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Enhancing the content of biologically active components in cluster tomatoes using organic fertilizers

Iryna Vardanian¹, Gayane Sargsyan^{1*}, Oksana Sementchouk², Hayk Martirosyan¹, Laura Khachatryan¹, Irina Tsereteli¹, Alvina Avagyan¹, and Laura Tadevosyan¹

¹Scientific Centre of Vegetable and Industrial Crops of the Ministry of Economy of the Republic of Armenia, 38 D.Ladoyan St, com. Darakert, Ararat Marz, 0808, Republic of Armenia ² Charles R. Drew University of Medicine and Science, 1731 E 120th St, Los Angeles, CA 90059

*Corresponding Author: Gayane Sargsyan, Doctor, Professor, Scientific Centre of Vegetable and Industrial Crops, 38 D. Ladoyan St, com. Darakert, Ararat Marz, 0808, Armenia

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ABSTRACT

Tomatoes (Solanum lycopersicum L.) are a vital agricultural crop with significant nutritional value, attributed to their high content of vitamins, minerals, and antioxidants. The antioxidant properties of tomatoes contribute to reducing the risk of cardiovascular and oncological diseases, positioning them as an important component of a balanced diet and beneficial for public health. The application of organic fertilizers containing fulvic and humic acids is particularly relevant to ensure the production of high-quality and nutritious tomatoes. These compounds, recognized as bio stimulants in plant cultivation, enhance physiological processes in plant cells. They stimulate protein and nucleic acid synthesis, activate enzymatic activity, and regulate metabolic pathways, thereby improving the biochemical composition of tomato fruits, increasing their nutritional quality, and enriching the content of bioactive compounds.

The objective of this study is to evaluate the accumulation of bioactive compounds such as lycopene, total phenols, vitamin C, total sugars, and dry matter in cluster tomato fruits using an Armenian fertilizer containing fulvic and humic acids. Additionally, the research aims to provide practical insights into sustainable agriculture by identifying optimal agronomic practices that enhance the accumulation of these bioactive compounds in cluster tomatoes. The research was conducted on greenhouse-grown cluster tomato hybrids: Syune F1 (Armenian breeding), Prodezo F1 (Rijk Zwaan), Santiano F1 (Rijk Zwaan), Adventure F1 (Rijk Zwaan), and Climbo F1 (Syngenta) during the spring growing seasons from

the years 2022 to 2024. The experiment utilized an organic fertilizer, and applied by abiding the following treatment scheme: 1. Control (St) — no organic fertilizer application, 2. Root treatment (RT), 3. Foliar treatment (FT), 4. Combined root and foliar treatment (RT-FT). Biochemical analyses of the tomato fruits were performed to quantify lycopene, total phenols, ascorbic acid, and total sugars using spectrophotometry, while dry matter content was determined via refractometry. Statistical data analysis was conducted using analysis of variance (ANOVA).

The study demonstrated that all treatment types with fulvic-humic fertilizer contributed to improving tomato fruit quality and the accumulation of biologically active components. The most effective treatment was the combined root and foliar application (RT-FT), which resulted in the highest values across all measured parameters. Depending on the hybrid, lycopene content increased by 11.1–15.9%, total phenols by 14.7–22.8%, when vitamin C by 13.1–15.9%, total sugars by 13.5–21.7%, and dry matter by 14.6–22.5% compared to the control. The 'Syune' and 'Climbo' hybrids exhibited the highest accumulation of lycopene and phenols, highlighting their potential for enhancing antioxidant properties. The 'Santiana' and 'Adventure' hybrids were notable for their elevated ascorbic acid content, making them particularly valuable for improving nutritional quality. The best results for sugar and dry matter accumulation were observed in the 'Syune' and 'Prodezo' hybrids, indicating improved flavor profiles in these tomato varieties.

Keywords: tomatoes, lycopene, total phenols, ascorbic acids, total sugars, dry matter, organic fertilizer, fulvic acids, humic acids



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INTRODUCTION

The quality of tomato fruits (Solanum lycopersicum L.) is a key factor determining their nutritional and biological value. Tomatoes are rich in essential micronutrients, including copper, manganese, zinc, and selenium. They are also abundant in natural antioxidants, such as carotenoids (β -carotene and lycopene), ascorbic acid (vitamin C), tocopherol (vitamin E), and phenolic compounds, which collectively contribute to the prevention and management of chronic diseases [1-2].Regular consumption of tomatoes has been shown to strengthen the immune system [3-4], prevent cardiovascular diseases [5-10], reduce the risk of cancer [5, 11-12], and lower the risk of diabetes [13-16].

In response to growing consumer demand for healthier and more eco-friendly agricultural practices, attention has shifted toward sustainable methods that enhance the bioactive compound content of tomatoes, which improves both their antioxidant properties and flavor [17]. One of the promising methods for enhancing fruit quality is the use of organic fertilizers containing fulvic and humic acids. These compounds are widely utilized as biostimulants in agriculture due to their ability to activate essential physiological processes at the cellular level [18]. Their chelating properties improve the absorption of nutrients by plants [19-22], enhance protein and nucleic acid synthesis, and regulate enzymatic activity and metabolism [23], lead to the stimulation of root system growth [24], improve photosynthetic processes, and increase overall plant productivity [25]. Fulvic and humic acids also positively influence the biochemical composition of fruits, increasing the concentration of vital bioactive components such as lycopene, sugars, and vitamins [26].

Nevertheless, the impact of local organic fertilizers on the biochemical parameters of tomato fruits remains insufficiently studied, highlighting the need for further research in this area. The objective of this study is to investigate the effects of Armenian fertilizer containing fulvic and humic acids on the quality characteristics of tomato fruits. Additionally, the research aims to identify optimal agronomic conditions that promote the maximum accumulation of biologically valuable components in tomato fruits.

The quality of tomato fruits (Solanum lycopersicum L.) is a key factor determining their nutritional and biological value. Tomatoes are rich in essential micronutrients, including copper, manganese, zinc, and selenium. Due to their high concentration of natural antioxidants, such as carotenoids (β -carotene and lycopene), ascorbic acid (vitamin C), tocopherol (vitamin E), and bioactive phenolic compounds, tomatoes can alleviate many health conditions, particularly chronic diseases [1-2]. Regular consumption of tomatoes has been shown to strengthen the immune system [3-4], prevent cardiovascular diseases [5-10], reduce the risk of cancer [5, 11-12], and lower the risk of diabetes [13-16].

In recent years, there has been increasing attention to the application of eco-friendly methods to enhance the content of bioactive compounds in tomato fruits, which play a crucial role in developing their antioxidant properties and flavor quality [17].

One of the promising methods for enhancing fruit quality is the use of organic fertilizers containing fulvic and humic acids. These compounds are widely utilized as biostimulants in agriculture due to their ability to activate essential physiological processes at the cellular level [18]. Their chelating properties improve the absorption of nutrients by plants [19-22], enhance protein and nucleic acid synthesis, and regulate enzymatic activity and metabolism [23], leading to the stimulation of root system growth [24], improved photosynthetic processes, and increased overall plant productivity [25]. Local organic fertilizers, such as the Armenian product used in this study, are of interest due to their high content of bioactive components and potential for sustainably improving fruit quality. However, specific effects on tomato fruit biochemistry have not been fully explored.

These compounds positively influence the biochemical composition of fruits, thereby enhancing their nutritional value and increasing the content of vital bioactive components such as lycopene, sugars, and vitamins [26]. Nevertheless, the impact of local organic fertilizers on the biochemical parameters of tomato fruits remains insufficiently studied, highlighting the need for further research in this area.

The objective of this study is to examine the effects of an Armenian fertilizer enriched with fulvic and humic acids on the quality characteristics of tomato fruits. Additionally, the research aims to offer practical insights into sustainable agriculture by identifying optimal agronomic practices that maximize the accumulation of biologically valuable components in tomato fruits.

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MATERIAL AND METHODS

The research was conducted at the Scientific Center of Vegetable, Melon, and Technical Crops of the Ministry of Economy of Armenia, within the glass greenhouse of the center, during the spring growing cycle from 2022 to 2024. The subjects of the study were selected cluster hybrids of tomatoes: Syune F1 (Armenian selection), Prodezo F1 (Rijk Zwaan), Santiano F1 (RZ), Adventure F1 (RZ), and Climbo F1 (Syngenta). Below is a brief description of the hybrids:

Syune F1	Medium-early cluster greenhouse hybrid characterized by indeterminate plants with robust foliage. The cluster-shaped fruit typically contains 5-6 round-flattened fruits, exhibiting an intense red color, weighing between 150-160 g [27].
Prodezo F1	Medium-early cluster greenhouse hybrid characterized by its indeterminate plant growth. It produces cluster-shaped fruits, typically consisting of 5-6 round-flattened fruits. These fruits are noted for their intense red color and weigh between 160-180g [28].
Santiana F1	Medium-early cluster greenhouse hybrid. Santiana F1 plants are indeterminate and are noted for their high early and total yields. The flat clusters contain 5-6 fruits, each weighing 160-170g and displaying a vibrant red color [28].
Adventure F1	Medium-early indeterminate tomato hybrid known for its high yield and fruit quality. It produces round, red fruits that typically weigh between 140-160 grams [28].
Climbo F1	Medium-early indeterminate tomato hybrid known for its high yield and fruit quality. It typically forms 5-6 fruits per cluster, producing round, red fruits that weigh between 140-160 g [29].

The organic fertilizer was characterized by the following parameters:

Dry matter 20–25%, organic matter (C) on a dry matter (DM) basis 20–30%, fulvic acids (DM) 12.0%, humic acids (DM) 7.0%, total nitrogen N (DM) 2.4%, total phosphorus (P_2O_5) (DM) 2.2%, total potassium (K_2O) (DM) 2.22%, pH 7.0–7.6.

The experiment followed a block-randomized design with three replications.

The experiment incorporated the following treatments with organic fertilizer:

1. Control (St) — This control variant used a complex NPK fertilizer without additional organic fertilizer treatment. In the other treatments, the same mineral fertilizer background was applied, supplemented with the following treatments of fulvic-humic fertilizer:

- 2. Root treatment (RT);
- Foliar treatment (FT);

4. Combined root and foliar treatment (RT-FT) comprehensive scheme.

The fertilizer was diluted with water and applied in the following proportions and frequencies: for root

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feeding — diluted at 1:100, four times during the growing season; for foliar feeding — diluted at 1:150 with an interval of 15 days.

The soil composition at a depth of 20-25 cm included: total nitrogen - 4.3-4.8 mg, phosphorus - 6.5-8.2 mg, and potassium - 16.5-18.5 mg per 100 g of soil. The soil electrical conductivity (EC) ranged from 1.5 to 2.5 dS·m⁻¹, with a pH of 7.0-7.5. The temperature in the greenhouse was maintained at 25-28°C during the day and 16-20°C at night. The relative humidity was kept between 60-70%.

Biochemical analyses of tomato fruits were conducted at the Laboratory of Plant Biotechnology, Phytopathology, and Biochemistry of the Scientific Center. Key quality indicators of the fruits were measured, including the content of lycopene, total phenols, ascorbic acid, total sugars, and dry matter.

The lycopene content was determined spectrophotometrically using a Cary 60 UV-Vis spectrophotometer (Agilent Technologies, USA) at a wavelength of 503 nm, with prior extraction using a solvent mixture of hexane, acetone, and ethanol. Results were calculated based on 100 grams of fresh weight (FW) of the sample [30].

The ascorbic acid content was determined spectrophotometrically according to the standard method using 2,4-dinitrophenylhydrazine, followed by measuring the absorbance at a wavelength of 520 nm. The calibration solutions were prepared using L-ascorbic acid (Merck, Germany) [31-32].

The total phenolic compound content was determined using the Folin-Ciocalteu reagent. For total phenolic content, gallic acid (Sigma-Aldrich, USA) was used as the standard, and results were expressed in gallic acid equivalents, per 100 grams of FW of the sample. Spectrophotometric measurements were conducted at a wavelength of 725 nm [33].

The sugar content was measured spectrophotometrically. For total sugars, the optical

density of the solution was measured at a wavelength of 490 nm. Calibration solutions were prepared using glucose (Merck, Germany) [34]. The dry matter content in the fruits was assessed using a refractometer.

The experimental data was analyzed statistically using ANOVA to evaluate the significance of treatment effects at a confidence level of $p \le 0.05$. The results are presented as means ± standard deviation (SD) based on three independent experimental replicates.

RESULTS

The research indicated that the lycopene content in the fruits of the cluster tomato hybrids increased with the intensity of organic fertilizer treatment. In the control group (St), the lycopene level in the 'Syune' hybrid was 9.41 mg/100g (FW). Following root treatment, the lycopene content increased to 10.21 mg/100g, while after foliar treatment, it reached 10.40 mg/100g, representing increases of 8.5% and 10.5% compared to the control, respectively. The maximum level was observed in the N4 treatment (combined application), achieving 10.91 mg/100g, which is 15.9% higher than the control (Fig. 1).

For the 'Prodezo' hybrid, the control lycopene content was 7.22 mg/100g. With root and foliar treatments, the lycopene levels were 7.68 mg/100g and 7.97 mg/100g, respectively, reflecting increases of 6.4% and 10.4% compared to the control. The highest values were recorded in the N4 treatment, where the lycopene content reached 8.20 mg/100g, indicating a 13.6% increase over the control.

In the 'Santiana' hybrid, the control group recorded a lycopene content of 7.78 mg/100g. Following root and foliar treatments, the lycopene levels increased to 8.39 mg/100g and 8.51 mg/100 g, respectively, reflecting increases of 7.8% and 9.4% compared to the control. In the N4 treatment, the lycopene content reached 8.78 mg/100g, which is 12.8% higher than the control. For the 'Adventure' hybrid, the initial lycopene level was 8.30 mg/100g. Root and foliar treatments resulted in lycopene content increasing to 8.87 mg/100g and 8.99 mg/100g, corresponding to increases of 6.8% and 8.3%, respectively. In the N4 treatment, the lycopene content reached 9.22 mg/100g, exceeding the control by 11.1%.

In the 'Climbo' hybrid, the control level was measured at 9.12 mg/100g. Following root and foliar treatments, the lycopene content increased to 9.87 mg/100g and 10.16 mg/100g, reflecting increases of

8.2% and 11.4% compared to the control,

respectively. The highest value of 10.45 mg/100g was achieved in the N4 treatment, which represents a 14.6% increase over the control.

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All hybrids exhibited superior lycopene content results with foliar treatment compared to root treatment. A clear upward trend in lycopene concentration was observed with increasing treatment intensity in the combined application of root and foliar treatments (RT-FT). Notably, the hybrids 'Syune' and 'Climbo' showed the most significant increases in lycopene content in response to the application of fulvic-humic fertilizers.



Figure 1. Lycopene content (mg/100 g FW) in the fruits of cluster-type tomato hybrids depending on the type of treatments ($p \le 0.05$)

Similar trends were observed in the analysis of other parameters, such as with the content of phenols, ascorbic acid, dry matter, and sugars, indicating an overall positive impact of the treatments on the quality of tomato fruits. As with lycopene, the maximum values were attained in treatment N4 (Fig. 2-5).

For the 'Syune' hybrid, the control values were as follows: total phenols – 107.5 mg/100g (FW), ascorbic acid – 22.13 mg/% (FW), total sugars – 3.27% (FW), dry matter – 6.57% (FW). The highest values were recorded

in treatment N4: the phenolic content increased to 132.1 mg/100g (+22.8% compared to the control), ascorbic acid rose to 25.03 mg/% (+13.1%), total sugars reached 3.98% (+21.7%), and dry matter increased to 8.05% (+22.5% compared to the control).

For the 'Prodezo' hybrid, the control values were as follows: total phenols – 95.4 mg/100g, ascorbic acid – 20.08 mg/%, total sugars – 3.01%, dry matter – 6.54%. The maximum values were recorded in treatment N4: phenolic content reached 111.7 mg/100g (+17.1%), ascorbic acid increased to 22.89 mg/% (+13.9% above control), total sugar rose to 3.47% (a 15.3% increase), and

dry matter reached 7.60% (16.2% higher than the control).

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Figure 2. Total phenolic content (mg/100g (FW)) in the fruits of cluster hybrids as affected by treatment types ($p \le 0.05$)



Figure 3. Ascorbic acid content (mg/% (FW)) in the fruits of cluster hybrids is affected by treatment types ($p \le 0.05$)

5.25



Figure 4. Total sugar content (% (FW)) in the fruits of cluster hybrids as influenced by treatment types ($p \le 0.05$)



■ 1. Control ■ 2. RT ■ 3. FT ■ 4. RT-FT



For the hybrid 'Santiana', the control values were established as follows: total phenolic content was 92.3

mg/100g, ascorbic acid concentration was 21.54 mg/%, total sugars content was 3.14%, and dry matter

constituted 6.34%. Notably, the highest measurements were observed under treatment N4, where phenolic content increased to 107.4 mg/100g, depicting a 16.4% enhancement. Ascorbic acid levels reached 24.97 mg/%, reflecting a 15.9% increase, while sugar content rose to 3.58%, marking a 14.0% augmentation. Additionally, dry matter increased to 7.29%, indicating a 14.9% elevation compared to the control.

In the case of the hybrid 'Adventure,' the control parameters recorded were: total phenols at 90.4 mg/100 g, ascorbic acid at 22.11 mg/%, sugars at 3.17%, and dry matter at 6.64%. The highest values recorded under treatment N4 included phenols at 103.7 mg/100 g, signifying a 14.7% increase, ascorbic acid at 25.31 mg/% (an increase of 14.5%), sugars at 3.60% (a 13.5% rise), and dry matter at 7.61% (a 14.6% increase compared to the control).

For the hybrid 'Climbo,' control measurements indicated a phenolic content of 112.3 mg/100 g, ascorbic acid concentration of 21.64 mg/%, total sugar content of 3.14%, and dry matter of 6.50%. Under treatment N4, the following enhancements were noted: phenolic content reached 136.0 mg/100 g, reflecting a 21.1% increase; ascorbic acid attained 24.69 mg/%, representing a 14.1% increase over the control; sugars amounted to 3.57%, marking a 13.7% elevation; and dry matter rose to 7.51%, a 15.5% increase compared to the control (fig. 2-5).

DISCUSSION

The selection of the tomato hybrids 'Syune,' 'Prodezo,' 'Santiana,' 'Adventure,' and 'Climbo' is driven by the rising market demand in Armenia for cluster tomatoes known for their superior sensory qualities and nutritional benefits. These hybrids exhibit a unique genetic makeup that confers various agronomic advantages. The presence of the rin gene, alongside the genes nor and norA in a heterozygous state, attenuates the ripening process of the fruits, thereby allowing the initial fruits at the base of the cluster to retain structural integrity and remain attached, even as the upper fruits commence ripening. Furthermore, the rin gene facilitates prolonged storage of mature fruits on the vine, preserving their organoleptic and commercial qualities [35].

Moreover, there is a growing demand for ecofriendly and high-quality products from both consumers and farmers. In this context, the selected hybrids play a crucial role as they facilitate the investigation of the effects of organic fertilizers, such as fulvic-humic complexes, on enhancing flavor characteristics, increasing antioxidant levels, and improving the overall quality of the fruits.

To effectively apply fertilizers based on fulvic and humic acids, it is crucial to consider both the dosage and the method of application, as these factors directly influence their efficacy. Research by Khan et al. (2014) [23] has demonstrated that foliar feeding yields positive results, particularly when applied at specific growth stages of the plants. Optimal doses of fulvic acids contribute to enhanced growth, increased chlorophyll content, improved nutrient uptake, and the stimulation of metabolic processes. Exceeding the recommended dosage can impair micronutrient absorption and disrupt balanced plant growth, underscoring the importance of precise dosing. Therefore, experimental studies on the methods of fertilizer application are necessary for each specific case. In our experiment, the best results were achieved through a combined treatment approach that integrated both root and foliar feeding (RT-FT), which demonstrated the most significant impact on the quality of tomato fruits. Conversely, root application exhibited a less pronounced effect compared to foliar application. This finding aligns with other studies that emphasize the importance of foliar feeding in stimulating plant metabolism and enhancing fruit quality [20, 23]. The enhancement of tomato fruit quality is closely linked to the significant effects of fulvic acids (FA) on nutrient absorption and redistribution. The application of FA improves the uptake of phosphorus (P) and potassium (K) in leaves and stems. Concurrently, nitrogen (N) is

redistributed from the roots to the fruits and leaves, leading to a reduction in its concentration within the stems. Importantly, FA enhances the absorption of micronutrients such as manganese (Mn), copper (Cu), and zinc (Zn) through a chelating effect, making these elements more bioavailable to plants [23]. Research by Shi et al. (2023) [36] reported that the application of fulvic acids increased the absorption of nitrogen (N), phosphorus (P), and potassium (K) via tomato fruits by 20.5% to 156%. Our study utilized an organic fertilizer containing both fulvic acids (predominantly) and humic acids at concentrations of no less than 12% and 7%, respectively.

These substances exert a synergistic effect on the plant, enhancing each other's actions. Humic acids (HA) contribute to the improvement of soil structure by activating microbial activity, which in turn increases nutrient availability. Furthermore, HA enhances the water retention capacity of the soil, which is particularly crucial in arid climatic conditions, and stimulates root development, positively affecting the overall biomass of the plants [37]. In addition, humic acids have been shown to influence the microbial community in the soil, promoting the growth of beneficial microorganisms that further contribute to the health of the plants and soil ecosystem.

Fulvic acids, being more mobile and readily absorbed, play a vital role in the transport of nutrients and assist plants in utilizing incoming elements more efficiently. Specifically, fulvic acids improve cellular metabolism, increase the rate of photosynthesis, and promote the synthesis of phytohormones, all of which contribute to the growth and development of plants [38-40].

Bioactive compounds play a vital role in enhancing the nutritional value and health benefits of food products, making them a key focus in the field of functional nutrition [41–46]. Among these compounds, lycopene—a powerful antioxidant found in tomatoes stands out. Its concentration in fruits depends not only on

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genetic factors but also on environmental conditions [47]. Studies have shown that the application of fulvic and humic acid-based fertilizers can significantly increase lycopene levels in tomatoes [25, 36]. In the present study, the combined treatment RT-FT (N4) facilitated the most pronounced increase in lycopene levels, ranging from 11.1% to 15.9%, contingent upon the specific hybrid, which may be attributed to enhanced nutrient assimilation by the plants. Among the hybrids investigated, 'Climbo' and 'Syune' demonstrated the greatest increments in lycopene content, at 14.6% and 15.9%, respectively, when compared to the control group. This suggests that the interaction between the plant's genetic traits and the applied organic fertilizers can have a substantial impact on the production of bioactive compounds, enhancing the overall quality of the fruits.

Research conducted by He et al. (2022) [25] indicates that the utilization of fulvic and humic fertilizers markedly improves the quality of lemon fruits, encompassing increases in sugar, ascorbic acid, and dry matter content. Furthermore, findings from Shi et al. (2023) [36] reveal that foliar applications of fulvic acids to tomato plants lead to significant enhancements in vitamin C and sugar concentrations within the fruits, exhibiting increases of 11.4% to 45.9% and 19.2% to 48.5%, respectively.

In our studies, foliar treatment (FT) exhibited a negligible impact on the quality indicators of cluster tomato fruits, with increases in vitamin C content ranging from 9.2 to 11.8 mg/%, total phenolic compounds from 12.6 to 17.7 mg/100g, total sugars from 5.1 to 12.8%, and dry matter from 9.8 to 15.1%. In contrast, the combined treatment RT-FT resulted in the maximum enhancements of vitamin C content, which increased by 13.1 to 15.9 mg/%, phenolic compounds by 14.7 to 22.8 mg/100g, sugars by 13.5 to 21.7%, and dry matter by 14.6 to 22.5% compared to the control group. This highlights the

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advantage of combining root and foliar treatments to achieve more significant improvements in fruit quality, with the synergistic effects of these two methods fostering more efficient nutrient absorption and utilization.

Vitamin C, sugars, and phenolic compounds are plant metabolites whose concentrations are regulated by both genetic and environmental factors. These metabolites play a crucial role in the nutritional value of plants and their resilience to stressors [25]. The hybrids 'Syune' and 'Climbo' exhibited the highest accumulation of phenolic compounds in their fruits, highlighting their potential for enhancing antioxidant properties. Simultaneously, the hybrids 'Santiana' and 'Adventure' were distinguished by their high levels of ascorbic acid, rendering them particularly valuable for improving nutritional quality. For the accumulation of sugars and dry matter, the best results were observed in the hybrids 'Syune' and 'Prodezo', indicating an improvement in the flavor quality of the tomatoes.

CONCLUSIONS

We have demonstrated the effectiveness of Armenian fertilizers containing fulvic and humic acids in enhancing the quality characteristics of cluster tomato fruits. The combined root and foliar treatment (RT-FT) resulted in the highest accumulation of lycopene, total phenol, ascorbic acid, total sugar, and dry matter when compared to individual root (RT) and foliar (FT) treatments, as well as the control groupThe increased accumulation of bioactive compounds enhances the nutritional profile of these tomatoes, underscoring their potential as functional foods that can contribute to disease prevention and overall health maintenance. Enriched with health-promoting components, these tomatoes can play a significant role in disease prevention and health maintenance, aligning with the growing interest in functional food development.

List of Abbreviations: FA — fulvic acids; HA — humic acids; RT- root treatment; FT- foliar treatment; RT-FT - root treatment- foliar treatment; RZ - Rijk Zwaan; DW- dry weight; FW — fresh weight; g — gram; mg — milligram.

Competing interests: The authors declare that they have no competing interests.

Authors' Contributions: IV and GS designed the study. IV and HM conducted the biochemical analyses, while GS performed the statistical analyses. OS, HM, and LT contributed to the interpretation of the biochemical and statistical results. LKh was responsible for graph preparation. ITs and AV edited the manuscript. All authors reviewed and approved the final version.

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