Phenotypic Traits and SSR Molecular Identification of Zhejiang × Guangning Camellia chekiangoleosa Hybrid Progeny Postprint

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Abstract

Camellia chekiangoleosa exhibits high seed kernel oil content and oleic acid content, while Camellia semiserrata demonstrates strong growth vigor and resistance. To utilize the advantages of both Camellia species and breed superior germplasm materials, this study conducted phenotypic trait analysis on 45 F1 hybrid progeny of C. chekiangoleosa × C. semiserrata to understand the phenotypic characteristics of the hybrid progeny, while simultaneously employing SSR markers for hybrid authenticity identification and screening SSR markers applicable for Camellia hybrid progeny identification. The results indicated: (1) The F1 progeny of C. chekiangoleosa × C. semiserrata exhibited tall tree stature and rapid growth, with leaf veins, sepals, and stigmas tending toward the paternal traits of C. semiserrata, whereas flower and leaf morphology traits were similar to the maternal parent C. chekiangoleosa, and characteristics such as leaf color and size were intermediate between both parents. (2) Eight fully complementary markers capable of distinguishing both parents and clarifying progeny origin were selected from 32 SSR markers for hybrid progeny identification, among which seven markers achieved 100% hybrid identification efficiency and one marker showed 55.56% identification efficiency; the eight markers complementarily identified all 45 hybrid progeny as true hybrids. (3) Validation of the identification capability of these eight SSR markers on hybrid progeny demonstrated that utilizing these SSR markers for authenticity identification of Camellia hybrid progeny is feasible. This study provides a reference for interspecific hybrid breeding of Camellia and also establishes a foundation for subsequent SSR marker identification of interspecific hybrid progeny in Camellia.

Full Text

Phenotypic Traits and SSR Molecular Identification of Hybrid Progenies of *Camellia chekiangoleosa* × *C. semiserrata*

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Abstract: *Camellia chekiangoleosa* exhibits high kernel oil content and oleic acid levels, while *Camellia semiserrata* demonstrates strong growth vigor and stress resistance. To combine these desirable traits and cultivate superior germplasm, we analyzed the phenotypic characteristics of 45 F_1 hybrid progenies from a cross between *C. chekiangoleosa* and *C. semiserrata*, and employed SSR markers for hybrid authenticity verification and marker screening. The results revealed: (1) The F_1 hybrids displayed tall stature and rapid growth, with leaf veins, sepals, and stigmas tending toward the paternal *C. semiserrata* phenotype, while floral and leaf morphology approximated the maternal *C. chekiangoleosa* characteristics. Leaf color and size were intermediate between the parents. (2) From 32 SSR markers, we identified eight fully complementary markers capable of distinguishing both parents and tracing progeny origin. Seven markers achieved 100% hybrid identification efficiency, while one marker showed 55.56% efficiency. Combined analysis with all eight markers confirmed all 45 progenies as true hybrids. (3) Validation of these eight SSR markers demonstrated their feasibility for authenticating oil-tea camellia hybrids. This study provides a reference for interspecific hybrid breeding in oil-tea camellia and establishes a foundation for future SSR-based identification of hybrid progenies.

Keywords: *Camellia chekiangoleosa*, hybrid identification, SSR markers, phenotypic traits, cross breeding

Oil-tea camellia refers to woody oil crops in the family Theaceae with high oil value. Camellia oil is rich in beneficial oleic acid, linoleic acid, tocopherols, and squalene, making it a high-quality functional edible oil [?, ?, ?, ?]. *Camellia chekiangoleosa* and *C. semiserrata* are major cultivated varieties within this group [?, ?]. *C. chekiangoleosa*, also known as Zhejiang red camellia, prefers cool summers and cold winters, showing poor heat tolerance. It is primarily distributed in mountainous regions of Jiangxi, Zhejiang, Hunan, Hubei, and southern Anhui at elevations of 600–1,400 m. *C. semiserrata*, or Nanshan tea, favors warm, humid conditions with partial shade and exhibits robust growth, mainly occurring in Guangdong and Guangxi provinces.

Compared with other *Camellia* species, red camellias possess significant advantages in both fatty acid content and nutritional value. *C. chekiangoleosa* particularly stands out, with average oleic acid content exceeding 80% and kernel oil content surpassing 60%, substantially higher than common oil-tea camellia (approximately 40%) [?, ?, ?, ?]. Since kernel oil content and oleic acid level are critical indicators of yield and quality, and their relative contents remain stable across harvest periods, *C. chekiangoleosa* represents excellent germplasm for high oil content and quality [?, ?, ?].

Hybrid breeding offers a cost-effective approach with broad segregation of traits in progeny, enabling the combination of desirable parental characteristics and serving as an important pathway for developing new oil-tea camellia varieties [?, ?]. Therefore, crossing the oil-quality elite *C. chekiangoleosa* with the vigorous and resistant *C. semiserrata* holds promise for producing high-yield hybrid progenies with superior comprehensive traits. Previous studies indicate that interspecific hybrids in oil-tea camellia typically exhibit intermediate traits with tendencies toward one parent [?, ?]. Yang et al. (2004) found that crosses using *C. chekiangoleosa* as the female parent with other *Camellia* species yielded the highest seed set rates, particularly in the *C. chekiangoleosa* × *C. semiserrata* combination. However, detailed characterization of the phenotypic traits of this specific hybrid combination remains unreported.

Oil-tea camellia is an insect-pollinated, outcrossing species with high genetic heterozygosity, presenting challenges such as long breeding cycles and potential contamination during hybridization that may produce false F_1 progeny. Some scholars propose that *C. chekiangoleosa* represents a transitional species in the evolution from *C. polyodonta* or *C. semiserrata* to the cultivated camellia group, or a crucial intermediate in the evolution from *C. semiserrata* to *C. hongkongensis* [?, ?]. This may explain the weak reproductive isolation between *C. chekiangoleosa* and its close relatives like *C. semiserrata* under natural conditions, resulting in spontaneous hybridization [?, ?]. Additionally, artificial hybridization may suffer from foreign pollen contamination, making verification of F_1 authenticity essential for subsequent genetic mapping and progeny testing [?, ?]. Early identification of hybrid progenies can improve breeding efficiency and reduce costs.

Progeny identification methods primarily include morphological characterization, chromosome counting, fluorescence in situ hybridization (FISH), and molecular markers. Morphological assessment, while intuitive and convenient, suffers from long identification periods, observer subjectivity, and environmental influences that compromise accuracy [?, ?, ?]. Cytological methods like FISH and chromosome counting offer high efficiency but are complex and labor-intensive. Molecular marker identification provides high efficiency, simplicity, and independence from environmental and developmental conditions while enabling genotype determination and revealing genetic differences between progeny and parents at the genomic level [?, ?, ?, ?]. Among molecular markers, simple sequence repeats (SSR) have been widely applied in hybrid identification for tea [?, ?], Shatian pomelo [?, ?], and chrysanthemum [?, ?] due to their co-dominance, reproducibility, reliability, and operational simplicity. However, studies on hybrid progeny identification in oil-tea camellia are scarce because hybrid populations are difficult to obtain. Only limited reports exist in related *Camellia* species: Xu et al. (2009) used five SSR markers from chloroplast DNA, rDNA internal transcribed spacers, and nuclear genome to identify six hybrids of *C. nitidissima* × *C. japonica* and *C. nitidissima* × *C. sasanqua*, achieving 83.33% identification efficiency.

This study focuses on molecular breeding and variety identification in oil-tea camellia. Using *C. chekiangoleosa* as the female parent and *C. semiserrata* as the male parent, we obtained 45 F_1 progenies through artificial hybridization. By phenotyping the hybrids and screening SSR markers for identification, we addressed three questions: (1) whether the hybrid progenies of *C. chekiangoleosa* × *C. semiserrata* tend toward the paternal, maternal, or intermediate phenotype; (2) whether specific SSR markers suitable for interspecific hybrid identification in oil-tea camellia can be obtained; and (3) whether SSR markers can authenticate the hybrids and what identification efficiency can be achieved. Our results provide a reference for interspecific hybrid breeding in oil-tea camellia and establish a foundation for future SSR-based identification of hybrid progenies.

1.1 Experimental Materials and DNA Extraction

We obtained 45 F_1 progenies from a conventional cross using *C. semiserrata* as the male parent and *C. chekiangoleosa* as the female parent. The five-year-old seedlings were planted at the experimental base of Jiangxi Academy of Forestry. For each sample, 3–5 young leaves were collected and stored at -80°C. DNA was extracted using a modified CTAB method [?, ?], and quality was assessed via 1% agarose gel electrophoresis. Concentration and purity were measured using a Nanodrop 2000 (Thermo Scientific, USA). DNA was diluted to 100 $\text{ng} \cdot \text{L}^{-1}$ and stored at -20°C for subsequent use.

1.2 SSR Primer Design and PCR Amplification

SSR primers were designed based on the full-length transcriptome sequence of *C. chekiangoleosa* using Primer 3.0 software. The PCR amplification system (10 µL) contained: 1.0 µL 10×Buffer, 1.0 µL Mg^{2+} (25 $\text{mmol} \cdot \text{L}^{-1}$), 1.0 µL dNTPs (10 $\text{mmol} \cdot \text{L}^{-1}$), 0.4 µL each of 10 $\mu\text{mol} \cdot \text{L}^{-1}$ forward and reverse primers, 0.1 µL Taq polymerase (5 $\text{U} \cdot \text{L}^{-1}$), 0.5 µL DNA template (100 $\text{ng} \cdot \text{L}^{-1}$), and sterile ddH_2O to a final volume of 10 µL. The PCR program consisted of: initial denaturation at 94°C for 5 min; 25 cycles of 94°C for 30 s, 57–60°C (primer-dependent) for 30 s, and 72°C for 30 s; final extension at 72°C for 1 min; and storage at 4°C. Amplification products were separated on 8% polyacrylamide gels at 150 V for 90 min, silver-stained, and photographed.

1.3 Primer Screening and Reliability Verification

Initial PCR screening identified 32 markers with clear bands and good polymorphism. These were further screened using both parents and six hybrid progenies (Nos. 10, 12, 13, 28, 33, and 40) to select SSR markers capable of distinguishing parents and determining progeny origin for subsequent analysis of all 45 F_1 progenies. To ensure reliability of hybrid identification results, three *C. semiserrata* individuals (non-paternal) and three *C. chekiangoleosa* individuals (non-maternal) were used to validate SSR markers with low identification rates. Parental and hybrid alleles were designated with letters A, B, C, and D.

2.1 Phenotypic Traits of Hybrid Progenies

The F_1 hybrids of *C. chekiangoleosa* × *C. semiserrata* exhibited intermediate phenotypes between the parents. Overall, they displayed tall tree stature and rapid growth, tending toward the paternal *C. semiserrata* phenotype (Table 1 , Figure 1 [Figure 1: see original paper]). The hybrids had smooth, hairless branches and petioles, with gray-white old branches and red new shoots. Leaves were greenish-yellow, thinly leathery, elliptic or oblong-elliptic, with approximately eight pairs of distinct lateral veins and serrations along three-quarters of the margin. Flowering occurred in the fourth year after planting, with terminal solitary red flowers 7–8 cm in diameter, 7–8 petals, and 5-lobed, medium-split stigmas. Bracts and sepals were yellow-green and hairy initially, later turning light brown with persistent pubescence, numbering 9–10 and remaining persistent.

2.2 Screening of SSR Primers for Hybrid Progeny Identification

All 32 primer pairs amplified successfully in both parents and six hybrid progenies (Nos. 10, 12, 13, 28, 33, and 40), with 20 pairs showing polymorphism between parents (62.5% polymorphism rate). Eight SSR primer pairs with clear, co-dominant amplification patterns were selected for identifying all 45 hybrid progenies. Detailed primer information is provided in Table 2 .

2.3 SSR Molecular Identification of Hybrid Progenies

As co-dominant markers, SSR loci in diploid materials enable hybrid authentication based on F_1 genotypes. Progeny displaying both parental characteristic bands or paternal-specific bands were classified as true hybrids, while those showing only maternal bands without paternal bands were deemed false hybrids [?, ?]. Analysis of 45 F_1 progenies using eight SSR primer pairs revealed all were true hybrids, with individual primer identification efficiencies ranging from 55.56% to 100% (Table 3). Primers CC_{eSSR152}, CC_{eSSR174}, and CC_{eSSR296} amplified two alleles in parents, showing homozygous complementary genotypes (AA×BB). All F_1 progenies exhibited AB genotypes, identifying 45 true hybrids with 100% efficiency—the most intuitive and effective approach. Primers CC_{eSSR162}, CC_{eSSR165}, CC_{eSSR171}, CC_{eSSR270}, and CC_{eSSR292} showed parental complementary genotypes. Among them, CC_{eSSR165} (AB×CC), CC_{eSSR171} (AA×BC), CC_{eSSR270} (CC×AB), and CC_{eSSR292} (AA×BC) amplified three alleles, while CC_{eSSR162} (AB×CD) amplified four alleles. Primers CC_{eSSR162}, CC_{eSSR165}, CC_{eSSR171}, and CC_{eSSR270} all produced progeny bands with both parental characteristics, achieving 100% identification efficiency. For primer CC_{eSSR292}, 25 F_1 progenies showed AB or AC genotypes, inheriting one allele from each parent (paternal AA, maternal BC), confirming them as true hybrids. The remaining 20 samples exhibited BB or CC genotypes, inheriting only maternal alleles without paternal contribution, and were classified as false progeny, yielding an identification efficiency of 55.56% (Table 3).

2.4 Verification of Hybrid Progeny Identification Results

To validate the identification results from primer CC_{eSSR292}, three non-paternal *C. semiserrata* individuals (G1, G2, G3) and three non-maternal *C. chekiangoleosa* individuals (Z1, Z2, Z3) were analyzed. As shown in Figure 3a [Figure 3: see original paper], true hybrids amplified by CC_{eSSR292} displayed heterozygous genotypes, perfectly inheriting one allele from each parent. In contrast, the six non-hybrid individuals in Figure 3b [Figure 3: see original paper] did not inherit parental alleles but instead showed novel alleles, confirming them as false hybrids. This demonstrates the reliability of CC_{eSSR292} for hybrid identification.

3.1 Phenotypic Analysis of Hybrid Progenies

Hybrid breeding aims to combine superior parental traits in progeny and represents a crucial approach for developing new oil-tea camellia varieties. In this study, we performed artificial hybridization using *C. chekiangoleosa* × *C. semiserrata*, selecting a maternal *C. chekiangoleosa* (GHY26) elite line characterized by high linoleic acid content (7.31%) and high fruit yield (average crown projection yield of 2.12 kg/m^2) [**?**, **?**], with the goal of breeding new high-yield oil-tea camellia varieties combining both parental advantages.

Previous studies using *C. chekiangoleosa* as the maternal parent reported progeny phenotypes biased toward maternal characteristics. For example, Wang et al. (2020) observed that hybrids between *C. chekiangoleosa* and *C. reticulata* largely inherited maternal traits in flowering, branch/leaf morphology, and tree growth. Similarly, Gao et al. (2016) found that *C. chekiangoleosa* × *C. azalea* hybrids showed maternal bias in petal number and floral form. In contrast, our F_1 hybrids resembled the maternal parent in floral and leaf morphology, while leaf color and size were intermediate, and leaf veins, sepals, stigmas, and growth vigor were more similar to the paternal *C. semiserrata*.

These findings differ from previous reports and demonstrate that our F_1 hybrids effectively combined parental advantages, with the paternal *C. semiserrata* exerting substantial phenotypic influence. This provides a basis for future breeding strategies leveraging paternal traits in *C. chekiangoleosa* hybrid variety development. The inheritance patterns for fruit yield and linoleic acid content require further investigation.

3.2 Screening of SSR Primers for Hybrid Progeny Identification

C. chekiangoleosa shows phenotypic similarity to *C. semiserrata*, *C. crassissima*, and *C. lucidissima* within the same section, with considerable intraspecific phenotypic variation, particularly in leaf morphology, making authenticity assessment based solely on morphological traits challenging [**?**, **?**]. Additionally, *C. chekiangoleosa* exhibits self-incompatibility and long-term outcrossing, resulting in highly heterozygous genetic backgrounds. Therefore, appropriate and effective co-dominant markers are essential to avoid misidentification. Researchers have noted varying identification capabilities among SSR markers, with homozygous markers generally showing higher efficiency than heterozygous ones, sometimes enabling complete progeny identification with a single marker [**?**, **?**]. Zhou et al. (2017) categorized SSR markers in rose hybrid progenies into three types: homozygous dominant AA×BB markers achieving 100% efficiency; AB×CC, AA×BC, and AB×CD markers with slightly lower efficiency; and least effective types like AA×AB, AB×BB, and AB×AC. Subsequently, Yin et al. (2019) classified nine SSR markers in apple hybrids into fully complementary (AA×BB, AB×CD, AB×CC) and incompletely complementary (AA×AB, AB×BC) types, with the former showing high efficiency and the latter requiring further validation. These studies consistently indicate that AA×BB, AB×CC, AA×BC, and AB×CD marker types have high theoretical identification rates, with AA×BB and AB×CD being most effective. In our study, all eight SSR markers used for oil-tea camellia hybrid identification were fully complementary types. CC_{eSSR152}, CC_{eSSR174}, and CC_{eSSR296} (AA×BB type) and CC_{eSSR162} (AB×CD type) achieved 100% identification efficiency, consistent with previous reports. Notably, CC_{eSSR165} (AB×CC), CC_{eSSR171} (AA×BC), and CC_{eSSR270} (CC×AB) also reached 100% efficiency, indicating a broad range of effective SSR primers for oil-tea camellia hybrid identification, which will benefit future studies on other species.

3.3 Analysis of SSR Marker Capability for Hybrid Progeny Identification

Han et al. (2010) suggested that at least five paternal-specific markers are required to identify 97% of true hybrids for heterozygous dominant markers. We screened eight high-efficiency markers from 32 SSR loci, seven of which individually identified all hybrid progenies in a single assay, demonstrating high screening and identification efficiency. Besides ensuring maximal accuracy, workload considerations are crucial in hybrid authenticity assessment. Lei et al. (2021) selected three markers from 32 SSR loci to identify two tea hybrid populations (Fuding Dabaicha × Baojing Huangjincha 1 and Anhui 1 × Baojing Huangjincha 1), achieving 85.42% and 79.55% identification rates, respectively. Yin et al. (2019) identified 225 true hybrids from 35 SSR markers in a 'Jiguan' × 'Fuji' apple F_1 population, with 93% identification efficiency. Li et al. (2021) successfully authenticated 35 rubber tree hybrids using only three polymorphic SSR markers, all with high identification efficiency. In this study, we used eight co-dominant markers to authenticate 45 F_1 progenies of *C. chekiangoleosa* × *C. semiserrata*. Seven markers (CC_{eSSR152}, CC_{eSSR162}, CC_{eSSR165}, CC_{eSSR171}, CC_{eSSR174}, CC_{eSSR270}, and CC_{eSSR296}) achieved 100% identification efficiency, while CC_{eSSR292} showed 55.56% efficiency. Combined analysis confirmed all 45 F_1 progenies as true hybrids. Thus, our selected SSR markers are fully applicable for oil-tea camellia hybrid identification, and reliability validation further supports the utility of SSR markers for this purpose.

References

DONG L, LI T, HUANG WY, et al., 2021. Selection and comprehensive evaluation of superior individual plant in *Camellia chekiangoleosa* [J]. Journal of Central South University of Forestry & Technology, 41(11):35-45. [Dong L, Li T, Huang WY, et al., 2021. Selection and comprehensive evaluation of superior individual plants in *Camellia chekiangoleosa* [J]. Journal of Central South University of Forestry & Technology, 41(11):35-45.]

DRIDI J, FENDRI M, BRETON CM, et al., 2018. Characterization of olive progenies derived from a Tunisian breeding program by morphological traits and SSR markers [J]. *Sci Hort-Amsterdam*, 236:127-136.

GAO JY, LIU XK, ZHAO QM. 2016. *Illustrations of the new camellia hybrids that bloom year-round* [M]. Hangzhou, Zhejiang Science and Technology Press:1-581. [Gao JY, Liu XK, Zhao QM, 2016. *Illustrated atlas of new year-round blooming camellia hybrids* [M]. Hangzhou: Zhejiang Science and Technology Press:1-581.]

GU ZJ, SUN XF, 1997. A karyomorphological study of seventeen species of Chinese *Camellia* [J]. *Acta Botan Yunnan*, 19(2): 159-170. [Gu ZJ, Sun XF, 1997. Karyomorphological study of seventeen species of Chinese *Camellia* [J]. *Acta Botanica Yunnanica*, 19(2):159-170.]

HAN GH, XIANG SQ, WANG WX, et al., 2010. Identification and genetic diversity of hybrid progenies from shatian pummelo by SSR [J]. *Sci Agricult Sin*, 43(22):4678-4686. [Han GH, Xiang SQ, Wang WX, et al., 2010. SSR identification and genetic diversity analysis of hybrid progeny populations from Shatian pummelo [J]. *Scientia Agricultura Sinica*, 43(22):4678-4686.]

HE YC, WU MJ, DONG L, et al., 2020. Analysis of kernel oil content and variation of fatty acid composition of *Camellia chekiangoleosa* in the main producing areas [J]. *Non-Wood For Res*, 38(3):37-45. [He YC, Wu MJ, Dong L, et al., 2020. Analysis of kernel oil content and fatty acid composition variation in *Camellia chekiangoleosa* from main production areas [J]. *Non-Wood Forest Research*, 38(3):37-45.]

HU WS, HUANG AP, JIANG F, et al., 2015. Identification and genetic diversity of reciprocal hybrids in Longan (*Dimocarpus longan*) by SSR [J]. *Acta Horticult Sin*, 42 (10):1899-1908. [Hu WS, Huang AP, Jiang F, et al., 2015. SSR identification and genetic diversity analysis of reciprocal hybrids in longan (*Dimocarpus longan*) [J]. *Acta Horticulturae Sinica*, 42(10):1899-1908.]

KHAJUDPARN P, PRAJONGJAI T, POOLSAWAT O, et al., 2012. Application of ISSR markers for verification of F_1 hybrids in mungbean (*Vigna radiata*) [J]. *Genet Mol Res*, 11(3):

KHAN H, SIVALINGAM P N, CHAUHAN S, et al., 2013. Improved crossing technique and identification of true F_1 hybrids of *Ziziphus mauritiana* Lam. by molecular markers [J]. *Sci Hort-Amsterdam*, 150: 164-171.

LI L, 2016. *Garden plant genetics and breeding* [M]. Chongqing: Chongqing University Press:157-173. [Li L, 2016. *Garden plant genetics and breeding* [M]. Chongqing: Chongqing University Press:157-173.]

LI WX, HE JJ, ZHANG HL, et al., 2021. Identification of F_1 hybrids of *Hevea brasiliensis* by SSR Markers [J]. *Chinese Journal of Tropical Crops*, 42(5):1305-1309. [Li WX, He JJ, Zhang HL, et al., 2021. Identification of true and false F_1 hybrids of *Hevea brasiliensis* using SSR markers [J]. *Chinese Journal of Tropical Crops*, 42(5):1305-1309.]

LEI Y, DUAN JH, HUANG FY, et al., 2021. Identification and genetic diversity of tea F_1 hybrids based on SSR markers [J]. *Journal of Plant Genetic Resources*, 22(03):748-757. [Lei Y, Duan JH, Huang FY, et al., 2021. SSR identification and genetic diversity analysis of true and false F_1 hybrids in tea [J]. *Journal of Plant Genetic Resources*, 22(03):748-757.]

LIU YX, LI PT, CHI TH, et al., 2019. Identification and genetic diversity analysis of interspecific F_1 hybrids between *Chrysanthemum nankingense* × *C. lavandulifolium* [J]. *Acta Horticult Sin*, 46(8):1553-1564. [Liu YX, Li PT, Chi TH, et al., 2019. Identification and genetic diversity analysis of interspecific F_1 hybrids between *Chrysanthemum nankingense* × *C. lavandulifolium* [J]. *Acta Horticulturae Sinica*, 46(8):1553-1564.]

LUO XL, ZHU WX, 2010. Processing technology of oil-tea camellia seed oil and comprehensive utilization of camellia oleifera resources [J]. *Chin Oils And Fats*, 35(9): 13-17. [Luo XL, Zhu WX, 2010. Processing technology of oil-tea camellia seed oil and comprehensive utilization of camellia resources [J]. *China Oils and Fats*, 35(9):13-17.]

QIN SY, RONG J, ZHANG WJ, et al., 2018. Cultivation history of *Camellia* *oleifera* and genetic resources in the Yangtze River Basin [J]. *Biodiversity Science*, 26(04): 384-395. [Qin SY, Rong J, Zhang WJ, et al., 2018. Cultivation history of *Camellia oleifera* and genetic resources in the Yangtze River Basin [J]. *Biodiversity Science*, 26(04):384-395.]

SUN PG, CHEN XY, XI RC, et al., 2012. Research progress on the evaluation of *Camellia oleifera* germplasm resources [J]. *Chin For Sci Technol*, 26(3): 1-6. [Sun PG, Chen XY, Xi RC, et al., 2012. Research progress on evaluation of *Camellia oleifera* germplasm resources [J]. *China Forestry Science and Technology*, 26(3): 1-6.]

XU J, HUANG LD, XU Y, et al., 2009. Identifying hybrids of golden camellia using SSR molecular markers [J]. *J Fudan Univ (Nat Sci)*, 48(5):668-673. [Xu J, Huang LD, Xu Y, et al., 2009. Identification of golden camellia hybrids using SSR molecular markers (in English) [J]. *Journal of Fudan University (Natural Science)*, 48(5):668-673.]

WEN Q, YE JS, LEI XL, et al., 2006. Study on the inter-simple sequence repeat condition of *Camellia oleifera* [J]. *J Centr S For Univ*, 26(6):22-26. [Wen Q, Ye JS, Lei XL, et al., 2006. Establishment and optimization of ISSR reaction system for *Camellia oleifera* [J]. *Journal of Central South University of Forestry & Technology*, 26(6):22-26.]

WEN Q, ZHU H, YE JS, et al., 2015. Authentication of *Camellia chekiangoleosa* and its close species using RPB2 gene sequences [J]. *Mol Plant Breed*, 13(11):2559-2565. [Wen Q, Zhu H, Ye JS, et al., 2015. Authentication of *Camellia chekiangoleosa* and its close relatives using RPB2 gene sequences [J]. *Molecular Plant Breeding*, 13(11):2559-2565.]

WANG XN, CHEN YZ, WANG R, et al., 2020. The breeding of two new *Camellia* varieties [J]. *J Centrl S Univ For Technol*, 40(8):1-6. [Wang XN, Chen YZ, Wang R, et al., 2020. Breeding of two new *Camellia* varieties [J]. *Journal of Central South University of Forestry & Technology*, 40(8):1-6.]

TIAN QQ, HUANG JJ, WEN Q, et al., 2021. The current situation and trend of molecular breeding in Oil-tea Camellia [J]. *S Chin For Sci*, 49(5): 53-59. [Tian QQ, Huang JJ, Wen Q, et al., 2021. Current status and trends of molecular breeding in oil-tea camellia [J]. *South China Forestry Science*, 49(5):53-59.]

TIAN XX, FANG XZ, SUN HZ, et al., 2018. Analysis of triacylglycerols in different oil-tea camellia cones [J]. *For Res*, 31(2):41-47. [Tian XX, Fang XZ, Sun HZ, et al., 2018. Analysis of triacylglycerols in fruits of different oil-tea camellia species and varieties [J]. *Forest Research*, 31(2):41-47.]

WU XH, SHEN B, HUANG YF, et al., 2016. Analysis and evaluation of nutrient ingredients in *Camellia chekiangoleosa* [J]. *Nonw For Res*, 34(3):130-134. [Wu XH, Shen B, Huang YF, et al., 2016. Analysis and evaluation of nutritional components in red camellia [J]. *Non-Wood Forest Research*, 34(3):130-134.]

YANG D, HU X, LIU Z, et al., 2010. Intergeneric hybridizations between

Opisthopappus taihangensis and *Chrysanthemum lavandulifolium* [J]. *Sci Hort-Amsterdam*, 125(4):718

YANG ZL, LI JY, FAN ZQ, 2004. A preliminary study on the Cross-compatibility among *Sect. japonica* cultivars in the genus *Camellia* [J]. *For Res*, 17(5):680-684. [Yang ZL, Li JY, Fan ZQ, 2004. Preliminary study on cross-compatibility among species of *Sect. japonica* in genus *Camellia* and their hybrids with cultivars [J]. *Forest Research*, 17(5):680-684.]

YE S, WANG Y, HUANG D, et al., 2013. Genetic purity testing of F_1 hybrid seed with molecular markers in cabbage (*Brassica oleracea* var. *capitata*) [J]. *Sci Hort-Amsterdam*, 155(2):92-96.

YIN BY, ZHANG Y, SUN FL, et al., 2019. Identification and genetic diversity of apple F_1 hybrids based on SSR markers [J]. *J Hebei Agric Univ*, 42(5):46-51. [Yin BY, Zhang Y, Sun FL, et al., 2019. SSR identification and genetic diversity analysis of apple F_1 population [J]. *Journal of Hebei Agricultural University*, 42(5):46-51.]

YUSUKE S. 1988. Studies on the flower colours in the genus *Camellia*, with special reference to the phylogenies of the genus [J]. *Bull Fac Agr Kagosh Univ*, 38: 9-62.

ZHOU NN, LI SB, LI YB, 2017. Hybrids identification and genetic analysis in diploid roses population (F_1) using SSR markers [J]. *Acta Hortic Sin*, 44(1):151-160. [Zhou NN, Li SB, Li YB, et al., 2017. SSR identification and genetic analysis of diploid rose F_1 population [J]. *Acta Horticulturae Sinica*, 44(1):151-160.]

ZHOU S, ZHU JH, XIAO JZ, et al., 2001. Distant crossing trial with oil tea camellia [J]. *Econom For Res*, 19(1):20-25. [Zhou S, Zhu JH, Xiao JZ, et al., 2001. Distant hybridization breeding experiment in oil-tea camellia [J]. *Economic Forest Research*, 19(1):20-25.]

ZHOU WC, HOU J, GUO W, et al., 2015. Identification of the true hybrids for *Populus deltoides* by using SSR markers [J]. *J Nanjing For Univ (Nat Sci Ed)*, 39(3):45-49. [Zhou WC, Hou J, Guo W, et al., 2015. Identification of hybrid progenies of *Populus deltoides* based on SSR markers [J]. *Journal of Nanjing Forestry University (Natural Sciences Edition)*, 39(3):45-49.]

ZHOU WC, XIAO XY, SHEN JL, et al., 2019. Review on germplasm resources and breeding strategy for *Camellia chekiangoleosa* [J]. *S Chin For Sci*, 47(6):20-24. [Zhou WC, Xiao XY, Shen JL, et al., 2019. Review on germplasm resources and breeding strategies for *Camellia chekiangoleosa* [J]. *South China Forestry Science*, 47(6):20-24.]

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