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Effects of Scion Variety on the Phosphorus Efficiency of Grafted *Camellia oleifera* Seedlings

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Abstract: Grafting provides a way to improve tolerance to low phosphorus (P) stress for plants, and has been extensively applied in commercial cultivars grafted onto appropriate rootstocks. However, little literature is available concerning the scion-mediated effect on P efficiency in grafted plants. In this study, three different *Camellia oleifera* Abel. scion cultivars (G8, G83-1, and W2) were grafted onto the same rootstock (W2) under controls (0.5 mM) and low-P (0 mM) availability for eight months. The results showed that the scions significantly affected root-to-shoot weight ratios, the root morphology with a diameter larger than 1 mm, P accumulation, and the P utilization efficiency (PUE) of the root. A higher increase in the root-to-shoot weight ratio under the low-P supply was observed in the G83-1/W2 (26.15%) than in the G8/W2 (0%) and the W2/W2 (5.32%). Root PUE of the scion G8, G83-1, and W2 was improved by up to 113.73%, 45.46%, and 20.97% under the low-P supply. Moreover, G8/W2 exhibited higher shoot P accumulation and the highest root PUE under the low-P supply, indicating a high capability to tolerate P deficiency by maximizing the cost-effectiveness of P remobilization to photosynthetic organs. This suggested the vigorous variety of G8 could be a promising scion to improve grafted *C. oleifera* tolerance to low-P stress. Our results would have important implications for exploration and identification of a superior scion variety to enhance the ability of resistance concerning P deficiency stress in *C. oleifera*.

Keywords: grafting; scion variety; *Camellia oleifera*; root morphology; low-P supply

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1. Introduction

Phosphorus (P), as an important component of macromolecular substances, which include nucleic acid and the cytomembrane, is intimately involved in plant growth and development [1,2]. Even when soil total P is relatively high, only 10–25% is available for plants owing to P's immobilization in soil [3,4]. Accordingly, P deficiency has become a primary factor limiting agriculture. Application of P fertilizers is required to improve and maintain crop yields worldwide, but only 10–20% of applied P fertilizer is directly utilized by plants [5–7]. The remaining P fertilizer is wasted and ultimately results in the loss of resources and surface water P pollution. As such, balancing the relationship between the amount of applied P fertilizer and P utilization of plants has been gaining extensive attention among policymakers and plant scientists.

Differences in the ability of plants to acquire P exist among different species or varieties within a single species [8–10]. Genetic improvement of P efficiency in plants, as achieved through the breeding of P-efficient cultivars, has been utilized to optimize plant production under lower fertilizer use conditions [11–13]. In many plants, rootstocks are widely employed to promote the P use efficiency of scion cultivars [14,15]. This is possible through rootstocks with high P efficiency being able to uptake more ions by efficient root morphologies and root architectures [16,17]. The selection of P-efficient rootstocks has been conducted in various species [18,19]. However, the P efficiency of grafted plants is both rootstock and scion dependent. Most of the available information on the P efficiency of plants has been obtained through experiments with rootstocks, while the P use of scions and P transportation between rootstocks and scions have been under-examined [20,21]. For example, the P efficiency of different scions grafted onto the same rootstock has not been reported yet.

The tea-oil camellia (*Camellia oleifera* Abel.) is an important woody edible-oil species cultivated in East Asia [22,23]. Tea-seed oil extracted from the seeds of this plant is well known as a healthy cooking oil owing to its high contents of unsaturated fatty acids, antioxidants, and vitamins [24]. In China, this species has been cultivated for over 2300 years. The cultivation areas were more than 4.5 million ha in 2020. *C. oleifera* is often planted in the hilly areas and low mountains of South China [22]. Owing to heavy rain leaching and adsorption of aluminum phosphate, the soil found in extensive areas of South China is characterized by P deficiency, which severely limits the growth and productivity of tea-oil cultivation [25,26].

Nurse seedling grafting is a primary way of propagating *C. oleifera* cultivars, in which semi-woody branches (scions) are joined to young seedling rootstocks without leaves. Because of high cell division activity between scions and rootstocks of the grafted plants with good compatibility, the young shoot tissue can enhance the survival probability of the grafted plant, and this technique is extensively applied in many camellia species [17]. There have been some studies focusing on the underlying physiological mechanisms determining the healing process and signaling pathways of the union formation process of *C. oleifera* [27,28]; however, our knowledge of whether the grafting alters the tolerance to abiotic stress in *C. oleifera* remains poor and somewhat fragmented. Additionally, some varieties with random rootstocks that influence the root development in grafted *C. oleifera* plants have been reported [29]. However, the effects of different vigorous scion varieties grated on the same rootstock on biomass allocation and strategies of P uptake and utilization under low-P stress have yet been estimated.

In this study, we evaluated the response of three different *C. oleifera* scions grafted onto the same rootstock cultivar under controls and low-P conditions (0.5 mM and 0 mM, respectively). The current research focused on the following: (1) Scion-mediated and P availability impact on the biomass allocation; (2) scion-mediated and P availability impact on root morphology in different diameter classes; (3) scion-mediated and P availability impact on P accumulation and P utilization efficiency.

2. Materials and Methods

2.1. Plant Materials and Treatments

This experiment used three *C. oleifera* cultivars ('Ganwu 2', 'Gan 8', and 'Ganshi 83-1') as the scions, which had obvious different morphology and had relatively greater planting areas in Jiangxi Province, eastern China. For example, 'Gan 8' (G8) has a greater crown and leaf area ratio [30]. 'Ganshi 83-1' (G83-1) has greater biomass [31]. 'Ganwu 2' (W2) has a relatively greater seedling height [32], of which seedlings were used as the rootstock in this experiment. In November, large, plump, and shiny seeds (W2) were collected from the *C. oleifera* germplasm bank in Jiangxi province, and stored outdoors in wet river sands until the following May. After germinating, the resulting plants were employed as rootstocks (Figure 1a). Robust half-lignified branches (W2, G8, and G83-1) were picked from the cutting orchard and used as scions for cleft grafting (Figure 1b). The nurse seedling grafting procedure for *C. oleifera* followed the methods of Feng et al. [32]. A total of three grafting combinations were generated, including W2 self-grafted (W2/W2) and two scion genotypes grafted onto W2 (G8/W2 and G83-1/W2).

Figure 1. *C. oleifera* nurse seedling grafting and the root morphology. (**a**) Rootstock; (**b**) Scion; (**c**) Grafted combination; (**d**) Root morphology for the grafted *C. oleifera*; (**e**) Grafted *C. oleifera* seedlings with two years.

2.2. Experimental Design

All seedlings were planted in a seedbed fertilized with farmyard manure and covered by a sun shelter. Because of high cell division activity for *C. oleifera* [32], all nurse grafting unions in this experiment almost survived. There were no significant differences in the affinity found among the three combinations. Until the next spring (January), uniformly growing plants were selected and transplanted into plastic containers (diameter and depth of 20.5 cm and 17.0 cm, respectively). In total, 36 grafting plants were transplanted. Each container filled with river sand contained one plant. The camellia seedlings were first rinsed with tap water for one month and then modified Hoagland nutrient solution. In this study, we employed 0.5 mM as the control condition, recognized as the optimum P availability for *C. oleifera* [33]. Owing to high adaptation in acidic red soils with P deficiency of wild *C. oleifera* trees, extremely low P (0 mM) was employed as deficient P in the experiment duration. The concentrations of the other macro- and micro-nutrient solution were: 2.0 mM $Ca(NO_3)_2$, 2.0 mM KNO_3, 1.0 mM $MgSO_4$, 1.0 mM $(NH_4)_2SO_4$, 50 µM H_3BO_3, 50 µM Fe-EDTA, 15 µM $ZnSO_4$, 2.0 µM $CuSO_4$, and 50 µM $MnSO_4$. KH_2PO_4 was used as the P source. There were six treatments, with three grafted combinations (W2/W2, G8/W2, and G83-1/W2), two P levels (0.5 mM, 0 mM), and six replicates with one grafting plant for each treatment. Every ten days, 200 mL of the corresponding nutrient solutions was replenished. All experiments were conducted in a greenhouse at the Science and Technology Park of Jiangxi Agricultural University, Nanchang, China (28°45′ N, 115°49′ E).

2.3. Determination of Biomass and Tissue Phosphorus Concentration

Eight months after starting low-P treatment, the whole plants were harvested and separated into different tissues (Figure 1e). Shoots and roots were oven-dried to weigh the shoot dry weight (SDW) and root dry weight (RDW). Total P contents were determined by the molybdenum antimony anti-colorimetric method [20]. P uptake efficiency was estimated as the total P accumulated in the plant. P accumulation and P utilization efficiency (PUE) were calculated as follows [33,34]:

$$\text{P accumulation (mg)} = \text{P concentration (mg/g)} \times \text{dry weight (g)}$$

$$\text{PUE (g/mg)} = \text{dry weight(g)/P accumulation (mg)}$$

2.4. Root Morphology

After cleaning using running water, the whole roots were dispersed in a transparent acrylic container over the Expression 10000XL 3.49 scanner (Epson Telford Ltd. Telford, UK) and scanned (Figure 1d). WinRHIZO (Pro2012b) software (Regent Instruments Company, Quebec, Canada) was employed to evaluate root length, root surface area, and root volume.

2.5. Statistical Analysis

Two-factor analysis of variance (ANOVA) was employed to explore the influence of scion cultivars, P availability, and their interaction among different grafted plants using SPSS 25.0. Throughout all figures, ***, **, and * indicate significance at the $p \leq 0.001$, $p \leq 0.01$, and $p \leq 0.05$ thresholds, respectively, while 'ns' indicates $p > 0.05$. The one-way ANOVA was used to determine any statistically significant differences between the control and low P conditions. The comparison was carried out using Duncan multiple range test at $\alpha = 0.05\%$.

3. Results

3.1. Scions Affected the Dry Weight of Grafted *C. oleifera*

We evaluated the shoot dry weight (SDW) and the root dry weight (RDW) among grafted *C. oleifera* with different scions on the same rootstocks under control and low-P availability. The results showed that the RDWs were not altered among different scions of grafted *C. oleifera* in either treatment (Figure 2a). However, the SDWs were significantly affected by the use of scion cultivars and the interaction between scion cultivar and P availability (Figure 2b). Considering total DW (TDW) for the whole plant, the grafted unions of G8/W2 and G83-1/W2 performed better than that of the self-grafted plants (W2/W2) under control conditions (Figure 2c). Furthermore, TDW of G8/W2 was enhanced by up to 22.7% compared with the G83-1/W2 under the low-P supply, but no significant differences were found between G8/W2 and G83-1/W2 under control conditions. Moreover, the RDW of G8 and G83-1 scion cultivars were higher compared with the self-grafted (W2/W2) under controls and the low-P supply (Figure 2a). The ratio of root to shoot was affected by the use of different scion cultivars, P availability, and their interaction (Figure 2d). The root-to-shoot ratio of G83-1/W2 under low P supply was significantly increased compared to controls; it was up to 26.15% higher than that of G8/W2 (0%) and W2/W2 (5.32%).

3.2. Scions Affected Root Morphology of Grafted *C. oleifera*

In this work, several root morphological indexes on different classes of root diameters were utilized to determine which scion cultivars, the P availability, and their interactions would influence the grafted *C. oleifera* plants. The results showed that scion cultivars significantly affected the total root surface area and root volume, but did not influence the total root length (Figure 3). On the other hand, scion impact on the root length with a root diameter larger than 1 mm was detected for grafted *C. oleifera* seedlings (Table 1). However, the root length with a root diameter less than 1 mm (accounting for 79.8% of the total root length), which were observably higher than the rest of the root diameter classes (Figure 3a), was not significantly affected by nutrient treatment and scion varieties (Table 1). Furthermore, the root volume with a root diameter larger than 3 mm, accounting for 64.2% of the total root volume, exceeded the total root volume of the remaining diameter classes (Figure 3c).

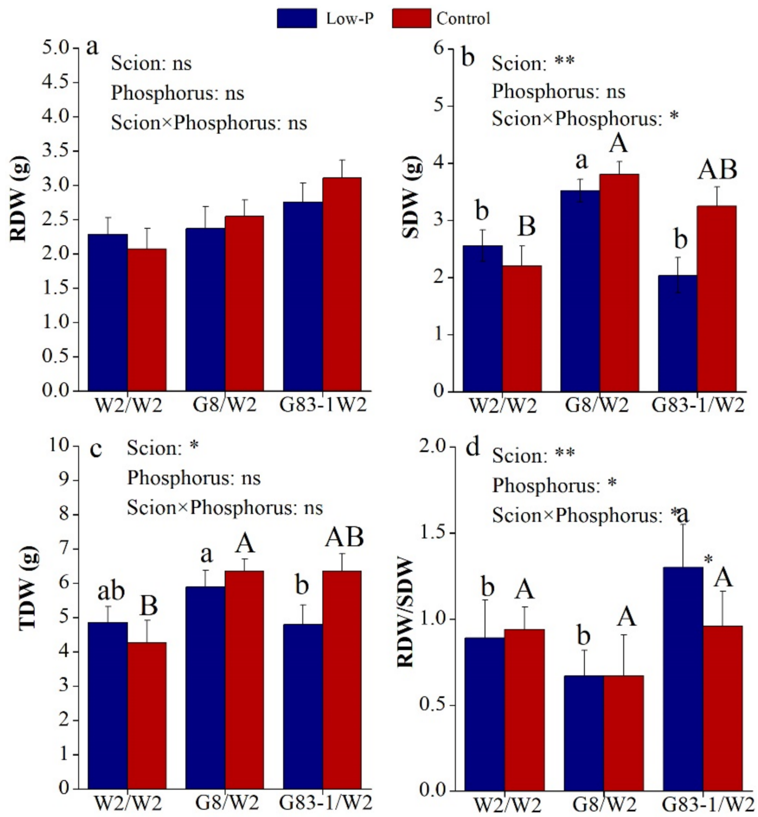

Figure 2. Root dry weight (RDW) (**a**), shoot dry weight (SDW) (**b**), total DW (TDW) (**c**), and root-to-shoot ratio (RDW/SDW) (**d**) of the scions (W2, G8, and G83-1) grafted onto W2 rootstock under control (0.5 mM) and low-P (0 mM) conditions during eight months. Lowercase and uppercase indicated significant differences among grafted combination under controls and the low-P supply treatments, respectively. * and ** in the figure legend indicated significant effect of Scion, P, and their interaction at level of $p \leq 0.05$ and $p \leq 0.01$, respectively. ns, no significant different between treatments. * on the bar indicated significant differences between control and low-P treated plants (α = 0.05%).

Table 1. Two-way ANOVA on the effects of scion cultivars, P availability, and their interaction on root length, root surface area, and root volume (*p*-values) for roots of diameters (d) ≤1 mm, 1 to 3 mm, and >3 mm (ns, nonsignificant).

Root Diameter (mm)	Factor	Root Length	Root Surface Area	Root Volume
Total roots	Scion	ns	<0.01	<0.05
	Phosphorus	ns	ns	ns
	Scion × Phosphorus	ns	ns	ns
$d \leq 1$	Scion	ns	<0.05	<0.05
	Phosphorus	ns	ns	ns
	Scion × Phosphorus	ns	ns	ns
$1 < d \leq 3$	Scion	<0.001	<0.001	<0.001
	Phosphorus	<0.01	<0.01	<0.01
	Scion × Phosphorus	ns	ns	ns
$d > 3$	Scion	<0.01	<0.01	<0.01
	Phosphorus	<0.01	<0.05	ns
	Scion × Phosphorus	ns	ns	ns

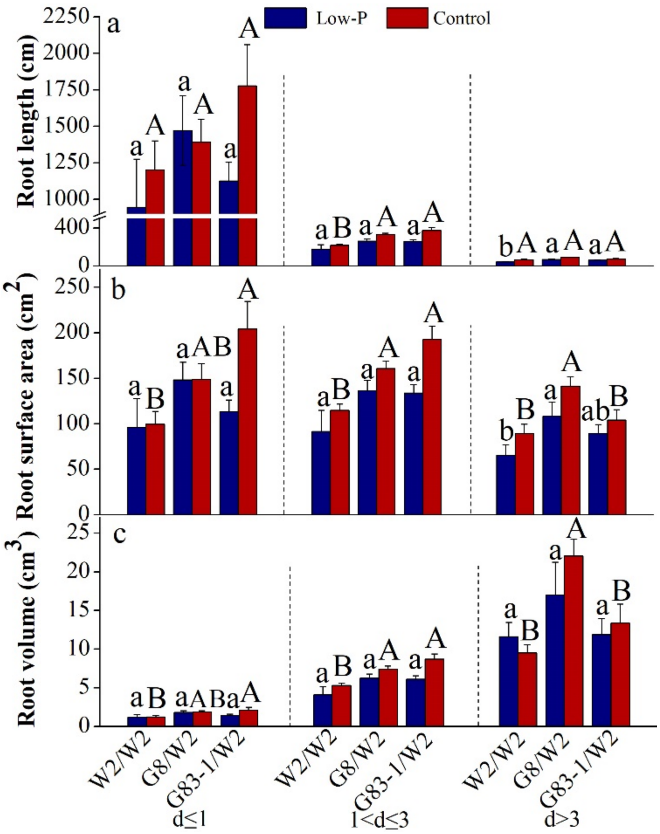

Figure 3. Root length (**a**), root surface area (**b**), root volume (**c**) of the scion (W2, G8, and G83-1) grafted onto W2 rootstock under control (0.5 mM) and low-P (0 mM) conditions during eight months. Lowercase and uppercase indicate significant differences among grafted combination under controls and the low-P supply treatments, respectively ($p \leq 0.05$).

The total root length, root surface area, and root volume for three scion cultivars of grafted plants under low-P supply were lower compared to controls (Figure 3). No significant differences in the root morphological parameters were detected among any combinations at any root diameter classes under low-P supply. Only the root length and root surface area (larger than 3 mm in a root diameter) of G8/W2 and/or G83-1/W2 were higher than that of the self-grafted plants (W2/W2) under low-P supply (Figure 3a,b). However, there were obvious differences in root surface area and root volume among three grafting combinations at all root diameter classes under control conditions ($p \leq 0.05$) (Figure 3). Moreover, different scions grafted onto W2 rootstock (including G8/W2 and G83-1/W2) under controls showed the greater potential of the root growth in comparison with the self-grafted plants (Figure 3). Interestingly, the scion G8 had the highest root surface area and root volume (larger than 3 mm in diameter) under controls ($p \leq 0.05$) and achieved relatively great performance on root length and root surface area (less than 1 mm in a diameter) even under the low-P supply (Figure 3).

3.3. *Scions Affected P Accumulation and P Utilization Efficiency (PUE) of the Root of Grafted C. oleifera*

The root P accumulation was apparently affected by scion cultivars and P availability ($p \leq 0.01$) (Table 2). P accumulation of G8/W2 and G83-1/W2 combinations in the root under low-P supply were apparently decreased compared to under controls, while no similar result was detected in grated W2/W2 plants. The percentage of P accumulation in the root was much lower in G8/W2 (23.08%) than in grafted plants G83-1/W2 (52.59%) under low-P conditions. Scion varieties significantly affected the shoot P accumulation under low-P supply, while no expectations were found under controls. Low-P treatments also decreased the P accumulation in the shoots of G8/W2 and G83-1/W2. However, the decreases of shoot P accumulation imposed by the P deficiency were smaller in G8/W2 (24.64%) than in grafted plants G83-1/W2 (56.55%).

Table 2. Effects of scion cultivars, P availability and their interaction on P accumulation and P uptake efficiency.

Scion/Rootstock	P Availability	Root P Accumulation	Shoot P Accumulation	Plant P Uptake Efficiency	Root P Accumulation/Plant P Uptake Efficiency
	mM	mg	mg	mg	%
W2/W2	Control	3.30 ± 0.46 B	6.70 ± 2.07 A	10.00 ± 3.92 B	33.00
	Low-P	2.98 ± 0.36 ab	5.74 ± 1.36 ab	8.72 ± 2.36 a	34.17
G8/W2	Control	5.03 ± 0.20 AB *	9.82 ± 1.44 A	14.85 ± 1.44 AB *	33.87
	Low-P	2.22 ± 0.36 b	7.40 ± 1.68 a	9.62 ± 2.10 a	23.08
G83-1/W2	Control	7.76 ± 0.55 A *	8.86 ± 2.96 A *	16.62 ± 3.00 A *	46.69
	Low-P	4.27 ± 0.88 a	3.85 ± 2.2 b	8.12 ± 2.61 a	52.59
Significance					
Scion (S)		**	**	ns	
Phosphorus (P)		**	**	***	
S × P		ns	ns	ns	

The values represent the means ± standard error. *, **, and *** denote $p \leq 0.05$, 0.01, and 0.001, respectively. Lowercase and uppercase indicate significant differences among grafted combination under controls and the low-P supply treatments, respectively ($p \leq 0.05$). * indicates significant differences between control and low-P treated plants (α = 0.05%).

The root PUE and the shoot PUE were significantly affected by scion cultivars, P availability, and their integration ($p \leq 0.001$) (Figure 4a). Compared with the plants grown under control conditions, low-P treatment significantly increased the PUE of the root, shoot, and whole plant of all grafting *C. oleifera* plants regardless of scion genotypes (Figure 4c). The increases of the root PUE imposed by the reduced P supply were higher in G8/W2 (113.73%) than in W2/W2 (20.97%) and G83-1/W2 (45.46%), while there was no significant difference in shoot PUE under the low-P supply.

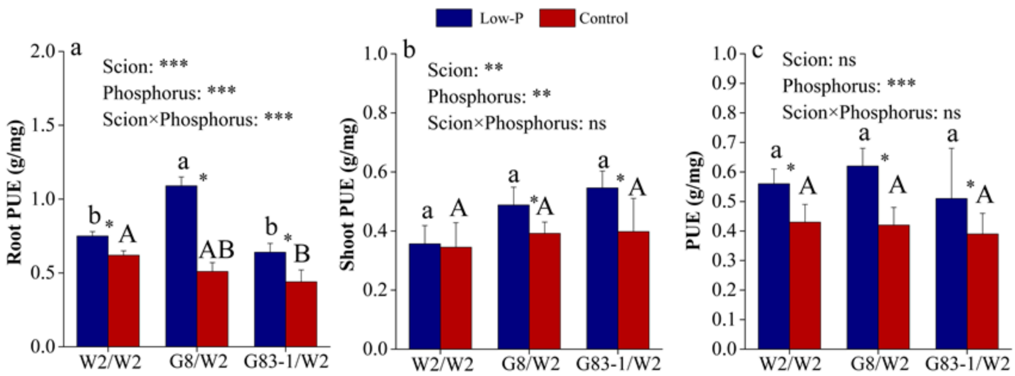

Figure 4. Root P utilization efficiency (Root PUE) (**a**), shoot P utilization efficiency (Shoot PUE) (**b**), and P utilization efficiency (PUE) (**c**) of the scions (W2, G8, and G83-1) grafted onto W2 rootstock under control (0.5 mM) and low-P (0 mM) conditions during eight months. Lowercase and uppercase indicate significant differences among the grafted combination under controls and low-P supply treatments, respectively. * on the bar indicated significant differences between control and low-P treated plants according to the one-way ANOVA test (α = 0.05%). ** and *** in the figure legend indicated significant effect of Scion, P, and their interaction at level of $p \leq 0.01$ and $p \leq 0.001$, respectively. ns, no significant different between treatments.

4. Discussion

To improve plant adaptation to a range of stress, grafting scion varieties onto rootstocks is extensively employed for many woody economic species [35,36]. A great deal of research has been conducted on rootstock-induced changes in scion vigor [37–39], but there has been a lack of literature that has examined the influence of scion genotypes on biomass allocation and root development in grafted plants, especially under nutrient limitation. A previous study reported variety differences in spatial distribution and monthly dynamics of fine roots for five different cultivars of *C. oleifera* using the minirhizotron technique [29]. However, they used the random rootstocks and also did not investigate the effect of P nutrient availability. This work found that the scion genotypes and P availability could affect the dry weights allocations, root morphology, root P accumulations, and root PUE among three different scion cultivars grafted onto the same *C. oleifera* rootstock.

Plant biomass allocation is generally influenced by nutrient availability, developmental stage, and genotype [40]. In the present study, the genetic variability among scions largely explained differences in the dry weights and allocation biomass of the aboveground organ among the grafted *C. oleifera* seedlings (Figure 2). The total DW of G8/W2 grafted plants performed better under two treatment conditions than the other grafted combinations (Figure 2c), indicating that G8 was a vigorous scion with relatively higher photochemical efficiency and higher dry weight. Wang et al. [41] reported that the *C. oleifera* scion cultivars of G8 had a relatively greater crown and leaf area. The RDW/SDW of G83-1/W2 under low P supply was higher compared to controls (Figure 2d), and no similar results were found in the other grafting unions, suggesting that scion cultivar G83-1 was sensitive to low P stress. The SDW of G83-1/W2 was lower (Figure 2b) and the root P accumulation was higher under the low-P level (Table 2), indicating that low P may restrict the shoot growth and promote P transfer from the leaves to the roots for scion cultivars G83-1.

Root development can be determined by the intrinsic genetic program of the rootstock and nutrient conditions in the external environment. In this study, we found that the scion genotypes also strongly impacted the root length (larger than 1 mm in diameter), root surface area, and root volume of the same rootstocks in different grafted *C. oleifera* combinations (Figure 3 and Table 1). Furthermore, the root growth of G8/W2 and G83-1/W2 under controls performed better than that of the self-grafted plants (Figure 3). These effects may have resulted from differences in the ability of the grafted plants to transport carbon supply from the shoot, which could thus determine root carbon acquisition and control root development [42,43]. Previous studies reported that coarse roots (larger than 3 mm in a diameter) could affect water and nutrient transport capacity [44,45]. In the current study, the scion cultivar of G8 with high SDW as a vigorous scion performed better on root surface area and root volume of coarse roots than that of the other grafted *C. oleifera* under controls ($p \leq 0.05$), suggesting vigorous scion can promote the growth of roots and enhance plants' ability to absorb P.

Fine roots (less than 1 mm in diameter), as a better indicator of root response to the nutrients in the soil [46,47], accounted for 79.8% of the total root length in this study (Figure 3a). However, no significant differences in root length were detected among fine roots (less than 1.0 mm in diameter) under both controls and low-P treatments (Figure 3a). Furthermore, no significant effect on root morphology was detected among combinations at the low-P supply, with a few exceptions (Figure 3). Because of the presence of P mainly in the upper layers of soil and decreasing with depth, root growth can be enhanced under P deficiency, especially with respect to the fine roots [48–51]. However, no effects were found in the current study, perhaps owing to our sampling only once for the whole experiment. Moreover, since nutrients and water were added regularly during the treatment, it was unlikely that differences in fine roots (less than 1 mm in diameter) resulted in different shoot performance and P uptake, especially for woody species. Similar results were detected in tomato roots under low P availability [21].

When facing nutrient stress, more efficient plants/genotypes have evolved underlying strategies allowing them to get access to obtain sufficient amounts of the nutrient (nutrient accumulation) and/or improve efficiency utilizing quantities (nutrient utilization efficiency) of the existing nutrients [52,53]. The scion variety of G8 significantly improved shoot P accumulation (Table 2) and root PUE under the low-P supply (Figure 4a). These results indicate that the higher tolerance of G8 to P deficiency was owing to a higher root PUE and a higher accumulation to transfer more P to the shoot. The capability to recycle P from non-photosynthetic organs like roots to upper shoots can maximize the cost-effectiveness of P remobilization to tolerate P deficiency [54]. However, the more P sensitive scion G83-1 grafted onto W2 showed higher P accumulation in the root and lower PUE in the shoot (Table 2 and Figure 2), which may affect the tolerance to the low-P stress.

5. Conclusions

This work comprised a comprehensive study of the scion-mediated effect on the root growth and strategies of nutrient uptake and utilization in grafted *Camellia oleifera* Abel. seedlings under low phosphorus (P) treatments. The more vigorous scion variety of 'Gan 8' with higher shoot dry weights can improve grafting plants' tolerance to the low-P supply, which appeared to result from a greater ability to take up P and translocate it to the shoot. Therefore, our results suggested 'Gan 8' as promising scions for farmers under low-P supply for grafted *C. oleifera* plants.

Author Contributions: J.Z., L.L. and A.X. conducted the research work and collected the data. J.Z. and J.L. analyzed the data and prepared the manuscript. L.Z., W.Z. and X.G. revised the manuscript. D.H. designed and supervised the work. All authors have read and agreed to the published version of the manuscript.

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