PLANT SCIENCE TODAY
Vol XX(1): 1-XX
https://doi.org/10.14719/pst.15457

eISSN 2348-1900
OPEN ACCESS

Research Article | Agriculture
2026, Volume XX, Issue X, pp. 1-XX

Harnessing traditional mango cultivars to validate the influence of rootstock and its age on softwood grafting in Kuttiattoor mango: A GI-registered cultivar of North Kerala

B Suchitra[1*], P K Reshmika[2], V Raju[3*], N M Mohan[1], K O Smitha[1], G K Krishna[4], M M Paul[5] & N S Sonia[1]

[1]Department of Fruit Science, College of Agriculture, Kerala Agricultural University, Padannakkad, Kasaragod 671 314, Kerala, India
[2]Department of Vegetable Science, College of Agriculture, Kerala Agricultural University, Thrissur 680 651, Kerala, India
[3]Department of Forest Products and Utilization, College of Forestry, Kerala Agricultural University, Thrissur 680 651, Kerala, India
[4]Department of Plant Physiology, College of Agriculture, Kerala Agricultural University, Thrissur 680 651, Kerala, India
[5]Department of Agricultural Statistics, College of Agriculture, Kerala Agricultural University, Thiruvananthapuram 695 522, Kerala, India

***Correspondence:** B Suchitra, suchitrabklm@gmail.com; V Raju, vishnu.r@kau.in

Abstract

Kuttiattoor mango, a geographical indication (GI)-registered traditional cultivar of North Kerala, is renowned for its unique taste and yellow-orange colour. However, being polyembryonic, it is mainly propagated through seeds, resulting in tall trees, a prolonged juvenile phase and difficulty in harvesting. In this context, the present study was undertaken to explore the potential of traditional mango cultivars as rootstocks for softwood grafting in Kuttiattoor mango. Four rootstocks viz. Vellaikolumban, Kurukkan, Kalapady and Kuttiattoor were assessed across three age groups (1, 2 and 3 months old) for softwood grafting. Grafts prepared with 3-month-old Kuttiattoor rootstocks recorded the highest sprouting percentage (73 %), survival percentage (41.92 %) and the fewest days to sprout (12.5). The same combination also produced superior vegetative growth, which was on par with 3-month-old Kalapady rootstocks at 140 days after grafting (DAG). The lower graft growth observed in Kuttiattoor grafts on Vellaikolumban and Kurukkan rootstocks suggests a dwarfing effect, highlighting their potential utility for developing compact, high-density mango orchards. Histological studies revealed better callus growth and vascular differentiation in grafts prepared with 3-month-old Kuttiattoor rootstocks followed by those with 3-month-old Kalapady rootstocks. Grafts with 3-month-old Kuttiattoor and Kalapady rootstocks were found to be the most suitable for nursery propagation of Kuttiattoor mango. The reduced vegetative growth observed on Vellaikolumban and Kurukkan rootstocks indicates their potential for future evaluation as dwarfing rootstocks in high-density mango production systems.

Keywords: histology; Kuttiattoor; mango; softwood grafting; Vellaikolumban

Received: 07 May 2026. **Accepted:** 18 August 2026. **Available online:** Version 1.0: 05 November 2026.

Cite this article: Suchitra B, Reshmika PK, Raju V, Mohan NM, Smitha KO, Krishna GK, Paul MM, Sonia NS. Harnessing traditional mango cultivars to validate the influence of rootstock and rootstock age on softwood grafting in Kuttiattoor mango, a GI-registered cultivar of North Kerala. Plant Science Today. 2026;XX(X):1-XX. https://doi.org/10.14719/pst.15457

1. Introduction

Mango (*Mangifera indica* L.) belongs to the family Anacardiaceae and is often known as the “King of Fruits” due to its flavour, high nutritional value, cultural significance, diverse varieties and economic importance (1). Kuttiattoor mango, a well-known traditional cultivar grown in the Kuttiattoor region of Kannur district, Kerala, India, received a geographical indication (GI) in 2021. It is known for its attractive yellow-orange colour and exceptional flavour. The ripe fruits have smooth skin without speckles, which enhances their market appeal. Owing to its superior fruit quality, characterised by a total soluble solids (TSS) content of 14.45 °Brix, carotenoid content of 6.47 mg 100 g^{-1} and ascorbic acid content of 43.92 mg 100 g^{-1} (2), Kuttiattoor mango possesses significant export potential. Its distinctive flavour and excellent processing quality further enhance its marketability, meeting the growing demand for value-added mango products in both domestic and international markets. An additional advantage of this cultivar is its early flowering, which mainly occurs during November–January. The fruits reach harvestable maturity during the 4th week of March and the 1st week of April (2).

The Kuttiattoor mango is a popular traditional cultivar of North Kerala, valued for its unique fruit quality and consumer preference. However, its commercial cultivation is constrained by several production-related challenges. The tall tree stature (Supplementary Fig. 1) makes harvesting difficult, particularly for fruits borne in the upper canopy, where the shortage of skilled labour

for climbing further increases production costs. In addition, seedling-derived trees are generally vigorous and begin bearing fruits only 6–8 years after planting, whereas vegetatively propagated trees exhibit a more manageable canopy and commence fruiting from the 3rd year onwards (3). Large-scale commercial propagation of Kuttiattoor mango therefore relies on vegetative methods, particularly grafting, to overcome the limitations associated with seed propagation. Grafting is a well-established propagation technique that enables rapid multiplication and can influence important horticultural traits such as tree vigour, canopy size, stress tolerance, yield and fruit quality (4). These attributes are largely determined by the rootstock, making the selection of a suitable and compatible rootstock essential for the successful propagation and long-term performance of the scion (5).

Although Kuttiattoor mango is polyembryonic, reliable discrimination between nucellar and zygotic seedlings at the juvenile stage based on morphological characters is difficult. Consequently, molecular marker-based approaches have been employed for their accurate identification. Marker systems such as randomly amplified polymorphic DNA (RAPD), directed amplification of minisatellite DNA (DAMD), inter-simple sequence repeat (ISSR) and simple sequence repeat (SSR) have been successfully used to distinguish nucellar and zygotic seedlings originating from the same seed in several fruit crops (6). Furthermore, Kuttiattoor mango seeds are highly susceptible to infestation by the mango nut weevil (*Sternochetus mangiferae*), which severely damages the seeds and further limits the availability of quality planting material.

The present study evaluated four mango cultivars, namely Kuttiattoor, Vellaikolumban, Kurukkan and Kalapady, as potential rootstocks. Earlier studies have demonstrated the dwarfing potential of Kalapady (7) and Vellaikolumban (8), while Kurukkan has also been classified as a dwarfing rootstock based on its morphological characteristics (9). In addition to their favourable horticultural traits, these locally available cultivars provide a continuous and economical source of rootstock seedlings for large-scale commercial propagation.

Successful graft establishment depends not only on vegetative growth but also on anatomical and physiological compatibility between the scion and rootstock. Histological examination of the graft union provides an early and reliable assessment of graft compatibility by revealing the extent of callus formation, cambial continuity and vascular tissue differentiation (10). Therefore, the present investigation also incorporated histological evaluation of graft union development using optical microscopy. Although graft success is influenced by several factors, including scion maturity, environmental conditions, season and grafting technique, the present study specifically evaluated the effects of rootstock cultivar and rootstock age under uniform experimental conditions. Considering the increasing demand for quality planting material of Kuttiattoor mango and the limited information available on suitable rootstocks for this cultivar, this investigation was undertaken to identify the most appropriate rootstock cultivar and rootstock age for successful softwood grafting and large-scale propagation of Kuttiattoor mango.

2. Materials and Methods

Location of the study area

The present study was conducted at the College of Agriculture, Padannakkad, Kasaragod district, Kerala, India, located at 12°15′23.97″ N latitude and 75°07′00.98″ E longitude with an elevation of 5–8 m above mean sea level. The area experiences minimum and maximum temperatures of 24 and 35 °C respectively and an average annual rainfall of 934.8 mm.

Experimental materials

Rootstock cultivars, namely Vellaikolumban, Kurukkan, Kuttiattoor and Kalapady were raised from mango stones collected from different locations in the Kasaragod and Kannur districts of Kerala. Mango stones were sown in a seedbed containing a medium consisting of soil, sand and decomposed farmyard manure in the ratio of 2 : 1 : 1 which was solar sterilised. Infestation of the mango nut weevil (*S. mangiferae*) in Kuttiattoor mango seeds was observed (Supplementary Fig. 2). Scions of the Kuttiattoor cultivar were collected from healthy and true-to-type mother trees located at Kuttiattoor, Kannur district, Kerala, for performing softwood grafting. Chemicals including acetone, ethyl alcohol, xylene (rectified 98 %), dibutylphthalate polystyrene distyrene (DPX) mountant and safranin used for fixation, staining and preparation of microsections were procured from Nice Chemicals Pvt. Ltd., Kochi, Kerala. All chemicals used in the study were of analytical grade.

Experimental design

The experiment was laid out in a completely randomised design (CRD) with a 4 × 3 factorial arrangement comprising 12 treatment combinations (4 rootstocks × 3 age groups). Softwood grafting was performed during August. Each treatment combination consisted of 25 grafted plants with 2 replications.

Grafting procedure

Healthy, well-developed and uniform mango stones were collected and sown in the nursery. A total of 1000 stones were sown for each rootstock type. Healthy, vigorous and uniform seedlings obtained

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https://doi.org/10.14719/pst.15457

from these stones were selected and used as rootstocks for grafting. Healthy, disease-free and uniform mother trees of the Kuttiattoor cultivar were selected for scion collection. Terminal shoots measuring 8–10 cm in length from 3- to 4-month-old mature flushes were selected as scions and defoliated 10 days before grafting. Softwood grafting was performed using the wedge grafting method. The pre-cured scion was detached from the mother tree and its basal end was shaped into a wedge by making two slanting cuts of 2–3 cm on opposite sides using a sharp knife. The wedge-shaped scion was carefully inserted into the vertical split of the decapitated rootstock, ensuring close contact between the cambial layers of the scion and rootstock. The graft union was secured firmly with transparent polythene tape (1–1.5 cm wide and 30 cm long). Following grafting, the plants were enclosed in tubular polyethylene covers to create a humid microclimate conducive to graft establishment. This enclosure helped reduce transpirational water loss during the critical period of vascular union formation and maintained relatively stable temperature and humidity conditions essential for successful graft healing. As grafting success is highly dependent on operator skill, all grafting operations were carried out by personnel with sufficient experience in mango grafting. In addition, appropriate cultural practices were adopted to keep the polybags weed-free and to maintain a favourable growing environment for the grafts. Immediately after placement under shade, the grafted plants were irrigated daily using a watering can to support uniform growth and development.

Histological analysis of the graft union

Preparation of sections for histological examination of the graft union was carried out following the standard microtomy procedures recommended for hardwoods (11). In brief, grafts were randomly selected for anatomical studies from all treatments using rootstocks of three different ages, viz., 1, 2 and 3 months. Immediately after collection, the samples were processed and preserved. Stem segments measuring approximately 3–4 cm in length were excised at the graft union, cleaned and defoliated. The samples were mounted on a Leica SM2000R sliding microtome and transverse sections of 30–60 µm thickness were prepared. The sections were stained with 1 % safranin at an appropriate concentration for 5–10 min, followed by dehydration through a graded alcohol series (30, 40, 50, 60, 70, 80, 90, 95 and 100 %) for 2–5 min at each step.

Subsequently, the sections were passed through an alcohol–xylene mixture (1 : 1) for 2–5 min and then through two changes of 100 % xylene for 2–5 min each. The sections were retained in xylene until they became completely transparent and free of air bubbles. Permanent slides were prepared using DPX as the mounting medium. After drying, the slides were labelled and examined under an optical microscope fitted with 4×, 10× and 40× objectives. Histological measurements and photomicrographs of selected sections were captured using Digi Pro 7 image analyser software attached to the microscope.

Data collection and analysis

The scions that remained green, whether sprouted or unsprouted, 15 days after grafting (DAG) were counted as the initial success. The percentage of graft survival was calculated using Eq. 1.

Graft survival = (Number of grafts alive/Total number of successful grafts) × 100 (Eq. 1)

The data on graft growth parameters, namely scion elongation, number of leaves, number of primary shoots, girth of the new growth, scion and rootstock were recorded at fortnightly intervals from the time of grafting. The detailed procedure for recording these measurements was adapted (12). Data collected from five randomly selected sample plants were subjected to statistical analysis using GRAPES 1.0.0 software.

3. Results and Discussion

The success of grafting depends on different factors, such as the influence of environmental parameters, genetic, physiological and anatomical factors of the stock and scion, the source of the rootstock, rootstock age, grafting time and grafting method (13). The selection of a suitable rootstock with respect to its age and cultivar is as important as the selection of the scion cultivar. It has a strong influence on growth, fruit maturity, yield, fruit quality and soil adaptability (14). Hence, the present study aimed to evaluate the effect of rootstock cultivar and its age on the success and growth of Kuttiattoor grafts developed through softwood grafting.

Effect of rootstock cultivars, its age and their interaction on graft success parameters

Statistical analysis showed that mango rootstock cultivars had a significant effect on graft success parameters, including the number of days required for graft sprouting, sprouting percentage and survival percentage (Table 1). The Kuttiattoor grafts with Kuttiattoor rootstocks required the fewest days for graft sprouting (12.5), performed best in terms of sprouting percentage (73 %), which was on par with that of grafts on Kalapady rootstocks (71.66 %) and also exhibited the highest graft survival (41.92 %). The Kuttiattoor grafts with Vellaikolumban rootstocks took the maximum number of days for graft sprouting (13.08), performed the lowest in terms of sprouting percentage (55 %) and survival percentage (36.47 %).

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Table 1. Effect of rootstock cultivars on graft success parameters

Varieties	Days required to graft sprouting	Percentage of sprouting (15 DAG)	Percentage of survival (140 DAG)
VEL	13.08 ± 0.63[a]	55.00 ± 8.74[c]	36.47 ± 4.07[d]
KUR	12.83 ± 0.69[b]	65.00 ± 8.74[b]	38.97 ± 3.97[c]
KAL	12.61 ± 0.74[c]	71.66 ± 9.07[a]	40.57 ± 4.84[b]
KUT	12.50 ± 0.81[d]	73.00 ± 9.52[a]	41.92 ± 4.55[a]
SE(m)	0.041	0.816	0.279
CD (0.05)	0.126	2.516	0.858
CV (%)	0.784	3.023	1.725

Mean values followed by different superscript letters (a–d) within a column are significantly different according to Duncan's multiple range test at $p < 0.05$. VEL: Vellaikolumban; KUR: Kurukkan; KAL: Kalapady; KUT: Kuttiattoor; CD: critical difference; CV: coefficient of variation; SE: standard error.

Graft success depends on three factors: precise physical alignment, coordinated physiological healing (callus formation, plasmodesmatal connectivity, vascular reconnection and hormone signalling) and genetic compatibility between the scion and rootstock. Among these, proper physical contact is fundamental. The superior performance of Kuttiattoor scion–rootstock combinations was evidenced by faster sprouting, higher sprouting percentage and greater survival, primarily because of uniform stem thickness ensuring effective cambial contact (15). A tight scion–rootstock fit enhances cambial activity, promoting stronger unions and earlier sprouting (16). Cambial alignment and stable contact are essential for vascular reconnection. Mechanical factors such as diameter matching, cut quality, cambial continuity and stability govern successful healing (17–19). Diameter mismatch and poor cambial contact lead to weak unions and vascular discontinuity, whereas clean cuts and firm stability enable rapid, uniform healing. Misalignment can cause early vascular disruption and eventual graft failure (20). The poor performance of Kuttiattoor grafts on Vellaikolumban rootstocks was characterised by delayed sprouting, lower sprouting and reduced survival, mainly because of diameter mismatch and inadequate cambial contact. Physiological compatibility determines the successful transition from physical union to functional integration by promoting coordinated callus formation, vascular differentiation and efficient transport of water, nutrients and signalling molecules. Disruption of these processes is a hallmark of graft incompatibility (20). The superior performance of the Kuttiattoor homograft was likely due to rapid vascular reconnection, which facilitated efficient water and nutrient transport, resulting in earlier sprouting, higher sprouting percentage and greater graft survival (19). This response reflects the combined effects of anatomical, physiological and genetic compatibility, which promote stable graft union formation (20). In contrast, reduced compatibility in heterografts likely delayed vascular integration and impaired resource translocation, leading to poorer graft performance. The significantly higher graft survival observed in the homogeneous Kuttiattoor–Kuttiattoor graft combination is consistent with previous reports indicating that graft compatibility is generally highest when the scion and rootstock belong to the same cultivar (20, 21). In the present study, the homogeneous graft combination was included as a reference treatment to facilitate comparison with the heterogeneous graft combinations. Its inclusion enabled differentiation between graft failures attributable to stock–scion incompatibility and those resulting from grafting technique or other experimental factors. Therefore, the homogeneous graft served as an important benchmark for interpreting the compatibility, graft success and survival of the heterogeneous rootstock–scion combinations evaluated in this study. Successful graft union formation depends on rapid callus proliferation followed by continuous xylem and phloem differentiation, ensuring efficient transport of water, nutrients and assimilates (18). Compatible graft unions generally exhibit faster vascular development, whereas incompatible combinations show delayed vascular differentiation and phloem discontinuity, resulting in poor graft establishment (20, 22, 23). These differences are associated with altered hormonal regulation and impaired wound-healing responses, ultimately reducing graft success (17, 24, 25).

The grafts with 3-month-old rootstocks required the fewest days for graft sprouting (11.96), performed best in terms of sprouting percentage (76.5 %) and graft survival (44.58 %). The grafts with 1-month-old rootstock took the maximum number of days for graft sprouting (13.55), performed the poorest in terms of sprouting percentage (57.5 %) and graft survival (34.88 %) (Table 2, Fig. 1). The interaction effect was found to be significant for all graft success parameters (Table 3).

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https://doi.org/10.14719/pst.15457

Table 2. Effect of rootstock age on graft success parameters

Age of rootstock (months)	Days required to graft sprouting	Percentage of sprouting (15 DAG)	Percentage of survival (140 DAG)
M_1	13.55 ± 0.24^{a}	57.50 ± 6.56^{c}	34.88 ± 1.75^{c}
M_2	12.76 ± 0.19^{b}	64.50 ± 9.48^{b}	39.24 ± 2.63^{b}
M_3	11.96 ± 0.37^{c}	76.50 ± 7.91^{a}	44.58 ± 2.12^{a}
SE(m)	0.035	0.707	0.241
CD (0.05)	0.109	2.179	0.743
CV	0.784	3.023	1.725

M1: 1-month; M2: 2-month; M3: 3-month; CD: critical difference; CV: coefficient of variation; SE: standard error. Mean values followed by different superscript letters (a–c) within a column are significantly different according to Duncan's multiple range test at $p < 0.05$.

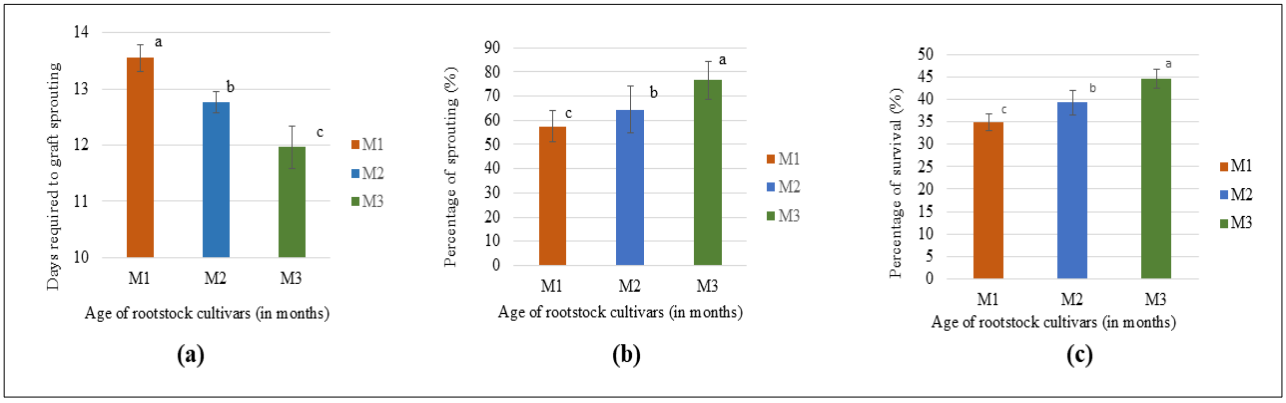


Fig. 1. Performance of grafts. a: Days required to graft sprouting; b: percentage of sprouting (%); c: percentage of survival (%) of grafts having rootstock with different ages.

Table 3. Interaction effect of rootstock cultivars and its age on graft success parameters

Varieties with rootstock age	Days required to graft sprouting	Percentage of sprouting (15 DAG)	Percentage of survival (140 DAG)
VEL M_1	13.85 ± 0.07^{a}	49.00 ± 1.41^{g}	32.54 ± 0.31^{h}
VEL M_2	12.95 ± 0.07^{d}	50.00 ± 2.82^{f}	35.89 ± 0.79^{fg}
VEL M_3	12.45 ± 0.07^{e}	66.00 ± 2.82^{d}	41.96 ± 0.30^{d}
KUR M_1	13.60 ± 0.14^{b}	55.00 ± 1.41^{f}	35.14 ± 0.60^{g}
KUR M_2	12.85 ± 0.07^{f}	66.00 ± 2.82^{d}	38.00 ± 0.70^{e}
KUR M_3	12.05 ± 0.07^{g}	74.00 ± 2.82^{b}	43.77 ± 0.94^{c}
KAL M_1	13.50 ± 0.14^{b}	61.00 ± 1.41^{e}	34.83 ± 0.70^{g}
KAL M_2	12.50 ± 0.14^{e}	73.00 ± 1.41^{bc}	41.38 ± 0.70^{d}
KAL M_3	11.85 ± 0.07^{f}	81.00 ± 1.41^{a}	45.50 ± 0.70^{b}
KUT M_1	13.25 ± 0.07^{c}	65.00 ± 1.41^{de}	37.00 ± 0.70^{ef}
KUT M_2	12.75 ± 0.07^{d}	69.00 ± 1.41^{cd}	41.67 ± 0.70^{d}
KUT M_3	11.50 ± 0.14^{h}	85.00 ± 1.41^{a}	47.11 ± 0.70^{a}
SE(m)	0.071	1.414	0.483
CD (0.05)	0.218	4.358	1.487
CV	0.784	3.023	1.725

VEL M1: Vellaikolumban 1-month-old; VEL M2: Vellaikolumban 2-month-old; VEL M3: Vellaikolumban 3-month-old; KUR M1: Kurukkan 1-month-old; KUR M2: Kurukkan 2-month-old; KUR M3: Kurukkan 3-month-old; KAL M1: Kalapady 1-month-old; KAL M2: Kalapady 2-month-old; KAL M3: Kalapady 3-month-old; KUT M1: Kuttiattoor 1-month-old; KUT M2: Kuttiattoor 2-month-old; KUT M3: Kuttiattoor 3-month-old; CD: critical difference; CV: coefficient of variation; SE: standard error. Mean values followed by different superscript letters (a–h) within a column are significantly different according to Duncan's multiple range test at $p < 0.05$.

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https://doi.org/10.14719/pst.15457

Grafts with 3-month-old Kuttiattoor rootstocks required the fewest days for graft sprouting (11.5) and exhibited the highest sprouting percentage (85 %), which was on par with grafts on 3-month-old Kalapady rootstocks. The grafts with 3-month-old Kuttiattoor rootstock also possessed the highest survival percentage (47.11 %). Grafts with 1-month-old Vellaikolumban rootstock took the maximum number of days for graft sprouting (13.85) and also recorded the lowest sprouting percentage (49 %). The grafts with 1-month-old Vellaikolumban rootstocks also possessed the lowest survival percentage (32.54 %).

Rootstock age significantly influenced graft success, with 3-month-old rootstocks exhibiting earlier sprouting, higher sprouting percentage and greater survival than younger rootstocks. Their superior performance is likely attributable to optimal physiological maturity, characterised by active cambial tissues, greater carbohydrate reserves and enhanced metabolic activity that promote rapid callus formation, vascular differentiation and graft union establishment (26). Similar improvements in graft success using physiologically mature juvenile rootstocks have been reported in mango, including higher survival in softwood and veneer grafts on 3- to 4-month-old rootstocks (27–30). However, the optimum rootstock age may vary among cultivars and grafting methods, with graft performance generally declining when rootstocks are either too young or physiologically over-mature (31).

Effect of rootstock cultivars, its age and their interaction on graft growth parameters

The growth assessments conducted at 140 DAG highlighted significant variations associated with different rootstock cultivars (Table 4). The Kuttiattoor scion grafted onto the Kuttiattoor rootstock exhibited the highest values for scion elongation (17.5 cm), girth of new growth (2.32 cm), scion girth (3.45 cm), rootstock girth (3.53 cm), number of leaves (22.86) and number of primary branches (2.45) followed by grafts on Kalapady rootstocks, while grafts with Vellaikolumban rootstocks exhibited reduced overall growth parameters (Supplementary Fig. 3). At 140 DAG, growth analysis demonstrated significant variation associated with rootstock age (Table 5).

The differential growth responses observed among rootstock cultivars are likely attributable to inherent differences in their vigour and compatibility with the scion. Post-grafting growth is governed by the combined effects of anatomical, physiological and genetic compatibility, which determine the efficiency of graft union formation and subsequent resource translocation (32, 33). Previous studies have demonstrated considerable variation in the growth potential of traditional mango rootstocks, with Vellaikolumban exhibiting relatively low vigour and Kurukkan being recognised as a dwarfing rootstock (9, 34). These inherent differences in rootstock characteristics, together with the quality of the graft union, are likely responsible for the variation in vegetative growth observed among the graft combinations in the present study (35).

The grafts with 3-month-old rootstock exhibited the highest values for scion elongation (18.55 cm), girth of new growth (2.42 cm), scion girth (3.51 cm), rootstock girth (3.6 cm), number of leaves (23.25) and number of primary branches (2.57) followed by those with 2-month-old rootstocks, while grafts with 1-month-old rootstocks exhibited reduced overall growth parameters (Fig. 2). The interaction effect of rootstock cultivars and rootstock age was found to be significant at 140 DAG (Table 6, Fig. 3). The Kuttiattoor graft with 3-month-old Kuttiattoor rootstocks exhibited the highest values for scion elongation (18.99 cm), girth of new growth (2.51 cm), scion girth (3.61 cm), rootstock girth (3.69 cm), number of leaves (24.9) and number of primary branches (2.9). This performance was statistically on par with that of 3-month-old Kalapady rootstocks for all graft growth parameters. The Kuttiattoor graft with 1-month-old Vellaikolumban rootstock exhibited the lowest values for scion elongation (14.1 cm), girth of new growth (2.11 cm), girth of scion (3.2 cm), girth of stock (3.29 cm), number of leaves (18.9) and number of primary branches (1.85). This performance was statistically on par with that of 1-month-old Kurukkan rootstocks for the number of primary branches and rootstock girth.

Table 4. Effect of rootstock cultivar on graft growth parameters (140 DAG)

Cultivars	Elongation of scion (cm)	Girth of new growth (cm)	Girth of scion (cm)	Girth of stock (cm)	Number of leaves	Number of primary branches
VEL	15.63 ± 1.63^{d}	2.20 ± 0.10^{c}	3.31 ± 0.10^{d}	3.41 ± 0.10^{d}	19.63 ± 0.63^{d}	2.05 ± 0.18^{b}
KUR	17.24 ± 1.18^{c}	2.23 ± 0.10^{b}	3.37 ± 0.09^{c}	3.44 ± 0.10^{c}	21.93 ± 1.59^{c}	2.11 ± 0.17^{b}
KAL	17.44 ± 1.23^{b}	2.30 ± 0.14^{a}	3.42 ± 0.11^{b}	3.50 ± 0.14^{b}	22.38 ± 1.92^{b}	2.36 ± 0.38^{a}
KUT	17.50 ± 1.23^{a}	2.32 ± 0.14^{a}	3.45 ± 0.11^{a}	3.53 ± 0.13^{a}	22.86 ± 1.88^{a}	2.45 ± 0.37^{a}
SE(m)	0.018	0.008	0.008	0.009	0.118	0.040
CD (0.05)	0.055	0.025	0.024	0.026	0.364	0.123
CV	0.257	0.877	0.567	0.605	1.333	4.359

VEL: Vellaikolumban; KUR: Kurukkan; KAL: Kalapady; KUT: Kuttiattoor; CD: critical difference; CV: coefficient of variation; SE: standard error. Mean values followed by different superscript letters (a–d) within a column are significantly different according to Duncan's multiple range test at $p < 0.05$.

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Table 5. Effect of root stock age on graft growth parameters (140 DAG)

Age of rootstock (months)	Elongation of scion (cm)	Girth of new growth (cm)	Girth of scion (cm)	Girth of stock (cm)	Number of leaves	Number of primary branches
M_1	15.64 ± 0.95^{c}	2.16 ± 0.04^{c}	3.28 ± 0.06^{c}	3.33 ± 0.04^{c}	19.93 ± 0.71^{c}	2.00 ± 0.13^{c}
M_2	16.67 ± 0.93^{b}	2.20 ± 0.04^{b}	3.38 ± 0.04^{b}	3.47 ± 0.04^{b}	21.92 ± 1.42^{b}	2.16 ± 0.15^{b}
M_3	18.55 ± 0.57^{a}	2.42 ± 0.08^{a}	3.51 ± 0.07^{a}	3.60 ± 0.08^{a}	23.25 ± 1.89^{a}	2.57 ± 0.32^{a}
SE(m)	0.015	0.007	0.007	0.007	0.102	0.035
CD (0.05)	0.047	0.022	0.021	0.023	0.315	0.107
CV	0.257	0.877	0.567	0.605	1.333	4.359

M1: 1-month; M2: 2-month; M3: 3-month; CD: critical difference; CV: coefficient of variation; SE: standard error. Mean values followed by different superscript letters (a–c) within a column are significantly different according to Duncan's multiple range test at $p < 0.05$.

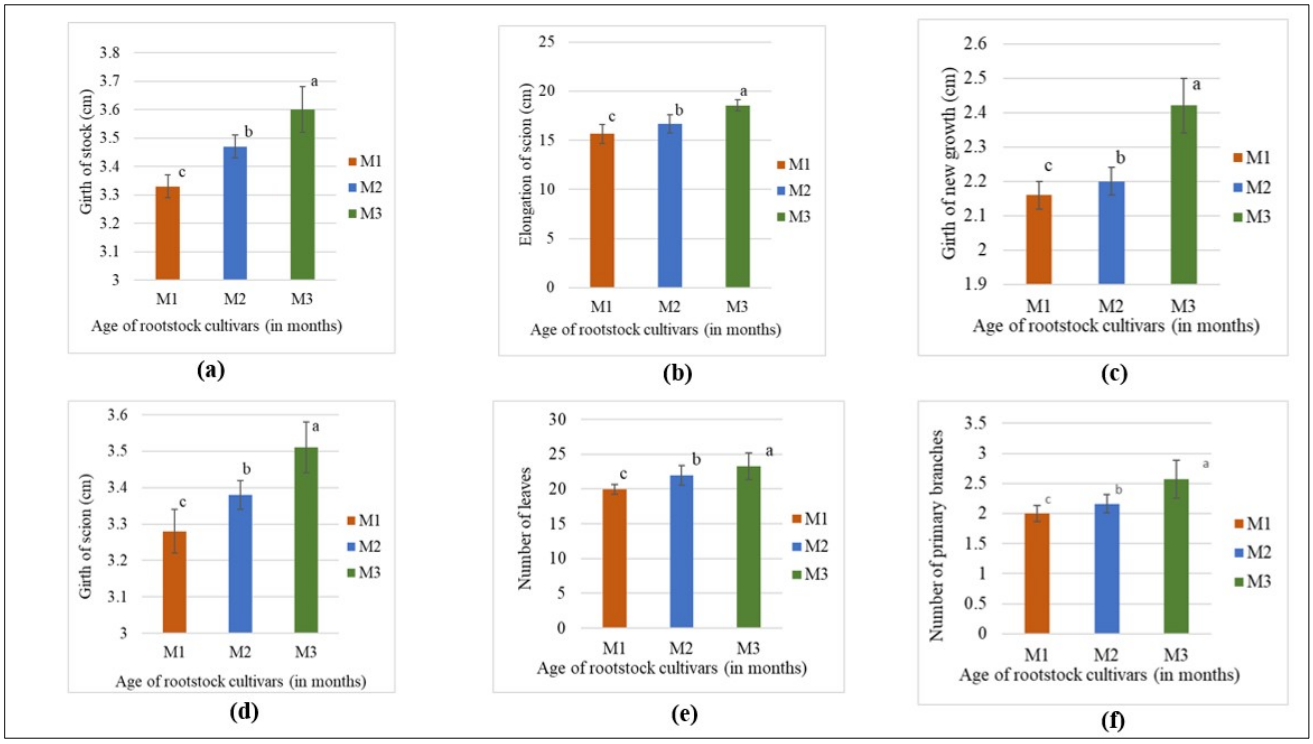


Fig. 2. Growth characteristics of grafts using rootstocks of different ages. a: girth of stock (cm); b: elongation of scion (cm); c: girth of new growth (cm); d: girth of scion (cm); e: number of leaves; f: Number of primary branches.

The superior vegetative growth observed in grafts on 3-month-old rootstocks is likely attributable to their optimal physiological maturity, characterised by active cambial tissues, greater carbohydrate reserves, enhanced metabolic activity and improved stress tolerance, which promote rapid graft union formation and vascular reconnection (36). Efficient vascular continuity enhances the translocation of water, nutrients and assimilates, resulting in greater scion elongation, stem girth and leaf production (18, 20). Similar responses have been consistently reported in mango, where physiologically mature rootstocks (3- to 4-month-old) exhibited superior vegetative growth compared with younger rootstocks (27, 29, 30, 37, 38). Comparable improvements in scion growth have also been reported in compatible homograft combinations, highlighting the importance of rootstock–scion compatibility in promoting post-grafting growth (36).

Table 6. Interaction effect of root stock cultivars and its age on graft growth parameters (140 DAG)

Varieties with rootstock age	Elongation of scion (cm)	Girth of new growth (cm)	Number of primary branches	Girth of scion (cm)	Girth of stock (cm)	Number of leaves
VEL M_1	14.1 ± 0.02^{i}	2.11 ± 0.014^{f}	1.85 ± 0.07^{f}	3.20 ± 0.01^{h}	3.29 ± 0.01^{i}	18.90 ± 0.14^{f}
VEL M_2	15.16 ± 0.05^{h}	2.17 ± 0.01^{e}	2.05 ± 0.07^{de}	3.32 ± 0.02^{ef}	3.42 ± 0.02^{ef}	19.70 ± 0.14^{e}
VEL M_3	17.65 ± 0.04^{c}	2.34 ± 0.02^{b}	2.25 ± 0.07^{bcd}	3.42 ± 0.007^{c}	3.52 ± 0.02^{bc}	20.30 ± 0.14^{de}
KUR M_1	16.02 ± 0.02^{g}	2.16 ± 0.02^{e}	2.00 ± 0.14^{ef}	3.27 ± 0.01^{g}	3.32 ± 0.02^{hi}	20.00 ± 0.28^{e}

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KUR M_2	17.06 ± 0.08^{e}	2.17 ± 0.04^{e}	2.05 ± 0.07^{de}	3.39 ± 0.01^{d}	3.45 ± 0.01^{de}	22.40 ± 0.56^{c}
KUR M_3	18.65 ± 0.04^{b}	2.37 ± 0.01^{b}	2.30 ± 0.14^{bc}	3.47 ± 0.01^{b}	3.55 ± 0.01^{b}	23.40 ± 0.28^{b}
KAL M_1	16.19 ± 0.01^{f}	2.19 ± 0.01^{de}	2.05 ± 0.07^{de}	3.31 ± 0.01^{f}	3.35 ± 0.04^{gh}	20.15 ± 0.07^{de}
KAL M_2	17.21 ± 0.01^{d}	2.23 ± 0.007^{c}	2.20 ± 0.14^{bcd}	3.41 ± 0.01^{cd}	3.49 ± 0.01^{cd}	22.60 ± 0.56^{c}
KAL M_3	18.93 ± 0.07^{a}	2.49 ± 0.01^{a}	2.85 ± 0.07^{a}	3.57 ± 0.01^{a}	3.67 ± 0.01^{a}	24.40 ± 0.28^{a}
KUT M_1	16.26 ± 0.02^{f}	2.21 ± 0.007^{cd}	2.10 ± 0.14c^{de}	3.35 ± 0.01^{e}	3.39 ± 0.01^{fg}	20.70 ± 0.14^{d}
KUT M_2	17.26 ± 0.02^{d}	2.25 ± 0.007^{c}	2.35 ± 0.07^{b}	3.43 ± 0.01^{c}	3.52 ± 0.007^{bc}	23.00 ± 0.14^{bc}
KUT M_3	18.99 ± 0.01^{a}	2.51 ± 0.01^{a}	2.90 ± 0.07^{a}	3.61 ± 0.04^{a}	3.69 ± 0.01^{a}	24.90 ± 0.14^{a}
SE(m)	0.031	0.014	0.069	0.011	0.015	0.205
CD (0.05)	0.095	0.043	0.213	0.034	0.046	0.631
CV	0.257	0.877	4.359	0.454	0.605	1.333

VEL M1: Vellaikolumban 1-month-old; VEL M2: Vellaikolumban 2-month-old; VEL M3: Vellaikolumban 3-month-old; KUR M1: Kurukkan 1-month-old; KUR M2: Kurukkan 2-month-old; KUR M3: Kurukkan 3-month-old; KAL M1: Kalapady 1-month-old; KAL M2: Kalapady 2-month-old; KAL M3: Kalapady 3-month-old; KUT M1: Kuttiattoor 1-month-old; KUT M2: Kuttiattoor 2-month-old; KUT M3: Kuttiattoor 3-month-old; CD: critical difference; CV: coefficient of variation; SE: standard error. Mean values followed by different superscript letters (a–i) within a column are significantly different according to Duncan's multiple range test at $p < 0.05$.



Fig. 3. Kuttiatoor grafts with 3-month-old rootstocks. a: Vellaikolumban; b: Kurukkan; c: Kalapady; d: Kuttiattoor (140 DAG).

Histological observations of graft union

The histological analysis of the graft unions revealed variations in callus formation, the presence of a necrotic line and tissue adhesion across different treatments, highlighting the influence of rootstock cultivar and rootstock age on graft compatibility during softwood grafting in Kuttiattoor mango.

Histological observation of graft union at 30 days after grafting

Histological analysis at 30 DAG showed a good connection between the tissues of the scion and rootstock in the Kuttiattoor grafts with 3-month-old Kuttiattoor rootstocks (Fig. 4a). They exhibited a very broad callus (430.64 µm) throughout the junction of the graft union without any gap. The callus was abundantly concentrated near the cambial ring. An adhesion line formed by thickened walls of cells belonging to the rootstock and scion was distinguishable to a varying extent at this stage. The necrotic patches disappeared in many regions. The cell walls of the scion and rootstock in the area of the graft junction were thicker. Early cell differentiation and formation of vascular tissue from the pre-existing vasculature were visible in grafts with 3-month-old Kuttiattoor rootstocks.

In the Kuttiattoor grafts with 2-month-old Kuttiattoor rootstocks (Supplementary Fig. 4b), callus formation initiated from the cambium junction between the rootstock and scion, extending towards the centre of the graft union. However, the presence of a thickened necrotic line and visible gaps at the junction suggested relatively lower compatibility compared with the Kuttiattoor grafts with 3-month-old Kuttiattoor rootstocks. The narrow callus width further indicated limited healing capacity, while the visible adhesion line pointed to incomplete tissue integration. These observations suggested that the physiological maturity of the grafts with 2-month-old rootstocks may not be sufficient to achieve optimal graft union at this stage. In the Kuttiattoor grafts with 1-month-old Kuttiattoor rootstocks (Supplementary Fig. 4a), callus formation had initiated but was limited to a small connection at the centre with gaps present in other regions, suggesting incomplete healing. The restricted callus formation may hinder the ability of the graft to fully establish vascular continuity, leading to reduced compatibility at this stage.

The Kuttiattoor grafts with 3-month-old Kalapady rootstocks (Fig. 4b) were characterised by a well-defined and highly thickened callus (242.25 µm) at the junction without any gap. The Kuttiattoor grafts with 2-month-old Kalapady rootstock (Supplementary Fig. 4d) exhibited necrotic lines and poor callus formation. In the Kuttiattoor grafts with 1-month-old Kalapady rootstocks (Supplementary Fig. 4c), a gap was present at the centre and a broad callus was formed along the sides of the graft union. The Kuttiattoor grafts with 3-month-old Kurukkan rootstocks (Supplementary Fig. 5b) exhibited

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moderate callus formation and improved tissue adhesion. The necrotic lines were still present. The tighter attachment suggested better graft integration compared with grafts on younger rootstocks, likely due to increased physiological maturity and greater storage of food reserves in the older rootstocks. The Kuttiattoor grafts with 2-month-old Kurukkan rootstocks (Supplementary Fig. 5a) showed a narrow callus connection and gaps at the graft junction. The Kuttiattoor grafts with 1-month-old Kurukkan rootstocks (Fig. 4c) exhibited a prominent necrotic line with minimal callus development. The callus was observed only along the sides of the graft, indicating that tissue integration was still in its early stages. This limited healing response reflects slower graft union formation.

The Kuttiattoor grafts with 3-month-old Vellaikolumban rootstocks (Supplementary Fig. 5d) showed low callus formation, highlighting that even with increasing age, the variety may have inherent limitations in achieving strong graft unions. The Kuttiattoor grafts with 2-month-old Vellaikolumban rootstocks (Supplementary Fig. 5c) exhibited limited callus formation. The Kuttiattoor grafts with 1-month-old Vellaikolumban rootstocks (Fig. 4d) displayed necrotic lines and minimal to very low connection between the scion and rootstock, indicating poor tissue compatibility. The lack of callus development suggested that the graft union might not progress effectively beyond this stage, resulting in low chances of graft success.

Compatible rootstock–scion combinations establish a continuous callus bridge, cambial continuity and organised vascular tissues, whereas incompatible unions are characterised by irregular callus formation, vascular discontinuity and tissue degeneration, ultimately reducing graft success (39, 40). Efficient graft healing depends on rapid cambial reactivation, carbohydrate mobilisation, vascular reconnection and coordinated hormonal regulation, which collectively promote successful graft union formation and functional integration (19, 24, 41–44). Kuttiattoor grafts on 3-month-old rootstocks, followed by Kalapady, showed reduced necrosis and better callus continuity, whereas 1-month-old rootstocks exhibited incomplete adhesion and necrotic barriers. Compatible combinations typically show earlier induction of hormone signalling and lignification-related genes, while incompatible unions display delayed or disrupted responses (44). Proper stock–scion contact enhances cambial activation and graft success, whereas excessive necrotic layers and undifferentiated callus impair union formation (16, 27). Although necrotic layers form early as a wound response, their presence does not necessarily prevent successful vascular reconnection (40, 45, 46).

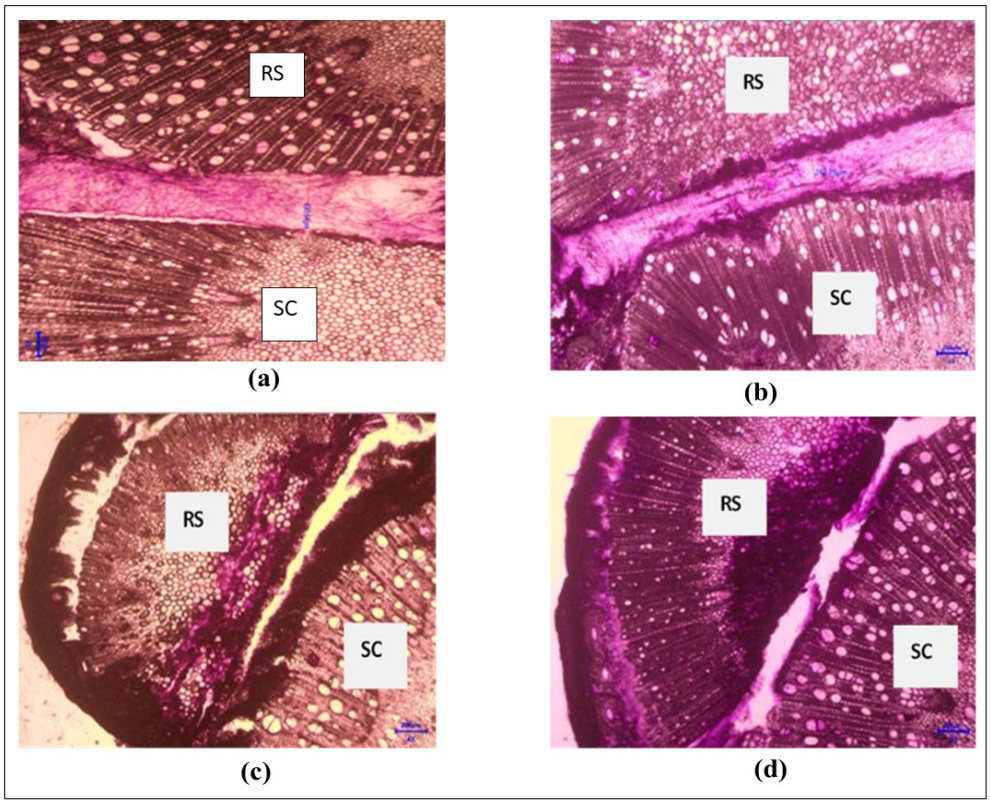


Fig. 4. Cross section of Kuttiattoor mango graft union at 30 DAG with different rootstocks. a: Kuttiattoor 3-month-old rootstocks; b: Kalapady 3-month-old rootstocks; c: Kurukkan 1-month-old rootstocks; d: Vellaikolumban 1-month-old rootstocks.
SC: scion; RS: rootstock.

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Rootstock maturity enhances graft integration through improved vascular development and carbohydrate reserves. In this study, 3-month-old rootstocks promoted faster callus formation, earlier sprouting and higher success, likely due to greater cambial activity and resource translocation (38, 47). Auxin-mediated signaling plays a central role in coordinating vascular bridge formation across the union (19, 43). In contrast, grafts on 1-month-old Vellaikolumban and Kurukkan rootstocks showed delayed union formation, reduced callusing and persistent necrotic lines, indicating stress and weaker compatibility (42). Carbohydrate dynamics also influence healing; starch accumulates above the graft and is later mobilised as vascular continuity is established. Adequate sugar availability supports callus proliferation and differentiation, while limitations or genotype-specific traits can restrict graft success (42, 43, 48).

Histological observation of graft union at 90 days after grafting

Kuttiattoor grafts on 3-month-old Kuttiattoor rootstocks (Fig. 5a) exhibited a very broad callus (787.46 µm) with early signs of cell differentiation, suggesting advanced integration and the establishment of functional vascular pathways that support nutrient transport and further growth. In Kuttiattoor grafts with 2-month-old Kuttiattoor rootstocks (Supplementary Fig. 6b) and 1-month-old Kuttiattoor rootstocks (Supplementary Fig. 6a), continuous vascular tissue connections were observed throughout the graft junction, indicating efficient healing and good scion-rootstock compatibility. The Kuttiattoor grafts with 3-month-old Kalapady rootstocks (Fig. 5b) exhibited a broad callus (359.71 µm) and cell differentiation, indicating stronger graft union development compared to younger rootstocks. The physiological maturity of the grafts with 3-month-old rootstock likely contributed to better tissue connection and enhanced nutrient flow across the graft junction. The Kuttiattoor grafts with 2-month-old Kalapady rootstocks (Supplementary Fig. 6d) displayed good callus formation. The Kuttiattoor grafts with 1-month-old Kalapady rootstocks (Supplementary Fig. 6c) showed a persistent adhesion line, suggesting that the healing process was still in progress. The Kuttiattoor grafts with Kurukkan 3-month-old rootstocks (Supplementary Fig. 7b), exhibited moderate callus connection and differentiation. The Kuttiattoor grafts with Kurukkan 2-month-old rootstock (Supplementary Fig. 7a) displayed good callus growth. The Kuttiattoor grafts with Kurukkan 1-month-old rootstock (Fig. 5c) showed low callus with gap at the junction. This may indicate that although Kurukkan rootstock have some capacity for graft union formation, they may require more time to establish strong functional connections between the scion and rootstock.

The Kuttiattoor grafts with 3-month-old Vellaikolumban rootstocks (Supplementary Fig. 7d) showed the presence of an adhesion line, suggesting incomplete vascular integration. The Kuttiattoor grafts with 2-month-old Vellaikolumban rootstocks (Supplementary Fig. 7c) exhibited good callus growth and differentiation. The Kutiattoor grafts with 1-month-old Vellaikolumban rootstocks (Fig. 5d) exhibited low callus growth and necrotic patches were observed throughout, highlighting poor compatibility and delayed healing. This suggested that Vellaikolumban rootstocks may have inherent limitations that prevent effective graft integration, particularly at younger stages. In summary, the histological observations revealed that at 90 DAG, cellular differentiation and vascular connectivity advanced in most treatments. The Kuttiattoor grafts with Kuttiattoor 3-month-old rootstocks, followed by Kalapady 3-month-old rootstocks, showed the most consistent vascular connections and advanced callus growth, which improved significantly with age. The Kuttiattoor grafts with 1-month-old Vellaikolumban rootstocks, followed by 1-month-old Kurukkan rootstocks, exhibited callus growth and vascular connectivity at a slower rate.

At 90 DAG, successful cambial continuity and vascular differentiation are typically established (49). In this study, rootstock age and genotype strongly influenced graft union development in Kuttiattoor mango. Grafts on 3-month-old Kuttiattoor and Kalapady rootstocks showed advanced healing, with extensive callus proliferation, clear cambial continuity and early xylem and phloem differentiation, reflecting optimal physiological maturity characterised by higher carbohydrate reserves, active cambium and enhanced lignification. Resource reallocation toward the graft interface supports intense metabolic demand during cell division and differentiation (42, 43). Grafts on 2-month-old rootstocks also developed continuous vascular connections, though tissue maturation was comparatively lower. The progressive improvement with age underscores the importance of physiological readiness for rapid meristematic activation and structural integration. In contrast, 1-month-old rootstocks, particularly Vellaikolumban and Kurukkan, exhibited limited callus formation, persistent adhesion lines and localised necrosis, indicating weak compatibility due to reduced metabolic reserves and delayed healing. Carbohydrate availability is a key limiting factor, as exogenous sugar supply enhances callus formation and vascular reconnection (42, 48).

Genotypic effects were evident: Kuttiattoor and Kalapady rootstocks ensured superior compatibility, whereas Vellaikolumban and Kurukkan showed delayed anatomical synchronisation, especially at younger stages. This highlights the role of genotype-dependent cambial responsiveness and carbohydrate metabolism in graft success, with altered sugar metabolism linked to slower healing in incompatible

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combinations (44, 48). The superior healing observed in 3-month-old rootstocks is attributed to coordinated vascular reconnection, carbohydrate mobilisation and cambial reactivation regulated by auxin signalling (47, 48). Adequate carbohydrate reserves promote vigorous callus formation, rapid cambial alignment and restoration of functional xylem and phloem (27). Conversely, limited reserves, delayed cambial activity and persistent necrosis in younger rootstocks disrupt vascular bridge formation and reduce compatibility (38, 42). Any imbalance in carbohydrate supply, auxin signalling, cambial activation or phloem differentiation can impair integration and lead to graft failure (44).

4. Conclusion

This study demonstrates that rootstock genotype and physiological age are key determinants of graft success, vegetative growth and graft union compatibility in softwood grafting of Kuttiattoor mango. Among the evaluated combinations, 3-month-old Kuttiattoor rootstocks exhibited superior graft establishment, characterised by earlier sprouting, higher survival, enhanced vegetative growth and improved vascular differentiation at the graft union. Comparable performance was also observed with 3-month-old Kalapady rootstocks. Histological observations further confirmed that successful graft establishment was associated with rapid callus proliferation, reduced necrotic tissue formation and early vascular reconnection, particularly in grafts involving 3-month-old Kuttiattoor and Kalapady rootstocks. These anatomical characteristics were reflected in their superior graft success and growth performance.

Although Vellaikolumban and Kurukkan rootstocks exhibited comparatively lower graft success and vegetative growth, their consistent suppression of scion vigour indicates their potential as candidate dwarfing rootstocks for Kuttiattoor mango. Such vigour-reducing effects could be advantageous for developing compact tree architectures suited to high-density orchards, improving canopy management, harvesting efficiency and overall orchard productivity. However, as the present study was confined to nursery-stage evaluations, the long-term effects of these rootstocks on tree vigour, canopy architecture, precocity, yield and fruit quality remain to be established. Based on the present findings, 3-month-old Kuttiattoor and Kalapady rootstocks can be recommended for efficient nursery propagation of Kuttiattoor mango, whereas 3-month-old Vellaikolumban and Kurukkan rootstocks warrant further evaluation as potential dwarfing rootstocks under long-term field conditions.

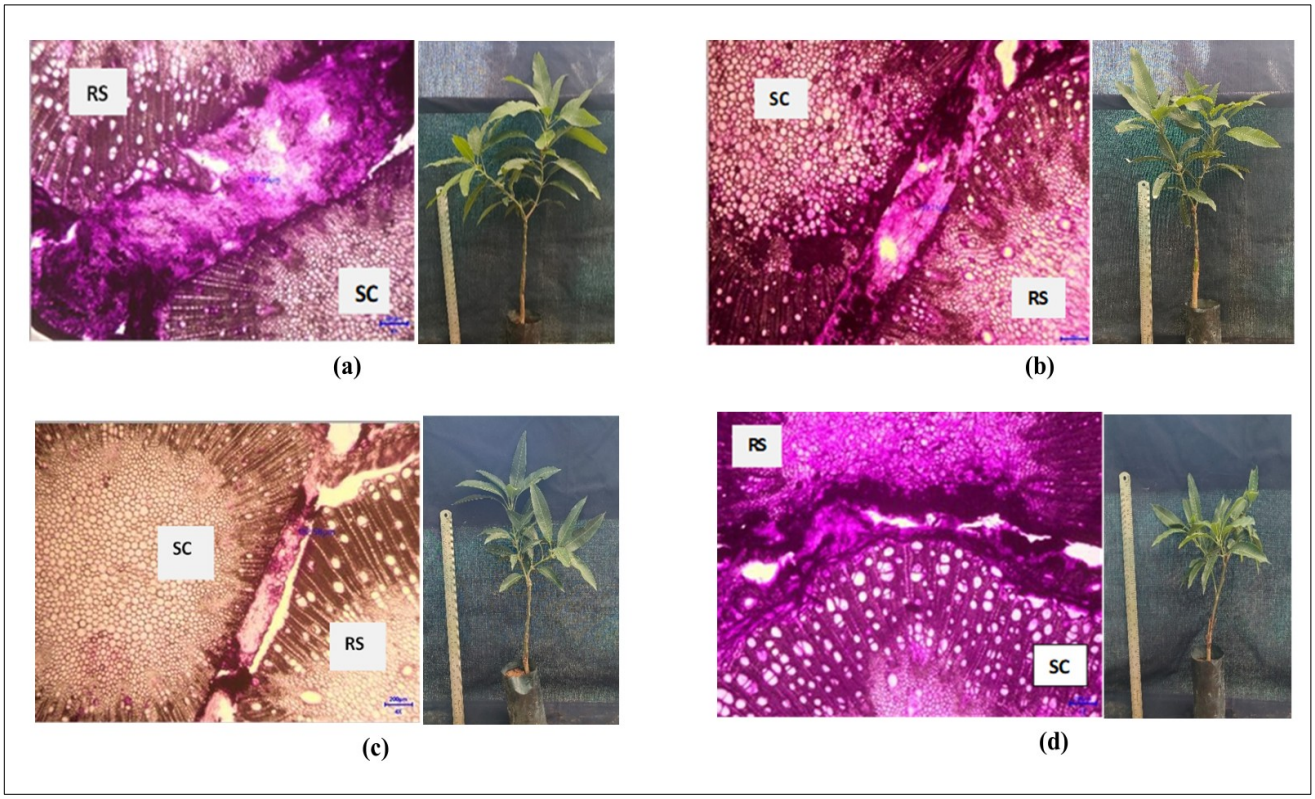


Fig. 5. Cross section of Kuttiattoor mango graft union at 90 DAG with different root stocks. a: Kuttiattoor 3-month-old; b: Kalapady 3-month-old; c: Kurukkan 1-month-old; d: Vellaikolumban 1-month-old.

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https://doi.org/10.14719/pst.15457

Acknowledgements

The authors gratefully acknowledge RF Wood Testing Unit, College of Forestry, Kerala Agricultural University, Thrissur, Kerala, India for providing support for sectioning of the plant material and for offering valuable assistance during research.

Authors' contributions

BS conceptualised the study, developed the methodology, carried out the investigation and prepared the original draft. PKR supervised the study, contributed to conceptualisation and validation, provided resources and reviewed and edited the manuscript. VR performed the formal analysis, supervised the study, provided resources and reviewed and edited the manuscript. NMM performed the investigation, validation and formal analysis, and supervised the study. KOS carried out the investigation, validation and formal analysis and supervised the study. GKK conducted the investigation, participated in validation and supervised the study. MMP developed the methodology, participated in validation and reviewed and edited the manuscript. NSS contributed to the methodology, provided resources and reviewed and edited the manuscript. All authors have read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest

Authors do not have any conflict of interests to declare.

Ethical issues

None

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https://doi.org/10.14719/pst.15457

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https://doi.org/10.14719/pst.15457