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REVIEW ARTICLE

Rootstock developments in avocado: Selection of rootstocks for biotic and abiotic stress mitigation

Gayathri S[1], Shanmugasundaram K A[2*], Auxcilia J[1], Shanthi A[1], Karthikeyan M[3,4] & Muthuvel I[5]

[1]Department of Fruit Science, Tamil Nadu Agricultural University, Coimbatore 641 003, Tamil Nadu, India
[2]Horticultural Research Station, Yercaud, Athiyur 636 601, Tamil Nadu, India
[3]Department of Plant Pathology, Tamil Nadu Agricultural University, Coimbatore 641 003 Tamil Nadu, India
[4]Centre for Crop Health, School of Agriculture and Environmental Science, University of 14 Southern Queensland, Toowoomba, Queensland 4350, Australia
[5]Horticultural College and Research Institute for Women, Tamil Nadu Agricultural University, Tiruchirappalli 620 009, Tamil Nadu, India

*Correspondence email - shanmugasundaramka@tnau.ac.in

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Abstract

Avocado (*Persea americana* Mill.) is a globally important fruit crop that is vulnerable to various biotic and abiotic stresses prevalent in subtropical regions, significantly affecting productivity. Rootstocks play a crucial role in mitigating stress factors and ensuring sustainable avocado cultivation. This review discusses the propagation methods for avocado rootstocks, including seed and clonal propagation techniques and examines the responses of different rootstocks to abiotic stresses such as salinity, poorly aerated soils, calcareous, alkaline soils and drought. It highlights the physiological, biochemical and molecular mechanisms involved in these stress responses. This review also covers resistance of various rootstocks against biotic stresses, including Laurel wilt (*Harringtonia lauricola*), root rot (*Phytophthora cinnamomi*), white root rot (*Rosellina necatrix*) and Verticillium wilt (*Verticillium dahliae*). Extensive research has identified promising rootstocks such as R0.05, Dusa, PP40 and R0.18 for salinity tolerance; West Indian rootstocks for tolerance to calcareous soils and rootstocks such as Duke 7, Toro Canyon and BG-83 for resistance against various other diseases. Understanding defense mechanisms such as callose deposition, lignification and pathogenesis-related protein production, will aid in developing molecular markers and screening techniques for tolerant rootstock selection. These specialized avocado rootstocks offer specific tolerance, making them ideal for diverse growing conditions. Enhancing stress resistance leads to more productive trees, which significantly boost the sustainability and profitability of commercial avocado cultivation.

Keywords : abiotic stress; avocado; biotic stress; defense mechanisms; rootstocks

Introduction

The Avocado is an important subtropical fruit crop that has gained global attention owing to its nutritional value, culinary use and increasing demand (1). Originally native to Mexico and Central America, avocado cultivation has expanded worldwide, particularly to warm and subtropical regions (2, 3). Avocado trees require well-drained soils, adequate moisture and temperatures between 16-30 °C for optimal growth and fruit production. The top three producers of avocado are Mexico, contributing approximately 2.3 million tons, followed by the Dominican Republic and Peru (4). Avocado belongs to the Lauraceae family and is known for its unique fruit composition. The fruit is rich in monounsaturated fatty acids, particularly oleic acid, which accounts for about 60-70 % of its total fat content (5). Additionally, avocados are an excellent source of dietary fibre, vitamins (including vitamins C, E, K and B-complex) and minerals such as potassium, magnesium and copper (6).

Avocado production is subject to various farming constraints, the most significant being susceptibility to pests and diseases (7), which can significantly impact productivity and yield. Implementing effective crop protection strategies, including the use of resistant cultivars, cultural practices and appropriate chemical formulations (8) can help address these challenges. Besides, sensitivity of the crop to environmental factors such as drought, cold or excessive heat adversely affects yield and fruit quality (9).

Researchers and growers continue to explore sustainable production practices to mitigate these stress factors, including the use of rootstocks, improved irrigation techniques, enhanced soil management practices and the development of new cultivars with desirable traits, such as disease resistance, higher yields and better adaptation to climatic conditions (10). Avocados naturally occur in the three distinct races and originate from different regions, differentiated by response to various environmental conditions (11). Rootstocks play a crucial role by providing the scion with enhanced resistance, improving nutrient and water uptake, triggering defense mechanisms and ultimately supporting growth and productivity.

Optimizing propagation techniques for superior avocado rootstocks

Avocados are generally propagated through seeds that require longer juvenile periods and produces plants that are not genetically identical to the mother plant. Alternatively, vegetative propagation methods include grafting and budding, in which rootstocks play a vital role in influencing tree performance and uniformity (12). The selection of appropriate rootstocks depends on various factors, including soil and climatic conditions, tree size, vigor and disease prevalence. Understanding avocado rootstock propagation is crucial for ensuring sustainable productivity (13).

Rootstocks are generally propagated through seed and clonal propagation techniques. This method involves sowing the seeds under protected conditions, followed by tip-grafting the seedlings earlier in the juvenile phase (14). There is a need for clonal propagation to overcome the constraints of seed dormancy and the inability to maintain true-to-type traits. It ensures genetic uniformity and is selected for its specific influence on the scion, including traits such as dwarfness, precocity, fruiting behaviour and resistance to biotic and abiotic stress conditions (15, 16). For better rooting success rates, the leafy stem buried etiolation technique was employed in combination with Indole Butyric Acid (IBA; 2500 mg/L) and 1:1 perlite: vermiculite medium, which enhanced rooting efficiency (17) Further studies have proved that the de-etiolation technique in plants enhances adventitious root formation. In the study, dark-grown plants were exposed to a short period of light, which increased chlorophyll content and induced changes in cell wall properties and hormonal levels, particularly auxins and ethylene (18). Recent findings focus on standardizing micropropagation protocols, aids in the large-scale production of genetically uniform and disease-free rootstock plants under controlled conditions. Anatomical and physiological variations in stem and leaf structures such as, continuous cambium structure and large xylem vessels in the rootstocks, enhances rooting efficiency and acclimatization rates (19).

Abiotic Stress Mitigation

Soil salinity and pH tolerance

Understanding salinity stress: Effects on plant physiology: Avocado is extremely sensitive to saline conditions, which significantly affects its' growth and development (20). Salt sensitivity positively correlates with yield reduction and survival rate due to toxic effects and undesirable osmotic adjustment (21). Salinity stress in avocados is primarily caused by Cl^- toxicity rather than Na^+, leading to leaf damage and reduced photosynthesis. Excess saline conditions in plants affect the photosynthetic pathway, with reduced stomatal conductance and water potential resulting in osmotic damage to the plant (22).

Grafting onto salinity-resistant rootstocks enables active energy production in leaves, mitigates Na^+ and Cl^- uptake to the above-ground portions of the plant and ensures normal root function. This is achieved through the absorption of soil minerals which leads to the accumulation of toxic ions and a reduction in the activity of nitrate reductase enzyme proportion to the level of damage (23). West Indian rootstocks thrive under saline conditions with increased nutrient acquisition, whereas Guatemalan rootstocks are susceptible and Mexican rootstocks show an intermediate response (24).

Physiological and biochemical responses to salinity stress in tolerant rootstocks: Rootstocks greatly influence Avocado trees' response to salinity. The Rootstocks R 0.05, R0.18 (Selections from Westfalia) and PP40 (UCR Experimental selection), have been identified for their ability to maintain growth and yield under saline conditions. This performance can be attributed to their low Cl^- concentrations in fully expanding leaves, along with higher yields, larger trunk diameters and greater survival rates (25). The performance of 'Hass' Avocado scion grafted onto different rootstocks viz., Dusa and PP was similarly maintained under salinity conditions. It was possibly due to a higher rate of stomatal conductance and water-use efficiency (WUE) causing non-apparent damage symptoms (26). The vegetatively cloned rootstocks (VC) belonging to the West Indian races (VC 140, VC 152, VC 159, VC 802) and the Mexican race (VC 840) were among the least salt-sensitive, as there was less incidence of visible salinity damage symptoms, lower level of leaf osmolytes Cl^- ion exclusion and high Leaf Area Index. An additional indicator was studied, where trichome density increased with higher salt concentration (27). Upregulation of genes and proteins promoting salinity tolerance induces the synthesis of phytohormones, including abscisic acid, ethylene and salicylic acid, which alleviates the effects of salinity, ion toxicity and Reactive Oxygen Species (ROS) generation (28). The reciprocity between scion and rootstock exhibiting salinity tolerance through the mechanisms of ionic accumulation and physiological alterations by impeding the transport of sugars and lipids are explained in Fig.1-3.

Nutrient availability and uptake challenges in calcareous and alkaline conditions: Generally, avocado thrives well in acidic soils (pH 3.5-5.5). Lime-induced chlorosis and alkalinity problems are found in major avocado-growing countries such as Florida, Spain, Israel and to a lesser extent, in California (29). The soils are highly saturated with $NaHCO_3$ and Na_2CO_3 restricting the water supply to the roots, resulting in nutrient unavailability. Excessive lime application, the use of phosphorous fertilizers and soil nutrient deficiencies of Fe, Zn and Mn are the major contributing factors, especially in sodic soils (30). Alkalinity stress in plants affects various metabolic pathways, resulting in stunted growth, leaf chlorosis and disrupted cell structures (31).

To alleviating alkalinity stress conditions, the isolation of key genes and identification of metabolic pathways are essential for developing of stress tolerance in rootstocks (32). The molecular components including iron reductases, iron transporters and other enzymes contribute to improved tolerance, by enabling iron absorption from calcareous soils, whereas sensitive rootstocks lack this ability (33). Studying the effect of NaCl and $NaHCO_3$ stress, West Indian rootstocks, specifically 'Julien' and 'Gallo 2', where found to exclude Na^+ and Cl^- by accumulating them in the roots, resulting in lower necrotic damage on leaves. Even though Cl^- toxicity is observed under high pH, Na^+ was found to cause nearly twice as much leaf necrosis as Cl^- (34).

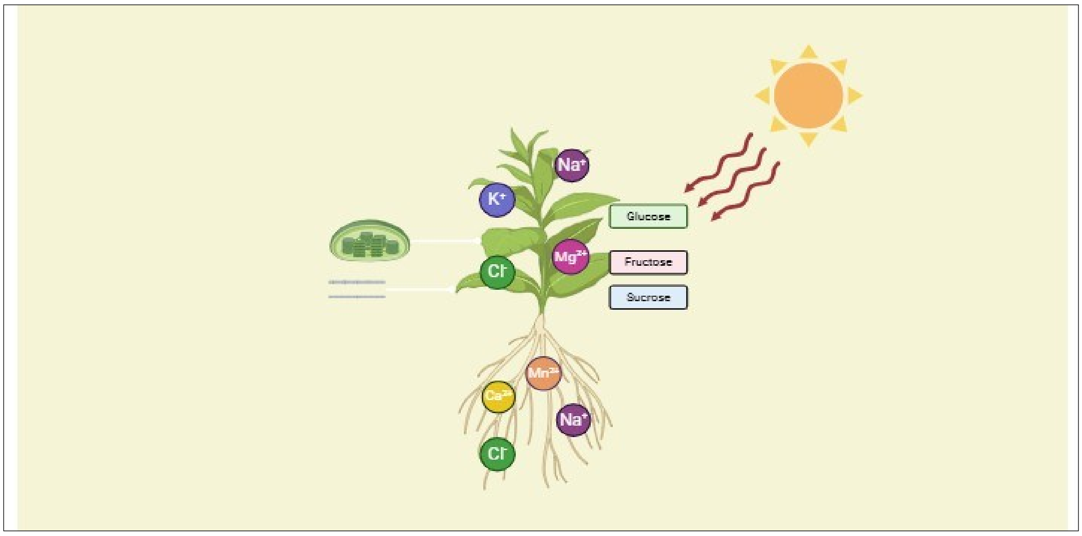

Fig. 1. Control rootstocks with low levels of 'Na' and 'Cl' having balanced supply of essential nutrients and no major Downward transport of Metabolites or stress-induced adjustments in membrane fluidity. [K]Glutathione-S-transferase[1]Oncogenes Transcription Factors of Myelocytomatosis family

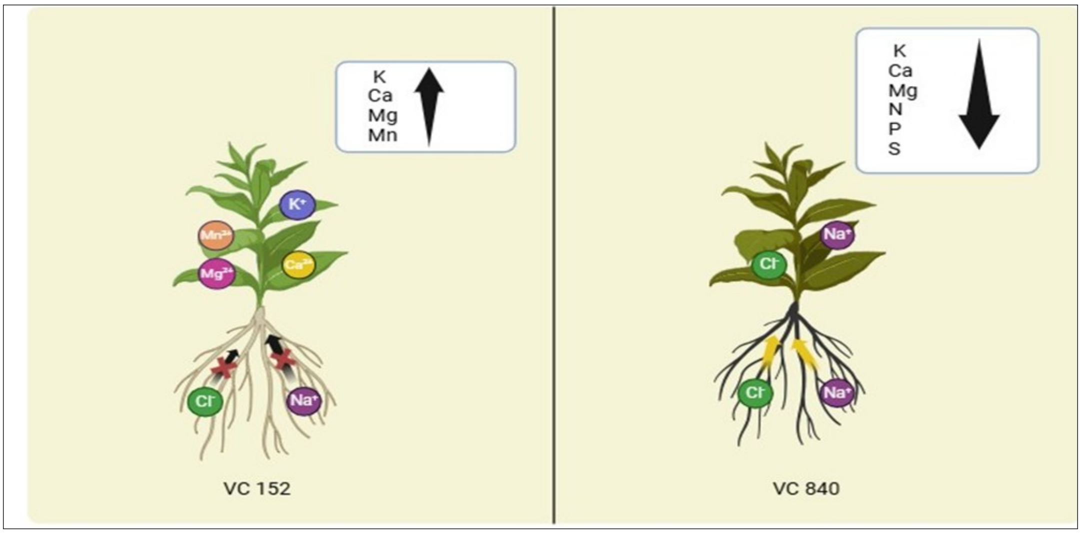

Fig. 2. Selective accumulation of 'Na' and 'Cl' in roots preventing ionic transport to leaves and maintaining stable concentrations of K, Ca, Mg and Mn in VC 152 (Left) and Increased concentration of 'Na' and 'Cl' in leaves shows visible damage symptoms with significant nutrient reduction in VC 840 (Right).

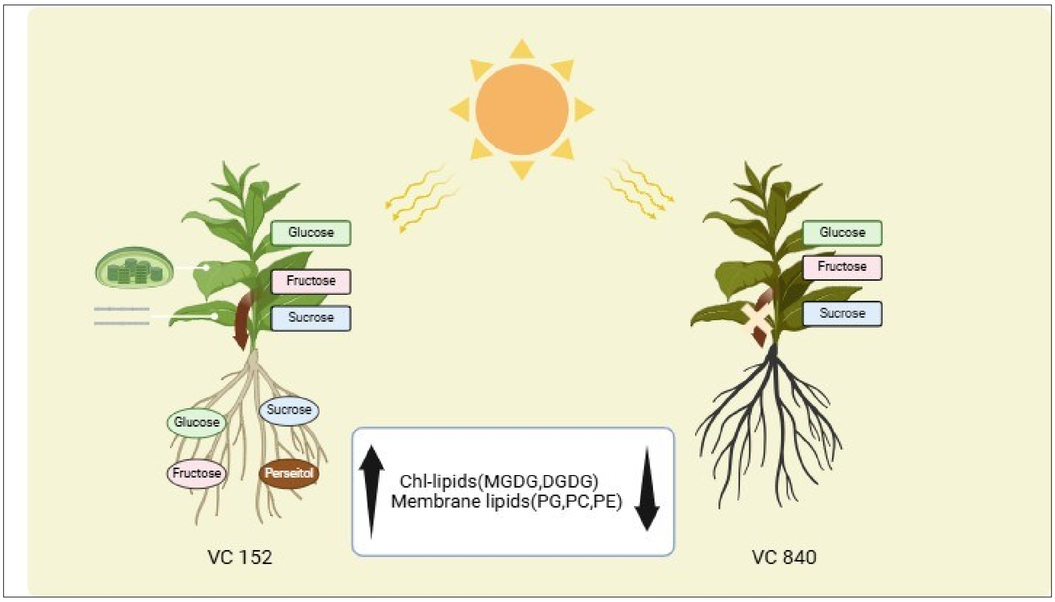

Fig. 3. Metabolic adjustments induced downward transport of Glucose, Fructose, Sucrose and Perseitol (Precursor of Mannoheptulose) and storage lipids with increasing concentration in Chloroplast and Membrane lipids in leaves sustained root function in VC 152 (Left) whereas the decreased concentration of lipids in leaves and restricted transport of sugars and other metabolites impairing them to cope up with salt stress in VC 840 (Right) (23) (Created in BioRender.com).

The Secondary metabolic pathways and phytohormones also play a crucial role; for instance, phenylpropanoid and phenylalanine metabolism exhibit improved tolerance in plants (35). Calcium signaling and antioxidants such as phenolics and flavonoids actively nullify the effects of alkali salts by inhibiting ROS generation (36). Under alkalinity stress, plants were more severely affected than under salinity stress, showing reduced photosynthetic rates (E-Transpiration rate, g_s-Stomatal Conductance) due to higher levels of NPQ-Non-photochemical quenching. Reversible photo-inhibition leads to oxidative stress with higher levels of α-tocopherol pigments (37). Overall, the rootstock '225' exhibited a stronger photoprotection mechanism, as indicated higher concentration of different photosynthetic pigments, such as Violaxanthin (VAZ- Sum of Violaxanthin Antheraxanthin and Zeaxanthin) and other protective pigments indicating the response of rootstocks to mitigate stress effects (38).

Defining water stress: Effects of soil moisture variability and plant responses

Consequences of waterlogging on plant development: Enhancing resilience using tolerant rootstocks: Poor aeration is also a major threat to avocado farming, resulting in poor soil structure and a subsoil hard pan that blocks water infiltration. Heavy rains, changes in soil pH, poor drainage and improper irrigation management cause lead to the lack of soil aeration (39). Plants exhibit stunted growth with premature defoliation and other physiological parameters such as intercellular CO_2concentration (C_i), transpiration rate (E), -stomatal Conductance (g_s), photosynthetic rate (A), water use efficiency (WUE), growth and survival rate being negatively affected (40). Genetic race and moisture stress levels highly influence the rootstock in response to flooding (41). Flooding significantly impacts avocado crops, primarily due to a deficiency of soil oxygen. This results in a condition known as hypoxia during short-term flooding, while long-term flooding leads to anoxia, i.e., the complete absence of oxygen (42). The combined effects of flooding and root rot were synergistic, resulting in complete defoliation and plant death.

Hung-Hsin-Yuan largely maintained $g_s$levels, whereas Black Beauty exhibited a continuous decrease in $g_s$during waterlogging, highlighting its sensitivity. The study noted that rootstock showed better stress response even during growth cessation, suggesting that growth status may influence the evaluation of waterlogging stress (43). Guatemalan rootstocks had better graft success and morphological indicators such as new flush buds, shoot development, scion elongation, with greater ability to suppress root suckers and the emergence of new shoots below the graft union due to the higher auxin concentrations compared to the Mexican race. Further research is to be carried out on various soil types and under different growth conditions to optimize the rootstocks in response to waterlogging conditions.

The transcriptomic response of rootstocks in response to flooding involves the upregulation of genes linked to glycolysis and ethanolic fermentation processes, compensating for limited ATP synthesis under hypoxia. Defense-related transcripts such as chalcone synthase were repressed, reducing root water uptake and downregulation of genes involved in energy-intensive processes such as cell wall synthesis (44). The oxidative stress in rootstocks under such conditions results in ROS generation and reduced activity of antioxidant enzymes such as Superoxide Dismutase (SOD), Peroxidase (POD), Glutathione peroxidase (GPX) and Ascorbate peroxidase (APX). The level of malondialdehyde which is considered to be a marker used in Lipid peroxidation, increases, causing significant cellular damage (45). Rootstock such as R 0.06 has been observed to be tolerant, with sustained photosynthetic rates, maintaining PS II efficiency and photochemical quenching ability (Fv/Fm) in flooded plants (46).

Molecular adaptations and transcriptomic responses in rootstocks to drought stress: Erratic rainfall patterns, temperature and moisture fluctuations, elevated CO_2concentrations, and climate change significantly affect plant water use efficiency (47). Avocado, being salt sensitive, is also extremely sensitive to drought conditions, highlighting the overlapping mechanisms of osmotic stress and ROS generation. This may occur due to poor quality water or improper irrigation management. Due to their shallow root system, the plants are unable to acquire water from the intense depth of soil (48). Molecular mechanisms and transcriptomic data have been analyzed to understand drought stress mitigation by emphasising the regulation of restricting enzymes, osmolytes, HSP-Heat Shock Proteins and phytohormones.

The rootstock 'Dusa' recovered from water stressed conditions after rewatering without any significant chlorophyll degradation or reduction in transpiration rates, exhibited no decline in the photochemical efficiency of PS II. Although hydraulic conductance decreased significantly, it approached to control values following rewatering likely due to embolism in Xylem conduits. Additionally, significant morphological changes were also observed in root growth and biomass, highlighting the adaptive strategies demonstrated by the rootstocks. The NCED-9 -cis-epoxy carotenoid dioxygenase genes, which are key regulators in Abscisic acid (ABA) biosynthesis, play an important role in early response to water deficit conditions (49).The hybridization rates of microarray in 'Dusa' rootstock were consistent with the expression of Differentially Expressed Genes (DEGs) under two conditions: Mild water stress (WS) (549 DEGs-identified; 47.2 % induced, 52.8 % repressed) and Severe WS (1066 DEGs identified; 40.4 % induced, 59.6 % repressed). The pattern of higher proportion of genes downregulated suggests a suppression of metabolic pathways that typically performs plant survival functions under water stress (50). Gene Ontology term enrichment was analyzed by identifying the molecular and biological functions in response to water deprivation (GO:0009414), cell wall organization (GO:0071555), methylation (GO:0032259) and cellular oxidant detoxification (GO:0098869), all of which are essential for the plant drought response (51). The molecular functions such as Heme binding and peroxidase activity along with the downregulation of aquaporins, play a prominent role in regulating water transport under severe WS conditions, reducing root hydraulic conductivity(52).

Biotic stress mitigation

Exploring Laurel wilt disease with early detection and its impact on plant health

Laurel wilt is a major fungal disease affecting the Lauraceae crops, prevailing in the Southeastern USA regions. The causal agent, *Harringtonia lauricola* (previously called *Raffaelea lauricola*) that affects avocado orchards has been reported in Florida, Georgia, South Carolina and Alabama (53). This severe infection is transmitted by the vectors called Redbay Ambrosia beetles (*Xyleborus glabratus)* which forms a symbiotic relationship with the fungus that causes lethal wilt (54). Other beetle species implicated in the spread include *X.gracilis, X.saxesenii, X.affinis, X.bispinatus, X.ferrugineus, X. volvulus* and *X.crassiusculus* (55). The further spread and infection of laurel wilt require low temperatures, heavy rainfall, high relative humidity and moist conditions. The symptoms are localized and include canopy wilting, where the oily green foliage turns brown, resulting in premature defoliation and sapwood discoloration ranging from reddish brown to bluish-grey (56). The pathogen enters the xylem vessels and further produces tyloses and gums, leading to vessel clogging (57). Leaf gas exchange parameters (Net Photosynthetic rate (P_{n-}), A, C_i, $g_s$and E) and chlorophyll parameters (Fv/Fm, Photochemical efficiency (Φ PS II) of PS II, NPQ) are the effective indicators of plant stress in response to Laurel wilt prior to the occurrence of visible symptoms (58).

The susceptibility to laurel wilt in avocado trees is influenced by botanical races related to the differences in xylem vessel size. West Indian cultivars, which possess wider vessels, exhibit higher hydraulic conductance and sap flow, thereby facilitating faster movement of pathogens leading to severe damage symptoms and decreased physiological processess (59). The interaction between scion and rootstock such as 'Duke-7' (a Mexican cultivar) grafted onto 'Reed' rootstock, influences xylem sap flow rates and disease severity. Under this graft combination, 'Duke-7' exhibited lower sap flow and less disease progression (60). Variations in disease incidence have been observed among different species, where *Persea americana* cv. Waldin exhibited fewer symptoms due to its higher xylem vessel density. In contrast, susceptible species suffer from vessel embolism which stimulates gel and tyloses production, blocking water transport and thereby reducing photosynthesis (61). Although the disease is found to be epidemic in the US, limiting the introduction of new invasive species becomes crucial. This can be achieved by monitoring global trade trends and implementing effective quarantine policies (62).

Combating root rot: Exploring tolerant rootstocks and implementing sustainable approaches: Root rot (*Phytophthora cinnamomi* Rands) is the most devastating disease occurring worldwide, affecting major avocado-growing countries (63). This pathogen can cause severe infection at any age of the plant growth, causing root damage and leading to secondary symptoms including wilting, yellowing of leaves, dieback of branches, premature defoliation and complete death at severe stages (64).In Mexican countries, the disease is called sadness, where the feeder roots show typical root rot symptoms, often leading to 100 % mortality (65). The disease was reported in Greece and assured by its morphological traits, such as thick-walled chlamydospores with ovoid to obpyriform-shaped non-papillate oospores and was sequenced using ITS1/ITS4 (Internal Transcribe Sequences) and FM83/FM84 (Reverse primer) primers in gene bank (GenBank accession nos. PP506613 to PP506615 and PQ063867 to PQ063869, respectively) (66). Lack of aeration, poor drainage, low pH, shallow soils, etc., are the major causes. The eradication of this disease is difficult since it forms resistant spores that survive up to 4 - 6 years in the absence of a host (67).The selection for root rot resistant rootstocks began in the early 1940s resulting in Duke 7 being recommended as the commercial rootstock, which later turned out to exhibit only mild tolerance besides being sensitive to waterlogging (68).

Eighteen accessions were selected from the avocado germplasm bank in Columbia and were inoculated with different strains of *Phytophthora*, namely Ag-A-041 and Ag-A-003 in which 'NATU-0011' and 'CAN008'exhibited highest tolerance compared to the other accessions (69). The germination rate of zoospores and hyphal penetration was very high in the susceptible rootstocks R 0.12 at 1-hpi. In contrast, R 0.06 exhibited the unique ability to interfere with cyst germination and hyphal networks were observed only after 6 hpi, indicating reduced disease progression (70).In the evaluation of ten different genotypes from various races, Hass(a hybrid of Mexican x Guatemalan race) and Duke-7 (Clonal origin, Mexican race) showed intermediate tolerance. Todo el A~no (a Mexican race) emerged as the sole resistant genotype, resulting from the recombination of desirable alleles inherited from its single female parent and its unique ability to produce two flowering cycles (65).

Unraveling the mechanisms of tolerance and physiological adaptations to root rot: Various defense strategies have been reported in avocado rootstocks for resistance against root rot, primarily attributed to the enhanced biochemical responses and enzymatic activities (71). Callose (β-1,3 glucan polymer) deposition along the epidermal cells and increased levels of defense-related enzymes such as APX, GPX and SOD in R 0.06, restricts zoospore germination and hyphal development. In contrast, the accumulation of lignin and tyloses in xylem vessels of susceptible rootstocks such as R 0.12 was less effective in preventing the disease incidence (70).

The Salicylic Acid (SA) pathway, plays a major role in the early detection of pathogens and stimulates plant defense mechanisms by inducing peroxidase activity in chitin catabolism and ABA signalling pathways (72). The Jasmonic Acid (JA) pathway mainly mediates resistance against necrotrophy. Jasmonate (JAZ) ZIM-domain proteins, involved in the JA biosynthesis and signalling, would be upregulated, thereby instigating auxin-related processes, Ca^{2+}-dependent interactions and cell wall strengthening functions. The interaction between SA and JA signalling pathways is associated with ROS-detoxification and cell wall degradation, leading to the activation of other defense proteins in the Microbe-associated molecular pattern (MAMP) pathway (73). A type of protease inhibitor called subtilases which is upregulated in 'Dusa' plays a crucial role in inducing hypersensitive responses as a defensive technique, resulting in localized cell death to prevent pathogen spread (74). In 'Dusa', genes of *P. cinnamomi* genes encoding receptors such as kinases and apoplastic proteases were highly upregulated constituting an important part of the pathogen sensing mechanism in plants (75).The nested qPCR assay facilitates the quantification of pathogen infection, while the double-phase plant hormone profile facilitates the expression of pathogens-related genes via the NPR 1 defense response pathway. Molecular markers like Single Nucleotide Polymorphisms (SNPs) have been used to estimate genetic diversity, construct high-density linkage maps and genotype rootstocks with varying levels of resistance to *Phytophthora*, to some extent (76). Variations in the number of differentially expressed genes in response to *P. cinnamomi* indicate that the resistant rootstock 'Dusa' remained active in defense-related pathways at 12 and 24 hours post-inoculation, whereas R 0.12 exhibited an early breakdown in the defense mechanism by shifting focus to growth and development pathways (77). Increased expression of effector proteins such as Necrosis and Ethylene-inducing peptide 1-like protein (NLPS) and Crinkling and Necrosis Effectors (CRNS) in R 0.12 is crucial for the enhancement of pathogen virulence, leading to higher vulnerability levels (78).

Impact and resilience of white root rot with pathogen dynamics and soil health practices: The disease is caused by *Rosellina necatrix* (Dematophora root rot) belonging to the order Xyrlariales and division Ascomycota. It is one of the most devastating diseases affecting the woody species in tropical and sub-tropical regions of the world (79). This soil-borne fungus thrives in humid, poorly drained and waterlogged soils**,** which create ideal conditions for mycelial growth and root infection (80). The fungal pathogen penetrates roots of Avocado through natural openings and wound infections, causing aerial symptoms such as premature defoliation, wilting, chlorosis and dieback of twigs, branches. Symptoms observed include damaged roots with white cottony mycelium and release of toxins, ultimately leading to root rot (81). Similar disease symptoms have been attributed to another saprophytic fungi belonging to the Basidiomycota division called *Irpex rosettiformis*, reported in Hass Avocado trees at Michoacán, México. This pathogen was characterized using molecular markers (82) and the its data were deposited in gene banks.

The BG83 genotype exhibited consistent gas exchange parameters throughout the progression of the disease, indicating its ability to mitigate the pathogen's effects compared to 'Dusa'. The increased values of WES (A/gs) serve as an effective strategy for minimizing water loss (83). Mild WS-induced plants (50 %), also referred to as primed plants, exhibited improved tolerance to white root rot, with significantly reduced values of Area under the disease progress curve (AUDPC) and delayed onset of external visible symptoms (84). Studies conducted on tolerant rootstocks such as BG 48 and BG 181 demonstrates water-saving mechanisms that maintains leaf water potential and hydraulic conductance, involving defense mechanisms and physiological pathways similar to those activated during water stress (85). Effective traits such as stomatal density, partitioning of assimilates and genetic expression related to osmoprotectants could be valuable strategies for withstanding *R. necatrix* infection.

Comparative analysis of gene expression and defensive responses tolerant to white root rot: Recent studies have shown that *Raffaelea lauricola* possesses a broad range of genes linked to pathogenicity, including genes associated with enzymatic activities that alter the host's defense mechanisms and increase the pathogen's level of virulence (86). Upregulation of six defensive- related genes was observed under water-stressed conditions, including protease inhibitors, glutathione-S-transferase, metallothionein-like protein, Nascent polypeptide-associated Complex (NAC) domain-containing protein 72, universal stress proteins and Miraculin (87). Mild WS-primed plants exhibited repression of certain genes such as Nonexpressor of Pathogenesis-Related 1(NPR 1) and PR 5, attributed to ABA signalling which influences salicylic acid pathways (88). This repression may facilitate the osmotic adjustment as a defense technique. It acts as a dual response that can either enhance tolerance by promoting rapid recovery from water stress and restoring photosynthetic performance thereby preventing susceptibility to pathogens such as *R.necatrix* (84).Avocado plants release toxins such as cytochalasin and rosnecatrone in response to fungal culture filtrates from *R.necatrix*, which trigger defense mechanisms. These responses include the release of antifungal compounds like paclitaxel and podophyllotoxin. (89). Gene expression studies show that resistant callus lines exhibit more controlled and efficient responses, indicated by a lower number of differentially expressed genes (DEG). This is attributed to somaclonal variation with increased enzyme activity related to lignin synthesis, which strengthens the cell wall and increase resistance (90). Pathogenesis-related proteins such as PR-4, thaumatin-like proteins (PR-5) and transcriptional factors known as WRKY (named after WRKYGQK amino acid sequence)and NAC are induced at 1.5 fold higher levels to regulate the plant defense response in resistant lines (91). Additionally, protease inhibitor genes and ethylene response transcription factors were more highly expressed in resistant callus line L-3 compared to the susceptible AN-9 line (92).The gene expression and defensive mechanisms expressed by susceptible 'Dusa' and resistant 'BG 83' rootstock in response to white root rot infection is illustrated in Fig. 4.

Deciphering verticillium wilt by pathogen behavior and holistic management strategies

The causal agent *Verticillium dahliae* is one of the most important soil-borne pathogens, with wide range of hosts over 200 plant species (93). This disease is considered to be very difficult to control since as the pathogen survives in the soil as dormant resistant spores called microsclerotia and lacks effective management practices (94). A report on *V.dahliae* causing wilt in avocado was recorded for the first time in Turkey where the cv. Hass grafted onto Fuerte rootstock showed dieback symptoms with internal bark discoloration. The presence of pathogen was confirmed through reisolation and sequencing of the Internal Transcribed Region (ITS) of rDNA using ITS1/ITS4 primers (95). The fungus penetrates the roots of susceptible plants and reaches the vascular system, interfering with the water transport in the xylem vessels (96). It also produces toxins like verticillins and other compounds that disrupts plant cell functions, leading to wilting and necrosis (97). The symptoms of *V.dahliae* include sudden wilting and dieback of single or multiple branches, accompanied by discoloration in vascular tissues; and in severe cases, wilting of inflorescence is also observed (98). Differences in Rootstock performance in response to wilt infection indicate genetic variability, that could be used as a successful strategy for exhibiting tolerance against *V.dahliae,* thereby decreasing tree mortality and loss in productivity.VC 804 demonstrated fewer visible damage symptoms with reduced proportion of tree loss when compared to other rootstocks (99). Nonetheless, further studies are essential to understand the mechanisms underlying rootstock tolerance against wilt conditions. The prominent stress tolerant genes in biotic and abiotic stress conditions identified in resistant rootstocks are mentioned in Table1.

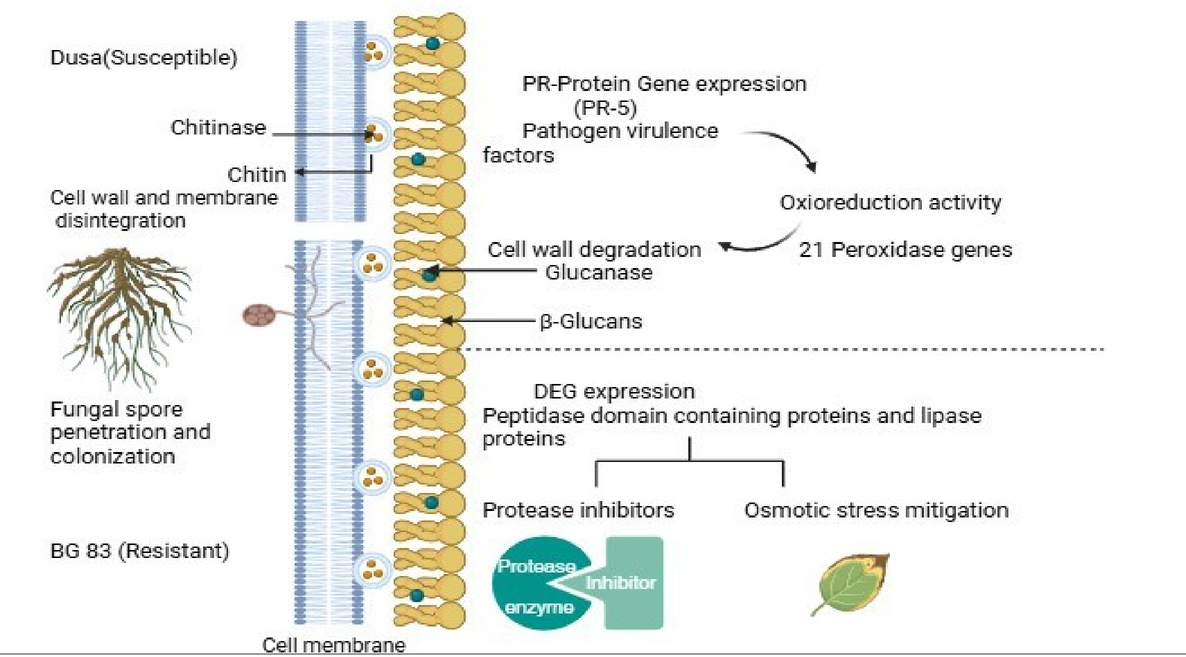

Fig. 4. Pathogenesis-related genes were in greater numbers for susceptible rootstock 'Dusa' stimulating the upregulation of chitinase, glucanase, peroxidase and specific proteins leading to the oxioreduction process with cell wall degradation (100). In contrast, resistant rootstock BG 83 had more stable defense mechanism with the presence of protease inhibitors, glu protease, trypsin, endopeptidase inhibitors and upregulation of genes related to osmotic stress with no visible symptoms even after 30 days (83) (Created in BioRender.com).

Table 1. Genes associated with biotic and abiotic stress tolerance in resistant avocado rootstocks

Stress factor	Genes involved	Function	Reference
Poorly aerated soils	Pa_Sin_GI32N0T02IUGTU	Induces ethanol fermentation under hypoxia conditions, regenerating NAD+ and maintaining ATP production.	(44)
	Pa_Contig00411	Regulates glycolysis under low-energy conditions, augmenting carbohydrate metabolism under waterlogging.	
	MRP: Pa[a]_Contig06346	Facilitates detoxification and stress adaptation.	
Drought	NAC[b]: Pa_Contig00313 (12.71 FC), Pa_Contig03450 (5.30 FC), Pa_Contig01191 (4.15 FC)	Managing drought-responsive genes, including those involved in root development and stress signaling.	(49)
	MYB[c] : Pa_Contig03985, Pa_Contig05714	Modulates hormonal signaling and lateral root growth under drought stress.	
	WRKY[d] : Pa_Contig03801, Pa_Contig04109	coordinated with biotic and abiotic stress signalling pathways.	
	NCED[e] : Pa_Sin_GI32N0T02JL4B4, Pa_Sin_HA66E9C01AOCH8	Key enzymes in ABA biosynthesis, promoting stomatal closure and osmotic adjustment.	
	Small HSP[f] : Pa_Sin_FZ03KKT01BNH1K, Pa_Sin_HA66E9C01AIWJ3	Inhibits protein denaturation and aggregation under drought-induced oxidative stress.	
Root rot	RLKs[g] : DUF26	expressed in early and late infection stages with signaling defense responses.	(75)
	LRR[h] : I, VIII and XII	Expressed during preliminary pathogen recognition.	
	WAKs[i] :	Stabilizing cell walls and signal defense responses.	
	PR1, PR3, PR5[j] :	Antifungal activity and strengthening cell wall defenses.	
	Extensins	Reinforce the extracellular matrix to block pathogen entry.	
	Metallothionein-like genes	Takes part in ROS scavenging and detoxification.	(76)
	GST[k]	Functions in redox regulation.	
	Callose Synthase	Implicated in callose deposition as a barrier against pathogen ingress.	
White Root Rot	Pag44234	Basic endochitinase-like protein (cell wall degradation of pathogens).	(92)
	Pag191108	Lignin-forming anionic peroxidase (critical for cell wall fortification).	
	Pag378827	Cytochrome P450 704B1 (detoxifies reactive oxygen species).	
	Pag296108	MYC2-like protein (key in jasmonic acid signaling).	

[a]Multidrug Resistance Protein, [b]Nascent polypeptide-associated Complex Domain-Containing Proteins, [c]Oncogenes Transcription Factors of Myeloblastosis family, [d]Transcription Factors comes from WRKYGQK amino acid sequence, [e]9-cis-Epoxycarotenoid Dioxygenase, [f]Heat Shock Proteins , [g]Receptor-Like Kinases, [h]Leucine-Rich Repeat , [i]Wall-Associated Kinases, [j]thaumatin-like proteins

Conclusion

Avocado cultivation faces various biotic and abiotic challenges that can significantly affect productivity, making the selection of appropriate rootstocks crucial for mitigating these stresses. Distinct avocado races exhibit varying levels of tolerance to these stress factors, with Mexican and West Indian rootstocks generally performing better than Guatemalan rootstocks under specific conditions. Emphasizing a narrow range of rootstocks and the continued use of homogenous farming practices can aggravate stress on rootstocks, making the ecosystem less resilient. The current review exemplifies rootstock-scion interactions and the genetic regulation of plant responses in attenuating biotic and abiotic stress factors. There is a need for long-term studies in rootstock innovations, integrating effectively with precision agriculture technologies and molecular breeding techniques ensuring sustainable avocado cultivation. The comparison of biotic and abiotic stress resistance among the avocado rootstocks is presented in Fig. 5.

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Authors' contributions

GS contributed to the collection of articles and formulated the concept. SKA prepared the draft for the review. AJ and SA compiled the references. KM and MI corrected and revised the manuscript. All the authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

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Salinity	R 0.05	PP40	R 0.18	Dusa	PP 4	PP 24	R 0.07	PP14	PP45	R0.06
	R 0.17	R 0.16	VC 840	VC 802	Degania 189	VC 801	VC 207	Degania 62	Nachlat 3	VC 320
	VC 55	VC 66	VC 96	VC 28	VC 140	VC 159	VC 55	VC 804	VC 68	VC 152
Root rot	Topa Tope	QUIQUI-0303	Bolivar	Caldas	Cauca	Cesar	Huila	Meta	Narino	Quindo
	Santander	Tolima	Valle del Cauca	NATU-011	CANO-0808	R 0.12	R 0.10	R 0.06	María Elena	Bola
Verticillium wilt	Latas	VC152	VC66	VC162	VC140	VC26	VC27	VC28	VC840	Gallo3
	VC55	VC159	VC320	Waldin	Degania 62	VC 207	VC 802	VC 804	Dusa	Degania 189
Calcareous and alkaline soils	Thomas	Topa-Topa	Gallo3	Julian	Gallo 2	225				
Laural wilt	Nabal	Zutano	Waldin	Duke-7						
White root rot	BG 83	Dusa								
Poorly aerated soils and waterlogging	Black-Beauty	Hung-Hsin-Yuan								

Susceptible | Moderately Tolerant | Tolerant

Fig. 5. Resistant status of different avocado rootstocks.

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