Review

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

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*Review*

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

**Xuena Liu [1,2,†], Shikai La [1,2,†], Chang Chen [3], Ainong Shi [4], Mingjiao Wang [1,2], Yingying Zhang [1,2], Jinghua Guo [1,2,*] and Lingdi Dong [1,2,*]**

[1] Institute of Cash Crops, Hebei Academy of Agriculture and Forestry Sciences, Shijiazhuang 050051, China
[2] Institute of Cash Crops of Hebei Academy of Agricultural and Forestry Sciences, Hebei Vegetable Engineering Technology Centre, Shijiazhuang 050051, China
[3] Hebei Academy of Agriculture and Forestry Sciences, Shijiazhuang 050051, China
[4] University of Arkansas, Fayetteville, AR 72701
* Correspondence: 15831138918@163.com (J.G.); donglingdi@163.com (L.D.)
† These authors contributed equally to this work.

## Abstract

Grafting is an effective horticultural technique that can significantly enhance the disease resistance and stress resistance of watermelon. This review summarizes the types of rootstocks used in watermelon grafting and investigates the responses of graft-cucurbits to viral/fungal pathogens, root-knot nematodes, and stresses (such as drought, temperature, and salinity). The reviews also summarize the changes in fruit quality and underlying mechanisms induced by graft resistance. With recent research advances summarizing and analyzing, this review will provide valuable insight and reference for promoting resistance improvement and sustainable production in cucurbit and other vegetable crops by grafting. In summary, grafting can effectively improve the stress resistance and yield of watermelon, but optimizing fruit quality is still the focus of future research.

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

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## 1. Introduction

Grafting technology is a horticultural method and it is very important for agriculture, especially to improve the quality of crops and yields and disease resistance as well as improve biotic stress and abiotic stress resilience of plants [1,2]. It combines the superior rootstocks and scions, so the advantages of rootstocks and scions could be made use of while the deficiencies were reduced in individual rootstocks or scions [3]. Grafting technology is often applied to planting watermelon (*Citrullus lanatus*), selecting rootstock varieties, improving grafting methods and developing effective seedling management techniques and cultivating methods to enhance fruit quality and stress resistance significantly [4].

Watermelon is an important economic and nutrient supply crop. Cultivation watermelon suffers from a wide variety of problems throughout the world [5]. During the process of huge domestication and trait breeding, today's watermelon can rarely resist environmental stress in favor of good fruit appearance and higher yield. Many problems will thus occur. Biological stresses are also a significant problem of production. Fusarium wilt causes serious loss of watermelon cultivation because of pathogens known as Fusarium oxysporum f. sp. niveum (FON) [6]. In addition to biological stresses, nematodes, viruses, fungal diseases are still some problems that affect considerable reductions in fruit quality[7–9].

A large number of agricultural losses may result from biotic or abiotic stress. Climate changes have caused serious drought (drought stress), soil saltification (salt stress), extremes temperatures (heat or cold stress), and these would decrease plant yield considerably [10]. Drought is recognized one of the most destructive factors on global farm production [11]. Imbalances between nutrients in soil and heavy metal toxicity, extreme environment conditions including waterlogging greatly affect watermelons growth and yield. In planting watermelon, the issues like insufficient root system and low nutrient uptake ability associated with some types of stress.

Grafting technology can enhance the resistance of watermelon to both biotic and abiotic stresses. Therefore, in-depth research on how grafting improves the resistance of watermelon to disease and stress resistance and its application value in production is of great theoretical significance and practical guidance [1,6]. This paper makes a review of the latest research on using grafting technology to improve watermelon's resistance to biotic and abiotic stresses. By knowing how grafting affects the physiological and biochemical processes, root exudation components and gene expression of watermelon, the best combination of watermelon grafting can be selected, and high stress-resistant watermelon varieties can be bred. Which helps increase yield and quality and reduce the use of pesticides, promote the sustainable development of the watermelon industry, ensure global food security and nutrition supply.

## 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) [9,12,13].

Currently, there are few reports of reducing the damage of viral diseases in watermelon through grafting, but some studies have found that grafting watermelon could help increase plant resistance to virus (Table 1). Grafting effect depends on the choice of antiviral rootstock. It can greatly limit virus disease spread and proliferation in plants. Grafting increased watermelon production by 115% in MNSV-infected fields [14]. Felipe et al., reported that grafting watermelon onto a hybrid squash rootstock, RS-841 significantly increased the resistance of watermelon scion to MNSV [15].

Previous research has proven that grafting can generally enhance the overall tolerance of seedless watermelon to virus [16]. But the efficacy of grafting watermelon depends on the selected rootstock, for certain viruses, for example, CGMMV, if it was already infected in scion before grafting, grafting would not cure existing viral infection directly [16]. Therefore, the selection and utilization of high-resistant rootstocks is the basement to achieve effective resistance to viruses.

Furthermore, it is worth developing resistant rootstocks by genetic engineering technology [17]. Researchers created transgenic rootstocks resistant to CGMMV by introducing cDNA encoding coat protein gene of CGMMV [18]. More importantly, rootstocks generated antiviral transgene using RNA silencing technologies could provide systemic resistance against viruses for susceptible scions grafted on them [19], which could develop new strategies via grafting to manage watermelon viruses.

### *2.2. Fungal Diseases*

Fusarium wilt, gummy stem blight, colletotrichum orbiculare and powdery mildew are the main fungal diseases that cause serious threats to the production of watermelon [8,20]. Grafting is very effective for managing fungal diseases in watermelon, especially those caused by soil-borne pathogens [3] (Table 1).

The use of gourds, pumpkin or wild watermelon can significantly enhance resistance to Fusarium wilt in scions, reducing disease indexes and incidence rates significantly. Grafting even could eliminate Fusarium wilt. Compared with non-grafted seedlings, the occurrence rate of fusarium was lower by 100% and 88% in grafted watermelons [21]. In the study of grafting watermelons against fungi by Qiao et al., researchers constructed the bacterial community existing in the rhizosphere soil of grafted plants by utilizing the core strains of the bacteria on roots of grafted watermelon, which significantly increased growth and disease resistance of non-grafted watermelon grown in non-sterilized soil [22].

Rootstocks resistant to fungal diseases are important options to enhance the resistance to fungi diseases in grafted watermelons, for example, Kousik et al. used 25 watermelon cultivars and 4 gourd cultivars as rootstocks for grafting experiments, then cultivated and compared their scion watermelon cultivar 'Mickey Lee', susceptible to powdery mildew. Results showed that compared with watermelon, rootstock gourds (USVL482-PMR and USVL351-PMR) could significantly increase scion powdery mildew disease resistance in watermelons [7].

### *2.3. Root-Knot Nematode*

Watermelon root-knot nematode disease has always been a challenge of watermelon industry caused mainly by Meloidogyne spp., among which Meloidogyne incognita is the most predominant one[23]. This root-nematode produces much damage to the roots of watermelons by causing galls or nodules in roots, which leads to shorter roots, rooting deterioration, and decreased root activities [24,25]. The above-ground symptoms are stunting, curling, and yellowing of leaves and wilting [26,27], even in some cases resulting in plant death. Therefore, growth and vigor of watermelon decrease with reduction in fruit setting, decrease in yield, lower fruit qualities as well [28] (Table 1).

The root-knot nematodes resistance is strong so that chemical control against them is almost useless and very dangerous as well as risky, such as pollute environmental elements, develop resistance, etc. [29]. Therefore, grafting has emerged as a viable strategy for managing this disease [3,30]. This technique is also one way of controlling root-knot nematode, which uses the resistant rootstock cultivars being grafted onto the susceptible ones for control root-knot nematode infection [31].

It was reported that there are some varieties of gourd (*Lagenaria siceraria*) or pumpkin (*Cucurbita moschata* × *C. maxima*) were found to be effective resistant rootstocks to reduce significantly the nematodes infections, decreased number of root knots, and improved yield of watermelon [31]. In field trials, these rootstocks such as 'Emphasis', 'Carnivor' and 'Strongto' had showed high resistance against root-knot nematodes. Wild watermelon (*Citrullus amarus*) as well as some wild cucumber resources (e.g., *Cucumis myriocarpus*) were also reported to have resistance against root-knot nematodes [32], which could be possible as their rootstocks materials. Germplasm resources of *Citrullus lanatus* var. citroides (i.e., forage watermelon or wild watermelon type) are good sources of possible materials of rootstocks resistance to root-knot nematodes [33]. Several series of wild watermelon rootstocks, RKVL series, developed from wild watermelons by United States Department of Agriculture has been reported with significant better performance against the nematode than commercial rootstocks and non-grafted watermelons, because in field situations under high nematode root infection, their root knot rates were only 9–16%, significantly lower than those (41%) for non-grafted cultivars [34].

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

| **Type of coercion** | **Rootstock** | | **Scion** | **Resistance** | **References** |
|---|---|---|---|---|---|
| Virus | *Cucurbita maxima* × *C. moschata* | RS841,<br>Shintosa Camelforce | Tri-X 313 | Increased yield; fruit hardness increased, but did not affect the soluble solids content. | [14] |
| | *Cucurbita maxima* × *C. moschata* | RS-841, Ercole | Mielheart | Significantly increased the resistance of scions to MNSV. | [15] |
| | *Citrullus lanatus* var citroides | Robust | | | |
| | *Citrullus mucosospermus* | 938-16-B | | Resistant to virus disease. | [35] |

| | | | | | |
|---|---|---|---|---|---|
| | *Citrullus lanatus* | H1, Hongzi | 938-16-B, H1, Hongzi | Susceptible to viral diseases. | |
| Fungus | *Cucurbita moschata* | Landrace | Crimson Tide | The incidence rate was reduced by 88 % -100 %, and even completely controlled. | [21] |
| | *Cucurbita maxima* | Landrace | | | |
| | *Lagenaria siceraria* | Landrace | | | |
| | *Luffa cylindrica* | Landrace | | | |
| | *Benincasa hispida* | Landrace | | | |
| | *Lagenaria* hybrid | 216, Emphasis, Skopje, FR Gold | | | |
| | *Cucurbita* hybrid | P360, Strong Tosa | | | |
| | *Lagenaria siceraria* | USVL482-PMR, USVL351-PMR | Mickey Lee | Significantly enhance the resistance of the scion to powdery mildew. | [7] |
| | *Lagenaria siceraria* | Chaofengkangshengwang | Sumi 1 | High resistance to Fusarium wilt, and the incidence was only 3.4 %. | [6] |
| | *Cucurbita maxima* × *C. moschata* | Tetsukabuto | Secretariat | Resistance to verticillium wilt. | [36] |
| | *Citrullus lanatus* var. *citroides* | IIHR-82, IIHR-617, BIL-53 | NS-295 | Resistance to gummy stem blight. | [37] |
| | *Lagenaria siceraria* | BG-95, BG-77-6-1 | | | |
| | *Citrullus lanatus* var. *citroides* | IIHR-617×Arka Manik, IIHR-82 × Arka Manik, IIHR-82 × IIHR-617 | | | |
| | *Cucurbita maxima* × *C. moschata* | Nun 6001, Strongtosa, Tetsukabuto, Ferro, Shintoza | Aswan F1 | Enhance disease resistance. | [38] |
| | *Lagenaria siceraria* | IT207112 | Sambokkul | Resistance to Fusarium wilt, single spore root rot, and vine recession. | [39] |
| | *Lagenaria siceraria* | FRD22 | | Moderate resistance to single spore root rot and vine decline disease. | |
| Nematodes | *Lagenaria siceraria* | Emphasis, WMXP 3938, WMXP 3944, WMXP3445 | Fiesta, Tri-X 313 | Significantly reduce the root knot rate and infection level; increase production. | [31] |
| | *Cucurbita moschata* × *C. maxima* | Strong Tosa | | Significant nematode resistance in field trials. | |
| | *Citrullus lanatus* var. citroides | RKVL 301, RKVL 302, RKVL 303, RKVL 315, RKVL 318, Ojakkyo | | Significant resistance; root knot index and nematode reproduction were low. | |
| | *Cucumis africanus*, *Cucumis myriocarpus* | | Congo, Charleston Gray | Resistance to root-knot nematodes. | [32] |

## 3. Grafting Affected the Tolerance of Watermelon to Abiotic Stress

### *3.1. Drought Stress*

Drought can pose a major problem for plants, and this especially affects crops that have high water requirements in arid regions or semi-arid areas, such as the Mediterranean Basin, parts of southwestern United States, and sub-Saharan Africa (for example: watermelon [40] (Table 2). Grafting onto rootstocks of drought tolerance is a way to alleviate such difficulties. Drought tolerant rootstocks usually develop better root systems which allow for more efficient absorption of soil water and nutrients, thus providing a stronger basis for the scions for drought stress [40]. Studies have confirmed that under continuous severe water stress, normal watermelon plants will suffer yield loss of up to 40% as a result of smaller single fruit weight and lower number of set fruits [41,42].

Watermelon grafted onto drought-resistant rootstocks can enhance the ability to avoid drought stress, including maintaining high leaf relative water content with low water transpiration by quickly adjusting stomatal state to control transpiration [43,44] and improving WUE [45]. However, scions also benefit from rootstocks. Grafting onto the pumpkin rootstock 'Naihan 1' was proven to increase the ClTCP4 gene expression in scions of grafted watermelon, leading to a better photosynthetic rate of plants (with a net $CO_2$ absorbing rate higher by 38%), as well as cell membrane stability with low malondialdehyde (MDA) levels by 45% [46]. Chen et al., (2024) studied the variation of various genes and metabolites under different drought stresses, providing useful key data to study the mechanism of improvement of drought resistance caused by grafting [47]. Moreover, antioxidant enzyme activity in watermelon grafted on some drought-resistant rootstocks often showed significantly high levels under drought stress, but the indices of oxidative damage were obviously lower than those in self-rooted watermelon [43].

Field trials have also 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’) [43,48] and other types of bottle gourd rootstocks, such as ‘Illapel’ and ‘Osorno’ [11], 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 (Table 2). Low-temperature stress can seriously affect plant growth and development, interfere with plant physiological functions, and even result in plant death [49,50]. After the watermelon planting period, the temperature (2°C) remained nearly 14–15 h, and watermelon yields were reduced by more than 10% [51]. The grafting technique is widely used to improve the low-temperature resistance of watermelon.

Watermelon plants grafted onto pumpkin rootstocks showed resistance to low temperatures. Watermelons can maintain a high chlorophyll content and photosynthesis rate, and the MDA content obviously decreased [49,52]. The decline in MDA levels indicates that grafting could reduce low-temperature damage to the cell membrane. Under low-temperature treatment, the activity of watermelon antioxidant enzymes decreases [49], which damages the process of photosynthesis and root development [53]. However, grafting significantly improved the ability of watermelon plants to remove reactive oxygen species (ROS) under low temperatures and reduced oxidative damage, which was closely related to the time-and-space dynamic response of ROS and salicylic acid (SA), indicating a possible interaction and could be the main reason for watermelon induced resistance during grafting [52]. Previous research has also found that using pumpkins or black-seeded pumpkin rootstocks can improve the cold resistance of watermelon seedlings, enhance the accumulation of melatonin and methyl jasmonate (MeJA), and increase hydrogen peroxide ($H_2O_2$) levels [54].

Transcriptome comparison of watermelon to rootstocks revealed that many low-temperature-related genes of seedlings can respond to expression changes under the influence of grafting, and also provides an important molecular basis for enhancing survival rate and growth under low temperature conditions [55]. Research has also demonstrated that the arginine decarboxylase (ADC) gene in pumpkin rootstock is upregulated, resulting in the biosynthesis of more putrescine, which effectively mitigates the detrimental effects of low temperatures [56]. Moreover, we have noticed that the expression level of some genes relevant to the Calvin cycle could be altered via grafting during low-temperature stress, further enhancing the resistance of seedlings to cold [49] By performing small RNA sequencing relative to muskmelon (a member of the same family as watermelon), we can speculate that gene regulation through differentially expressed miRNAs in response to cold stress may be one of the reasons contributing to the improved cold resistance [57].

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 [49]. Grafting watermelon onto a bottle gourd rootstock could improve cold tolerance, especially at the early stages of growth, and enhance its commercial quality without compromising fruit quality [39].

High temperatures caused by global warming threaten the harvest and yield of watermelon [58]. Although little research on the heat tolerance of grafted watermelon has been conducted systematically, the benefits have already been proven. For example, it has been proven that grafting benefits the increase in cucumber yield under combined stress conditions of (heat and salt) [59]. Rootstocks, mostly pumpkin or bottle gourds, have a higher ability to absorb soil water and nutrition, and a larger root area can help sustain a higher level of water under high temperatures, which indirectly improves the plant's resistance to heat [60].

### *3.3. Salt Stress*

Soil salinization is a major abiotic factor that affects the yield of crops worldwide (Table 2), whereas watermelon is mainly inhibited in growth, suffering from osmotic stress, ion toxic injury, and secondary oxidative stress, which severely constrain plant growth and development [61–66]. Therefore, grafting salt-resistant rootstocks is an effective way to improve salt stress resistance [65].

It was found that rootstocks could exhibit different levels of Na transport tolerance by various types [67–70]. Pumpkin rootstocks, such as 'Kaijia No.1', showed much better salt tolerance [68]. 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 [71].

Grafting salt-resistant rootstocks could improve plant salt resistance through their ‘ion exclusion’ effects, intercepting $Na^+$ from roots to significantly reduce ion transportation capacity from roots to shoots, such as the leaves of scion parts [69]. For example, watermelon leaves grafted onto 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 [68,72], with an accumulation of osmotic adjustment substances, such as soluble sugars [67].

In addition, under salt stress conditions, the grafted plants can maintain or even significantly enhance the activities of antioxidant enzymes in leaves [65,73,74], efficiently reducing ROS and damage, such as membrane lipid peroxidation, to protect the stability of the cell membrane structure and function [65,75].

Transcriptomic and proteomic analyses indicated a comprehensive molecular reaction network initiated by grafting. Wang et al. screened 8462 differential genes in watermelon seedlings grafted with gourd rootstock under salt stress [65]. The results showed that grafting onto gourd rootstock could greatly improve the damage caused by salt stress on the growth and photosynthesis of watermelon. The expression of 40 proteins was clearly altered after grafting on the rootstock and/or salt stress [76]. These proteins are mainly related to the Calvin Cycle, biosynthesis of amino acids, sugar and energy metabolism, ROS defense system, hormone biosynthesis, and hormone signaling pathways. Yang et al. used gourd as a rootstock for grafting and observed that at least 12 proteins exhibited significant changes with prolonged stress exposure using a 50 mmol/L NaCl treatment [77]. In addition, we found that after grafting, some other genes were obviously changed, such as genes involved in response to salt stress, including ion transporter genes SOS, HKT1, and NHX1, pump proton PMA, etc., and gene transcription factors, including NAC and WRKY [65,78]. Yuan et al. found that the positive regulation of transcription factor ClaDREB14 to peroxidase gene ClaPOD6, so ClaDREB14 upregulated peroxidase activity to enhance salt tolerance in watermelon rootstocks [75].

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

| **Type of coercion** | **Rootstock** | | **Scion** | **Resistance** | **References** |
|---|---|---|---|---|---|
| Drought stress | *Lagenaria siceraria* | Illapel, Osorno, GC<br>BG-48, Philippines | Santa Amelia | Drought tolerance, significantly increased yield; improve root structure.<br>Not drought-tolerant. | [11] |
| | *Cucurbita maxima* × *C. moschata* | Shintoza | Crimson Sweet | Better growth performance and water status. | [43] |
| | *Citrullus colocynthis* (L.) Schrad | Esfahan | | Better drought resistance, growth and biomass decreased less, and showed higher antioxidant activity and lower oxidative stress. | |
| | *Cucurbita moschata* | Naihan 1 | | Up-regulation of ClTCP4 gene expression in scions helped to maintain higher photosynthetic efficiency and cell membrane stability. | [46] |
| | *Lagenaria siceraria* | Jingxinzhen 1 | Zaojia 8424 | Better growth performance. | [48] |
| | *Cucurbita maxima* × *C. moschata* | Qingyanzhen 1 | | | |
| | *Citrullus lanatus* subsp. *mucosospermus* | | Crimson Sweet | Improve the ability to resist water stress, improve growth and yield. | [40] |
| | *Cucurbita maxima* × *C. moschata* | Strong Tosa | Crimson Tide F1 | Enhance drought tolerance. | [45] |
| | *Citrullus lanatus* var. *citroides* | | Crimson Tide | Enhance drought tolerance and affect physiological characteristics and nutrient uptake. | [44] |
| | *Cucurbita maxima* × *C. moschata* | TZ-148 | | | |
| | *Citrullus lanatus* var. *citroides* | A1, A2 | Crimson Tide | Enhance drought tolerance. | [79] |
| | *Cucurbita maxima* × *C. moschata* | TZ-148 | | Enhance drought resistance and improve fruit quality. | |
| Temperature stress | *Lagenaria siceraria* | FR79 | Sambokkul | Tolerance to low temperature, little effect on fruit quality. | [39] |
| | *Lagenaria siceraria* | 0526, 2505 | Zaojia 8424 | Enhance cold resistance. | [49] |
| | *Cucurbita maxima* × *C. moschata* | Qingyan No.1 | 97103 | Enhance cold resistance. | [50,52] |
| | *Cucurbita moschata* | Weizhen No.1 | Nongkeda No.5 | Enhance cold resistance. | [54] |
| | *Cucurbita ficifolia* Bouché | Cf | | | |
| Salt stress | *Lagenaria siceraria* | Chaofeng Kangshengwang | Xiuli | Enhance salt tolerance. | [65,73,74,76] |
| | *Cucurbita maxima* | Cma | Crimson Tide | Enhance salt tolerance. | [67] |
| | *Lagenaria siceraria* | Skp, Birecik | | | |
| | *Citrullus lanatus* | Jingxin No.2 | | General salt tolerance. | [68] |

| | | | | |
|---|---|---|---|---|
| *Cucurbita moschata* | Quanneng Tiejia | Jingxin No.2 | General salt tolerance. | |
| | Kaijia No.1 | | High salt tolerance. | |
| *Lagenaria siceraria* | Hanzhen No.3 | | High salt tolerance. | |
| *Citrullus lanatus* | Zhongyu No.9 tetraploid | Zhongyu No.9 | Enhance salt tolerance. | [71] |
| *Lagenaria siceraria* | | *C. lanatus* | Enhance salt tolerance. | [72,77,78] |
| *Cucurbita maxima* × *C. moschata* | Shintosa F-90 | *C. lanatus* | Enhance salt tolerance. | [72] |

## 4. Effects of Grafting on Fruit Quality of Watermelon

The quality of watermelon fruit includes many properties affecting human taste perception, such as 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) [80]. 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 [81–83]. 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 [81,84] (Table 3).

### *4.1. Soluble Solids Content*

Grafting may decrease SSC and total sugar content in watermelons. Fredes Sivoplás et al. indicated that the SSC of fruits grafted onto rootstocks from *Citrullus lanatus* var. citroides would decrease [85]. Liu et al. found that fruit quality, such as sugar content in watermelon, might be decreased if seedless watermelons were grafted onto pumpkin rootstocks [86]. Conversely, other reports have indicated that grafting could enhance the SSC in watermelon, especially on gourd rootstocks, where the SSC increased by 12 to 15% in the rootstock [87–89]. In addition, Sun et al. found that grafting pumpkin rootstocks altered the sugar composition and increased the weight of watermelon fruits through the action of invertase and sugar transporters [83]. Transcriptome analyses have shown that pumpkin rootstocks can upregulate genes involved in fructose/mannose metabolism in the pulp, increase the activity of sucrose synthase, and enhance the transfer of carbohydrates into fruits. Rootstocks can improve the effectiveness of sugar transport in sink tissues via SWEET, affecting diverse aspects of sink growth, such as the sugar transporter SWEET10 [88,89]. The mRNAs exchanged between rootstocks and scions may have beneficial effects on the quality of watermelon fruits. They may be responsible for the regulation of watermelon sugar metabolism [90].

### *4.2. Organic Acid*

Grafting alters organic acid metabolism in watermelon fruits, affecting their quality and flavor. Some studies have indicated that grafting can increase the total organic acids and acidity of watermelon during fruit ripening [84,91]. Different rootstock combinations in grafting experiments showed significant differences in fruit organic acids [82,92]. On the one hand, the types of organic acids in watermelons differ, and grafting influences the synthesis and accumulation of various organic acids in watermelons, such as citric and malic acids. One study on watermelons grafted onto a pumpkin reported 56 primary metabolites, among which the abundance of some organic acids between grafted and self-rooted seedlings showed great differences, including increased citric acid and decreased malic acid compared to self-rooted plants, thereby influencing the acid-sweet ratio of fruits [93]. These effects determine the accumulation of citric and malic acids, which are directly associated with the quality of watermelons.

The regulation of organic acids mainly involves related enzymes, such as citrate synthase (CS) and malate dehydrogenase (MDH). Grafting can cause changes in enzyme activity in the plant body or even at the cellular level, thus indirectly affecting organic acid metabolism. For example, in an experiment using watermelon 'Zaojia' as a scion in grafting, changes were found in the activities of acid invertase, neutral invertase, sucrose synthase, and sucrose phosphate synthase. These enzymes are also involved in sugar metabolism; thus, their activity changes are also associated with organic acid accumulation in watermelon fruits [82].

Transcriptome analysis reveals the influence of grafting on organic acids. Comprehensive transcriptome analysis combined with metabolome data revealed that pumpkin rootstocks can induce gene expression associated with the regulation of secondary metabolic pathways. More than 216 differentially accumulated metabolites between non-grafted and grafted watermelon were significantly changed, and the genes corresponding to them were mostly related to biosynthesis pathways, such as flavonoid and flavanol synthesis, which were closely related to fruit flavor quality [89]. Moreover, key gene networks linked to sugar and organic acid accumulation have been identified through transcriptome analysis [94,95].

The transfer of long-distance signals, especially mobile RNA (mb-mRNA), between rootstocks and scions could be an important factor in improving grafted fruit quality. Recently, 834 mb-mRNAs in the flesh and stems of pumpkin rootstock-grafted watermelons were identified as potential genes participating in the regulation of fruit quality enhancement [90].

### 4.3. Lycopene

Lycopene is a main carotenoid and also acts as a powerful antioxidant. High lycopene intake benefits human health [96]. Studies have found that lycopene bioavailability in watermelons is higher than that in tomatoes, with an efficiency of more than 60% [97,98]. 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 [99–101].

Grafting techniques can give advantages for increase the lycopene content. Much evidence has demonstrated that specific graft combinations can increase the lycopene content in watermelon fruits. For instance, grafting watermelon onto pumpkin interspecific hybrid rootstocks increased lycopene levels [102,103]. In addition, watermelons grafted onto gourd and pumpkin hybrid rootstocks exhibited higher lycopene content than non-grafted controls [102,104]. This may be because rootstocks promote fruit lycopene accumulation by regulating the transcriptional expression levels of lycopene metabolism-related genes related to lycopene in watermelon fruit [104]. Several studies have confirmed that grafting combinations can increase lycopene content [105].

However, different rootstocks could yield inconsistent effects on the quantity of lycopene in watermelon fruit with the same or different fruiting statuses under plantation and degrees. Possible reasons could be the rootstock scion combinations, planting environment, and fruit maturity age [38,106–109]. Additionally, other researchers did not find much difference in lycopene levels between grafted and non-grafted watermelon fruits [38,108,110].

Grafting can delay the lycopene accumulation rate during fruit flesh development, causing the color peak to be postponed after ripening. Studies have shown that in some cases, grafting can delay the accumulation of lycopene in the pulp and the appearance of color peaks [84,111]. 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. The decrease in ABA concentration may indirectly affect the accumulation rate and final lycopene content [112].

### 4.4. Physical and Sensory Quality

Grafting, especially with Cucurbita rootstocks, may be a method for enhancing the hardness of watermelon flesh [84,113,114]. For instance, compared with the non-grafting control, the pulp hardness of watermelon grafted with pumpkin rootstocks was significantly higher [115]. The high hardness could be related to the variation in the structure and/or compactness of cells in the pulp tissue [114]. However, not all studies have shown similar results. Some studies have shown that grafting does not influence hardness [108,116], and the flesh hardness can even be weakened by some rootstocks or scions [86,117]. For instance, watermelon fruits are grafted onto zucchini rootstocks [117]. This change often correlates with rootstock genotypes, scion varietal species, and cultivation environments [109].

In addition to influencing flesh hardness, grafting may also affect other traits related to watermelon fruits. Grafting sometimes increases peel thickness [113], providing fruits with a longer shelf life and more resistance to damage and cracking during transportation. Grafting onto some rootstocks could weaken the fruit cracking sensitivity of watermelons, showing enhanced watermelon toughness [114]. Investigations have shown that grafting influences watermelon fruit weight or size [118], increasing individual fruit weights [83].

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

| **Rootstock** | | **Scion** | **Changes in quality after grafting** | References |
|---|---|---|---|---|
| *Lagenaria siceraria* | Yongzhen No.1,<br>Yongzhen No.3,<br>Yongzhen No.8 | Zaojia 8424 | Increase SSC content. | [82] |
| *Cucurbita maxima* × *C. moschata* | Yongzhen No.7 | Zaojia 8424 | Increase fruit weight (SSC content did not change ). | [83] |
| *Cucurbita maxima* × *C. moschata* | 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. | [84] |
| *Cucurbita maxima* × *C. moschata* | Super Shintosa | Melody | Increase the lycopene content. | [86] |
| *Cucurbita moschata* | Marvel | | Increase fruit hardness. | |
| *Cucurbita maxima* × *C. moschata* | Root Power | | | |
| *Lagenaria siceraria* | Macis | Crimson Sweet | Increased the size and rind thickness of fruits. | [88] |
| *Cucurbita moschata* | SiZhuang | 8424 | Improve quality, increase beneficial metabolites, and reduce bitter compounds. | [89] |
| *Cucurbita moschata* | Xi Jia Qiang Sheng | Zhongyu No.1 | Increase the total sugar, total amino acid and total acid content. | [93] |
| *Lagenaria siceraria* | FR STRONG | RX 467 | Reduce the lycopene content. | [103] |

| | | | | |
|---|---|---|---|---|
| *Cucurbita maxima* × *C. moschata* | RS 841 | | Increase the lycopene content. | |
| *Lagenaria siceraria* | Jingxinzhen No.1 | Zaojia | Increase the lycopene content. | [104] |
| Citrullus lanatus var. citroides | Yongshi | | | |
| *Cucurbita maxima* × *C. moschata* | Qingyanzhen No.1 | | No effect on lycopene content. | |
| *Cucurbita maxima* × *C. moschata* | Ferro, Nun 6001, Shintoza | Aswan | Increase the lycopene content. | [38] |
| *Cucurbita maxima* × *C. moschata* | TZ148 | Pegasus | Increase fruit hardness and citrulline content. | [111] |
| *Cucurbita maxima* × *C. moschata* | Jingxinzhen No. 2 | 97103 | Maturity extended. | [112] |
| *Cucurbita argyrosperma* | 451 | Summer Flavor 800,<br>Summer Sweet 5244 | Reduce fruit weight, lycopene content (diploid). | [113] |
| *Cucurbita maxima* × *C. moschata* | N101 | Pegasus | Increase fruit hardness. | [114] |
| *Cucurbita maxima* × *C. moschata* | TZ148, Bombo, N101 | Celebration, Gallery, Pegasus, Torpilla | Increase fruit hardness, lycopene content; SSC content decreased slightly. | [115] |
| *Cucurbita maxima* × *C. moschata* | Ferro RZ, Nun 9075 | Crimson Tide | Increase SSC content, peel thickness, fruit hardness. | [116] |
| | RS 841, Strong Tosa | | Increase lycopene content, peel thickness, fruit hardness. | |
| *Citrullus lanatus* var. *citroides* | BGV0005167 | Oneida | Increase fruit thickness, flesh hardness, SSC content. | [117] |
| *Cucurbita maxima* VAV 1860× *C. moschata* PI 550689 | GMM1 Cobalt | | Increase fruit thickness and flesh hardness; change the fruit aroma. | |
| | TZ-148 | 1262 | Improve fruit taste. | [118] |

| | | | | |
|---|---|---|---|---|
| *Cucurbita maxima* × *C. moschata* | Nurit | | Improve fruit taste, increase lycopene and SSC content. | |
| *Lagenaria siceraria* | A3 | Crimson Tide | Increase the sugar content of fruit. | [79] |
| *Lagenaria* spp. | Argentario, 3335 | 187×125, 11×162 | Increase the SSC content, fruit diameter, peel thickness and fruit weight. | [119] |
| *Cucurbita maxima* × *C. moschata* | TZ148, Nun9075 | | Increase fruit weight. | |

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

### *5.1. Biotic Stress Resistance*

The core of grafting plants for resistance to biotic stress lies in the relationship between the rootstock and scion. Selecting suitable rootstocks plays a pivotal role in plant resistance to diseases or soil diseases [120,121]. Grafting can mainly improve plant disease resistance by enabling materials to transmit and allowing signals to be induced over long distances between rootstocks and scions [122,123]. For example, various substances, including nutrients and hormone signals, as well as mRNAs, small molecules, miRNAs, and proteins, can pass between the rootstock and scion after grafting [124–127]. Some compounds, such as jasmonic acid (JA) and its similar compounds, are very important for systemic immunity, and grafting experiments have confirmed their important function in immunity [128]. They are important components of long-distance signal transmission and play an important role in triggering defensive reactions, which are achieved through signals mediated by roots to herbivory. Other compounds, such as SA, are essential for defense signaling systems. Through systemic acquired resistance (SAR), their levels increase in plants, which activates the protein NPR1 and widespread resistance in plants against different pathogens [129–131].

Moreover, grafting also affects the activation and regulation of the plant's immune system. Plants can respond to pathogens by sensing conserved signature molecular patterns of pathogens and activating pattern-triggered immunity (PTI) using pattern recognition receptors or activating effector-triggered immunity (ETI) mediated by effector recognition receptors [132,133]. By passing on the signal molecule to the scion, rootstocks can help enhance PTTI or ETI. Beneficial microorganism groups, including bacterial and fungal microorganisms in the rhizosphere, could induce systemic resistance (ISR), which may be enhanced and transmitted via grafting to increase plant resistance against pathogens and insects [131,134–136]. ISR is primarily achieved by regulating hormone signaling pathways, such as JA, ethylene (ET), and SA, and related gene expression [134].

Grafting not only mediates signal transmission between two parts, but may also activate epigenetic modification at certain locus or loci in the plant genome, leading to changes in gene expression via epigenetic regulation [124,137,138]. For example, the demethylation occurring in DNA during the grafting of eggplant would correlate to higher grafting activity [138], and these epigenetic modifications might trigger lasting improved resistance, since this can affect how far the plants can develop an adaptive memory towards stress, and how they react to it in the future.

Finally, grafting could also induce plants to produce antioxidant enzymes, such as superoxide dismutase, catalase, and peroxidase, that are required for plants to scavenge the existing radicals in the body to decrease oxidative stress [139,140]. Grafting also affects the distribution of secondary metabolites necessary for resistance to some diseases and insect pests [126,127]. Some rootstocks can influence the accumulation of plant secondary metabolites, which play an active defense role in their shoot parts, improving their tolerance and resistance to diseases [127].

### *5.2. Abiotic Stress Resistance*

The mechanism of grafting to increase plant tolerance to abiotic stresses is complex and involves morphology, physiology, biochemistry, and molecular levels [126,141]. Choosing suitable rootstocks is crucial for grafting adjustments at the morphological and physiological levels. Strong rootstock roots can absorb more water and nutrients, which effectively improves the stress resistance of the entire plant [121,142,143]. Grafting increases the photosynthetic characteristics and water-use efficiency of crops [144]. Under drought stress, the negative effect on the scions of grafted cucumber was significantly less, meaning that the rootstocks prevented the negative effect of drought stress on scions [145]. In addition, the physiological and biochemical responses of grafted grapes to drought stress were more positive, such as osmotic adjustment and antioxidant enzyme activity [146]. In addition, grafting resistant or salt-resistant rootstocks into scions could restrict harmful ion ($Na^+$) transfer from the rootstocks to the scions, hence enhancing the ability of scions to survive in salt-alkali land [143,147].

Intricate and long-distance signal transmission and communication between rootstocks and scions are the basic mechanisms through which grafting enhances resistance [122,124,141]. Plant hormones are essential for this process [148,149]. For instance, rootstocks improve scion cold tolerance by facilitating scion signals of melatonin, MeJA, and $H_2O_2$ accumulation in grafted watermelon plants [54]. Hormones, including ABA, ET, JA, CKs, and SA, are associated with the regulation of signal pathways in grafted plants under stress response cascade control processes [148,149]. In addition, mobile mRNAs from rootstocks are delivered to scions, which receive and produce similar cellular functions [150]. Although its specific transference mechanism is still being elucidated, the molecular communication between rootstock and scion is a key factor in the scion's ability to adapt to adverse environments [124].

Grafting-induced abiotic stress tolerance involves complex mechanisms and gene regulation [151,152]. Abiotic stress can cause the expression of a series of stress-related genes in plants [153], while grafting can enhance plant tolerance by modifying the expression of such stress-related genes. Transcriptome analysis showed that the expression levels of heat tolerance-related genes changed in grafting roses under high-temperature stress [154], and the genes in grafted grapes in response to drought showed a differential expression pattern under drought stress [146]. Epigenetic regulation plays a crucial role in this process and in the formation of plant stress memory [124,149,152,155]. For example, self-grafted tomatoes can induce changes in histone modifications and DNA methylation, which are closely related to the enhanced tolerance of plants to drought [156]. As an important mechanism for plants to adapt to extreme environments, DNA methylation can lead to fluctuations in the expression levels of stress-related genes, thereby enhancing stress tolerance [155]. The relationship between plant and microorganism interactions and abiotic stress regulation is important. Plant bio-stimulants and rhizosphere-beneficial microorganisms (such as extracellular polysaccharide EPS produced by rhizosphere bacteria) interactions in the vicinity of roots play important roles, which are beneficial for plants to be resistant to abiotic stresses such as drought, salt stress, and heavy metals [157,158]. However, grafting can promote beneficial plant-microbial rhizosphere interactions of roots, thus increasing plant resistance and adapting to adverse changes in the environment or climate [159].

## 6. Conclusions and Prospects

To conclude, watermelon plants can be strengthened through grafting technology, which is a very efficient and sustainable method that can be applied to overcome numerous obstacles. It offers significant resistance to biotic stresses since it relies on rootstocks to prevent the proliferation of virus, fungi and nematodes physically and physiologically and potentially transfer systemic resistance signals to scions at the molecular level. On abiotic stress, the rootstocks which are drought-, salt-, and cold-tolerant enhance the performance of scions through the formation of better root systems to get access to resources efficiently, enhance physiological processes like photosynthesis, and activate proper antioxidant systems to minimize oxidative injuries. Long-distance communication of hormones, proteins, and mobile RNAs that mediate synergistic relationships between rootstocks and scions regulate functional changes in transcriptomes and metabolomes of progeny to elicit a stress response.

Nevertheless, the grafting outcomes on the quality of fruits are multifaceted and indirect. Although the use of grafting has the potential to raise fruit size, lycopene concentration and shelf life due to a thicker pericarp, it can also cause underlying quality measures and alter natural rhizome-grafting interactions depending on the combination applied. As such, effective use of grafting needs to be implemented, such as rootstocks resistance trait selection combined with graft compatibility to eliminate adverse effects to fruit sensory and nutritional quality thus to achieve high yield and acceptance.

Recent studies have focused on the short-term impacts of grafting on the watermelon yield and disease resistance but its long-term impact on the soil ecosystems have not been exhaustively researched. It has been demonstrated that, in the case of continuous Cucurbitaceae cropping systems, it is beneficial since grafting can increase rhizosphere microbial activity, soil enzyme activity, through regulating root exudates release [160]. However, the effects of grafting on microbial communities and biochemical processes in deep soil layers (>30 cm) remain unclear [161]. Significant improvements in soil versatility occurred through the long-term joint use of bio-organic fertilizer and grafting, but the primary indicators, including soil salinity and actin-fungal community structure, were not significantly enhanced.

Secondly, it can be added that grafting technology may work as a supplement to normal breeding technologies. The next direction in watermelon rootstocks breeding should concentrate on conducting breeding of the rootstocks varieties which can be perennial, highly resistant to pests and diseases, resistant to biotic and abiotic stresses and how they may influence the quality of the fruits. Based on this, potential ways the study can look further into the overall pre-infectious prevention and control impact of the grafting technology in co-infection with multiple pathogens.

As a result of the variations in the production systems, economic benefits of grafted watermelon production differ greatly. In commercial appraisals, the grafting technology may double/trip the yield thus nullifying the raise made in the labor expenses of grafting seedlings [38]. Smallholder production systems on the other hand are faced with a lot of challenges: the price of the grafted seedlings is typically 3-5 times as high as of the non-grafted ones and the rate of growth in the yield of the small-scale environment is typically between 10% and 15%. Break-even of 25 - 30% is difficult to attain, and therefore break-even is not economically feasible.

It is noted that majority of the existing grafting research work is in the greenhouse production system but few studies that are systematic with reference to compatibility of grafted varieties in direct field and performance of grafted seedlings under varying climatic conditions are available. Hence, the adaptability, stress stability and affinity of rhizomes to open-air cultivation systems needs to be carefully considered in order to enhance the ubiquitous use of grafting technology in the production systems of the given field.

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