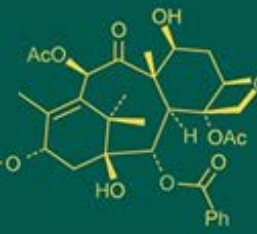
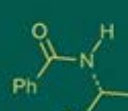
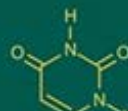
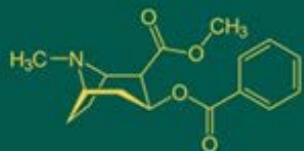


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Vegetable grafting for climate-resilient production systems: Physiological, molecular and technological advances

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Abstract

Vegetable crops are now facing several stresses associated with climate change, including drought, salinity, high temperature, flooding and soil-borne diseases. Vegetable grafting has proven itself to be an advanced and effective technology that promotes climate-smart agriculture through the integration of superior scions and resilient rootstocks, resulting in enhanced water and nutrient absorption, improved photosynthesis, increased hormone control and effective antioxidative defences that enable plants to perform well even under stressful environments. Molecular biology studies have shown that the interaction between the rootstock and scion includes the transport of signals like RNA, protein, hormone and metabolites for enhanced stress adaptation and better plant performance. The benefits of grafting include the sustainable management of biotic stress without the use of hazardous chemical pesticides. Moreover, modern technologies like the development of grafting machines, marker-assisted breeding of rootstocks, genomics, artificial intelligence and digital phenotyping are improving grafting techniques. Although some limitations like the problems of compatibility, economic feasibility and the lack of rootstock are faced during vegetable grafting, the practice holds great potential for sustainable horticulture.

Keywords: Vegetable grafting, precision agriculture, climate resilience, stress, ai

1. Introduction

The impacts of climate change are evident in the increased prevalence of stresses that affect vegetable productivity globally. Rising temperatures, erratic rainfall, prolonged droughts, increased levels of soil salinity and higher disease rates constitute major threats to vegetable crops (IPCC, 2023) [1]. Vegetables are highly susceptible to environmental stress Singh *et al.*, 2020) [2, 3, 4]. Agricultural practices such as grafting have gained increasing significance recently in the context of climate-smart agriculture (Lee *et al.*, 2010; Kumar *et al.*, 2017) [5]. The term grafting refers to the merging of a particular scion cultivar with a resistant rootstock to produce a better composite plant (King *et al.*, 2010; Warschefsky *et al.*, 2016) [6, 7]. Currently, the practical application of grafting technology in the agricultural production of vegetable plants in the case of tomatoes, cucumbers, watermelons, melons, eggplants and peppers, is common (Lee *et al.*, 2010; Davis *et al.*, 2008) [5, 8]. Recent scientific studies prove the potential of grafting as a way to enhance the resistance of vegetables to abiotic and biotic stress factors (Rouphael *et al.*, 2018; Kyriacou *et al.*, 2017) [9, 10]. Moreover, the study of plant physiology and molecular biology has indicated that hormonal, RNA, protein and metabolite-based signals from rootstocks play a major role in stress resistance and plant improvement (Goldschmidt, 2014; Albacete *et al.*, 2015; Kubota *et al.*, 2008; Grieneisen *et al.*, 2018) [11, 12, 13, 14].

2. Development and Impact of Grafting Vegetables

2.1 Development

Earliest commercial use of vegetable grafting dates back to Japan during the 1920s when watermelons were grafted on resistant rootstock varieties in order to overcome the issue of soil borne diseases as well as to increase crop yield (Oda, 2002) [15]. Later on, the technology spread all across East Asia, followed by Europe and North America as farmers needed ways other than chemical treatment of soils to avoid soil borne diseases (Bie *et al.*, 2017) [16].



Fig 1: Grafted seedling of Watermelon

In recent years, due to increasing soil-borne diseases, root-knot nematodes and replant disorders caused by the intensification of cultivation of vegetables, the need arose for grafted plants that could sustain productivity in the face of continuous cultivation (Louws *et al.*, 2010 and Miguel & Maroto, 2002) ^[17, 18].

2.2 The Role of Grafting in Climate-Smart Agriculture

Vegetable grafting plays a vital role here, as it not only improves their resilience to different environmental stresses but also decreases dependence on the use of external resources (Schwarz *et al.*, 2013). Rootstocks that have powerful root systems help plants take up more water and nutrients under stressful environmental conditions (Savvas *et al.*, 2010) ^[19]. Grafted vegetables do not require additional pesticides, which reduces not only costs but also pollution, as they are less susceptible to nematodes and soil-borne diseases (Flores *et al.*, 2010) ^[20]. Grafting also increases both the water-use efficiency and nutrient use efficiency of plants, thus ensuring a better crop yield at lower inputs (Sánchez-Rodríguez *et al.*, 2016) ^[21].

3. Physiological Mechanisms for Plant Resilience to Climatic Variations

3.1. Enhanced Water Relations

Plants with rootstock tolerance to abiotic stresses have more developed and effective root systems; thus, the plants explore soil more efficiently, absorbing more water (Martínez-Rodríguez *et al.*, 2008) ^[22]. Increased hydraulic conductivity of roots improves translocation of water to aerial parts of a plant, resulting in maintenance of leaf water potential and cell turgor when drought occurs (Edelstein *et al.*, 2011) ^[23]. Grafted plants tend to improve water management by enhancing stomata regulation and osmoregulation. Stomata opening can be controlled via the signalling pathway from the root to the shoot by rootstocks. The latter use abscisic acid (ABA) to reduce transpiration and, consequently, conserve water without decreasing the effectiveness of photosynthesis (Cantero-Navarro *et al.*, 2016) ^[24]. Proline, soluble sugars and glycine betaine accumulation in a plant's tissue improves osmoregulation and increases a plant's resistance to drought and salinity (Penella *et al.*, 2014) ^[25]. Therefore, vegetables obtained by grafting are characterized by a higher yield stability under stress conditions.

3.2 Effective Utilization and Acquisition of Nutrients

The function of rootstock has an immense influence on enhancing nutrient uptake and efficient use. The robust nature

of roots leads to high absorption of nutrients such as NPK and Ca, along with iron (Fe), Zn, Mn and B (Martínez-Ballesta *et al.*, 2010) ^[26]. Higher nutrient uptake is achieved through larger root surface area, more active roots and upregulated expression of nutrient transporters (Colla *et al.*, 2013) ^[27]. Proper mineral nutrition has a direct effect on chlorophyll formation, activation of enzymes, carbon metabolism, and photosynthesis efficiency (Moya *et al.*, 2017) ^[28].

3.3 Photosynthetic Efficiency

Another physiological strength of grafting that enhances plant survival under environmental stress conditions is the preservation of efficient photosynthesis. There have been several studies that reported elevated levels of chlorophylls, high photosynthetic rates and stomatal conductance in drought, saline and heat-stressed grafted vegetable plants (He *et al.*, 2009) ^[29]. The rootstocks play an essential role in defending the integrity of photosystem II and the chloroplast from oxidative and osmotic damage (Nawaz *et al.*, 2016) ^[30].

3.4 Hormone Regulation

Hormonal regulation is an essential factor for stress adaptation via grafting. The effects of rootstocks on the production, translocation, and distribution of phytohormones result in regulated growth, development and stress tolerance. For example, cytokinins secreted by roots stimulate shoot development, leaf expansion and chlorophyll maintenance, while auxins control vascular development and graft healing processes (Albacete *et al.*, 2015) ^[12]. Another important hormone involved in drought and salinity stress is abscisic acid, which regulates stomata closure and stress response gene expression. It has been found that there is usually increased ABA regulation in stressed grafted plants, allowing them to cope with environmental stresses (Nilsen *et al.*, 2014) ^[31]. Moreover, gibberellins and ethylene hormones are important in terms of their involvement in rootstock-scion interaction, which is manifested through changes in plant morphology, fruit development and stress tolerance.

3.5 Antioxidant Defence Systems

Grafted plants have been known to possess better antioxidant defence systems in order to reduce oxidative stress and ensure cellular integrity (Liu *et al.*, 2016) ^[32]. High levels of antioxidant enzymes like superoxide dismutase (SOD), catalase (CAT), peroxidase (POD) and ascorbate peroxidase (APX) in response to abiotic stress conditions have been observed among grafted vegetable plants (Wei *et al.*, 2019) ^[33].

4. Molecular Mechanisms of Rootstock-Scion Interaction

4.1 Graft Union Formation

Graft union formation is a well-coordinated biological process of wound detection, callus development and regeneration of the vascular system. (Melnyk *et al.*, 2015) ^[34]. The initial signals induce the dedifferentiation of parenchymal cells, resulting in callus formation. Next, auxin-induced vascular differentiation followed by the reactivation of the cambium layer leads to the connection of xylem and phloem. Transcriptome analysis has demonstrated substantial transcriptional control on cell wall modification, lignin biosynthesis, and hormone signalling networks in grafting (Gautier *et al.*, 2019) ^[35]. The successful vascular connection plays a significant role in maintaining water and nutrient exchange between rootstock and scion.

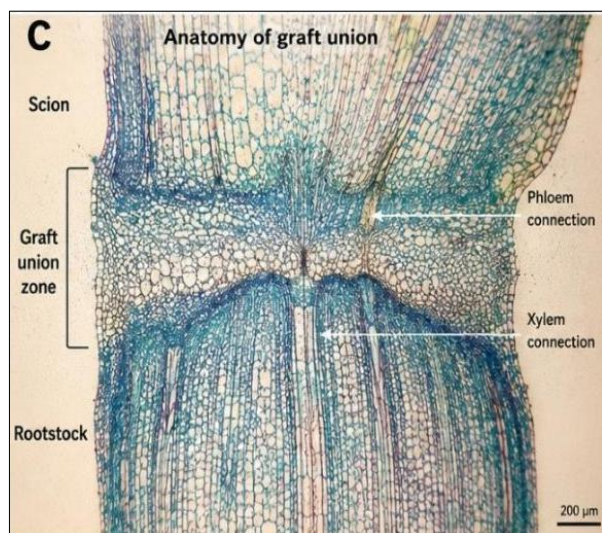


Fig 2: Anatomy of graft union

4.2 Long-distance molecular signalling

An important process involved in grafting is the transfer of mobile molecules via vascular connections. Following successful grafting, mRNA molecules, siRNA, miRNA, proteins, peptides and metabolites move to target tissues (Kehr & Buhtz, 2013; Notaguchi & Okamoto, 2015) [36, 37].

Molecular mobility includes mRNAs capable of regulating flowering, transportation of nutrients and response to stress factors in the recipient tissue. Small RNAs are responsible for post-transcriptional gene regulation and epigenetics, binding to complementary mRNA molecules (Lewsey *et al.*, 2016) [38]. The hormonal pathway comprises molecules such as auxins, cytokinins and abscisic acid (Harada, 2010) [39].

4.3 Transcriptomic and Proteomic Responses

Modern omics technologies have been instrumental in elucidating many aspects of molecular changes occurring in response to grafting. Transcriptome profiling indicated that grafting affected transcriptional regulation of genes related to

photosynthetic activity, hormonal signalling, antioxidative and stress response pathways (Stegemann & Bock, 2012) [40].

Changes in differential expression of genes in grafted plants correlate with enhanced abiotic stress tolerance, especially when exposed to drought and salt stresses. The use of proteomics helps identify some stress-regulated proteins, including heat-shock proteins, antioxidants and pathogenesis-related proteins upregulated during the development of the graft union under stress conditions (Shen *et al.*, 2016) [41].

4.4 Gene Expression Induced by Rootstocks

Some genes related to osmotic adjustment, ionic regulation, detoxification and antioxidative metabolism are induced in scions grafted on rootstocks adapted to stresses. Rootstocks can manipulate the transcription of genes in the scions, affecting processes such as nutrition, water transport, photosynthesis and stress resistance (Loupit & Cookson, 2020; Stegemann & Bock, 2012) [42, 40].

5. Grafting for Management of Abiotic Stress

The modern vegetable production system is facing increased exposure to multiple abiotic stresses acting separately or simultaneously. Global climate change has led to increases in drought incidences, salt encroachment, heat waves and flooding, resulting in poor performance and decreased production stability (Schwarz *et al.*, 2010; Venema *et al.*, 2008) [19, 43].

5.1 Drought Stress

One of the biggest limiting factors in vegetable cultivation is drought stress, especially in arid and semi-arid environments. Drought resistance of grafted plants is mainly attributed to improvements in root system structure and increased root biomass, leading to better soil moisture exploration capabilities (Kumar *et al.*, 2015; Nardini *et al.*, 2014) [44, 45]. Other physiological traits include better osmotic adjustment through increased levels of osmotically active compounds, such as proline and carbohydrates (He *et al.*, 2009) [29].

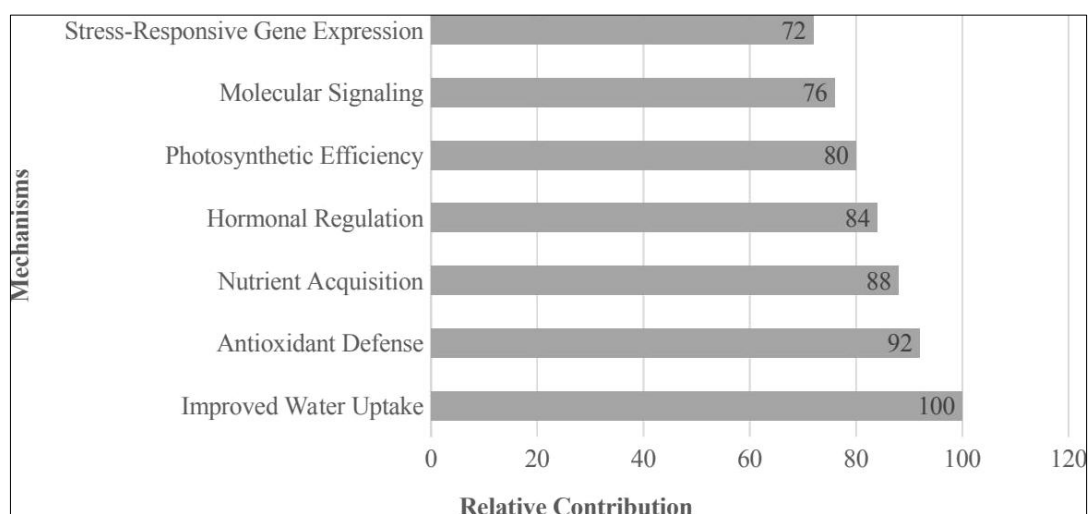


Fig 3: Integrated mechanisms through which vegetable grafting enhances climate resilience

A conceptual ranking of the relative contributions of the main physiological and molecular pathways involved in graft-mediated climate resilience is shown in the graph. Values are derived from published literature and are not meant for quantitative comparison, but rather for trend visualization (Lee *et al.*, 2010; Colla *et al.*, 2010; Albacete *et al.*, 2015;

Warschefsky *et al.*, 2016; Kyriacou *et al.*, 2017; Rouphael & Colla, 2020) [5, 46, 12, 7, 10].

5.2 Salt Stress

The mechanism that plays a crucial role in increasing resistance to salt stress is the reduction of Na⁺ transport from roots to

shoots, preventing toxic effects of ions on photosynthetic tissues. Another beneficial function of rootstocks is the increase in K⁺ accumulation, ensuring the appropriate K⁺/Na⁺ balance necessary for enzymatic and metabolic processes (Colla *et al.*, 2013) [27]. Increased antioxidative enzyme activity prevents the development of oxidative stress and protects chloroplasts (Martínez-Ballesta *et al.*, 2010) [26].

5.3 Heat Stress

Heat resistant rootstocks result in enhanced levels of heat shock protein (HSP), which act as molecular chaperones preventing protein denaturation and aggregation under the effect of increased temperature (Bita & Gerats, 2013) [47]. Chlorophyll content and photosystem II efficiency of grafted plants are maintained higher even during heat stress conditions, thereby ensuring carbon assimilation. Furthermore, antioxidants help in minimizing heat stress-induced ROS build-up (Rivero *et al.*, 2003) [48].

5.4 Hypoxia and Flooding Tolerance

Flood stress results in oxygen deficiency (hypoxia), negatively impacting root respiration and nutrient acquisition. Plants grafted on rootstocks that have tolerance to floods show increased survival rates and ability to recover from flooded conditions. The role of improved ethylene signal transmission is important as far as adaptive morphogenesis is concerned (Sauter, 2013) [49].

6. Grafting for Management of Biotic Stresses Grafting differs from the other control measures by its long-term safety and effectiveness as a means of disease management in sustainable agriculture systems of vegetable production (Louws *et al.*, 2010; King *et al.*, 2010) [17, 6].

6.1 Resistance to Fusarium Wilt

Grafting onto rootstock with resistance to Fusarium wilt greatly decreases the occurrence of



Fig 4: Grafted seedlings of Tomato

this disease due to prevention of fungal growth into vascular tissues (Zhou *et al.*, 2013; Lee *et al.*, 2010) [50, 5]. Furthermore, the plants grafted onto rootstocks exhibit higher expression of PR proteins including chitinases and β -1,3-glucanases responsible for fungal cell wall degradation (King *et al.*, 2010) [6].

6.2 Verticillium Wilt Tolerance

Verticillium wilt caused by *Verticillium dahliae* is another vascular infection of solanaceous crops. It can be controlled using grafting, because it helps minimize pathogen entry and reduces the clogging of vessels in plants. In addition, grafted

plants demonstrate higher levels of SAR, due to salicylic acid signalling pathways (Pflieger *et al.*, 2011) [51].

6.3 Resistance to Bacterial Wilt

R. solanacearum is a particularly damaging bacterium causing bacterial wilt in tropical and subtropical areas. Grafting is among the best means of controlling this pathogen (Rivard *et al.*, 2010) [52].

Resistance to the bacteria in grafts involves restriction in bacterial colonization due to reduction in bacterial movement and preservation of vascular tissue. Furthermore, increased synthesis of antibiotics and the oxidative burst play an essential role in suppressing bacterial action (Cohen *et al.*, 2017) [53].

6.4 Root-Knot Nematode Resistance

Root-knot nematodes (*Meloidogyne spp.*) have a negative impact on vegetable yield because they attack the roots of plants and interfere with their ability to absorb nutrients. The use of grafting to resistant rootstocks is a highly effective method, as it hinders nematode infection and reproduction. Production of defence compounds, such as phenolic compounds and alkaloids, further increases resistance to nematodes (Hussey & Janssen, 2002) [54].

6.5 Soil-Borne Fungal Pathogens

Grafting can increase resistance by improving the defence capabilities of the root system. The grafting process causes an increase in the activity of antioxidant enzymes and the phenylpropanoid pathway that helps in reinforcing the cell walls of roots and preventing penetration by the fungus (Savvas *et al.*, 2010) [19].

7. Technological Developments in Vegetable Grafting

The technology of vegetable grafting has changed from being done manually in a nursery to an automated process that is highly informed by data.

7.1 Grafting Using Robotics and Automation Technologies

Recent advancements in automation have seen successful grafting because of the ability to accurately manage stem alignment, pressure application and healing environment conditions. Vision systems used in automated grafting processes have enabled precise monitoring of stem diameter and alignment problems (Vázquez *et al.*, 2020) [55]. The use of automation technologies in industry has greatly helped save on labour costs and improve hygiene levels.

7.2 Breeding of Rootstocks Using Marker-Assisted Selection

High-density molecular markers like SNPs and SSRs facilitate quick screening of large breeding populations without requiring phenotyping. Thus, the selection process becomes very efficient and can be used to select rootstocks that have superior compatibility and adaptation to the environment (Xu & Crouch, 2019) [56].

7.3 Genomics and Gene Editing

The CRISPR/Cas system has opened up new possibilities in terms of genome editing in which important traits such as stress resistance and pathogen resistance may be edited. Vegetable crops have been studied using gene-edited rootstocks for enhancing nutrient absorption (Chen *et al.*, 2021) [57].

7.4 Digital Phenotyping

The techniques facilitate identification of stress effects like drought, malnutrition and pathogens in plants even before the onset of observable symptoms. The thermal imaging technique is highly efficient in determining plant water status and stomatal conductance. The combination of phenotyping systems with analytical capabilities on cloud-based systems allows the tracking of plant growth patterns (Singh *et al.*, 2020) ^[3, 4, 2].

8. Challenges and Future Prospects

Although many achievements have been made in plant grafting research and application, some biological, technological and economic barriers to adopting plant grafting remain to be overcome. The limited availability of superior and polygenic rootstocks that are stress-tolerant, resistant to disease and graft-compatible is one of the important limitations in plant grafting (López *et al.*, 2020) ^[58]. Another important limitation associated with grafting is the limited knowledge regarding molecular communication between the rootstock and scion (Szymański *et al.*, 2021). High labour and production costs associated with grafting seedlings constitute a major impediment, especially in less developed countries (Costa *et al.*, 2021) ^[59]. Biologically, incompatibility between species and cultivars is still an issue (Singh & Singh, 2020) ^[3, 4, 2]. The absence of standardized methods for determining graft performance, stress tolerance and compatibility is another biological barrier (Fiorani & Schurr, 2013) ^[60].

Conclusion

Grafting of vegetables is another sustainable practice that has proven to be extremely successful for making vegetable plants resistant to climate change. Grafting has made use of the favourable rootstock and the scion plant variety to make the crop more resistant to various types of abiotic stress like drought, salinity, extreme heat and waterlogging. In addition to being resistant to adverse climatic factors, grafted plants are also more resistant to soil-borne diseases and pests.

The recent developments in molecular biology show that the ability to withstand stress due to grafting occurs via various interactions between the rootstock and scion through the movement of RNAs, proteins, hormones, metabolites and epigenetic changes. Such breakthroughs in science have expanded knowledge about grafting compatibility and provided new opportunities for developing vegetables that are resistant to climate change without using direct genetic engineering. Moreover, automation, marker-assisted breeding, genomics, artificial intelligence and digital phenotyping techniques have led to increased efficiency and application of grafting technologies.

Thus, vegetable grafting can be considered a prospective approach for implementing climatesmart horticulture, improving the efficiency of resources usage, decreasing the use of agrochemicals and ensuring sustainable vegetable production under changing climatic conditions.

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