Review

Scion–Rootstock Relationship: Molecular Mechanism and Quality Fruit Production

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Abstract: Most tree fruits are commercially grown on different root systems, hence called composite plants. The section provides the root system as the rootstock, and the atop ground portion is called the scion. The combination is selected based on different traits of scion varieties, rootstock, and prevailing edaphic situations. The dated back plant propagation technique of joining two plants (grafting/budding) that directly communicates new physiological traits to the desirable scion variety from the rootstock remains unclear. In spite of this, the propagation technique continues widely applied in the multiplication of several fruit plant species. In a grafted plant, rootstocks impacted the scion variety’s growth, yield and quality attributes, physiology, nutrient accumulation as well as biotic and abiotic stress tolerance in many ways. Modern research in plant science for next-generation sequencing providing new vital information about the molecular interactions in composite plants multiplied using grafting. Now it was confirmed that genetic exchange is occurring between rootstock and scion variety through grafting joints. In this aspect, we discuss the process and the molecular mechanism of rootstock scion interactions. This review finally explains the dynamics of rootstock–scion interactions as well as their effect on physiology in terms of production, environmental stresses, and fruit quality. The morphological, physiochemical, and molecular mechanisms have been reviewed to develop an integrated understanding of this unknowable process that questions existing genetic paradigms. The present review summarizes the reported molecular mechanism between scion and rootstock and the impact of rootstocks on the production biology of scion varieties of economically important fruit crops and identifies numerous key points to consider when conducting rootstock scion interaction experiments. Rootstocks may offer a non-transgenic approach to rapidly respond to the changing environment and expand agricultural production of perennial fruit crops where grafting is possible in order to meet the global demand for fruit, food, and demands of the future.

Keywords: graft-union; hormones; molecular breeding; rootstock

1. Introduction

Horticulture is currently a major potential sector for increasing agricultural production, income generation, and nutritional security through export, employment generation, value addition, and diversification. In addition to new major challenges, low productivity per unit area continues a problem in most of the horticultural crops, with climate change impacting the greater effect on fruit productivity. Biotic (causal agents of disease, insect, nematode, etc.), and abiotic (temperature, humidity, drought, wind, water logging, salinity, etc.), stresses are also challenges. Numerous studies on graft union
formation and graft compatibility between scion–rootstock plants have given rise to several scientific hypotheses in herbaceous plants. However, due to long juvenile periods and generation times, and large plant size, studies at different growth stages of grafts in woody fruit plants are meager [1,2].

Rootstock selection is one of the most important factors in orchard management because it affects the growth, nutrient accumulation, environmental tolerance, and fruit quality of scion varieties [2–4]. Conventional breeding must be supplemented with molecular approaches to refine biotic and abiotic stress tolerance in fruit crops as lack of knowledge, breeding programs will often be time-consuming and costly. The identification of molecular markers linked to desirable rootstock traits must first be identified. For example, DNA fragments (genes), may be related to the production of an enzyme that promotes fruit set. If the location of this genetic material (marker) has been determined and the benefits of the marker have been identified, DNA from other rootstocks can be quickly screened for the gene of interest [5]. Parental genetic maps and delineated genomic regions associated with graft (in)-compatibility parameters in apricot has been studied by Pina et al. [6]. Therefore, the selection of desirable rootstocks at the nursery seedling stages can help to reduce the testing duration and exposure required for expensive field trials. Small interfering RNAs (silencing RNA) are now being used to grow virus-resistant transgenic rootstocks [7]. In rootstocks, the potential movement of RNA and DNA genetic or epigenetic factors and the transformation of proteins can be evaluated because of their unique and identifiable characteristics. It is commonly believed that grafted rootstocks and scions maintain their genetic identity, transcription factors, regulatory small interfering RNAs (siRNAs), micro RNAs (miRNAs), mRNAs, peptides, and proteins are mobile in the plant vascular system and may cross the graft union [8,9]. The present review explains how macromolecules such as DNA, RNA, and protein are transported between rootstock and scion via vascular tissues and affect scion in various fruit crops.

2. Molecular Mechanism between Scion and Rootstock

Earlier, researchers focused on the role of hormones in vascular reconnection [10]. Now, a successful graft union formation is the function of molecular signaling via phloem which leads to the anatomical and physiological changes in both components for the smooth connectivity of vascular tissues [11,12]. It is an established fact that the transfer of the intact plastid genome is essential across the graft junction at the molecular level for the uninterrupted communication between the scion and rootstock of the grafted plant [13,14]. The protein migrates from the companion cells of the shoot into the root cells and controls various physiological processes in plants [9]. The rapid development of molecular biotechnology and “omics” approaches will allow researchers to unravel the physiological and molecular mechanisms involved in the rootstock–scion interaction [15].

DNA, RNA, and Protein Transfer during Rootstock–Scion Interaction

As essential components of the RdDM pathway in Arabidopsis, sRNAs migrate bidirectional (from shoot to root and vice versa) [7]. The graft union allows molecules such as DNA, RNA, proteins, and hormones to be transferred bidirectionally between both the component of grafted plants [16,17] as shown in Figure 1.
DNA is able to transfer from rootstock to scion via vascular uptake. During the graft union formation, generation of plasmodesmata and re-establishment of vascular bundles provide horizontal gene transfer (HGT) transport channels [14,18,19]. Plant graft hybridization may result in the horizontal transfer of nuclear DNA and the transfer of cpDNA genetic material between the rootstock and scion, but no nuclear gene exchange occurs [19]. The entire chloroplast genome can be transferred through inter-specific grafting, regardless of graft orientation, and is relatively stable [20]. The movement of the nuclear genome occurs between grafting sections, resulting in the development of stable allopolyploid and fertile plants [21].

Small RNA regulates epigenetic alteration by counteracting DNA methylation in grafted and budded plants [22]. Small interfering RNAs (siRNAs) play an important role in signaling and gene silencing [12,23]. Micro RNAs (miRNAs) play a role during the development of graft union for example cca-miR159 and cca-miR156 are upregulated at the graft site of hickory plants during graft growth, stimulating the tissue attachment process. Furthermore, miR390b is downregulated, resulting in an increase in ATP-binding protein accumulation [24]. Superoxide radical scavenging enzyme superoxide dismutase 4 (SOD4) helps in the protection of plant cells due to oxidative stress caused during the early stages of the grafting due to tissue injury. SOD4 is a target of the miRNA cca-miR827, which has been found to be down-regulated during the early stages of grafting, preferring SOD4 activation to scavenge harmful superoxide radicals at graft unions [20]. Messenger RNAs (mRNAs), which are primarily responsible for the coding of various proteins, also regulate various functional proteins involved in the normal growth and development of plant tissues after they have been transported through the graft unions [25–27].

Many proteins (such as chaperones) have the ability to bind mRNAs and are known for their roles in promoting molecular transport and preventing mRNA degradation. One of these chaperones CmPP16 has been found in Cucurbita maxima (winter squash) and play role in RNA transfer from the rootstock to the scion via graft union [28]. The
cyclophilin protein SICyp1 is transported from the scion to the rootstock via the phloem. It increases auxin response and helps to promote root development. Proteins from the companion cells of the shoot can be transferred into the stele cells of the roots and regulate the physiology of grafted plants [29–31]. Plasma membrane intrinsic proteins (PIPs) are involved in the grafting process, and aquaporins are involved in cellular water transport controlling active cell proliferation [32,33]. At the grafting site, stimulated expression of an aquaporin (PIP1B) is accompanied by cell elongation and increased water levels, leading to good callus formation [34,35].

The role of differentially expressed proteins (DEPs) in grafting had been observed. In hickory plants, 369 and 341 DEPs are found to be downregulated and upregulated at graft unions, respectively [36], and increased expression of CcPIP1;2 during grafting has been found to be functional in Carya cathayensis [37]. Guo et al. [38] studied the differentially expressed genes (DEGs) to understand the mechanism of pumpkin grafting’s effect on watermelon fruit ripening and quality development. Loupit and Cookson [39] well explained the changes in transcript abundance during graft union formation indicate that grafting responses are similar to responses to wounding and include the differential expression of genes related to hormone signaling, oxidative stress, formation of new vascular vessels, cell development, and secondary metabolites, in particular polyphenols. The details of the differential expression of protein are shown in Table 1.

<table>
<thead>
<tr>
<th>Protein</th>
<th>Response</th>
<th>Crop</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>CmPP16</td>
<td>Favoring the process of molecular transport and reduce the degradation of</td>
<td>Cucurbita maxima</td>
<td>[28]</td>
</tr>
<tr>
<td></td>
<td>mRNAs.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>PbPTB3</td>
<td>Play role in long-distance movement of mRNAs across the graft junction</td>
<td>Pyrus betlaefolia</td>
<td>[31]</td>
</tr>
<tr>
<td></td>
<td>by binding of PbPTB3 to PbWoxT1 mRNA.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cyclophilin, SICyp1</td>
<td>Play role in increased auxin response and promoting the growth of roots.</td>
<td>Tomato</td>
<td>[40]</td>
</tr>
<tr>
<td>PIP1B</td>
<td>Enhanced water levels and cell elongation, leading to better callus formation and successful grafting.</td>
<td>Carya cathayensis</td>
<td>[35]</td>
</tr>
<tr>
<td>DEPs</td>
<td>At graft unions, 341 and 369 DEPs were found to be upregulated.</td>
<td>Carya cathayensis</td>
<td>[41]</td>
</tr>
<tr>
<td>PIN</td>
<td>Reunion of vascular tissues is favored by the auxin movement from top to downward direction mediated by PIN proteins.</td>
<td>Arabidopsis</td>
<td>[42]</td>
</tr>
</tbody>
</table>

3. Role of Hormones during Rootstock–Scion Interaction

Auxins play a key regulatory function in plants during the process of grafting and budding development. The polar auxin transport (PAT) maintains the levels of auxins in the plant portion and is involved in the development of xylem tissue [43]. In plants, auxins are needed for both shoot and root growth [20]. The production and proliferation of cambium and procambium cells are dependent on cytokinin (CK) signaling. Type-B ARR transcription factors, which are involved in callus formation and cell division, are activated by CK signaling. Plant immunity against biotic factors is provided by CK-activated ARR2 via salicylic acid (SA) mediated cell signaling [44]. Gibberellins (GAs) promote cell expansion, proliferation, and differentiation [20].

Ethylene is a gaseous hormone that regulates a wide range of processes, fruit ripening, and senescence, including root initiation and biotic and abiotic stress response. Abscisic acid (ABA) is essential for abiotic and biotic stress responses. How these phyto-
hormones and cell signals transported and regulated callus and vascular tissue formation is well explained in Figure 2. Further, details of growth regulators along with gene names are given in Table 2.

Table 2. Function of phytohormones encoding genes in graft compatibility in various fruit crops.

<table>
<thead>
<tr>
<th>Phytohormones</th>
<th>Genes</th>
<th>Response</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Auxin</strong></td>
<td><strong>Aux/IAA</strong></td>
<td>Control graft union healing and graft compatibility.</td>
<td>[45]</td>
</tr>
<tr>
<td></td>
<td><strong>GH3</strong></td>
<td>Showed positive responses to grafting.</td>
<td>[46]</td>
</tr>
<tr>
<td></td>
<td><strong>VviGH3-21</strong></td>
<td>Role in the grafted plant growth.</td>
<td>[46]</td>
</tr>
<tr>
<td></td>
<td><strong>PIN1 and ABCB1</strong></td>
<td>Carriers in auxin transport, regulate the graft development.</td>
<td>[47]</td>
</tr>
<tr>
<td></td>
<td><strong>CcPIN1b and CcLAX3</strong></td>
<td>Carriers for PAT and favor the process of grafting.</td>
<td>[37]</td>
</tr>
<tr>
<td></td>
<td><strong>ARF</strong></td>
<td>The process of grafting further regulates various biochemical pathways promoting vascular connection between the scion and the stock.</td>
<td>[35]</td>
</tr>
<tr>
<td></td>
<td><strong>MrPIN1, MrSHR</strong></td>
<td>Downregulation in the gene expression of MrPIN1 and MrSHR in roots of the grafted plants.</td>
<td>[48]</td>
</tr>
<tr>
<td></td>
<td><strong>MrPIN3</strong></td>
<td>Upregulation and enhanced distribution of auxins, which further induces the division of pericycle cell.</td>
<td>[49]</td>
</tr>
<tr>
<td></td>
<td><strong>HCA2</strong></td>
<td>Grafting site which is important for the reconnection of phloem.</td>
<td>[47]</td>
</tr>
<tr>
<td></td>
<td><strong>Type-B ARRss</strong></td>
<td>Induction of cell division and callus formation.</td>
<td>[50]</td>
</tr>
<tr>
<td></td>
<td><strong>LHW</strong></td>
<td>Growth and development of stele cells as well as in formation of protoxylem.</td>
<td>[50]</td>
</tr>
<tr>
<td></td>
<td><strong>VND7</strong></td>
<td>Expresses during protoxylem formation.</td>
<td>[51]</td>
</tr>
<tr>
<td></td>
<td><strong>VND6</strong></td>
<td>Expresses during metaxylem formation.</td>
<td>[51]</td>
</tr>
<tr>
<td></td>
<td><strong>CRE1/WOL</strong></td>
<td>Regulation of proliferation and specifica.</td>
<td>[52]</td>
</tr>
</tbody>
</table>
4. Effect of Rootstock on Scion

The effect of rootstock on the scion cultivars is one of the most important influences in fruit production. The effects differ depending upon the nature of the scion and stock and environmental conditions [58]. The effects of rootstock on the scion cultivars include tree vigor (dwarfing and vigor), flowering, fruiting, time of maturity, fruit size and fruit quality, resistance to biotic (disease, insect–pest, nematodes, etc.), and abiotic (cold, drought, flooding, salt, nutrients, etc.) stresses and post-harvest fruit quality is well studied in mango, apple, citrus, tomato, etc. [2,59–61]. Rootstock–scion interactions
demonstrated that rootstock had a greater influence than scion on tree weight and growth rate [62]. The rootstock–scion interaction affects the quality of fruit production by mitigating various biotic and abiotic stresses (Figure 1).

4.1. Effect on Tree Vigor

Most fruit crops have a wide shape and size canopy, and the development of small or even dwarf trees is of great importance from an economic point of view. Roots provide water and nutrients to shoots, while shoots provide assimilates to roots. In mango, some pre-selection criteria of rootstock selection for dwarfness are higher phloem to xylem and lower stomatal density per unit area on the leaf surface [63]. Higher phenolics content in the apical bud is associated with a reduction in vigor and causes dwarfness. In mango, Vellaikulumban seedling imparted dwarfing in contrast to Alphonso grafted on its own seedling [64]. The grape cultivar “Sultana” grows vigorously when grafted on 1103P, R2, and Ramsey, rootstocks [65]. *Psidium pumilum* rootstock had dwarfing effect [66,67] found that guava rootstock aneuploid No. 82 imparts dwarfness to “Allahabad Safeda” in terms of plant spread, plant volume and tree height and also reported to contribute high yield in this rootstock. Commercial citrus production relies on grafting with rootstocks that reduce tree vigor to control plant height very well studied in detail by several workers [68–73]. The detailed study on dwarfing rootstocks is very well reviewed [74,75]. In addition, the relationships between trunk radial growth and fruit yield in apple and pear trees on size-controlling rootstocks were well studied by Plavcova et al. [76]. In apples, 1rolB transgenic stock is less vigorous than the scion cultivars [77]. Upregulation of BAK1 in the dwarf combination in apples grown on dwarfing rootstocks, and a possible function for brassinosteroid signaling in scion dwarfing control in sweet cherry cv. grafted onto dwarfing rootstock (Gisela 5) and semi-vigorous rootstocks, 99 transcripts were differentially expressed (Gisela 6), and genes involved in transcription regulation, flavonoid metabolism, brassinosteroid signaling, and cell-wall modification or biosynthesis [78]. Apple rootstock has a dwarfing effect when TFs are methylated, they fail to bind the IPT5b promoter region, resulting in lower gene expression, which reduces cytokinin synthesis in the roots and causes dwarfism. Unmethylated promoters resulted in increased gene expression and proper cytokinin synthesis in roots, as well as increased vigor [79]. Epigenetic changes at the union affect chromatin architecture through DNA methylation, histone modification, and the action of small RNA molecules. The mechanism triggering these effects likely is affected by hormonal crosstalk, protein and small molecules movement, nutrient uptake, and transport in the grafted trees [80]. Hence, the influence of rootstocks on scion growth and dwarfing mechanisms is induced by multiple factors, including hormone signaling, photosynthesis, mineral transport, water relations, anatomical characteristics, and genetic markers. It has been shown that the complex interactions between scion and rootstock can regulate plant development and its structure [81]. The mechanism involved in imparting rootstock-induced dwarfing is presented in Table 3 and Figure 3.
Figure 3. Effect of differential gene expression to regulate canopy of fruit plant. This figure well explains how methylated (A) and unmethylated (B) condition regulate the plant height along with concentration of cytokinin. DNA methylation are epigenetic marks and are highly conserved and involved in altering the canopy of the plants by catalyzing changes in the chromatin structure through methylation and demethylation. Cytosine methylation (5 mC) is the key regulator in DNA.

<table>
<thead>
<tr>
<th>Fruit Crop</th>
<th>Rootstock</th>
<th>Effect</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peach</td>
<td>Okinawa and Capdebosq</td>
<td>Vigor</td>
<td>[82]</td>
</tr>
<tr>
<td></td>
<td>Nano</td>
<td>Semi-dwarf</td>
<td>[83]</td>
</tr>
<tr>
<td>Mango</td>
<td>Ollour and Vellaicolamban</td>
<td>Dwarfing</td>
<td>[64]</td>
</tr>
<tr>
<td>Pear</td>
<td>Quince C</td>
<td>Dwarfing</td>
<td>[84]</td>
</tr>
<tr>
<td></td>
<td>Pyrodwarf</td>
<td>Dwarfing</td>
<td>[58]</td>
</tr>
<tr>
<td></td>
<td><strong>Poncirus trifoliate</strong></td>
<td>Dwarfing</td>
<td>[83]</td>
</tr>
<tr>
<td>Citrus</td>
<td>Flying Dragon</td>
<td>Dwarfing</td>
<td>[83]</td>
</tr>
<tr>
<td></td>
<td>Troyer citrange</td>
<td>Dwarfing</td>
<td>[58]</td>
</tr>
<tr>
<td></td>
<td>Fand A 418</td>
<td>Dwarfing</td>
<td>[85]</td>
</tr>
<tr>
<td>Guava</td>
<td>Pusa srijan (Aneuploid 82)</td>
<td>Dwarfing</td>
<td>[58]</td>
</tr>
<tr>
<td></td>
<td>M-2, MM-104</td>
<td>Vigorous</td>
<td>[58]</td>
</tr>
<tr>
<td>Apple</td>
<td>B-9</td>
<td>Semi-dwarfing</td>
<td>[58]</td>
</tr>
<tr>
<td></td>
<td>M-9</td>
<td>Dwarfing</td>
<td>[86]</td>
</tr>
</tbody>
</table>
4.2. Effects of Rootstock on Biotic Resistance

Biotic stresses are the most detrimental factors in fruit production, resulting in lower yields and tree longevity. In fruit crops, biotic stresses such as disease, insect pests, and nematodes are a major concern. As a result, advanced breeding approaches such as trans grafting and gene silencing must be used to increase biotic stress resistance in fruit crops. A silenced rootstock expressing a small RNA homologous to a region of the viral genome produces a double-strain dsRNA that passes to the scion and activates the siRNA silencing signal, which interferes with viral genetic machinery replication, including virus resistance and systemic silencing. Apple rootstocks MM 109, MM 106, MM 111, and MM 104 are woolly aphid-resistant [87]. In cherry, the Mahaleb rootstock is resistant to the buckskin virus. Myrobalan B has been described as a plum rootstock resistant to bacterial canker disease [62]. Many diseases, such as exocortis, xyloporosis, and tristeza, are resistant to rough lemon, but nematode and gummosis are susceptible. According to Sathisha et al. [88], grape rootstocks such as 99 R, 1103 P 110 R, and 99 R had high levels of proline, total phenols, and total protein, and increased phenolic content in rootstocks may help in the reduction of disease incidence in grapes. In citrus rootstock breeding, seven RAPD markers were found linked to the Citrus tristeza virus resistance gene by bulked sergeant [89]. Guava rootstocks such as P. friedrichsthalianum (Chinese guava), P. lucidum (lemon guava), and P. cattleianum (strawberry guava) are resistant or immune to the root-knot nematode (M. enterolobii) [90] and Psidium guineense showed tolerance to the nematode [91] (Table 4).

Table 4. Details of rootstock to mitigate biotic stresses in fruit crops.

<table>
<thead>
<tr>
<th>Crop</th>
<th>Rootstock</th>
<th>Resistant/Tolerant Trait</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mango</td>
<td>Carabao, Pico Manga d Agua</td>
<td>Resistant to wilt</td>
<td>[92]</td>
</tr>
<tr>
<td>Guava</td>
<td><em>Psidium friedrichsthalianum, P. cattleianum var. lucidum</em></td>
<td>Resistance to root-knot nematode</td>
<td>[90]</td>
</tr>
<tr>
<td></td>
<td><em>Psidium guineense</em></td>
<td>Resistance to root-knot nematode</td>
<td>[91]</td>
</tr>
<tr>
<td></td>
<td>Dimple, Jonelle, GU 8</td>
<td>GWD resistance</td>
<td>[93]</td>
</tr>
<tr>
<td></td>
<td>GU8 P. longipes and P. arayan</td>
<td>Nematode tolerance</td>
<td>[94]</td>
</tr>
<tr>
<td>Avocado</td>
<td>Duke 7 and G6</td>
<td>Resistance to <em>P. cinnamomi</em></td>
<td>[95]</td>
</tr>
</tbody>
</table>
Citrus Star ruby and ruby red Resistant against citrus psylla [96]

*Vitis champinii* rootstock Dog Ridge and Ramsey have been discovered to have resistance to root-knot nematodes for a long time (RKN). VR O39-16 and UCD GRN1 rootstocks were selected for their resistance to the root lesion nematode [97]. Viorica is a promising rootstock for grafting to produce high resistance against papaya dieback disease, with a > 90% success rate, and has been used to reduce the susceptibility of elite scion [98]. Genetic modification of stone fruit rootstocks with genes encoding the BT (*Bacillus thuringiensis*) toxin for the control of Lepidopteran pests is one possible avenue [99]. The grape rootstock 41 B Mgt has the ability to induce a variety of genes involved in early responses to biotic stresses (*VvNBS-LRRs*, *VvLOXs*, *VvPRs*, *VvNACs*, *VvWRKYs*), with secondary metabolism genes *VvSTSs* being especially active [100]. The Gala/M.7 gene, which encodes a metallothionein-like protein, has the potential to play a role in *E. amylovora* resistance in apples.

4.3. Effect of Rootstock on Abiotic Resistance

Many unfavorable pedo-climatic conditions, such as salinity, drought, temperature, and light, cause plants to react biochemically, physiologically, and genetically. Plants respond to salinity using a variety of mechanisms, including salt excretion, salt exclusion, salt avoidance, antioxidant protection, and osmotic adjustment. Rootstocks produce ABA plant hormone in drought stress, which may be involved in water conservation processes through stomatal closure [101]. Gomera-1 is salt tolerant, limiting the transport and uptake of Na+ and Clions from the root system to the plant’s above-ground portions [101]. In mango, some rootstocks such as 13-1, Kurakkan, Gomera-1, and Bappakai are tolerant to salinity. Citrus rootstock and scion have a significant effect on each other under unfavorable conditions. Nevertheless, their specific response can be different depending on the way to translocate and compartment the toxic ions, or induce antioxidant systems. Findings showed that Cl ion accumulation presents a robust correlation with stress indicators and their scavenging enzymes in leaves and roots [102,103]. Valizadeh et al. [104] reported that Daneshgah 32, Daneshgah 8 and Daneshgah 13 used as rootstocks showed maximum drought tolerance among the cultivars. Many grape rootstocks, such as 110 R, Dogridge, B2-56 salt creek, and B2-56, have high relative water content and water use quality, allowing them to withstand drought conditions [101]. The high drought resistance in *Vitis vinifera* often decreases yield while higher water use efficiency [105]. *Pyrus betulaefolia* rootstock is well adapted to different soil conditions and it is winter hardy [66]. *Poncirus trifoliata* is the cold hardy rootstock of citrus. Apple rootstocks, M-16 and M-9 are resistant to winter injury. In *V. vinifera*, there are two genes, *VvNCED* and *VvZEP*, that have been described thought to be involved in the ABA biosynthetic pathway in response to soil water deficit in the roots [105].

In chimanritta/rootstock combinations, water deficit alters the expression of genes linked to osmotic modification, such as *SDH*, *SIP1*, *GTL*, and *P5CS*. The expression of genes involved in carbohydrate (*SDH*, *GTL*, *SIP1*, and *S6PDH*) and proline (*P5CS*) metabolism can be used to identify variability in *Prunus persica* water-deficit tolerance [106]. The *PtADC* gene in *P. trifoliata* is involved in stress resistance, including low temperature and dehydration [107]. Identified a clone from Gala/M.7 with homology to *HVA22*, which is a member of a family of stress-regulated (ABA, drought, salt, cold) genes of unknown function believed to play a role in stress tolerance [108] and another clone from Gala/M.7 had homology to *SP1/POP3*, a protein implicated in drought tolerance (Table
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5). Mutual scion–rootstock relationships enable marked tolerance to salt stress through selective ion transport and metabolic modifications in avocado [109].

Table 5. List of abiotic resistant/tolerant rootstocks in fruit crops.

<table>
<thead>
<tr>
<th>Crop</th>
<th>Rootstock</th>
<th>Resistant/Tolerant Trait</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mango</td>
<td>Kurukan</td>
<td>Tolerant to salinity</td>
<td>[110]</td>
</tr>
<tr>
<td></td>
<td>13/3</td>
<td>Tolerant to salinity</td>
<td>[111]</td>
</tr>
<tr>
<td>Guava</td>
<td>Crioula</td>
<td>Tolerant to salinity</td>
<td>[112]</td>
</tr>
<tr>
<td></td>
<td>Beta</td>
<td>Cold hardiness</td>
<td>[113]</td>
</tr>
<tr>
<td>Grape</td>
<td>140Ru</td>
<td>Tolerance to water deficit condition</td>
<td>[114]</td>
</tr>
<tr>
<td></td>
<td>A15 and A17</td>
<td>Tolerance to alkalinity</td>
<td>[115]</td>
</tr>
<tr>
<td>Loquat</td>
<td>Anger</td>
<td>Tolerance to saline conditions</td>
<td>[116]</td>
</tr>
</tbody>
</table>

4.4. Effect of Rootstock on Tree Flowering and Fruiting

The apple cultivar “Pinova” was induced to flower early by over-expressing a silver birch (Betula pendula Roth) floral meristem identity MADS-box gene (BpMADS4) in the rootstock [117]. Ectopic expression of citrus FT (CiFT) in trifoliate orange (Poncirus trifoliata) induced early flowering [118]. In apple high-density plantings (HDP), dwarfing rootstocks induces precocious flowering, which enables earlier fruit production [119]. Fruiting precocity is correlated with dwarfing rootstocks and delay in fruiting with vigorous rootstocks [120]. The Tarocco Scire/C35 citrange combination showed the highest expression levels for CiFT2. This increased expression was correlated with yield and a higher number of flowers [121].

4.5. Effect of Rootstock on Fruit Quality

The rootstocks can influence fruit quality by affecting fruit size and color, fruit maturity, firmness, and soluble solids content [122–126]. Pacific Gala on B.9 rootstock had a smaller fruit size and earlier fruit maturity but a higher fruit starch degradation pattern (SDP) on this rootstock [127]. In pistachio, P. terebinthus and P. atlantica rootstocks led to kernels with high quality, by increasing the contents of betulinic acid and total polyphenols as compared to the fruits obtained with P. integerrima rootstock [128]. Different scion–rootstock combinations could be modulating the volatile compound composition and sensory profile in fruit crops such as citrus [129], peach [130], and lemon [131]. Kagzi Kalan lemon budded on RLC-4 and Karna Khatta rootstocks led to enhanced TSS and acid contents in the fruit juice. Similarly, the rootstocks, RLC-4 and Troyer citrange proved their superiority in terms of imparting higher ascorbic acid content to the scion [3].

5. Conclusions

A compatible rootstock can transfer outstanding traits to the scion varieties. Composite plants are the forthcoming research directions to understand the molecular mechanism involved in transferring important traits from the rootstock to the scion varieties so that more rootstocks with excellent traits and broad genetic bases can be selected for
the scion varieties. It is evident from the observations that an exchange of compounds between rootstocks and scions is happening. The present review highlights the molecular mechanism of scion rootstock interactions and the involvement of single nucleotide polymorphism markers, differentially expressed genes, and proteins in composite plants. Further, it emphasized the role of macromolecules such as DNA, various types of RNA even plastid genome movement via graft union bidirectional from rootstock to scion and scion to rootstock. It is very important to know the molecular and physiological mechanism of how rootstock imparts quality scion to mitigate various biotic and abiotic stresses. Moreover, epigenetic changes at the union affect chromatin architecture by DNA methylation, histone modification, and the action of small RNA molecules with crosstalk of hormone and small molecules signaling in the grafted trees.

Understanding the molecular mechanisms underlying these effects certainly would simplify future rootstock selection for diverse agro-climatic conditions as well as for different varieties. More research is needed on molecular aspects of rootstocks for evolving rootstocks tolerant to biotic and abiotic stresses in different tropical, subtropical and temperate fruit crops. In a future where sustainable agricultural production is the need of the future, grafting could play a key role to develop products with better fruit quality, and higher yield, and minimizing the use of the chemical in a safe and “green” way.

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**References**


