Effects of Water Stress on Grape Sugar Content and Sucrose-Metabolizing Enzyme Activity (Postprint)

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Abstract

To analyze the effects of water stress on fruit sugar composition and related metabolic enzyme activities, a field experiment was conducted using greenhouse table grape cultivar 'Red Globe' as experimental material, with four water treatment levels (severe water stress TS, moderate stress TA, mild stress TM, and well-watered control CK). The results indicated that sugar accumulation in Red Globe grape berries was predominantly hexoses (fructose and glucose); at fruit maturity, all categories of sugar content were highest under mild stress treatment and lowest under severe stress; sufficient water supply during the early fruit expansion stage combined with mild stress during the late expansion stage and the coloring-maturation period facilitated effective sugar accumulation in berries; mild stress promoted both sucrose metabolic enzyme activity and fruit quality in grapes, with a yield increase of 12.15%, whereas severe stress exhibited strong inhibitory effects, resulting in an 18.6% yield reduction. Fruit sugar metabolism represents the integrated outcome of related enzyme activities, with water stress indirectly regulating it through effects on enzyme activity.

Full Text

Abstract

To analyze the effects of water stress on fruit sugar component content and related metabolic enzyme activity, field experiments were conducted using greenhouse table grape Red Globe as test material under four water treatment levels: severe water stress, moderate stress, mild stress, and fully irrigated control. Results showed that sugar accumulation in Red Globe grape fruit is dominated by hexose (fructose and glucose). At fruit maturity, the content of various sugar types was highest under mild stress treatment and lowest under severe stress. Sufficient water supply during the early fruit expansion period, combined with mild stress at the end of the expansion period and during the coloring and maturation period, facilitated effective sugar accumulation in fruit. Mild stress promoted sucrose metabolism enzyme activity and quality in grape fruit while increasing yield by 12.15%, whereas severe stress showed strong inhibition with yield reduction reaching 18.6%. Fruit sugar metabolism results from the combined effects of related enzyme activities, which are indirectly regulated by water stress through its influence on enzyme activity.

Keywords: water stress; greenhouse grape; sugar accumulation; enzyme activity; fruit quality

Introduction

Rising living standards have driven growing market demand for off-season fruits, and greenhouse fruit cultivation satisfies the need for fresh fruit availability during the off-season. In the cool regions of northwest China, large diurnal temperature differences give greenhouse grapes distinct economic advantages through light avoidance in spring and warming in winter, leading to significant economic benefits and rapid development. However, large-scale promotion has made consumer demands for off-season grape quality increasingly stringent, making high-quality stable production a critical scientific challenge for sustainable greenhouse grape development. Previous studies have shown that controlling water use efficiency or applying varying degrees of water stress during different grape growth periods can improve grape yield while promoting sugar accumulation. Some reports also indicate that moderate water stress can enhance certain enzyme activities. However, few studies have reported on the response mechanism of greenhouse grape sugar accumulation and sucrose synthesis enzyme activity to water stress.

Sugar composition and content in grape (*Vitis vinifera*) fruit are key factors affecting quality and important indicators for judging fruit maturity. Sucrose, widely present in plants, serves as an energy substance and material synthesis raw material while also participating in sugar signal transduction. For sucrose to be utilized within the fruit, it must undergo a series of metabolic processes involving related enzymes to be converted into usable forms. Sucrose synthase (SS), sucrose phosphate synthase (SPS), and sucrose invertase (Inv) play irreplaceable roles in this metabolic process. Water is an indispensable factor for all living organisms to maintain life activities, and water deficiency has become a decisive environmental factor affecting the growth and yield formation of economic plants. In the cool regions of northwest China, greenhouse grape cultivation holds significant economic importance, but relative soil water deficiency constrains grape growth and development.

This study used greenhouse Red Globe grape as test material to analyze the physiological relationship between sugar accumulation and sucrose metabolism-related enzyme activity under water stress conditions, as well as its mechanism of action on grape yield and quality. The aim was to provide a theoretical basis for improving water regulation models for greenhouse grapes in northwest cool regions and further elucidating the formation and regulation mechanisms of grape quality.

1 Materials and Methods

1.1 Experimental Site Overview

The experiment was conducted from March to September 2019 at the facility cultivation grape test base in Yongdeng County, Lanzhou City, Gansu Province, located at 102°36 ~103°45 E, 36°12 ~37°07 N. The area is in a semi-arid region with a continental climate, annual average temperature of 5.9°C, and annual precipitation of 290 mm, approximately 1/14 of the evaporation rate. The soil in the test area is primarily loam with a bulk density of 1.42 $g \cdot cm^{-3}$ and field capacity of 27.2%.

1.2 Experimental Design

The experiment used four-year-old Red Globe grapes cultivated at a row spacing of 2.0 m and plant spacing of 0.8 m in a soil-wall straw-curtain greenhouse with single-arm Y-shaped dwarf trellis. Based on irrigation test specifications, the greenhouse grape growth period was divided into three phenological stages (Table 1). A single-factor completely randomized water regulation experiment was conducted with four treatments throughout the growth period: severe water stress (W_1), moderate water stress (W_2), mild water stress (W_3), and fully irrigated control (W_4). The lower limits of soil average water content as a percentage of field capacity (_f) for the 0–80 cm layer were 45%$±5±5±5±$5%, respectively, with upper limits of 60%, 70%, 80%, and 90%, respectively. Each treatment had three replications randomly distributed, with each plot area being 6 m × 2 m. Drip irrigation was used, with one drip line laid on the same side of each row, controlled by valves before each branch. Irrigation timing was determined by measured soil water content. When the average soil water content (0–80 cm) reached the designed lower limit, irrigation was applied with a quota of 270 $m^3 \cdot hm^{-2}$, bringing each treatment' s soil water content to its respective upper limit. A 60 cm thick polyethylene geomembrane was laid between plots to prevent soil water diffusion. All fertilization, pruning, pest control, and weeding measures were consistent with local greenhouse grape cultivation management practices.

1.3 Measurement Items and Methods

1.3.1 Soil Water Content Three measurement points were selected along the grape row direction at one-third of the length from each end on the same side, 10 cm from the trunk. Soil samples were taken at depths of 20 cm, 40 cm, 60 cm, and 80 cm using the drying method (oven model 9036A at 105°C) to determine water content at each depth. The water content at each measurement point was the arithmetic mean of values at all depths, and the plot water content was the average of the two measurement points. Samples were taken every 7 days throughout the growth period, with additional measurements before and after irrigation when soil water content approached the control lower limit.

1.3.2 Yield and Growth Indicators In each plot, three grape vines were selected from the front, middle, and back sections. On each plant, three vines were marked with red string, and the main stem length was measured with a tape every 7 days. The stem diameter at upper, middle, and lower positions was measured with vernier calipers and averaged. Three fruit clusters were selected on each test plant, with three representative berries chosen from upper, middle, and lower positions on each cluster. Berry vertical and transverse diameters were measured every 7 days with vernier calipers. During rapid growth, measurements were taken every 7 days; during slow growth, every 14 days. At grape maturity, 30 uniformly growing, healthy berries were selected from each test plant to measure size and weight. Each plot was harvested and sealed separately, and yield was measured with a 0.01 kg precision electronic balance (GB/T7722-2005) and converted to standard yield ($kg \cdot hm^{-2}$).

1.3.3 Quality and Sucrose Metabolism Enzyme Activity Three uniformly growing vines were selected for each treatment, with approximately 90 berries randomly sampled each time and placed in an ice box for laboratory analysis. The flesh was separated with a blade, collected, and stored at -80°C. Following the methods of Long et al. [cite], titratable acid was determined by titration, anthocyanin by spectrophotometer, vitamin C by 2,6-dichlorophenolindophenol titration, soluble solids by handheld sugar meter, and glucose content by high-performance liquid chromatography.

SS and SPS activities were determined following the methods of Guo et al. [cite], while Inv activity was determined following Xu et al. [cite].

1.4 Data Processing

Data on grape growth, fruit quality, and enzyme activity indicators were statistically analyzed using Excel 2013. SPSS 21.0 was used for significance and correlation analysis of grape growth and fruit quality indicators.

2 Results

2.1 Effects of Water Stress on Greenhouse Grape Growth and Development

As shown in Table 2 , under water stress conditions, all growth indicator values were largest in the W_3 treatment, with yield and average single fruit weight increasing by 12.15% and 3.12% compared to the fully irrigated control (W_4), though differences were not significant. The W_1 treatment reduced these metrics by 18.60% and 29.57%, respectively, significantly lower than W_4. The fruit shape index in W_3 was 3.53% higher than W_4, but no significant differences existed among treatments. The stem diameter and length growth rates in W_3 increased by 14.89% and 38.30%, respectively, compared to W_4, while W_1 decreased them by 12.94% and 23.91%, respectively, with no significant differences among treatments. These results indicate that mild water stress benefits grape yield increase, while severe stress significantly reduces yield, though water variation has relatively minor effects on stem diameter and length.

2.2 Effects of Water Stress on Fruit Sugar Content and Quality

2.2.1 Effects on Sugar Components During Fruit Development Figure 1 [Figure 1: see original paper] shows that grape fruit primarily accumulates glucose and fructose, with total sugar content showing an overall upward trend during fruit development, though the increase rate varies among sugar types and periods. Under water stress, total sugar content in all treatments showed a "fast then slow" continuous growth trend (Figure 1a [Figure 1: see original paper]). The growth rate during fruit expansion (March 30–May 10) was significantly higher than during coloring and maturation (May 10–June 6), though the rate varied among treatments. The W_3 treatment maintained the highest total sugar content throughout the growth period, while W_1 remained the lowest. On June 6 (coloring and maturation period), total sugar content in W_3 reached 17.26%, significantly higher than W_4 (9.09%) and W_1 (8.23%), with no significant difference between W_4 and W_2. This indicates that mild water stress contributes to total sugar accumulation.

Sucrose content in all treatments showed a slow 微量增长 trend throughout fruit development (Figure 1b [Figure 1: see original paper]). The fastest growth rate occurred from March 30 to April 20 (early fruit expansion), but differences among treatments were not significant. On June 6, sucrose content was highest in W_3, not significantly different from W_4 but significantly higher than W_1 and W_2. From May 10 to June 6, the sucrose content growth rate in all treatments was slower than in the previous period, with W_3 and W_4 showing similar rates that gradually leveled off, while W_1 and W_2 growth rates decreased significantly.

Fructose content in all treatments gradually increased with fruit development (Figure 1c [Figure 1: see original paper]), though growth rate patterns varied considerably. From March 30 to April 20, fructose content was highest in W_1, significantly higher than W_3 but not significantly different from W_2 and W_4. During mid-to-late fruit expansion (April 20–May 10), fructose content increased rapidly, with W_3 showing the fastest growth rate at $14.39\% \cdot d^{-1}$, significantly higher than W_1 ($7.65\% \cdot d^{-1}$) but not significantly different from W_2 and W_4. From May 10 to June 6 (coloring and maturation), fructose content was highest in W_3 and W_4, significantly higher than W_1, with no significant difference between them. This demonstrates that mild stress during mid-to-late fruit expansion and coloring maturation benefits fructose accumulation, while severe stress is detrimental.

Glucose content in all treatments increased gradually with fruit development

(Figure 1d [Figure 1: see original paper]), though growth rate patterns differed. During fruit expansion (March 30–May 10), W_1 showed the fastest growth rate at $0.17\% \cdot d^{-1}$. From late fruit expansion to early coloring maturation (May 10–May 24), W_3 grew fastest at $0.15\% \cdot d^{-1}$, while W_1 grew slowest at $0.05\% \cdot d^{-1}$. During coloring maturation (May 24–June 6), W_3 and W_4 had similar growth rates ($0.07\% \cdot d^{-1}$ and $0.02\% \cdot d^{-1}$, respectively), both significantly higher than W_1 ($0.03\% \cdot d^{-1}$). These results show that sufficient water supply during early fruit expansion and mild stress during late expansion and coloring maturation help accumulate effective sugars.

2.2.2 Effects on Fruit Flavor Quality Indicators Greenhouse grape fruit flavor quality indicators were affected by water stress (Table 3). Soluble solids and anthocyanin content followed the order: $W_3 > W_2 > W_4 > W_1$. Soluble solids content in W_3 was 27.32% higher than W_4, and anthocyanin content was 23.91% higher, both significantly different, while W_2 and W_4 showed no significant differences. Vitamin C content in W_3 was significantly higher than W_1 and W_2 but not significantly different from W_4. Titratable acid content was highest in W_1, significantly different from other treatments and 52.67% higher than W_4. W_2 was second highest, also significantly higher than W_3 and W_4, while W_3 was lowest but not significantly different from W_4. These results indicate that moderate and severe water stress promote titratable acid content, increasing fruit astringency, while mild stress not only reduces acidity but also promotes vitamin C accumulation and improves fruit flavor quality.

2.3 Effects of Water Stress on Sucrose Metabolism Enzyme Activity

Under water stress conditions, enzyme activity patterns over time remained fundamentally unchanged, though significant differences existed among treatments (Figure 2 [Figure 2: see original paper]). SS activity showed a "decrease-increase-decrease" trend (Figure 2a [Figure 2: see original paper]), reaching its lowest point on May 10 (fruit expansion period) and peaking on May 24 (coloring maturation period). W_3 maintained the highest SS activity throughout, while W_1 remained the lowest. SPS activity showed a "rapid increase then sharp decrease" pattern (Figure 2b [Figure 2: see original paper]), peaking on May 24 in all treatments. W_3 activity was significantly higher than W_1 and W_2 but not significantly different from W_4. Acid invertase (AI) activity showed a single-peak "increase then decrease" pattern (Figure 2c [Figure 2: see original paper]), peaking on May 24 (coloring maturation period) in all treatments. W_3 activity was significantly higher than W_1 and W_2 but not significantly different from W_4. Neutral invertase (NI) activity increased slowly throughout fruit development (Figure 2d [Figure 2: see original paper]), consistent with the trend of sucrose content change. On May 24, NI activity reached its maximum in all treatments, with W_3 significantly higher than W_1 and W_2 but not significantly different from W_4.

2.4 Correlation Between Fruit Sugar Content and Sucrose Metabolism Enzyme Activity

Correlation analysis (Table 4) showed that Red Globe grape fruit sugar content was closely related to sucrose metabolism enzyme activity. SS activity was extremely significantly positively correlated with total sugar and glucose content and significantly positively correlated with fructose. SPS activity was significantly positively correlated with total sugar, glucose, and fructose. No significant correlations existed between enzyme activities and sucrose content. NI activity showed positive correlations with all sugar types but without significance. These results indicate that SS is a key enzyme regulating glucose and fructose, particularly a determinant for glucose accumulation, while SPS has some influence on final sugar accumulation but the effect is not obvious.

3 Discussion

Scientific water management is crucial for greenhouse grape growth and intensive water resource utilization. Water regulation for quality improvement is considered one of the safest measures to enhance grape quality. Moderate water deficit can inhibit fresh weight increase while improving sugar content and fruit quality. The results show that mild and moderate water stress positively affected soluble solids and anthocyanin accumulation, while severe deficit was detrimental. Moderate and severe stress promoted titratable acid content, while mild stress not only reduced astringency but also promoted vitamin C accumulation. Under mild stress, grape total yield increased by 12.15% compared to the control, while severe stress reduced yield by 18.6%, which is unfavorable for yield formation and significantly affects fruit shape.

Red Globe grape fruit primarily accumulates glucose and fructose (hexoses). At maturity, fructose and glucose contents under mild stress were significantly higher than the control and significantly higher than under severe stress. Studies have confirmed that timely moderate water stress can effectively inhibit ineffective shoot growth, increase the effective content of photosynthetic products transferred to fruit, and improve economic yield. Severe drought stress significantly reduces fruit sugar content, likely because severe water deficit cannot meet normal plant metabolic water requirements, inhibiting photosynthesis and affecting assimilate transport, which is consistent with this study' s conclusions.

Grape fruit sugar content is mainly determined by the sugar accumulation process. Sugar accumulation is the sucrose metabolism process where photosynthates from source organs (leaves) are transported via phloem and unloaded into fruit. As a metabolic storage sink, grape fruit' s ability to obtain assimilates during ripening depends on sink strength, which is determined by sucrose metabolism-related enzyme activity. Therefore, enzyme activity should be decisive for fruit sugar accumulation. Various measures such as applying water-retaining agent adsorbed urea or foliar selenium spraying can regulate glucose accumulation and metabolism by changing related enzyme activities. Studies show that sucrose unloading in grape fruit shifts from symplastic to apoplastic pathways during the peak hexose accumulation period, and apoplastic unloading changes with extracellular sugar concentration. Water stress increases SS activity, enhancing fruit sucrose metabolism capacity and improving assimilate acquisition from source tissues.

This study found that although the basic patterns of enzyme activity over time did not fundamentally change under water stress, severe stress inhibited all enzyme activities while mild stress enhanced them, particularly during coloring maturation (after May 24), where SS and SPS activities in W_3 were significantly higher than the control, corresponding to differences in sugar content among treatments. Increased SPS activity enhanced sucrose synthesis capacity, promoting sugar accumulation. Correlation analysis showed that enzyme activity changes had varying effects on sugar accumulation: SS is a key enzyme regulating glucose and fructose, particularly determining glucose accumulation, while SPS has some influence on final sugar accumulation but the effect is not obvious. In summary, water stress indirectly regulates fruit sugar metabolism by affecting sucrose metabolism-related enzyme activity. In studying the mechanism of sugar accumulation in Red Globe grape fruit, net enzyme activity should be considered comprehensively, as sugar metabolism throughout fruit development is co-regulated by related metabolic enzymes, and net enzyme activity reflects their comprehensive effect, consistent with Liu et al.' s findings.

Some literature explains that increased sugar content under water stress results from active osmotic regulation in fruit, while others suggest complex internal links between sugar response and plant hormone synthesis or signal transduction mutants. Further exploration of the response mechanism of grape fruit sugar metabolism to water regulation and revealing plant growth and development regulatory mechanisms will be the main research direction. Based on these results, it is recommended that local facility-cultivated grapes undergo water stress during the coloring maturation period to achieve water saving and promote sugar accumulation. The optimal water regulation model is mild stress with soil water at 65%–75% of field capacity and irrigation quota of 270 $m^3 \cdot hm^{-2}$.

4 Conclusion

Analysis of sugar content and sucrose metabolism enzyme activity changes in greenhouse grape fruit under water stress yielded the following main conclusions:

1) Red Globe grape is a hexose-type fruit. Water stress had minor effects on plant growth. Mild stress improved fruit sugar content, yield, appearance, and taste quality, while severe stress was detrimental.

2) Water stress did not change the temporal variation patterns of fruit sucrose metabolism enzyme activity. Mild stress promoted enzyme activity, while severe stress inhibited it.

3) Water stress indirectly regulated fruit sugar metabolism by affecting sucrose metabolism-related enzyme activity. SS is a key enzyme regulating glucose and fructose, particularly determining glucose accumulation, while SPS has some influence on final sugar accumulation but the effect is not obvious.

4) The optimized water regulation model for grapes in northwest cool regions is mild stress with soil water at 65%-75% of field capacity and irrigation quota of 270 $m^3 \cdot hm^{-2}$.

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Note: Figure translations are in progress. See original paper for figures.