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Characterisation of Breadfruit (*Artocarpus altilis*) Plants Growing on Lakoocha (*A. lakoocha*) Rootstocks

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Abstract: Breadfruit (*Artocarpus altilis*) is a traditional fruit tree of 15–30 m tall in Oceania. The species is a staple crop for food security in the tropics. Tree loss from tropical windstorms, together with transition toward high-density planting has driven an interest in the dwarf phenotype of the species. Information on dwarfing rootstocks for breadfruit is currently limited. The aim of this study was to assess the performance of breadfruit growth with lakoocha (*Artocarpus lakoocha*) as rootstocks. We compared the phenotype of breadfruit trees on lakoocha rootstocks with those on self-graft and non-graft within 21 months after grafting. These led to the discovery of a rootstock-induced dwarf trait in breadfruit species. Breadfruit scions on lakoocha rootstocks displayed a reduction in tree height, stem thickness, and internode length, with fewer branches and leaves, resulting in about 32% of the standard height at the end of 21 months after grafting. These suggest lakoocha rootstocks have the potential to control breadfruit tree vigor. Non-structural carbohydrate analysis showed the composite trees exhibited lower hexose concentration in both scion stems and roots, but higher sucrose level in scion stems, and higher starch level in roots. The significance of these parameters in rootstock dwarfing is discussed.

Keywords: rootstock; scion; dwarfing; phenotype; non-structural carbohydrate; stems; roots; *Artocarpus altilis*; *Artocarpus lakoocha*

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1. Introduction

Breadfruit [*Artocarpus altilis* (Parkinson) Fosberg)] is a traditional fruit tree in the tropics. With significant nutritional and ecological benefit, the species is regarded as a staple crop for food security in Oceania [1–4]. However, as an evergreen tree of 15 to 30 m, breadfruit is prone to wind damage. Intense tropical windstorms, such as cyclones and hurricanes on the islands in recent decades, have resulted in the destruction or uprooting of numerous mature breadfruit trees [5–8]. Tree height also creates major constraint for disease control and fruit harvesting, leading to increase in production cost [5,9]. In response to these constraints, there is increasing interest in searching for the dwarf phenotype of the species. Breadfruit has hundreds of cultivars, displaying great morphological and agronomic diversity; however, a naturally dwarf variety of the species has not been discovered [10–12]. Dwarfism has been achieved largely through the use of dwarfing rootstocks in many other fruit tree species, including the M9 and M27 for apple rootstocks [13], the Controller™ series for peach rootstocks [14], the Gisela 5 (*Prunus cerasus* × *Prunus canescens*) for sweet cherry rootstocks [15], the trifoliata 'Flying Dragon' orange (*Poncirus trifoliata* L. Raf.) for citrus rootstocks [16], and the Pectinifera for Fremont mandarin rootstocks [17]. These dwarfing rootstocks have revolutionised fruit production by conferring smaller tree size, increasing precocity, and substantially decreasing production costs in high-density planting [18,19]. Dwarfing rootstocks for breadfruit are still less known. Vegetative propagation is essential for the seedless breadfruit varieties, but also preferred for the seeded varieties as a result of their recalcitrant seeds [12]. Breadfruit vegetative propagation is generally

through cuttings, air layering, and root suckers [12]. Breadfruit grafting was practised in the tropics where its closely related species, *A. mariannensis* and *A. camansi*, were used as rootstocks [20–22]. Breadfruit grafting onto other interspecific rootstocks, including pedalai (*A. sericicarpus*) and marang (*A. odoratissimus*), were also reported [23]. Of these rootstocks, marang rootstock has been shown to induce dwarfing of breadfruit scions [24]. A recent assessment suggested that the dwarf phenotype on marang rootstock was not associated with graft incompatibility [25], but rather caused by an intriguing interaction of scions and rootstocks that involved disruption in networks of hormone transduction, nutrient transport, and sucrose utilisation, leading to inhibition of cell elongation in scions [25,26]. There is currently limited information on the impact of other *Artocarpus* rootstocks on the performance of breadfruit species. The genus *Artocarpus* comprises approximately 60 species, including *A. heterophyllus* (jackfruit), *A. integer* (chempedak), *A. hirsutus* (wild jack), *A. lanceifolius* (keledang), *A. anisophyllus* (entawak), and lakoocha (*A. lakoocha*) [27]. While most of these species are tall rainforest trees, they display great diversity in tree stature [28]. Notably, *Artocarpus lakoocha* Roxb. (Syn: *A. lacucha* Buch.-Ham.), also known as 'lakoocha' or 'monkey jack', is a tropical evergreen tree species of 6 to 15 m tall [28–30]. Native to India, the species is widely distributed in tropical counties, ranging from south-east Asia to the Himalayan countries of the Indian subcontinent [30,31]. Breadfruit grafting onto lakoocha rootstocks has not been reported. We hypothesized that the smaller tree size habit of the lakoocha species could create potential for rootstock-induced control over the vigor of breadfruit trees.

In this study, we investigated the morphological characteristics of breadfruit trees growing on lakoocha rootstocks following a recent success in generating the composite trees. We identified a distinct dwarf habit in breadfruit trees when lakoocha was used as a rootstock. Further comparative biochemical analysis revealed lakoocha rootstocks also affected the content of non-structural carbohydrates, including sucrose, glucose, fructose, and starch in stems and roots of the composite plants. The potential role of these biochemical properties in rootstock-induced dwarfism of breadfruit is further discussed.

2. Materials and Methods

2.1. Plant Materials

Breadfruit plants (*Artocarpus altilis* cv. Noli), grown from stem cuttings and seedlings of lakoocha (*Artocarpus lakoocha*), were obtained from a commercial nursery in northern Queensland. Both scions and rootstocks were grown as pot plants in glasshouse at 25~28 °C with water supply and fertilizers as previously described [24]. Breadfruit scions were grafted onto lakoocha seedlings (cross-species graft), and also grafted onto the same breadfruit cultivar as rootstocks (self-graft). Graft success was determined as the survival rate at 3 months after the beginning of grafting. The final survival percentage was measured at 21 months after grafting. Any survival graft after 3 months from grafting was sampled as one biological replicate for further observation. For grafting, breadfruit scions of 30~50 cm were grafted onto lakoocha seedlings of similar size using approach grafting [23]. Six months after grafting, every established grafted plant was transferred to an 85-litre pot and continued to grow under the same condition. The non-graft controls (own-rooted breadfruits) were selected with similar height to the self-graft at the end of 3 months after grafting and were grown alongside for comparison. Breadfruit scions were also grafted onto the same breadfruit cultivar as the self-graft control. Four trials were performed, each trial started with at least six replicates for each scion/rootstock combination at 3 months after grafting.

2.2. Morphological Comparison of Breadfruit Trees on Different Rootstocks

Stem elongation of grafted and non-grafted plants was measured as previously described [24]. Internode length was measured from the second internodes after elongation ceased. Node and branch number (with at least one node) was counted on the main scion stems. Stem diameter was calculated based on the averaged stem circumference of the

top five internodes. Leaf size was examined from three fully matured leaves per plant as previously described [24]. Leaf characteristics, such as leaf shape, leaf lobe number, leaf margin, base, and apex were inspected concurrently. The ratio of stem diameter above and below graft union was examined at 5 cm above and below the graft union at 21 months after grafting. Graft compatibility rate was assessed at both 12 and 21 months after grafting. Plants showing graft compatibility were defined as displaying active growth with continuous development of green leaves from the apex, and progressive emergence of new internodes from apical buds (Supplementary Figure S1). The 1-year or final (21 months) graft compatibility was determined by the percentage of compatible plants collected from two independent trials (each with 8 replicates for each graft combination from the beginning) out of the total survived grafts at 3 months after grafting. Phenotype comparison was only performed on compatible grafts.

2.3. Measurement of Leaf Chlorophyll Content

Chlorophyll concentration was estimated every 3 months with a chlorophyll meter (atLeaf Chl meter, FT GREEN LLC, Wilmington, DE, USA), and converted to total chlorophyll content [24]. The final chlorophyll content at 21 months after grafting was determined analytically as previously described [25].

2.4. Non-Structural Carbohydrate Analysis

All sampling occurred between 8 am and 9 am. Upon separation from plants, tissues were snap-frozen in liquid N_2 immediately. Stem tissues were sampled at the second internode from the top in each plant. For root sampling, roots were carefully removed from pots, washed to remove soils, and healthy fine roots were collected under water. Soluble sugars of each sample (50 mg) were extracted in 80% ethanol at 60 °C for 2 h. Supernatants were evaporated and dissolved in sterile water. Soluble sugars were determined enzymatically, with glucose and fructose according to D-Fructose/D-Glucose assay kit (Megazyme, Bray, Ireland), and sucrose according to Birnberg and Brenner [32]. The pellets of ethanol extraction were digested with amyloglucosidase and α-amylase, as previously described [25], and the released glucose units were determined enzymatically as above.

2.5. Statistical Analyses

Statistical analysis of all data was performed in SPSS (IBM Statistics version 27). Significant differences related to concentration, growth rate, stem height, and diameter were analysed using analysis of variance (ANOVA) followed by Tukey's multiple comparison test at $p < 0.05$. Significant differences in number of leaves, nodes, and branches were analysed with the Kruskal–Wallis test. Significant differences of graft compatibility were analysed by Fisher's exact test.

3. Results

3.1. Growth Habit of Breadfruit Plants on Different Rootstocks

Grafting of breadfruit scions was achieved on lakoocha rootstocks (Supplementary Figure S2). The graft success rate for the breadfruit/lakoocha combination was 51.6% at the end of 3 months after grafting. The successful grafting events were initially identified by survival of grafted scions for >4 weeks only dependent on the rootstocks at 3 months after grafting, consistent with previous findings in breadfruit grafting on interspecific rootstocks of marang (*A. odoratissimus*) and pedalai (*A. sericicarpus*) [23]. By 6 months, the successful grafts could be confirmed by the emergence of new leaves and new shoot growth (Supplementary Figure S2).

Growth curve analysis in the period from 3 to 21 months after grafting (Figures 1 and 2, also see Supplementary Table S1) showed plants growing on lakoocha rootstocks displayed significantly shorter stature compared with the standard size (non-grafted plants). The decrease in scion height began to appear from 9 months, where a reduction of 52.2% was observed compared with those of the self-graft. The height of scions between the

self-graft and the non-graft was not significantly different at any time point in the period (Figure 2). Consistently, the self-graft scions elongated at a similar rate as those of the non-graft, while a decreased elongation rate was shown in plants growing on lakoocha rootstocks (Table 1). As a result, at the end of 21 months, plants on lakoocha rootstocks were significantly shorter, with a reduction of 68.3% and 67.9% in height, respectively, compared with those on self-graft and non-graft, resulting in a dwarf phenotype (Figure 1, Table 1). Apart from shorter stature, the stem thickness on lakoocha rootstocks was reduced by 52.9% and 49.8%, respectively, compared with those on self-graft and non-graft (Table 1). Node number of scion main stems between rootstocks was not changed, but the internode length on lakoocha rootstocks displayed a reduction of 61.9% compared with those on self-graft, whereas no difference was found between those of the self-graft and non-graft (Figure 1, Table 1). By the end of 21 months, plants on lakoocha rootstocks also displayed reduction in branch number and leaf number. While they had smaller leaves, plants on lakoocha rootstocks displayed no change in other leaf characteristics, such as leaf shape and surface, apex, margin, vein, and lobe number (Figures 1 and S1). Total chlorophyll content measured every three months by a non-destructive method showed insignificant differences in scion leaves between different rootstock types in the tested period (Figure 3). Consistently, analytical measurement at 21 months after grafting showed no significant difference in leaf chlorophyll (Chl) concentration, including Chl *a*, Chl *b*, Chl *a* + *b*, and Chl *a/b* in scion leaves of different rootstocks (Table 1).

Figure 1. Representatives of breadfruit plants growing on different rootstocks. (**a**) Breadfruit plants growing on lakooch rootstocks (BL), self-graft (BB), and non-graft (N) at 21 months after grafting. (**b**–**d**) Breadfruit shoots showing internode length growing on lakoocha rootstocks (**b**), self-graft (**c**), and non-graft (**d**).

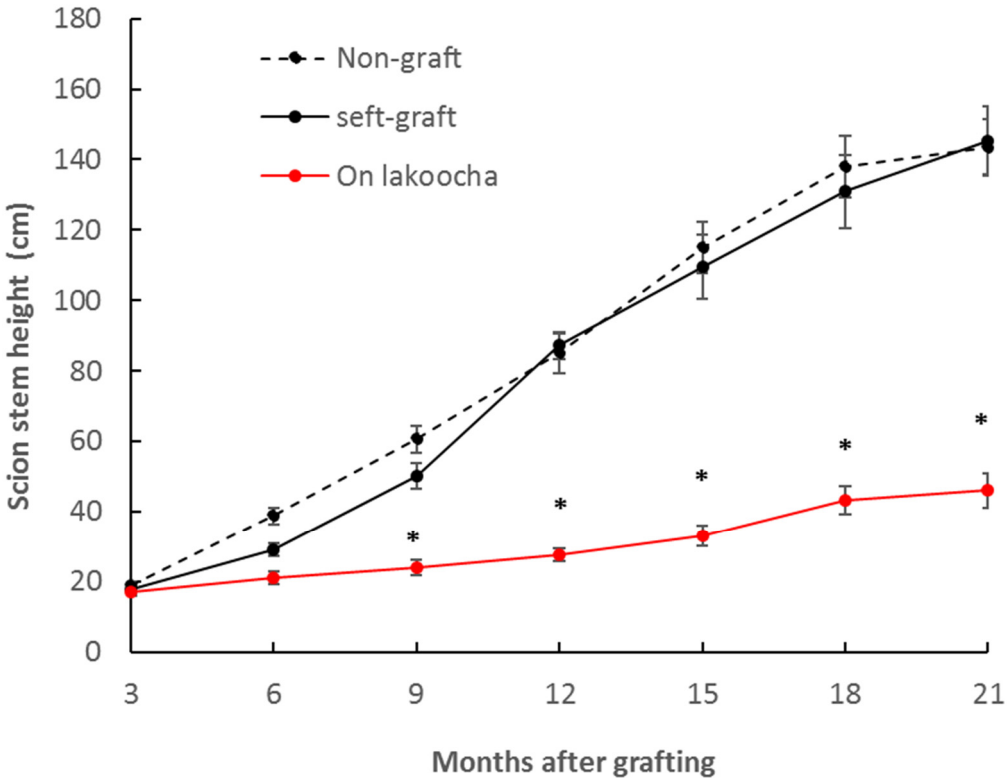

Figure 2. Growth curve comparison of breadfruit plants on different rootstocks. All values represent mean ± SE from five biological replicates. * Significant difference ($p < 0.05$).

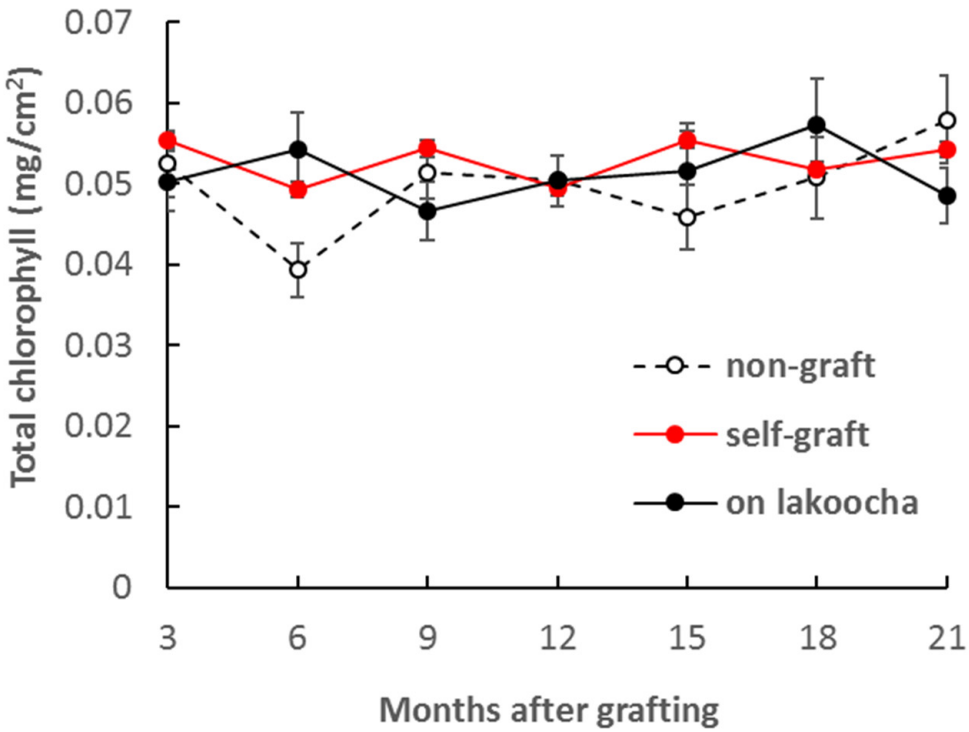

Figure 3. Total chlorophyll content of scion leaves growing on different rootstocks from 3 to 21 months after grafting. Chlorophyll contents were measured by hand-held chlorophyll meter (see Methods).

Table 1. Morphological assessment of breadfruit plants growing on different rootstocks *.

	Non-Graft	Self-Graft	On Lakoocha
Final scion height (cm)	151.17 ± 8.60 *b*	156.67 ± 10.14 *b*	47.97 ± 5.05 *a*
Main stem diameter (cm)	2.91 ± 0.80 *b*	3.10 ± 0.78 *b*	1.46 ± 0.37 *a*
Node number on main stems	28.22 ± 4.53 *a*	27.04 ± 4.61 *a*	22.48 ± 2.56 *a*
Number of branches per plant	2.20 ± 0.42 *b*	2.42 ± 0.27 *b*	0.61 ± 0.45 *a*
Main stem elongation rate (cm/month)	7.32 ± 2.19 *b*	6.96 ± 0.75 *b*	2.21 ± 0.62 *a*
Second internode length in Main stems (cm)	5.62 ± 1.20 *b*	5.91 ± 1.25 *b*	2.25 ± 0.23 *a*
Leaf numbers per plant	7.23 ± 0.53 *b*	8.40 ± 0.60 *b*	4.00 ± 0.35 *a*
Leaf chlorophyll *a* (mg/g)	2.22 ± 0.55 *a*	2.49 ± 0.61 *a*	2.12 ± 0.42 *a*
Leaf chlorophyll *b* (mg/g)	0.83 ± 0.10 *a*	0.87 ± 0.12 *a*	1.32 ± 0.34 *a*
leaf chlorophyll *a* + *b* (mg/g)	2.76 ± 0.81 *a*	3.36 ± 0.61 *a*	3.44 ± 0.63 *a*
Leaf chlorophyll *a/b*	3.04 ± 0.56 *a*	3.01 ± 0.88 *a*	1.97 ± 0.47 *a*
Leaf length	82.55 ± 1.16 *b*	78.50 ± 3.18 *b*	55.89 ± 5.90 *a*
Leaf width	58.50 ± 2.43 *b*	60.25 ± 2.56 *b*	39.25 ± 3.67 *a*
Stem diameter at 5 cm above graft union		3.25 ± 0.25 *a*	1.71 ± 0.10 *b*
Stem diameter at 5 cm below graft union		3.31 ± 0.34 *a*	1.60 ± 0.16 *b*
Stem diameter difference above and below graft union		0.18 ± 0.06 *a*	0.17 ± 0.09 *a*
Ratio of stem diameter above and below graft union		0.99 ± 0.04 *a*	1.09 ± 0.08 *a*
Final survival (%)		59.72 ± 6.15 *a*	40.05 ± 4.85 *b*
1-year graft compatibility (%)		81.25 ± 8.84 *a*	68.75 ± 8.84 *a*
Final graft compatibility (%)		75.00 ± 0.00 *a*	62.50 ± 0.00 *a*

The 1-year and final compatibility represent the mean ± SD of two independent trials, with eight replicates for each graft combination at each trial. All other values represent the mean ± SE of five replicates. Values with different letters in the same row are significantly different ($p < 0.05$). * Measurement conducted at 21 months after grafting.

Apart from dwarf habit, the composite trees on lakoocha rootstocks grew normally in the current condition. Regardless of the rootstock types, all grafted plants displayed continuous emergence of green leaves from the apex, with new internodes progressively formed from apical buds or axillary buds (Supplementary Figure S1). Of the grafts that survived for >3 months after grafting, the differences between the 1-year and final graft compatibility rates across types of rootstocks were not significant (Table 1).

3.2. Effect of Rootstocks on Non-Structural Carbohydrate Contents

Non-structural carbohydrate contents (NSC) of root and scion stem tissues were measured at 15, 18, and 21 months after grafting. Significantly lower levels of glucose and fructose were detected in scion stems growing on lakoocha rootstocks at all the three time-points, with a reduction of 36.6%, 37.2%, and 45.6%, respectively, at 15, 18, and 21 months in glucose, and a reduction of 43.1%, 33.1%, and 41.8%, respectively, at 15, 18, and 21 months in fructose, compared with those on self-graft at the same time points (Figure 4a,b). In contrast, scion stems on lakoocha rootstocks showed higher levels of sucrose in all the three time-points, with an increase of 42.2%, 99.2%, and 128.1%, respectively, at 15, 18, and 21 months compared with those on self-graft (Figure 4c). These sugar levels were not significantly different between those on self-graft and non-graft. The difference in starch content of scion stems across different rootstocks was not significant (Figure 4d).

In root tissues, significantly lower glucose and fructose levels were also detected in lakoocha rootstocks at both 18 and 21 months after grafting, with a reduction of 43.1% (18 months) and 39.7% (21 months) in glucose, and a reduction of 45.6% (18 months) and 39.2% (21 months) in fructose compared with those of self-graft at the same time (Figure 5). Levels of glucose and fructose in root tissues were not significantly different between the self-graft and non-graft. While there was no difference in sucrose levels between the types of rootstocks, higher starch contents were detected in roots of lakoocha rootstocks for all the time-points, all with an increase of over 50% compared with the self-graft and non-grafted. Levels of starch in root tissues were not significantly different between the self-graft and non-graft (Figure 5).

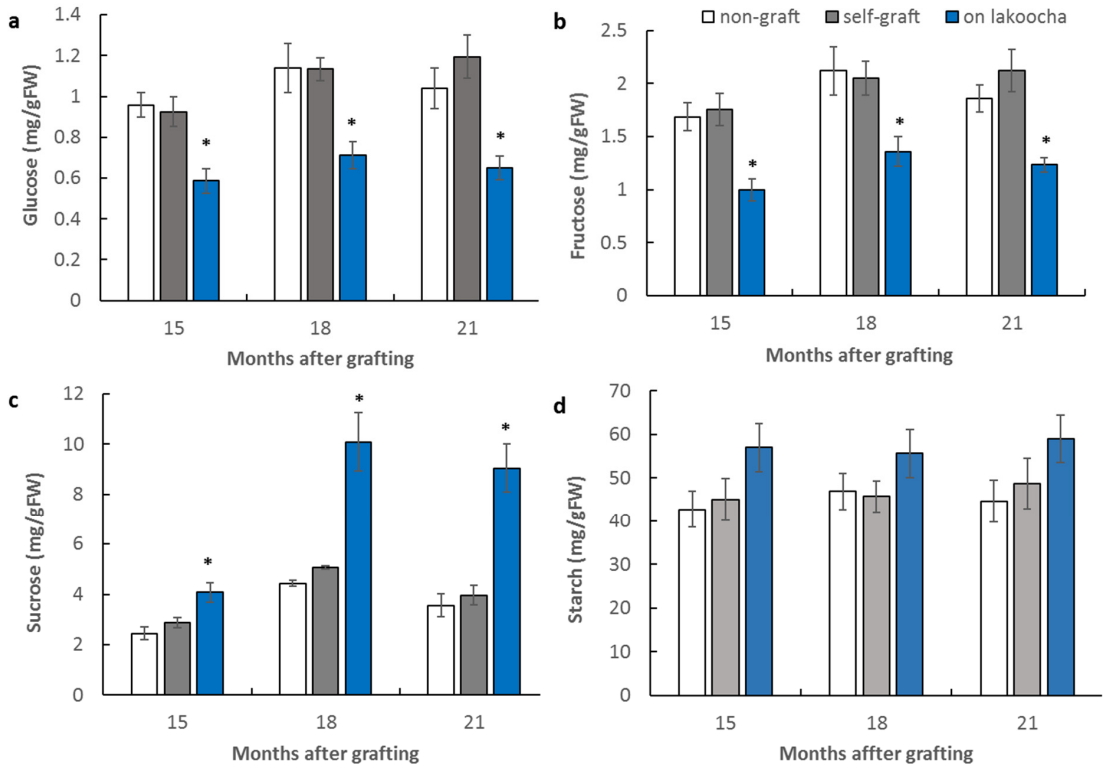

Figure 4. Non-structural carbohydrate contents in scion leaves of breadfruit plants growing on different rootstocks. (**a**) Glucose contents; (**b**) Fructose contents; (**c**) Sucrose contents; (**d**) Starch contents. All values represent mean ± SE from five biological replicates (* $p < 0.05$).

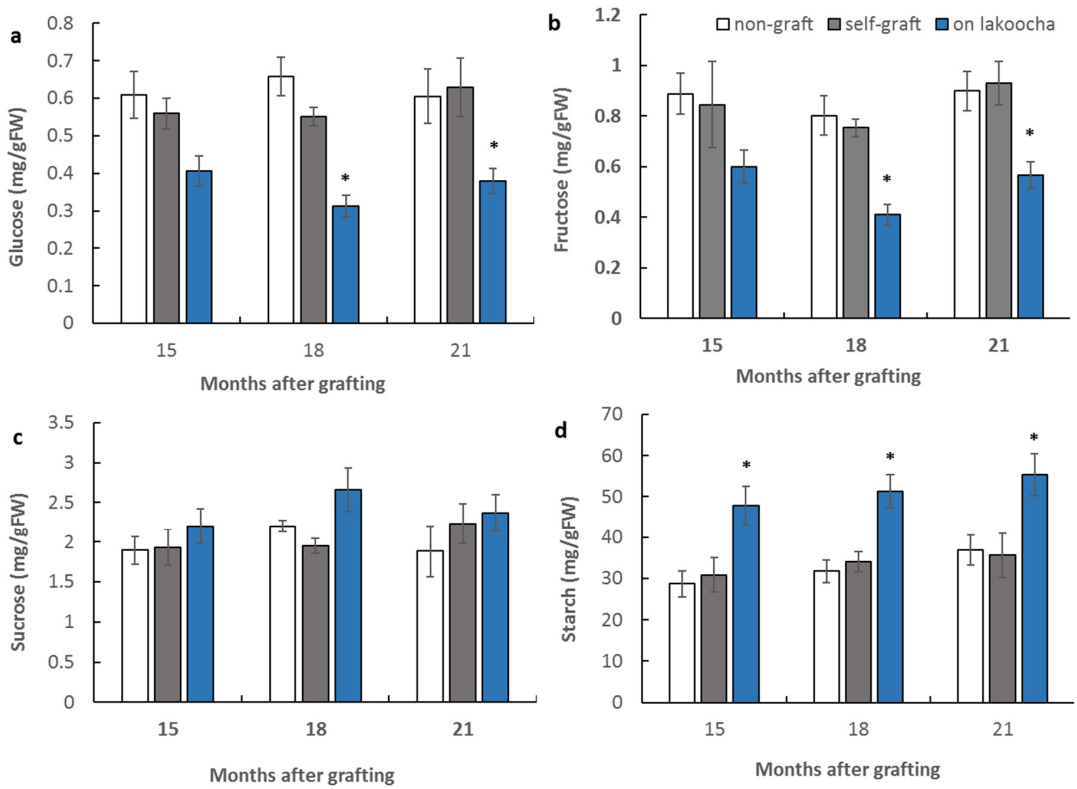

Figure 5. Non-structural carbohydrate contents in root tissues of different rootstocks. (**a**) Glucose contents; (**b**) Fructose contents; (**c**) Sucrose contents; (**d**) Starch contents. All values represent mean ± SE from five biological replicates (* $p < 0.05$).

4. Discussion

In the current study, breadfruit scions were successfully grafted onto lakoocha rootstocks, and the phenotype of the composite plants was characterised for the first time. As expected from the lakoocha species being a smaller tree in nature [29,30], breadfruit scions on these rootstocks displayed a distinct dwarf habit compared with their standard size (self-graft and non-graft), and were also characterised by decreased stem thickness and internode length. The composite trees also had fewer branches and smaller leaves (Figures 1 and 2, Table 1). The difference in growth pattern between the self-graft and the self-rooted breadfruits (non-graft) was negligible, suggesting the impact of the graft union on the growth of self-graft was not significant during the tested period. The growth habit of breadfruit trees on lakoocha rootstocks is in agreement with the rootstock-induced dwarfing of many other species [16,33–35]; it also shared similarity to the dwarf traits of the species on marang rootstocks [24]. In addition, our findings that the rootstock-induced dwarf traits in breadfruit scions developed in the early stage of vegetative growth support previous findings that the effect of most dwarfing rootstocks on scion architecture occurs in the first or second year after grafting [36,37]. Furthermore, architectural modelling in the rootstock-induced dwarfing of apple trees suggests that several growth parameters, including internode length, stem cross-sectional area, and number of axillary shoots observed in the early growth season are highly correlated with the long-term dwarfing potential [36,38]. Therefore, the growth parameters affected by lakoocha rootstocks, including decrease in stem thickness and internode length, and reduction in branch numbers could be applied to the prediction of dwarfing phenomenon over time for the breadfruit/lakoocha composite trees. Our results that breadfruit scions growing on lakoocha rootstocks were less than 32% of the standard height at 21 months after grafting point to the potential of lakoocha rootstocks in breadfruit tree vigor control for wind resistance and high-density planting. However, long-term assessment for the effect of lakoocha rootstocks on breadfruit growth, and other agronomic traits, including flowering and fruiting, is required in the future.

Rootstock performance and its ultimate success in commercial application not only depends on the interaction between genotypes of scion and rootstock, but also the compatibility of the rootstock with scion [18,39,40]; it is therefore necessary to assess the graft combination of breadfruit/lakoocha for graft compatibility. Graft compatibility indexes, including the ratio and difference of diameter in stems above and below the graft union, examined at 21 months after grafting showed these values were not significantly different between the self-graft and breadfruit/lakoocha graft (Table 1). In both combinations, the difference between diameter in stems above and below the graft union was very small, and the ratio of scion to rootstock stem diameter in the breadfruit/lakoocha combination was very close to 1. The growth differences above and below the graft union has often been used to correlate growth characteristics with graft incompatibility [41]; in particular, the ratio of the stem diameter above and below the graft union has been applied as an early determinant of long-term graft incompatibility [41–43]. Based on these indexes, the incompatibility was not apparent in the breadfruit/lakoocha combination at 21 months after grafting. Consistent with the compatibility indexes, scion leaf chlorophyll (Chl) on lokoocha rootstocks, including Chl *a*, Chl *b*, Chl *a* + Chl *b*, and Chl *a/b* was not significantly different from those of the self-graft (Figure 3, Table 1). Chlorophyll content served as an indicator of carbon assimilation, nitrogen uptake, and stress adaptation for the proper functioning of a composite plant, and has provided a sensitive tool to identify graft incompatibility [41–43]. Furthermore, there was no difference in the 1-year and the final compatibility rates between the breadfruit/lakoocha grafts and the self-grafts. Taken together, these evidences suggest that, at this stage, the dwarf phenotype of breadfruit scions on lakoocha rootstocks was not associated with graft incompatibility. Over the course of the experiment, we observed some breadfruit/lakoocha combinations developed a thinner rootstock stems compared with their scion stems at the early stage of graft establishment (during 3~6 months after grafting). However, this structure did not sustain to the second year after grafting (Figure S2). It is not known whether this pattern is associated with the approach grafting techniques. In this

procedure, both scions and rootstocks were bound tightly together in the first 2 months; they were self-sustained by their own roots [44]. During this period, some breadfruit scions grew faster than lakoocha rootstocks, resulting in thicker scions by the time they were separated from the scion roots. It was also possible that there was scion swelling above the graft union at the early stage of graft establishment. The nature of this pattern or whether it could be used as a reliable indicator for graft incompatibility in the long run for breadfruit species needs further investigation. Given that an incompatible graft can grow for years without any external indication in woody species [45], and not all methods are reliable indicators for graft incompatibility for a given species [41], it is essential that evaluation for graft compatibility of the breadfruit/lokoocha combination be done in actual field conditions over a long period of time for its efficiency to produce satisfactory yields at a commercial scale.

The lower hexose levels in combination with higher sucrose levels detected in scion stems on lakoocha rootstocks (Figure 4) may reflect a disruption of sucrose utilisation induced by the rootstocks. In higher plants, sucrose produced during photosynthesis in leaves (sources tissues) is transported to different sink tissues, such as roots and stems. Sucrose is hydrolysed to produce hexose in sink tissues (such as stems and roots) for cell metabolism, energy production, and macromolecule biosynthesis [46]. The lower levels of hexose observed in scion stems and roots growing on lakoocha rootstocks are in agreement with previous findings in apple trees on dwarfing rootstocks 'M27' and 'M9' [13]. These evidences suggest that hexose depletion leading to reduction of carbon and energy metabolism may have a role in the growth inhibition of composite trees growing on dwarfing rootstocks. On the other hand, as a signalling molecule, intracellular sucrose can communicate metabolic demand to regulate sucrose influx [47]; the evidences that high sucrose concentration negatively regulates phloem loading through repressing its own transport [46] also point to the potential role of disruption in carbon partitioning in the dwarfing effect of lakoocha rootstocks.

Our findings that roots of the breadfruit/lakoocha composite trees accumulated higher levels of starch than those in self-graft are in agreement with previous findings that dwarfing citrus and apple rootstocks contained more starch than vigorous rootstocks [13,48,49], and suggest an impaired balance of starch reserve and hexose level in dwarfing rootstocks. Higher starch concentration in roots of woody plants was associated with inhibition of shoot elongation, such as during dormancy [44]. On the other hand, root starch plays a crucial role in plant growth and development under depressed photosynthesis, as it can be immediately degraded to supply respiratory substrates, therefore maintaining root functions, such as water and nutrient uptake [50,51]. For example, perennial plants with disturbed aerial parts often have higher starch content in their roots [52]. Therefore, increase in starch reserve at the expense of hexose for cellular activity and growth may be a strategy for continuous root function following reduction of total photosynthetic leaf area in scions growing on lakoocha rootstocks. In support of this hypothesis are findings that scion leaf chlorophyll contents were not significantly changed when compared with the self-graft and non-graft. Leaf chlorophyll content is an indicator of carbon assimilation and nitrogen uptake, and reflects the proper functioning of the composite trees [41–43].

5. Conclusions

We reported the phenotype of grafted breadfruit plants growing with lakoocha as rootstocks following the successful development of the composite trees. Within the period up to 21 months after grafting, the composite plants displayed shorter stem height in combination with decreased stem thickness and internode length, fewer branches, and smaller leaves, consistent with the phenotype of rootstock-induced dwarfing. Breadfruit plants on lakoocha rootstocks also showed lower hexose concentration in both scion stems and roots, but higher sucrose concentration in scion stems, and higher starch concentration in roots. The information provides opportunity to design rootstock breeding programs that confer vigor control over breadfruit scions. However, evaluation for graft compatibility

of the breadfruit/lokoocha combination is required in actual field conditions over a long period of time for its efficiency to produce satisfactory yields at a commercial scale.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/horticulturae8100916/s1, Figure S1: Representatives of graft-compatible phenotype of breadfruit plants on different rootstocks, Figure S2: Representatives of grafted breadfruit plants on lakoocha rootstocks at 3 and 6 months after grafting; Table S1: Raw data of scion height of breadfruit plants on different rootstocks.

Author Contributions: Conceptualization and methodology, Y.Z. and S.J.R.U.; investigation and data analysis, Y.Z.; writing and review, Y.Z. and S.J.R.U. All authors have read and agreed to the published version of the manuscript.

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Conflicts of Interest: The authors declare no conflict of interest.

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