

Review

Research Progress on the Effect of Grafting Technology on Disease Resistance and Stress Resistance of Watermelon

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Abstract

Grafting is an effective horticultural technique that significantly enhances disease resistance and stress tolerance in watermelon. This review systematically summarizes the types of rootstocks used in watermelon grafting and analyzes the effects of grafting on plant responses to biotic stresses, such as viral and fungal pathogens, root-knot nematodes infections, and abiotic stresses, including drought, temperature extremes, and salinity. Furthermore, it discusses the changes in fruit quality and explores the underlying mechanisms associated with graft-induced resistance. By synthesizing recent research advances, this review aims to offer valuable insights and practical references for improving resistance and promoting sustainable production in cucurbit and other vegetable crops through grafting. As a sustainable cultivation strategy, grafting demonstrates considerable potential for enhancing watermelon resilience and yield; however, optimizing fruit quality remains a critical focus for future research.

Keywords: watermelon; grafting; biotic stress; abiotic stress; quality



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1. Introduction

Grafting, a horticultural technique that enhances crop resistance and yield by integrating selected rootstocks and scions, is extensively utilized in agricultural production [1–3]. It has proven particularly effective in enhancing the productivity and quality of cucurbit vegetables, such as watermelon, in many countries [4].

During long-term domestication and selective breeding focused on fruit appearance and yield, watermelons have experienced a significant decline in innate stress tolerance. Biotic stresses, such as Fusarium wilt, pose a serious threat to production. Similarly, abiotic challenges, including drought, salinity, and temperature extremes, substantially constrain watermelon growth and quality [5–9]. Grafting technology offers a viable solution to enhance watermelon resistance to both biotic and abiotic stresses [10] (Figure 1).

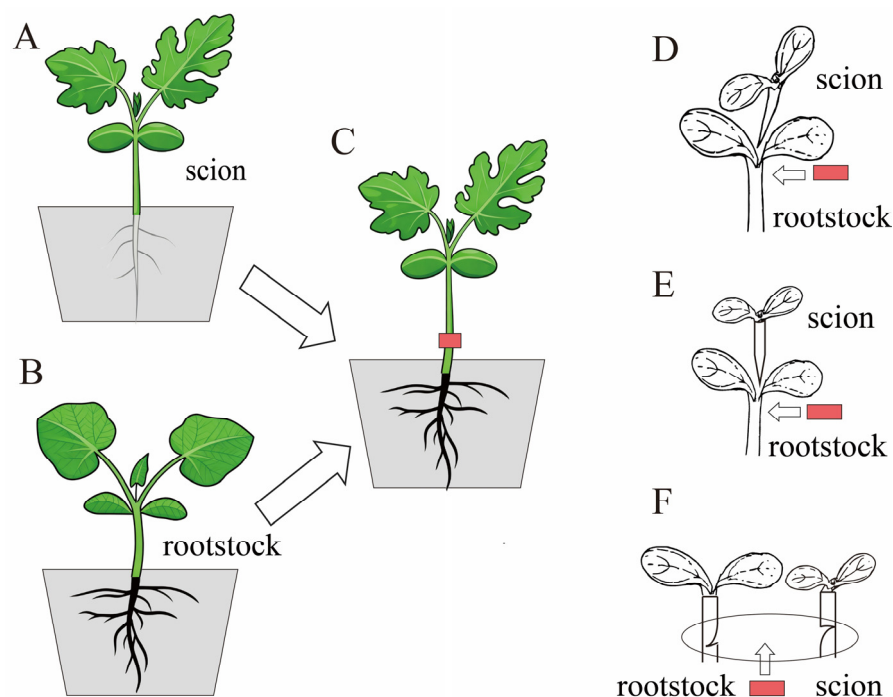


Figure 1. The main steps of watermelon grafting and suitable grafting methods. (A) Watermelon seedling was used as scion. (B) Rootstock seedling. (C) Grafted watermelon seedling after the process. (D–F) represent the three commonly used grafting methods suitable for watermelon. (D) Top-inset grafting: A sharp tool is used to pierce the stem at the growing point of the rootstock without penetrating it. The scion is then inserted, positioning the cotyledons of the scion and rootstock in a cross shape relative to each other. (E) Cleft grafting: A blade is used to make a vertical incision approximately 1–1.5 cm long at the growing point of the rootstock. The scion is inserted into the incision and secured using a grafting clip or tube. (F) Approach grafting: After removing the growing point of the rootstock, a downward incision of approximately 1 cm in length was made with a blade. The scion was prepared with an upward slanting cut of approximately 1 cm. The scion and rootstock are then fitted together and secured with grafting clips or tubes. The red rectangles in the figure indicate the positions of the graft clips or tubes.

This paper systematically reviews the effects of grafting technology on disease resistance (including viruses, fungal, and root-knot nematodes), stress resistance (such as drought, temperature, and salt stress), and fruit quality of watermelon. Furthermore, it summarizes the underlying mechanisms through which grafting confers enhanced disease and stress resistance. The aim is to provide a reference for both theoretical research and practical applications aimed at improving resistance in watermelon and other cucurbit vegetables by grafting technology.

2. Grafting Affects the Tolerance of Watermelon to Biotic Stress

2.1. Virus Disease

There are several virus diseases for watermelon such as watermelon mosaic virus (WMV), watermelon curly mottle virus (WCMV), melon yellow spot virus (MYSV), melon necrotic spot virus (MNSV), papaya leaf distortion mosaic virus (PLDMV), papaya ringspot virus watermelon strain (PRSV-W), cucumber green mottle mosaic virus (CGMMV), melon aphid-borne yellows virus (MABYV), and *Citrullus lanatus* cryptic virus (CiLCV) [9,11,12].

Although reports on the use of grafting to mitigate viral diseases in watermelon remain limited, some studies indicate that grafting can enhance plant resistance to certain viruses (Table 1). This protective effect depends on the choice of rootstock with antiviral properties. Selecting appropriate rootstocks can significantly restrict viral spread and replication within

plants. For example, grafting increased watermelon production by 115% in fields infected with MNSV [13]. In another study, Ref. [14] reported that grafting watermelon onto a hybrid squash rootstock (RS-841) significantly improved scion resistance to MNSV.

Table 1. Effects of grafting on biotic stress resistance of watermelon.

Type of Stress	Rootstock		Scion	Resistance	References
Virus	<i>Cucurbita maxima</i> × <i>C. moschata</i>	RS841, Shintosa Camelforce	Tri-X 313	Increased yield; fruit firmness increased, but did not affect the soluble solids content.	[13]
	<i>Cucurbita maxima</i> × <i>C. moschata</i>	RS-841, Ercole	Mielheart	Significantly increased the resistance of scions to MNSV.	[14]
	<i>Citrullus lanatus</i> var. <i>citroides</i>	Robust			
	<i>Citrullus mucosospermus</i>	938-16-B	938-16-B, H1, Hongzi	Resistant to virus disease.	[15]
	<i>Citrullus lanatus</i>	H1, Hongzi		Susceptible to viral diseases.	
Fungus	<i>Cucurbita moschata</i>	Landrace	Crimson Tide	The incidence rate was reduced by 88–100%, and even completely controlled.	[16]
	<i>Cucurbita maxima</i>	Landrace			
	<i>Lagenaria siceraria</i>	Landrace			
	<i>Luffa cylindrica</i>	Landrace			
	<i>Benincasa hispida</i>	Landrace			
	<i>Lagenaria</i> hybrid	216, Emphasis, Skopje, FR Gold			
	<i>Cucurbita</i> hybrid	P360, Strong Tosa			
	<i>Lagenaria siceraria</i>	USVL482-PMR, USVL351-PMR	Mickey Lee	Significantly enhance the resistance of the scion to powdery mildew.	[7]
	<i>Lagenaria siceraria</i>	Chaofengkangshengwang	Sumi 1	High resistance to Fusarium wilt, and the incidence was only 3.4%.	[6]
	<i>Cucurbita maxima</i> × <i>C. moschata</i>	Tetsukabuto	Secretariat	Resistance to verticillium wilt.	[17]
	<i>Citrullus lanatus</i> var. <i>citroides</i>	IIHR-82, IIHR-617, BIL-53	NS-295	Resistance to gummy stem blight.	[18]
	<i>Lagenaria siceraria</i>	BG-95, BG-77-6-1			
	<i>Citrullus lanatus</i> var. <i>citroides</i>	IIHR-617 × Arka Manik, IIHR-82 × Arka Manik, IIHR-82 × IIHR-617			

Table 1. Cont.

Type of Stress	Rootstock	Scion	Resistance	References
Fungus	<i>Cucurbita maxima</i> × <i>C. moschata</i>	Nun 6001, Strongtosa, Tetsukabuto, Ferro, Shintoza	Aswan F1	Enhance disease resistance. [19]
	<i>Lagenaria siceraria</i>	IT207112	Sambokkul	Resistance to Fusarium wilt, single spore root rot, and vine recession. [20]
	<i>Lagenaria siceraria</i>	FRD22		Moderate resistance to single spore root rot and vine decline disease.
Nematodes	<i>Lagenaria siceraria</i>	Emphasis, WMXP 3938, WMXP 3944, WMXP3445	Fiesta, Tri-X 313	Significantly reduce the root knot rate and infection level; increase production. [21]
	<i>Cucurbita moschata</i> × <i>C. maxima</i>	Strong Tosa		Significant nematode resistance in field trials.
	<i>Citrullus lanatus</i> var. <i>citroides</i>	RKVL 301, RKVL 302, RKVL 303, RKVL 315, RKVL 318, Ojakkyo		Significant resistance; root knot index and nematode reproduction were low.
	<i>Cucumis africanus</i> , <i>Cucumis myriocarpus</i>		Congo, Charleston Gray	Resistance to root-knot nematodes. [22]

Previous research has shown that grafting can generally enhance the overall virus tolerance of seedless watermelons [23]. However, their efficacy entirely depends on the rootstock selected. It is also important to note that grafting cannot cure existing viral infections. For certain viruses, such as CGMMV, infection present in the scion before grafting will persist post-grafting [23]. Therefore, the selection and use of highly resistant rootstocks are essential for effective viral disease management.

Furthermore, the development of antiviral rootstocks through genetic engineering represents a promising research direction [24]. Transgenic rootstocks resistant to CGMMV have been successfully developed by introducing cDNA encoding the viral coat protein gene [25]. Notably, antiviral transgenic rootstocks engineered via RNA silencing technology can confer systemic resistance to susceptible scions grafted onto them [26]. This advancement presents new opportunities for integrated management of watermelon viral diseases through grafting in future agricultural practices.

2.2. Fungal Diseases

Fusarium wilt, gummy stem blight, colletotrichum orbiculare, and powdery mildew are the principal fungal diseases that pose serious threats to watermelon production [8,27]. Grafting is recognized as an effective management strategy for these diseases, particularly those caused by soil-borne pathogens [3] (Table 1).

The selection of resistant rootstocks, such as bottle gourds, pumpkins, and wild watermelons relatives, can significantly improve scion resistance to Fusarium wilt. Grafting onto these rootstocks has been shown to substantially reduce disease indices and incidence rates. In some cases, grafting can eliminate the disease entirely; one study reported 100% and 88% reductions in Fusarium wilt occurrence in grafted plants compared to non-grafted seedlings [16]. Furthermore, Ref. [28] indicated that grafting can modulate the rhizosphere bacterial community. By utilizing core bacterial strains isolated from the roots of grafted plants, they successfully constructed a synthetic beneficial microbial that enhanced both growth and disease resistance in non-grafted watermelons cultivated in non-sterilized soil.

Therefore, selecting rootstocks with inherent resistance is a critical component for improving fungal disease management in grafted watermelons. Ref. [7] grafted the scion cultivar ‘Mickey Lee’, which is susceptible to powdery mildew, onto 25 watermelon cultivars and four gourd rootstocks. The results demonstrated that specific gourd rootstocks (USVL482-PMR and USVL351-PMR) conferred a significantly higher level of powdery mildew resistance to the scion than watermelon rootstocks.

2.3. Root-Knot Nematode

Watermelon root-knot nematode disease, primarily caused by *Meloidogyne* spp. (especially *Meloidogyne incognita*), poses a significant challenge to watermelon production worldwide [29]. This pathogen damages the root system by forming galls or root nodules. These structures result in shortened roots, impaired root development, and reduced root activity [30,31]. The corresponding above-ground symptoms include plant stunting, leaf curling, yellowing, and wilting [32,33], which can lead to plant death in severe cases. Consequently, plant growth and vigor are compromised, leading to reduced fruit set, lower yields, and inferior fruit quality (Table 1).

Chemical control of root-knot nematodes often shows limited efficacy due to their adaptability, while also posing environmental risks and potential for resistance development [34]. Consequently, grafting has been developed as a viable management strategy for this disease [3,35]. This technique involves grafting susceptible watermelon scions onto rootstock cultivars that are resistant to root-knot nematodes, thereby controlling infection [21].

Certain varieties of bottle gourd (*Lagenaria siceraria*) and interspecific hybrid pumpkin (*Cucurbita moschata* × *C. maxima*) have been identified as effective resistant rootstocks for this disease. Their use significantly reduces nematode infection levels and root gall formation while improving watermelon yield [21]. Field trials have demonstrated high resistance in rootstock cultivars such as ‘Emphasis’, ‘Carnivor’ and ‘Strongto’. Resistance has also been reported in wild watermelon (*Citrullus amarus*) and some wild cucumber resources (e.g., *Cucumis myriocarpus*), suggesting their potential as rootstocks [22]. Germplasm resources of *Citrullus lanatus* var. *citroides* represents another source of potential rootstock material with resistance to root-knot nematodes [36]. The RKVL rootstocks series, developed by the United States Department of Agriculture from wild watermelons, has shown superior performance against nematodes compared to commercial rootstocks and non-grafted plants. Under field conditions with high nematode pressure, the root-knot rates for RKVL rootstocks were 9–16%, which was significantly lower than the 41% rate observed in non-grafted cultivars [37].

3. Grafting Affected the Tolerance of Watermelon to Abiotic Stress

3.1. Drought Stress

Drought stress presents a significant challenge to plant cultivation, particularly for high-water-demand crops, like watermelon, in arid and semi-arid regions. Grafting commercial varieties onto drought-tolerant rootstocks offers a potential strategy for mitigating these challenges. Tolerant rootstocks typically develop more extensive root systems, facilitating more efficient absorption of soil water and nutrients, thereby providing a stronger foundation for the scion under water-deficit conditions [38] (Table 2). Under continuous severe water stress, non-grafted watermelon plants can suffer yield losses of up to 40%, a consequence of reduced single-fruit weight and a lower fruit set [39,40].

Table 2. Effects of grafting on abiotic stress resistance of watermelon.

Type of Stress	Rootstock		Scion	Resistance	References
Drought stress	<i>Lagenaria siceraria</i>	Illapel, Osorno, GC	Santa Amelia	Drought tolerance, significantly increased yield; improve root structure.	[10]
		BG-48, Philippines		Not drought-tolerant.	
	<i>Cucurbita maxima</i> × <i>C. moschata</i>	Shintoza	Crimson Sweet	Better growth performance and water status.	[41]
	<i>Citrullus colocynthis</i> (L.) Schrad	Esfahan		Better drought resistance, growth and biomass decreased less, and showed higher antioxidant activity and lower oxidative stress.	
	<i>Cucurbita moschata</i>	Naihan 1		Up-regulation of CITCP4 gene expression in scions helped to maintain higher photosynthetic efficiency and cell membrane stability.	
	<i>Lagenaria siceraria</i>	Jingxinzheng 1	Zaojia 8424	Better growth performance.	[43]
	<i>Cucurbita maxima</i> × <i>C. moschata</i>	Qingyanzheng 1			
	<i>Citrullus lanatus</i> subsp. <i>mucosospermus</i>		Crimson Sweet	Improve the ability to resist water stress, improve growth and yield.	[38]
	<i>Cucurbita maxima</i> × <i>C. moschata</i>	Strong Tosa	Crimson Tide F1	Enhance drought tolerance.	[44]
	<i>Citrullus lanatus</i> var. <i>citroides</i>		Crimson Tide	Enhance drought tolerance and affect physiological characteristics and nutrient uptake.	[45]
	<i>Cucurbita maxima</i> × <i>C. moschata</i>	TZ-148			
	<i>Citrullus lanatus</i> var. <i>citroides</i>	A1, A2	Crimson Tide	Enhance drought tolerance.	[46]
<i>Cucurbita maxima</i> × <i>C. moschata</i>	TZ-148	Enhance drought resistance and improve fruit quality.			
Temperature stress	<i>Lagenaria siceraria</i>	FR79	Sambokkul	Tolerance to low temperature, little effect on fruit quality.	[20]
	<i>Lagenaria siceraria</i>	0526, 2505	Zaojia 8424	Enhance cold resistance.	[47]
	<i>Cucurbita maxima</i> × <i>C. moschata</i>	Qingyan No. 1	97103	Enhance cold resistance.	[48,49]
	<i>Cucurbita moschata</i>	Weizhen No. 1	Nongkeda No. 5	Enhance cold resistance.	[50]
	<i>Cucurbita ficifolia</i> Bouché	Cf			

Table 2. Cont.

Type of Stress	Rootstock		Scion	Resistance	References
Salt stress	<i>Lagenaria siceraria</i>	Chaofeng Kangshengwang	Xiuli	Enhance salt tolerance.	[51–54]
	<i>Cucurbita maxima</i>	Cma	Crimson Tide	Enhance salt tolerance.	[55]
	<i>Lagenaria siceraria</i>	Skp, Birecik			
	<i>Citrullus lanatus</i>	Jingxin No. 2	Jingxin No. 2	General salt tolerance.	[56]
	<i>Cucurbita moschata</i>	Quanneng Tiejia		General salt tolerance.	
		Kaijia No. 1		High salt tolerance.	
	<i>Lagenaria siceraria</i>	Hanzhen No. 3		High salt tolerance.	
	<i>Citrullus lanatus</i>	Zhongyu No. 9 tetraploid	Zhongyu No. 9	Enhance salt tolerance.	[57]
	<i>Lagenaria siceraria</i>		<i>C. lanatus</i>	Enhance salt tolerance.	[58–60]
	<i>Cucurbita maxima</i> × <i>C. moschata</i>	Shintosa F-90	<i>C. lanatus</i>	Enhance salt tolerance.	[58]

The use of drought-resistant rootstocks enhances the ability of grafted watermelon plants to both avoid and tolerate drought stress. Physiological improvements include the maintenance of a high leaf relative water content and improved water-use efficiency (WUE) [44]. This is partly achieved through the rapid adjustment of the stomatal aperture to control transpiration [41,45]. Furthermore, grafting induces beneficial molecular and biochemical changes in the host. For example, grafting onto the pumpkin rootstock ‘Naihan 1’ upregulates CITCP4 gene expression in the watermelon scion. This genetic change is associated with a 38% increase in the net CO₂ assimilation rate and a 45% reduction in malondialdehyde (MDA) levels, indicating enhanced photosynthetic capacity and greater cell membrane stability [42], respectively.

Ref. [61] provided key multi-omics data on the variation in genes and metabolites under drought stress, which is important for understanding the mechanisms underlying graft-induced drought resistance. Additionally, grafted plants exhibit significantly higher antioxidant enzyme activity during drought stress. Concurrently, indices of oxidative damage were markedly lower in these plants than in self-rooted watermelon [41].

Field trials have confirmed the influence of rootstock type on the extent of increased drought resistance. Commercial pumpkin hybrid rootstocks (*Cucurbita maxima* Duch. × *Cucurbita moschata* Duch. rootstock ‘Shintoza’) [41,43] and other types of bottle gourd rootstocks, such as ‘Illapel’ and ‘Osorno’ [10], can effectively increase the yield of grafted watermelon under drought or less water conditions.

3.2. Temperature Stress

Watermelon is a thermophilic crop, and it is highly sensitive to low temperatures stress (Table 2). Low-temperature stress can seriously affect plant growth and development, interfere with plant physiological functions, and even result in plant death [47,48]. For instance, when post-planting temperatures remain around 2 °C for 14–15 h, watermelon yields can decrease by more than 10% [62]. The grafting technique is widely used to improve the low-temperature resistance of watermelon.

Grafting watermelon onto pumpkin rootstocks improves chilling resistance by maintaining higher chlorophyll content and photosynthetic rates under cold stress. Additionally, they exhibit a significant reduction in MDA content, indicating diminished cell membrane damage due to cold stress [47,49]. Typically, low temperatures suppress the activity of antioxidant enzymes in watermelon, adversely affecting photosynthesis and root develop-

ment [47,63]. However, grafting significantly enhances the capacity of plants to eliminate reactive oxygen species (ROS), thereby mitigating oxidative damage. This enhancement is closely associated with the dynamic interactions between ROS and salicylic acid (SA), which may be a key mechanism underlying grafting-induced cold tolerance [49]. Further studies have indicated that pumpkin rootstocks improves cold resistance in watermelon seedlings by promoting the accumulation of melatonin and methyl jasmonate (MeJA) and increasing the levels of hydrogen peroxide (H_2O_2) [50].

Transcriptome analyses revealed that grafting altered the expression of many low-temperature-related genes in watermelon seedlings. This provides a molecular basis for better survival and growth under low temperatures [64]. For example, pumpkin rootstocks upregulate the arginine decarboxylase (ADC) gene, leading to the production of more putrescine, which helps mitigate the harmful effects of low temperatures [65]. Grafting can also alter the expression of genes related to the Calvin cycle, further enhancing cold adaption [47]. Insights from muskmelon studies suggest that miRNA-mediated gene regulation may also contribute to enhanced cold tolerance [66].

However, it is also necessary to mention that there are many differences in cold tolerance among various rootstocks. Rootstocks with good cold tolerance, such as the bottle gourd varieties '2505' and '0526', help improve the cold tolerance of grafted watermelons [47]. Grafting onto bottle gourd rootstocks can enhance cold tolerance, particularly during early growth stages, without compromising fruit commercial quality [20].

Elevated temperatures resulting from global warming have emerged as a significant threat to the yield and quality of watermelon [67]. Although systematic studies on heat tolerance in grafted watermelon remain limited, existing evidence have indicated their potential advantages. Grafting has been shown to have a beneficial effect on cucumber yield under combined stress conditions (heat and salt) [68]. Rootstocks, mostly pumpkin or bottle gourds, generally feature more extensive root systems with superior water and nutrient uptake capacity, which helps maintain plant water status under high-temperature conditions and indirectly enhances heat [69].

3.3. Salt Stress

Soil salinization is a major abiotic factor that affects the yield of crops worldwide (Table 2). In watermelon, salt stress leads to growth inhibition, osmotic stress, ion toxicity, and secondary oxidative stress, collectively limiting plant development and productivity [51,70–74]. Research indicates that grafting salt-tolerant rootstocks is an effective strategy for enhancing salt stress tolerance [51].

Variations in salt tolerance mechanisms are observed among different rootstocks, such as the Na translocation strategy [55,56,75,76]. Pumpkin rootstocks, such as 'Kaijia No. 1', showed much better salt tolerance [56]. Interestingly, autotetraploid watermelon rootstocks showed more salt-stress tolerance than diploid watermelon rootstocks, suggesting that autotetraploid watermelon may have a larger ion transportation capability of K^+ and Na^+ accumulation for its replication genome to enhance these functions, including ion absorption/transportation adjustment ability and antioxidant capability [57].

Grafting with salt-resistant rootstocks enhances plant salt resistance through 'ion exclusion' mechanisms, whereby Na^+ transport from roots to shoots is restricted. This significantly reduces Na^+ accumulation in leaves and helps maintain a balanced K^+/Na^+ ratio in scion tissue [75]. For example, watermelons grafted onto bott gourd rootstock showed much less accumulation of Na^+ and significantly maintained leaf ion levels (the K^+/Na^+ ratio) in a balanced range, and also preserved stable cell osmotic pressure [56,58], with an accumulation of osmotic adjustment substances, such as soluble sugars [55].

In addition, under salt stress, grafted plants maintain or enhance the activity of antioxidant enzymes in leaves [51–53]. This increased enzymatic activity mitigates reactive oxygen species (ROS) overproduction and reduces oxidative damage, including membrane lipid peroxidation, thereby protecting cellular membrane integrity and function [51,77].

Transcriptomic and proteomic analyses have revealed a comprehensive molecular network activated by grafting, which may represent an adaptive response initiated by alterations in the local hormonal balance. Ref. [51] studied that 8462 differentially expressed genes were identified in grafted watermelon seedlings under salt stress, demonstrating that grafting onto gourd rootstock significantly alleviated salt-induced growth inhibition and photosynthetic decline. This widespread transcriptomic reprogramming likely reflects the systemic adjustments triggered by rootstock-induced hormonal signals. Similarly, proteomic analyses have indicated that grafting and/or salt stress alters the expression of 40 proteins involved in key processes, such as the Calvin cycle, amino acid biosynthesis, sugar and energy metabolism, ROS defense system, and hormone signaling pathways [54]. Ref. [59] further reported that grafting onto gourd rootstock led to dynamic changes in at least 12 proteins under prolonged 50 mmol/L NaCl stress. Additional studies have highlighted grafting-induced modulation of salt-responsive genes, including ion transporters (e.g., SOS, HKT1, NHX1, and PMA) and transcription factors, such as NAC and WRKY [51,60]. Moreover, ref. [77] demonstrated that the transcription factor ClaDREB14 positively regulates the peroxidase gene ClaPOD6, enhancing peroxidase activity and contributing to improved salt tolerance in grafted watermelons. These multilevel molecular changes collectively underscore grafting-induced adaptive mechanisms, potentially orchestrated by hormonal rebalancing, which enhances stress resilience.

4. Effects of Grafting on Fruit Quality of Watermelon

Watermelon fruit quality is a multifaceted concept that encompasses several key attributes that influence consumer perception and acceptance. These attributes primarily include appearance characteristics (size, shape, and color), internal quality characteristics (flesh color and texture), nutrients (lycopene and vitamin C), and flavor characteristics (soluble solids, soluble sugars, and organic acids) [78]. Sugar and soluble solid contents (SSC) both affect the sweetness of fruits, and consumer taste is directly influenced. Among them, SSC is an important index for evaluating watermelon sweetness [79–81]. Lycopene is one of the essential pigments that can give red coloration to watermelon but it also works as the antioxidant functions, plays an important role in measuring the nutritional value of watermelons [79,82] (Table 3).

Table 3. Effects of grafting on fruit quality of watermelon.

Rootstock		Scion	Changes in Quality After Grafting	References
<i>Lagenaria siceraria</i>	Yongzhen No. 1, Yongzhen No. 3, Yongzhen No. 8	Zaojia 8424	Increase SSC content.	[80]
<i>Cucurbita maxima</i> × <i>C. moschata</i>	Yongzhen No. 7	Zaojia 8424	Increase fruit weight (SSC content did not change).	[81]

Table 3. Cont.

Rootstock		Scion	Changes in Quality After Grafting	References
<i>Cucurbita maxima</i> × <i>C. moschata</i>	TZ148	Pegasus	The flesh firmness, color and other physical qualities were improved, and the contents of bioactive compounds such as lycopene and citrulline were increased, but the acidity was slightly increased.	[82]
<i>Cucurbita maxima</i> × <i>C. moschata</i>	Super Shintosa		Increase the lycopene content.	
<i>Cucurbita moschata</i>	Marvel	Melody	Increase fruit firmness.	[83]
<i>Cucurbita maxima</i> × <i>C. moschata</i>	Root Power			
<i>Lagenaria siceraria</i>	Macis	Crimson Sweet	Increased the size and rind thickness of fruits.	[84]
<i>Cucurbita moschata</i>	SiZhuang	8424	Improve quality, increase beneficial metabolites, and reduce bitter compounds.	[85]
<i>Cucurbita moschata</i>	Xi Jia Qiang Sheng	Zhongyu No. 1	Increase the total sugar, total amino acid and total acid content.	[86]
<i>Lagenaria siceraria</i>	FR STRONG		Reduce the lycopene content.	
<i>Cucurbita maxima</i> × <i>C. moschata</i>	RS 841	RX 467	Increase the lycopene content.	[87]
<i>Lagenaria siceraria</i>	Jingxinzen No. 1			
<i>Citrullus lanatus</i> var. <i>citroides</i>	Yongshi	Zaojia	Increase the lycopene content.	[88]
<i>Cucurbita maxima</i> × <i>C. moschata</i>	Qingyanzhen No. 1		No effect on lycopene content.	
<i>Cucurbita maxima</i> × <i>C. moschata</i>	Ferro, Nun 6001, Shintoza	Aswan	Increase the lycopene content.	[19]
<i>Cucurbita maxima</i> × <i>C. moschata</i>	TZ148	Pegasus	Increase fruit firmness and citrulline content.	[89]
<i>Cucurbita maxima</i> × <i>C. moschata</i>	Jingxinzen No. 2	97103	Maturity extended.	[90]
<i>Cucurbita argyrosperma</i>	451	Summer Flavor 800, Summer Sweet 5244	Reduce fruit weight, lycopene content (diploid).	[91]
<i>Cucurbita maxima</i> × <i>C. moschata</i>	N101	Pegasus	Increase fruit firmness	[92]
<i>Cucurbita maxima</i> × <i>C. moschata</i>	TZ148, Bombo, N101	Celebration, Gallery, Pegasus, Torpilla	Increase fruit firmness, lycopene content; SSC content decreased slightly.	[93]

Table 3. Cont.

Rootstock		Scion	Changes in Quality After Grafting	References
<i>Cucurbita maxima</i> × <i>C. moschata</i>	Ferro RZ, Nun 9075	Crimson Tide	Increase SSC content, peel thickness, fruit firmness.	[94]
	RS 841, Strong Tosa		Increase lycopene content, peel thickness, fruit firmness.	
<i>Citrullus lanatus</i> var. <i>citroides</i>	BGV0005167	Oneida	Increase fruit thickness, flesh firmness, SSC content.	[95]
<i>Cucurbita maxima</i> VAV 1860 × <i>C. moschata</i> PI 550689	GMM1		Increase fruit thickness and flesh firmness; change the fruit aroma.	
	Cobalt			
<i>Cucurbita maxima</i> × <i>C. moschata</i>	TZ-148	1262	Improve fruit taste.	[96]
	Nurit		Improve fruit taste, increase lycopene and SSC content.	
<i>Lagenaria siceraria</i>	A3	Crimson Tide	Increase the sugar content of fruit.	[46]
<i>Lagenaria</i> spp.	Argentario, 3335	187 × 125, 11 × 162	Increase the SSC content, fruit diameter, peel thickness and fruit weight.	[97]
<i>Cucurbita maxima</i> × <i>C. moschata</i>	TZ148, Nun9075		Increase fruit weight.	

4.1. Soluble Solids Content

Grafting has been observed to potentially reduce SSC and total sugar content. Ref. [95] indicated that the SSC of watermelon fruits grafted onto rootstocks from *Citrullus lanatus* var. *citroides* decrease. Ref. [83] found that fruit quality, including sugar content, of seedless watermelons grafted onto pumpkin rootstocks might be adversely affected. Conversely, some studies have indicated that grafting could enhance the SSC in watermelon, especially on gourd rootstocks, where the SSC increased by 12 to 15% [84,85,98]. Ref. [81] found that grafting pumpkin rootstocks altered the sugar composition and increased the weight of watermelon fruits through the action of invertase and sugar transporters. Transcriptome analyses have shown that pumpkin rootstocks upregulated the expression of genes involved in fructose/mannose metabolism in the flesh, increase the activity of sucrose synthase, and enhance the transfer of carbohydrates into fruits. Furthermore, grafting onto pumpkin rootstocks leads to an optimization of sugar distribution efficiency in sink tissues by regulating key factors such as the sugar transporter SWEET10 [84,85]. The mRNAs exchanged between the rootstock and scion have been implicated in improving watermelon fruit quality, potentially involving the regulation of sugar metabolism pathways [99].

4.2. Organic Acid

Grafting influences organic acid metabolism in watermelon fruits, thereby affecting their quality and flavor. Some studies have indicated that grafting can increase the total organic acids and titratable acidity of watermelon during fruit ripening [82,100]. Different rootstock combinations in grafting experiments showed significant differences in fruit organic acids [80,101]. Regarding specific organic acid types, grafting exerts a regulatory effect on the content of key organic acids such as citric acid and malic acid. In a metabolomic study of pumpkin rootstock-grafted watermelon, 56 primary metabolites were identified,

with notable differences in organic acid profiles between grafted and self-rooted plants. Specifically, citric acid content increased while malic acid decreased, leading to an altered sugar-acid balance in the fruit [86].

The regulation of organic acid accumulation is primarily regulated by key metabolic enzymes. Grafting has the potential to influence the metabolic pathways of organic acids by altering the enzyme activity. For instance, in the ‘Zaojia’ watermelon grafting experiment, variations in the activities of acid invertase (AI), neutral invertase (NI), sucrose synthase (SS), and sucrose phosphate synthase (SPS) were documented. These enzymes play a role in sugar metabolism, and changes in their activity are indirectly associated with the accumulation of organic acids [80].

A comprehensive analysis of transcriptome and metabolome revealed that pumpkin rootstocks modify gene activity in plant biochemical processes. Over 216 chemical compounds differed between non-grafted and grafted watermelon, mainly in flavonoid biosynthesis affecting fruit flavor [85]. Gene networks linked to sugar and organic acid accumulation were identified through transcriptome analysis [102,103]. The translocation of signals between plant parts, including 834 mobile RNAs identified in pumpkin-grafted watermelon, may enhance grafted fruit quality [99].

4.3. Lycopene

Lycopene is a powerful antioxidant, and its increased consumption positively influences human health [104]. Studies have found that lycopene bioavailability in watermelons is higher than that in tomatoes, with an efficiency of more than 60% [105,106]. Many studies on lycopene and its biological activities have verified that lycopene possesses bioactivities, including anti-cancer, antioxidant, anti-aging, and prevention or cure of cardiovascular diseases [107–109].

Specific graft combinations have been shown to increase the lycopene content in watermelon fruits. For instance, grafting watermelon onto interspecific hybrid pumpkin rootstocks increased lycopene levels [87,110]. Similarly, watermelons grafted onto bottle gourd and pumpkin hybrid rootstocks exhibited higher lycopene content than non-grafted controls [88,110]. This enhancement may result from rootstock-mediated transcriptional regulation of lycopene metabolism genes [88]. Comparative analyses further corroborated that grafting combinations can augment lycopene content [111].

Regarding the impact of rootstocks on lycopene content in watermelon, current research findings remain inconclusive. Some studies suggest that different rootstocks can have varying effects on lycopene content due to factors such as the combination of scion and rootstock, planting environment, and fruit maturity. This influence may also differ depending on fruit set conditions and cultivation practices [19,112–114]. However, other studies have indicated that there is no significant difference in lycopene content between grafted and non-grafted watermelon fruits [115].

Grafting also influences the temporal pattern of lycopene accumulation. Research indicates that grafting can delay lycopene accumulation during fruit development, resulting in postponed color peaks in mature fruits [82,89]. This delay may be attributed to the fact that grafting significantly reduced the concentration of abscisic acid (ABA) in the fruit, which is essential for promoting fruit ripening. Reduction in ABA concentration may indirectly affect both the rate of accumulation and final lycopene content [90].

4.4. Physical and Sensory Quality

Grafting, particularly with Cucurbita rootstocks, is widely considered as a method for improving watermelon flesh firmness [82,91,92]. For instance, compared with the non-grafting control, the flesh firmness of watermelon grafted with pumpkin rootstocks

was significantly higher [93]. This increase may be attributed to alterations in the cell wall structure or increased cell density of the fruit flesh [92]. However, not all studies support this finding. Some studies have indicated that grafting does not influence firmness [94,113], and may result in a reduction in firmness under specific rootstock/scion combinations [83,95]. For instance, watermelon is grafted onto zucchini rootstocks [95]. This change often correlates with rootstock genotypes, scion varietal species, and cultivation environments [114].

Beyond flesh firmness, grafting may also affect other fruit quality traits. Several studies have indicated that grafting can increase peel thickness [91], which may extend the shelf life of fruits and enhance their resistance to damage during transportation. Furthermore, grafting onto certain rootstocks may reduce the sensitivity of watermelons to fruit cracking, a condition associated with increased fruit toughness [92]. Regarding fruit morphology, grafting has been found to affect fruit weight and size [96] and increasing the weight of individual fruits [81].

5. Mechanism of Grafting Affecting Disease and Stress Resistance of Plants

5.1. Biotic Stress Resistance

The core of grafting technology in enhancing plant resistance to biotic stress is the synergistic interaction between the rootstock and scion. The selection of appropriate rootstocks is crucial, particularly for conferring resistance against soil-borne pathogens [116,117]. Grafting primarily augments plant disease resistance by facilitating efficient material exchange and long-distance signal transduction between rootstocks and scions [118,119]. This physical connection facilitates the transport of nutrients and hormone signals, and defense-related molecules [120–123]. For instance, jasmonic acid (JA) and its derivatives participate in systemic defense responses. Grafting experiments have demonstrated their involvement in long-distance signal transduction by activating defense mechanisms against herbivores [124]. Similarly, SA acts as a key signaling molecule in systemic acquired resistance (SAR), where its accumulation promotes NPR1 protein activation and confers broad-spectrum disease resistance [125–127].

Grafting can influence activation and regulation of the plant innate immune system. Plants respond to pathogens via pattern-triggered immunity (PTI), mediated by pattern recognition receptors (PRRs), and effector-triggered immunity (ETI), mediated by effector recognition receptors (NLRs) [128]. Rootstocks can transfer signal molecules to scions, thereby enhancing their PTI or ETI response. Moreover, beneficial rhizosphere microorganisms, including bacteria and fungi, can induce systemic resistance (ISR), which may be enhanced or transmitted through grafting to improve plant resistance to pathogens and pests [127,129–131]. ISR largely depends on the modulation of hormone signaling pathways involving JA, ethylene (ET), SA, along with associated gene expression changes [129].

Beyond signal transduction, grafting may induce epigenetic modifications that regulate gene expression without altering the DNA sequence [120,132,133]. For instance, the DNA demethylation observed during eggplant grafting is correlated with increased grafting activity [133]. These epigenetic changes may underlie the long-term enhancement of resistance in grafted plants as they can influence the plant's memory effect regarding stress and its future response capabilities.

Furthermore, grafting can stimulate the production of antioxidant enzymes such as superoxide dismutase, catalase, and peroxidase, which help scavenge reactive oxygen species and alleviate oxidative stress [134,135]. Grafting may influence the accumulation of secondary metabolites that are vital for the defense against pathogens and pests [122,123].

Certain rootstocks enhance the accumulation of secondary metabolites with defensive properties in scions, thereby improving disease resistance [123].

5.2. Abiotic Stress Resistance

The mechanism by which grafting influences plant tolerance to abiotic stress is multifaceted, involving morphological, physiological, biochemical, and molecular adaptations [122,136]. Selecting suitable rootstocks is essential for optimizing morphological and physiological adjustments. Robust rootstock roots can absorb more water and nutrients, thereby effectively improves the stress resistance of the entire plant [117,137,138]. Grafting has been shown to increase the photosynthetic efficiency and water-use efficiency of crops [139]. Under drought stress, grafted cucumber plants exhibit significantly less damage in scions, indicating that rootstocks can effectively mitigate the adverse effects of water deficit [140]. Similarly, grafted grapes exhibit improved physiological and biochemical responses under drought stress, including enhanced osmotic adjustment and antioxidant enzyme activity [141]. Furthermore, salt-tolerant rootstocks can limit the translocation of harmful ions (such as Na^+) to aerial parts, thereby improving the tolerance of plants to saline-alkali stress [138,142].

Long-distance signal and communication between rootstocks and scions constitute a fundamental mechanism underlying grafting enhanced stress resistance [118,120,136]. The formation of local hormone gradients is pivotal for orchestrating this process [143,144]. For instance, rootstocks improve scion cold tolerance by facilitating scion signals of melatonin, MeJA, and H_2O_2 accumulation in grafted watermelon plants [50]. Various hormones, including ABA, ET, JA, CKs, and SA, are involved in regulation of signal pathways in grafted plants [143,144]. In addition, rootstocks can transmit mobile mRNAs to scions, contributing significantly to enhanced stress tolerance [145]. Although the specific molecular transport mechanism is still under investigation, molecular communication between rootstock and scion is clearly a key factor in the adaptation of grafted crops to adverse environments [120].

The molecular basis of grafting-induced abiotic stress tolerance involves gene regulatory networks [146,147]. Abiotic stress typically triggers the expression of a series of stress-related genes in plants [148], while grafting can enhance plant tolerance by modulating the expression of such stress-related genes. Transcriptome studies have revealed the altered expression of heat tolerance-related genes changed in grafting roses under high-temperature stress [149], and differential gene expression patterns in grafted grapevines under drought conditions [141]. Epigenetic regulation plays a crucial role in this process and in the formation of plant stress memory [120,144,147,150]. For example, self-grafted tomato plants can induce changes in histone modifications and DNA methylation, which are closely associated with the enhanced tolerance of plants to drought [151]. As a key mechanism for plants to adapt to extreme environments, DNA methylation can lead to fluctuations in the expression levels of stress-related genes, thereby enhancing resilience [150]. Plant-microorganism interactions represent another important dimension. Plant biostimulants and rhizosphere-beneficial microorganisms (such as extracellular polysaccharide EPS produced by rhizosphere bacteria) can enhance plant tolerance to drought, salinity, and heavy metals [152,153]. However, grafting can promote this beneficial interaction, thereby enhancing plant adaptability to environmental stresses [154].

6. Conclusions and Prospects

Grafting is an effective technique for enhancing the disease and stress resistance of watermelon. It confers resistance to biotic stresses using rootstocks to prevent virus, fungi, and nematode proliferation and transfers systemic resistance signals to scions. In response to abiotic stress, drought-, salt-, and cold-tolerant rootstocks improve scion performance

through enhanced root architecture, increased photosynthetic efficiency, and activated antioxidant systems. Hormones, proteins, and mobile RNAs mediate the relationships between rootstocks and scions to regulate transcriptomes and metabolomes for stress response. While grafting can increase fruit size, lycopene concentration, and shelf life, its effects on other quality traits vary with rootstock–scion combinations. Therefore, selecting rootstocks with strong stress resistance and high graft compatibility is essential to maintain fruit quality and achieve high yields.

Future research should focus on two key directions: first, the strategic integration of breeding with grafting to develop advanced rootstocks that provide perennial multi-stress resistance and ensure fruit quality, potentially enabling pre-emptive control against complex diseases. Second, a comprehensive investigation into the long-term effects on soil ecosystems is essential, particularly concerning the impact of grafting on microbial communities and biochemical processes in deeper soil layers and how these effects can be optimized together with soil amendments to amendments soil health and sustainability.

For widespread adoption, economic and agronomic feasibility must be considered. While grafting is highly profitable in commercial systems where yield gains offset costs, its economic viability remains challenging for small-scale farmers [19]. Bridging this gap requires the development more accessible and affordable grafting solutions. Finally, future studies should extend beyond greenhouse conditions to systematically evaluate grafted plant performance, stress stability, and rootstock–scion compatibility under diverse open-field conditions.

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