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ROOTSTOCK BREEDING AND COMPATIBILITY ISSUES IN FRUIT CROPS – CURRENT ADVANCES AND FUTURE PROSPECTS

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ABSTRACT

Rootstocks play a fundamental role in shaping the productivity, adaptability, and sustainability of fruit crop production systems. The stock of a have a substantial impact on tree vigour, nutrition and water absorption, resistance to soilborne pests and diseases, tolerance to abiotic stressors, blooming behaviour, production efficiency, and fruit quality in addition to providing anchoring. The significance of well-adapted and compatible rootstocks has increased as the world's fruit supply is under growing pressure from new diseases, land and water limits, and climate change. However, because to lengthy juvenile periods, intricate rootstock scion environment interactions, and ongoing graft compatibility issues, rootstock breeding has historically advanced more slowly than scion improvement. Because incompatible pairings can result in poor vascular connections, physiological problems, decreased production, and ultimately tree death, graft compatibility is a crucial factor in determining long-term orchard success. Anatomical, physiological, metabolic, and genetic aspects, such as callus development, vascular differentiation, hormonal balance, and mobile signal exchange across the graft union, all influence compatibility. Recent developments in molecular biology and plant physiology have improved our knowledge of these processes and provided new ways to identify and treat incompatibility early on. Advanced techniques including marker-assisted selection, genomic selection, high-throughput phenotyping, and multi-omics methods, which allow for more accurate and effective identification of better genotypes, are increasingly supporting modern rootstock breeding. Furthermore, although sociological and regulatory issues still need to be taken into account, biotechnological advancements like gene editing show promise for the targeted development of root-specific features without changing scion genetics. Apple, citrus, stone fruit, grapevine, and other perennial species are examples of crop-specific breeding programs that successfully combine traditional and contemporary methods to create rootstocks with enhanced compatibility and stress tolerance. In order to support sustainable fruit production, this review highlights recent scientific and technological advancements, summarises current knowledge on rootstock breeding strategies and compatibility issues in fruit crops, and addresses key challenges and future prospects for developing resilient, compatible rootstocks.

Key words: Rootstock breeding; Graft compatibility; Rootstock–scion interaction; Graft union formation; Genomic selection; Abiotic stress tolerance; Disease resistance; Sustainable fruit production

Introduction

In fruit crop production systems, rootstocks are an essential but sometimes overlooked component. The rootstock in grafted perennial fruit crops creates the subterranean structure that sustains the scion and has a significant impact on the overall performance of the plant

(Castle, 2010). Beyond anchoring, rootstocks control the intake of water and nutrients, establish the architecture and depth of roots, and alter hormonal signalling that influences fruit quality, yield efficiency, scion development, and blooming. Rootstocks are essential to modern horticulture because they allow fruit crops to be grown in a variety of soil types, climates, and management approaches. As fruit production methods have become more intensive, the significance of rootstocks has grown significantly. Rootstocks that can regulate tree vigour, promote early bearing, and guarantee consistent development are crucial for precision horticulture, high-density orchards, and automated management. Climate unpredictability, soil degradation, salinity, water shortages, and the advent of novel pests and diseases all pose growing challenges to fruit production. By boosting resistance to soilborne diseases and nematodes, increasing tolerance to abiotic stressors, and stabilising productivity under less-than-ideal growth circumstances, rootstocks provide an efficient biological tool to alleviate many of these limitations (Reig & Moreno, 2018). As a result, the creation of better rootstocks has emerged as a global strategic priority for sustainable fruit production. Rootstock breeding has generally advanced more slowly than scion improvement, despite its significance. This discrepancy results from a number of intrinsic difficulties. Because rootstocks are perennial in nature, it takes a considerable time to fully evaluate their influence on scion performance. Selection is complicated by the fact that many rootstock characteristics, such compatibility and stress tolerance, are quantitatively inherited and heavily modified by environmental influences. Breeding projects are further complicated by the need for rootstocks to function consistently across a variety of scion cultivars. Graft compatibility continues to be one of the most important and unpredictable limitations among these difficulties. The capacity of the rootstock and scion to create a stable, functional graft union that promotes long-term growth and production is known as graft compatibility. Poor vascular connections, physiological diseases, decreased vigour, yield decline, or abrupt tree loss can all be signs of incompatible combinations, sometimes years after orchard creation. Such hidden incompatibility restricts the use of otherwise promising rootstocks and presents producers with significant financial concerns. At the graft interface, complex anatomical, physiological, pharmacological, and genetic interactions many of which are still poorly understood control compatibility. Rootstock research is starting to change as a result of recent developments in molecular biology, plant physiology, and breeding technology. New opportunities for targeted rootstock improvement are being made possible by increased knowledge of graft union formation, hormonal and molecular signalling between rootstock and scion, and the genetic foundation of rootstock-mediated characteristics (Soumelidou *et al.*, 1994). Simultaneously, contemporary breeding techniques including genomic selection, marker-assisted selection, and high-throughput phenotyping provide chances to expedite the discovery and use of improved rootstocks. It is appropriate to provide a thorough synthesis of compatibility concerns and rootstock breeding techniques. In order to support sustainable fruit crop production in the face of shifting environmental and production demands, this review aims to critically examine the biological basis of rootstock–scion interactions, evaluate recent developments in rootstock breeding and compatibility research, and highlight important challenges and future prospects for developing resilient, compatible rootstocks.

Historical development of Rootstock Breeding

The foundation of contemporary fruit production systems is rootstock breeding, which has developed from straightforward empirical methods to an organised scientific field. Rootstocks were first utilised incidentally for clonal multiplication, but as time went on, it became clear that they had a significant impact on orchard performance, tree vigour, and adaptability. The development of horticultural knowledge, evolving production problems, and the slow integration of genetic and physiological insights are all reflected in the historical evolution of rootstock breeding. It is crucial to comprehend this development in order to contextualise contemporary technical developments in rootstock enhancement as well as to recognise the benefits and drawbacks of conventional methods.

Evolution of rootstock use in fruit crops

Rootstocks were first used in fruit crops in ancient horticulture systems, when grafting was used to increase tree longevity and preserve exceptional varieties. At this time, the rootstock was not thought of as a genetically significant element but rather as a physical support for the scion (Mudge *et al*., 2009). Growers saw that some rootstocks offered greater vigour, adaptability, and durability as fruit farming spread across many conditions, gradually realising their functional significance. The phylloxera problem in European vineyards in the nineteenth century marked an important turning point. The effective application of American grape species resistant to phylloxera as rootstocks for Vitis vinifera scions demonstrated that rootstocks might confer resistance to soilborne pests without compromising fruit quality (Castle, 2010). This discovery revolutionised viticulture and encouraged the methodical investigation of rootstocks in other fruit crops. Organised research initiatives in apple led to the creation of clonal rootstocks, especially the Malling series, which categorised rootstocks based on their ability to manage vigour. These rootstocks facilitated the transition to intensive, high-density production systems and allowed for predictable orchard construction (Webster, 2004). Similarly, in order to increase orchard production and stability, citrus businesses chose rootstocks that were appropriate for calcareous soils, salinity, and changing climatic conditions (Forner-Giner *et al*., 2003). By the middle of the 20th century, rootstocks were no longer just instruments for multiplication but were essential to orchard management (Beede & Klonsky, 1998).

Conventional breeding approaches and limitations

Phenotypic selection and interspecific hybridisation were the main methods used in conventional rootstock breeding to solve particular production restrictions. Breeders chose rootstocks with beneficial characteristics such tolerance to unfavourable soil conditions, moderate vigour, and apparent compatibility with widely grown scions. Through interspecific crosses, stone fruit breeding in the genus prunus concentrated on adding resistance to root-knot nematodes, tolerance to calcareous soils, and winter hardiness (Reig & Moreno, 2018). Similar emphasis was placed on hybrid rootstocks in citrus breeding projects to prevent tristeza virus, salt stress, and inadequate drainage (Castle, 2010). Traditional breeding methods have intrinsic drawbacks despite significant achievements. Because rootstocks are perennial, it takes a long time to adequately evaluate their impact on scion development, production, and lifespan. Phenotypic selection is less effective and predictable since many rootstock properties are quantitatively inherited and heavily modified by environmental influences (Hancock & Kumar, 2016). Furthermore, genuine rootstock performance was frequently obscured by scion impacts, making reliable evaluation more difficult. The inability to accurately estimate graft compatibility was one of the biggest obstacles to traditional breeding. Years after orchard establishment, several rootstock scion pairings showed signs of delayed incompatibility, including vascular discontinuity, decreased vigour, and ultimately tree loss (Pina & Errea, 2005). These mistakes reduced the uptake of recently produced rootstocks and caused financial losses. Moreover, selection decisions were not supported by molecular and genetic techniques in early breeding efforts. With little knowledge of the physiological and genetic processes controlling rootstock performance, selection was based virtually solely on long-term field observations. Despite laying the groundwork for contemporary fruit production systems, these conventional methods' shortcomings highlighted the need for more accurate, scientifically grounded breeding techniques, which ultimately led to the incorporation of physiological, molecular, and genomic tools in modern rootstock breeding (Goldschmidt, 2014; Warschefsky *et al*., 2016).

Biological basis of grafting and rootstock scion interaction

The biological processes that take place at the graft interface and the long-term physiological integration between the rootstock and scion are essential to the success of grafted fruit crops. Grafting is a complicated biological process that involves wound healing, tissue regeneration, vascular reconnection, and coordinated signalling between genetically different people. It is not only the mechanical joining of two plant parts. These procedures decide if a graft union is successful and long-lasting or fails because of incompatibility. Therefore, enhancing graft success and directing rootstock breeding strategies require an understanding of the physiological and molecular processes underpinning graft union formation and rootstock–scion interactions.

Physiological processes involved in graft union formation

In grafting, both the rootstock and the scion experience a wound reaction that initiates the development of the graft union. According to (Melnyk and Meyerowitz, 2015), the damaged tissues trigger defence and healing pathways, resulting in the creation of a protective necrotic layer that stops pathogen entrance and desiccation. The contact between the transplanted components is subsequently filled with parenchymatous callus tissue that grows from both partners. In order to proceed with differentiation and vascular reconnection, these callus cells must successfully adhere. Cellular differentiation and reorganisation take place at the graft interface after callus development. New xylem and phloem strands can form throughout the union thanks to the restoration of continuity by cambial cells from the rootstock and scion (Yin *et al*., 2012). Restoring water, nutrient, and assimilate movement between the two partners depends on this vascular reconnection. Xylem reconnection typically occurs before phloem differentiation in suitable grafts, allowing for early water transport prior to the establishment of complete assimilate exchange. During the development of graft unions, hormonal control is crucial. At the graft interface, auxin carried from the scion builds up and promotes vascular differentiation and cambial activity (Aloni *et al*., 2010). While ethylene is involved in wound signalling and stress responses, cytokinin produced in the rootstock affect cell division and differentiation. The pace of vascular reconnection and the effectiveness of union formation are determined by the temporal and geographical balance of these hormones. Another important physiological aspect affecting graft effectiveness is the availability of carbohydrates. A sufficient supply of carbohydrates from the scion is necessary for the energy-intensive processes of callus development and vascular differentiation. Union formation is frequently delayed or partial in grafts carried out in environments that restrict photosynthesis or carbohydrate transport (Loupit & Cookson, 2020). By affecting metabolic activity and cell division rates, environmental variables like humidity and temperature also have an impact on graft healing. Physiological disturbances happen at one or more of these phases in incompatible transplants. Transport might be limited and the union weakened by insufficient vascular connections, poor callus adhesion, and uneven cambial alignment. Such flaws might eventually result in decreased vigour, nutritional imbalances, or mechanical failure, underscoring the need of physiological compatibility for long-term orchard success.

Molecular and hormonal signaling between rootstock and scion

Grafted plants depend on substantial molecular communication between rootstock and scion in addition to anatomical reconnection. Numerous signalling molecules, including as hormones, proteins, messenger RNAs, and short RNAs, may travel across graft unions and control growth and stress responses in distant tissues, according to developments in molecular biology (Notaguchi & Okamoto, 2015). Numerous rootstock-mediated effects on scion phenotypic are supported by this long-distance signalling. It has been demonstrated that small RNAs, especially microRNAs (miRNAs), may traverse graft interfaces and alter recipient tissue gene expression. These mobile RNAs offer a way for rootstocks to affect scion development and adaptability by controlling processes including phase transition, nutritional balance, and stress responses (Tsikou *et al.*, 2018). Similarly, phloem sap has been found to contain graft-transmissible messenger RNAs, indicating direct genetic communication between graft partners. The connection between rootstock and scion is still dominated by hormonal signalling. By changing the production, transport, and perception of hormones such auxins, cytokinins, gibberellins, and abscisic acid, rootstocks affect scion vigour and architecture. For instance, dwarfing rootstocks are frequently linked to altered cytokinin distribution and decreased auxin transport, which results in reduced shoot elongation and improved reproductive development (Tworkoski & Fazio, 2016). By altering stomatal conductance and hydraulic behaviour, abscisic acid signalling from the rootstock is essential for controlling scion responses to water stress. Differential expression of genes related to cell wall modification, lignin production, defence responses, and oxidative stress regulation has been found in recent transcriptome studies comparing compatible and incompatible graft unions (Chen *et al.*, 2017). Excessive phenolic compound and reactive oxygen species buildup at the graft interface in incompatible combinations might impair vascular differentiation and cell survival, which can lead to long-term failure. Another possible mediator of graft-induced effects is epigenetic regulation. Both partners' gene expression patterns may be impacted by DNA methylation and histone alterations brought on by grafting stress, which might have long-term effects on growth and stress tolerance (Gautier *et al.*, 2019). This field is crucial for comprehending graft compatibility at a deeper molecular level, even if it is still understudied in fruit crops.

Rootstock-scion compatibility and incompatibility

A key need for the long-term viability of grafted fruit crops is rootstock–scion compatibility. Throughout the tree's life, a suitable graft union guarantees stable anatomical integration, effective water and nutrient delivery, balanced physiological functioning, and continuous productivity. On the other hand, incompatibility frequently appears many years after orchard formation and can lead to poor growth, reduced production, structural weakness, and early demise. Graft incompatibility is still a significant problem in rootstock breeding and commercial deployment because it is hard to forecast in the early stages and is impacted by genetic, physiological, and environmental variables.

Types and symptoms of graft incompatibility

According to the timing and manifestation of symptoms, graft incompatibility in fruit crops is often classified into early (localised) and delayed (systemic) variants. Early incompatibility, which results in graft failure during the nursery phases, manifests shortly after grafting and is characterised by inadequate vascular differentiation, tissue necrosis at the graft interface, and lack of callus development (Andrews & Marquez, 1993). Severe physiological or biochemical differences between the rootstock and scion are frequently linked to such incompatibility. Graft unions look successful at first, with normal development throughout the early years, but structural and physiological problems emerge progressively, making delayed incompatibility increasingly troublesome. Swelling or constriction at the graft union, bark cracking, differing trunk diameters above and below the union, decreased vigour, chlorosis, and abrupt tree breakage under wind or crop load are typical signs (Herrero, 1951). Growers may suffer large financial losses if these signs don't appear until the trees reach reproductive maturity. Physiological incompatibility, in which anatomical connections seem normal but functional abnormalities continue, is another significant manifestation. In these situations, poor canopy growth, decreased output efficiency, poor fruit quality, and chronic stress are caused by limited water or assimilate movement across the graft union (Moore, 1984). It might be challenging to identify physiological incompatibility in ideal growth conditions since it can be made worse by stressors like drought, nutrient shortages, or heavy fruit loads. External variables have a significant impact on how graft incompatibility manifests. In somewhat suitable combinations, environmental pressures such as temperature extremes and soil limitations might hasten the onset of symptoms (Goldschmidt, 2011). The degree of incompatibility symptoms may also be influenced by orchard management techniques including pruning intensity and watering schedule. As a result, long-term examination in a variety of field settings is necessary for accurate compatibility assessment.

Genetic, Biochemical and Anatomical causes of incompatibility

Genetic divergence, biochemical interference, and anatomical mismatches at the graft interface are among the biological variables that interact to cause graft incompatibility. One of the main factors influencing compatibility between rootstock and scion is genetic relatedness; closely related genotypes often show more compatibility than distant interspecific or intergeneric combinations (Warschefsky *et al.*, 2016). Asynchronous development and poor coordination of vascular differentiation might result from genetic mismatch. Graft failure is mostly caused by biochemical processes, especially the buildup and oxidation of phenolic chemicals. Excessive phenolic buildup at the graft interface in unsuitable grafts can impede cambial activity, cause oxidative stress, and damage cellular integrity (Errea, 1998). Tissue browning and necrosis have been seen in incompatible unions due to increased activity of enzymes such polyphenol oxidase and peroxidase (Irisarri *et al.*, 2015). Normal wound healing and vascular reconnection are hampered by these metabolic disruptions. Incompatibility is further exacerbated by anatomical discontinuities. Asynchronous differentiation or poor cambial tissue alignment can produce discontinuous or poorly linked xylem and phloem elements, which limit assimilate transport and hydraulic conductivity (Soumelidou *et al.*, 1994). Long-term effects on the mechanical stability and physiological effectiveness of the graft union might result from even minor anatomical mismatches, such as variations in vessel diameter or orientation. Additionally, defense-related reactions have been linked to graft incompatibility in recent studies. The graft partner may be seen as non-self in some incompatible pairings, which might set off defence signalling pathways akin to pathogen reactions. Tissue regeneration at the graft interface is hampered by the activation of stress-related genes and programmed cell death pathways (Flaishman *et al.*, 2008). These results imply that plant immune responses and graft incompatibility are mechanistically comparable.

Modern approaches in rootstock breeding

Rootstock breeding has seen a substantial revolution in recent decades, moving away from purely empirical selection and towards more predictive, technologically driven techniques. Despite being successful in producing fundamental rootstocks, traditional breeding techniques are constrained by lengthy generation periods, complicated trait inheritance, and the delayed manifestation of important characteristics like compatibility and stress tolerance. By combining molecular genetics, sophisticated phenotyping, and biotechnological technologies to speed up the identification and creation of better rootstocks with consistent performance and wide adaptability, modern breeding tactics seek to overcome these limitations.

Marker-assisted and genomic selection for rootstock improvement

A key technique for increasing the effectiveness of rootstock breeding is marker-assisted selection (MAS), especially for qualities governed by main genes or quantitative trait loci (QTLs). Early screening of breeding populations is made possible by molecular markers associated with resistance to diseases, nematodes, and soilborne pests. This eliminates the need to maintain a large number of subpar genotypes during extended field assessment cycles (Collard & Mackill, 2008). MAS has been effectively used in fruit crops to find rootstocks with better vigour control and disease resistance, cutting down on breeding times. Many rootstock properties, including compatibility, drought tolerance, and nutrient-use efficiency, are polygenic and impacted by environmental interactions, whereas MAS is useful for traits controlled by a small number of loci. This constraint is addressed by genomic selection (GS), which predicts breeding values for complex characteristics using genome-wide marker information (Meuwissen *et al.*, 2001). GS allows for the early identification of potential rootstock candidates, even before trait expression is completely apparent, by combining rich marker data and phenotypic information from training populations. Recent uses of GS in perennial fruit crops show that it can speed up rootstock development, especially when paired with data from multi-environment trials (Muranty *et al.*, 2015). GS is particularly useful for rootstock breeding since it may increase selection accuracy for characteristics with low heritability and lessen dependency on drawn-out field trials. However, the availability of sizable, well-characterized training populations and reliable phenotypic datasets which continue to be obstacles in many breeding programs is necessary for GS to be effective. Breeders may leverage the advantages of both methods by integrating GS and MAS into rootstock breeding pipelines, employing GS for complicated quantitative characteristics and MAS for important resistance traits. The creation of rootstocks suited to certain production settings and scion requirements is supported by this integrated method, which also improves selection efficiency.

Role of gene editing and biotechnological tools

Modern rootstock breeding now has a wider range of tools because to biotechnological advancements. Rapid clonal multiplication of elite rootstocks is made possible by tissue culture and micropropagation methods, which guarantee genetic homogeneity and enable widespread deployment (George *et al*., 2008). The efficacy of early-stage selection can be increased by screening rootstock genotypes under controlled stress conditions through somatic embryogenesis and in vitro selection. Technologies for gene editing, especially CRISPR/Cas systems, provide previously unheard-of accuracy for altering certain genes linked to rootstock characteristics. In contrast to conventional genetic alteration, gene editing may induce specific mutations without introducing foreign DNA, which may increase regulatory acceptability in particular areas (Zhang *et al.,* 2020). Gene editing is particularly appealing in rootstocks because it allows for changes to be limited to the root system while leaving the scion, or fruit-bearing portion, genetically intact. Enhancing resistance to soilborne diseases, altering root architecture for better water and nutrient absorption, and controlling hormone production or transport to manage scion vigour are some possible uses of gene editing in rootstock breeding (Bortesi & Fischer, 2015). Modifying genes related to stress signalling pathways may also enhance resistance to salinity and drought, characteristics that are becoming more crucial in the context of climate change. Despite its potential, issues with transformation efficiency, lengthy regeneration durations, and regulatory ambiguity continue to limit the practical implementation of gene editing in woody perennials. Molecular techniques are complemented by high-throughput phenotyping and "phenomics" technologies, which allow accurate assessment of rootstock properties. Large datasets produced by technologies like automated growth analysis, sensor-based water-use monitoring, and root imaging systems can be combined with genetic data to enhance selection choices (Furbank & Tester, 2011). These methods are especially useful for characteristics like hydraulic conductivity and root system architecture that are challenging to evaluate visually.

Rootstock-mediated stress tolerance and disease resistance

Fruit crops are more resilient to biotic and abiotic stressors when they have rootstocks. A tree's capacity to withstand drought, salt, temperature extremes, and soilborne infections is primarily determined by its rootstocks since the root system is the main interaction with the soil environment. Because the scion genotype in many fruit crops is insufficient to defend against these limitations, rootstock-mediated tolerance is a crucial tactic for maintaining yield under more unpredictable climatic and edaphic environments. Therefore, one of the main goals of contemporary fruit crop development is to comprehend how rootstocks provide stress tolerance and disease resistance.

Rootstock influence on Abiotic stress tolerance

Rootstocks have a substantial impact on plant responses to abiotic conditions such as drought, salt, floods, and temperature extremes by affecting root architecture, hydraulic conductivity, and hormonal signalling. According to Comas *et al.*, (2013), rootstocks with deeper or more widespread root systems boost water acquisition during drought circumstances, improving scion water status and sustaining photosynthetic activity during stressful times. In tolerant rootstocks, improved xylem architecture and hydraulic conductivity also help to improve water transport efficiency when soil moisture levels are low. Another crucial characteristic controlled by rootstocks is salinity tolerance, especially in citrus, grapevine, and stone fruits cultivated in marginal soils. By limiting the absorption and transfer of harmful ions like sodium and chloride, salt-tolerant rootstocks shield the scion canopy from osmotic stress and ion toxicity (Munns & Tester, 2008). Increased salt compartmentalisation in root tissues and changed ion transporter gene expression are frequently linked to this selective ion exclusion. A key component of rootstock-mediated abiotic stress tolerance is hormone control. Abscisic acid (ABA) generated from roots functions as a long-distance signal that controls the scion's stomatal conductance, allowing for quick reactions to soil water deficiency (Lovisolo *et al*., 2016). Additionally, cytokinin and ethylene signalling, which regulate shoot development and stress response, are influenced by rootstocks. Grafted plants are able to balance growth and survival in challenging environments because to these hormonal connections. Rootstock selection also affects temperature stress tolerance, especially cold hardiness. In order to lessen susceptibility to frost damage during crucial growth phases, several rootstocks improve carbohydrate storage and alter phenological timing (Wisniewski *et al*., 2014). When taken as a whole, these processes show how rootstocks improve scion performance under abiotic stress by acting as physiological buffers.

Role of Rootstocks in managing soilborne diseases and pests

In order to control soilborne diseases and pests that are challenging to manage with chemical or cultural methods, rootstocks are frequently employed as a biological technique. In many fruit crops, rootstock growth has been significantly influenced by resistance to diseases including Phytophthora, Verticillium, and Armillaria (Agrios, 2005). By limiting pathogen colonisation of root tissues, resistant rootstocks avoid systemic infection and the ensuing scion deterioration. Through increased vigour and root health, rootstocks can improve disease tolerance in addition to direct resistance, making plants more resilient to infection load. By triggering defence signalling pathways, rootstocks can also cause systemic resistance in the scion a phenomena that is becoming more well acknowledged in grafted plants (Pieterse *et al*., 2014). Even in the absence of full resistance, such generated resistance can lessen the severity of the disease. Another important characteristic that rootstocks provide is nematode resistance, especially in citrus and stone fruits. Rootstocks that are resistant to lesion and root-knot nematodes enhance nutrient absorption, lessen root damage, and stop opportunistic pathogens from causing subsequent infections (Nyczepir & Thomas, 2009). Because of this resilience, orchards last longer and require less soil fumigants. Disease suppression is also influenced by the rhizosphere microbiota connected to rootstocks. According to Berendsen *et al*., (2012), some rootstock genotypes support advantageous microbial communities that either improve plant immune responses or compete with diseases. Even though fruit crop research in this field is still in its infancy, it offers a potential path towards long-term disease control.

Crop-specific advances in rootstock development

Crop biology, production strategies, and regional limitations have all influenced the varied pace of rootstock improvement among fruit crops. While certain crops, like citrus and apples, have benefitted from long-standing, well-funded rootstock breeding projects, others have just lately begun to receive systematic attention. Different breeding objectives and tactics have been driven by crop-specific difficulties, such as soilborne pathogens, abiotic stress sensitivity, and scion compatibility needs. More specialised rootstock creation for specific crops is now possible thanks to developments in genetics, physiology, and breeding technology. Analysing crop-specific success reveals transferable tactics that may be applied to different fruit species and provide insightful information on how rootstock breeding goals are turned into useful results. With a focus on how rootstock innovation has enhanced orchard performance, resilience, and sustainability, this section examines recent developments in important fruit crops.

Progress in major fruit crops (Apple, Citrus, Stone fruits, and Grapevine)

Apple (Malus domestica) has one of the most sophisticated rootstock breeding histories, driven by the requirement for size control in high-density orchard systems. Dwarfing ability, resistance to soilborne diseases, and enhanced tolerance to abiotic stressors have all been included into modern apple rootstocks. In addition to improving nutrient absorption efficiency and fruit quality consistency, recent breeding efforts have focused on rootstocks that sustain yield under replant disease pressure and varied climatic circumstances (Fazio *et al*., 2014). Compared to conventional standards, more recent rootstock series have shown increased orchard longevity and fire blight resistance. Citrus rootstock growth has accelerated due to the global danger of Huanglongbing (HLB), as well as increased soil salinity and water constraint. In order to extend orchard output, breeding strategies concentrate on creating rootstocks that maintain root function and nutrient absorption even when scions are impacted by HLB (Albrecht & Bowman, 2019). Improved resistance to salt, alkalinity, and Phytophthora root rot has been demonstrated by hybrid rootstocks produced via interspecific crossings, underscoring the significance of using genetic diversity for stress resilience. Stone fruit crops of the *Prunus* genus (peach, plum, apricot, cherry) have specific hurdles due to graft compatibility limits, sensitivity to nematodes, and calcareous soils. Clonal rootstocks with better nematode resistance, moderate vigour control, and increased adaptation to marginal soils are examples of recent developments (Fonti Forcada *et al*., 2020). Dwarfing rootstocks have made intensive orchard systems possible for sweet cherries, but research on striking a balance between vigour management and long-term tree health is still ongoing. Grapevine rootstock breeding has historically centred on phylloxera resistance, but current efforts are increasingly focussing on drought tolerance, salt resistance, and fruit composition. Growers can customise rootstock selection to particular terroirs and production objectives because rootstocks range significantly in their impacts on vine vigour, phenology, and fruit chemistry (Ollat *et al*., 2016). The significance of rootstocks that increase heat tolerance and water-use efficiency in viticultural systems has increased due to climate change.

Comparative performance and adoption of commercial rootstocks

Commercial rootstock performance varies greatly between settings and management regimes, highlighting the significance of region-specific assessment. Strong rootstock environment interactions are seen in comparative experiments, where certain rootstocks perform extraordinarily well in certain soil or climate circumstances but badly in others (Atkinson *et al*., 2013). Such heterogeneity emphasises the necessity for localised testing and draws attention to the shortcomings of general rootstock advice. Adoption of novel rootstocks is impacted by practical and economic factors in addition to biological performance. Even though more recent options may have benefits, growers often prefer rootstocks with shown long-term performance. In perennial systems, where starting an orchard is a long-term commitment, risk aversion is especially prominent (Robinson, 2011). Therefore, for improved rootstocks to be successfully adopted, comprehensive multi-year trial data and explicit extension guidelines are crucial. The gap between research and adoption is being filled in part by recent developments in regional trial networks and decision-support technologies. These tools let producers choose rootstocks that are most appropriate for their particular environment by combining soil and climatic data with field performance data (Trought & Howell, 2019). It is anticipated that these strategies will become more crucial as production systems grow more specialised and climatic unpredictability increases.

Challenges, opportunities and future prospects

The quick development and use of superior rootstocks in fruit crops is still hampered by a number of biological, technological, and socioeconomic issues, despite significant advancements in graft compatibility research and rootstock breeding. Trait prediction is challenging and frequently incorrect because rootstock performance is controlled by intricate interactions between genotype, scion cultivar, environment, and management techniques. Breeding process is further slowed by lengthy juvenile periods, the requirement for multi-year field trials, and the possibility of delayed graft incompatibility. Furthermore, current rootstock–scion pairings are under unprecedented strain due to soil degradation, climate change, and the introduction of new pests and diseases. Simultaneously, developments in biotechnology, data science, phenotyping, and genomics are opening up new ways to get around long-standing limitations. Developing next-generation rootstocks that guarantee orchard resilience, productivity, and sustainability will require addressing present issues while seizing new opportunities. The main obstacles to rootstock breeding are highlighted in this section, along with potential future paths that might redefine rootstock improvement techniques.

Key constraints and rootstock breeding and deployment

The lengthy breeding cycle of perennial fruit crops is one of the biggest obstacles in rootstock development. It is sometimes difficult to adequately evaluate the impacts of rootstock on scion vigour, production, and lifespan until many years after planting, which causes selection decisions to be delayed and expenses to rise (Grattapaglia *et al*., 2018). For characteristics like stress tolerance and graft compatibility, which could only show up in certain environmental circumstances, this temporal lag is especially troublesome. Graft incompatibility is still a recurring and unpredictable limitation. Reliable early-stage diagnostic methods are still missing, despite breakthroughs in our knowledge of the anatomical and molecular mechanisms of incompatibility (Gainza *et al*., 2015). Because of this, a large number of potentially useful rootstocks are rejected at the end of the assessment process, which lowers breeding efficiency and stifles creativity. The significant impact of genotype environment interactions on rootstock performance is another significant constraint. Recommendations may be complicated and widespread adoption may be restricted if rootstocks that do well in one area fail in another due to different soil or climate conditions (Bassi *et al*., 2021). Due to this unpredictability, large-scale multi-location studies are required, which require a lot of resources and are challenging to sustain over time. Rootstock deployment is also influenced by socioeconomic and regulatory variables. Without long-term performance data, growers are frequently hesitant to embrace novel rootstocks, especially considering the high establishment expenses of orchards (Costa *et al*., 2020). Furthermore, in certain areas, the use of cutting-edge biotechnologies may be restricted and commercialisation may be delayed due to regulatory ambiguity around genetically modified or gene-edited rootstocks.

Emerging opportunities and future research directions

Many of the difficulties in rootstock breeding may be solved with the help of recent technical developments. Predictive breeding models are being supported by the more accurate identification of genetic areas linked to important rootstock properties made possible by high-throughput genotyping and whole-genome sequencing (Heslot *et al*., 2015). These technologies can shorten the breeding cycle and increase selection accuracy when paired with sophisticated statistical and machine-learning techniques. Platforms for high-resolution phenotyping offer yet another significant possibility. Non-destructive evaluation of rootstock performance in field settings is made possible by developments in root imaging, sensor-based water and nutrient monitoring, and remote sensing technologies (Yang *et al*., 2020). To improve genomic selection models specific to perennial crops, phenotypic data and genetic information must be integrated. Future breeding efforts may potentially heavily rely on cisgenic techniques and rootstock-specific gene editing. Breeders can improve rootstock performance without altering scion genetics by focussing on root-specific characteristics such pathogen resistance, hormone biosynthesis, or ion transport (Van Nocker & Gardiner, 2014). In certain nations, this approach could streamline regulatory clearance and boost public acceptability. The influence of rootstocks on the microbiota of the rhizosphere is another new area of study. Nutrient uptake and disease suppression may be improved in a sustainable way by choosing or creating rootstocks that support beneficial microbial communities (Compant *et al*., 2019). This strategy fits with the increasing interest in crop resilience solutions based on nature. Lastly, the conversion of scientific discoveries into useful results will depend on improved interaction between breeding programs, growers, and extension agencies. Decision-support tools, regional trial networks, and participatory breeding can all assist guarantee that novel rootstocks satisfy grower demands and function consistently in practical settings (Keller *et al*., 2022).

Conclusion

A key component of sustainable fruit crop production, rootstock breeding supports orchard resilience, performance, and long-term profitability. Rootstocks have a significant impact on tree vigour, nutrition and water intake, stress tolerance, disease resistance, graft compatibility, and ultimately fruit output and quality, as this review makes clear. Fruit breeding projects have historically focused on improving the scion, but increasing environmental challenges and changing production methods have brought the rootstock back into the spotlight as a crucial element for adjusting fruit harvests to a variety of shifting situations. Understanding the biological underpinnings of grafting and rootstock–scion interactions has advanced significantly. Key mechanisms involved in the creation of graft unions, including as wound healing, vascular reconnection, hormone modulation, and long-distance signalling, have been made clearer by developments in physiology and molecular biology. Better understanding of the anatomical, physiological, and genetic reasons of graft incompatibility has also shed light on why some rootstock–scion pairings don’t work out after first succeeding. In order to reduce the hazards associated with delayed incompatibility, our findings highlight the intricacy of compatibility and the necessity of early diagnostic techniques and long-term assessment. Rootstock development is changing from an empirical process to a more predicted and focused undertaking thanks to modern breeding techniques. It is possible to speed up breeding cycles and increase selection accuracy for complex characteristics by combining marker-assisted selection, genomic selection, high-throughput phenotyping, and biotechnological technologies. Simultaneously, crop-specific breeding initiatives in grapevine, apple, citrus, and stone fruits show how customised rootstock creation may address crop-specific and region-specific issues such abiotic stress, soilborne pathogens, and climate change. These achievements highlight the benefits of fusing cutting-edge technology with conventional breeding knowledge. Rootstock breeding still faces significant obstacles in spite of these developments. The quick deployment of novel rootstocks is hampered by long generation durations, significant genotype environment interactions, regulatory ambiguity surrounding modern biotechnologies, and cautious farmer acceptance. Breeders, physiologists, molecular scientists, farmers, and legislators must work together to address these issues. Aligning breeding goals with real-world orchard requirements may be greatly aided by decision-support tools, regional trial networks, and participatory breeding techniques. Innovative and suitable rootstocks that can boost resistance, productivity, and sustainability are becoming increasingly important for fruit crop development. Unlocking the full potential of rootstock breeding will need sustained investment in multidisciplinary research, data integration, and technology transfer. Horticulture may better address the issues of resource scarcity, global food security, and climate change by putting rootstocks at the core of fruit crop improvement initiatives.

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