

Vanadium stimulates growth and flower production in tomato without affecting seed germination

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Abstract

Vanadium (V) is easily absorbed by plants and has been proposed as a novel beneficial element and inorganic biostimulant, since at low doses it can enhance plant metabolism. However, its effects on the biology of cultivated species have not been fully explored. Therefore, we evaluated the effect of V on tomato (*Solanum lycopersicum* L.) during seed germination and initial seedling growth. We tested 0, 5, 10, and 15 μM V in seeds during the germination process and in 37-day-old plants over four weeks. The application of V did not alter seed germination percentage. Plant height increased with the application of 5 μM V at 21 days after treatment application (DAT), while root volume increased with the application of 10 μM V at 28 DAT. Stem diameter, number of leaves, and number of flower buds showed the highest values with 10 μM V, while 5 μM V produced higher means in number of leaves as well as fresh and dry biomass weight of flowers. However, the fresh and dry biomass of leaves, stems, and roots decreased significantly with the application of 15 μM V. The total concentrations of amino acids and sugars in leaves, stems, and roots decreased in the treatments with V. We conclude that V is a beneficial element with high potential to be used in the biostimulation of horticultural crops such as tomato.

Keywords: beneficial elements; flowering; inorganic biostimulants; plant development; Solanaceae; *Solanum lycopersicum*

Introduction

Vanadium (V) is a metal naturally distributed in the environment, including soil, water, air, and biota. It is the fifth most abundant transition element in the Earth's crust, and is found at an average concentration of 100 mg/kg in at least 65 different minerals. Volcanic emissions, continental dust, and marine aerosol are natural sources of atmospheric V. Furthermore, oil refineries and thermoelectric power stations that use V-rich fuel oils also contribute to emissions of this element into the environment (ATSDR, 2012).

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Once released into the environment, V is an element that cannot be destroyed or decomposed, and can only change its form, or adhere to or separate into air, soil, or water particles or sediments. The transport and distribution processes of V in the environment are affected by many factors including the pH and redox potential of the medium, and the presence of particles (Wehrli and Stumm, 1989; Roberts *et al.*, 2016). Due to its many uses, exposure to high concentrations of V is common today in different environments. Excessive exposure to V-carrying particles in the air has been associated with various pathologies like hypertension, dysrhythmia, systemic inflammation, hypercoagulation, and bronchial hyper-responsiveness, among other disorders observed in humans (Fortoul *et al.*, 2014). Algae, plants, invertebrates, and fish can have certain levels of V in their tissues, while mollusks and crabs are bioaccumulators of V, and can present higher contents of this element than the levels found in seawater (Umunnakwe-Johnboscoe and Ogamba-Adindu, 2013; Anani and Olomukoro, 2020; Labuschagne *et al.*, 2020).

The intake of high levels of V through the food chain increases the risk of lesions to the nervous system, liver, kidneys, and spleen, among others (Chen *et al.*, 2021), and in some cases can produce alterations in DNA molecules, but its carcinogenic potential has not been reliably demonstrated (ATSDR, 2012; Ścibior *et al.*, 2020). On the other hand, V has enormous potential in medical applications due to its antiviral, antibacterial, antiparasitic, antifungal, anticancer, anti-hypercholesterolemic, antidiabetic, cardioprotective, and neuroprotective activity, as well as its potential ability to regulate appetite in the treatment of overweight and obesity (Ścibior *et al.*, 2020). In particular, V can restore the normal function of glycolytic enzymes in the liver, such as L-pyruvate kinase (L-PK), phosphoenolpyruvate carboxykinase (PEPCK), and glucokinase (GK), in diabetic organisms (Xie *et al.*, 2014). Therefore, V biofortification as a means of enhancing crop nutritional quality could be of great importance in future research approaches.

In nature, the existing concentration of V is similar to that of zinc (Zn), and twice that of copper (Cu) and lead (Pb) (Schlesinger *et al.*, 2017). However, V shows low mobility in the soil, since less than 1% of V is leachable and extractable with water (Tian *et al.*, 2015). V has different valence states in nature (i.e. -3 , -1 , 0 , $+2$, $+3$, $+4$, and $+5$), with the most common being $+5$ (Gan *et al.*, 2020).

In plants, the application of low concentrations of V can promote growth and improve other attributes, while high concentrations of V inhibit growth and can be toxic to various living organisms (Aihemaiti *et al.*, 2019).

Plants can easily absorb V, and its stimulating or inhibitory effect depends on various factors such as dose, source, type of compound, ionic valence, route of exposure, duration of exposure, and tested genotype (Ścibior *et al.*, 2020). At concentrations above 2 ppm V, chlorophyll degradation, growth retardation, root deformation, and nutritional imbalances can be observed (García-Jiménez *et al.*, 2018; Nawaz *et al.*, 2018). For example, high doses of V can decrease P absorption capacity and the enzymatic activity of proteins that contain phosphate groups, which reduces growth and causes water imbalances, among other important physiological disorders (Imtiaz *et al.*, 2018). Therefore, the study of the impacts that this element can have on human health, the environment, and plants is of paramount importance for life sciences.

The dose, chemical species, and oxidation state in which V is supplied, as well as the prevailing environmental conditions and root development are factors that influence V absorption processes by plants (Imtiaz *et al.*, 2017). In the environment, the factors that most affect V uptake by plant roots are soil properties like pH, redox potential, microbial activity, and organic matter content, as well as the plant species (Shaheen *et al.*, 2014). Most plants mainly accumulate V in the roots and the translocation of V from the roots to the shoots is limited. When there is an excessive availability of V in the growth medium, some plants may slow down their metabolism and decrease translocation of this element from roots to shoots, which probably provides a selective advantage to cope with toxic V levels (Chen *et al.*, 2021).

In rice (*Oryza sativa* L.), the application of 35 mg L^{-1} V decreased growth and caused root deformation and damage, cell death, and high production of reactive oxygen species (ROS) that increased the activity of the enzymes superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD), as well as the concentration of malondialdehyde (MDA) (Altaf *et al.*, 2020). However, in pepper (*Capsicum annuum* L.), concentrations of

5 μM V increased the concentrations of amino acids, chlorophylls, and sugars, stimulated growth and flowering, and modified the nutrient concentrations in the plants (García-Jiménez *et al.*, 2018). In chickpea (*Cicer arietinum* L.), low V concentrations improved nitrogen fixation, regulated plant growth, and increased K utilization and chlorophyll synthesis (Imtiaz *et al.*, 2018). In corn (*Zea mays* L.), the application of 20 ppm V increased plant height, flowering, leaf area, number of leaves, root length, concentrations of chlorophylls and carotenoids, and grain yield (Magar *et al.*, 2018). In diazotrophs (bacteria that fix atmospheric N into a more available form such as ammonium), V acts as a cofactor of V-dependent nitrogenase (Sippel and Einsle, 2017), whose function is the reduction of dinitrogen (N_2) to ammonia (NH_3) (Hu *et al.*, 2012). V also interacts with other elements like P and Mo (Venkataraman and Sudha, 2005). When supplied as monomeric vanadate, the molecule is structurally and electronically similar to phosphate, so it can participate in the inhibition and activation of enzymes related to phosphorus metabolism such as phosphatases, ATPases and phosphotransferases (Akabayov and Akabayov, 2014).

Tomato (*Solanum lycopersicum* L.) is one of the most cultivated crops worldwide, with important nutraceutical properties. In 2019, the last year for which production statistics are available, more than 243.64 million tons of fresh tomato fruits were produced worldwide in a total of 6.12 million hectares, translating into an average yield of 494 t/ha (FAOSTAT, 2021). The tomato fruit is an important source of vitamins, carotenoids, and phenolic compounds, thereby contributing to a better state of health (Quinet *et al.*, 2019). This cultivated species has been the subject of numerous studies, although the effect of inorganic biostimulants like V has not been fully explored. The objective of the present study was to evaluate the effect of different V concentrations on seed germination and initial growth of tomato seedlings, as well as on the concentration of amino acids and total sugars. Thus, two independent experiments were established. In the first experiment, the effect of V on seed germination was tested under controlled laboratory conditions. In the second experiment, the effect of V on the growth and metabolism of seedlings in their first growth stages was evaluated, in a hydroponic system under greenhouse conditions.

Materials and Methods

Germination test

To test the effect of V on seed germination, tomato seeds of the DRD8561[®] (Seminis; Mueang Khon Kaen, Thailand) variety were used. Seeds were disinfected and placed on sterilized filter paper inside 120 x 110 mm closed plastic containers, which were previously disinfected with 70% ethanol. In each container, 25 seeds were distributed and 15 mL of solution was added with the following treatments: 0, 5, 10, and 15 μM V in the form of NH_4VO_3 (Sigma-Aldrich; St. Louis, MO, USA). Each treatment was carried out in quadruplicate (i.e. four replicates per treatment). The solution was adjusted to a pH of 5.5. The containers were placed in the dark at 28 °C for three days; subsequently, they were kept at room temperature and in natural light under laboratory conditions. Irrigation was done every third day with distilled water in order to maintain moisture. Seeds with a 2 mm long radicle were considered germinated. From day 1 to day 7 after applying the treatments, the number of germinated seeds was recorded, following methodologies as previously described (Ranal and De Santana, 2006; Mehrian *et al.*, 2016).

Tests during initial seedling growth

To test the effect of V on initial seedling growth, a second experiment was established where seeds were germinated in germination trays with 200 cavities, using Canadian peatmoss as substrate. The seeds were only watered with tap water and kept under greenhouse conditions for 30 days. At this stage, no V treatments were applied.

Once the seedlings reached 30 days of age, they were placed in 35 L plastic containers containing Steiner's nutrient solution at 20%, with 1.29 mM $\text{Ca}(\text{NO}_3)_2 \cdot 4\text{H}_2\text{O}$, 0.81 mM $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, 0.19 mM

KH_2PO_4 , 0.60 mM KNO_3 , and 0.30 mM K_2SO_4 (Steiner, 1984). This base Steiner solution was supplemented with a microelement mixture containing 89.97 μM Fe, 42.68 μM Mn, 7.17 μM Zn, 40.28 μM B, 2.95 μM Cu, and 1.81 μM Mo.

The seedlings remained under these conditions for seven days as an adaptation period. After this time, the evaluation treatments were added: 0, 5, 10, and 15 μM V in the form of NH_4VO_3 (Sigma-Aldrich). The solution was adjusted to a pH of 5.5 and oxygenated for 15 min every 2 h. The nutrient solution containing the different V treatments was replaced every 7 days. The experiment was established in a completely randomized design, where each plant was designated as an experimental unit, and there were 12 replicates per treatment. The experiment was carried out in a greenhouse with an average daytime temperature of 26 °C, relative humidity of 60%, with 14 hours of light, and photosynthetically active radiation (PAR) of 275 W m^{-2} during the day.

Measurements of initial plant growth and development

Plant height was measured at 7, 14, 21, and 28 days after the application of the V treatments. At 28 days, the variables number of leaves, stem diameter, root volume, leaf area, weight of fresh and dry root, stem and leaf biomass, and number of flowers, were recorded.

Plant height was measured from the base of the plant stem to its apical zone. Stem diameter was measured with an electronic caliper. To quantify root volume, the water displacement method was used. The weight of the fresh biomass was determined separately; to do this, the plants were divided into stem, leaves, flowers and roots. Later, the fractions were weighed on an analytical scale (Pro AV213C, Adventurer Ohaus; Parsippany, NJ, USA). Finally, the separated samples were dried at 70 °C in a forced air convection oven (HCF-125D, Riossa; Monterrey, NL, Mexico) for 48 h to determine the weight of the dry biomass.

Total amino acids

The amino acid concentration in plant tissue was determined according to the ninhydrin method (Moore and Stein, 1954). Accordingly, a volume of 500 μL of the mixtures of three sequential ethanolic extractions was taken and added to 500 μL of a sodium citrate buffer solution (16 mM citric acid and 34 mM sodium citrate, pH 5.2.) and ascorbic acid (0.2% w/v). This solution was mixed with 1000 μL ninhydrin (1% w/v) in 70% ethanol (v/v). The samples were incubated at 95 °C in a water bath for 20 min, and subsequently cooled to room temperature. The standard curve was done with 10 mM leucine in 70% ethanol. Finally, the samples were read at 570 nm in a 6715 UV/Vis spectrophotometer (Jenway; Staffordshire, UK). Each treatment had four replicates and two technical replicates were read per run.

Total soluble sugars

The concentration of total soluble sugars was determined according to the anthrone method (Bailey, 1958). The extraction was done in 0.5 g of fresh plant material, to which 50 mL of 80% ethanol was added, with constant heating at 125 °C on a thermal plate (Corning; New York, NY, USA) with sporadic stirring (approximately 5 s each). Upon completion, the samples were filtered and the extracts were filled up to a final volume of 20 mL. Subsequently, 500 μL of 80% ethanol was added to a 500 μL aliquot. The samples were placed on ice and then a volume of 5 mL anthrone (Meyer; Querétaro, Querétaro, Mexico) was added. Following this, they were placed for 15 min at 95 °C in a water bath, and immediately after they were placed on ice to stop the reaction. To read the samples, a 6715 UV/Vis spectrophotometer was used, a standard curve was done with glucose (Sigma-Aldrich) and they were read at 620 nm. Each treatment had four replicates and two technical replicates were read per run.

Statistical analysis

In order to verify the normality and homogeneity of variances, a Shapiro-Wilk and Bartlett test ($P \leq 0.05$) was performed with the data obtained. In some cases, the data were subjected to logarithmic transformations,

although the results are shown untransformed. Once these assumptions were verified, a one-way analysis of variance (ANOVA) was carried out and Duncan's method ($P \leq 0.05$) was used for means comparison using SAS 9.0 statistical software.

Results

V application does not affect tomato seed germination

Two days after the application of the treatments (DAT), the germination percentage was significantly reduced when applying 10 μM V, as compared to the control. Three, four, and five days after treatment application (DAT), the means of all the treatments were statistically similar to each other. However, at 3 DAT, the application of 5 μM V produced a germination percentage 4% higher than that of the control, though this increase was not statistically different from the control (Figure 1).

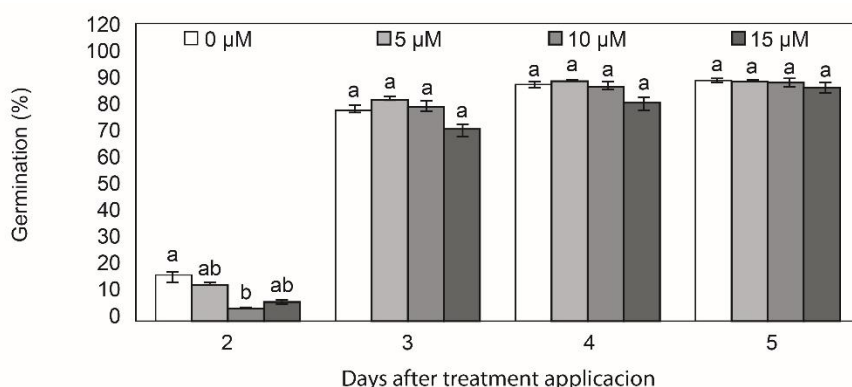


Figure 1. Germination percentage of tomato seeds treated with different V concentrations (0, 5, 10, and 15 μM V) 2, 3, 4, and 5 days after treatment application (DAT)

Means with different letters on the columns of each measurement indicate statistically significant differences among treatments (Duncan; $\alpha = 0.05$). Means \pm Standard Error

Vanadium stimulates initial tomato plant growth and development

Plant height

At 7 DAT, the application of 5 and 10 μM V significantly decreased plant height as compared to the control. Nevertheless, in measurements made at 14 DAT, no statistical differences were observed among treatments. In the measurement carried out 21 DAT, the greatest plant height was observed in the treatment with 10 μM V, while the other treatments were statistically similar. At 28 DAT, plant height was higher in the treatment with 5 μM V, but similar to the control and the treatment with 10 μM V. It is important to note that in the measurements made at 28 days, the lowest height was obtained in plants treated with 10 and 15 μM V (Figure 2).

Root volume

Root volume was measured at the end of the experiment, 28 DAT. The highest mean for this variable was observed in plants treated with 10 μM V. The results for the other treatments were similar to each other and lower than those of the treatment with 10 μM V (Figure 3). It is important to note that in the plants treated with 5 and 15 μM , a greater number of secondary roots was observed, as compared to plants treated with 10 μM V (data not shown).

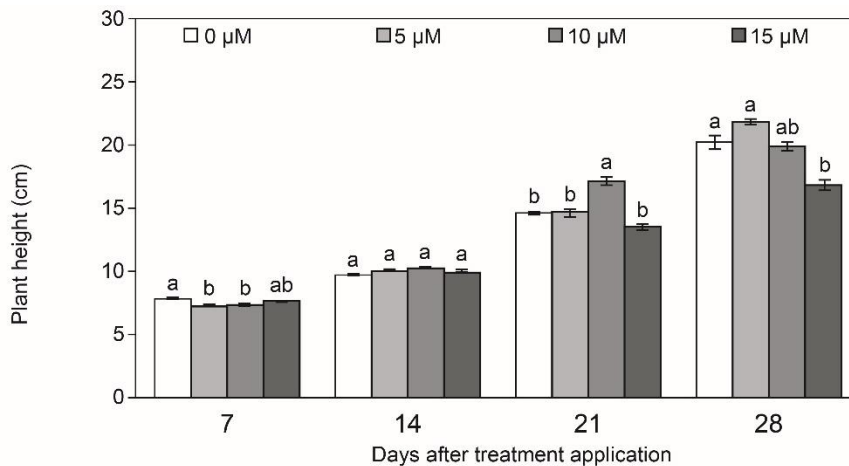


Figure 2. Plant height of tomato plants treated with different V concentrations (0, 5, 10, and 15 μM V) 7, 14, 21, and 28 days after treatment application (DAT). Means with different letters on the columns of each measurement indicate statistically significant differences among treatments (Duncan; $\alpha = 0.05$). Means \pm Standard Error

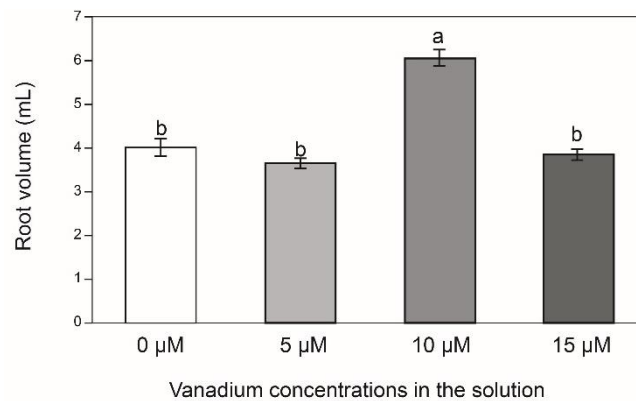


Figure 3. Root volume of tomato plants grown in nutrient solution with different V concentrations (0, 5, 10, and 15 μM V) for 28 days. Means with different letters on the columns indicate statistically significant differences among treatments (Duncan; $\alpha = 0.05$). Means \pm Standard Error

Stem diameter, number of leaves, number of flower buds, and weight of fresh and dry flower matter

The variables stem diameter, number of leaves, number of flower buds, and weight of fresh and dry flower matter, recorded at 28 DAT, are shown in Table 1. It can be observed that the stem diameter of the tomato plants treated with 10 μM V was greater than that of the other treatments. Nevertheless, with a concentration of 15 μM V, the diameter decreased even more than that of the control. Plants treated with 5 and 10 μM V showed the highest number of leaves, while those treated with 15 μM V displayed the lowest values for this variable. Control plants had an intermediate number of leaves. The number of flower buds per plant was higher with the application of 5 and 10 μM V, while the application of 15 μM V decreased the value of this variable. The lowest value of this variable was observed in control plants, although it was similar to the treatments with 5 and 15 μM V. The fresh and dry biomass weight of flowers was higher with the application of 5 μM V. The means in the other treatments showed no significant statistical differences among them, and they were lower than the mean observed in plants receiving 5 μM V. Interestingly, the application of 5 μM V accelerated flowering and generated larger flowers. The application of 15 μM V also accelerated flowering, but the flowers were smaller than those produced by the plants treated with 5 μM V. In contrast, in the control, only the presence of flower buds was observed (data not shown).

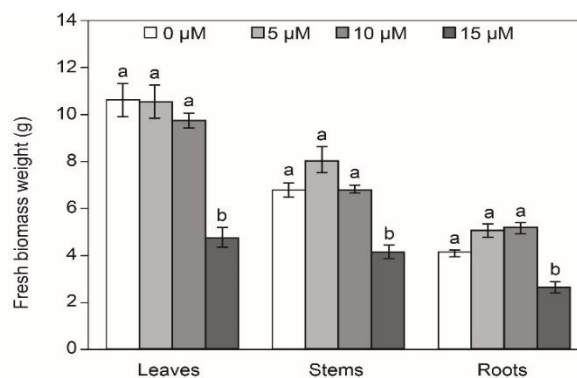
Table 1. Stem diameter, number of leaves, number of flower buds, and fresh and dry biomass weight of flowers of tomato plants exposed to different vanadium (V) concentrations in the nutrient solution for 28 days

Vanadium concentration	Stem diameter (mm)	Number of leaves	Number of flower buds	Fresh biomass weight of flowers (g)	Dry biomass weight of flowers (g)
Control	5.72 ± 0.09 b	8.87 ± 0.20 b	7.50 ± 0.71 b	0.32 ± 0.03 b	0.03 ± 0.004 b
5 µM	5.67 ± 0.12 b	9.14 ± 0.13 a	9.00 ± 0.55 ab	0.50 ± 0.07 a	0.06 ± 0.005 a
10 µM	6.15 ± 0.11 a	9.14 ± 0.13 a	9.14 ± 0.36 a	0.34 ± 0.01 b	0.04 ± 0.002 b
15 µM	4.31 ± 0.11 c	7.66 ± 0.10 c	8.14 ± 0.27 b	0.31 ± 0.04 b	0.04 ± 0.005 b
Pr > F	<0.0001	<0.0001	<0.0001	0.0072	0.0061

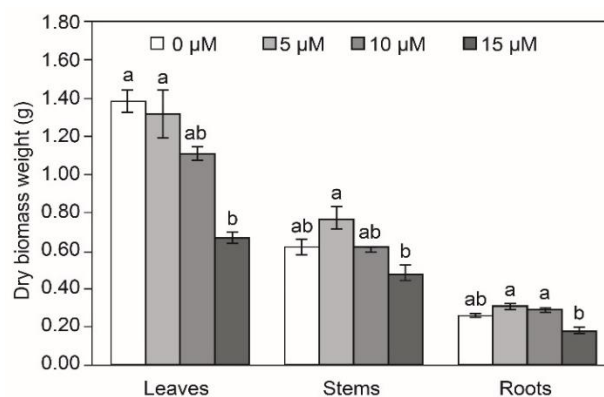
Means with different letters in each column, indicate statistical differences among treatments (Duncan; $\alpha = 0.05$). Means \pm Standard Error

Weight of fresh and dry biomass of leaves, stems, and roots

Regarding the weight of the fresh and dry biomass of leaves, the low and medium levels of V (i.e. 5 and 10 µM V) produced means similar to the control, while when applying 15 µM V the value of this variable was statistically lower than the rest of the treatments. The same behavior was observed for the variables fresh weight of stems and roots. However, in these last two tissues, a tendency of the value of this variable to increase was observed when applying 5 and 10 µM V (Figures 4 and 5).

**Figure 4.** Fresh biomass weight of leaves, stems, and roots of tomato plants grown in nutrient solution with different V concentrations (0, 5, 10, and 15 µM V) for 28 days

Means with different letters on the columns of each tissue indicate statistically significant differences among treatments (Duncan; $\alpha = 0.05$). Means \pm Standard Error

**Figure 5.** Dry biomass weight of leaves, stems, and roots of tomato plants grown in nutrient solution with different V concentrations (0, 5, 10, and 15 µM V) for 28 days

Means with different letters on the columns of each tissue indicate statistically significant differences among treatments (Duncan; $\alpha = 0.05$). Means \pm Standard Error

Concentration of total free amino acids and total soluble sugars in leaves, stems, and roots are negatively affected by V

The concentration of amino acids in the three analysed plant tissues was higher in the control plants than in those treated with V. In general, the highest concentrations of free amino acids were observed in stems and the lowest in leaves, while the roots showed intermediate concentrations (Figure 6).

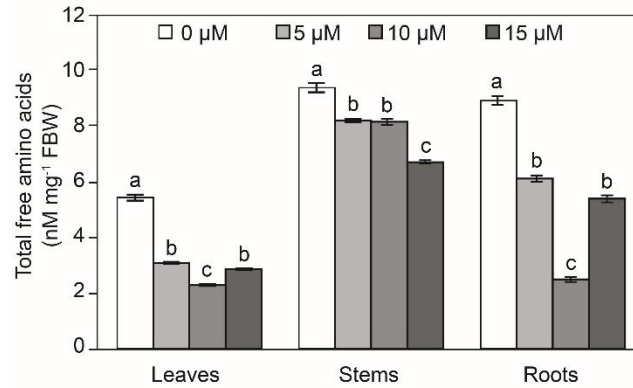


Figure 6. Concentration of total free amino acids in leaves, stems, and roots of tomato plants grown in nutrient solution with different V concentrations (0, 5, 10, and 15 μM V) for 28 days. Means with different letters on the columns of each tissue indicate statistically significant differences among treatments (Duncan; $\alpha = 0.05$). Means \pm Standard Errors. FBW: Fresh Biomass Weight

In leaves, the highest concentration of total soluble sugars was observed in the control plants and in those treated with 15 μM V, while the values of this variable in leaves of plants exposed to 5 and 10 μM V were lower than the other two treatments. In stems, a similar behavior to that observed in leaves was evident, since the highest concentration of sugars was obtained in the control plants, followed by plants exposed to 15 μM V, and the lowest value was observed at the 5 μM V dose. In roots, the highest concentrations of soluble sugars were obtained in control plants and those treated with 5 μM V; plants exposed to 10 and 15 μM V showed lower means as compared to the other treatments, though the 5 and 15 μM V applications were statistically similar. Regardless of the treatments to which the plants were exposed, the highest concentrations of total soluble sugars were observed in the stems, while the lowest concentrations were observed in the roots, with the leaves showing intermediate concentrations when comparing the tissues (Figure 7).

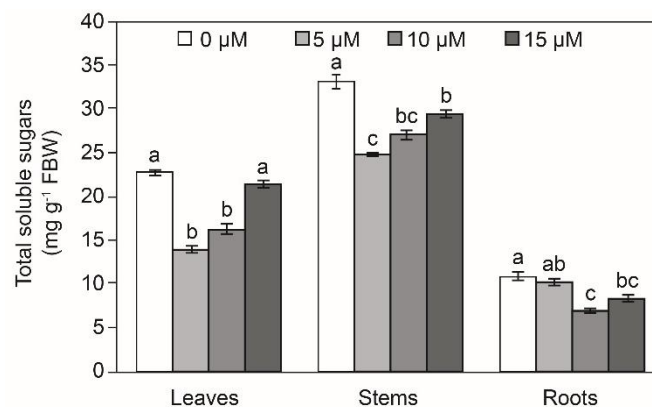


Figure 7. Concentration of total soluble sugars in leaves, stems, and roots of tomato plants grown in nutrient solution with different V concentrations (0, 5, 10, and 15 μM V) for 28 days. Means with different letters on the columns of each tissue indicate statistically significant differences among treatments (Duncan; $\alpha = 0.05$). Means \pm Standard Error. FBW: Fresh Biomass Weight

Discussion

Beneficial elements are not considered necessary for plant development, but they can promote plant growth and development while stimulating better crop yields and quality (Carvalho *et al.*, 2020). Among the elements that are considered beneficial are cerium (Ce), aluminum (Al), iodine (I), cobalt (Co), lanthanum (La), silicon (Si), selenium (Se), titanium (Ti), sodium (Na), and vanadium (V) (Pilon-Smits *et al.*, 2009; Gómez-Merino and Trejo-Téllez, 2018). However, beneficial elements can have different effects and functions in the plant depending on various factors such as concentration, source, and method of application of the element, as well as the genotype, phenological stage, and agronomic management of the crop species. It should be noted that there is increasing experimental evidence that these elements can produce hormesis, a natural phenomenon by which low concentrations stimulate the development, growth, and production of the plant, while high concentrations cause toxicity (Jalal *et al.*, 2021). In this work, the application of V had no effect on the germination of tomato seeds at 3, 4, and 5 days after treatment application (DAT), although at 2 DAT there was a decrease in the values of this variable when applying 10 μM V, as compared to the control (Figure 1). Metals like V affect cell division and alter the seed coat, which decreases germination. Given this, the seeds trigger survival strategies like chelation of the element within cellular compartments, decreasing the absorption of the element and activating antioxidant mechanisms, which can cause reduced germination rates at the beginning of the process (Wu *et al.*, 2020).

Regarding the growth variables, positive effects of the application of V were observed. At 21 DAT, plant height was higher with the application of 10 μM as compared to the control, while at 28 DAT, the application of 5 μM produced the greatest height in absolute terms, although the mean was statistically similar to the control and to the treatment with 10 μM V (Figure 2). Also in tomato, the addition of 5 μM and 10 μM V increased seedling height (Saldaña-Sánchez *et al.*, 2019), which can be attributed to the fact that V confers greater elasticity to the tissue, increased water volume, greater growth, and better cell expansion (Emadian and Newton, 1989). Depending on the dose and environmental conditions, V acts as a redox catalyst during electron transport in photosystems I and II, besides participating in the accumulation and fixation of N in plants. Thus, growth promotion is probably due to the stimulation of chlorophyll biosynthesis, the translocation and absorption of essential elements and N use efficiency (Imtiaz *et al.*, 2017; 2018). These determinations are in progress in our laboratory.

In our study, the application of 10 μM V stimulated root volume (Figure 3), which could be because there was a greater number of secondary roots compared to the control. Coincidentally, in *Arabidopsis thaliana* exposed to 25 μM , a higher formation and density of root hairs was observed (Lin *et al.*, 2015). In tomato, root volume increased when applying 3, 5, or 10 μM V (Saldaña-Sánchez *et al.*, 2019). In common beans (*Phaseolus vulgaris* L.), the application of 320 μM V inhibited root growth, dry weight, and leaf size (Saco *et al.*, 2013). This is probably because when V surpasses concentrations that the plant can tolerate, it causes deformation of the roots, which in turn decreases the absorption and use efficiency of essential elements (García-Jiménez *et al.*, 2018; Nawaz *et al.*, 2018).

The application of 10 μM V produced stems with greater diameter, as well as a greater number of leaves per plant as compared to the control, while 15 μM V resulted in stems of lesser diameter and fewer leaves (Table 1). In sugarcane (*Saccharum* spp. hybrids), the application of 0, 10, and 20 μM V increased stem diameter as the dose of applied V increased (Senties-Herrera *et al.*, 2018). In pepper cv. Mysterio, stem diameter increased with the application of 5 μM V and decreased with 10 μM V (García-Jiménez *et al.*, 2018). These stimulating effects of V at low concentrations can be attributed to the fact that V increases the availability of N and fosters growth and photosynthetic activity, as well as being essential for the peroxidase holoenzyme of bromine, iodine, and chlorine (Basiouny, 1984; McLauchlan *et al.*, 2018). Additionally, V can act through N-fixing microorganisms and increase the supply of this essential element thus stimulating plant growth (Eady, 1989).

However, higher concentrations of V can inhibit or delay the growth of plants. For example, in rice, the application of 0, 15, 25, 35, and 70 mg L^{-1} V decreased the number of leaves and length of shoots and roots as

the dose of V supplied increased (Altaf *et al.*, 2020). These responses may be because high V doses can induce cellular degradative processes that result in slower growth (Imtiaz *et al.*, 2017).

An important effect to observe in our study was that the application of 10 μM V stimulated the formation of flower buds (Table 1). These results coincide with those already observed in this same species, since applying 250 ng mL^{-1} V increased flower production (Basiouny, 1984). Although in stems and roots the application of 5 and 10 μM V tended to increase the production of fresh and dry biomass, the differences with the control were not significant. Contrarily, when applying 15 μM V, the means of the variables fresh and dry biomass weight decreased in the three tissues analyzed. Similar results were obtained in pepper flower biomass weight, which increased with applications of concentrations of 5 and 10 μM V (García-Jiménez *et al.*, 2018). In rice, when the applications were increased to 30 mg L^{-1} V, the production of fresh biomass, shoot height, and root length decreased (Yuan *et al.*, 2020). These detrimental effects may be attributed to the fact that high doses of V can trigger oxidative stress and suppress the absorption of essential elements, which inhibits the growth and development of different plant structures (Roychoudhury, 2020).

These results suggest that V has a hormetic effect, as it promotes the growth and development of different plant species when applied at low concentrations, while at high concentrations it is toxic to plants and inhibits their growth. This effect has also been reported in other beneficial elements such as Al, Co, and Se (Poschenrieder *et al.*, 2006; Kaur *et al.*, 2016; Moreno-Alvarado *et al.*, 2017).

The concentration of free amino acids in leaves, stems, and roots was the highest in control plants, and decreased with the application of V (Figure 6). Massive bioaccumulation of V beyond the threshold limit has serious consequences, inhibiting growth, chlorophyll content, and photosynthesis, in addition to causing oxidative damage, breakage and aberrations of chromosomes, alteration of mineral homeostasis, and disruption of the proper functioning of various metabolic processes (Roychoudhury, 2020). In rice, the application of at least 1 mM V increased lipid peroxidation and the activity of mitogen-activated protein kinase (MAPK) and calcium-dependent protein kinase (CDPK) in roots (Lin *et al.*, 2009). Furthermore, 0.25-2.0 mM V exposure induced changes in the expression of genes related to cell metabolism, signaling, response to stimuli, ion transport, and auxin, abscisic acid (ABA), and jasmonic acid (JA) biosynthesis (Lin *et al.*, 2013). In contrast, the application of 5 and 10 μM V increased the concentrations of amino acids and total sugars in pepper plants (García-Jiménez *et al.*, 2018), which was attributed to the function of V as a redox catalyst in the transport of electrons in photosystems I and II, and its contribution to the accumulation and fixation of N in plants, as well as the absorption and translocation of essential elements (Imtiaz *et al.*, 2018; Meisch and Becker, 1981). It is possible that the stimulatory or inhibitory effects of V are linked to genetic and physiological attributes of certain plants, and their ability to harness V in specific functions (Chen *et al.*, 2021).

The concentration of total soluble sugars was higher in control plants in the three tissues analyzed, the concentration being the highest in stems, followed by leaves and finally roots. The lower concentrations of applied V decreased the concentrations of soluble sugars in leaves and stems, while increasing the levels of V upped the concentration of these biomolecules were observed (Figure 7). In sunflower (*Helianthus annuus* L.), the application of $\geq 7.5 \text{ mg L}^{-1}$ V was found to increase the concentration of sugars (Abedini and Mohammadian, 2018). V can increase sucrose synthase activity and sucrose synthesis, which in turn increases total sugar content (Singh and Wort, 1969). A higher sucrose content is associated with a higher rate of CO_2 fixation and the activity of sucrose biosynthesis enzymes, which in turn increases the photosynthetic efficiency resulting in a greater source of energy, and therefore contributes to the development of the plant and stimulates flowering. In fact, sucrose can promote floral transition in several plant species (Ohto *et al.*, 2001), so V could be an important external factor to activate the regulatory pathways of the floral transition in tomato.

In ongoing research in our workgroup, we are analyzing the effect of V on nutrition, production, and fruit quality, as a strategy to supply V given the benefits it can have on human health. V has low absorption by the oral route, which decreases its toxicity during the medicinal use of V compounds. There is a strong similarity between the structure of vanadate and that of phosphate that makes the former assume metabolic regulatory functions, which is reflected in functional regulation between vanadate and phosphate-dependent enzymes,

where vanadate blocks the protein-binding domain for phosphate (Rehder, 2013). The antagonism of vanadate with phosphate, the direct influence that V has on DNA, and the participation of V in the removal of reactive oxygen species (ROS) are the modes of action of V that have been identified for its probable medicinal application, with high potential applications as a neuroprotective, as well as in approaches aimed at controlling cancer and protozoal, viral, and bacterial diseases (Rehder, 2016).

The daily V intake in humans is between 10 and 160 μg , which comes from foods like parsley, seafood, wine, beer, spinach, and mushrooms, among others. V participates in the metabolism of bones and teeth, in addition to acting as an enzymatic cofactor, regulating the action of enzymes such as Na^+ - and K^+ -ATPases, phosphotransferases, adenyl cyclases, and protein kinases (Grzanka *et al.*, 2020).

The importance of V in the human diet, its low absorption by the oral route, and its beneficial effects in plants together provide an opportunity for its use in the production of commonly consumed crops, which favors both the development of crops and the human diet. When there is excessive V in plants, they have developed detoxification mechanisms such as V precipitation in the root system, sequestration in the vacuole or cell wall, localization in the apoplast, or activation of the antioxidant defense systems (Chen *et al.*, 2021; Yang *et al.*, 2017). In fact, much of the V that reaches the plant remains in the roots and only small amounts are translocated to the stem and leaves, while the root system tends to accumulate more V than is found in the soil where the plants grow (Chen *et al.*, 2021; Chételat *et al.*, 2021). Nevertheless, it is necessary to carry out precise studies to determine the mechanisms that its application triggers in the cell, as well as the thresholds between beneficial and toxic effects of V in the plant, in order to guarantee the application of optimal doses for the development of plants, while being suitable for humans when consuming the obtained products (i.e. leaves, fruits, roots, etc.).

A summary of the results we observed in this study are depicted in Figure 8.

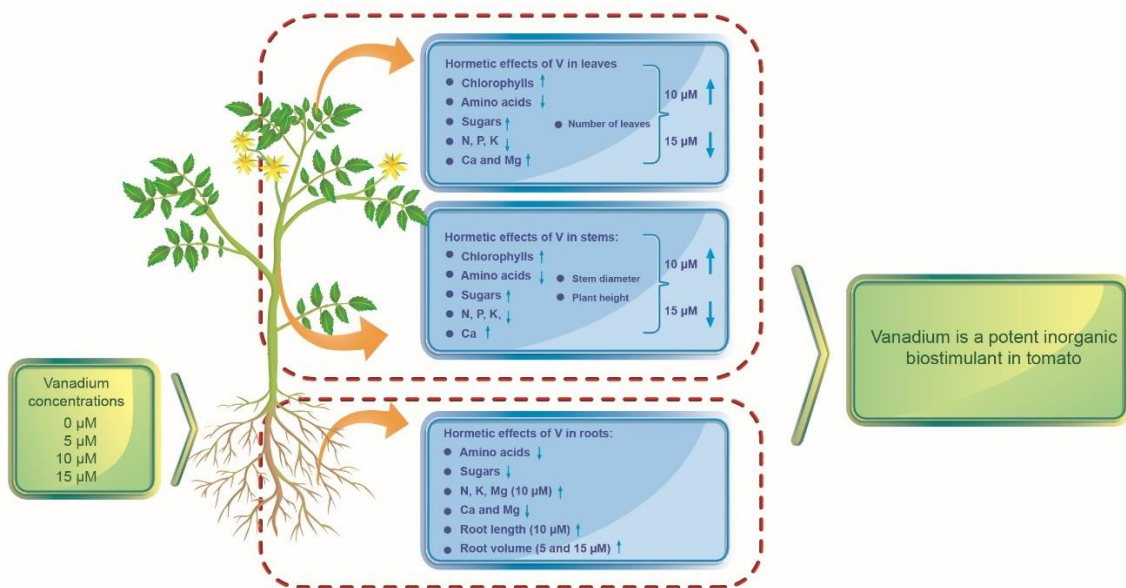


Figure 8. Summary of the effects of vanadium application to tomato plants on biomolecule and nutrient concentrations observed in leaves, stems and roots

Conclusions

Vanadium did not affect germination in tomato, but it did have significant effects on growth and flowering. Concentrations of 5 to 10 μM V helped stimulate plant growth, promoting greater height, root volume, stem diameter, number of leaves, number of flower buds, and weight of fresh and dry flower matter.

However, inhibitory effects of V were observed in the measured amino acid and sugar concentrations. We conclude that low doses of V (5-10 μ M V) can be used in the initial stages of tomato plant development to enhance growth and induce floral transition.

Authors' Contributions

Conceptualization, L.I.T.-T. and F.C.G.-M.; methodology, A.G.-J., L.I.T.-T. and F.C.G.-M.; software, L.I.T.-T.; validation, L.I.T.-T. and A.C.-O.; formal analysis, M.G.P.-S., L.I.T.-T. and A.C.-O.; investigation, A.G.-J. and M.G.P.-S.; resources, F.C.G.-M. and L.I.T.-T.; writing—original draft preparation, A.G.-J. and M.G.P.-S.; writing—review and editing, F.C.G.-M.; supervision, F.C.G.-M.; project administration, F.C.G.-M. and L.I.T.-T. All authors read and approved the final manuscript.

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Conflict of Interests

The authors declare that there are no conflicts of interest related to this article.

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