary, our key findings reveal significant differences in flower-visiting insect diversity between sexes, with males supporting more diverse and abundant communities. Critically, multiple pollinator groups visited only male plants, while none were observed on females, likely contributing to poor natural pollination. Leaf volatile profiles also differed substantially between sexes in both dominant and unique compounds. We hypothesize that these chemical differences drive insect preference for male plants, causing divergence in flower-visiting communities. Future research should employ wind tunnel experiments, Y-tube olfactometry, and electroantennography to systematically test insect responses to specific *S. grosvenorii* volatiles and further elucidate mechanisms of pollination failure. Additionally, comparative studies on wild *S. grosvenorii* populations would provide valuable insights.

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Note: Figure translations are in progress. See original paper for figures.