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Foliar Arginine Application Improves Tomato Plant Growth, Yield, and Fruit Quality

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Abstract

Tomatoes are important for human health, and there is an urgent need to increase tomato yield and quality worldwide. Arginine is proven to be beneficial for crop storage quality and stress resistance in plants; however, its effects on tomato production and quality have not been fully investigated. This study demonstrated the effects of spray application of arginine on tomato growth, yield, and quality. Arginine treatment significantly increased the nitrogen concentration in the aboveground tomato plant parts and fruit, net photosynthetic rate, stem diameter, dry mass weight, and root activity. It is suggested that increased nitrogen accumulation following arginine application is mainly due to arginine uptake as organic nitrogen, higher expression of the *LeNRT1.1* gene, and increased root activity. The increased nitrogen levels improved photosynthesis and promoted tomato plant growth. Moreover, foliar arginine application enhanced fruit size, weight, and yield. Arginine treatment had a positive effect on tomato quality as indicated by the concentrations of lycopene, vitamin C, soluble solid, soluble sugar, and titratable acids, and the sugar-acid ratio. Arginine application has potential to improve tomato production by regulating plant development and enhancing fruit yield and quality.

Introduction

The tomato (*Lycopersicum esculentum*) is one of the most widely available vegetables and is a common food. Tomatoes are rich in beneficial ingredients, including lycopene, vitamins, and mineral elements. (Khachik et al., 2002; Viuda-Martos et al., 2014; Padayatty and Levine, 2016). The risk of numerous diseases, including heart disease, cardiovascular disease, and various cancers, can be reduced by a regular consumption of tomatoes (Li et al., 2020). With increased living standards, satisfying the demand for tomato production and quality has become an increasingly important issue.

Amino acids positively promote the growth and yield of plants (Moreira and Moraes, 2016; Mohammadipour and Souri, 2019; Souri and Hatamian, 2019), but various amino acids have distinct effects on plants, and their mechanisms of action may differ (Souri, 2016; Aghaye Noroozlo et al., 2019). For example, several studies revealed that glutamate and histidine affected root architecture and micronutrient uptake, respectively (Walch-Liu, 2006; Ghasemi et al., 2012). Arginine has been identified as a crucial contributor to nitrogen storage and transport in plants because of its high nitrogen-carbon ratio (Cheng et al., 2004). Morris (2006) showed that arginine is the primary precursor of cellular metabolites in many organisms. Plant metabolism is efficiently enhanced by exogenous arginine, and the antioxidant system activity is promoted (Babalar et al., 2018). Previous studies exploring the effects of arginine focused mainly on increased abiotic stress tolerance in plants. Recently, the effect of arginine on fruit quality has received more attention from researchers. Several studies reported that plants treated with arginine had improved fruit storage quality and harvest delay (Zhang et al., 2017; Li et al., 2019; Shu et al., 2020). However, the impact of arginine on tomato plant growth, yield, and fruit quality has not been investigated previously, in terms of its effects and mechanisms, despite the apparent benefits that this would bring.

Based on the evidence above, we speculated that arginine could increase the growth, yield, and quality of tomato plants. We studied the effects of arginine on nitrogen concentration and net photosynthetic rate to investigate mechanisms affecting tomato growth. We characterized the expression of the *LeNRT1.1* gene, which is the primary gene responsible for nitrogen uptake in the tomato root and also plays a role in root development to examine possible pathways for the effects of arginine. In addition, we determined the effect of arginine on tomato fruit yield and quality by measuring fruit weight, size, nutritional quality, and flavor. Our study confirms the value of arginine as a potential new crop treatment and provides a novel strategy for improving tomato production.

Materials And Methods

2.1 Plant culture and treatment

The experiment took place in a greenhouse of China Agricultural University. Arginine was supplied by Jiangsu Hanling Fertilizer Corporation (Jiangsu, China), and the tomato variety used for the experiments was "FenGuan No.1". Tomato seed germination was started in July 2018, and tomato fruits were harvested in October and November, respectively. Individual tomato plants were transplanted into single pots filled with 8 kg of nutrient soil one month after germination. Cultivated soil consisted of black soil:vermiculite:chicken manure in a 4:1:0.33 ratio. The tops of the tomato plants were sheared off after the third flower had bloomed to ensure sufficient nutrition for each plant. Each plant was sprayed with 50 ml of 1 mmol/L arginine once a week from 45 d after transplanting until harvest, and deionized water was sprayed as the control. Arginine was applied 12 times during this experiment. The arginine concentration used was based on a previous study in which 1 mM arginine was the optimal concentration for improving fruit quality (Zheng et al., 2011; Zhang et al., 2017). Tween 80 was used as a surface-active agent in both treatments. Each treatment included ten tomato plants. Five tomato plants were harvested at 90 d after transplanting, and the stem diameter, dry mass, net photosynthetic rate, nitrogen concentration in the aboveground parts, relative gene expression, and root activity were measured. At 120 d after transplanting, we determined the nitrogen concentration in the fruits, fruit yield, and mature fruit quality from the remaining five tomato plants.

2.2 Determination of tomato growth indicators, photosynthesis rate, nitrogen concentration, and relative gene expression

Electronic digital calipers were used to measure the stem diameter between the first and second stem nodes above the tomato root. Root activity was determined by the triphenyl tetrazolium chloride (TTC) method (Zhang et al., 2013). Fresh root (0.5 g) was immersed in a mixed solution of 0.4% TTC and phosphate buffer and kept in the dark for 2 h at 37°C. After addition of 2 mL of 1 mol/L H_2SO_4, the root was dried with filter paper and extracted with ethyl acetate. The red extractant was stabilized with ethyl acetate (10 ml), and the absorbance was determined at 485 nm. TTC reduction intensity was used to express root activity.

Root activity = amount of TTC reduction (μg) / [fresh root weight (g) × time (h)].

After drying at 60°C until a constant weight was reached, we ascertained the dry mass of the tomato aboveground parts and the roots. We used mature leaves from the third node to test the net photosynthetic rate using a portable photosynthesis measurement system (LI-6400, LI-COR, Lincoln, NE, USA). The aboveground parts were crushed, and the nitrogen concentration was determined using a Carbon Nitrogen Analyzer (vario MACRO cube; Elementar, Hanau, Germany). Tender roots and mature leaves from the third node of the tomato plants were used to test gene expression. Total RNA was extracted with TRIzol reagent (Invitrogen, Carlsbad, CA, USA) and then treated with RNase-free DNase I (Takara Bio Inc., Shiga, Japan) to remove genomic DNA contamination. ReverTraAce reverse transcriptase (Toyobo, Osaka, Japan) was used to synthesize first-strand cDNA. Quantitative real-time PCR was performed with the StepOnePlus real-time PCR system (Applied Biosystems, Waltham, MA, USA) and SYBR Premix Ex Taq (Perfect Real Time) reagent (Takara). The primers used for the quantitative real-time PCR are listed in Table S1. Each treatment was carried out with five biological replicates (n = 5).

2.3 Analysis of tomato yield and fruit quality

Tomato fruit yield, single fruit weight, transverse diameter, and vertical diameter were determined using mature fruits, and the mean values of fruits from each tomato plant were considered as single repetitions. Ripe tomato fruits were pulped to measure the fruit quality and nitrogen concentration with five biological replicates. Tomato fruit yield and weight per fruit were determined using an electronic balance. Electronic digital calipers were used to measure the transverse and vertical diameters of the fruits. The nitrogen concentration in tomato fruits was determined by the method described above. Lycopene and vitamin C concentrations were measured by the spectrophotometric method according to the procedure of Muzolf-Panek et al. (2017). Homogenized fruit flesh (5 g) was mixed with 50 ml of hexane:acetone:ethanol (2:1:1, v/v) and kept in the dark for 60 min. Then, 10 ml of water was added to each sample and shaken for 5 min. The solution was separated into polar and non-polar layers, and the absorbance of the non-polar layer was measured at 472 nm. The lycopene content was calculated using the molar extinction coefficient of 17.2×10^4 $L \cdot mol^{-1} \cdot cm^{-1}$. To measure the vitamin C concentration, homogenized fruit flesh containing 1.0–60.0 mg ascorbic acid was added to a mixed solution, which included 1 ml of 40 mg/ml iron (III), 4 ml of 0.03% 2-(5-bromo-2-pyridylazo)-5-diethylaminophenol (Br-PADAP), and 2.5 μl of acetate buffer (pH 4.75). After 5 min under dark conditions, 1 μl of 0.1% EDTA solution was added, and the solution was mixed. This mixture was diluted with deionized water to 25 ml. The absorbance was measured at 560 nm or 748 nm, and a standard curve was drawn for ascorbic acid. After homogenization, the tomato tissues were filtered through filter paper, and the soluble solid content was determined using an RA-600 digital refractometer (KEM, Kyoto, Japan). Soluble sugar was measured as described by Goncalves et al. (2006). The fruit pulp (2 g) was mixed with 10 ml of 80% ethanol and heated at 60°C for 30 min. The extract was filtered through a filter paper, and 200 μl of the filtrate with 3 ml of anthrone was immersed in boiling water for 10 min. After cooling, we measured the absorbance at 625 nm to evaluate the soluble sugar content. The fruit pulp was diluted 5-fold with deionized water and filtered using filter paper for the titratable acid and soluble protein assays. The filtrate was titrated with

0.1 mol/L NaOH to pH 8.2, and the titratable acid was calculated as described by Panthee et al. (2012). Next, the sugar-acid ratio was calculated using the soluble sugar and titratable acid as follows:

Sugar-acid ratio = Soluble sugar / titratable acids

2.4 Statistical analysis

Data are means + SD, and statistical analyses were analyzed using GraphPad Prism 8 software (San Diego, USA) and the Student's *t*-test ($P < 0.05$).

Results

3.1 The effects of arginine on tomato growth

Arginine treatment increased tomato plant growth compared with the control treatment (Fig. 1). The stem diameters of the tomato plants were increased significantly by arginine treatment (Fig. 1a), and the dry mass weights of the aboveground parts and roots were increased by 12.6% and 14.7%, respectively, compared to the control (Fig. 1b, c). A positive effect on tomato root activity was also observed (Fig. 1d).

Exogenous application of arginine promoted photosynthesis in tomato leaves, increased the nitrogen concentration in leaves and fruit, and increased *LeNRT1.1* gene expression (Fig. 2). Arginine treatment resulted in a 17.1% increase in the net photosynthetic activity in tomato leaves compared to the control (Fig. 2a). Moreover, following arginine application, the nitrogen concentrations in the aboveground plant parts and in fruit increased by 7.1% and 32.9%, respectively (Fig. 2b, c). *LeNRT1.1* expression was 7-fold higher in the roots of treated plants than in those of the control plants (Fig. 2d). These results indicated that plant growth, photosynthesis, and nitrogen content were promoted by treatment with exogenous arginine.

3.2 The effects of arginine on fruit yield and quality

There were significant increases in fruit yield and size following arginine application (Fig. 3). The fruit yields and weight per fruit of arginine-treated tomato plants increased by 67.5% and 48.8%, respectively (Fig. 3a, b). The transverse and vertical diameters of the arginine-treated tomato fruits increased (Fig. 3c, d). These results showed that the external application of arginine stimulated tomato fruit production.

The nutritional quality and flavor of the tomato fruits were greatly improved following arginine treatment. Additionally, the lycopene concentration was enhanced by 123% compared with the control (Fig. 4a). The vitamin C concentration was 13% higher in the treated plants than in the control plants (Fig. 4b). The fruits of arginine-treated tomato plants contained a higher concentration of soluble sugar and titratable acid than those of the control plants, and the sugar-acid ratio was also higher (Fig. 4c, d, and e). Arginine treatment also significantly increased the soluble protein concentration and soluble solid content in the tomato fruits compared to the control (Fig. 4f, g). The above results demonstrated the positive effects of arginine on tomato fruit nutritional quality and flavor.

Discussion

4.1 The effects of foliar arginine on plant growth, fruit yield and quality

In this study, tomato plants treated with arginine showed increased plant growth, fruit yield, and fruit quality compared with the control plants. Foliar application significantly promoted plant biomass and stem diameter. Notably, arginine treatment resulted in increased tomato fruit weight, size, and yield per plant. Additionally, exogenous arginine increased the concentrations of lycopene, vitamin C, and soluble protein; the contents of soluble sugar, titratable acid, and soluble solids; and the sugar-acid ratio.

We showed that arginine induced increased growth of the aboveground plant parts and increased root development (Fig. 1). A previous study indicated a similar positive effect of arginine on plant growth in which the growth of bean seedlings was improved by the application of arginine (Zeid, 2009). Naser and Azeez (2019) found that the stem diameters and leaf areas of apricot trees were significantly increased following spraying with arginine. Our results showed that tomato fruit yield, weight, and size were significantly increased following spraying with arginine (Fig. 4). These results match those observed in earlier studies showing improved yields following arginine application. Abdul-Qados (2009) concluded that spraying plants with arginine effectively increased wheat growth and all yield components. Mohseni et al. (2017) demonstrated that for strawberry, the yield, the mean weights of primary and secondary fruits, and the number of achenes were increased following foliar application of arginine.

Our study also found that the exogenous application of arginine significantly enhanced tomato quality. Foliar application of arginine resulted in increased concentrations of lycopene and vitamin C in tomato fruits (Fig. 5a, b). Lycopene and vitamin C are vital for the nutritional quality of tomato fruits (Frusciante et al., 2010). In recent years, lycopene has been increasingly used in the food industry and in medicines, and has shown benefits for human health (Grabowska et al., 2019). One study showed that the lycopene concentration in tomato fruits declined with nitrogen fertilizer supplementation (Dumas et al., 2003). However, our data contradict this finding, and this difference is difficult to explain due to a lack of evidence in the literature. Further investigation is needed to clarify the reasons behind the differing findings. Vitamin C deficiency is a crucial issue affecting people's health and results in scurvy (Brickley et al., 2020). A previous study indicated that nitrogen application increased the vitamin C concentration in leafy parsley (Koota, 2011). Other studies have also reported increases in vitamin C concentration in various crops following the application of amino acids (Noroozlo et al., 2019; Mohammadipour and Souri, 2019; Souri et al., 2017; Souri and Hatamian, 2019; Shooshtari et al., 2020). Thus, the enhanced vitamin C concentration in tomato fruits could be due to the organic nitrogen supplied by the foliar arginine treatment.

Soluble solids, soluble sugar, and titratable acids are important components of flavor in tomato fruit (Atanassova et al., 2003). Several studies showed that soluble solids are related to nitrogen supplementation in various plants (He et al., 2003; Pierre et al., 2008). Our results showed that soluble

sugar, titratable acids, and the sugar-acid ratio in tomato fruits were promoted by exogenous arginine (Fig. 5c, d, e). Our findings agree with Mohseni et al. (2017), who demonstrated significantly increased induction of sugars and titratable acids in strawberry following arginine application. Recent evidence has shown that arginine plays a vital role in organic acid metabolism in plants (Hildebrandt et al., 2015). Another crucial, and novel finding was that the sugar-acid ratio was higher than the control, indicating that the tomato became sweeter following external arginine application.

4.2 Mechanisms by which arginine improves tomato plant and fruit growth

Our study found that foliar application of arginine resulted in a significant improvement in the rate of photosynthesis in tomato leaves, and this was also seen in previous studies (Stephan et al., 2000). Yagi and Al-Abdulkareem (2006) demonstrated that arginine showed positive effects on chlorophyll synthesis and improve photosynthesis in *Eruca sativa* Mill. Marschner (2011) illustrated that carbohydrates accumulated via photosynthesis formed the basic framework of plants. Increased photosynthesis following the external application of amino acids has been identified as a major factor that promotes plant growth (Yagi and Al-Abdulkareem, 2006; Mohammadipour and Souri, 2019; Noroozlo et al., 2019). Petridis et al. (2018) reported that increased tomato fruit yield was mainly associated with improved carbohydrate content due to increased photosynthesis. Meanwhile, the increased accumulation of soluble solids and soluble sugar in arginine-treated tomato fruits was consistent with the increase in carbohydrates. Arginine induced photosynthesis, therefore, might be responsible for the increased tomato fruit yield and quality. Nitrogen is vital for photosynthesis as it participates in chlorophyll synthesis, chloroplast structure stabilization, and the activation of relevant enzymes (Marschner, 2011). It is likely that the increased photosynthetic rate we observed in tomato leaves could be related to the increased nitrogen (Fig. 2). In summary, exogenous arginine increased the nitrogen concentration leading to improved photosynthesis in tomato leaves, resulting in a significant increase in growth of the aboveground plant parts and the roots, as well as fruit yield and quality.

In plants, arginine is regarded as an organic nitrogen storage sink and nitrogen transformation medium due to its high nitrogen-to-carbon ratio (Winter et al., 2015). It has been reported that amino acids can be absorbed and utilized directly as organic nitrogen sources by plants (Nasholm et al., 2009; Ganeteg et al., 2017). Jonas and Torgny (2001) demonstrated that pine trees assimilate arginine and showed a similar response to treatment with ammonium and nitrate. In recent years, improved nitrogen utilization in plants following arginine application has been well documented (Abdul-Qados *et al.*, 2009; Ghasemi et al., 2012). We found a similar effect on nitrogen accumulation in tomato, which is likely due to arginine uptake. In our experiment, 50 ml of 1 mmol/L arginine was applied 12 times per tomato plant, resulting in a total application of 104.52 mg of arginine during the experimental period. We calculated that the tomato plants absorbed a maximum of 33.6 mg of nitrogen with arginine treatment. However, the nitrogen content in the aboveground parts of the tomato plants was increased by 0.3 g compared with the control plants (Figure S1). Obviously, the nitrogen supplied by the direct uptake of arginine was

insufficient for the nitrogen increment observed in the aboveground parts. Therefore, other factors may be involved in the improved nitrogen accumulation in the arginine-treated tomato plants.

In plants, nitrogen uptake is mainly regulated by the gene families encoding nitrite transporter (NRT) and ammonium transporter (AMT) proteins. Moreover, *LeNRT1.1* and *LeAMT1.1* are reported to be the primary regulatory genes for the uptake of nitrate and ammonium in tomatoes (Lauter et al., 1996; Filiz and Akbudak, 2020). Nitrogen metabolism in plants is regulated primarily by nitrate reductase, glutamine synthetase, and glutamate synthase, encoded by the *LeNR*, *LeGS1*, and *LeGOGAT* genes, respectively (Becker et al., 1993; Yao et al., 2008). Compared with the control, the expression of *LeNRT1.1* was upregulated markedly by arginine treatment in our study (Fig. 2c). However, we found no differences in the expression of *LeAMT1.1*, *LeNR*, *LeGS1*, or *LeGOGAT* (Figure S2). Hence, we conclude that arginine has a positive effect on nitrate uptake but not on ammonium uptake and nitrogen transport in tomato plants. Our findings indicate a potential second mechanism underlying the increased nitrogen concentration in the tomato plant aboveground parts. However, further research is needed to fully determine the relationship between external arginine application and the nitrate absorption pathway in tomato.

Studies have shown that arginine is essential for root growth and elongation, and other amino acids cannot replace arginine (Xia et al., 2014a, b). White *et al*. (2015) demonstrated that increased root development in grass enhanced the capacity to absorb nitrogen. Additionally, the promotion of root activity had a positive effect on nitrogen uptake in tomato plants under root-zone heating conditions (Kawasaki et al., 2014). In our study, the significant increase in root activity and plant growth following arginine treatment helped tomato plants assimilate nitrogen from the soil (Fig. 1c, d). Hence, arginine application leading to increased root growth might underlie the enhanced accumulation of nitrogen in the tomato aboveground plant parts and in the fruit.

In summary, the increase in nitrogen seen in the aboveground parts and fruit of the tomato plant is related to three possible arginine-induced mechanisms (Fig. 5). These mechanisms involve arginine uptake as organic nitrogen, increased *LeNRT1.1* expression, and increased root development and activity. It is possible that a small amount of arginine applied as a foliar spray could result in considerable nitrogen accumulation in the tomato plant and fruit. This increased nitrogen concentration significantly promotes photosynthesis in the tomato leaves, which stimulates plant growth. Moreover, tomato fruit yield, flavor, and nutritional quality were directly improved by the exogenous application of arginine. In addition, arginine is a main component of proteins found in living organisms and does not harm the environment, making it an excellent candidate for agricultural application.

Conclusion

We analyzed three primary methods by which nitrogen is accumulated in tomato plants following arginine treatment; a) arginine uptake as organic nitrogen, b) upregulation of *LeNRT1.1* gene expression, and c) the promotion of root activity. Furthermore, we showed that increases in growth, yield, and quality were associated with photosynthesis, which increased with nitrogen accumulation following arginine

application. More generally, this work indicates the capacity of arginine to increase tomato yield and quality and has shown the potential for its use in tomato crop production.

Declarations

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Author contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Qingqing Liu and Tianqi Wang. The first draft of the manuscript was written by Tianqi Wang and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Compliance with Ethical Standards

Conflicts of interest

The authors declare no conflict of interest.

Research Involving Human and Animal Rights

This work is not against human and animal rights.

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Figures

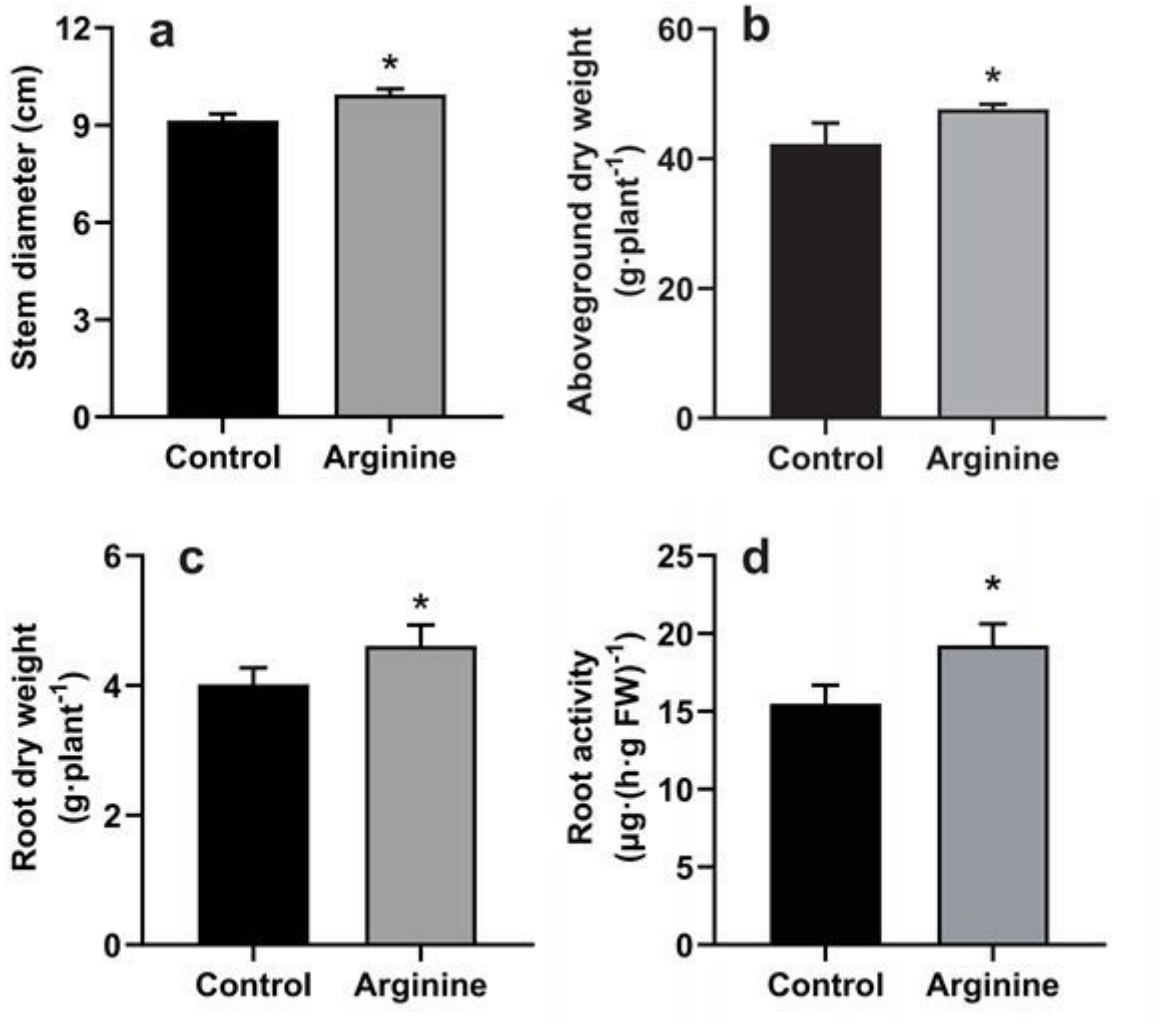

Figure 1

Application of arginine exhibited batter growth traits of tomato plants. The effect on stem diameter (a), dry mass of aboveground (b) and root (c), root activity (d) of tomato plant under control and arginine treatment. Bars and lines represent mean and standard deviation, respectively (n = 5). Asterisks indicate $P<0.05$ by Student's t-test.

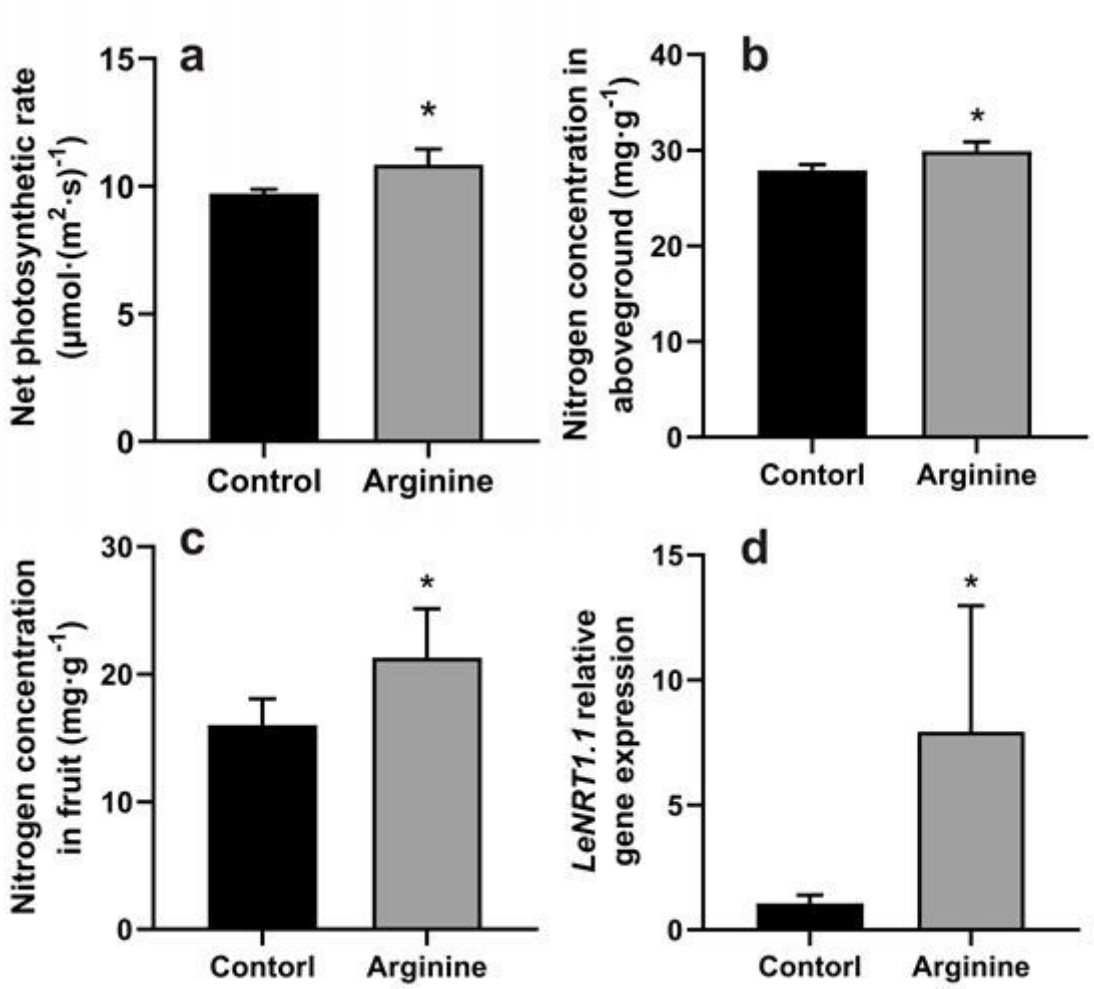

Figure 2

Arginine treatment significantly promoted photosynthesis of tomato leaves by enhancing nitrogen accumulation. Net photosynthetic rate in leaves (a), nitrogen concentration in aboveground (b) and fruit (c), relative gene expression of LeNRT1.1 in root (d) of tomato with spraying arginine and water (control). Bars and lines represent mean and standard deviation, respectively (n = 5). Asterisks indicate $P<0.05$ by Student's t-test.

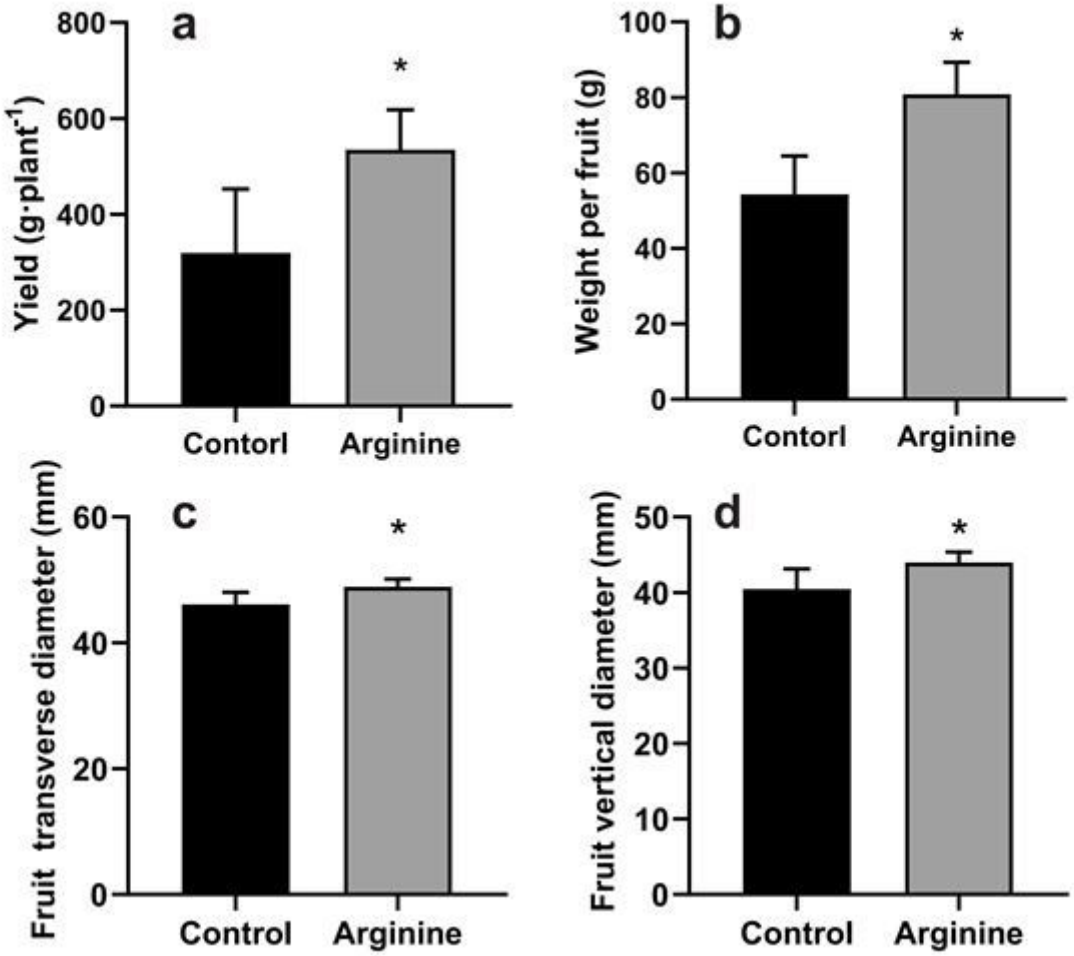

Figure 3

Spray of arginine increased yield traits of tomato. The spraying arginine on yield (a), weight per fruit (b), fruit vertical diameter (c), and fruit transverse diameter (d) of control and arginine-treated tomato. Bars and lines represent mean and standard deviation, respectively (n = 5). Asterisks indicate $P<0.05$ by Student's t-test.

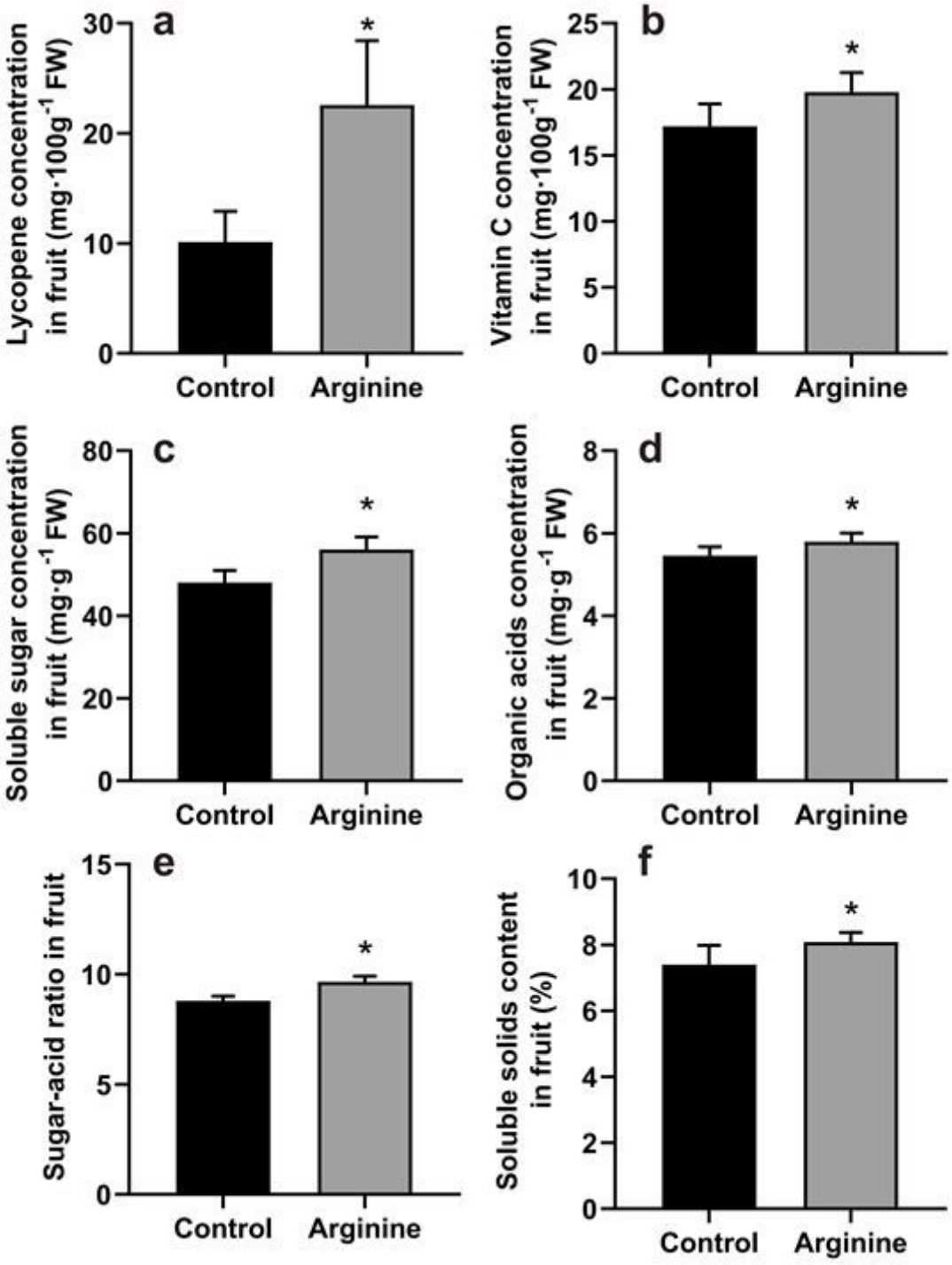

Figure 4

Varied quality traits were promoted by arginine treatment. Lycopene concentration (a), vitamin C concentration (b), soluble sugar concentration (c), titratable acids concentration (d), sugar-acid ratio (e) and soluble solid content (f) of tomato fruit with external arginine and water (control). Bars and lines represent mean and standard deviation, respectively (n = 5). Asterisks indicate $P<0.05$ by Student's t-test.

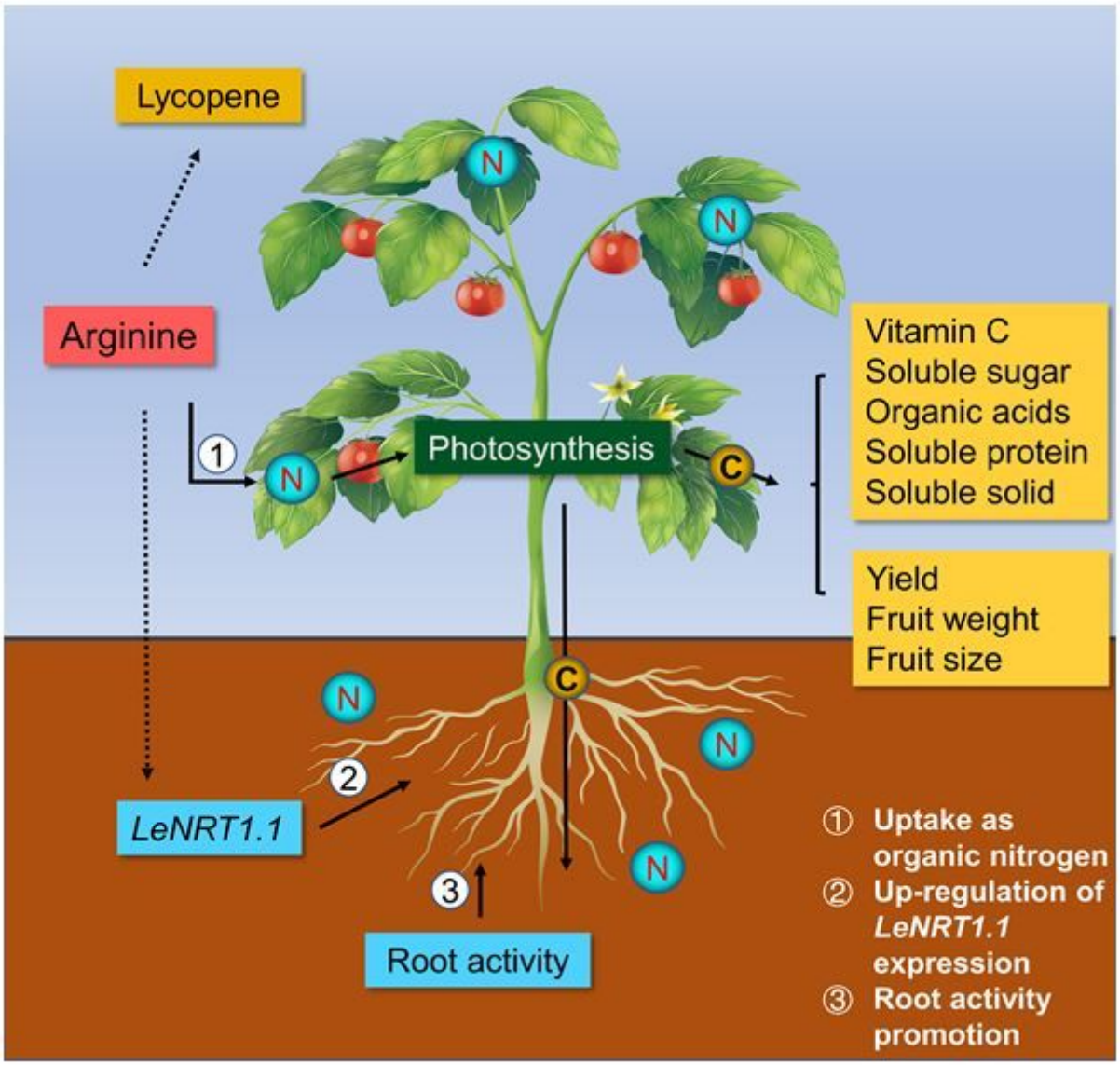

Figure 5

The mechanisms of foliar arginine application on improving growth, yield, and quality of tomato. With foliar applicated, more nitrogen accumulated in tomato aboveground by three primary mechanisms: uptake as organic nitrogen, up-regulation of LeNRT1.1 expression, and root activity promotion. Furthermore, the photosynthesis could be increased by promoted nitrogen, and then the synthesized carbohydrates might make great contribution to fruit yield and quality.

Supplementary Files

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