horticulturae

MDPI

Article

Variation in Fruit Traits and Seed Nutrient Compositions of Wild *Camellia oleifera*: Implications for *Camellia oleifera* Domestication

Kai-Feng Xing [1,†], Yu-Jing Zou [1,2,†], Hao-Xing Xie [1,†], Shang Chen [1], Jun Zhou [1], Xie-Tian Luo [3], Gong-Hu Chen [1,4], Yao Zhao [1], Ze-Yuan Deng [5], Jun Rong [1], Jing Li [5,*] and Jian Zhang [1,*]

1 Center for Watershed Ecology, School of Life Sciences, Key Laboratory of Poyang Lake Environment and Resource Utilization, Ministry of Education, Nanchang University, Nanchang 330031, China; 5601118087@email.ncu.edu.cn (K.-F.X.); yujing-zou@foxmail.com (Y.-J.Z.); haoxingxie@foxmail.com (H.-X.X.); 15256627188@163.com (S.C.); kuso2014@foxmail.com (J.Z.); chengonghu@foxmail.com (G.-H.C.); yaozhao@ncu.edu.cn (Y.Z.); rongjun@ncu.edu.cn (J.R.)
2 Yichun Academy of Sciences, Yichun 336000, China
3 School of Basic Medical Sciences, Nanchang University, Nanchang 330031, China; luoxietian@ncu.edu.cn
4 China Rural Special Technology Association Science and Technology Backyards, Nanchang 330031, China
5 State Key Laboratory of Food Science and Resources, Nanchang University, Nanchang 330031, China; dengzy@ncu.edu.cn
* Correspondence: lijing66@ncu.edu.cn (J.L.); zhangjianlab@126.com (J.Z.)
† These authors contributed equally to this work.

Abstract: *Camellia oleifera* is a woody oil crop with the highest oil yield and the largest cultivation area in China, and *C. oleifera* seed oil is a high-quality edible oil recommended by the Food and Agriculture Organization of the United Nations. The objectives of this study were to investigate the variation in fruit yield traits and seed chemical compositions of wild *C. oleifera* in China and to identify the differences between wild *C. oleifera* and cultivated varieties. In this study, we collected wild *C. oleifera* samples from 13 sites covering the main distribution areas of wild *C. oleifera* to comprehensively evaluate 25 quantitative traits of wild *C. oleifera* fruit and seed chemical compositions and collected data of 10 quantitative traits from 434 cultivated varieties for a comparative analysis of the differences between wild and cultivars. The results showed that the coefficients of variation of the 25 quantitative traits of wild *C. oleifera* ranged from 2.605% to 156.641%, with an average of 38.569%. The phenotypic differentiation coefficients ranged from 25.003% to 99.911%, with an average of 77.894%. The Shannon–Wiener index (H') ranged from 0.195 to 1.681. Based on the results of principal component analysis (PCA) and phenotypic differentiation coefficients, 10 traits differed significantly between wild *C. oleifera* and cultivated varieties, while the differentiation coefficients (V_{ST}) for fresh fruit weight, oleic acid, unsaturated fatty acids, stearic acid, and saturated fatty acids were more than 95%, of which fresh fruit weight and oleic acid content were potential domestication traits of *C. oleifera*. The results of this study can contribute to the efficient excavation and utilization of wild *C. oleifera* genetic resources for *C. oleifera* breeding.

Keywords: *Camellia oleifera*; domestication; fatty acid; fruit trait; genetic resource; oil content; seed nutrient composition

Citation: Xing, K.-F.; Zou, Y.-J.; Xie, H.-X.; Chen, S.; Zhou, J.; Luo, X.-T.; Chen, G.-H.; Zhao, Y.; Deng, Z.-Y.; Rong, J.; et al. Variation in Fruit Traits and Seed Nutrient Compositions of Wild *Camellia oleifera*: Implications for *Camellia oleifera* Domestication. *Horticulturae* **2024**, *10*, 450. https://doi.org/10.3390/horticulturae10050450

Academic Editor: Julė Jankauskienė

Received: 28 March 2024
Revised: 23 April 2024
Accepted: 26 April 2024
Published: 29 April 2024

1. Introduction

Camellia oleifera (oil camellia) is the predominant woody oil crop in China and one of the four major woody oil crops in the world, together with oil palm (*Elaeis guineensis*), oil olive (*Olea europaea*), and coconut (*Cocos nucifera*) [1]. In 2022, the planting area of *C. oleifera* in China was about 4.67 million ha, and the *C. oleifera* seed oil production exceeded 1 million tons. The *C. oleifera* seed oil is rich in oleic acid, making up over 80% of the fatty acid compositions, known as 'oriental olive oil' [2]. In addition, *C. oleifera* seed oil also contains

many functional nutrient concomitants, such as phytosterols, squalene, tocopherols, and saponin [3,4]. The nutrient components of *C. oleifera* seed oil have good antioxidant and anti-inflammatory activities and can help lower blood cholesterol and lipids for reducing the risks of cardiovascular and cerebrovascular diseases [5–8]. *Camellia oleifera* seed oil is therefore one of the healthy and high-quality edible vegetable oils recommended by the Food and Agriculture Organization of the United Nations (FAO) [5].

The first record clearly indicating *C. oleifera* as an oil crop was in the Ming dynasty, so the cultivation history may be less than 1000 years in China [1]. Cultivated *C. oleifera* was domesticated from wild *C. oleifera* probably in the middle reach of the Yangtze River Basin [1]. As the essential genetic resource for *C. oleifera* breeding, wild *C. oleifera* is widely distributed in the subtropical evergreen broadleaved forests of the Yangtze River Basin and South China [9]. With high-throughput sequencing-based microsatellite genotyping, rich genetic diversity and clear genetic differentiation have been found among wild *C. oleifera* populations from different latitudes and longitudes [10]. As a perennial woody oil crop with a short cultivation history, the domestication bottleneck of *C. oleifera* may be mild compared to annual herbaceous crops [11]. Nevertheless, differentiations may be expected between wild and cultivated *C. oleifera* leading to so-called 'domestication traits' in the latter, especially for fruit and seed traits under strong human selection [12–16]. The enlargement of *C. oleifera* fruits plays a pivotal role in the enhancement of *C. oleifera* oil production [5,6]. Nevertheless, there is a lack of systematic study on the variation in the fruit and seed traits of wild *C. oleifera* and the differentiations in key traits between wild and cultivated *C. oleifera*.

In this study, representative wild *C. oleifera* populations were investigated across the main distribution regions of wild *C. oleifera*. Fruits were collected from wild *C. oleifera*, and fruit traits and seed nutrient compositions of wild *C. oleifera* were measured and analyzed. In addition, fruit traits, seed oil contents and fatty acid compositions of 434 cultivated *C. oleifera* were collected from the literature. The differences in fruit traits and seed nutrient compositions were compared between wild and cultivated *C. oleifera* to infer the key domestication traits. This study comprehensively and systematically evaluated the variation in fruit traits and seed nutrient compositions of wild *C. oleifera* germplasm resources in China, providing the support for the selection of wild *C. oleifera* with valuable nutrient compositions. Moreover, this study can facilitate the understanding of *C. oleifera* domestication, especially for the formation of key domestication traits.

2. Materials and Methods

2.1. Plant Material Collection

According to the main distribution regions of wild *C. oleifera* in China [9], 13 representative wild *C. oleifera* populations within natural subtropical evergreen broadleaved forests are investigated (Supplementary Table S1). The range of samples covers the major habitats of wild *C. oleifera* [9]. A total of 206 wild *C. oleifera* sample trees and 927 wild *C. oleifera* sample fruits are collected (Supplementary Table S1). The wild *C. oleifera* populations show diverse individual plant types with obvious age structures. In each population, well-grown wild *C. oleifera* trees are selected and fruit samples are collected from each tree. In this study, the living *C. oleifera* trees in the investigated natural forests with less human interference are called wild *C. oleifera*. The judgment criteria of wild *C. oleifera* forests in this study are as follows: the habitat is a natural forest; the living *C. oleifera* trees are scattered in patches or sporadically, with no obvious traces of artificial cultivation, such as uniform spacing between rows and rows, continuous distribution, and the grafting of *C. oleifera* trees; and the *C. oleifera* populations have an obvious age structure, and there are a large number of young plants that can be naturally regenerated [9]. The main soil types of the various source sites include red soil and brown soil, and the landforms are mainly plains and low hills; the basal diameter of oil tea ranges from 10 to 25 cm, and the age structure is obvious, with sparse branches and leaves and fewer fruits, which are mixed with other forest trees.

Based on the Oil-Tea Camellia Genetic Resource in China, the phenotypic data of *C. oleifera* cultivars were counted, and the missing data for *C. oleifera* cultivars were excluded, so a total of 434 cultivated *C. oleifera* cultivars were collected and collated with quantitative trait data on fruit yield traits and seed chemical composition, from which 10 quantitative trait data such as oil yield and fatty acid content were selected. The catalog of cultivars and related trait data are shown in Supplementary Table S2.

2.2. Data Collection (or Evaluated Traits) for Wild C. oleifera

2.2.1. Fruit Trait Measurement

Fresh fruit weight and fresh seed weight were weighed using an electronic balance with an accuracy of 0.01 g. Fruit height, fruit diameter, and pericarp thickness were measured using calipers with an accuracy of 0.01 mm. The number of seeds per fruit was determined by direct counting (Figure 1). Fresh seed yield and fruit shape index were calculated as follows:

$$\text{Fresh seed yield} = \text{fresh seed weight}/\text{fresh fruit weight} \times 100\%.$$

$$\text{Fruit shape index} = \text{fruit height}/\text{fruit diameter} \times 100.$$

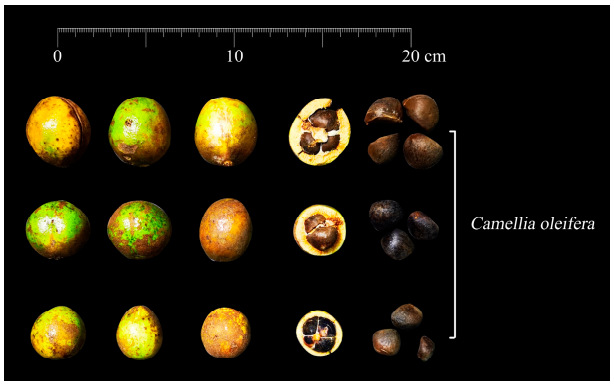

Figure 1. Images of the wild *C. oleifera* fruits and seeds. Schematic diagram of measuring fruit traits such as fresh fruit weight, fruit height, fruit diameter, peel thickness, number of seeds per fruit, and fresh seed weight.

2.2.2. Determination of Chemical Composition of Fruits

Determination of the Oil Content of the Kernel

The *C. oleifera* samples were subjected to a series of preparatory steps. First, they were hulled and subsequently crushed using a crusher. The resulting material was then passed through a 60 mesh sieve. Following this, the samples were obtained using the four-part method, as outlined in the national standard GB5491-85 "Grain and Oilseed Inspection Cuttings and Splitting Method".

For the determination of oil content, in accordance with the national standard GB5009.6-2016 "Determination of oil content in food", a certain quantity of prepared *C. oleifera* seed sample powder was accurately weighed. Soxhlet extraction was performed using a petroleum ether solution. Subsequently, the oil content of the seed kernel obtained from each *C. oleifera* sample was calculated based on the extracted oil [17]. The experiment was performed in triplicate.

Determination of Fatty Acid Composition

The methyl esterification of fatty acids: *C. oleifera* seed oil (2 mg) was aspirated with a pipette gun, followed by the addition of 1.5 mL of hexane solution. The mixture was vortexed for 30 s. Then, 40 uL methyl acetate solution and 100 µL sodium methanol/methanol solution were added, and the mixture was vortexed for another 30 s. The reaction was allowed to proceed in a water bath at 37 °C for 20 min. Upon completion, the reaction

mixture was transferred to a refrigerator set at −20 °C for 10 min. Immediately thereafter, 100 µL oxalic acid–methyl acetate solution was added, and the mixture was centrifuged at 4200 rpm for 5 min. The supernatant was carefully collected and passed through anhydrous sodium sulfate to remove residual moisture. The sample was then dried under a nitrogen stream. Finally, 1 mL of n-hexane solution was added, and the mixture was vortexed for 30 s before passing through a 0.45 µm membrane. The resulting solution was then prepared for measurement.

The measurement conditions were as follows: the gas chromatography column was a CP-7489 capillary column (100 mm × 0.25 mm × 0.2 µm); the carrier gas was N2, and the combustion gases were H2 and air; the inlet temperature was 250 °C; the pressure was 24.52 psi; and the total flow rate was 29. The flow rate in the column was 1.8 mL/min, and the column temperature was 45 °C (4 min), increased at 13 °C/min to 175 °C (27 min), and then decreased at 4 °C/min to 135 °C (35 min). The temperature was increased to 215 °C (35 min), the detector temperature was 250 °C, and the flow rates of hydrogen, nitrogen, and air were 30.0, 30.0, and 300 mL/min, respectively. The relative fatty acid content was determined by area normalization against a fatty acid methyl ester standard [5,17]. The experiment was performed in triplicate.

Determination of the Tocopherol Content

Tocopherol standard curve: We accurately weighed 25.28 mg of α-tocopherol standard using a precision balance. We mixed the weighed α-tocopherol standard thoroughly with hexane solution to make a 10 mL solution. We transfered 1 mL of the prepared solution to a new 25 mL volumetric flask and dilute to 25 mL with hexane solution. Then, we transfered 0.5 mL, 1 mL, 1.5 mL, 2 mL, and 3 mL aliquots of the diluted solution into separate 10 mL volumetric flasks and diluted each to 10 mL with hexane solution. High-performance liquid chromatography (HPLC) was used to analyze each sample. Each sample was run three times in parallel. The standard curve for α-tocopherol was then constructed from these measurements.

Determination of tocopherol content: 0.3 g of *C. oleifera* seed oil was accurately weighed using a balance. The *C. oleifera* seed oil was then diluted to 10 mL with n-hexane solution. The diluted solution was then passed through a 0.45 µm filter membrane. The filtered solution was analyzed by high-performance liquid chromatography (HPLC), with each sample measured three times in parallel. The tocopherol content of each *C. oleifera* sample was calculated from the tocopherol standard curve. The liquid chromatography column used was Elite Hypersil ODS2 (5 µm, 4.6 mm × 150 mm), and the mobile phase consisted of methanol and water in a ratio of 98:2 (*v/v*). For each injection, 3 µL of sample was injected into the column, and the flow rate was set at 0.8 mL/min. The ultraviolet detector (DAD) was set to a maximum excitation wavelength of 295 nm. The column temperature was maintained at 25 °C and the analysis time was 10 min [5,17]. The experiment was performed in triplicate.

Measurement of Squalene

Squalene standard curve: 5.78 mg of squalene was accurately weighed and the volume was adjusted in a 25 mL volumetric flask with hexane. Then, 1 mL was aspirated and transferred to a 10 mL volumetric flask containing hexane. Aliquots of 0.5 mL, 1.0 mL, 1.5 mL, 2.0 mL, and 2.5 mL were then pipetted, and each volume was made up to 10 mL with hexane. The standard curve was generated by high-performance liquid chromatography. Chromatography was performed on a Hypersil ODS2 column (250 mm × 4.6 mm, 5 µm) with acetonitrile–methanol (60:40, *v/v*) as the mobile phase. The flow rate was set to 1.0 mL/min, and the sample injection volume was 10 µL.

The determination of squalene content: 0.5 g of *C. oleifera* seed oil was accurately weighed and dissolved in 5 mL of petroleum ether. The solution was then passed through a 160–200-mesh silica gel column. The sample solution collected after passing through the column was concentrated to dryness under a stream of N2 and then dissolved in

2.5 mL of hexane. Moreover, 1 mL of the resulting solution was passed through a 0.45 μm filter membrane before measurement by high-performance liquid chromatography. The squalene content of the sample was calculated from the squalene standard curve [5,17]. The experiment was performed in triplicate.

Reagents and Equipment

Main reagents: methyl acetate and ethyl acetate (all analytical reagents), Shanghai Chemical Reagent Company (Shanghai, China); distilled water, sodium methanol/methanol solution, petroleum ether, oxalic acid–methyl acetate, and anhydrous sodium sulfate (all analytical reagents), Shanghai Xilong Chemical Company (Shanghai, China); methanol, acetonitrile, and n-hexane (all chromatography pure reagents), Tedia Company (Columbus, OH, USA); and silica gel powder, Qingdao Ocean Chemical Factory (Qingdao, China). The other reagents were analytical reagents.

The main equipment used in this study is as follows: The laboratory is equipped with an Anke TDL-5-A low-speed centrifuge manufactured by Shanghai Anting Scientific Instrument Factory (Shanghai, China); we use a HH-4 digital thermostatic water bath manufactured by Changzhou Guohua Electric Appliances Company, Ltd (Changzhou, China); and a 1100 high-performance liquid chromatograph and 6890 N gas chromatograph manufactured by the Agilent Company (Palo Alto, CA, USA) is used. The AR1140 electronic analytical balance is manufactured by the OHAUS trading company (Parsippany, NJ, USA). The QL-861 vortex machine is manufactured by Qilimbeier Instrument Manufacturing Company of Haimen (Haimen, China).

2.3. Data Collection (or Evaluated Traits) of the Cultivated C. oleifera

To facilitate the comparative analysis with wild *C. oleifera*, the following 10 quantitative traits were selected from the collected data set of cultivated *C. oleifera*: fresh fruit weight, fresh seed yield, oil rate of kernel, stearic acid, palmitic acid, saturated fatty acid, oleic acid, linoleic acid, linolenic acid, and unsaturated fatty acid. The catalog of cultivars and related trait data are shown in Supplementary Table S2. The range of origin of the cultivars is a representation of the main *C. oleifera* production areas. The 19 bioenvironmental climate factors were obtained from the World Climate Database website (http://www.worldclim.org, accessed on 15 January 2024) based on the coordinate information of the sample plots.

2.4. Statistical Analysis

Data statistics were performed using Microsoft Office 2021 software (Home and Student 2021 version); multiple comparisons, analysis of variance, nested ANOVA, and correlation analysis between wild *C. oleifera* fruit yield traits and seed chemical composition were performed using SPSS 27.0 software. The correlation analysis between environmental climatic factors and wild *C. oleifera* fruit yield traits with seed chemical composition was carried out using SPSS 27.0 software. Ten traits of wild and cultivated *C. oleifera* were resampled to estimate their means (30 at a time, with 10,000 replications). The 99.9% confidence interval (99.9% CI) of the estimate was inferred by resampling means positions (10,000 bootstrap samples). Correction for significance was performed using the Bonferroni method [18]. Principal component analysis and cluster analysis were performed on 444 germplasm resources using Origin 2021 software (Version 2021b). TOPSIS was achieved by SPSSPRO (https://www.spsspro.com, accessed on 22 January 2024).

V_{ST} is the coefficient of phenotypic differentiation, which indicates the percentage of interpopulation variation to total genetic variation, $V_{ST}(\%) = [\delta^2{}_{t/S}/(\delta^2{}_{t/S} + \delta^2{}_S)] \times 100$, where $\delta^2{}_{t/S}$ is the between-population variance component and $\delta^2{}_S$ is the within-population variance component.

The Shannon–Wiener index is a quantitative expression describing the degree of variability in trait diversity, and the formula is as follows: $H' = -\sum_{i=1}^{n} PilnPi$, where H′ is the diversity index, and Pi is the effective percentage of the distribution frequency within the material at level i of a trait.

The degree of trait dispersion is expressed by the coefficient of variation (CV) of trait characteristics, CV(%)= $s/\overline{x} \times 100$, where $\overline{x}$ is the trait mean, and s is the standard deviation.

3. Results

3.1. Comprehensive Evaluation of Yield Traits and Seed Chemical Composition of Wild C. oleifera Fruits from Different Seed Sources

The results of the study showed (Supplementary Table S3) that there was a wide variation in yield characteristics and seed chemical composition of wild *C. oleifera* fruits collected from 13 wild *C. oleifera* sample plots. The fresh fruit weight ranged from 0.939 to 11.477 g, the peel thickness ranged from 0.128 to 0.293 cm, the number of seeds per fruit ranged from 1.697 to 3.836, the fresh seed weight ranged from 0.530 to 4.453, the fresh seed yield ranged from 25.851 to 50.276%, the α-tocopherol content ranged from 0.057 to 0.286 mg/g, squalene content ranged from 0.035 to 0.255 mg/g, the oil rate of kernel ranged from 32.860 to 55.725%, palmitic acid content ranged from 7.784 to 10.782%, stearic acid content ranged from 1.625 to 3.097%, saturated fatty acid content ranged from 10.524 to 13.466%, palmitoleic acid content ranged from 0.067 to 0.173%, oleic acid content ranged from 71.156 to 80.164%, monounsaturated fatty acid content ranged from 73.324 to 81.660%, linoleic acid content ranged from 4.531 to 10.829%, linolenic acid content ranged from 0.264 to 0.552%, polyunsaturated fatty acid content ranged from 4.990 to 11.277%, and unsaturated fatty acid content ranged from 83.949 to 89.746% (Supplementary Table S3).

The coefficients of variation of the 13 seed sources of wild *C. oleifera* ranged from 9.592 to 27.374%, with a mean of 16.977. The coefficients of variation among seed sources for the 25 quantitative traits ranged from 2.605 to 156.641%, with a mean of 38.569%, with higher variation (CV value > 50%) for nervonic acid, myristic acid, margaric acid, squalene, α-tocopherol content, fresh seed weight, and fresh fruit weight (Supplemental Table S4).

The phenotypic differentiation coefficients of 25 quantitative traits for the fruit yield traits and seed chemical composition of wild *C. oleifera* ranged from 25.003 to 99.911%, with a mean of 77.894% (Supplementary Table S5). The phenotypic differentiation coefficient for fruit size-related traits (86.602%) was higher than that for seed chemotaxonomy (73.796%). In addition, the lowest phenotypic differentiation coefficient for saturated fatty acid content (25.003%) was found in wild *C. oleifera* from different seed sources, while the higher phenotypic differentiation coefficient for unsaturated fatty acid content (87.185%) was found in wild *C. oleifera* (Supplementary Table S5). In addition, phenotypic differentiation coefficients were lower for saturated fatty acid content and higher for unsaturated fatty acid content in different seed sources of wild *C. oleifera* (Supplementary Table S5). The 25 quantitative traits H′ varied in the range of 0.195 to 1.681, indicating that different seed sources of wild *C. oleifera* exhibited a high level of phenotypic diversity (Supplementary Table S3).

3.2. Correlations between 25 Quantitative Traits of Wild C. oleifera and Meteorological Factors

Correlation analyses using Pearson's correlation coefficients were performed on 13 wild *C. oleifera* populations, and complex relationships among 25 quantitative traits were estimated (Supplemental Table S6). Significant positive correlations were found between fresh fruit weight, fruit height, fruit diameter, and fresh seed weight, with coefficients ranging from 0.872 to 0.963. α-Tocopherol showed a significant negative correlation with saturated fatty acid ($r = -0.616$) and cis-11-vaccenic acid ($r = -0.759$) and a significant positive correlation with the oil rate of kernels ($r = 0.639$), linoleic acid ($r = 0.558$), and unsaturated fatty acid ($r = 0.849$). Palmitic acid showed a significant positive correlation with saturated fatty acid content ($r = 0.907$) and a significant negative correlation with oleic acid ($r = -0.596$) and unsaturated fatty acid content ($r = -0.687$). Stearic acid showed a significant negative correlation with linoleic acid content ($r = -0.612$). Oleic acid showed a significant negative correlation with palmitic acid ($r = -0.596$) and palmitoleic acid ($r = -0.603$) content. Unsaturated fatty acids showed a significant negative correlation ($r = -0.756$) with saturated fatty acids content (Supplementary Table S6).

Based on the correlation between environmental variables (correlation coefficient > 0.800), only six environmental climatic factors were selected, namely, annual mean temperature (Bio1), mean diurnal range (mean of monthly (max temp–min temp)) (Bio2), temperature annual range (Bio7), annual precipitation (Bio12), precipitation seasonality (Bio15), and the precipitation of the warmest quarter (Bio18) (Supplementary Table S7). The results of the correlation between environmental climatic factors and the chemical composition of wild *C. oleifera* seeds showed that Bio1 and stearic acid content showed a significant negative correlation (r = −0.610), Bio2 showed a significant positive correlation with palmitic acid (r = 0.559) and saturated fatty acids (r = 0.570), and Bio7 and squalene content (r = −0.615) showed significant negative correlation. Bio12 showed a significant positive correlation with the number of seeds per fruit (r = 0.585), Bio15 showed a significant positive correlation with neuronic acid content (r = 0.578), and Bio18 showed a significant positive correlation with squalene content (r = 0.745) (Supplementary Table S8). The α-tocopherol content of wild *C. oleifera* showed a significant decreasing trend with increasing latitude ($p < 0.05$), with a linear regression equation of y = −0.01559x + 0.58673 ($R^2 = 0.25$) (Supplementary Figure S1).

3.3. Trait Characteristics of 434 Cultivated C. oleifera Varieties

The statistical analysis of 434 *C. oleifera* cultivars revealed that the fresh fruit weight was 1.390 g~83.210 g, fresh seed yield was 6.180~79.380%, the oil rate of kernels was 11.800~70.630%, stearic acid content was 0.300~6.040%, palmitic acid content ranged from 0.300% to 12.020%, saturated fatty acid content ranged from 2.800% to 15.130%, oleic acid content ranged from 70.100% to 87.200%, linoleic acid content ranged from 0.480% to 17.200%, linolenic acid content ranged from 0.000% to 1.400%, and unsaturated fatty acid content ranged from 81.980% to 91.400% (Supplementary Table S9). The CV values of the 10 quantitative traits of cultivated *C. oleifera* ranged from 1.307% to 49.423%, with the largest variation in linolenic acid content and the smallest variation in unsaturated fatty acid content. The H′ values of 10 quantitative traits ranged from 0.267 to 1.626, indicating that cultivated *C. oleifera* varieties are also characterized by rich diversity (Supplementary Table S9).

The oil content, fresh fruit weight, and saturated fatty acid content of cultivated *C. oleifera* showed a significant decreasing trend with increasing latitude ($p < 0.01$), and the linear regression equations were y = −0.55076x + 58.92634 ($R^2 = 0.05337$), y = −1.55853x + 67.56822 ($R^2 = 0.15494$), and y = −0.07872x + 12.60323 ($R^2 = 0.03587$). The unsaturated fatty acid content showed a significant increasing trend with increasing latitude ($p < 0.01$), and the linear regression equation was y = 0.10644x + 85.8808 ($R^2 = 0.05979$) (Figure 2).

3.4. Principal Component Analysis

In this study, PCA analysis was performed on wild *C. oleifera* and *C. oleifera* cultivars. The comparative analyses of fruit traits (fresh fruit weight and fresh seed yield) revealed a clear differentiation between wild *C. oleifera* and the cultivars in terms of fresh fruit weight (Figure 3A). The principal components of seed chemical composition revealed that the dimensions implied by the eight quantitative traits could be simplified into two significant components, with a cumulative contribution of 91.914% (Figure 3C; Supplementary Table S10). The first factor was kernel oil rate with a contribution of 70.088% and can be called kernel oil rate factor. The second factor was oleic acid content with a contribution of 21.827% and can be referred to as the oleic acid factor. The differentiation between wild *C. oleifera* and the cultivars on PC2 (oleic acid factor) was more pronounced (Figure 3B). In this study, the phenotypic differentiation coefficients (V_{ST}) between wild *C. oleifera* and the cultivars were calculated. The results showed that the phenotypic differentiation coefficients of fresh fruit weight, stearic acid, saturated fatty acid, oleic acidm and unsaturated fatty acid content were all greater than 95%, and the degree of differentiation between wild *C. oleifera* and the cultivars was high (Table 1). Therefore, fresh fruit weight, oleic acid content,

and other indicators can be used as important indicators to distinguish wild *C. oleifera* from the cultivars.

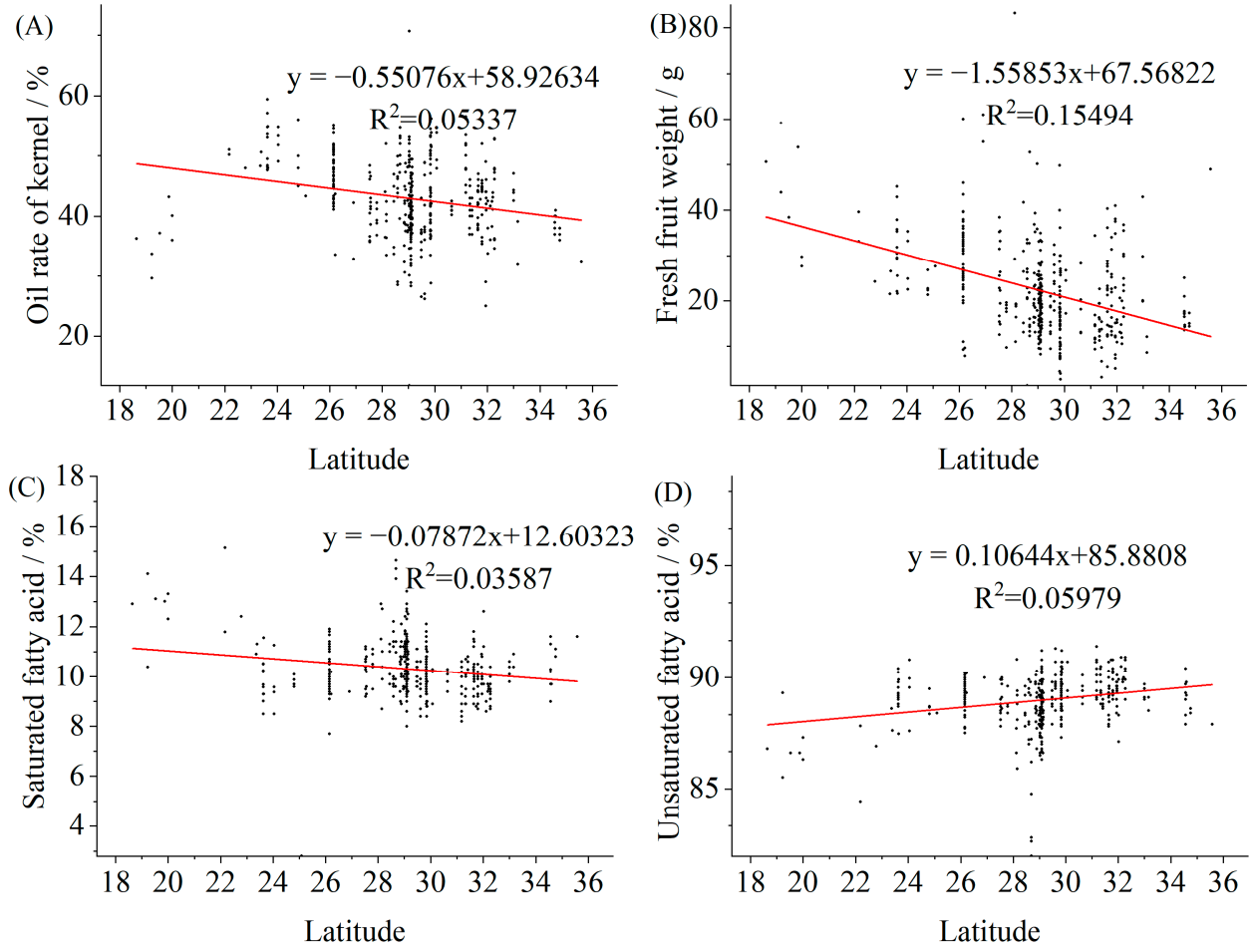

Figure 2. Correlation of oil content, fresh fruit weight, saturated fatty acid content, and unsaturated fatty acid content of cultivated *C. oleifera* with latitude. (**A**) Oil rate of kernel; (**B**) Fresh fruit weight; (**C**) Saturated fatty acid; (**D**) Unsaturated fatty acid.

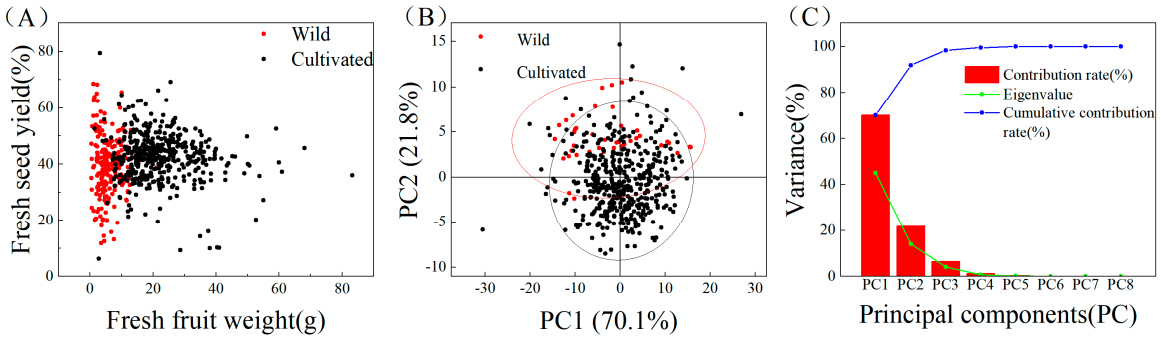

Figure 3. Principal component analysis of wild *C. oleifera* and cultivars. (**A**) Distribution plots of fresh fruit weight and fresh seed yield. (**B**) Principal component analysis of seed chemical constituents. (**C**) PCA eigenvalues, contribution rate (%), and cumulative contribution rate (%) of eight quantitative characters of seed chemical components.

Table 1. Comparison of nested ANOVA and phenotypic differentiation coefficients between wild and cultivated *C. oleifera* [(1)].

Fruit Characters and Nutrients	Among Provenances			Within Provenances			Random Error		Phenotypic Differentiation Coefficient/%
	Mean Square	F Value	Component/%	Mean Square	F Value	Component/%	Mean Square	Component/%	
Fresh fruit weight	36604.016	475.468 **	95.637	1592.856	20.69 **	4.162	76.985	0.201	95.830
Fresh seed yield	1754.040	19.957 **	82.193	292.123	3.324	13.689	87.893	4.119	85.723
Oil rate of kernel	214.558	5.062 *	45.778	211.747	4.996 *	45.179	42.384	9.043	50.330
Palmitic acid (C16:0)	5.015	14.588 **	84.272	0.592	1.723	9.948	0.344	5.781	89.442
Stearic acid (C18:0)	18.061	14.402 **	91.383	0.449	0.358	2.272	1.254	6.345	97.574
Saturated fatty acid (SFA)	63.088	49.85 **	94.978	2.070	1.636	3.116	1.266	1.906	96.823
Oleic acid (C18:1n-9)	853.657	106.001 **	98.906	1.386	0.172	0.161	8.053	0.933	99.838
Linoleic acid (C18:2n-6)	27.434	4.628 *	76.644	2.432	0.410	6.794	5.928	16.561	91.857
Linolenic acid (C18:3n-3)	0.336	16.782 **	66.142	0.152	7.597 **	29.921	0.020	3.937	68.852
Unsaturated fatty acid (UFA)	185.992	111.317 **	99.110	0.000	0.000	0.000	1.671	0.890	100.000
Mean	3972.620	81.806	83.504	210.381	4.091	11.524	22.580	4.972	87.627

[(1)] "*" indicted $p < 0.05$, "**"indicted $p < 0.01$.

3.5. Comparative Analysis of Fruit Yield Traits and Seed Chemical Composition between Wild C. oleifera and Cultivars

The comparative analysis of fruit yield traits and seed chemical composition between wild *C. oleifera* and the cultivars in this study showed that wild *C. oleifera* had significantly lower fresh fruit weight, fresh seed yield, oil rate of kernel, oleic acid content, and unsaturated fatty acid content traits than the cultivars ($p < 0.001$) (Figure 4; Supplemental Table S11). The stearic acid content, palmitic acid content, linoleic acid content, linolenic acid content, and saturated fatty acid content of wild *C. oleifera* were significantly higher than those of the cultivars ($p < 0.001$) (Figure 4; Supplementary Table S11).

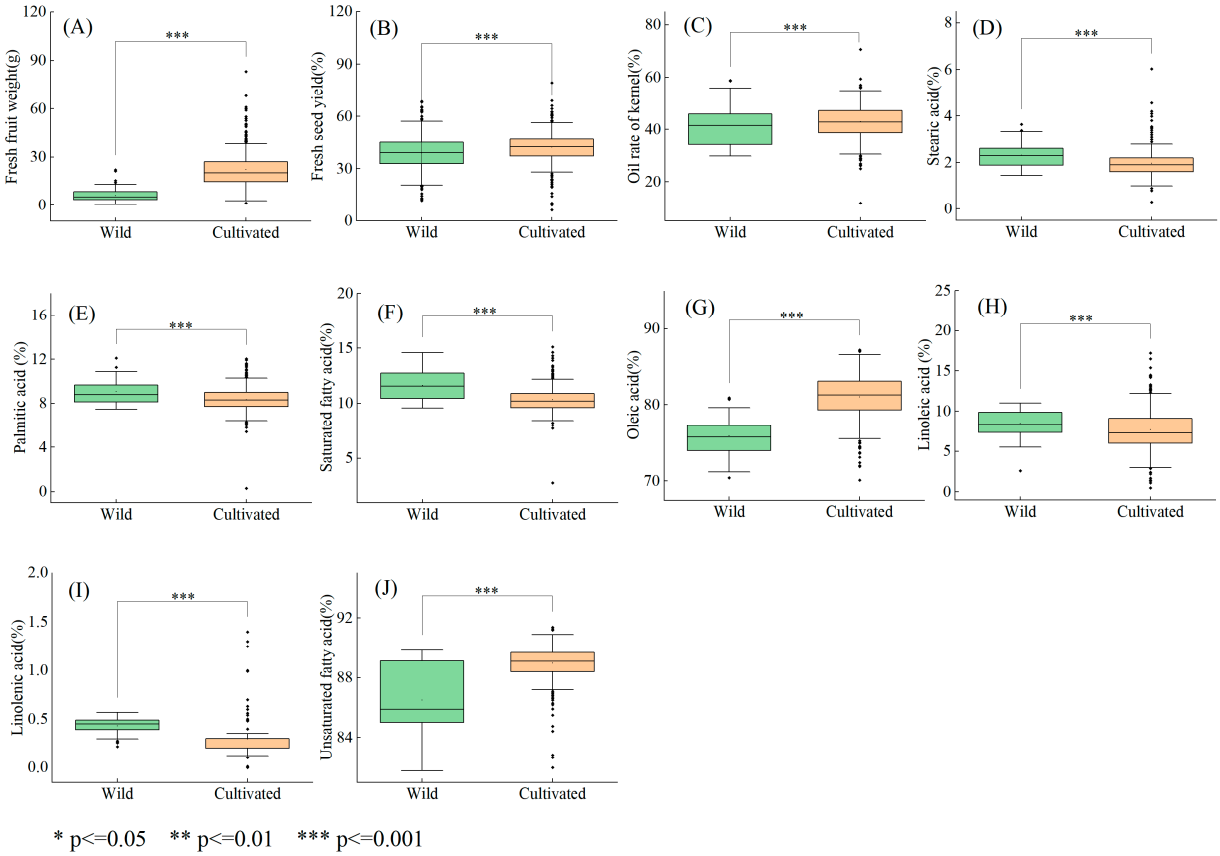

Figure 4. Comparative analysis of fruit yield traits and seed chemical composition between wild and cultivated *C. oleifera*. (**A**) Fresh fruit weight; (**B**) Fresh seed yield; (**C**) Oil rate of kernel; (**D**) Stearic acid; (**E**) Palmitic acid; (**F**) Saturated fatty acid; (**G**) Oleic acid; (**H**) Linoleic acid; (**I**) Linolenic acid; (**J**) Unsaturated fatty acid.

3.6. Cluster Analysis

In this study, the relationships between 13 wild *C. oleifera* populations and 434 cultivated *C. oleifera* varieties were analyzed by hierarchical cluster analysis. The results showed that all the germplasm resources could be classified into six different groups. The 13 populations of wild *C. oleifera* showed a clustering trend, of which 11 populations were clustered in Group I, and the other 2 populations were clustered in Group III (Figure 5; Supplementary Table S12).

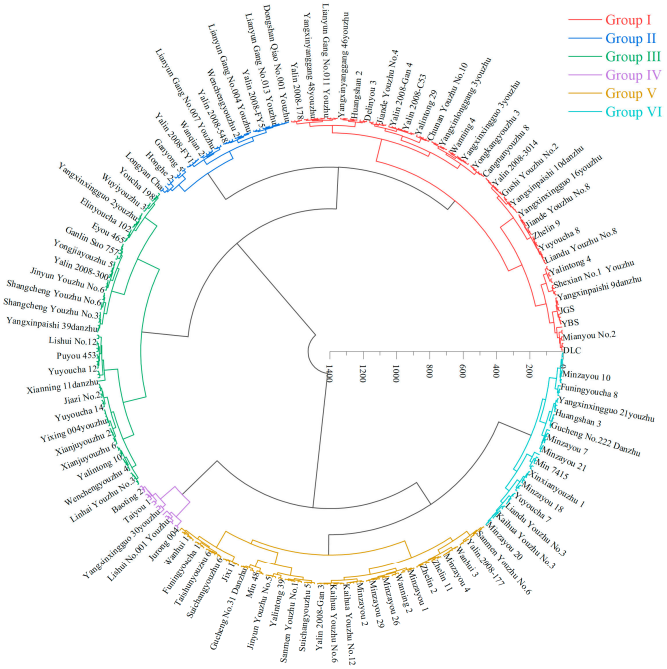

Figure 5. Clustering of 447 *C. oleifera* germplasm resources.

Group I contained 124 germplasm resources, accounting for 27.740% of the total accessions. This group was characterized by the smallest fresh fruit weight (Group I: 15.175 g; Wild: 5.952 g), the lowest oil rate of kernel (Group I: 38.777%; Wild: 41.443%) and the highest linolenic acid content (Group I: 0.331%; Wild: 0.430%) (Figure 5; Table 2; Supplementary Table S11). Group II contained 46 germplasm resources, representing 10.291% of the total accessions, with the highest fresh seed yield (55.272%) and the lowest stearic acid content (1.811%). Group III contained 97 resources, accounting for 21.700% of the total accessions, with the lowest linolenic acid content (0.282%). Group IV contained 18 germplasm resources, representing 4.027% of the total accessions, and this group was characterized by the highest fresh fruit weight (50.387 g), palmitic acid (9.143%), linoleic acid (9.338%), and saturated fatty acid content (11.301%) and the lowest fresh seed yield (28.946%), oleic acid (78.487%), and unsaturated fatty acid content (88.153%). Group V contained 102 germplasm resources, representing 22.819% of the total accessions. This group was characterized by the lowest content of saturated fatty acids (10.002%). Group VI contained 60 germplasm resources, representing 13.423% of the total accessions, and was characterized by the highest oil rate of kernel (49.165%), stearic acid (2.173%), oleic acid (82.161%), and unsaturated fatty acid content (89.255%) and the lowest palmitic acid (7.893%) and linoleic acid content (6.809%) (Figure 5; Table 2).

3.7. TOPSIS Comprehensive Evaluation

By using the TOPSIS method, we conducted a comprehensive score rank of wild and cultivated *C. oleifera* (Supplementary Table S13). LS, LFS, and JGS were the top three wild *C. oleifera*. Yunyoucha 9, Xianning 15youzhu, yunyoucha 14, Minzayou 22, Yangxintongcha 208, Shihe Youzhu No.2, Yongkangyouzhu 7, Wanning 2, Minzayou 25, Nanzheng 1 were the top 10 *C. oleifera* varieties (Table 3).

Table 2. Phenotypic characteristics of the cluster groups (X ± SE) [(1)].

Groups	Fresh Fruit Weight (g)	Fresh Seed Yield (%)	Oil Rate of Kernel (%)	Fatty Acid Composition of *C. oleifera* Oils(%)						
				Stearic Acid (C18:0)	Palmitic Acid (C16:0)	Saturated Fatty Acid (SFA)	Oleic Acid (C18:1n-9)	Linoleic Acid (C18:2n-6)	Linolenic Acid (C18:3n-3)	Unsaturated Fatty Acid (UFA)
I	15.175 ± 0.535 d	43.781 ± 0.357 b	38.777 ± 0.469 c	1.892 ± 0.044 bc	8.568 ± 0.085 b	10.483 ± 0.085 b	79.710 ± 0.266 c	8.516 ± 0.209 ab	0.331 ± 0.016	88.714 ± 0.114 a
II	15.979 ± 0.604 d	55.272 ± 0.947 a	42.816 ± 0.719 b	1.811 ± 0.093 c	8.710 ± 0.163 b	10.521 ± 0.172 b	80.341 ± 0.450 bc	7.939 ± 0.459 bc	0.309 ± 0.021	88.589 ± 0.249 ab
III	15.708 ± 0.532 d	35.030 ± 0.680 d	43.556 ± 0.628 b	2.058 ± 0.060 ab	8.460 ± 0.106 bc	10.523 ± 0.112 b	81.162 ± 0.243 ab	7.300 ± 0.205 cd	0.282 ± 0.011	88.782 ± 0.136 bc
IV	50.387 ± 3.117 a	28.946 ± 3.372 e	38.781 ± 1.853 c	2.158 ± 0.263 a	9.143 ± 0.291 a	11.301 ± 0.379 a	78.487 ± 1.038 d	9.338 ± 0.975 a	0.328 ± 0.029	88.153 ± 0.374 a
V	25.896 ± 0.460 c	44.541 ± 0.544 b	44.385 ± 0.513 b	1.943 ± 0.048 abc	8.059 ± 0.130 cd	10.002 ± 0.117 c	81.897 ± 0.262 a	7.062 ± 0.212 cd	0.281 ± 0.015	89.240 ± 0.094 c
VI	34.531 ± 0.747 b	41.179 ± 0.641 c	49.165 ± 0.623 a	2.173 ± 0.079 a	7.893 ± 0.114 d	10.065 ± 0.131 c	82.161 ± 0.325 a	6.809 ± 0.257 d	0.285 ± 0.016	89.255 ± 0.131 c

[(1)] Different lowercases in the same column indicate the significant difference at 0.05 level.

Table 3. Composite scores and groupings of the top 13 ranked wild *C. oleifera* and top 20 ranked cultivated *C. oleifera*.

Cultivated				Wild			
Variety	**Cluster Group**	**Comprehensive Score**	**Rank**	**Population**	**Cluster Group**	**Comprehensive Score**	**Rank**
Yunyoucha 9	VI	0.690	1	LS	III	0.440	260
Xianning 15youzhu	I	0.681	2	LFS	I	0.428	285
Yunyoucha 14	VI	0.644	3	JGS	I	0.398	335
Minzayou 22	VI	0.636	4	NL	I	0.354	387
Yangxintongcha 208	III	0.628	5	DLC	I	0.335	401
Shihe Youzhu No.2	I	0.623	6	TK	I	0.328	407
Yongkangyouzhu 7	VI	0.616	7	HK	I	0.327	409
Wanning 2	V	0.607	8	HLT	I	0.322	415
Minzayou 25	VI	0.606	9	DCP	I	0.321	416
Nanzheng 1	VI	0.604	10	EM	III	0.317	421
Yangxinyanggang 48youzhu	I	0.604	11	BR	I	0.312	428
Minlong No.31	II	0.602	12	QL	I	0.309	430
Xianning 11danzhu	III	0.601	13	YBS	I	0.290	438
Wanhui 2	I	0.600	14				
Minzayou 24	VI	0.599	15				
Minzayou 1	V	0.598	16				
Yuyoucha 7	VI	0.596	17				
Wanqi 2	V	0.595	18				
Minzayou 9	V	0.591	19				
Wanqi 3	V	0.589	20				

In order to better illustrate the changes in the traits of cultivated *C. oleifera*, we showed the trends of the five traits with the largest differentiation coefficients mentioned above. From the results, we can see that the fresh fruit weight, oleic acid content, and unsaturated fatty acid content of the top 20 germplasm resources of cultivated *C. oleifera* were significantly higher than those of wild *C. oleifera*, and stearic acid and saturated fatty acid content were significantly lower than those of wild *C. oleifera* ($p < 0.001$) (Figure 6).

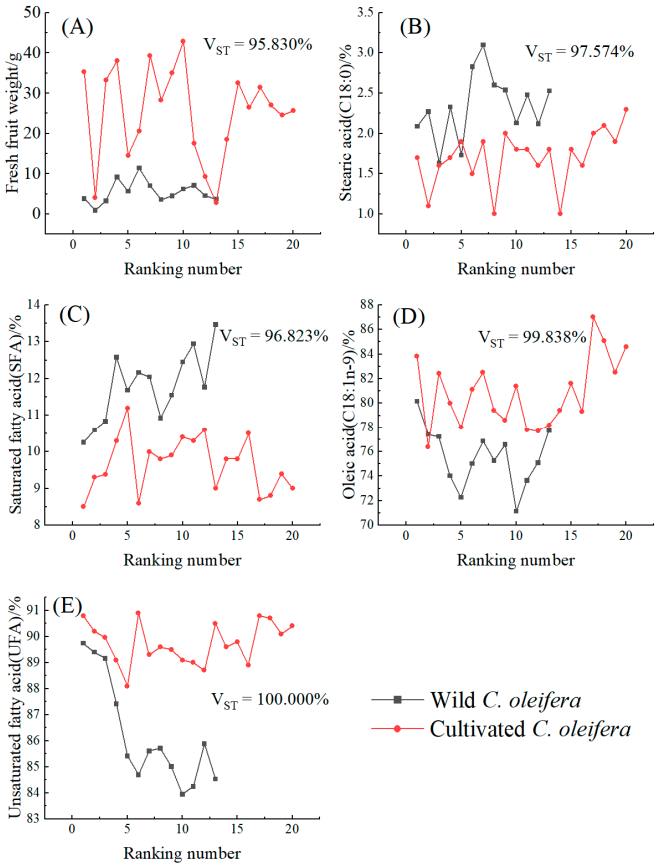

Figure 6. Comparison of fruit traits and seed chemical composition between top 13 ranked wild *C. oleifera* and top 20 ranked cultivated *C. oleifera*. (**A**) Fresh fruit weight; (**B**) Stearic acid (C18:0); (**C**) Saturated fatty acid (SFA); (**D**) Oleic acid (C18:1n-9); (**E**) Unsaturated fatty acid (UFA).

4. Discussion

Genetic diversity is a fundamental component of biological diversity. Phenotypic diversity is an important area of genetic diversity research [19]. The coefficient of variation and the coefficient of phenotypic differentiation can reflect the degree of difference between different phenotypic traits [20]. By analyzing 25 phenotypic traits of 13 wild *C. oleifera* populations, it was found that wild *C. oleifera* varied significantly among different populations and that inter-population variation was greater than intra-population variation. Similar results were found in the genetic structure analysis of wild *C. oleifera* by Cui et al. [10]. This is mainly due to the fact that wild *C. oleifera* is widely distributed in the Wuyi Mountain Range, Luoxiao Mountain Range, Nanling Mountain Range of Guangdong Province, Huangshan Mountain Range, and other low mountainous areas, where the habitat differences between individual populations are large and gene flow is somewhat hindered [10]. Bioactive compounds such as tocopherols and squalene found in *C. oleifera* have antioxidant, anti-inflammatory, and other health benefits. It has been shown that tocopherols and squalene can be used to identify potential markers for *C. oleifera* oils [21]. In this study, we found that wild *C. oleifera* with high Shannon–Wiener index scores for oil content (1.681), tocopherols (1.548), and squalene (1.201) contained rich variants, and these rich variants may be important fingerprints for the identification and evaluation of *C. oleifera* [5,21].

In this study, 434 *C. oleifera* cultivars were selected, and there was a wide variation in traits among the cultivars (H': 0.267 to 1.626; CV: 1.307% to 49.423%). The study suggests that plant domestication by artificial selection is diverse and driven by cultural traits, crop characteristics, and geo-environmental factors [22]. For example, there are more than 2,000 cultivated olive varieties in the Mediterranean basin, with a wide variety of fruit morphology, stone size, and shape [23]. The samples selected for this study were collected, as far as possible, from selected varieties within the main habitats of *C. oleifera*, geographically covering a wide area of the middle and lower reaches of the Yangtze River, with obvious differences in habitat and culture between regions. Therefore, the current major *C. oleifera* varieties in China have a high diversity of traits rather than a single variety. Through cluster analysis, we found that Group I was characterized by smaller fruits (15.175 g) and a higher linolenic acid content (0.331%), Group II varieties had a higher fresh seed yield (55.272%), Group IV varieties had a larger fresh fruit weight (50.387 g), and Group VI varieties had a higher oil content (49.165%) and oleic acid content (82.161%). Further correlation analysis with latitude revealed that fresh the fruit weight, oil content, and saturated fatty acid content of the cultivars were significantly negatively correlated with latitude, and unsaturated fatty acid content was significantly positively correlated with latitude (Figure 2). The ability to regulate membrane lipid fluidity by altering unsaturated fatty acid levels is an important characteristic of plants domesticated by environmental stress [24]. In plants, an increase in fatty acid unsaturation helps to increase the fluidity of cell membranes, prevent stress-induced membrane hardening and membrane damage, and maintain the structural and functional integrity of cell membranes, thus improving the plant's resistance to environmental stress [25–27]. Xie et al. [28] found significant gene enrichment in the fatty acid elongation pathway in *C. oleifera* during cold domestication. Thus, the increase in unsaturated fatty acids with latitude in the cultivars may be related to the evolution of their adaptations to cold stress. In summary, the domestication of *C. oleifera* is driven by a combination of artificial directional selection and environmental factors [12,23].

The domestication of wild plants to produce high-yielding and high-quality crops is an important event in the advancement of human civilization [16,29]. Strong human selection pressure on crop plants can rapidly alter phenotypic traits in crops [30]. Cultivated plants typically show changes in traits adapted to the cultivated environment, such as the greater morphological integrity of individual plants, increased yields, altered nutrient content, and reduced defenses, compared to wild species [31,32]. For example, cultivated olives have heavier fruits, larger leaves, and a significantly higher oil content than wild olives [33,34].

The results of the present study also showed that among the 10 selected traits, fresh fruit weight, fresh seed yield, seed kernel oil content, oleic acid, and unsaturated fatty acid content were significantly higher, while stearic acid, palmitic acid, linoleic acid, linolenic acid, and saturated fatty acid content were significantly lower in the cultivars compared to wild *C. oleifera* (Figure 4; Supplementary Table S11). This indicates that after nearly a thousand years of artificial selection and cultivation, the cultivars are clearly distinguishable from wild *C. oleifera*.

By comparing the differentiation coefficients of wild and cultivated *C. oleifera* traits, we found that the differentiation coefficients of five traits, including fresh fruit weight, oleic acid, unsaturated fatty acid, stearic acid, and saturated fatty acid, were greater than 95% (Table 1), which is a very high degree of differentiation and may be a potential domestication trait for *C. oleifera*. *Camellia oleifera* varieties are rich in trait variation, and the direction of selection and breeding of cultivated *C. oleifera* traits, as well as the degree of domestication, varies in different regions and at different times, resulting in the formation of a rich diversity of cultivated *C. oleifera* varieties, which can be classified into six major groups according to the degree of trait domestication (Figure 5). In order to further verify that the above five traits are the main indicators of domestication, our study used the TOPSIS method to rank the *C. oleifera* cultivars in terms of their comprehensive scores and selected the top 20 cultivars (mainly clustered in the V and VI branches) for a comparison with wild *C. oleifera*, which showed a more significant trend in the differentiation of fresh fruit weight, oleic acid, unsaturated fatty acid, stearic acid, and saturated fatty acid (Figure 6). Studies have shown that heterogamous pollinated perennials are susceptible to domestication bottlenecks due to factors such as generation overlap, generation reduction, and hybridization. These bottlenecks manifest themselves in the form of domestication that is not readily achieved or reduced trait differentiation, especially for some composite traits such as seed yield and oil content [35]. As a self-incompatible perennial flowering plant, the cultivars of pear (*Pyrus*) are mainly propagated by grafting. This has resulted in a low number of sexual generations in the history of pear domestication, which may also have led to insufficient selection pressure and phenotypic differentiation during the pear domestication process [36]. Similarly, *C. oleifera* is also a self-incompatible perennial woody oilseed plant, and most cultivars are selected from wild *C. oleifera* plants and then propagated by grafting. Such asexual lines may not undergo further selection and breeding in the later stages of propagation, which may result in the under-domestication of some complex traits of *C. oleifera* [1]. Therefore, composite traits such as fresh seed yield and oil content may still require longer-term continuous selection over multiple generations. Furthermore, through results such as PCA analysis, we found that cultivated *C. oleifera* differed significantly from wild *C. oleifera* only in terms of fresh fruit weight and oleic acid content (Figure 3). In crops where the fruit is an economically important organ, fruit size is a key component of crop yield and has been a typical trait for crop domestication [34,37]. Th enhancement of fruit size significantly increases *C. oleifera* oil production [20,38,39]. Therefore, according to the results of this study, fresh fruit weight is an important trait in the domestication process of *C. oleifera*.

Another important domestication trait of *C. oleifera* is the increase in oleic acid content in the seed. First, according to previous studies, crop seeds with high oleic acid content can effectively improve the oxidative stability and significantly increase the shelf life of seeds. Soybean seeds with high oleic acid content can be better preserved and germinated and can be easily selected by directional selection [40,41]. Similarly, wild *C. oleifera* seeds with high oleic acid content also have better antioxidant activity, which not only improves seed germination but also improves the shelf life of the pressed tea oil [42,43]. In addition, the modern breeding standard for *C. oleifera* (GBT28991-2020) also specifies the oleic acid content ($\geq$78%) of cultivars. This has led to a further increase in the oleic acid content of cultivated *C. oleifera*. In the fatty acid synthesis pathway, since the domestication of *C. oleifera* is directed to increase oleic acid synthesis, this results in a corresponding decrease in the synthesis of stearic, linoleic, and linolenic acids. Studies have shown that in the fatty

acid synthesis pathway of *C. oleifera*, the SAD gene (stearoyl-ACP desaturase) primarily catalyzes the desaturation of stearic acid to produce oleic acid [44]. The gene FAD2 (fatty acid desaturase 2) mainly regulates the desaturation of oleic acid to linoleic acid [45]. The high expression of the SAD gene and low expression of the FAD2 gene are regulatory mechanisms for oil accumulation in *C. oleifera* seeds [46]. The genes FAD3, FAD7, and FAD8 are key regulators of the conversion of linoleic acid to linolenic acid, and the reduced expression of these genes at later stages of seed development also contributes to the accumulation of oleic acid [38,45,46]. With the increasing demand for high-quality edible oil and the rapid development of molecular breeding, the results of our study can provide better theoretical support for the selection and breeding of *C. oleifera* varieties in the future.

5. Conclusions

In this study, 25 quantitative traits of wild *C. oleifera* fruit yield characteristics and seed chemical composition were determined and comprehensively evaluated, and 10 major traits were selected for comparative analyses with cultivated varieties. The results of this study showed that wild *C. oleifera* phenotypic traits contain rich variation, and fresh fruit weight and oleic acid content can be potential domestication traits for cultivated *C. oleifera*. The results of this study can help the effective excavation and utilization of wild *C. oleifera* genetic resources and enable positive explorations into *C. oleifera* breeding.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/horticulturae10050450/s1, Supplementary Table S1: Sample plot information; Supplementary Table S2: Fruit yield traits and seed chemical composition of 434 cultivars of *Camellia oleifera*; Supplementary Table S3: Fruit yield traits and seed chemical composition of wild *Camellia oleifera*; Supplementary Table S4: Average coefficient of variation (CV) of fruit yield traits and seed chemical composition of wild *Camellia oleifera*; Supplementary Table S5: Comparison of nested ANOVA and phenotypic differentiation coefficients of wild *Camellia oleifera* fruit yield traits and seed chemical composition; Supplementary Table S6: Correlation analysis among 25 quantitative traits in wild *Camellia oleifera*; Supplementary Table S7: Correlation analysis between 19 environmental climate factors; Supplementary Table S8: Correlation analysis of wild *Camellia oleifera* fruit traits and climatic factors; Supplementary Table S9: Main characteristics of 434 cultivars of *Camellia oleifera* fruit; Supplementary Table S10: Loading coefficients and contribution of wild and cultivated *Camellia oleifera* varieties on each principal component; Supplementary Table S11: Comparative analysis of nutritional composition of wild and cultivated varieties of *Camellia oleifera*; Supplementary Table S12: Cluster analysis of wild and cultivated varieties of *Camellia oleifera*; Supplementary Table S13: Comprehensive score and ranking of germplasm resources of 13 wild populations and 343 cultivars of *Camellia oleifera*; Supplementary Figure S1: Correlation of wild *Camellia oleifera* α-tocopherol with latitude.

Author Contributions: K.-F.X., Y.-J.Z. and H.-X.X. contributed equally to this work and shared first authorship. K.-F.X. and Y.-J.Z. carried out the experiment and data processing. K.-F.X. and H.-X.X. drafted the manuscript. Z.-Y.D., J.L., J.Z.(Jian Zhang), Y.Z. and J.R. assisted in reviewing the manuscript critically. S.C., J.Z.(Jun Zhou), X.-T.L. and G.-H.C. helped to prepare material for the whole experiment. All authors have read and agreed to the published version of the manuscript.

Funding: This study was funded by the National Natural Science Foundation of China (32260306), the National Natural Science Foundation of China (32270238), the National Natural Science Foundation of China (42061022), and Jiangxi Provincial Natural Science Foundation (20232BAB215014).

Data Availability Statement: Data are contained within the article or Supplementary Materials.

Conflicts of Interest: The authors declare no competing interest.

Abbreviations

FAO: the Food and Agriculture Organization of the United Nations; H′, the Shannon–Wiener index; PCA, principal component analysis; V_{ST}, the differentiation coefficients; CV, the coefficient of variation; C14:0, myristic acid; C16:0, palmitic acid; C17:0, margaric acid; C18:0, stearic acid; SFA, saturated fatty acid; C16:1, palmitoleic acid; C18:1n-9, oleic acid; C18:1n-11, Cis-11-Vaccenic

acid; C24:1n-9, nervonic acid; MUFA, monounsaturated fatty acid; C18:2n-6, linoleic acid; C18:3n-3, linolenic acid; PUFA, polyunsaturated fatty acid; UFA, unsaturated fatty acid; DLC, Daling Village, Anhui Province; TK, Tangkou Village, Anhui Province; LFS, Luofu Mountain, Guangdong Province; NL, Nanling, Guangdong Province; YBS, Yuanbao Mountain, Guangxi Province; DCP, Dengcunping Village, Hubei Province; HK, Hengkou Village, Hubei Province; HLT, Huangliantai, Hunan Province; JGS, Jinggang Mountain, Jiangxi Province; LS, Lushan Mountain, Jiangxi Province; BR, Prajna Temple, Sichuan Province; EM, Emei Mountain, Sichuan Province; QL, Qinglong Village, Sichuan Province.

References

1. Qin, S.; Rong, J.; Zhang, W.; Chen, J. Cultivation history of *Camellia oleifera* and genetic resources in the Yangtze River Basin. *Biodivers. Sci.* **2018**, *26*, 384–395. [CrossRef]
2. Ma, J.; Ye, H.; Rui, Y.; Chen, G.; Zhang, N. Fatty acid composition of *Camellia oleifera* oil. *J. Verbrauch Lebensm.* **2011**, *6*, 9–12. [CrossRef]
3. Kong, Q.; Jiang, H.; Guo, C.; Chen, T.; Feng, S.; Ding, C.; Zhou, L. Research Progress on Main Chemical Constituents and Pharmacological Activities of *Camellia oleifera*. *J. Chin. Cereals Oils Assoc.* **2022**, *37*, 194–202.
4. Gong, W.; Song, Q.; Ji, K.; Gong, S.; Wang, L.; Chen, L.; Zhang, J.; Yuan, D. Full-Length Transcriptome from *Camellia oleifera* Seed Provides Insight into the Transcript Variants Involved in Oil Biosynthesis. *J. Agric. Food Chem.* **2020**, *68*, 14670–14683. [CrossRef] [PubMed]
5. Zhang, F.; Zhu, F.; Chen, B.; Su, E.; Chen, Y.; Cao, F. Composition, bioactive substances, extraction technologies and the influences on characteristics of *Camellia oleifera* oil: A review. *Food Res. Int.* **2022**, *156*, 111159. [CrossRef] [PubMed]
6. Quan, W.; Wang, A.; Gao, C.; Li, C. Applications of Chinese *Camellia oleifera* and its By-Products: A Review. *Front. Chem.* **2022**, *10*, 921246. [CrossRef] [PubMed]
7. Gao, J.; Ma, L.; Ma, J.; Xia, S.; Gong, S.; Yin, Y.; Chen, Y. Camellia (*Camellia oleifera* Abel.) Seed Oil Regulating of Metabolic Phenotype and Alleviates Dyslipidemia in High Fat-Fed Mice through Serum Branch-Chain Amino Acids. *Nutrients* **2022**, *14*, 2424. [CrossRef] [PubMed]
8. Yang, R.; Qiu, S.; Yang, R.; Tian, H.; Tang, T.; Liao, D.; Li, J.; Li, S. Research Progress of Edible and Medicinal Value of *Camellia Oleifera* Seeds. *Mod. Tradit. Chin. Med. Mater. Medica-World Sci. Technol.* **2019**, *21*, 2770–2774.
9. Cui, X.; Wang, W.; Yang, X.; Li, S.; Qin, S.; Rong, J. Potential distribution of wild *Camellia oleifera* based on ecological niche modeling. *Biodivers. Sci.* **2016**, *24*, 1117–1128. [CrossRef]
10. Cui, X.; Li, C.; Qin, S.; Huang, Z.; Gan, B.; Jiang, Z.; Huang, X.; Yang, X.; Li, Q.; Xiang, X.; et al. High-throughput sequencing-based microsatellite genotyping for polyploids to resolve allele dosage uncertainty and improve analyses of genetic diversity, structure and differentiation: A case study of the hexaploid *Camellia oleifera*. *Mol. Ecol. Resour.* **2022**, *22*, 199–211. [CrossRef]
11. Miller, A.J.; Gross, B.L. From forest to field: Perennial fruit crop domestication. *Am. J. Bot.* **2011**, *98*, 1389–1414. [CrossRef] [PubMed]
12. Purugganan, M.D. Evolutionary Insights into the Nature of Plant Domestication. *Curr. Biol.* **2019**, *29*, R705–R714. [CrossRef] [PubMed]
13. Gao, L.; Kantar, M.B.; Moxley, D.; Ortiz-Barrientos, D.; Rieseberg, L.H. Crop Adaptation to Climate Change: An Evolutionary Perspective. *Mol. Plant* **2023**, *16*, 1518–1546. [CrossRef]
14. Song, B.; Ning, W.; Wei, D.; Jiang, M.; Zhu, K.; Wang, X.; Edwards, D.; Odeny, D.A.; Cheng, S. Plant genome resequencing and population genomics: Current status and future prospects. *Mol. Plant* **2023**, *16*, 1252–1268. [CrossRef] [PubMed]
15. Meyer, R.S.; Purugganan, M.D. Evolution of crop species: Genetics of domestication and diversification. *Nat. Rev. Genet.* **2013**, *14*, 840–852. [CrossRef] [PubMed]
16. Doebley, J.F.; Gaut, B.S.; Smith, B.D. The molecular genetics of crop domestication. *Cell* **2006**, *127*, 1309–1321. [CrossRef]
17. Li, G.; Ma, L.; Yan, Z.; Zhu, Q.; Cai, J.; Wang, S.; Yuan, Y.; Chen, Y.; Deng, S. Extraction of Oils and Phytochemicals from *Camellia oleifera* Seeds: Trends, Challenges, and Innovations. *Processes* **2022**, *10*, 1489. [CrossRef]
18. Lesack, K.; Naugler, C. An open-source software program for performing Bonferroni and related corrections for multiple comparisons. *J. Pathol. Inform.* **2011**, *2*, 52. [CrossRef] [PubMed]
19. Zhang, Z.; Yao, Z.; Ma, Q.; Liu, J.; Liu, Y.; Liang, W.; Zhang, T.; Yin, D.; Liu, W.; Qiao, Q. A study on the phenotypic diversity of *Sinopodophyllum hexandrum* (Royle) ying. *Pak. J. Bot.* **2022**, *54*, 2291–2302. [CrossRef]
20. Chen, T.; Liu, L.; Zhou, Y.; Zheng, Q.; Luo, S.; Xiang, T.; Zhou, L.; Feng, S.; Yang, H.; Ding, C. Characterization and comprehensive evaluation of phenotypic characters in wild *Camellia oleifera* germplasm for conservation and breeding. *Front. Plant Sci.* **2023**, *14*, 1052890. [CrossRef]
21. Shi, T.; Wu, G.; Jin, Q.; Wang, X. Camellia oil authentication: A comparative analysis and recent analytical techniques developed for its assessment. A review. *Trends Food Sci. Technol.* **2020**, *97*, 88–99. [CrossRef]
22. Milla, R.; Osborne, C.P.; Turcotte, M.M.; Violle, C. Plant domestication through an ecological lens. *Trends Ecol. Evol.* **2015**, *30*, 463–469. [CrossRef] [PubMed]

23. Breton, C.; Terral, J.-F.; Pinatel, C.; Médail, F.; Bonhomme, F.; Bervillé, A. The origins of the domestication of the olive tree. *CR Biol.* **2009**, *332*, 1059–1064. [CrossRef] [PubMed]
24. Upchurch, R.G. Fatty acid unsaturation, mobilization, and regulation in the response of plants to stress. *Biotechnol. Lett.* **2008**, *30*, 967–977. [CrossRef] [PubMed]
25. Xiao, R.; Zou, Y.; Guo, X.; Li, H.; Lu, H. Fatty acid desaturases (FADs) modulate multiple lipid metabolism pathways to improve plant resistance. *Mol. Biol. Rep.* **2022**, *49*, 9997–10011. [CrossRef] [PubMed]
26. Zhang, M.; Barg, R.; Yin, M.G.; Gueta-Dahan, Y.; Leikin-Frenkel, A.; Salts, Y.; Shabtai, S.; Ben-Hayyim, G. Modulated fatty acid desaturation via overexpression of two distinct ω-3 desaturases differentially alters tolerance to various abiotic stresses in transgenic tobacco cells and plants. *Plant, J.* **2005**, *44*, 361–371. [CrossRef] [PubMed]
27. Mikami, K.; Murata, N. Membrane fluidity and the perception of environmental signals in cyanobacteria and plants. *Prog. Lipid Res.* **2003**, *42*, 527–543. [CrossRef] [PubMed]
28. Xie, H.; Zhang, J.; Cheng, J.; Zhao, S.; Wen, Q.; Kong, P.; Zhao, Y.; Xiang, X.; Rong, J. Field plus lab experiments help identify freezing tolerance and associated genes in subtropical evergreen broadleaf trees: A case study of *Camellia oleifera*. *Front. Plant Sci.* **2023**, *14*, 1113125. [CrossRef] [PubMed]
29. Zeder, M.A. Core questions in domestication research. *Proc. Natl. Acad. Sci. USA* **2015**, *112*, 3191–3198. [CrossRef]
30. Chen, Y.H.; Gols, R.; Benrey, B. Crop Domestication and Its Impact on Naturally Selected Trophic Interactions. *Annu. Rev. Entomol.* **2015**, *60*, 35–58. [CrossRef]
31. Levis, C.; Costa, F.R.C.; Bongers, F.; Peña-Claros, M.; Clement, C.R.; Junqueira, A.B.; Neves, E.G.; Tamanaha, E.K.; Figueiredo, F.O.G.; Salomao, R.P.; et al. Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. *Science* **2017**, *355*, 925–931. [CrossRef]
32. Whitehead, S.R.; Turcotte, M.M.; Poveda, K. Domestication impacts on plant-herbivore interactions: A meta-analysis. *Philos. Trans. R Soc. B Biol. Sci.* **2017**, *372*, 20160034. [CrossRef]
33. Kassa, A.; Konrad, H.; Geburek, T. Molecular diversity and gene flow within and among different subspecies of the wild olive (*Olea europaea* L.): A review. *Flora* **2019**, *250*, 18–26. [CrossRef]
34. Besnard, G.; Terral, J.-F.; Cornille, A. On the origins and domestication of the olive: A review and perspectives. *Ann. Bot.* **2018**, *121*, 385–403. [CrossRef]
35. Gaut, B.S.; Diez, C.M.; Morrell, P.L. Genonics and the Contrasting Dynamics of Annual and Perennial Domestication. *Trends Genet.* **2015**, *31*, 709–719. [CrossRef]
36. Wu, J.; Wang, Y.; Xu, J.; Korban, S.S.; Fei, Z.; Tao, S.; Ming, R.; Tai, S.; Khan, A.M.; Postman, J.D.; et al. Diversification and independent domestication of Asian and European pears. *Genome Biol.* **2018**, *19*, 77. [CrossRef]
37. Jahed, K.R.; Hirst, P.M. Fruit growth and development in apple: A molecular, genomics and epigenetics perspective. *Front. Plant Sci.* **2023**, *14*, 1122397. [CrossRef]
38. Ye, C.; He, Z.; Peng, J.; Wang, R.; Wang, X.; Fu, M.; Zhang, Y.; Wang, A.; Liu, Z.; Jia, G.; et al. Genomic and genetic advances of oiltea-camellia (*Camellia oleifera*). *Front. Plant Sci.* **2023**, *14*, 1101766. [CrossRef]
39. Yan, C.; Lin, P.; Lyu, T.; Hu, Z.; Fan, Z.; Li, X.; Yao, X.; Li, J.; Yin, H. Unraveling the Roles of Regulatory Genes during Domestication of Cultivated *Camellia*: Evidence and Insights from Comparative and Evolutionary Genomics. *Genes* **2018**, *9*, 488. [CrossRef]
40. La, T.C.; Pathan, S.M.; Vuong, T.; Lee, J.D.; Scaboo, A.M.; Smith, J.R.; Gillen, A.M.; Gillman, J.; Ellersieck, M.R.; Nguyen, H.T.; et al. Effect of High-Oleic Acid Soybean on Seed Oil, Protein Concentration, and Yield. *Crop Sci.* **2014**, *54*, 2054–2062. [CrossRef]
41. Bachleda, N.; Grey, T.; Li, Z.L. Effects of high oleic acid soybean on seed yield, protein and oil contents, and seed germination revealed by near-isogeneic lines. *Plant Breed* **2017**, *136*, 539–547. [CrossRef]
42. Wang, Z.; Huang, B.; Ye, J.; He, Y.; Tang, S.; Wang, H.; Wen, Q. Comparative transcriptomic analysis reveals genes related to the rapid accumulation of oleic acid in *Camellia chekiangoleosa*, an oil tea plant with early maturity and large fruit. *Plant Physiol. Biochem.* **2022**, *171*, 95–104. [CrossRef] [PubMed]
43. Wei, Z.; Guo, M.; Wang, Y.; Duan, Z.; Yang, K.; Luan, X. Recent Advances in Research on Polyphenol Compounds in *Camellia oleifera* Seed Oil. *Food Sci.* **2021**, *42*, 311–320.
44. Yang, J.; Chen, B.; Manan, S.; Li, P.; Liu, C.; She, G.; Zhao, S.; Zhao, J. Critical metabolic pathways and SAD/FADs, WRI1s, and DGATs cooperate for high-oleic acid oil production in developing oil tea (*Camellia oleifera*) seeds. *Hortic Res.* **2022**, *9*, uhac087. [CrossRef] [PubMed]
45. Wu, B.; Ruan, C.; Han, P.; Ruan, D.; Xiong, C.; Ding, J.; Liu, S. Comparative transcriptomic analysis of high- and low-oil *Camellia oleifera* reveals a coordinated mechanism for the regulation of upstream and downstream multigenes for high oleic acid accumulation. *3 Biotech* **2019**, *9*, 257. [CrossRef]
46. Lin, P.; Wang, K.; Zhou, C.; Xie, Y.; Yao, X.; Yin, H. Seed Transcriptomics Analysis in *Camellia oleifera* Uncovers Genes Associated with Oil Content and Fatty Acid Composition. *Int. J. Mol. Sci.* **2018**, *19*, 118. [CrossRef]