PLANT SCIENCE TODAY
Vol x(x): xx–xx
https://doi.org/10.14719/pst.8154

eISSN 2348-1900

REVIEW ARTICLE

Papaya grafting: Advance, mechanisms and future prospects

Meichander P[1], D Vidhya[1*], J Auxcilia[1], M Djanaguiraman[2], P Renukadevi[3] & I Muthuvel[4]

[1]Department of Fruit Science, Horticultural College and Research Institute, Tamil Nadu Agricultural University, Coimbatore 641 003, Tamil Nadu, India
[2]Department of Crop Physiology, Tamil Nadu Agricultural University, Coimbatore 641 003, Tamil Nadu, India
[3]Department of Plant Pathology, Tamil Nadu Agricultural University, Coimbatore 641 003, Tamil Nadu, India
[4]Horticultural College and Research Institute for Women, Tamil Nadu Agricultural University, Trichy 620 027, Tamil Nadu, India

*Correspondence email - dv79@tnau.ac.in

Received: 09 March 2025; Accepted: 20 April 2025; Available online: Version 1.0: 08 May 2025

Cite this article: Meichander P, Vidhya D, Auxcilia J, Djanaguiraman M, Renukadevi P, Muthuvel I. Papaya grafting: Advance, mechanisms and future prospects. Plant Science Today (Early Access). https:/doi.org/10.14719/pst.8154

Abstract

Papaya (*Carica papaya* L.) is a nutritionally rich and economically significant tropical fruit crop. Despite its importance, papaya cultivation faces challenges such as dioecy, inconsistent seed propagation and environmental influence on sex expression. Grafting has emerged as a viable vegetative propagation technique to overcome these constraints, ensuring uniformity, improved plant vigor and extended economic lifespan. Among various grafting methods, cleft grafting has demonstrated high success rates, producing hermaphrodite plants with desirable traits such as reduced fruiting height and increased productivity. The process involves intricate physiological and molecular mechanisms. These include callus formation, vascular regeneration and hormonal interactions that facilitate graft union success. Cytokinins and gibberellins play a crucial role in lateral shoot development, aiding scion production by mitigating apical dominance. Additionally, molecular studies reveal the movement of RNAs and proteins across graft unions, influencing growth regulation. Despite its advantages, papaya grafting faces challenges like bacterial rot, which can be managed through silicon application and optimized grafting conditions. This review highlights advancements in grafting techniques, emphasizing their role in enhancing propagation efficiency and improving papaya cultivation. Standardizing these techniques could provide sustainable solutions for commercial papaya production, ensuring consistent fruit quality and yield. Future research should focus on optimizing grafting methodologies, exploring resistant rootstocks and understanding genetic interactions and promoting field-level adoption to enhance commercial cultivation.

Keywords: grafting methods; hormonal balance; lateral shoot production; papaya propagation

Introduction

Papaya (*Carica papaya* L.) is a tropical fruit crop native to Americas and widely cultivated in tropical and subtropical region worldwide (1). India is the largest producer, contributing over 13.9 million tonnes annually-more than 50 % of global papaya production. As of 2023-2024, papaya is grown on approximately 148.13 thousand hectares in India, yielding around 5304.28 thousand metric tonnes (2). While Mexico dominates global papaya exports (3), the United States remains the largest consumer of this fruit (1). Papaya cultivation is widespread across India states such as Andhra Pradesh, Tamil Nadu, Assam, Maharashtra, Bihar, Uttar Pradesh, Gujarat, Kerala, West Bengal, Madhya Pradesh and Karnataka (4, 5). Gujarat leads in area and production (18.04 thousand ha and 1050.21 thousand MT), while Karnataka records in highest productivity (76.35 MT/ha) (2). Papaya is rich in fibre, flavonoids, antioxidants, iron, thiamine, vitamin C and vitamin A (6). It thrives in tropical climates with temperature 21 °C-33 °C, annual rainfall around 1200 mm and an altitude ranging from sea level to 1500 m (7). The crop adapts well to diverse soils, including volcanic and calcareous types and prefers a pH range of 6 to 6.5 (8).

Papaya is a soft-wooded, semi-herbaceous plant with a columnar growth habit, often resembling palm trees. It typically remains unbranched, wearing a crown of leaves with long, hollow petioles and deeply lobed blades (9). Botanically, papaya is trioecious-individual plants produce male, female, or hermaphrodite flowers. Male trees bear long, pendulos inflorescences with slender flowers that usually lack pistils. Female plants produce large pistil-bearing flowers without stamens, while hermaphrodites bear bisexual flowers capable of sexual variation (7). The fruit shape varies accordingly-female trees yield globose fruits, whereas hermaphrodites produce elongated fruits with higher market preference.

Environmental conditions strongly influence sex expression in papaya (10). Optimal growth occurs at 25-30 °C during the day and 11-16 °C at night. Intrestingly, sex reversal may occur under specific photothermal conditions; for instance, male plants may transform into hermaphrodites when exposed to 12 °C-night temperatures and shorter day lengths.

Early identification of plant sex is crucial for efficient field planting and cost saving. Molecular markers such as

RAPD and SCAR have been effectively used for sex determination at the seedling stage, reducing the chances of false negatives and improving breeding efficiency (11).

Earlier, the formation of callus and graft union was caused by the application of Plant Growth Regulators (PGR), like Benzyl Amino Purine (BAP) and chemical Zinc Sulfate ($ZnSO_4$), to the graft union during grafting, as well as by pre-treating the root stock and scion (12). Zinc is a crucial component that aids in the preservation and storage of Indole-3-acetic acid (IAA) in large amounts, which in turn causes the creation of xylem in the graft union after phloem formation. Auxin plays a crucial regulatory role in the development of plant grafts. Polar auxin transport (PAT) regulates auxin distribution in plant tissues, including xylem formation (13).

An effective graft union requires the advancement of "de novo" generated meristematic regions between the scion stick and the stock (14). For gynodioecious cultivars, bisexual varieties that yield fruits with distinct forms, sizes and flavours are favoured over round fruits from female plants because they command higher prices in the market (15). Globally, scientists are working on the possibility of vegetative propagation of papaya for crop improvement. Compared to other vegetative propagation methods, grafting makes papaya more efficient and promising (16). Traditionally, farmers follow the seedling method, raising the seeds in polybags and taking them to the field for production. Commercially, farmers do not practice asexual propagation in papayas. Despite its potential, vegetative propagation particularly grafting has not been widely adopted in commercial papaya cultivation. This review compiles current advancement in grafting methods, mechanisms and molecular insights, providing a foundation for researchers, breeders and growers to explore innovative approaches for sustainable papaya production.

History of papaya grafting

Papaya is naturally dioecious, meaning male and female flowers are produced on separate plants. However, growers typically prefer hermaphrodite plants due to their higher yield and superior fruit quality. Traditionally, when seedlings begin to flower, growers identify and retain a hermaphrodite plant while removing the others from each planting hole (17). Although commonly practiced, this seed-based method presents several challenges. To overcome such limitations, alternative propagation techniques-such as grafting, cuttings and in vitro culture-have been introduced (17). Among these, grafting is particularly recognized as an effective method for vegetative propagation of papaya (18). Early attempts at grafting using mature papaya tissues were largely unsuccessful, primarly due to excessive latex exudation at the graft site, which interfered with successful union formation. As a result, subsequent research shifted focus toward using juvenile plant material, which showed higher graft compatibility and success rate (4).

One of the earliest documented cases of papaya grafting involved field grafting of female branches onto male plants within the same dioecious variety (19). Further field experiment was reported in cultivars such as ‘Coorg Honey Dew’ and ‘Coimbatore 01’, demonstrating initial success in vegetative propagation through grafting (20). Nevertheless, few studies have been conducted on papaya grafting (21) and the tongue, approach and cleft grafting procedures are widely acknowledged as the most suitable grafting approaches (22). A number of variables, such as the grafting technique employed, suitability, vigour, health of the plants involved and post-grafting management, might affect the quality of the grafts (23).

Tongue grafting is simple and requires only a micro-environment with low relative humidity. Nonetheless, it demands more floor space and labor compared to other methods. Since the grafting point is close to the ground, it allows easier soil penetration by the adventitious roots of the scion, which in turn improves seedling survival rates. In this method, scions and rootstocks should be of similar diameter. The rootstock is sliced at an angle of 35 to 45 degrees through the hypocotyl. By making a partial cut, the developing tip can be left intact or removed using a grafting knife.

To overcome some limitations of traditional tongue grafting, modified tongue grafting approaches have been developed (24). For example, in the Apatzingan Valley, grafted seedlings showed high success rates (80-90 %) using both standard and modified tongue techniques. When seedlings were raised in plastic bags, graft survival increased to 92.5 %, indicating that environmental management post-grafting plays a critical role (25).

Grafting becomes intriguing when stronger rusticity traits are seen in rootstocks (26). Consequently, grafting between other Caricaceae genera and species has also been confirmed (27) and the grafts of *Vasconcellea cauliflora* and *Carica papaya*, *V. microcarpa* and *C. papaya* and *V. monoica* and *C. papaya* were compatible.

For tomato species splice grafting was effectively habituated in Almeria, Spain and also productive for the auto-graft of the ‘BH65’ papaya (28), where biodegradable tweezers are used for the “scion” and “rootstock” junction, speeding up the process and advancing the process towards automation (29). Grafting of standard sized “Solo” papaya variety scion onto “Dwarf Solo” rootstock, gave effective in reducing the height of flowering and fruit production on the stem, as well the vigour of the tree also minimized, while *vice versa* on grafting with “Dwarf Solo” scion onto the “Solo” rootstock (30). The timeline of papaya grafting is shown in Fig. 1.

Need of papaya grafting

Grafting plays a vital role in enhancing the genetic uniformity, robustness and resistance of plants to various environmental stresses, including those caused by living and non-living factors (31). Seed propagation, on the other hand, poses limitations such as producing offspring that do not consistently match the parent plant’s traits. Moreover, seeds from open-pollinated flowers often lead to variations in physical characteristics and disease susceptibility due to genetic unpredictability (16). In species with separate male and female plants, particularly in dioecious papaya varieties, maintaining a proper sex ratio is crucial for economic yields. To manage this, removing unwanted plants is necessary and vegetative propagation offers a more reliable alternative to

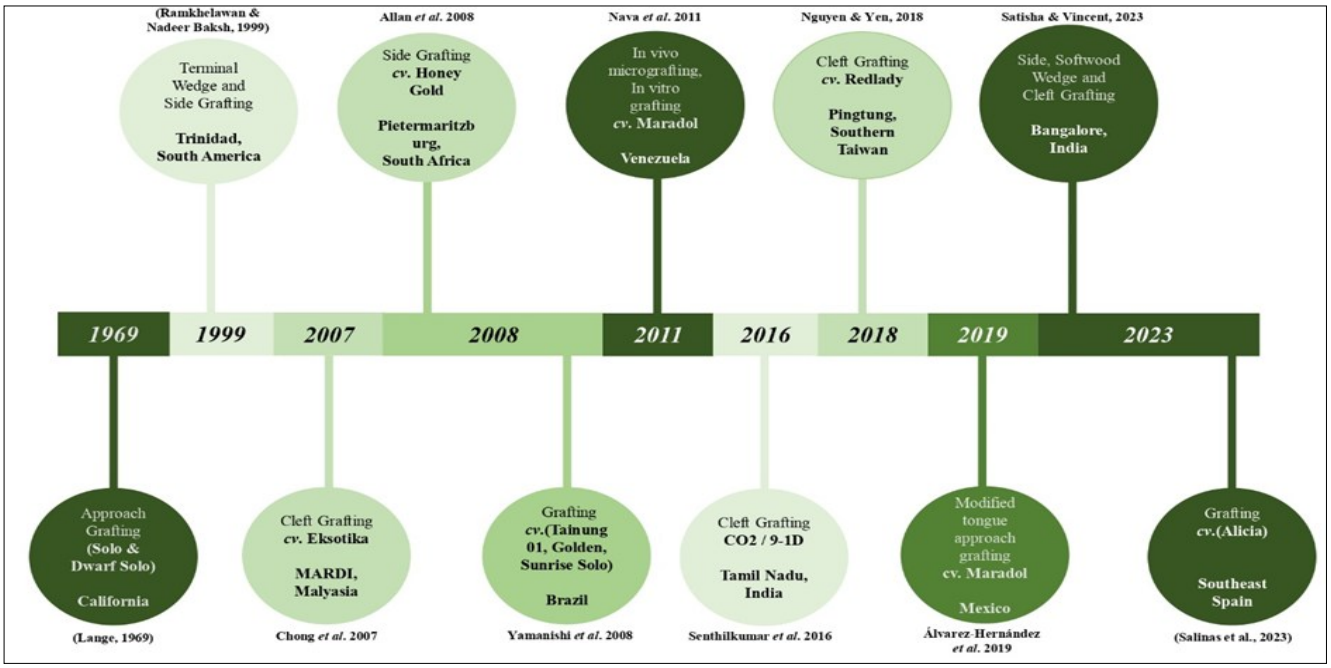

Fig. 1. Timeline of major grafting methods and advancements in papaya cultivation across different countries. This figure illustrates the chronological evolution of grafting techniques-such as approach, cleft and side grafting-along with the corresponding cultivars and geographic locations from 1969 to 2023. The timeline emphasizes the shift towards higher compatibility and success rates in grafting methods, contributing to improved papaya production and regional adoption strategies.

traditional seed methods (32). Commercial propagation of certain fruit crops remains difficult using seeds alone, prompting the adoption of grafting and other asexual techniques like layering and cutting. As a result, grafting is widely favored for its consistency and efficiency. Specifically, grafted papaya trees benefit from a compact growth form, allowing them to produce fruit earlier and closer to the ground, which increases their commercial value (26, 33).

Despite successive generations of inbreeding or sib-mating, considerable variation still exists in yield and phenotypic traits among plants of the same sex. This suggests that even with controlled breeding efforts, complete uniformity remains elusive. Moreover, progenies from such breeding programs often exhibit a mix of sex types, further complicating orchard management. These challenges underscore the genetic complexity of papaya and the limitations of breeding alone in achieving consistent performance (33). Due to its greater yield and superior fruit quality, growers prefer to cultivate hermaphrodite plants (17). However, a grower must transplant three to four seedlings in each planting hole to boost the likelihood of obtaining at least one hermaphrodite plant per hole (18). When the seedlings begin to bloom, the grower pulls the surviving plants from each planting hole, examines the sex of the flowers and select one hermaphrodite plant.

Seed propagated papaya plants display a broad mix of sex types-hermaphrodite, male and female-leading to inconsistencies in fruit quality and marketability (15). Early sex determination of papaya seedlings in nurseries is possible by using molecular markers (34). Nonetheless, certain disadvantages originating from the sexual origins of plants still exist. For example, although seedlings have a juvenile stage that delays their entry into production, their sexual origin causes significant heterogeneity in the field, with some productive specimens coexisting with others that, despite equal management, do not yield the same amount of fruit as nearby plants (35).

There are numerous problems associated with this seed multiplication method (36). The most noticeable, increase in price is related to the consumption of more plantlets than ultimately required; however, there are extra expenses associated with cultivating excess seedlings initially and the detrimental impact of their competition on plant growth.

The primary benefit of vegetative propagation especially grafting, is the ability to produce crops for bisexual and female plant population that have 100 % hermaphrodite plants (bisexual). In dioecious cultivars, female plants are propagated vegetatively with the help of certain male plants that are required for pollination to be ensured (37). Remarkably, 100 % of female plants that are developed through asexual propagation are established and there is a market for seedless papaya fruits. This also applies to other dioecious cultivars.

Grafted papaya trees exhibit a longer commercial lifespan, combined with dwarf growth habits and earlier fruiting. In Malaysia, farmers practicing grafting in the cultivar 'Eksotika' reported better fruit quality and productivity, leading to the removal of seed-propagated female plants (38). Similarly, in Taiwan, grafted plantlets are preferred over those produced via cuttings or micropropagation, due to their stronger root systems and better field establishment (39).

Scion and rootstock production in papaya grafting

Auxin and cytokinin are the hormones that governs the apical dominance in plants. The major antagonist to the auxin in the apical dominance is the cytokinin. Till now, to induce the lateral bud from the dormancy is the cytokinin (40). Generally, in the young leaves and in the shoot apex the auxins are involved (41), which is carried polarly and basipetally down the stem by the active movement of the vascular tissue. There are many proteins that handle the movement of auxin in which the auxin efflux messengers like PIN-formed (PIN

protein) and p-glycoprotein and the auxin influx mediator such as Auxin Resistant 1 (42). The presence of auxin in the plant's meristem zone causes apical dominance, which prevents the production of lateral branches in papaya (43). The ability of axillary buds to emerge from mature plants may be diminished because lignification of the nodal zones of the plant (44). Cytokinins promote cell division and play a critical role in initiating lateral bud development. Following apical bud removal (decapitation), lateral buds show increased auxin production and reduced abscisic acid (ABA) levels, facilitating outgrowth. The stem also synthesizes cytokinins, which are transported to axillary buds to stimulate their activation (40, 45). A clear pictorial representation for the scion production is given in Fig. 2.

In papaya, the application of gibberellins and cytokinins, when combined with apical segment cutting, has been shown to promote the emergence of lateral shoots (46). The rootstock, also referred to as the understock, forms the root system of the grafted plant, while the scion becomes the new shoot system. Scions are typically grafted onto selected rootstocks that possess resistance to both biotic and abiotic stressors. Selection of scions is usually based on traits related to yield potential (14).

A major limitation in papaya grafting is the restricted production of lateral shoots due to strong apical dominance in certain genotypes (4). However, the use of hormones such as benzyladenine (BA) and gibberellic acid (GA) can effectively overcome this dominance, stimulating the formation of side shoots. These hormones are particularly useful for generating scions suitable for grafting. A detailed list of hormones involved in scion production is presented in Table 1.

There is sturdy apical dominance, particularly in papaya trees. To overcome this, a different combination of BA and GA was used to promote the lateral shoots for grafting purposes in papayas and they also founded that BA (500 mg^{-1}) and GA (1000 mg^{-1}) with the combination of lanolin paste were applied to the matured part of the selected papaya plants, which resulted in a higher number of axillary buds (48). BA (500 mg^{-1}) and GA (100 mg^{-1}) spray solutions at an interval of three times per week showed efficient lateral shoot production. To produce high-quality scion materials, the mother blocks were placed under an insect-proof net.

Other plant growth regulators such as indole-3-acetic acid (IAA), indole-3-butyric acid (IBA), naphthaleneacetic acid (NAA), 2,4-dichlorophenoxyacetic acid (2,4-D) and parachlorophenoxyacetic acid (PCPA) have also been incorporated into basal media to stimulate shoot growth. Among these, auxin-based treatments have shown particularly promising results for enhancing lateral shoot development (52).

Rootstocks significantly influence the vigor, water transport and compatibility of the scion (14). For instance, one-month-old 'Red Lady' rootstocks performed well when grafted in both summer and autumn seasons (53). Other rootstocks such as 'Viorica' have shown high tolerance to papaya die-back disease, particularly when paired with susceptible scions like 'Eksotika'. Rootstock of three-months-old rootstock of CO2 papaya variety grafted with 9-1(D) showed the best result. Intervarietal grafts, such as 'CO8' scion onto 'CO8' rootstock, also enhanced chlorophyll content and soluble protein levels, indicating improved physiological performance (54-59).

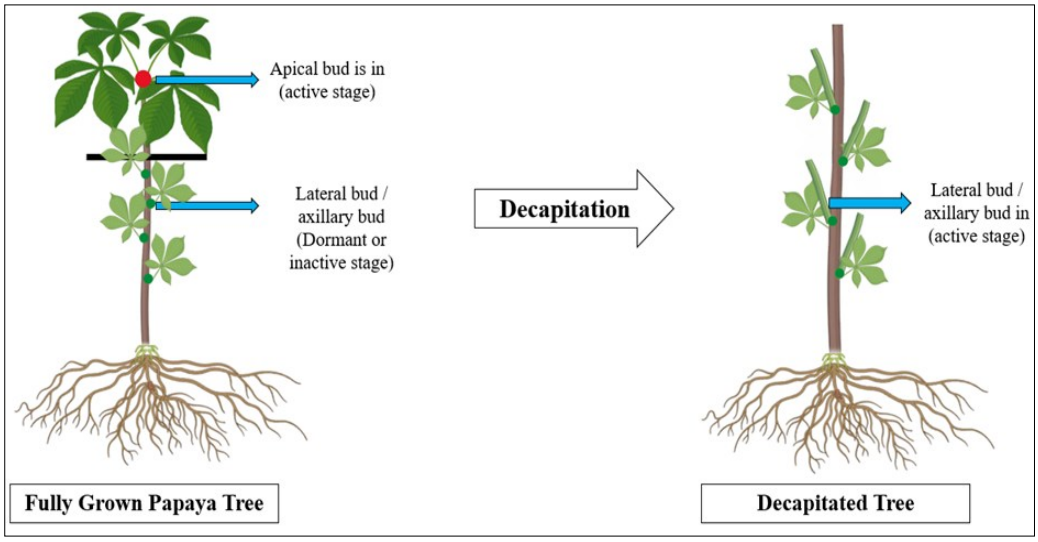

Fig. 2. A schematic representation on scion production in papaya.

Table 1. Different kind of hormones used for induction of lateral shoots

Plant age	Shoot induction treatment	Application interval	Days to scion stage	Reference
8-month-old	Defoliation+ GA_3 125 ppm + BA 125 ppm	3times/week & apical portion removed after 1st spray	35 days	(47)
2-year-old	BA 500 mg/l + GA_3 1000 mg/l	3times/week	5-6 weeks	(48)
1-year-old	De-topping + (500 ppm BAP + 100 ppm GA)	PGR were sprayed just once	50-60 days	(43)
5-6-month-old	Spraying BA @ 100 ppm + GA_3 @ 250 ppm	After 3 weeks 200ppm GA_3 were sprayed for all treatment	2 months	(44)
6-months-old	GA_3 250 mg/l + BA 250 mg/l	Three sprays were given at weekly intervals	45 days	(49)
-	Spraying BA @ 500 mg/l + GA_3 @ 100 mg/l	Three times at weekly intervals	30 days	(50)
12-months-old	Spraying BAP @ 500 mg/l + GA @ 500 mg/l	-	-	(51)

Role of cytokinin and GA_3 in shoot production

Branching of lateral shoots is mainly ruled by auxins, cytokinin and strigolactone (60). Cytokines are plant hormones that are generated from adenine, which quickens cell division and mitosis differentiation which are created at the tip of the root and carried out through xylem vessels. There are two types of cytokinin which are present and the first one is kinetin, zeatin and 6-Benzylaminopurine (6-BAP) which are examples of adenine developed in active cell division parts of plants. The other type is the artificial derivation of cytokinin, which is not produced by plants such as tidiazuron (TDZ), difeniluera meanwhile 6-BAP (Benzylaminopurine) plays a major role in the production of buds compared to other types of cytokinins (61). Based on physiological reasons, a growing apex produces a great amount of auxin, which circulates downwards to the stem to stop axillary bud growth and support apex expansion. Branching occurs when the apical portion is removed, during which the axillary buds are released and start to grow (62). In peas, the growth of axillary buds occurs when strigolactone biosynthesis decreases and cytokinin biosynthesis increases (63). Cytokinin biosynthesis is inhibited by auxin. Katyayini NU (60) minimal stem amount of auxin and strigolactones may be required for cytokinin induced expansion of the active axillary buds.

The major effect of gibberellins (GA's) has been identified, due to its shoot elongation property in larger plants, the increase in leaf growth with a decrease in the root development and the addition of adverse effects on shoot growth in normal and in dwarf plants were identified in gibberellins (64). Phytohormones like cytokinin and auxin have important, although sometimes conflicting, roles during the development of graft unions. It is well known that auxin builds up near the graft interface, encouraging cell proliferation and vascular differentiation-two processes necessary for effective graft healing (68). On the other hand, cytokinin promotes callus development and cell proliferation, especially in the rootstock area. However, cytokinin production can be inhibited by high auxin concentrations, indicating a carefully controlled antagonistic interaction. However, when auxin triggers cytokinin sensitivity in specific tissues, it can also have a synergistic effect by promoting coordinated cell division and tissue reconnection. For vascular reconnection and graft establishment to be effective, these hormones' balance and spatial distribution are consequently essential.

Methods of grafting in papaya

Various grafting techniques have been employed globally to propagate papaya, with varying levels of success and compatibility. Among these, cleft grafting has emerged as the most effective method, consistently demonstrating higher success rates and compatibility compared to other techniques. Although side grafting has also shown promising results (24), cleft grafting is generally considered more reliable for papaya propagation. Cleft grafting involves cutting the scion into a wedge shape and the rootstock into a cleft shape and inserting the wedge-shaped scion into the cleft-shaped rootstock (16). The procedure for cleft grafting in papaya is shown in Fig. 3. Cleft grafting showed 80 % success in the papaya variety eksotika compared to all other grafting methodologies and cleft grafting showed excellent propagation with vegetative means (26). Cleft-grafted eksotika plants are hermaphrodites that, produce fruits at

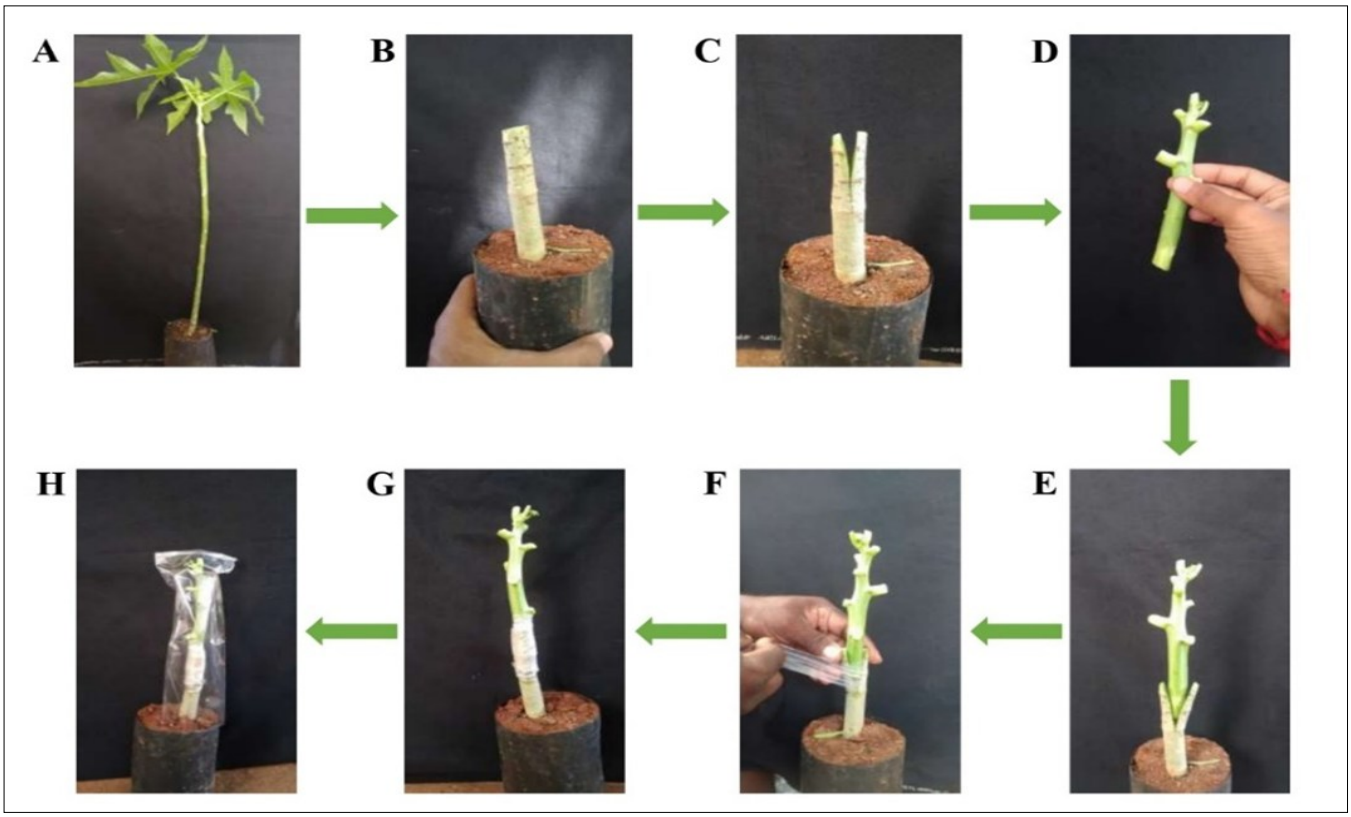

Fig. 3. A pictorial representation of Cleft grafting followed in papaya. (A) Selection of rootstock; (B) making a cut of stock (8-10 cm) from the soil; (C) cleft-shaped cut in the stock; (D) desirable girth of scion should be cut into wedge shape; (E) wedge-shape scion inserted into the stock; (F) wrapping of stock and scion with grafting tape; (G) grafted Papaya; (H) grafted Papaya covered with polythene cover to maintain humidity for graft union (own image).

lower heights and have a longer economic life cycle. The CO2 papaya variety grafted with the 9-1(D) papaya variety in the vegetative propagation of cleft grafting showed a nearly 96 % success rate in papaya grafting (58).

Apart from cleft grafting, there are other methods of grafting such as side grafting, wedge grafting, modified tongue approach grafting and in-vivo and in-vitro micrografting. Using a heavy knife at an angle of 20 to 30 degrees, an oblique incision was made into the rootstock branch for side grafting. The cut should be around 2.5 cm deep. The scion was inserted after pulling back the top of the stock branch and two or three buds were present on the scion (65). Side grafting with the honey gold variety of papaya showed an 81 % success rate after 105 days of grafting, but the major disadvantage was that scion rot caused by bacteria could not be prevented by the investigated biological therapies (24).

Wedge grafting, also known as the "Saw-Kerf Graft," involves scions typically 10-13 cm in length and 10-13 mm in diameter. The rootstock used has a similar diameter of 5-10 cm. The base of the scion is shaped into a wedge, which is then inserted into a corresponding slit in the rootstock. Proper alignment of the vascular cambium layers is critical. If matched accurately, the wedge fits securely and supports stable union formation (65).

Softwood grafting has outperformed both cleft and side grafting in terms of success rate (44). Approach grafting, although effective in the 'Honey Gold' variety (66), is labor-intensive and time-consuming. Similarly, splice grafting has been tested, but stem rot has often led to graft failure, limiting its practical utility. Tongue grafting, when secured with tape, achieved an 80 % success rate, comparable to cleft grafting (25). Modifications of this method, such as raising seedlings in polythene bags, increased graft success up to 92.5 %. Micrografting techniques have also been employed for papaya, pushing the boundaries of vegetative propagation and enabling precision in early-stage plant development. A comparison of the success rates of various practices of grafting in papaya has shown in Fig. 4 in which cleft grafting showed the highest percentage of successful grafts compared with other grafting methods. Although papaya grafting methods such as cleft and side grafting have a high compatibility and success rate, questions have been raised about their possible effects on genetic integrity over the course of several generations. Since grafting is a non-sexual propagation technique, it does not change the nuclear genome of the scion or rootstock. Recent studies have demonstrated that graft partners can share mobile genetic elements (such as proteins and short RNAs) and epigenetic changes, which may have an impact on gene expression in later vegetative generations (101). These modifications may impact characteristics like fruit yield, stress response, or disease resistance even if they are not actual mutations. Therefore, to guarantee the stability and uniformity of desired features in commercial production, grafted papaya lines must be monitored over an extended period of time.

Grafting mechanism

Successful grafting depends on the formation of a functional union between the scion and rootstock. This involves several key steps: adhesion of the graft partners, callus formation at the wound site and subsequent development of vascular connections (67, 68). Tissue compatibility between scion and rootstock is critical for the establishment of a successful graft union. Adhesion among the stock and scion, growth of callus cells or the forming of callus bridges and vascular differentiation over the graft interface are the primary steps in the formation of a compatible graft union (65). The scion cannot continue to grow effectively when vascular tissues are connected between the scion and rootstock (69). The new xylem and phloem gain vascular linkage again and it is a necessary step for forming fresh shoots from scion buds (70). The rigid graft grows exponentially at the beginning of the graft without deviation and tissue attachment occurs quickly (71). The success of grafting depends on the rootstock and scion used to produce graft union. Tissue healing following injury is accomplished via physiological, biochemical and

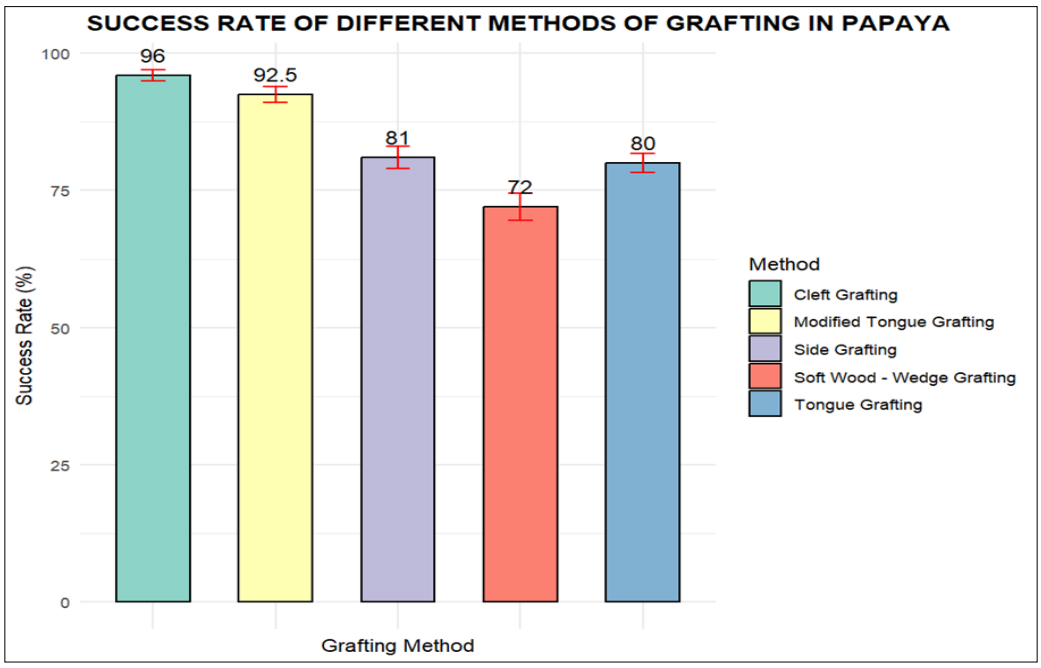

Fig. 4. Methods of grafting and its success rate in papaya (Source: R Studio).

molecular pathways that also form graft junctions (70). Five steps are followed in the graft union process 1. Necrotic layer development and alignment 2. Increased callus cell formation during graft union 3. At the graft junction, the callus bridge grows 4. Emergence of vascular cambia 5. Regeneration of vascular tissue at the junction of the scion and rootstock (14). Furthermore, the volume of cultivation affects papaya grafting's commercial feasibility. Grafting may not be widely adopted by small-scale farmers due to its time and effort required, unless there is adequate technical assistance and training for this process. Grafting, on the other hand, could be more practical for large-scale farmers since they have greater access to infrastructure, expert labour and resources. Therefore, even though grafting has several agronomic advantages, its use at all farming sizes is contingent upon logistical and financial factors.

Plant hormones involved in graft formation

Plant hormones, also referred to as phytohormones, are secreted by plants. These phytohormones are present in plants at minimal concentrations and exist in the form of chemical compounds such as auxins, cytokinins, gibberellins, abscisic acid and gaseous compounds like ethylene. In recent studies, researchers have utilized grafting techniques to demonstrate the transportation of molecules over long distances, including phytohormones, proteins and RNAs (72). Initially, grafting stimulates cells at the incision site to release pectins, facilitating the adhesion of the scion and stock (68). Subsequently, the connection of vascular cambium represents a critical step in the formation of the graft union (14). Phytohormones govern all aspects of the growth of the plant and control their reactions to both living and non-living environmental factors.

Auxin plays a critical role in promoting graft union compatibility. Cell division in proximity to vascular tissues is essential for the formation of callus tissue and the cellularization of graft unions (73). Low concentrations of auxin induce callus differentiation into phloem in several plant species, whereas high concentrations promote both phloem and xylem development. PIN proteins facilitate auxin transport to wound sites, which subsequently induces vascular tissue regeneration in Arabidopsis stems and pea epicotyl (74) . Auxins demonstrate a crucial role in citrus graft compatibility. Compatible combinations exhibited upregulation of nine auxin pathway genes and downregulation of three, in comparison to incompatible combinations (75). Along with gibberellin and cytokinin, auxin stimulates cell differentiation and triggers the emergence of the vascular connection and reconnecting of the graft junction which preserves the symmetry of auxin (14). Following grafting, nine differentially expressed genes (DEGs), categorized as TAA, YUC, Aux/IAA, auxin-responsive protein IAA and auxin-induced protein involved in IAA signal transduction or IAA biosynthesis pathways, were initially upregulated in a compatible combination (76).

Ethylene promotes cell growth, callus development and proliferation in the wound response during the formation of the graft interface and plays a role in the activity of auxin during grafting (73). AVG, an inhibitor of ethylene production, decreased scion development in WT/iaaM grafts three weeks after grafting. Abiotic stresses are linked to ethylene. For example, injury causes ethylene to be produced around the wound site (77).

During the wound-healing process, cytokinins can cause the graft union's callus to proliferate (78). Zeatin riboside levels increased 15 and 30 days after grafting in cells of the *Carya illinoinensis* graft union during examination (79) . Exogenous cytokinin treatment, such as benzyl adenine or kinetin, has been shown to promote graft union formation and greatly boost callus production in grapevines (80).

Gibberellin also plays a notable role in graft union formation. Plant vascular development is primarily regulated by GAs, which can influence xylem fibre differentiation, cambium activity, xylem expansion and secondary plant growth (81). Spraying GA_3 at 10 ppm immediately after grafting and again 21 days later improved grafting success (56.05 %) and shoot development in the Mallika mango cultivar (82). Additionally, GAs can stimulate and accelerate wood production through their signalling pathways. The concentration of gibberellins (GAs) increases at the site of graft union and the gene GA20OX, which is involved in GA biosynthesis, exhibits elevated expression in this region. Gibberellins and auxin function synergistically to facilitate tissue emergence through cellular proliferation (68, 78).

ABA's role in graft union formation has not been widely studied. The effects of ZR and IAA are counterbalanced by ABA, promoting differentiation and suppressing excessive cell division, which may be due to reduced ABA production or signal transduction (70). Among other phytohormones, these five play a major role in graft union formation. Other phytohormones like jasminoides and brassinosteroids have not been identified as involved in graft union formation.

Molecular aspects in graft union

Recent molecular studies in grafting biology have focused on understanding the long-distance transport of signaling molecules, especially RNAs and proteins, across the graft junction (14, 83). Short-distance DNA transfer in cells, close to the ends of the rootstock and scion during grafting has significant effects on scion growth and performance, including grafting success (84). Mobile mRNAs, small RNAs and proteins travel bidirectionally across the graft site, affecting chromatin remodeling and transcriptional activity (86, 90). For example, small RNAs have been shown to move from rootstock to scion and vice versa, reprogramming gene expression patterns and facilitating graft success as represented in Fig. 5 (70, 90).

Additionally, cell wall-associated molecules such as pectins, extensins, hemicellulose and arabinogalactan proteins are released during the early stages of graft union formation (86, 87). These aid in cell adhesion and stimulate callus development. Gene expression studies in model plants such as Arabidopsis have revealed the upregulation of graft-responsive genes like ERF114, ERF115, DOFs and ANAC071, which are associated with vascular tissue differentiation and wound healing (89). Proteins such as cyclophilin SICyp1 have been observed to migrate from scion to rootstock, amplifying auxin responses and promoting root growth (87). Differentially expressed proteins (DEPs), including aquaporins

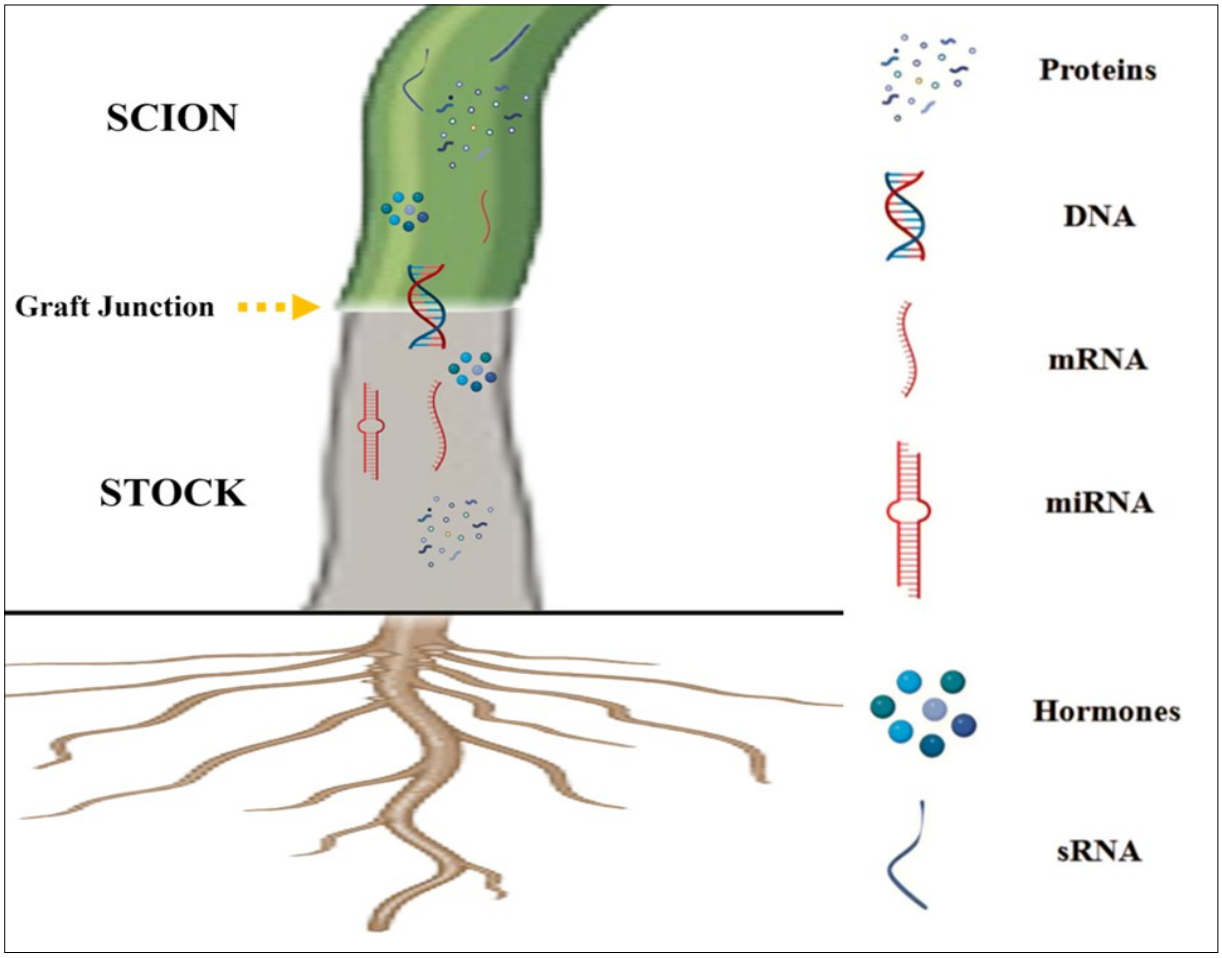

Fig. 5. An illustrative representative of exchanging signals between the graft interface (14).

like PIP1B, play roles in enhancing water transport and promoting callus integrity (93). Enhancer of Visual and Grafting 1 (EVG1), in coordination with receptor-like protein RLP44, has been linked to xylem differentiation and graft success (94). Recent findings also suggest horizontal gene transfer (HGT) and DNA movement across the graft union via plasmodesmata and the vascular cambium (87, 91). This suite of molecular and cellular signals collectively ensures functional integration between graft partners. In addition to providing insight on graft compatibility, an understanding of the molecular transport of proteins and RNAs provides new opportunities for the deliberate selection of improved rootstock-scion pairings. For example, it has been demonstrated that mobile mRNAs and short RNAs that travel across the graft union affect characteristics including the scion's resilience to illness, ability to withstand stress and growth vigour (95). The compatibility potential and physiological synergy between particular genotypes can also be communicated to breeders by protein signalling molecules involved in vascular differentiation or hormone responses. Now that transcriptome and proteomic studies are combined, researchers may find and filter the best graft partners to guarantee long-term performance, especially in high-density orchards or under abiotic stress (96). Therefore, molecular markers made from mobile proteins and RNAs are becoming useful instruments in contemporary grafting techniques.

Constraints in papaya grafting

The primary difficulty faced after grafting is bacterial rot in the scion, which occurs frequently (24). Silicon has emerged as a potential management tool due to its antimicrobial properties and role in plant defense. Present in the soil as monosilicic acid (H_4SiO_4) at concentrations of 0.1-0.6 mM, silicon is absorbed by plant roots and strengthens cell walls, reducing pathogen entry (97, 98). A favourable link has been discovered between silicon and decreased severity of bacterial infections in both monocot and dicot host plants (99). The application of silicon fertilizers, both in solid and liquid forms, enhanced plant resistance to various bacterial pathogens. Solid calcium silicate ($CaSiO_3$) fertilizers are incorporated into the soil (100). Liquid potassium silicate (K_2SiO_3) or sodium silicates (Na_2SiO_3) are applied as a soil drench or as a foliar spray. Sakr N (97) elicitors are known as biocompatible molecules and biological agents in combination with silicon can exhibit significant resistance against bacterial pathogens. For instance, the negative yeasts *Rhodotorula aurantiaca*, *R. glutinis* and *Pichia anomala* lessen the intensity of bacterial blotch (*Acidovorax citrulli*) on melon (101), while chitosan and the rhizobacteria strain *Bacillus pumilis* (102) lessen the extent of bacterial wilt (*Ralstonia solanacearum*) on tomatoes. Silicon is used for better effect to control the bacterial rot in the plants. The success of papaya grafting is restricted by a number of factors in addition to bacterial infections. A major problem is graft incompatibility, which frequently leads to poor graft unions or delayed graft failure, especially when mixing genetically

dissimilar scions and rootstocks (103). It has been shown that environmental stressors such high temperatures, low humidity and water stress have a detrimental effect on the graft healing process and lower success rates (65). Furthermore, because grafting requires specialised labour, regulated settings and extra inputs like grafting equipment and materials, its economic viability is an issue, particularly for smallholder farmers. These restrictions make it difficult for grafting techniques to be widely used in papaya farming, both on a local and big scale.

Conclusion and future prospects

Vegetative propagation, especially through grafting, holds transformative potential for improving papaya cultivation. Grafting enables the production of true-to-type plants, reduces variability and eliminates the challenge of managing male and female plants in dioecious cultivars. Additional benefits include reduced plant height, early fruiting and extended economic lifespan, all of which enhance productivity and facilitate orchard management field trials across various countries have shown high grafting success rates in papaya, affirming its feasibility. However, its adoption must be supported through standardized protocols, nursery-level training and research on compatible rootstock-scion combinations. In the future, papaya grafting could serve as a reliable solution to major cultivation challenges-offering uniformity, improved disease resistance and adaptability to climate variability. Therefore, the wider adoption and commercialization of grafting practices should be prioritized to ensure sustainable and profitable papaya production system.

Acknowledgements

The authors acknowledge the support of the Tamil Nadu Agricultural University, Coimbatore to allow to provide technical guidance. The GOI - DUS Papaya, PPVFRA, New Delhi to provide research assistantship during 2024-2025.

Authors' contributions

All the authors contributed equally to conceptualizing the work, interpretation, analysis, review writing and editing of the manuscript. All the authors 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

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the author(s) used ChatGPT to use to improve language and readability, with caution. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

References

1. Koul B, Pudhuvai B, Sharma C, Kumar A, Sharma V, Yadav D, et al. *Carica papaya* L.: a tropical fruit with benefits beyond the tropics. Diversity. 2022;14(8):683. https://doi.org/10.3390/d14080683
2. Indiastat. Area, Production and Productivity of Papaya in India (2023-2024-3rd Advance Estimates) 2023-2024. Available from: https://www-indiastat-com.elibrarytnau.remotexs.in/table/agriculture/selected-state-wise-area-production-productivity-p/1455632#
3. Husin F, Ya'akob H, Abd Rashid SN, Shahar S, Soib HH. Cytotoxicity study and antioxidant activity of crude extracts and SPE fractions from *Carica* papaya leaves. Biocatalysis and Agricultural Biotechnology. 2019;19:101130. https://doi.org/10.1016/j.bcab.2019.101130
4. Senthilkumar S, Kumar N, Soorianathasundaram K, Kumar PJ. Aspects on asexual propagation in papaya (*Carica papaya* L.) - a review. Agricultural Reviews. 2014;35(4):307-13. https://doi.org/10.5958/0976-0741.2014.00919.2
5. Sharma S, Gupta RK, Rana VS, Sankhyan N, Sharma U, Sharma S. Forecasting the future of papaya in india: predicting area and production through autoregressive integrated moving average. Applied Fruit Science. 2024;66(1):183-91. https://doi.org/10.1007/s10341-023-01009-0
6. Boshra V, Tajul A. Papaya - an innovative raw material for food and pharmaceutical processing industry. Health and the Environment Journal. 2013;4(1):68-75.
7. Ávila-Hernández JG, del Rosario Cárdenas-Aquino M, Camas-Reyes A, Martínez-Antonio A. Sex determination in papaya: current status and perspectives. Plant Science. 2023;335:111814. https://doi.org/10.1016/j.plantsci.2023.111814
8. Hernández-Salinas G, Luna-Cavazos M, Soto-Estrada A, García-Pérez E, Pérez-Vázquez A, Córdova-Téllez L. Distribution and eco-geographic characterization of *Carica papaya* L. native to Mexico. Genetic Resources and Crop Evolution. 2022;69(1):99-116. https://doi.org/10.1007/s10722-021-01207-3
9. Storey W. Carica papaya. Handbook of flowering. CRC Press; 2019. p. 147-57. https://doi.org/10.1201/9781351072540-23
10. Babhare U, Singh SK. Regulation of sex expression and flowering in papaya (Carica papaya). Journal of Pharmacognosy and Phytochemistry. 2020;9(6):549-51.
11. Modi A, Suthar K, Thakkar P, Mankad MC, Kumari S, Narayanan S, et al. Evaluation of sex specific RAPD and SCAR markers linked to papaya (*Carica papaya* L.). Biocatalysis and Agricultural Biotechnology. 2018;16:271-6. https://doi.org/10.1016/j.bcab.2018.08.004
12. Ikeuchi M, Sugimoto K, Iwase A. Plant callus: mechanisms of induction and repression. The Plant Cell. 2013;25(9):3159-73. https://doi.org/10.1105/tpc.113.116053
13. Růžička K, Ursache R, Hejátko J, Helariutta Y. Xylem development-from the cradle to the grave. New Phytologist. 2015;207(3):519-35. https://doi.org/10.1111/nph.13383
14. Rasool A, Mansoor S, Bhat K, Hassan G, Baba TR, Alyemeni MN, et al. Mechanisms underlying graft union formation and rootstock scion interaction in horticultural plants. Frontiers in Plant Science. 2020;11:590847. https://doi.org/10.3389/fpls.2020.590847
15. Silva Jd, Rashid Z, Nhut DT, Sivakumar D, Gera A, Souza MT, et al. Papaya (*Carica papaya* L.) biology and biotechnology. Tree and Forestry Science and Biotechnology. 2007;1(1):47-73.
16. Kumar PV. Comparative analysis of metabolomics associated with intra-varietal graft of dioecious papaya var. TNAU Papaya CO 8; 2021.
17. Ramos HCC, Pereira MG, Silva FFd, Viana AP, Ferreguetti GA. Seasonal and genetic influences on sex expression in a backcrossed segregating papaya population. Crop Breeding and Applied Biotechnology. 2011;11:97-105. https://doi.org/10.1590/s1984-70332011000200001

18. Salinas I, Hueso JJ, Força Baroni D, Cuevas J. Plant growth, yield and fruit size improvements in 'Alicia' papaya multiplied by grafting. Plants. 2023;12(5):1189. https://doi.org/10.3390/plants12051189
19. Hancock W. Grafting male papaw trees. Queensland Agricultural Journal. 1940;54:377-9. https://doi.org/10.1080/03670074.1943.11664351
20. Airi S, Gill S, Singh S. Clonal propagation of papaya (*Carica papaya* L.). Journal of. Agriculture Research. 1986;23:237-9.
21. Van Hong Nguyen VHN, Yen Chung Ruey YC. Rootstock age and grafting season affect graft success and plant growth of papaya (*Carica papaya* L.) in greenhouse. 2018;78(1). https://doi.org/10.4067/s0718-58392018000100059
22. Lee J-M, Oda M. Grafting of herbaceous vegetable and ornamental crops. Horticultural Reviews-Westport then New York 2002;28:61-124. https://doi.org/10.1002/9780470650851.ch2
23. Kawaguchi M, Taji A, Backhouse D, Oda M. Anatomy and physiology of graft incompatibility in solanaceous plants. The Journal of Horticultural Science and Biotechnology. 2008;83(5):581-8. https://doi.org/10.1080/14620316.2008.11512427
24. Allan P, Clark C, Laing M, editors. Grafting papayas (*Carica papaya* L.). II International Symposium on Papaya 851; 2008. https://doi.org/10.17660/actahortic.2010.851.38
25. Álvarez-Hernández JC, Castellanos-Ramos JZ, Aguirre-Mancilla CL. Adaptation of a grafting method for *Carica papaya* based on seedling behavior. HortScience. 2019;54(6):982-7. https://doi.org/10.21273/hortsci13800-18
26. Chong S, Prabhakaran R, Lee H, editors. An improved technique of propagating 'Eksotika' papaya. International Workshop on Tropical and Subtropical Fruits 787;2007. https://doi.org/10.17660/actahortic.2008.787.30
27. Jimenez H. Injertos entre especies de Carica. Agriculture Tropical. 1957;7(1):33-7.
28. Schmildt ER, Schmildt O, Alexandre RS, do Amaral JAT, Campostrini E, Ferreguetti GA, et al. Propagação assexuada de mamoeiro. Fruticultura Tropical. 2015:158.
29. Lee J-M, Kubota C, Tsao S, Bie Z, Echevarria PH, Morra L, et al. Current status of vegetable grafting: Diffusion, grafting techniques, automation. Scientia Horticulturae. 2010;127(2):93-105. https://doi.org/10.1016/j.scienta.2010.08.003
30. Lange A. Reciprocal grafting of normal and dwarf Solo papaya on growth and yield. HortScience. 1969;4(4):304-6. https://doi.org/10.21273/hortsci.4.4.304
31. Leonardi C, Romano D, editors. Recent issues on vegetable grafting. XXVI International Horticultural Congress: Issues and Advances in Transplant Production and Stand Establishment Research. ISHS Acta Horticulturae 631;2002. https://doi.org/10.17660/actahortic.2004.631.21
32. Preece JE. A century of progress with vegetative plant propagation. HortScience. 2003;38(5):1015-25. https://doi.org/10.21273/hortsci.38.5.1015
33. Allan P, editor. Propogation of 'Honey Gold' papayas by cuttings. International Symposium on Tropical Fruits. ISHS Acta Horticulturae 370;1993. https://doi.org/10.17660/actahortic.1995.370.15
34. Salinas I, Salehi M, Hueso J, Cuevas J. Assessment of two sex-determining procedures in 'BH-65' papaya from an economical and developmental point of view. Fruits. 2018;73(3):184-90. https://doi.org/10.17660/th2018/73.3.5
35. Chan LaiKeng CL, Teo C. Micropropagation of Eksotika, a Malaysian papaya cultivar and the field performance of the tissue culture derived clones. ISHS Acta Horticulturae 575: International Symposium on Tropical and Subtropical Fruits; 2002. https://doi.org/10.17660/actahortic.2002.575.8
36. Araya-Valverde E, Bogantes A, Holst A, Vargas-Mora C, Gómez-Alpízar L, Brenes A, et al. Field performance of hermaphrodite papaya plants obtained through molecular selection and micropropagation. Crop Breeding and Applied Biotechnology. 2019;19:420-7. https://doi.org/10.1590/1984-70332019v19n4a59
37. Schmildt O, Silva C, Ferreguete GA, Schmildt E, Czepak MP. Correlação canônica entre caracteres vegetativos e de Capacidade de brotação em mamoeiro. Enciclopédia Biosfera. 2011;7(13). https://doi.org/10.18227/1982-8470ragro.v10i3.3021
38. Cheah L, Yau K, Subramaniam S, Lai F, editors. Cleft grafting and quality improvements of papaya cv.'Eksotika'. Proc Seminar on the Fruit Industry in Malaysia. MARDI Johor Bahru, Malaysia; 1993.
39. Nguyen V-H, Yen C-R, Hsieh C-H. Effects of Rootstock Age and Grafting Time on Cleft Grafting in 'Tainung No. 2'Papaya. International Journal of Research in Agricultural Sciences 2018;5(2):2348-3997.
40. Shimizu-Sato S, Tanaka M, Mori H. Auxin-cytokinin interactions in the control of shoot branching. Plant Molecular Biology. 2009;69:429-35. https://doi.org/10.1007/s11103-008-9416-3
41. Ljung K, Bhalerao RP, Sandberg G. Sites and homeostatic control of auxin biosynthesis in Arabidopsis during vegetative growth. The Plant Journal. 2001;28(4):465-74. https://doi.org/10.1046/j.1365-313x.2001.01173.x
42. Murphy AS, Hoogner KR, Peer WA, Taiz L. Identification, purification and molecular cloning of N-1-naphthylphthalmic acid -binding plasma membrane-associated aminopeptidases from Arabidopsis. Plant Physiology. 2002;128(3):935-50. https://doi.org/10.1104/pp.010519
43. Das S, Wangchu L, Raghavan M, Langstieh LB. Effect of plant growth regulators, detopping and their combination on lateral shoots initiation in papaya (*Carica papaya*) var. vinayak. IJCS. 2018;6(3):3085-8. https://doi.org/10.13140/RG.2.2.24640.15365
44. Satisha J, Vincent L. Vegetative propagation of papaya (*Carica papaya* L.) through grafting. Current Science. 2023;124(2):00113891. https://doi.org/10.18520/cs/v124/i2/239-244
45. Lazar T. Annals of botany. In: Taiz L, Zeiger E, editors. Plant physiology. 3rd ed. Oxford University Press; 2003. https://doi.org/10.1093/aob/mcg079
46. de Souza Barros FL, Schmildt ER, Amaral AT, Coelho RI. Influence of the pruning to different heights in papaya tree 'Golden'. Revista Ciência Agronômica. 2009;40(4):596.
47. Senthilkumar S, Kumar N, Soorianathasundaram K, Jeyakumar P. Effect of plant bio-regulators in induction of lateral shoots in papaya cv. CO. 2. Plant Archives. 2014;14(2):707-10.
48. Reuveni O, Shlesinger D, editors. Rapid vegetative propagation of papaya plants by cuttings. International Symposium on the Culture of Subtropical and Tropical Fruits and Crops 275; 1989. https://doi.org/10.17660/actahortic.1990.275.36
49. Dhanyasree K, Rafeekher M, Simi S. Effect of plant bio-regulators on side shoot induction in papaya (Carica papaya) var. red lady. Pharma Innovation. 2022;11(12):5593-7.
50. Allan P, MacMillan C. Advances in propagation of *Carica papaya* L. cv. Honey Gold cuttings. 1991. https://doi.org/10.21273/hortsci.27.6.691f
51. Giampan JS, Cerqueira TS, Jacomino AP, Rezende JAM, Sasaki FF. Induction of lateral shoots of papaya tree (*Carica papaya* L.). Revista Brasileira de Fruticultura. 2005;27:185-7. https://doi.org/10.1590/S0100-29452005000100050
52. Drew R, Smith N. Growth of apical and lateral buds of papaw (*Carica papaya* L.) as affected by nutritional and hormonal factors. Journal of Horticultural Science. 1986;61(4):535-43. https://doi.org/10.1080/14620316.1986.11515737
53. Nguyen V-H, Yen C-R. Rootstock age and grafting season affect graft success and plant growth of papaya (*Carica papaya* L.) in

greenhouse. Chilean Journal of Agricultural Research. 2018;78 (1):59-67. https://doi.org/10.4067/s0718-58392018000100059

54. Sarip J, Nur Sulastri J, Sanimah S, Salehudin M, Razali M, Noor Faimah G, et al. Viorica: a promising rootstock in producing highly tolerance grafted papaya against papaya dieback disease. Transactions of the Malaysian Society of Plant Physiology. 2017;25(1):56-60.

55. Amin NM, Bunawan H, Redzuan RA, Jaganath IBS. Erwinia mallotivora sp., a new pathogen of papaya (*Carica papaya*) in Peninsular Malaysia. International Journal of Molecular Sciences. 2010;12(1):39-45. https://doi.org/10.3390/ijms12010039

56. Edelstein M, Cohen R, Burger Y, Shriber S, Pivonia S, Shtienberg D. Integrated management of sudden wilt in melons, caused by *Monosporascus cannonballus*, using grafting and reduced rates of methyl bromide. Plant Disease. 1999;83(12):1142-5. https://doi.org/10.1094/pdis.1999.83.12.1142

57. Mohd-Azhar H, Sarip J, Ghazali NF, Razikin MZM, Mariatulqabtiah AR. Tolerance level of grafted papaya plants against papaya dieback disease. Malaysian Applied Biology. 2021;50(1):95-103. https://doi.org/10.55230/mabjournal.v50i1.16

58. Senthilkumar S, Kumar N, Soorianathasundaram K, Jeyakumar P. A histological investigation on graft formation in papaya (*Carica papaya* L.). Ecology Environment and Conservation. 2016;22 (December Suppl.):69-72.

59. Akino A, Auxcilia J, Soorianathasundaram K, Muthulakshmi P. Evaluation of seedlings and intervarietal grafts on biochemical properties and biotic stress tolerance enzymes activities of papaya (*Carica papaya* L.). IJCS. 2018;6(4):2333-4.

60. Katyayini NU, Rinne PL, Tarkowská D, Strnad M, van der Schoot C. Dual role of gibberellin in perennial shoot branching: inhibition and activation. Frontiers in Plant Science. 2020;11:736. https://doi.org/10.3389/fpls.2020.00736

61. Amelia Z, Wulandari A, editors. Effect of 6-BAP application on shoot production of *Melaleuca alternifolia* seedlings. IOP Conference Series: Earth and Environmental Science. IOP Publishing; 2020. https://doi.org/10.1088/1755-1315/528/1/012063

62. Cline MG. Concepts and terminology of apical dominance. American Journal of Botany. 1997;84(8):1064-9. https://doi.org/10.2307/2446149

63. Tanaka M, Takei K, Kojima M, Sakakibara H, Mori H. Auxin controls local cytokinin biosynthesis in the nodal stem in apical dominance. The Plant Journal. 2006;45(6):1028-36. https://doi.org/10.1111/j.1365-313x.2006.02656.x

64. Jones RL, Kaufman PB. The role of gibberellins in plant cell elongation. Critical Reviews in Plant Sciences. 1983;1(1):23-47. https://doi.org/10.1080/07352688309382170

65. Hartmann HT, Kester DE. Plant propagation: principles and practices. Torrey Botanical Society; 1975. https://doi.org/10.2307/2483997

66. Allan P, editor. Vegetative propagation and production of 'Honey Gold' papayas. Symposium on Tropical Fruit in International Trade 269; 1989. https://doi.org/10.17660/actahortic.1990.269.13

67. Mudge K. A history of grafting. In: Janick J, editors. Horticulture reviews. Vol. 35. Wiley-Blackwell; 2009. https://doi.org/10.1002/9780470593776.ch9

68. Nanda AK, Melnyk CW. The role of plant hormones during grafting. Journal of Plant Research. 2018;131(1):49-58. https://doi.org/10.1007/s10265-017-0994-5

69. Pina A, Errea P. A review of new advances in mechanism of graft compatibility–incompatibility. Scientia Horticulturae. 2005;106 (1):1-11. https://doi.org/10.1016/j.scienta.2005.04.003

70. Habibi F, Liu T, Folta K, Sarkhosh A. Physiological, biochemical and molecular aspects of grafting in fruit trees. Horticulture Research. 2022;9:uhac032. https://doi.org/10.1093/hr/uhac032

71. Feng M, Augstein F, Kareem A, Melnyk CW. Plant grafting: molecular mechanisms and applications. Molecular Plant. 2024;17(1):75-91. https://doi.org/10.1016/j.molp.2023.12.006

72. Turnbull CG. Grafting as a research tool. In: Hennig L, Köhler C, editors. Plant developmental biology: methods and protocols. Vol. 655. Totowa (NJ): Humana Press; 2010:11-26. https://doi.org/10.1007/978-1-60761-765-5_2

73. Zhai L, Wang X, Tang D, Qi Q, Yer H, Jiang X, et al. Molecular and physiological characterization of the effects of auxin-enriched rootstock on grafting. Horticulture Research. 2021;8:74. https://doi.org/10.1038/s41438-021-00509-y

74. Aloni R. Vascular differentiation and plant hormones: Springer; 2021. https://doi.org/10.1007/978-3-030-53202-4

75. He W, Wang Y, Chen Q, Sun B, Tang H-R, Pan D-M, et al. Dissection of the mechanism for compatible and incompatible graft combinations of *Citrus grandis* (L.) Osbeck ('Hongmian Miyou'). International Journal of Molecular Sciences. 2018;19(2):505. https://doi.org/10.3390/ijms19020505

76. Chen Z, Zhao J, Hu F, Qin Y, Wang X, Hu G. Transcriptome changes between compatible and incompatible graft combination of Litchi chinensis by digital gene expression profile. Scientific Reports. 2017;7(1):3954. https://doi.org/10.1038/s41598-017-04328-x

77. Asahina M, Azuma K, Pitaksaringkarn W, Yamazaki T, Mitsuda N, Ohme-Takagi M, et al. Spatially selective hormonal control of RAP2. 6L and ANAC071 transcription factors involved in tissue reunion in Arabidopsis. Proceedings of the National Academy of Sciences. 2011;108(38):16128-32. https://doi.org/10.1073/pnas.1110443108

78. Sharma A, Zheng B. Molecular responses during plant grafting and its regulation by auxins, cytokinins and gibberellins. Biomolecules. 2019;9(9):397. https://doi.org/10.3390/biom9090397

79. Mo Z, Feng G, Su W, Liu Z, Peng F. Transcriptomic analysis provides insights into grafting union development in pecan (*Carya illinoinensis*). Genes. 2018;9(2):71. https://doi.org/10.3390/genes9020071

80. Köse C, Güleryüz M. Effects of auxins and cytokinins on graft union of grapevine (*Vitis vinifera*). New Zealand Journal of Crop and Horticultural Science. 2006;34(2):145-50. https://doi.org/10.1080/01140671.2006.9514399

81. Dayan J, Voronin N, Gong F, Sun T-p, Hedden P, Fromm H, et al. Leaf-induced gibberellin signaling is essential for internode elongation, cambial activity and fiber differentiation in tobacco stems. The Plant Cell. 2012;24(1):66-79. https://doi.org/10.1105/tpc.111.093096

82. Choudhury AG, Ghosh SN. Improvement of grafting success of mango through application of plant growth regulators. 2021;7 (2):105-8. https://doi.org/10.53552/ijmfmap.2021.v07ii02.012

83. Kehr J, Buhtz A. Endogenous RNA constituents of the phloem and their possible roles in long-distance signaling. In: Thompson GA, van Bel AJE, editors. Phloem: molecular cell biology, systemic communication, biotic interactions. Wiley; 2012. p. 186-208. https://doi.org/10.1002/9781118382806.ch9

84. Thomas HR, Frank MH. Connecting the pieces: uncovering the molecular basis for long-distance communication through plant grafting. New Phytologist. 2019;223(2):582-9. https://doi.org/10.1111/nph.15772

85. Toscano-Morales R, Xoconostle-Cázares B, Martínez-Navarro AC, Ruiz-Medrano R. AtTCTP2 mRNA and protein movement correlates with formation of adventitious roots in tobacco. Plant Signaling & Behavior. 2016;11(3):e1071003. https://doi.org/10.1080/15592324.2015.1071003

86. Frey C, Hernández-Barriuso A, Encina A, Acebes JL. Non-invasive monitoring of tomato graft dynamics using thermography and

fluorescence quantum yields measurements. Physiologia Plantarum. 2023;175(3):e13935. https://doi.org/10.1111/ppl.13935

87. Shivran M, Sharma N, Dubey AK, Singh SK, Sharma N, Sharma RM, et al. Scion–rootstock relationship: molecular mechanism and quality fruit production. Agriculture. 2022;12(12):2036. https://doi.org/10.3390/agriculture12122036

88. Xie L, Tian J, Peng L, Cui Q, Liu Y, Liu J, et al. Conserved regulatory pathways for stock-scion healing revealed by comparative analysis of Arabidopsis and tomato grafting transcriptomes. Frontiers in Plant Science. 2022;12:810465. https://doi.org/10.3389/fpls.2021.810465

89. Zhang A, Matsuoka K, Kareem A, Robert M, Roszak P, Blob B, et al. Cell-wall damage activates DOF transcription factors to promote wound healing and tissue regeneration in *Arabidopsis thaliana*. Current Biology. 2022;32(9):1883-94. https://doi.org/10.1016/j.cub.2022.02.069

90. Kapazoglou A, Tani E, Avramidou EV, Abraham EM, Gerakari M, Megariti S, et al. Epigenetic changes and transcriptional reprogramming upon woody plant grafting for crop sustainability in a changing environment. Frontiers in Plant Science. 2021;11:613004. https://doi.org/10.3389/fpls.2020.613004

91. Zhao L, Liu A, Song T, Jin Y, Xu X, Gao Y, et al. Transcriptome analysis reveals the effects of grafting on sugar and α-linolenic acid metabolisms in fruits of cucumber with two different rootstocks. Plant Physiology and Biochemistry. 2018;130:289-302. https://doi.org/10.1016/j.plaphy.2018.07.008

92. Buhtz A, Pieritz J, Springer F, Kehr J. Research article Phloem small RNAs, nutrient stress responses and systemic mobility. 2010;10:64. https://doi.org/10.1186/1471-2229-10-64

93. Zheng BS, Chu HL, Jin SH, Huang YJ, Wang ZJ, Chen M, et al. cDNA -AFLP analysis of gene expression in hickory (*Carya cathayensis*) during graft process. Tree Physiology. 2010;30(2):297-303. https://doi.org/10.1093/treephys/tpp102

94. Paultre DSG, Gustin M-P, Molnar A, Oparka KJ. Lost in transit: long -distance trafficking and phloem unloading of protein signals in Arabidopsis homografts. The Plant Cell. 2016;28(9):2016-25. https://doi.org/10.1105/tpc.16.00249

95. Notaguchi M, Okamoto S. Dynamics of long-distance signaling via plant vascular tissues. Frontiers in Plant Science. 2015;6:161. https://doi.org/10.3389/fpls.2015.00161

96. Kappagantu M, Brandon M, Tamukong YB, Culver JN. Rootstock-induced scion resistance against tobacco mosaic virus is associated with the induction of defence-related transcripts and graft-transmissible mRNAs. Molecular Plant Pathology. 2023;24 (9):1184-91. https://doi.org/10.1111/mpp.13353

97. Winslow MD. Silicon, disease resistance and yield of rice genotypes under upland cultural conditions. Crop science. 1992;32(5):1208-13. https://doi.org/10.2135/cropsci1992.0011183x003200050030x

98. Ma JF, Yamaji N. Silicon uptake and accumulation in higher plants. Trends in Plant Science. 2006;11(8):392-7. https://doi.org/10.1016/j.tplants.2006.06.007

99. Sakr N. Silicon control of bacterial and viral diseases in plants. Journal of Plant Protection Research. 2016;56(4):331-6. https://doi.org/10.1515/jppr-2016-0052

100. Datnoff L. Mineral nutrition and plant disease. APS Press; 2007. https://doi.org/10.2478/v10045-008-0034-5

101. Conceição CS, Felix KCS, Mariano RL, Medeiros EV, Souza EB. Combined effect of yeast and silicon on the control of bacterial fruit blotch in melon. Scientia Horticulturae. 2014;174:164-70. https://doi.org/10.1016/j.scienta.2014.05.027

102. Kurabachew H, Wydra K. Induction of systemic resistance and defense-related enzymes after elicitation of resistance by rhizobacteria and silicon application against *Ralstonia solanacearum* in tomato (*Solanum lycopersicum*). Crop Protection. 2014;57:1-7. https://doi.org/10.1016/j.cropro.2013.10.021

103. Goldschmidt EE. Plant grafting: new mechanisms, evolutionary implications. Frontiers in Plant Science. 2014;5:727. https://doi.org/10.3389/fpls.2014.00727

Additional information

Peer review: Publisher thanks Sectional Editor and the other anonymous reviewers for their contribution to the peer review of this work.

Reprints & permissions information is available at https://horizonepublishing.com/journals/index.php/PST/open_access_policy

Publisher's Note: Horizon e-Publishing Group remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Indexing: Plant Science Today, published by Horizon e-Publishing Group, is covered by Scopus, Web of Science, BIOSIS Previews, Clarivate Analytics, NAAS, UGC Care, etc
See https://horizonepublishing.com/journals/index.php/PST/indexing_abstracting