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Regulation of Fruit Sugar Accumulation by Humidity Control Techniques in Protected Melon Cultivation

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Abstract This study discusses how controlling air humidity in protected cultivation can influence the sugar accumulation of melon fruits, explaining how humidity affects the transportation of photosynthetic products, the formation of fruit "sink", the activity of enzymes related to sugar synthesis, and the expression of related genes. It also analyzes how humidity interacts with other factors, such as temperature and light. The performance of several different humidity management methods in actual planting was summarized. The response differences of different melon varieties under different humidity conditions were also compared, and their potential in breeding was discussed. This study aims to provide some theoretical and technical references for improving the quality of melons and promoting intelligent planting.
Keywords Melon breeding; Humidity regulation; Sugar accumulation; Protected cultivation; Molecular regulation

1 Introduction

The sweetness of melons is an important criterion for evaluating their quality and market appeal. Melons with high sugar content taste better, are more acceptable to consumers, and are also more expensive (Albuquerque et al., 2006; Freilich et al., 2015; Ren et al., 2023). Therefore, whether it is breeding or planting management, increasing the sugar content in fruits is an important goal.

Protected cultivation such as greenhouses or plastic sheds can artificially regulate the environment (Sabir and Singh, 2013). It can help melons avoid bad weather and extend the planting time, which is conducive to increasing yield and quality. In this environment, temperature and humidity can be regulated to better meet the growth requirements of melons, thereby enabling better accumulation of sugar in the fruits (Buczkowska et al., 2023).

This study mainly explored how to control air humidity in protected cultivation to influence sugar accumulation in melon fruits, and further analyzed the related physiological changes and molecular mechanisms. This study hopes that these results can provide some theoretical support and assistance in planting techniques for improving the quality and industrial benefits of melons.

2 Physiological Basis of Sugar Accumulation in Melon Fruit

2.1 Photosynthate production and translocation pathways

The sugar in melon fruits mainly comes from the photosynthesis of the leaves. The sugars produced by leaves, especially sucrose, are transported through the phloem to "sink" sites such as fruits. This transportation process requires the collaboration of some sugar metabolism enzymes and sugar transporters to deliver sugar from the "source" (that is, the leaves) to the "sink" (that is, the fruits) (Ren et al., 2023).

2.2 Sink strength and carbohydrate allocation during fruit development

Whether a fruit can consume more sugar mainly depends on its "sink strength". "Sink strength" refers to the ability of fruits to absorb and store photosynthetic products. This ability will increase with the growth of the fruit and is also regulated by genes and hormones (Ren et al., 2023). During the growth of melons, the "sink strength" of the fruit gradually increases, enabling it to absorb and accumulate more carbohydrates. Key enzymes such as sucrose phosphosynthase (SPS) control the process of sucrose production and affect the amount of sugar (Gao et al., 2023). Therefore, changes in sink strength will directly affect the final sugar content and quality in the fruit.

2.3 Temporal pattern of sugar composition during ripening

During the process of fruit ripening, the sugar content inside will also gradually change. At the beginning, reducing sugar and starch were mainly used. When the fruit was nearly ripe, the activity of sucrose synthase and sugar transporter became stronger, and sucrose would increase rapidly and become the main sugar. The signal transduction of ethylene and some transcription factors (such as CmMYB44, CmERFI-2) can regulate the key genes of sucrose synthesis, thereby facilitating sucrose accumulation (Gao et al., 2023). In addition, environmental factors such as low temperature can also affect ethylene production and the activity of glucose metabolism enzymes, thereby changing the rate and total amount of sugar accumulation (Yang et al., 2025).

3 Environmental Factors Affecting Sugar Accumulation in Protected Cultivation

3.1 Overview of microclimatic variables: temperature, light, CO_2, and humidity

Temperature can directly affect the activity of enzymes that control sugar synthesis, regulate ethylene production, and influence sucrose accumulation and fruit ripening (Gao et al., 2023; Yang et al., 2025). Light provides energy and is the foundation of photosynthesis. The sugar produced by the leaves is transported to the fruits by it. Ren et al. (2023) thought that the concentration of carbon dioxide affects the rate of photosynthesis and indirectly influences the synthesis and transportation of sugar. Humidity affects the opening and closing of stomata, the intensity of transpiration and the flow of water, ultimately influencing whether sugar can be smoothly transported into the fruit.

3.2 Unique challenges of humidity control under enclosed conditions

In facilities like greenhouses and sheds, humidity regulation can be more troublesome. Due to the closed space and poor air circulation, it is very easy for the humidity to be too high or too low. These changes will affect the accumulation of sugar. When the humidity is too high, transpiration weakens and sugar is not easily transported away from the leaves. When the humidity is too low and there is insufficient moisture, the fruit cells may not function properly (Ren et al., 2023). Moreover, humidity is also related to the occurrence of diseases and the improvement of fruit quality, making its management more complicated.

3.3 Interactions between humidity and other abiotic factors

At low temperatures, if the humidity changes, it may affect the production of ethylene, influence some genes that regulate sugar, and thereby affect the sucrose content and the flavor of melons (Gao et al., 2023; Yang et al., 2025). Humidity may also alter the activity of glucose metabolism enzymes and glucose transport proteins, which can affect how sugar is distributed and stored in the fruit (Ren et al., 2023). Buczkowska et al.'s research in 2023 found that humidity also plays a role in conjunction with irrigation. When the two work well together, they can significantly increase the total sugar and reducing sugar content in melon fruits.

4 Role of Humidity in Melon Sugar Metabolism

4.1 Influence on transpiration, stomatal conductance, and plant water status

Environmental humidity directly affects the transpiration rate and stomatal conductance of melons. When the air humidity is high, it will weaken evaporation and reduce water loss. However, in this case, the stomatal conductance of the leaves may also decrease, and the efficiency of water and nutrient transport will be affected. Jeenprasom et al. (2019) found that under high humidity conditions, the plant height and leaf area of melons were slightly smaller than those under normal humidity conditions, indicating that appropriate transpiration is actually beneficial for maintaining water balance and normal growth.

4.2 Impact on sugar transport via phloem loading and unloading

Humidity can also affect the accumulation of sugar in melon fruits, as it can alter the efficiency of sugar transport in the phloem. Under high humidity, the TSS content of the fruit will significantly decrease, indicating that high humidity may cause the sugar in the leaves to be unable to transport or transport slowly, resulting in less sugar in the fruit (Jeenprasom et al., 2019). Appropriate humidity can maintain the pressure gradient in the phloem, which is crucial for the smooth flow of sugar to the fruit.

4.3 Regulation of enzymatic activity in sugar biosynthesis under different humidity levels

Changes in humidity can also affect the activity of enzymes related to sugar metabolism. Studies have found that in melons planted in spring (with low humidity), the contents of soluble sugar, sucrose phosphate synthase (SPS), and sucrose synthase (SS) are all higher than those in autumn (with high humidity), indicating that a low-humidity environment is more favorable for the activities of these enzymes and conducive to sugar synthesis and accumulation (Diao et al., 2022). As the fruit ripens, the activities of enzymes such as acid invertase, neutral invertase and sucrose synthase usually increase first and then decrease. Humidity affects the amount of sugar in the fruit indirectly by influencing their activity (Wu et al., 2020).

5 Humidity Control Technologies in Protected Melon Cultivation

5.1 Passive vs. active ventilation systems

Passive ventilation mainly relies on the structure of the greenhouse, such as the roof and side Windows, to allow air to circulate naturally, thereby regulating temperature and humidity. Active ventilation uses equipment such as fans to forcibly drive the air, achieving a faster and more obvious regulatory effect. Seo et al. (2022) pointed out that relying solely on rooftops and side Windows for ventilation has very limited effects in summer, as the temperature cannot be lowered and the humidity is difficult to control. If active ventilation is added, such as using circulating fans, the situation will improve a lot. Seo et al. (2022) also found that when the atomization system is used in conjunction with the circulating fan, it can reduce the temperature in the greenhouse by 3.2°C to 7.0°C and increase the humidity by 12% to 28%. This is beneficial for the melon to grow taller and can also enhance its sweetness and texture. Using fans for ventilation in high temperatures also helps reduce pests and diseases, allowing plants to grow better.

5.2 Fogging, misting, and dehumidification devices

Fogging and misting devices can increase air humidity and counteract the negative impacts brought by high temperatures and droughts. Experiments show that this method can help melons grow faster and have better fruit quality. However, if the humidity is too high, the fruit weight and sugar content of melons will decrease instead. Therefore, the humidity should be controlled within an appropriate range (Jeenprasom et al., 2019). When the humidity is too high, using dehumidification equipment can lower it, prevent diseases from occurring, and also protect the quality of the fruits. Different humidity control methods will all have an impact on the growth time, fruit weight and stress resistance of melons. Reasonable humidity regulation can not only make the fruits grow better, but also prolong the harvest time and increase the total yield (Adinegara et al., 2017).

5.3 Sensor-based smart control systems for humidity optimization

Nowadays, many melon greenhouses have begun to adopt intelligent control systems that combine the Internet of Things (IoT) and various sensors. These systems can monitor temperature, humidity and light in real time, and then automatically control devices such as fans, atomizers and heaters to achieve relatively precise regulation (Figure 1) (Parenreng et al., 2024; Supriyanto et al., 2025). Furthermore, machine learning algorithms such as XGBoost and VAR have also been used to predict environmental changes and make regulatory responses in advance, which helps melons accumulate sugar and improve quality (Jeon et al., 2024). Some low-cost and easy-to-operate intelligent systems have also begun to be promoted, enabling small and medium-sized farmers to use scientific humidity management solutions.

6 Genotypic Variation in Melon Response to Humidity

6.1 Differential sugar accumulation under varying humidity among cultivars

Different melon varieties show significantly different performances under changes in humidity. When the humidity is high, some varieties grow larger fruits and have a longer harvest time. However, some varieties perform better in drought or low-humidity environments, not only being drought-resistant but also having a relatively high yield (Adinegara et al., 2017). The sugar content is greatly influenced by the interaction between environmental humidity and varieties. Neto et al. (2025) demonstrated that different melon hybrids respond differently to humidity, with some being particularly sensitive to it and others having strong adaptability.

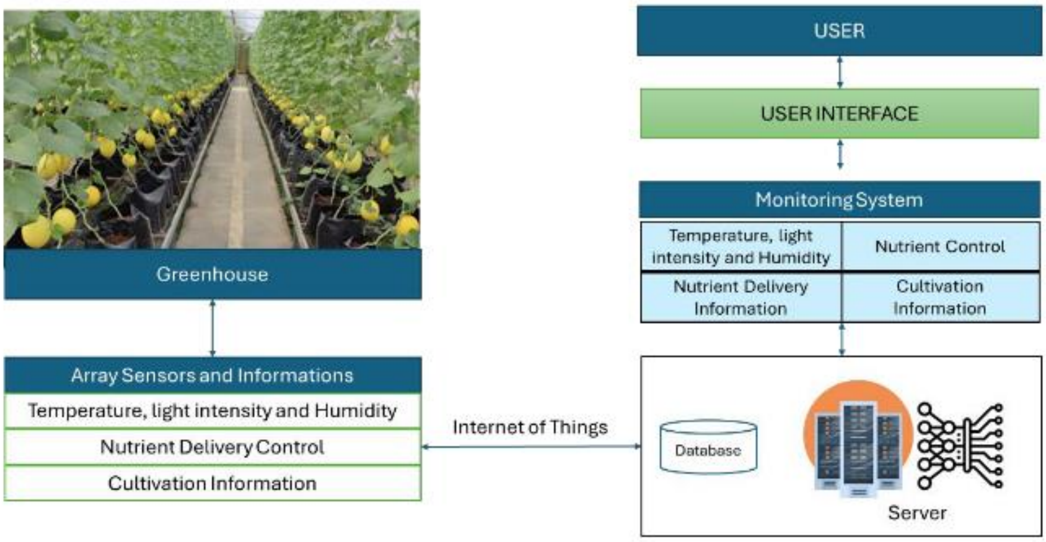

Figure 1 Schematic diagram of the monitoring system using Internet of Things (Adopted from Supriyanto et al., 2025)

6.2 Genetic markers linked to humidity tolerance and sugar traits

Through the analysis of plant physiological responses and transcriptome, researchers found that some melon varieties that are tolerant to high temperature and high humidity have advantages in antioxidant enzyme activity, leaf water content and the expression of photosynthetically related proteins (Weng et al., 2022). These characteristics may be related to moisture resistance and sugar accumulation, and can be used as reference indicators for breeding moisture-tolerant and high-sugar varieties. There are also some graphical analysis methods like "genotype-trait-yield (GYT)" that can help identify good varieties with high yield and strong resistance (Rad et al., 2025).

6.3 Implications for breeding humidity-resilient high-sugar melon varieties

Because different varieties respond differently to humidity, during breeding, good genes can be selected by combining molecular markers and some agronomic traits. By testing the sugar accumulation and stability of different varieties in multiple environments, it is possible to more quickly screen out those good varieties that can maintain stable high yields and high sugar content under various humidity conditions. This is of great help for the quality improvement and stress-resistant breeding of melons under facility conditions such as greenhouses (Weng et al., 2022; Neto et al., 2025; Rad et al., 2025).

7 Hormonal and Molecular Regulation Mediated by Humidity Signals

7.1 Hormonal crosstalk (ABA, ethylene) under high/low humidity

Ethylene is an important hormone that controls the ripening of melons and the increase of sugar content. When the temperature is low and the humidity is high, ethylene synthesis decreases. For example, the expression of the *CmACO1* gene will decline, thereby slowing down starch decomposition and sucrose accumulation (Lao et al., 2023; Guan et al., 2024). Some ethylene-responsive factors (such as *CmERFV-2* and *CmERFI-5*) regulate genes related to ethylene synthesis and glucose metabolism, sometimes promoting and sometimes inhibiting, which directly affects the sweetness of melons (Gao et al., 2023; Yang et al., 2025). ABA (abscisic acid) is also related to sugar accumulation. Although its role in melons is not yet fully understood, in watermelons, studies by Durán-Soria et al. (2020) and Wang et al. (2023b) found that ABA-related genes (such as *SnRK2.3*) delay fruit ripening and affect sugar levels by controlling the synthesis of ABA and sucrose.

7.2 Expression patterns of sugar metabolism-related genes

During the growth and ripening of fruits, the genes related to sugar metabolism constantly change. Genes such as sucrose phosphosynthase (*CmSPS1*), sucrose synthase (SS), acid or neutral invertase (AI/NI), and sucrose transporter (CmSWEET10) usually have increased expression levels near fruit ripening, which contributes to sugar synthesis and accumulation (Schemberger et al., 2020; Zhou et al., 2023). In different types of melons, *CmSPS1* promotes sucrose synthesis in all fruits, while sucrose synthase 2 is expressed more in respiratory leap varieties, whose hexose levels are generally lower (Dai et al., 2011; Stroka et al., 2024). Some transcription factors, such as CmMYB44 and CmERFI-2, also affect sugar accumulation by regulating the expression of key genes (such as *CmSPS1* and *CmACO1*) (Figure 2) (Gao et al., 2023; Wang et al., 2023a). Other genes related to glucose metabolism, such as *CmINH3*, *CmTPP1*, and *CmTPS5/7/9*, also have special expressions at the fruit ripening stage, suggesting that they may also be involved in regulating glucose accumulation.

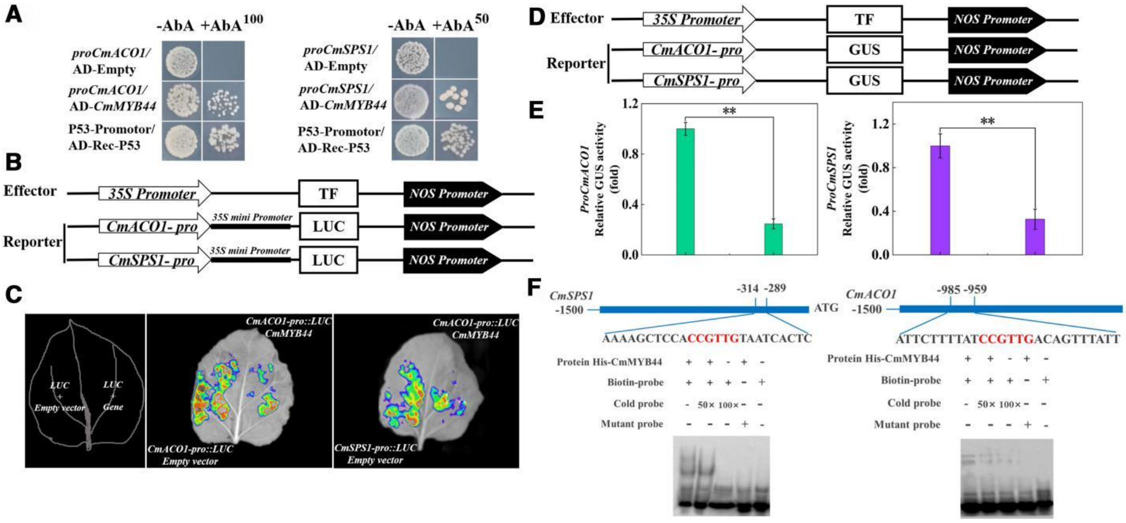

Figure 2 CmMYB44 directly binds to the promoters of *CmSPS1* and *CmACO1* and acts as a transcriptional repressor (Adopted from Gao et al., 2023)

Image caption: A) Y1H analysis of CmMYB44 binding to the promoters of *CmSPS1* and *CmACO1*. The growth status of transformed yeasts on two mediums. Normal yeast growth on a defective medium containing the antibiotic Aureobasidin A indicates CmMYB44 can bind to the promoters of *CmSPS1* and *CmACO1*. B and C) Luciferase reporter assay showed the binding of CmMYB44 to the *CmSPS1* and *CmACO1* promoters in vivo. The infected *Nicotiana benthamiana* was measured by a living fluorescence imager. The fluorescence intensity weaker than control (empty vector) means that CmMYB44interacts with promoter, and represses the gene expression. D and E) GUS activity assays analysis of CmMYB44 binding to the *CmSPS1* and *CmACO1* promoters in N. benthamiana leaves. Relative GUS activity decreasing indicates transcriptional regulation is repressed. An independent t-test was used to analyze the difference between the treatment group and control. Significant differences are marked with asterisks (**P < 0.01). Error bars are shown with the three biological replicates. F) Electrophoretic mobility shift assay (EMSA) analysis of CmMYB44 binding to the *CmSPS1* and *CmACO1* promoters. The hot probe was biotin-labeled *CmSPS1* and *CmACO1* promoters, while the cold probe was a nonlabeled competitive probe (with a 50/100-fold higher concentration than the hot probe). His-tagged CmMYB44 (CmMYB44-His) was purified and used for DNA-binding assays. The sequence of the biotin-labeled probe is shown and the CCGTTG motif is highlighted in bold (Adopted from Gao et al., 2023)

7.3 Potential gene targets for regulating sugar accumulation under humidity stress

There are some key genes that can be targeted for improvement regarding the impact of humidity on sugar content. *CmACO1*, *CmERFV-2*, and *CmERFI-5* in the ethylene pathway, *CmSPS1* and *CmVINV2* in sucrose metabolism, *CmSWEET10* in glucose transport, and the transcription factors *CmMYB44* and *CmPIF8* that regulate them, are all very important targets (Zhou et al., 2023; Guan et al., 2024; Yang et al., 2025). Wen et al. (2025) indicated that proteins like CmFLA8 might also have an inhibitory effect on fruit development, and their expression would be influenced by hormones and stress signals. If these key genes can be controlled through gene editing or molecular markers, it is possible to improve the sugar accumulation capacity and fruit quality of melons under different humidity conditions (Lao et al., 2023; Ren et al., 2023).

8 Case Study: Controlled Humidity Effects on Sugar Accumulation in Greenhouse Melons

8.1 Experimental design: RH treatments in commercial greenhouses

In commercial greenhouses, researchers often observe the growth of melons and changes in fruit quality by adjusting the air humidity (RH). Some experiments set normal humidity and fogging treatment (increasing humidity), and combined with different substrate moisture contents (such as 100%, 130%, 160% field capacity) to systematically study the effects of humidity on melon growth and sugar accumulation (Jeenprasom et al., 2019). When the temperature is high in summer, there are also studies that use atomization systems and air circulation fans to increase humidity while cooling down, in order to simulate the management methods in real production.

8.2 Measurement of sugar content, enzyme activity, and fruit quality

Brix, central sugar content and total sugar content of the fruit are commonly used indicators for judging sugar accumulation (Jeenprasom et al., 2019). Diao et al. (2022) found that the activities of sugar metabolism enzymes such as sucrose phosphate synthase and sucrose synthase would also be measured to understand how sugar is synthesized and accumulated. Jeenprasom et al.'s experiment in 2019 found that under low humidity (normal conditions), the single fruit weight and Brix value of melons were higher than those treated with high humidity (fogging). However, after moderately increasing the humidity under the atomization system, the fruit weight and sugar content actually rose. The fruit weight increased by approximately 300 g, and the Brix increased by 1.5. This indicates that an appropriate increase in humidity is beneficial to fruit quality. Wang et al. (2022) also indirectly adjusted soil moisture by covering it with degradable film, promoting sugar accumulation and quality improvement.

8.3 Practical insights for growers on optimizing humidity regimes

Several studies suggest that when growing melons in greenhouses, the air humidity should be well controlled. Too high humidity will reduce the sweetness and quality of fruits. However, in hot weather, temporarily increasing humidity can reduce heat damage and promote sugar accumulation. The water content of the substrate is best controlled around 100% of the field capacity. If there is too much water, the fruit quality will decline (Jeenprasom et al., 2019). The combined use of degradable films and intelligent prediction systems is helpful for more precise regulation of greenhouse humidity, thereby increasing the yield and sugar level of melons (Wang et al., 2022; Jeon et al., 2024).

9 Challenges and Research Gaps

9.1 Integration of environmental control with plant physiology

Nowadays, many studies mainly focus on how humidity affects the quality of melon fruits, such as their sweetness. However, there is still insufficient understanding of the relationship between humidity and some physiological processes within plants, such as the activity of sugar metabolism enzymes and the synthesis of ethylene. Studies have found that changes in temperature and humidity can affect the contents of soluble sugar and sucrose synthase in melon fruits, but it is not very clear how these changes cooperate with cell wall enzymes and ethylene signaling (Diao et al., 2022). In addition, it is not quite clear at present how to precisely act on these molecular regulatory links by adjusting environmental conditions to enable fruits to accumulate sugar more efficiently (Gao et al., 2023; Yang et al., 2025).

9.2 Lack of long-term and multi-environment field trials

At present, many studies are conducted in greenhouses and the experimental time is relatively short. There is not yet sufficient long-term field trails on melons grown under different climates, soil conditions and planting methods. For instance, the current data on whether humidity control is effective in different varieties, seasons or irrigation methods is not comprehensive enough (Diao et al., 2022; Buczkowska et al., 2023). So it is still very difficult to formulate a universal, stable humidity management solution suitable for large-scale promotion at present.

9.3 Need for predictive models linking humidity profiles to sugar outcomes

Although many people have noticed that humidity can affect sugar accumulation, there is still no model that can accurately predict the impact of humidity changes on sugar. Most studies have only made qualitative descriptions and have not integrated multi-faceted information such as environmental data, enzyme activity and gene expression into a mathematical model (Diao et al., 2022; Gao et al., 2023; Yang et al., 2025). In the future, it can be considered to utilize big data and molecular physiological indicators to establish predictive tools, which can help regulate humidity more precisely and make the sugar content of melons increase more stably.

10 Concluding Remarks

Air humidity directly affects the accumulation of sugar in melon fruits. Generally speaking, when the air humidity is low, the content of soluble sugar in fruits will be higher, and the activities of sucrose phosphate synthase (SPS) and sucrose synthase (SS) will also increase, which is conducive to sugar accumulation. Humidity changes can also indirectly affect the activity of enzymes related to sucrose synthesis and decomposition by regulating the synthesis of ethylene and the expression of some key transcription factors. For instance, some ethylene reaction factors (CmERFI-2, CmERFI-5, CmERFV-2) regulate genes related to glucose metabolism (such as *CmSPS1*, *CmVINV2*, *CmACO1*), thereby influencing the accumulation of sucrose and reducing sugars. In addition, the combination of temperature and humidity can also affect the activity of cell wall enzymes, which will change the taste of the fruit and the speed of sugar conversion.

In recent years, environmental monitoring and automatic control technologies in greenhouses have developed rapidly. Now, air and soil humidity can be monitored in real time through sensors, and combined with automatic irrigation and ventilation systems, the growth environment of melons can be precisely controlled. This not only enables more timely regulation of humidity but also automatically adjusts the conditions according to the different growth stages of melons, ensuring better quality and yield of the fruits.

In the future, research still needs to integrate environmental science, molecular biology and crop breeding to deeply understand how environmental factors such as humidity affect sugar accumulation at the molecular level. On the one hand, it is possible to continue studying the differences in the responses of various melon varieties to humidity to identify which varieties are suitable for precise humidity management in greenhouses. On the other hand, combining automated environmental control technology with molecular marker breeding is expected to achieve a complete technical chain of “environmental regulation - gene optimization - quality improvement”.

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Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

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