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Rootstock-Scion Physiological and Molecular Aspects in Plants: A Review of Interactions between Biotic and Abiotic Stress in Horticultural Crops

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ABSTRACT: Grafting is frequently employed in fruit, vegetable, and flower propagation to increase quality, yield, and resilience to biotic and abiotic stress. The processes governing the rootstock-scion relationship can have an impact on a plant's physiology and biochemistry, growth and development, and environmental adaption. Model plants like *Arabidopsis thaliana* have mostly been used to research long-distance signal transfer between rootstock and scion, as well as the systemic changes caused by grafting. The study of model plants only serves as a theoretical foundation and point of reference for the associated research on grafted vegetables because these features of grafting alter when other plant materials are grafted. This review includes the use of transgenic rootstocks, the causes of poor grafting success or graft incompatibility, the effects of rootstocks on scion development, including both abiotic and biotic stress tolerance/resistance, as well as potential molecular mechanisms involved. Grafting has the potential to make a significant contribution in this climate change situation, provided that it would allow for the growth of advantageous crops in increasingly marginal conditions. The lack of information regarding the long-distance movement of signalling molecules in grafted fruits and vegetables contrasts with the rapid growth of their large-scale production, emphasizing the requirement for further research into the processes controlling rootstock-scion interaction. Researchers will be able to understand the physiological and molecular mechanisms involved in the rootstock-scion interaction in horticultural crops thanks to the quick development of molecular biotechnology and "omics" methods.

Keywords: Grafting, physiological, omics, rootstock, scion.

INTRODUCTION

Global population growth, climate change, and resource depletion are all major threats to future generations' access to food, both in terms of quantity and quality (Fanzo *et al.,* 2018). As a result, we are driven to develop novel cropping systems in order to meet expanding worldwide demand for plant foods and essential nutrients while also improving sustainability and resistance to environmental shocks (Rivero *et al.,* 2021).

Grafting is one of the most popular methods for horticulture crops including fruits, vegetables, and flowers to reproduce asexually. It's widely used to help crops recover from biotic and abiotic stress, such as that produced by insect pests, pathogens and other climatic factors. Grafting can also influence fruit characteristics such size, rind thickness (Fredes *et al*., 2017), and flesh firmness (Bertucci *et al.,* 2018). The processes that control the rootstock–scion relationship can have an impact on plant growth and development, as well as physiological and biochemical features. Grafting, for example, can enhance vegetable quality by enhancing endogenous hormone synthesis as well as the acquisition and distribution of mineral elements.

About 200 species of plants in nature have spontaneous root grafts reported, but countless more likely do as well. By the end of the 20th century, grafting had become commonplace in many horticultural systems across the globe, including herbaceous crops (solanaceous and cucurbits) grown under a variety of conditions, both in the field and greenhouse (Fullana-Pericas *et al.,* 2020). For a range of horticultural crops today, graft-induced alterations in scion phenotypic are extensively documented and include important attributes including yield potential, fruit maturation period, canopy traits, tolerance to suboptimal temperature regimes, mineral toxicity, soil nutrient deficit, or salinity.

This review includes the use of transgenic rootstocks, the causes of poor grafting success or graft incompatibility, the effects of rootstocks on scion development, including both abiotic and biotic stress tolerance/resistance, as well as potential molecular mechanisms involved.

Graft union formation and success of grafting. Graft union success is based on the formation of new vascular cambium, also known as de novo meristems. Rapidly dividing callus cells form the connection between the scion and rootstock. Later, the cells divide to produce the vascular cambium (lateral meristem) and the vascular system. During the process of compatible graft union, three primary events occur. These include rootstock and scion adhesion, callus cell production at the graft interface, and vascular cell differentiation. The following procedure describes the formation of graft union in details.

Wound periderm Formation: A necrotic layer is created from the cell walls of the cut scion and rootstock cells when an incision is made during grafting. Callus tissue is formed by actively dividing paranchyma cells near and internal to necrotic cells.

Parenchyma cell interlocking: The cambial areas of rootstock and scion must be close enough to connect the parenchyma cells produced by both rootstock and scion. When rootstock and scion are of uneven thickness, at least one side of rootstock and scion must always be matched to ensure appropriate vascular cambium connectivity in a mismatched graft component.

Callus bridge formation: within seven days, new parenchymatous callus proliferates from both the rootstock and the scion. The outer layers of intact parenchyma cells in the rootstock and scion continue to divide, resulting in callus formation. The necrotic layer produces new parenchyma cells that are contiguous and internal. They intertwine and fill in the gaps between the scion and rootstock.

Differentiation of vascular cambium: Before the bridges of vascular cambium of both rootstock and scion, the early xylem and phloem are distinct. To bridge the graft union, wound-repair xylem is generated first, followed by wound-repair phloem. The vascular cambium unites, and wound-bridging xylem and phloem remain connected. As a result, secondary vascular growth ensues, resulting in effective graft union.

Secondary xylem and phloem production: Cambial activity commences in the freshly produced cambial layer. As a result, secondary xylem develops on the interior of the wood, while phloem forms on the outside. The vascular link between the rootstock and the scion is made up of xylem and phloem. This stage must be accomplished before the appearance of many leaves on the scion for successful graft union. The loss of water through transpiration is not compensated otherwise, and the scion shoots perish.

Grafting success and graft compatibility are required for commercial use of rootstocks. As a result, it's critical to anticipate potential incompatibility issues early in the growing process in order to assure the long-term viability of scion/rootstock pairs. Transport of proteins, hormones, mRNA, and short RNA across the graft junction is now being recognized as a significant mechanism mediating rootstock-scion communication, as well as a key component in comprehending the physiology of grafting.

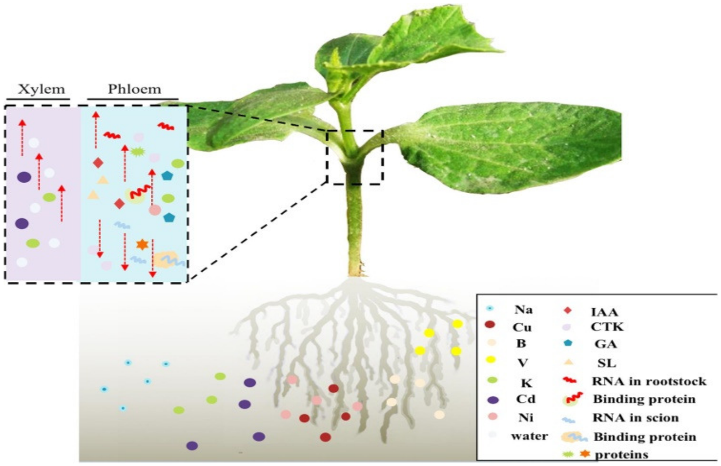

Fig. 1. Model that is suggested for the directed transfer of mRNA and protein to sieve components in grafted cucurbits.

Loupit and Cookson (2020) examined current knowledge of changes in metabolism and transcript abundance during graft union formation and in cases of graft incompatibility in order to find molecular markers. Incompatibility appears to be linked to secondary metabolism and growth-regulating hormone metabolism, with results that are very species-specific. Prunacin was the first marker of graft compatibility discovered in pear/quince grafts, but later studies have found other markers in Prunus include the activity of UDP-glucose pyrophosphorylase (UGPase). Among the potential indicators of graft incompatibility in other species, such as grapevine, are stilbenes and certain flavanols.

"Omics" Analyses of Macromolecule Signal Exchanges Induced by Grafting: Genome-wide study has made it possible to learn about probable roles of the encoded transporters by analyzing the expression patterns of IAA-related transporter genes like ClLAX, ClPIN, and ClABCB in grafted watermelon in response to abiotic stimuli (such as salt, drought, and cold). Using watermelon scions grafted to squash rootstocks, transcriptome profiling has been extensively used to examine the functions of DEGs/DEMs in graft compatibility and abiotic stress resistance (Xu *et al.*, 2016). Proteomics can be used to examine the key protein categories in treatment options to investigate the mechanisms of graft-enhanced stress tolerance in scions. Comparative proteome analysis, for instance, was used to show how cucumber scions grafted to Momordica rootstocks could respond to heat stress by accumulating proteins involved in photosynthesis in different ways (Xu *et al.,* 2018).

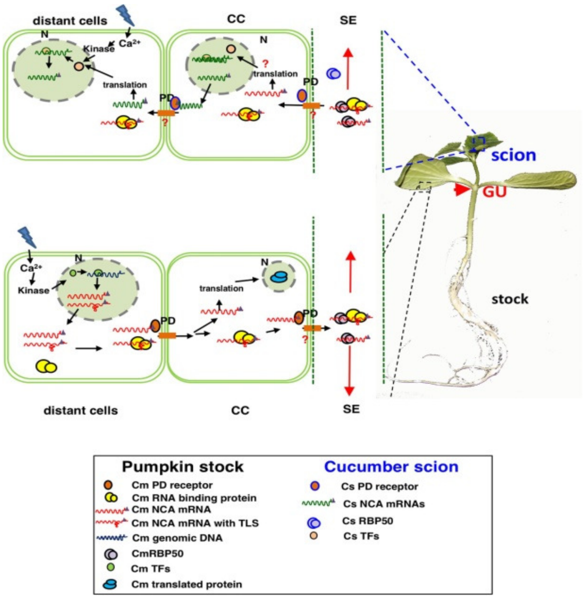

Fig. 2. Model for systemic long-distance signal transmission in grafted vegetables' far-flung tissues. Grafting material: cotyledon-insertion grafts from cucumber and pumpkin.

As a result, "omics" analyses are crucial tools that can be utilized to understand how macromolecular signals are transported and accumulated differently in grafted plants. The selection of appropriate rootstock resources would be made possible by unravelling the mechanisms that control vascularly supplied signalling molecules in grafted vegetables. It would also help to explain how grafting enhances vegetable quality. The modifications and transport of phytohormones, minerals, mRNAs, ncRNAs, and proteins brought on by grafting has been the subject of several investigations. Certain proteins, mRNAs, ncRNAs, and phytohormones that can travel through the circulatory system have been shown to have specific uses. Directionality, minerals, and water that the rootstock has acquired can be transferred to the scion through the xylem, and in grafted vegetables, the phloem rootstock-scion communication channel can transfer plant hormones, certain microRNAs, and proteins. A few binding proteins can also transport RNAs. Rootstocks of grafted vegetables will selectively absorb or reject mineral elements in the rhizosphere in order to establish tolerance of grafted plants to high/low mineral element levels.

It is necessary to combine additional biological investigations, such as fluorescence quantitative analysis of gene expression pattern, in order to confirm the findings using "omics" datasets. However, "omics" analyses are direct and quick ways to find mobile and differentially expressed materials in grafted vegetables, such as DEGs (Xu *et al*., 2016), DEMs (Ren *et al*., 2018); DAPs (Xu *et al*., 2018).

Modulation of crops response to biotic stress. Flores-Leon *et al.* (2021) examined the performance of grafted snake melons in organic farming under extreme biotic and salinity stress conditions. More than 50% of the output was lost due to soil-borne illnesses, viruses

(WMV, ZYMV, and ToLCNDV), and *Podosphaera xanthii* assaults. Although it worked synergistically with the biotic stress, salt stress had a little effect. Grafting consistently decreased plant mortality under biotic stress, but had a detrimental impact on consumer acceptance. This negative effect was reduced by the Cucumis F1P at 81 rootstock. Thus, the use of *Cucumis* rootstocks seems to be a strategy to enable resilient organic farming production of snake melon targeted to high-quality markets in organic farming.

In grape, citrus and different temperate fruits, considerable variability exist among their rootstocks for their response to diseases, pests and nematodes. Rough lemon rootstock, which is tolerant to Tristeza, and xyloporosis, is also tolerant to gummosis but susceptible to Exocortis viral disease. Similarly, guava varieties grafted on Chinese guava, can tolerate wilt disease and nematodes

In many genotypes of *Physalis* spp., Chaves-Gomez *et al*. (2020) employed various physiological variables to test possible rootstocks for resistance to vascular wilt induced by *Fusarium oxysporum* f. sp. *physali* (FOph). While *P. peruviana* "Colombia" and "Sudafrica" plants showed higher susceptibility to the vascular wilt, with net photosynthesis rate, stomatal conductance, leaf water potential, and Fv/Fm being lower than in the non-inoculated plants, *P. floridana* and *P. ixocarpa* plants inoculated with FOph showed similar behaviour to non-inoculated plants. The former genotypes can be used as rootstocks to plant cape gooseberry in soils with FOph infestations or in breeding operations.

When compared to ungrafted plants, tomato and melon grafted onto the resistant rootstocks "Aligator" and *Cucumis metuliferus* (acc. BGV11135), respectively, did not always offer higher tolerance levels to *Meloidogyne incognita*, but the relative crop yields observed both in spring and summer were improved (Exposito *et al*., 2020). In particular, the only significant difference between the grafted and ungrafted summer-grown melons was the presence of nematode tolerance (but not in spring). Regarding this latter harvest, crop season affects fruit quality.

Modulation of crops' response to biotic and abiotic stressors. Various rootstocks can increase resistance to subpar growth conditions, according to other sources. The tomato cultivar BHN-589 was subjected to both optimal soil temperature (24°C) and inadequate soil temperature (SST, 13.5°C) (Bristow *et al*., 2021). Under SST, stomatal conductance (gs), plant biomass, and root hydraulic conductivity and conductance all reduced, but only two rootstocks retained increased stomatal conductance. Higher (20%) root-to-shoot ratios were observed in all phenotypes due to greater reductions in shoot biomass than in root biomass. Some commercial rootstocks maintained higher levels of shoot N content and stomatal conductance, which helped them function better under SST.

Cold-tolerant pumpkin (Cm) rootstock was used in the research work by Fu *et al*. (2021) to increase the grafted cucumber's ability to withstand cold temperatures. The endogenous salicylic acid (SA) level was raised by cooling stress, particularly in cucumber (Cs) scions grafted onto Cm rootstocks. These alterations were connected to the up-regulation of crucial SA biosynthesis genes. Under aerial and root-zone freezing stress, respectively, SA production in leaves and transport from roots both increased, which was primarily responsible for the buildup of SA in the Cs/Cm leaves. Additionally, exogenous SA markedly increased the expression of genes that respond to cold (COR) as well as physiological processes related to cold tolerance.

CONCLUSION

Grafting is now successfully used in many nations throughout the world and is directly related to the success of numerous crops. Since the nineteenth century, this method's largely empirical progress has made it possible for entire woody crops, such citrus groves or vineyards, to survive. Grafting has developed in herbaceous cultivation systems since the turn of the 20th century in tandem with scientific curiosity about the underlying physiological and molecular mechanisms, helping to meet the rising need for securing a sustainable food supply. Practically speaking, this accomplishment was partly due to the significant advantages of grafting (such as resistance to infections and pests, improved yields, and regulation of the production phases), which outweighed the disadvantages associated with higher prices (e.g., related to seeds, skilled labor, facilities and equipment to rise grafted plants). Due to the increased sensitivity of ecosystems and the depletion of natural resources, climate change effects forced agriculture to design environmentally sound methods that can produce more nutrient-dense crops. Grafting has the potential to make a significant contribution in this situation, provided that it would allow for the growth of advantageous crops in increasingly marginal conditions. The most recent developments in physiological, biochemical, molecular, and -omic studies, according to this theory, are anticipated to make a substantial contribution to understanding and regulating the complex nature of plant scion-rootstock interactions. This is a difficult but compelling task, and the solution will have an impact on how much more sustainable agriculture is able to develop the genetic and agronomic potential of many important crops for human nourishment.

FUTURE SCOPE

Despite the current state of research, the mechanisms that control the changes in and transport of specific molecules in grated horticulture crops remains poorly understood and therefore understanding Rootstock-

Scion Physiological and Molecular Aspects can help to improve the genetic potential of most of the horticulturally important crops.

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Conflict of Interest. None.

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