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Flowering Biology and Reproductive Characteristics of Four *Camellia oleifera* Cultivars in Northeastern Guizhou, China

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Abstract. **This study aimed to investigate the flowering biology and reproductive characteristics of *Camellia oleifera* Abel. in northeastern Guizhou, China, by focusing on four locally cultivated cultivars (Minyu 2, Minyu 3, Qianyu 1, and Qianyu 2). Assessed parameters included flowering phenology, floral morphology, pollen viability dynamics, stigma receptivity, and reproductive characteristics classification. All cultivars exhibited concentrated flowering between October and November, with 'Minyu 3' categorized as mid-flowering and the others characterized as early-flowering types. Average flower longevity was 8 days. Visible wilting began 5 to 6 days postanthesis. Significant floral variation was noted. All cultivars had large flowers, with androecium lengths surpassing pistil heights; however, 'Minyu 2' exhibited notably larger corollas than those of the others ($P < 0.05$). Stigmas reached receptivity 2 days before anthesis, peaked at 1 to 3 days postanthesis, and lost receptivity by day 7. A strong correlation ($P < 0.05$) between 2,3,5-Triphenyltetrazolium chloride (TTC) staining (0.5%) and in vitro germination confirmed TTC as an efficient viability assay, whereas acetocarmine and peroxidase staining overestimated viability. Scanning electron microscopy revealed tricolporate pollen with reticulate–vermiculate exine ornamentation across cultivars and significant variations in lumina size, density, and spatial configuration. Pollen-to-ovule (P/O) ratios and outcrossing indices (OCI) confirmed obligate xenogamy requiring pollinator mediation. These findings offer essential insights for regulating flowering periods in high-yield cultivation and inform parental selection and optimal pollination timing in hybrid breeding programs.**

Oil tea (*Camellia oleifera* Abel.), a species within the *Camellia* genus of the Theaceae family, is a vital woody oil crop in China with a cultivation history spanning over 2300 years. Along with olive (*Olea europaea*), oil palm (*Elaeis guineensis*), and coconut (*Cocos nucifera*), it ranks among the world's four major woody oil crops. The oil extracted from *C. oleifera* is a high-quality edible oil distinguished by its clarity, rich nutritional profile, and exceptional storage stability (Wu et al. 2022). Because of its high content of unsaturated fatty acids, it boasts significant antioxidant and anti-inflammatory properties as well as benefits such as improving vascular elasticity, reducing blood lipid levels, and lowering blood pressure (Wang et al. 2017). By-products of *C. oleifera*, including tea seed meal and tea husk, are widely used across industries as detergents, dyes, paper-making products, chemical fibers, textiles, and pesticides, thus underscoring its industrial value (Quan et al. 2022). In China, *C. oleifera* is cultivated extensively, primarily between lat. 18°28′ and 34°34′N and long. 100° to 122°E; however, the core production belt is centered in Hunan, Jiangxi, Guangxi, and Guizhou provinces (Wu et al. 2022). In recent years, rapid growth has occurred in the *C. oleifera* industry. Traditional production areas like Hunan and Jiangxi have doubled their yield per unit area through clonal breeding of superior cultivars, such as the Xianglin, Changlin, and Ganwu series (Xiao and Liu 2021). Conversely, Guizhou Province, an emerging production area, has approved 19 provincially certified elite cultivars, including Minyu 2–3 and Qianyu 1–2 from Yuping County in northeastern Guizhou and Qianbi 1–2 from Bijiang District. Nevertheless, the overall efficiency of germplasm innovation in Guizhou lags behind that of traditional regions. To overcome industrial development bottlenecks, Guizhou has prioritized germplasm innovation and cultivar breeding. In 2023, Guizhou launched the Implementation Plan for Accelerating the Development of the *C. oleifera* Industry (2023–25), which set strategic targets to expand the cultivation area to 293,000 hm^2 and achieve an annual tea oil production capacity of 90,000 tons by 2025. Superior cultivars, such as Minyu 2, Minyu 3, Qianyu 1, and Qianyu 2, bred in Yuping Dong Autonomous County, have been widely promoted across various regions. However, fundamental biological research of their flowering characteristics and reproductive systems remains insufficient, thus limiting the widespread adoption and yield enhancement of these superior cultivars.

The high and stable yield of *C. oleifera* is intricately linked to its reproductive biology, with sexual reproduction involving complex biological mechanisms. Floral characteristics and the reproductive characteristics, as core components of plant reproductive biology (Chen et al. 2015), reflect crucial aspects such as flowering phenology, floral development, pistil–stamen maturation patterns, and gametophyte development (Fan et al. 2019). Research has indicated that the regulation of flowering timing is a sophisticated physiological process controlled by both endogenous genetic factors and various environmental parameters (Wang and Ding 2023). In cross-pollinated species, the temporal alignment of pollen viability and stigma receptivity directly influences pollination efficiency and hybrid breeding success (Douglas and Freyre 2010; Huang et al. 2004). In recent years, oil-tea *Camellia* cultivation has faced severe flower drop, which has become a key bottleneck to yield improvement, with only approximately 10% of flower buds successfully maturing into fruit (Ye et al. 2022). This issue is particularly pronounced in Hezhang County, Guizhou Province, where environmental factors further exacerbate flower drop and low yield problems in local *C. oleifera* cultivation (Du et al. 2017). Such challenges not only hinder the sustainable development of local woody

oil crop industries but also pose risks to national edible oil security and the achievement of strategic "oil self-sufficiency" goals.

Flowering biology is a critical factor for improving plant yield (Strelin et al. 2023). Recent studies have advanced the understanding of *C. oleifera* biology. Wei et al. (2021) documented stable floral organ variation in *C. weiningensis*, thus offering valuable insights into its evolutionary relationships. Cheng et al. (2023) conducted a study of the biological flowering characteristics of 10 major cultivated cultivars of *C. oleifera* in Jiangxi Province and provided a scientific basis for enhancing yield. Liu et al. (2025) explored how flowering traits affect pollination efficiency in the Changlin 4 and Changlin 53 cultivars and emphasized floral phenology as a pivotal determinant of yield and oil quality. While significant research has focused on nationally recognized cultivars such as the Changlin and Xianglin series, investigations of locally bred cultivars from northeastern Guizhou, specifically, Minyu 2, Minyu 3, Qianyu 1, and Qianyu 2, remain limited. Existing studies include one by Du et al. (2023), who explored phytohormone coordination during flower bud formation in 'Minyu 2' and 'Qianyu 2', and one by Liu et al. (2021), who developed high-grafting techniques for improving 'Minyu 2', 'Minyu 3', and 'Qianyu 1'. However, comprehensive analyses of their flowering phenology and reproductive biology are notably lacking. To fill this gap, this study systematically examined four locally adapted *C. oleifera* cultivars from northeastern Guizhou by focusing on floral phenology, developmental chronology, morphometric floral traits, pollen viability dynamics, stigma receptivity patterns, pollen morphology, and reproductive characteristics. This study aimed to establish a theoretical framework to enhance yield stability, optimize hybridization strategies, and improve cultivation practices in oil-tea *Camellia* production systems.

Materials and Methods

This study was conducted in Yuping Dong Autonomous County, Tongren City, Guizhou Province, China (lat. 108°54′16″E, long. 27°17′47″N, elevation 513 m). This region has a mid-subtropical monsoon humid climate, with extreme maximum and minimum recorded temperatures of 39.7 °C and −10.7 °C, respectively. Annual precipitation ranges from 1100 to 1200 mm, with mean annual relative humidity of 80%. Sunshine totals 1733.3 h annually, and the average frost-free period spans 299 d. The terrain features a 15° eastern slope with well-drained yellow loam soil and deep soil layers. The optimal growing conditions include abundant sunlight, sufficient rainfall, and a planting density of 70 to 80 trees per 667 m^2. The experimental stand consists of 7-year-old trees spread over 2 ha managed using conventional water and fertilizer practices.

Four *C. oleifera* cultivars bred in Yuping Dong Autonomous County were used as scions (Minyu 2, Minyu 3, Qianyu 1, and Qianyu 2), and the rootstock seedlings were propagated from seeds of 'Changlin 3'. For the experiments, we selected healthy trees that exhibited uniform growth vigor and normal flowering and fruiting patterns.

Flower buds containing mature anthers before pollen release were selected. Anthers were carefully extracted using tweezers and evenly spread on sulfuric acid paper. The samples were dried under an incandescent lamp for 12 h; an ambient temperature of 25 °C was maintained to promote natural anther dehiscence and pollen dispersal. The collected mature pollen was divided into two portions: one portion was immediately used for viability testing and the other was stored under low-temperature conditions for subsequent scanning electron microscopy observations of pollen morphology. An in vitro germination medium was prepared using 1% agar, 10% sucrose, and 0.01% boric acid (Zhao et al. 2022). Pollen grains were incubated in this medium at 28 °C for 4 h, with three replicates. Pollen counts and germination rates were recorded. To minimize methodological bias, comparative assessments of pollen viability were performed using peroxidase staining (He et al. 2024), acetocarmine staining (Skrzypkowski et al. 2023), and 2,3,5-Triphenyltetrazolium chloride (TTC) staining (Hu et al. 2021). Random sampling and observation were conducted using an Olympus BX-43 microscope (Evident Corp., Tokyo, Japan). For each sample, three random fields were selected for statistical analysis, ensuring ≥50 pollen grains per field. The pollen germination rate (%) was calculated as follows: germination rate (%) = (number of germinated pollen grains/total pollen grains per field) × 100%, where germination was defined as a pollen tube length exceeding twice the pollen grain.

Observations were conducted during the full-bloom stage between early Oct and early Dec 2024. A standardized fixed-branch observation method was used. Healthy secondary branches selected from sun-exposed areas with consistent growth vigor that were free from pests or diseases and exhibited uniform developmental stages were chosen as experimental materials and randomly labeled. For each sample plant, one flowering plant at full bloom was selected from each of the east, west, south, and north orientations. Flowers at identical developmental stages were strictly selected for measurements, with 15 standard flowers collected per plant. The following floral morphological traits were measured using a vernier caliper and stereomicroscope: petal size (length and width); petal count; corolla dimensions; sepal count; androecial length; and style length. Measurements were repeated multiple times, and average values were calculated to ensure data accuracy and reliability.

Branches bearing abundant young buds were hydroponically maintained in the laboratory. Buds were labeled at 2 d before flowering and 1 to 7 d after flowering, with five samples collected daily at fixed intervals. Excised stigmas were placed on concave glass slides, and a reaction mixture (1% benzidine: 3% H_2O_2:H_2O = 4:11:22 v/v/v) was applied. After 2 to 5 min of reaction, bubble formation on the stigma surface was observed and recorded under a stereomicroscope. Stigma receptivity was evaluated based on bubble quantity and diameter, with increased receptivity indicated by a higher bubble count and larger diameters.

Pollen grains were evenly spread on a sample stage coated with conductive adhesive, gold-coated, and observed using a JSM-6380LV scanning electron microscope (JEOL, Tokyo, Japan) at an accelerating voltage of 10 kV. Pollen morphological parameters, including polar axis length (P), equatorial axis length (E), germination furrow length, reticulum ridge width, and germination furrow spacing, were measured using Image J software (National Institutes of Health, Bethesda, MD, USA). Maximum and minimum values were recorded to indicate the variation range, with results expressed as the mean ± standard deviation. Pollen shape was classified as prolate or prolate spheroidal, and pollen size was categorized based on polar axis length into small (10–25 μm), medium (25–50 μm), and large (50–100 μm).

Anthers (20/sample) were vortexed in 1% cellulase (1 mL) to release pollen. The pollen quantity per anther was calculated as follows: (counted grains × 500)/20. Ovaries (n = 10) were dissected to count locules and ovules. Pollen-to-ovule (P/O) ratios were used to determine outcrossing types, with a P/O ratio of 2108 to 195,525 indicating obligate xenogamy (Cruden 1977).

Microsoft Excel 2016 (Microsoft Corporation, Redmond, WA, USA) was used for data processing. Statistical analyses were performed using SPSS 27 software (IBM, Chicago, IL, USA), and a one-way analysis of variance (ANOVA) was applied to assess differences in pollen traits across ploidy levels. Graphs were generated with OriginPro 2024 (OriginLab Corporation, Northampton, MA, USA) and R Studio 4.4.1 (Posit Software PBC, Boston, MA, USA).

Results

Population flowering dynamics. In this study, the flowering periods of four *C. oleifera*

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We declare that these experiments comply with the ethical standards in China.
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Table 1. Flowering times of four cultivars of *C. oleifera*.

Variety	Early flowering stage	Full flowering	Late flowering	Whole flowering stage/days
Minyu 2	10.09–10.21	10.22–11.02	11.15–12.03	55
Minyu 3	10.24–11.05	11.06–11.20	11.21–12.12	49
Qianyu 1	10.02–10.19	10.20–11.05	11.06–11.18	47
Qianyu 2	10.10–10.26	10.27–11.12	11.13–11.22	43

cultivars occurred primarily between early October and mid-December. Among these, 'Qianyu 1' was the earliest-flowering cultivar, with a blooming duration of 47 d, while 'Minyu 3' exhibited the latest flowering period, lasting 49 d, with a 22-d delay in initial flowering compared with 'Qianyu 1'. 'Minyu 2' had the longest flowering duration, with an initial flowering time similar to 'Qianyu 2'. However, 'Qianyu 2' had the shortest blooming period, ending 12 d earlier than the final flowering stage of 'Minyu 2'. Despite variations in individual flowering periods, significant overlap in the collective blooming phases was observed across cultivars (Table 1).

Single-flower development. Individual flowers progressed through five distinct stages over 7 to 8 d (Fig. 1). During the bud stage (before anthesis, 2 d), sepals remained tightly overlapped, stigma secretory activity initiated, and petal bases slightly expanded. The initial opening phase (days 1–2) featured cup-shaped corolla expansion and commencement of anther dehiscence. At full bloom (days 3–4), complete petal expansion, stamen–pistil separation, maximal pollen release (characterized by a golden coloration), and heightened stigma secretion were observed. During subsequent senescence (days 5–6), petal wilting, anther browning, and reduced stigma secretory activity occurred. Finally, the abscission phase (days 7–8) marked complete petal drop, >90% stigma browning, and full senescence of floral organs.

Floral organ morphology. All cultivars were bisexual flowers, including sepals, petals, androecium, and gynoecium. The petals were white, obcordate, ranged from five to eight per flower, and often featured apical notches. The sepals, numbering four to eight per flower, exhibited an ovate–elliptic shape with brown–yellow to yellow–green coloration, pubescent surfaces, and an imbricate arrangement. The androecium consisted of filament–anther complexes fused to the petal bases, while the gynoecium featured a trichome-covered three- to five-locular ovary and styles (three to five branches) extending beyond the height of the filaments. A comparative analysis revealed significant morphological variations among cultivars. 'Minyu 2' exhibited notably wider corollas than those of 'Qianyu 1' ($P < 0.01$) and longer corollas than those of other cultivars ($P < 0.05$). Its style length was shorter than that of 'Qianyu 1' (8.52 mm vs. 9.99 mm; 22.22% difference; $P < 0.01$) but longer than that of 'Minyu 3' ($P < 0.05$) and had longer corollas than those of other cultivars ($P < 0.05$) (Fig. 2).

Stigma receptivity dynamics. Stigma receptivity of the four *C. oleifera* cultivars was assessed using the benzidine–H_2O_2 method spanning from 2 d before anthesis to 7 d postanthesis (DPA) (Fig. 3). All cultivars showed stigma receptivity as early as 2 d before flowering following a unimodal curve, with peak receptivity occurring between 1 and 3 DPA. Receptivity declined significantly by 4 to 5 DPA, coinciding with perianth abscission and filament wilting. Notably, 'Qianyu 1' maintained nonbrowned stigmas until 5 DPA, while other cultivars began stigma browning at this stage. Complete stigma browning (dark brown coloration), desiccation, and stamen abscission were observed by 6 DPA, with receptivity fully lost by 7 DPA. These findings indicate an optimal stigma receptivity window of 1 to 3 DPA across all cultivars, and receptivity progressively declines thereafter.

Pollen morphological traits. Scanning electron microscopy revealed significant pollen morphological variations among cultivars (Fig. 4). All pollen grains were prolate [polar axis/equatorial axis (P/E) ratio: 1.14–1.87]. Based on the size criteria of Kadluczka et al. (2022), 'Minyu 2', 'Minyu 3', and 'Qianyu 2' produced medium-sized pollen (25–50 μm), while 'Qianyu 1' bore larger pollen grains (>50 μm). All pollen exhibited tricolporate apertures with elongated grooves and distinct pore depressions (Tables 2 and 3). 'Minyu 2' displayed the widest intergroove distance (12.85 μm). An exine ornamentation analysis revealed a reticulate–vermiculate pattern across cultivars with intraseries similarities: Minyu cultivars had irregularly shaped lumina and stratified spatial structures, whereas Qianyu cultivars featured predominantly subcircular or oblong lumina of varying sizes (Fig. 4A1–D1). Notably, 'Qianyu 1' showed significantly higher lumina density (1.25 μm) and muri width compared with those of the other cultivars ($P < 0.05$). Morphologically, pollen exhibited a triangular ambitus in the polar view and an oblong equatorial view, with the aperture mid-region protruding during hydration, thus causing a transition from a prolate to a pyramidal shape.

Pollen viability evaluation. Pollen viability was assessed using peroxidase staining, acetocarmine staining, TTC staining, and in vitro germination assays. The in vitro germination method directly reflected pollen viability through observable pollen tube elongation. (Fig. 5C). Using this method, the pollen germination rates of the four *C. oleifera* cultivars were measured as 56.90% ('Minyu 2'), 46.59% ('Minyu 3'), 62.04% ('Qianyu 1'), and 49.25% ('Qianyu 2'). Notably, pollen tube lengths of 'Qianyu 1' and 'Qianyu 2' were significantly greater than those of 'Minyu 2' and 'Minyu 3'

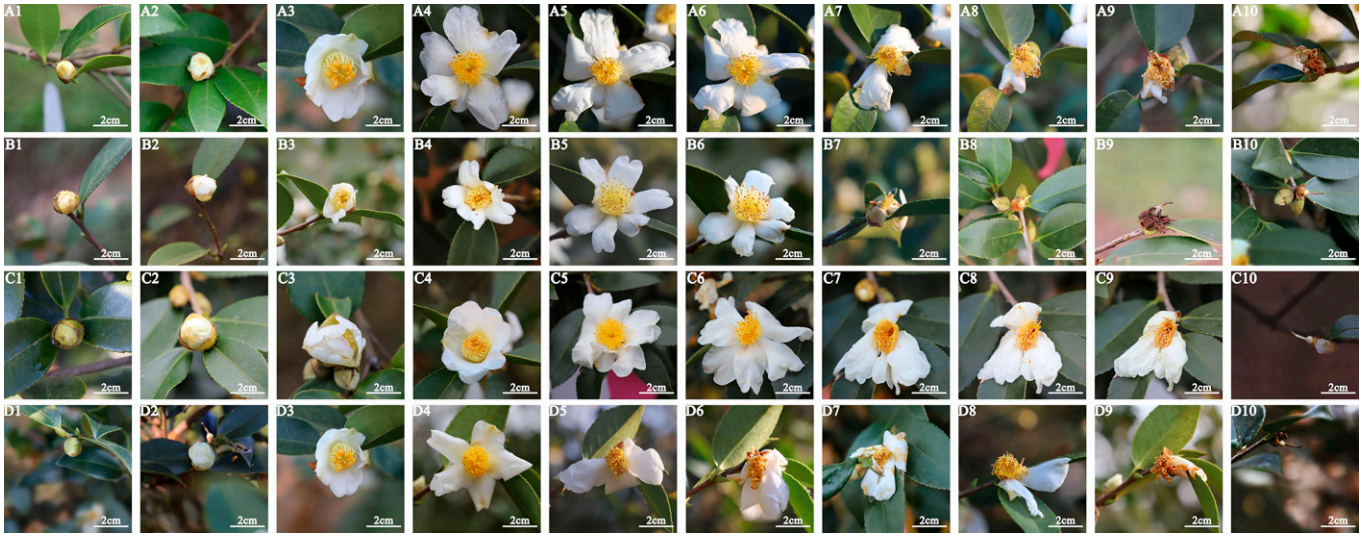

Fig. 1. Floral phenology of four *C. oleifera* cultivars. (**A**) 'Minyu 2', (**B**) 'Minyu 3', (**C**) 'Qianyu 1', and (**D**) 'Qianyu 2'. Developmental stages: 1–2: 1–2 d before anthesis (DBA); 3: anthesis day (0 DPA); 4–10: 1–7 d postanthesis (DPA).

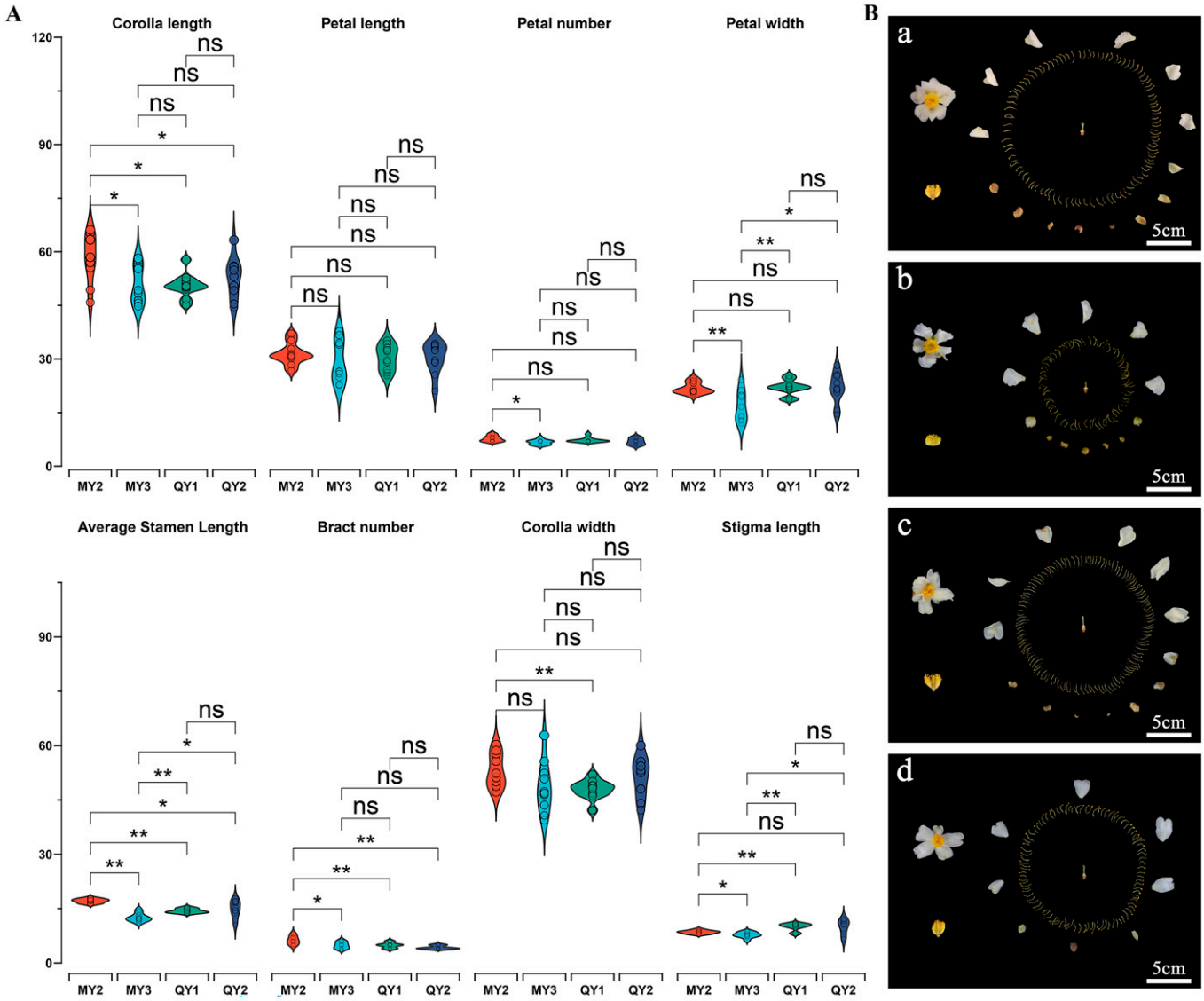

Fig. 2. Comparative analysis of floral characteristics of four *C. oleifera* cultivars. (**A**) Violin plot illustrates the differences in floral organs among four cultivars. MY2 = 'Minyu 2'; MY3 = 'Minyu 3'; QY1 = 'Qianyu 1'; QY2 = 'Qianyu 2'. Significance levels: $*P < 0.05$, $**P < 0.01$, ns (not significant). (**B**) Representative floral morphology. (**A**) 'Minyu 2', (**B**) 'Minyu 3', (**C**) 'Qianyu 1', and (**D**) 'Qianyu 2'. Scale bar: 5 cm.

($P < 0.05$). However, the in vitro germination method exhibited high sensitivity to environmental conditions, with results prone to bias because of operational interference. In contrast, acetocarmine staining and peroxidase staining yielded significantly higher germination rates than the in vitro method ($P < 0.05$) (Fig. 5A), which did not align with actual viability. For TTC staining, active pollen cells showed red formazan deposits caused by mitochondrial dehydrogenase activity. Viability was determined by color intensity; deep or light red indicated viable pollen and yellow indicated nonviable pollen (Fig. 5B). The germination rates measured by TTC staining did not differ significantly from those observed with the in vitro method. Furthermore, the TTC method proved to be rapid, simple, and reliable, making it the preferred approach for pollen viability assessment.

P/O ratio of C. oleifera. Cruden's method calculated mean P/O ratios of 43,992 ('Minyu 2'), 55,501 ('Minyu 3'), 42,200 ('Qianyu 1'), and 68,550 ('Qianyu 2') using 20 flowers per cultivar (Table 4). All values were within the obligate xenogamy range (2108–195,525), indicating pollinator-dependent outcrossing systems.

OCI of C. oleifera. The OCI was evaluated for each cultivar according to criteria reported by Dafni (1994) and considering three parameters: (1) flower diameter (>6 mm; scored as 3); (2) protogyny, characterized by stigma maturation preceding anther dehiscence (scored as 0); and (3) spatial separation of reproductive organs, with anthers positioned above stigmas at anthesis (scored as 1). A cumulative OCI value of 4 confirmed obligate outcrossing reproductive characteristics relying on pollinator-mediated fertilization (Table 5).

Discussion

Flowering plays a pivotal role in plant reproduction and evolution, marking a crucial transition from juvenile to adult and from vegetative to reproductive stages (Teotia and Tang 2015). A comprehensive understanding of flowering biology is essential for studying plant life cycles as well as for conserving, using, and breeding germplasm resources (Wan et al. 2024). Plant flowering phenology generally follows two distinct patterns: the mass-flowering pattern, characterized by synchronized, intensive blooming across a population over a short period (e.g., a single day or week), and the sequential-flowering pattern, with individuals flowering intermittently over extended periods and lower frequencies of blooming (every few days or weeks) (Augspurger 1983). In this study, the four *C. oleifera* cultivars exhibited clustered flowering periods, aligning with the mass-flowering pattern. Based on the classification reported by Wang (2011), 'Qianyu 1', 'Qianyu 2', and 'Minyu 2' were categorized as early-flowering types, while 'Minyu 3' was classified as mid-flowering. The significant

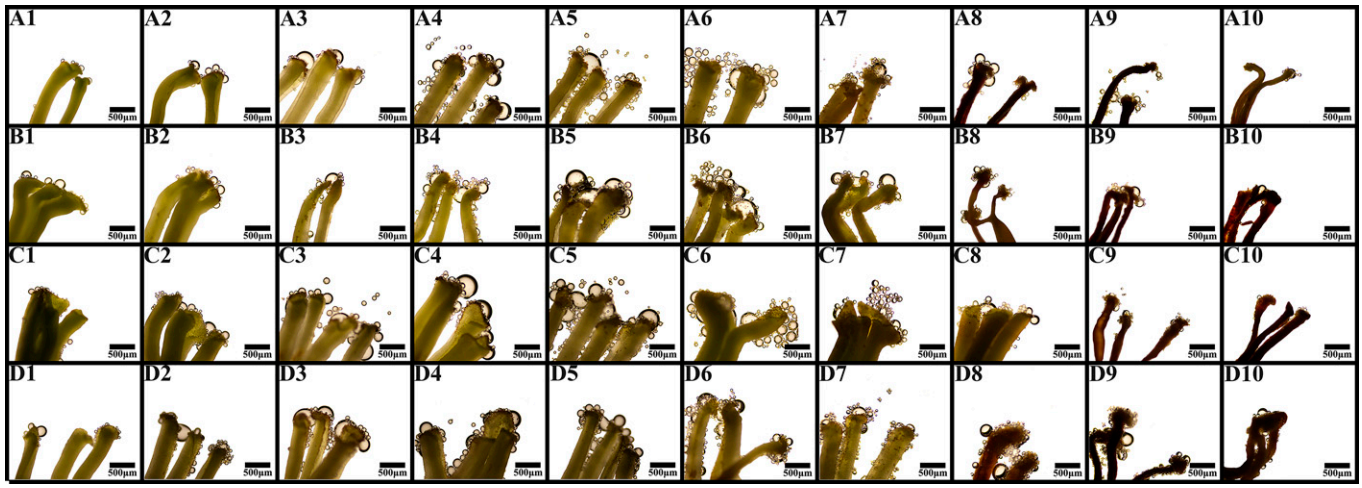

Fig. 3. Stigma receptivity of four *C. oleifera* cultivars assessed by the benzidine–H_2O_2 method. (**A**, **B**, **C**, and **D**) 'Minyu 2', 'Minyu 3', 'Qianyu 1', and 'Qianyu 2'. Developmental stages: 1–2: 1–2 d before anthesis (DBA); 3: anthesis day (0 DPA); 4–10: 1–7 d postanthesis (DPA).

overlap in blooming periods across the cultivars suggests that synchronized flowering may be an adaptive reproductive strategy to enhance pollination success under low-temperature conditions in winter. Furthermore, an analysis of individual flower dynamics showed that the blooming duration for all cultivars ranged from 6 to 7 d, consistent with findings by Liu (2023). These results offer a theoretical foundation and practical guidance for future research of flowering regulation, artificial pollination, and the development of new cultivars with optimized flowering traits.

Floral morphology directly influences pollination efficiency and reproductive fitness (La Rosa and Conner 2017), with pollinators often prioritizing corolla size over subtle shape variations (Kaczorowski et al. 2012). According to Abe (2006), flowers with diameters exceeding 27.86 mm in diameter significantly attract pollinators through enhanced visual signals, thereby increasing outcrossing rates. The observed corolla diameters in this study met this threshold (29.22–31.45 mm), suggesting morphological adaptations that increase with pollinator visitation frequency or duration. These conclusions are based on single-year (2024) observations. Future studies should integrate multiyear phenological monitoring and environmental correlation analyses to further understand flowering plasticity and climate response mechanisms.

Stigma receptivity represents a critical temporal window for plant female reproductive success, typically lasting hours to days, and directly influences pollen adhesion, germination, and fertilization efficiency (Ferreira et al. 2021; Kumari et al. 2021). This study found that stigmas of all four *C. oleifera* cultivars (Minyu 2, Minyu 3, Qianyu 1, and Qianyu 2) became receptive as early as 2 d before anthesis, consistent with the findings by Xie (2015). Protogynous maturation, where stigmas mature before anthers, likely reduces self-pollination by temporal isolation, thereby

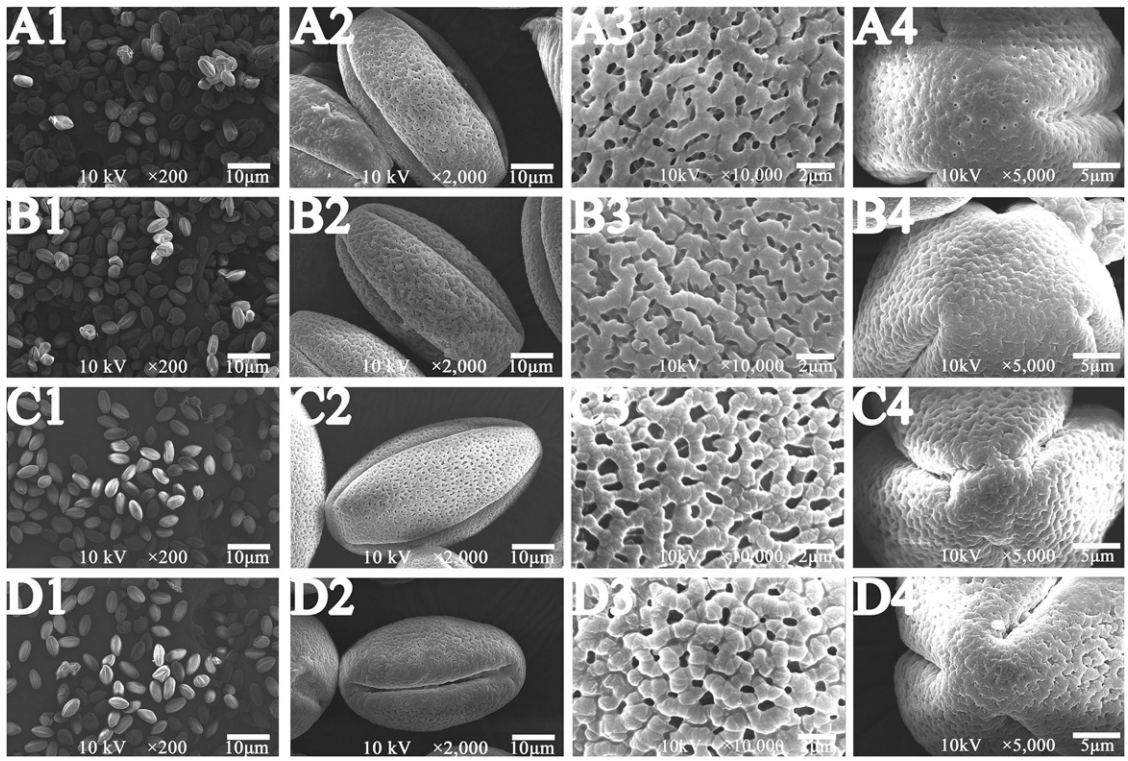

Fig. 4. Observation of pollen morphology of four *C. oleifera* cultivars by scanning electron microscopy. (**A–D**) 'Minyu 2', 'Minyu 3', 'Qianyu 1', and 'Qianyu 2', respectively. 1–4 indicate the group view, outer wall decoration, equatorial view, and polar view of pollen, respectively.

Table 2. Pollen shape categories of *C. oleifera* genotypes.

Variety	Pollen shape	Outer wall decoration	Shape of germination pores	Polar view	Equatorial view	Pollen size (polar axis × equatorial axis)/μm^2
Minyu 2	Prolate	Regulate–foveolate	Tricolporate	Trilete rounded	Oblong	48.25 (54.79–45.75) × 28.14 (27.34–31.18)
Minyu 3	Prolate	Regulate–foveolate	Tricolporate	Trilete rounded	Oblong	27.37 (26.27–28.90) × 49.96 (54.67–45.70)
Qianyu 1	Prolate	Regulate–foveolate	Tricolporate	Trilete rounded	Oblong	28.60 (55.19–51.34) × 48.40 (29.65–26.23)
Qianyu 2	Prolate	Regulate–foveolate	Tricolporate	Trilete rounded	Oblong	29.76 (49.77–43.11) × 46.87 (32.42–26.72)

Table 3. Quantitative traits of pollen grains among *C. oleifera* genotypes.

Cultivar	Mesh ridge width/μm	Distance between colporates/μm	Length of germination colpus/μm	Length of polar axis/μm	Length of equator axis/μm	P/E
Minyu 2	0.70 ± 0.11 b	12.85 ± 0.42 a	43.90 ± 0.66 b	48.47 ± 0.65 bc	28.06 ± 0.41 bc	1.73 ± 0.04 b
Minyu 3	0.70 ± 0.11 b	12.66 ± 0.71 a	44.27 ± 1.12 b	50.33 ± 0.95 b	27.38 ± 0.22 c	1.84 ± 0.03 a
Qianyu 1	1.16 ± 0.19 a	10.19 ± 0.25 b	48.55 ± 0.44 a	53.58 ± 0.31 a	28.64 ± 0.31 ab	1.87 ± 0.01 a
Qianyu 2	0.56 ± 0.06 b	7.73 ± 0.26 c	42.77 ± 0.89 b	47.12 ± 0.86 c	29.67 ± 0.51 a	1.59 ± 0.04 c

Different lowercase letters within a column indicate significant differences at $P < 0.05$ by Duncan's multiple range test.
P/E = polar axis/equatorial axis.

enhancing outcrossing opportunities (Wada and Uemura 2000; Wang and Ding 2012). Postpollination stigma browning, as observed in this study, may reflect cellular senescence or oxidative stress induced by pollen–pistil interactions (Lankinen et al. 2006), which aligns with rapid floral senescence patterns that reduce reproductive investment after fertilization (Herrero and Arbeloa 1989). Benzidine–H_2O_2 assays identified peak receptivity between 1 and 3 DPA, with complete receptivity loss occurring by 6 to 7 DPA. These findings corroborate those of reports of *C. osmantha* (Lü 2023) and *C. gauchowensis* (Zhu 2017), but they contrast with those of studies of semi-wild *C. yunnanensis* (Li et al. 2012) and wild *C. hunanensis* (Deng et al. 2009), suggesting habitat-driven adaptive divergence among cultivars.

Pollen, a key carrier of genetic information in angiosperms (Hu and Gao 2022; Hu et al. 2021), is primarily influenced by its intrinsic genetic composition (Boavida et al. 2005), with distinct morphological recognition features observed across species. To date, over 70 *Camellia* species have been studied with a focus on sections such as *Camellia* sect. *Chrysantha* (Shi et al. 2022; Tan et al. 2016), sect. *Camellia* (Wei et al. 2012; Yin et al. 2024), and sect. *Theopsis* and *Eriandria* (Wu et al. 2023; Zhang et al. 2023). In this study, the P/E ratios of the four *C. oleifera* cultivars ranged from 1.14 to

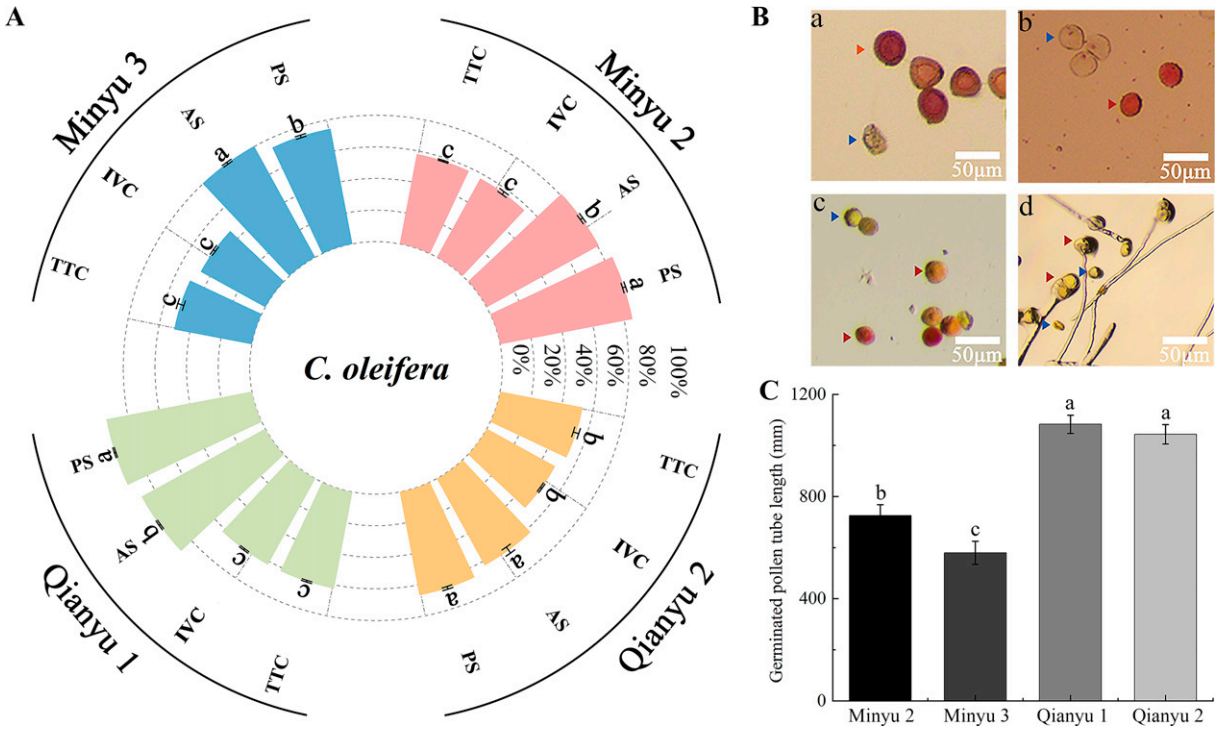

Fig. 5. Pollen viability assessment of four *C. oleifera* cultivars using multiple detection methods. (**A**) Comparative analysis of four detection methods: AS = acetocarmine staining; IVG = in vitro germination; PS = peroxidase staining; TTC = 2,3,5-Triphenyltetrazolium chloride. Different lowercase letters above columns indicate statistically significant differences ($P < 0.05$, Duncan's test). (**A**) Peroxidase staining. (**B**) Acetocarmine staining. (**C**) 2,3,5-Triphenyltetrazolium chloride. (**D**) In vitro germination. Viable pollen grains (red arrows) and nonviable pollen grains (blue arrows) are shown. Scale bars: 50 μm. (**C**) Pollen tube growth after 4 h in vitro culture. Data represent mean ± standard error.

Table 4. P/O of four *C. oleifera* cultivars based on Cruden's method.

Cultivar	Replicate 1	Replicate 2	Replicate 3	Avg	Pollen grains per flower	P/O ratio
Minyu 2	6233	8633	9267	8044	844,655	43992
Minyu 3	5733	6900	8933	7189	754,810	55501
Qianyu 1	6300	6967	7833	7033	738,500	42200
Qianyu 2	10,367	11,133	11,600	11,033	1,158,500	68550

P/O = pollen-to-ovule.

1.87, all classified as prolate, in line with previous reports of other *C. oleifera* cultivars (Xie 2016), confirming that prolate morphology is a characteristic feature of *Camellia* pollen. This further confirms that prolate morphology is a typical characteristic of *Camellia* pollen. Considerable interspecific variation in pollen exine ornamentation exists within *Camellia* (Xiao et al. 2024; Zavada and Wei 1993), thus serving as a key morphological marker for species classification and cultivar identification (Wang et al. 2010). Previous studies have emphasized the taxonomic importance of exine patterns among *Camellia* species (Xiao et al. 2024). In the current study, all four *C. oleifera* cultivars exhibited rugulate–foveolate exine ornamentation, consistent with the typical features of *Camellia* pollen (Li 2011). Notably, significant similarity in ornamentation was observed within cultivar groups; 'Minyu 2' and 'Minyu 3' shared comparable patterns, as did 'Qianyu 1' and 'Qianyu 2', suggesting convergent evolution these lineages. These findings align with those of Deng et al. (2020), who observed similar exine patterns between 'Changlin 4' and 'Changlin 18', as well as between 'Ganzhouyou 8' and 'Ganzhouyou 6'. Despite the shared macromorphological traits (e.g., size and shape) among the four *C. oleifera* cultivars, which suggest close phylogenetic relationships, palynological evidence alone is insufficient to fully resolve their systematic affiliations. Future research should integrate floral anatomy, molecular markers, and multidisciplinary approaches to further clarify their evolutionary trajectories and taxonomic status.

A pollen viability assessment is essential for hybrid breeding, influencing parental selection, artificial pollination, and the understanding of plant reproductive mechanisms (Althiab-Almasaud et al. 2024). Among the various viability assays, the in vitro germination method provides a direct indication of actual pollen vitality, while staining methods can yield biased results because of species-specific differences in pollen biochemical composition and reaction mechanisms. Both acetocarmine and peroxidase staining resulted in significantly higher germination rates than the in vitro method ($P < 0.05$), likely because of nonspecific staining of cellular contents, which causes false-positive results. Therefore, these methods are unsuitable for accurate viability assessments of *C. oleifera* pollen. In contrast, TTC staining, which evaluates viability through mitochondrial dehydrogenase activity, showed results closely aligned with those from the in vitro germination method, with only a slight upward trend. This finding corroborates studies by Wang et al. (2012) of *C. oleifera* cultivars Ma 1 and Ma 3 as well as by Liao et al. (2021) on three *Camellia* species, affirming TTC staining as a rapid and reliable method for pollen viability screening. Additionally, the P/O ratio serves as a predictor of angiosperm mating systems (Burd 2025), reflecting pollination dynamics and seed yield potential (Harder and Johnson 2023). In this study, the P/O ratios and OCI for the four *C. oleifera* cultivars indicated obligate outcrossing, confirming self-incompatibility. These results are consistent with findings by Ma et al. (2023) and Chang et al. (2023). However, while P/O and OCI values suggested outcrossing traits, controlled bagging experiments were not conducted to validate the reproductive characteristics. Future research should include pollination biology experiments to further confirm reproductive characteristics.

Conclusions

This research systematically examined the floral biological characteristics and reproductive characteristics traits of four superior *C. oleifera* cultivars from the northeastern Guizhou region. Through a comprehensive analysis of flowering phenology, floral organ development, and pollination biology, the optimal pollination window (1–3 DPA) for these cultivars was identified. These findings provide essential references for promoting elite cultivars and optimizing high-yield cultivation practices in northeastern Guizhou and offer valuable insights for improving the quality and productivity of the regional oil-tea *Camellia* industry.

Table 5. OCI values of four *C. oleifera* varieties based on Dafni's method.

Cultivars	Flower diam	Maturation timing of stigma and anther	Spatial relationship between stigma and anther	OCI value
Minyu 2	3	0	1	4
Minyu 3	3	0	1	4
Qianyu 1	3	0	1	4
Qianyu 2	3	0	1	4

OCI = outcrossing indices.

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