
NITROGEN AND POTASSIUM NUTRITION DIFFERENTIALLY AFFECT TOMATO BIOMASS AND GROWTH

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SUMMARY

We evaluated the effect of nitrogen and potassium nutrition on phenological stages on the vegetative biomass production and growth of tomato cultivated hydroponically. Nitrogen concentrations of 10, 12, 14, and 16 mol_c·m⁻³ in the vegetative stage were evaluated, while potassium concentrations of 5, 7, 9, 11, and 13 mol_c·m⁻³ were evaluated for the reproductive stage. In the vegetative stage, the addition of N caused significant differences in the vegetation dry biomass (VDB), with the largest responses observed at concentrations of 14 and 16 mol_c·m⁻³. For the reproductive stage, a significant re-

sponse was only observed for K. The 5-13 mol_c·m⁻³ increases in the K concentration raised the VDB. Growth (net assimilation rate NAR, relative growth rate RGR, and crop growth rate CGR) was characterized by a quadratic behavior in the vegetative stage. In the reproductive stage, NAR and RGR exhibited an asymptotic negative trend, while CGR exhibited a positive quadratic trend. Nitrogen and potassium positively affected the growth variables evaluated in the vegetative and reproductive stages, increasing the productive potential of hydroponically cultivated tomato.

Introduction

Direct measures of growth such as dry weight, leaf area, and time are used for the quantitative analysis of plant growth, and the following rates are calculated, among others: relative growth rate, crop growth rate, net assimilation rate, leaf area index, and leaf area duration. These indexes allow for the analysis of plant growth by measuring the accumulation of dry matter, which depends on the amount of leaf area, the time of leaf functioning (Tekalign and Hammes, 2005), the interception and use of solar radiation, and management practices during the growing season, which includes fertilization management (Santos *et al.*, 2010).

The content of particular elements in leaves changes over leaf lifetime, and these changes are partially associated with phenology during the growing season (Bueno *et al.*, 2011) in association with organ ageing, which affects the mineral composition of plant organs (Thomas, 2013). The nutrient concentrations of vegetative parts therefore often decline sharply during the reproductive stage (Marschner, 2012), and 60 to 70% of the absorbed N, P, or K is accumulated in the fruits (Dumas, 1990), which account for 52 to 72% of the total plant dry biomass at this time (Peil and Galvez, 2005). In this context, the establishment of appropriate N/K ratios for the various stages of the crop is a

fundamental factor for managing the production of tomato in a greenhouse (Hernández-Díaz *et al.*, 2009). Both nutrients affect the balance between processes that occur in the vegetative and reproductive stages. More than 90% of plant dry matter consists of organic compounds such as cellulose, starch, lipids and proteins; and part of these compounds determine the biological yield which is directly related to photosynthesis (Engels *et al.*, 2012). In turn, photosynthesis is a biological process that is affected by different factors, including the N status (Hawkesford, 2012), foliar area, and by chlorophyll, soluble proteins and RuBisCO contents (Li *et al.*, 2013), among others. Regarding K,

this element plays a central role in stomatal conductance, conversion of light energy into chemical energy, mesophyll resistance, photosynthetic CO₂ fixation and RuBisCO activity (Mengel and Kirkby, 2001; Cakmak, 2005). Therefore, there is a dare need to investigate the impact of N and K on biomass accumulation and growth in order to propose models that can predict the behavior of growth rates in response to the supply of N in the vegetative stage and K in the reproductive age. Importantly, in addition to time, both N and K represent critical factors for growth during different phenological stages of the tomato crop. Hence, in this study we aimed to evaluate the combined

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NUTRIÇÃO DIFERENCIADA UTILIZANDO NITROGENIO E POTÁSSIO AFETA O CRESCIMENTO E A BIOMASSA EM TOMATEIROS

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RESUMO

Este estudo avaliou o efeito do nitrogênio e potássio, na nutrição, estádios fenológicos, produção de biomassa vegetal e crescimento do tomateiro cultivado em sistema hidropônico. As concentrações de nitrogênio (N) foram 10, 12, 14, e 16 mol_c.m⁻³, as quais foram avaliadas na fase vegetativa, enquanto que as concentrações de potássio (K) foram 5, 7, 9, 11, e 13 mol_c.m⁻³, avaliados na fase reprodutiva. Na fase vegetativa, a adição de N causou diferenças significativas na biomassa seca vegetativa (BSV), com as maiores respostas observadas nas concentrações de 14 e 16 mol_c.m⁻³. Para a fase reprodutiva, apenas para o K foi observada resposta signifi-

cativa. Para todas as concentrações de K, 5-13 mol_c.m⁻³, foi observado aumentou na BSV. O crescimento (taxa de assimilação líquida, TAL; taxa de crescimento relativo, TCR; e taxa de crescimento da cultura, TCC) foi caracterizado por um comportamento quadrático na fase vegetativa. Na fase reprodutiva, TAL e NAR exibiram uma tendência negativa assintótica, enquanto TCC exibiu uma tendência quadrática positiva. O nitrogênio e o potássio afetam positivamente as variáveis fisiológicas avaliadas no estágio vegetativo e reprodutivos, aumentando o potencial de produção de tomates cultivados em sistema hidropônico.

LA NUTRICIÓN NITROGENADA Y POTÁSICA AFECTA LA BIOMASA Y EL CRECIMIENTO DEL TOMATE

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RESUMEN

Se evaluaron los efectos de la nutrición con nitrógeno y potasio por etapas fenológicas en la producción de biomasa vegetativa y en el crecimiento de plantas de tomate cultivado en hidroponía. Las concentraciones de nitrógeno en la solución nutritiva evaluadas en la etapa vegetativa fueron 10, 12, 14 y 16 mol_c.m⁻³; mientras que las de potasio, evaluadas en la etapa reproductiva, fueron 5, 7, 9, 11 y 13 mol_c.m⁻³. En la fase vegetativa, dosis crecientes de N ocasionaron efectos significativos en la biomasa seca vegetativa (VDB), registrándose las medias más altas en esta variable con concentraciones de N entre 14 y 16 mol_c.m⁻³. En la fase reproductiva solamente para K se observaron efec-

tos significativos. El incremento de K en la solución nutritiva de 5 a 13 mol_c.m⁻³ aumentó la biomasa seca vegetativa (VDB). El crecimiento (tasa de asimilación neta NAR, tasa de crecimiento relativo RGR, y tasa de crecimiento del cultivo CGR) es caracterizado por un comportamiento cuadrático en el estado vegetativo. En el estado reproductivo, NAR y RGR exhiben una tendencia asintótica negativa, mientras que CGR muestra una tendencia cuadrática positiva. El nitrógeno y el potasio afectan positivamente las variables de crecimiento evaluadas tanto en la fase vegetativa como en la reproductiva, incrementándose con ello el potencial productivo de tomate cultivado en hidroponía.

effects of the N concentration in the vegetative stage and the K concentration in the reproductive stage on the vegetative biomass production and growth dynamics of tomato cv. Charleston under hydroponic greenhouse conditions.

Materials and Methods

The study was carried out at Colegio de Postgraduados Campus Montecillo, municipality of Texcoco, State of Mexico (19°29'N, 98°53'W and 2250masl), from July to December 2012. During this period, monthly average day lengths were 10.9, 11.0, 9.7, 9.8, 9.6 and 9.0h, respectively.

The research was conducted under greenhouse and hydroponics conditions. Inside the

greenhouse, a Hobo H8 Onset Computer Corporation[®] Data Logger that was located immediately above the canopy was used to record the daily maximum and minimum temperatures. Solar radiation was obtained from the weather station of Colegio de Postgraduados. The solar radiation data were transformed to photosynthetically active radiation (PAR) using a correction factor of 0.47 according to Blackburn and Proctor (1983) and then another correction was made because the plastic in the greenhouse had a transmittance of 74%, which was corroborated by random measurements collected with a light sensor (Spectrum Technologies 3415FX, USA). Climatic data are reported as

decadal means, and the PAR radiation corresponded to values between 12:00 and 14:00.

The experiment was conducted in two stages. First, 4 levels of nitrogen in the nutrient solution (10, 12, 14 and 16 mol_c.m⁻³) during the vegetative stage were evaluated under a completely randomized design with 4 replicates per treatment. Second, the plants that received N treatments in the first stage were used to evaluate 5 concentrations of potassium (5, 7, 9, 11, and 13 mol_c.m⁻³) during the reproductive stage. The combination of N×K originated 20 treatments, which were established under a design of plots divided completely randomly with 4 replications, using one plant per pot as the

experimental unit. The N level corresponded to the large plot, and the K level corresponded to the small plot.

Seeds of Campari tomato cv. Charleston were sown in a tray with 200 cavities in a mixture of peat:perlite 4:1 v/v. The seedlings were watered with tap water until the first true leaf appeared; then, a 25% concentration Steiner solution (Steiner, 1984) was applied until 37 days after planting. At this time the seedlings were transplanted at a density of 3.8 plants/m², placing each plant in a black polyethylene bag (40×40cm) with 13 liters of red volcanic rock (≤1.2mm diameter) used as substrate. After the transplant, the experiment lasted 170 days.

Eight daily irrigations (134ml for each event) were performed using a drip irrigation system during the first 30 days after transplantation (DAT). From this moment until the end of the growing season (170 DAT), 16 daily irrigations (140ml) were applied. The concentration and composition of the nutrient solution were varied according to the phenological stage (Steiner, 1984). In the first week, the nutrient solution was applied at 50% of its original concentration. After the first week and until 45 DAT, the N concentration of the nutrient solution was changed to 10, 12, 14, or 16mol_c·m⁻³, for the vegetative stage of the crop. Subsequently, for the reproductive stage, the K concentration of the nutrient solution was modified to 5, 7, 9, 11, or 13mol_c·m⁻³. For both the vegetative and reproductive phenological stages, the electrical conductivity of the nutrient solution was adjusted to a value of 2dS·m⁻¹, with an osmotic potential of -0.072MPa.

Destructive samplings were performed during the growing season to determine the variables during the vegetative (first 45 DAT) and reproductive (46-170 DAT) growth stages. Samples were collected at 14, 28, and 42 DAT from the vegetative stage and at 69, 126, 152, and 170 DAT from the reproductive stage, as indicated below.

Vegetation dry biomass (VDB)

The leaves and stems of the plants were separated and placed in an oven (Riosa HCF-125D, Mexico) with air circulating at 70°C for 72h to obtain a constant dry weight (g).

Growth rate analysis

Growth rates were also assessed during both the vegetative and reproductive stages by determining the net assimilation rate (NAR, mg·dm⁻²/day), the relative growth rate (RGR, mg·g⁻¹/day), and the culture growth rate (CGR, g/day) according to Hunt (1981) as follows:

$$NAR = \left(\frac{DW_2 - DW_1}{LA_2 - LA_1} \right) \left(\frac{\ln LA_2 - \ln LA_1}{t_2 - t_1} \right) \quad (1)$$

$$RGR = \left(\frac{\ln DW_2 - \ln DW_1}{t_2 - t_1} \right) \quad (2)$$

$$CGR = \left(\frac{DW_2 - DW_1}{t_2 - t_1} \right) \quad (3)$$

where DW₁ and DW₂: initial and final dry weights, respectively, of the time interval; LA₁ and LA₂: initial and final leaf areas, respectively, of the time interval; and t₁ and t₂: initial and final times.

The data were analyzed using analysis of variance, and the means compared by Tukey's test (P≤0.05). The Statistical Analysis System ver. 9.3 (SAS, 2011) program was used to perform the data analysis. The initial regression models were specified for the growth rates based on the response of the variable of interest to the factors under study, i.e., N for the vegetative stage and K for the reproductive stage. In addition, the time in days after transplantation (DAT) was also considered as an independent variable. The signs and interactions were also considered until the best-fit model was obtained, using the mean square error (MSE) as a criterion for the goodness of fit according to Volke *et al.* (2005).

Results and Discussion

Figure 1 shows the temperature range of 9-28°C during the course of the tomato crop cycle. During the vegetative stage, the mean maximum and minimum daily temperatures were 28 and 12°C, respectively; while they were 29 and 6°C, respectively, during the reproductive stage. The amount of PAR radiation varied, with mean maximum values of 300W·m⁻² from July to October, but the maximum PAR tended to decrease to 251W·m⁻² from November to December, which coincided with the final stage of crop growth. This information is important because tomato leaves can absorb up to 85%

of PAR light, but this capacity changes over time, and leaves may show different photosynthetic rates in response to environmental

cues (Heuvelink and Dorais, 2005) as it indeed happened in our experiment.

The responses of the vegetation dry biomass (VDB) differed significantly among N treatments (vegetative stage), and the effects of N on the VDB were observed from day 28 after treatments onwards (Table I). In the reproductive stage, N and the N×K interaction did not affect VDB. In contrast, at this stage, K treatments caused effects on VDB, but despite the effects exerted by K, the effect of the K×N interaction was not significant (Table I).

The N applied at the vegetative stage (from 10 to 16mol_c·m⁻³) increased the VDB by 16.6 and 30.6% at 28 and 42 DAT, respectively. Similarly, VDB increased significantly with an increase in K. The K concentrations of 11 and 13mol_c·m⁻³ elicited the highest VDB responses (Table II).

The dry matter production presents exponential or sigmoidal growth in the early days of crop development, according to the findings by De

Oliveira *et al.* (2014), followed by a linear growth phase or constant growth rate (Heuvelink and Dorais, 2005), which coincides with the results obtained for the vegetation dry biomass increases of 38.9, 32.2, and 6.07g between the initial and final sampling for the first, second, third, and fourth samplings (Table II).

The behavior of the net assimilation rate (NAR) fits a negative quadratic and a positive linear model, respectively, for the effects of N and of days after transplantation (DAT) (Table III). NAR reached the lowest values at 42 DAT (Figure 2a), whereas the increase in N from 10 to 16mol_c·m⁻³ enhanced the NAR by 8, 7.9, and 12.6% at 14, 28, and 42 DAT, respectively (Figure 2b).

Later in the reproductive stage, this expression of growth gradually decreased to an asymptote at the end of the cycle, adjusting to a model with a linear rate of change and an exponent of the DAT variable of 0.75 (Table III). Neither the N nor the K affected the NAR during the reproductive stage, with time (DAT) the only factor that affected the growth trend during this stage. Thus, the maximum leaf photosynthetic efficiency occurred 69 DAT (87mg·dm⁻²/day) and decreased to a value of 4mg·dm⁻²/day at 152 DAT (Figure 4a).

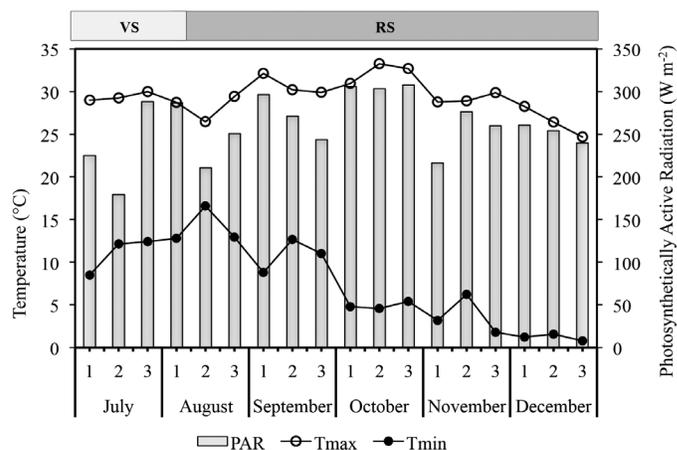


Figure 1. Maximum and minimum temperatures and photosynthetically active radiation (PAR) recorded during the vegetative (VS) and reproductive (RS) stages of a tomato crop cultivated hydroponically from July to December 2012.

TABLE I
STATISTICAL SIGNIFICANCES OF N, K, AND N×K
FOR VEGETATION DRY BIOMASS DURING
THE VEGETATIVE AND REPRODUCTIVE STAGES

Variation source	Vegetative stage			
	14	28	42	
	----- Days after transplantation -----			
N	0.621 ns	0.0016*	0.0006*	
CV (%)	19.3	5.3	8.8	
Variation source	Reproductive stage			
	69	126	152	170
	----- Days after transplantation -----			
N	0.392 ns	0.627 ns	0.949 ns	0.9239 ns
K	<0.0001*	<0.0001*	<0.0001*	<0.0001*
N×K	0.888 ns	0.990 ns	0.993 ns	0.990 ns
CV (%)	4.7	4.7	5.7	4.9

* P≤0.05; ns: not significant after ANOVA. C V: coefficient of variation.

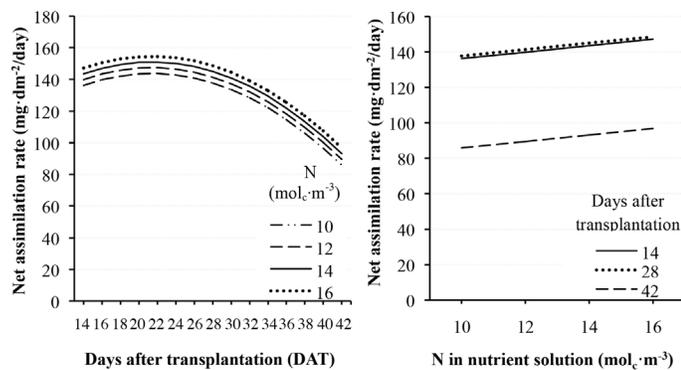


Figure 2. Net assimilation rate NAR as a function of time (a) or the concentration of N in the nutrient solution (b) during the vegetative stage of the tomato crop. Estimated values from the model (Table III).

TABLE III
BEST-FIT MODELS OF GROWTH RATES FOR THE VEGETATIVE AND
REPRODUCTIVE STAGES OF A HYDROPONIC TOMATO CROP

Growth rate	Model	P-value
----- Vegetative stage -----		
NAR	Y= 63.464 + 1.806N + 5.816DAT - 0.136DAT ² MSE= 172.108 CV= 9.1 R ² = 0.789	<0.0001
RGR	Y= 58.18659-2.24954N+8.20921DAT- 0.19527DAT ² MSE= 123.00231 CV= 8.0 R ² = 0.924	<0.0001
CGR	Y= 0.51063+0.16565DAT+0.00795DAT ² +0.00135NDAT ² -0.00001139 N ³ DAT ² MSE= 0.39116 CV= 9.8 R ² = 0.989	<0.0001
----- Reproductive stage -----		
NAR	Y= 87.42622+ 2.83946DAT- 11.58653DAT ^{0.75} MSE= 17.09178 CV= 15.6 R ² = 0.987	<0.0001
RGR	Y= 69.93256+ 2.32058DAT- 9.43408DAT ^{0.75} MSE= 8.15264 CV= 13.7 R ² = 0.990	<0.0001
CGR	Y= 6.63994-0.07918DAT+ 0.00029733DAT ² + 0.04714K MSE= 1.00055 CV= 27.0 R ² = 0.795	<0.0001

NAR: net assimilation rate, RGR: relative growth rate, CGR: culture growth rate, N: nitrogen, DAT: days after transplantation, K: potassium, MSE: mean square error, CV: coefficient of variation.

TABLE II
THE MINERAL CONCENTRATION IN THE NUTRIENT
SOLUTION ON VEGETATION DRY BIOMASS OF A
TOMATO CROP IN THE VEGETATIVE (N) AND
REPRODUCTIVE (K) STAGE

N (mol _c ·m ⁻³)	Vegetation dry biomass (g)			
	14	28	42	
	----- Days after transplantation -----			
10	1.76 a ¹	18.51 c	55.77 b	
12	2.00 a	19.54 bc	68.80 ab	
14	2.03 a	21.47 ab	77.07 a	
16	2.11 a	22.19 a	80.32 a	
HSD	0.80	2.28	11.2	
CV (%)	19.3	5.3	8.9	
K (mol _c ·m ⁻³)	Vegetation dry biomass (g)			
	69	126	152	170
	----- Days after transplantation -----			
5	119.5 c	157.8 c	184.8 b	189.5 b
7	119.6 c	157.7 c	189.1 b	194.2 b
9	125.1 bc	163.2 bc	192.9 b	198.7 b
11	130.8 ab	170.8 a	207.9 a	214.7 a
13	133.7 a	173.9 a	209.6 a	217.5 a
HSD	5.9	7.8	11.2	10.0
CV (%)	4.7	4.7	5.7	5.0

Same letters in each column indicate no significant difference (Tukey, P≤0.05). HSD: honestly significant difference. CV: coefficient of variation.

The NAR exhibits a behavior previously noted by Monte *et al.* (2013), i.e., initially increases and then decreases with plant age (Figures 4a and 6a). In the early phenological stages, the leaf area is constantly increasing with the development of new leaves (Segura *et al.*, 2006), which are more exposed to radiation and are more efficient at

capturing CO₂ (Carranza *et al.*, 2009); consequently, the production rate of photoassimilate (the product of photosynthesis) increases. As time passes, the amount of foliage increases, and thus, the outer leaves shade the inner leaves, decreasing the photosynthetic activity of the shaded leaves (Barraza *et al.*, 2004), on the one hand, because of the low concentrations of chlorophyll and soluble proteins (Azofeifa and Moreira, 2004) and, on the other hand, because senescence starts. In addition, the photoassimilate is mainly transported to fruits, which accounts for up to 72% of the total dry matter in tomato (Peil and Galvez, 2005). Therefore, the NAR is reduced in the reproductive stage. In addition, solar radiation also tends to decrease by the end of cultivation (Figure 1) because it is winter and the days are shorter (from 10.9 to 9h), which may affect the NAR.

The present study demonstrated that increasing the nitrogen concentration in the nutrient solution increases the NAR (Figure 2b), which may be attributed to the increased N concentration in the leaf, which in turn results in an

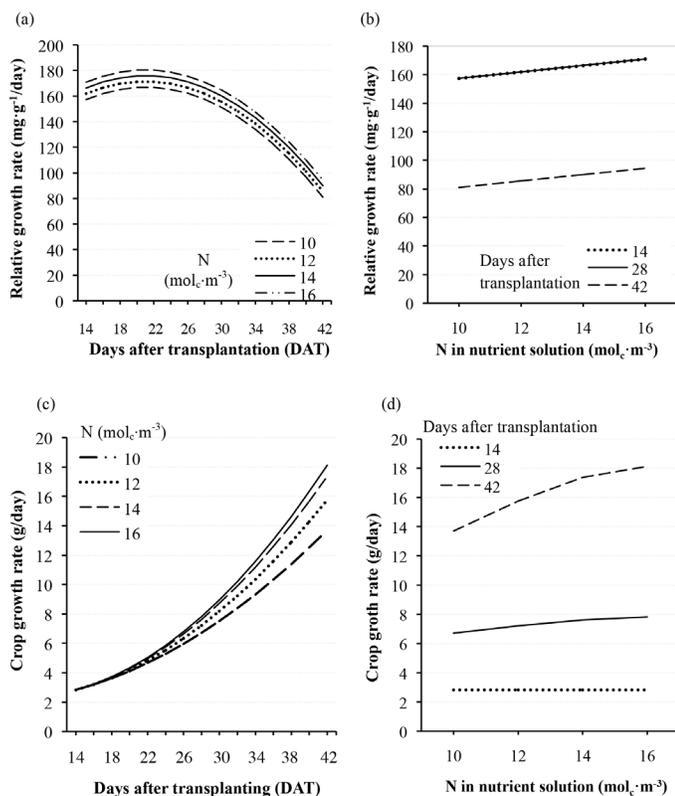


Figure 3. Relative growth rate RGR (a) and Crop growth rate CGR (c) as a function of time and Relative growth rate (b) and Crop growth rate (d) as a function of N concentration in the nutrient solution, for the vegetative stage of the tomato crop. Estimated values from models (Table III).

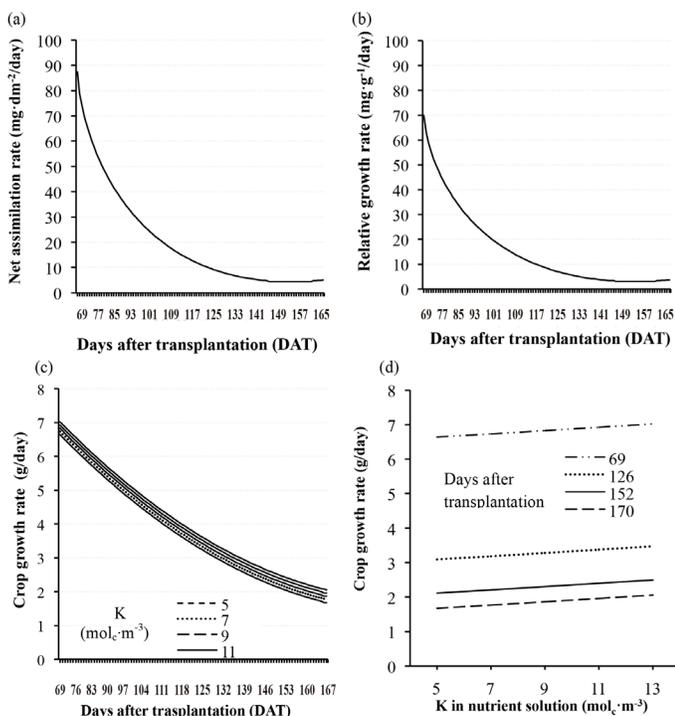


Figure 4. Net assimilation rate NAR (a), relative growth rate RGR (b), and crop growth rate CGR (c) as a function of time and the K concentration of the nutrient solution (d) during the reproductive stage of the tomato crop. Estimated values from models (Table III).

increase in photosynthetic capacity, as noted by Chechin and De Fátima-Fumis (2004). The photosynthetic capacity of the leaves is related to the nitrogen content (Mengel and Kirkby, 2001; Osaki *et al.*, 2001), mainly because the thylakoids (which account for 24% in spinach leaves) and proteins of the Calvin cycle account for the majority of the N in the leaf. Positive relationships between N content and RuBisCO (this enzyme represents 20-30% of total foliar N) and chlorophylls have been reported (Makino *et al.*, 2003; Heuvelink and Dorais, 2005; Bloomfield *et al.*, 2014). Therefore, N fertilization facilitates further incorporation of CO₂ (Wang *et al.*, 2012) through RuBisCO, since this enzyme is most required in order to maintain high photosynthetic rates (Engels *et al.*, 2012). Consequently, the concentration and activity of RuBisCO may have a very large impact on photosynthesis, and therefore, on growth, biomass production and fruit yield (Long *et al.*, 2006).

During the vegetative stage, the relative growth rate (RGR) initially increased and subsequently decreased with the number of DAT, while N produced a minimal effect. This trend defined a best-fit model with a linear rate of increase with N and a linear and negative quadratic response to DAT, which best describe the pattern of growth during the first 42 DAT (Table III). During this stage, the highest RGR was recorded at 22 DAT, with rates of 167, 171, 176, and 180 mg·dm⁻²/day. Nevertheless, in the end of this period (42 DAT), this index drastically decreased until minimum values of 81, 86, 90, and 95 mg·dm⁻²/day for concentrations of N from 10 to 16 mol·m⁻³ (Figure 3a). In addition, the RGR exhibited a directly proportional relationship with an increase in the concentration of N in the nutrient solution, and increased by 9% at 14 and 28 DAT and by 17% at 42 DAT, demonstrating a greater effect of this

nutrient over the course of this phenological stage (Figure 3b).

During the reproductive stage, the RGR decreased sharply until reaching an almost constant value by the end of the cycle at 170 DAT. This projection of the RGR fits a model with a linear rate of change and a fractional exponent ($3/4 = 0.75$) for DAT, the latter being the model explaining the dramatic decline in RGR (Table III). The N and K concentrations evaluated for the vegetative and reproductive stages elicited no effects on the efficiency of biomass production during this period. Thus, time (DAT) was the sole determinant of their variation. Consequently, the highest efficiency of dry matter production was observed at 69 DAT (70 mg·dm⁻²/day), followed by a sharp decrease to a constant and insignificant level at 142 DAT which caused minimal values of 3.7 mg·dm⁻²/day at 170 DAT (Figure 4b) because the crop was in senescence.

The RGR presented the same behavior as the NAR (Figures 2a and 3a) because both are dependent on photosynthesis, respiration, leaf area, and plant architecture (Gardner *et al.*, 1985). In the present study, the RGR increased during the vegetative stage because of the constant development of leaf tissue in which photosynthesis occurs, from which the assimilate can be reinvested (Azofeifa and Moreira, 2004) in the development of new leaf tissue. Furthermore, the influence of N treatments on leaf growth (Figure 3b) coincides with the results of Isah *et al.* (2014), who reported positive effects of N on RGR. This nutrient promotes greater leaf area (Lovelock *et al.*, 2004) and thus increases photosynthesis. Increased photosynthesis promotes greater plant efficiency in the production of dry matter, which promotes a better balance between photosynthesis and respiration (Carranza *et al.*, 2009).

In potato and tomato, RGR is high at the beginning of the crop cycle and then gradually

decreases towards the end of the cycle, coinciding with the onset of leaf senescence (Santos *et al.*, 2010) and shading of lower leaves (Heuvelink and Dorais, 2005). This finding is consistent with the results of this study because the RGR was the highest at the beginning of the reproductive stage and decreased dramatically by the end of the experiment (Figure 4b). This behavior may occur because the crop was producing fruits, which account for 52 to 72% of the total dry matter of the plant, as indicated by Peil and Galvez (2005), and additionally, leaves started the senescence process. Thus, both processes decreased CO₂ assimilation, total soluble proteins contents and the activity of the Calvin cycle related enzymes (Wingler *et al.*, 2006; Martínez *et al.*, 2008), which finally affected biomass accumulation.

The culture growth rate (CGR) increased gradually to a maximum at the end of the vegetative cycle. The behavior of the CGR was a product of the linear and quadratic effects of DAT, in addition to its interaction with the linear N and cubic N effects (Table III and Figures 3c and 3d). The lowest CGR (3g/day) occurred early in the vegetative cycle (14 DAT). Then, the CGR increased gradually until the end of this phenological stage, with maximum values at 42 DAT of 13.7, 15.7, 17.4, and 18.1g/day, which varied depending on the concentration of N (10-16mol_c·m⁻³) and its interaction with time (Figure 3c). Although the N concentrations evaluated at this stage influenced the performance in terms of the CGR, the effects of N became visible at 28 DAT and were clearly evident at 42 DAT, when a significant and positive response was observed, with increases of 15, 27, and 32% associated with increasing concentrations of N from 10 to 16mol_c·m⁻³ (Figure 3d).

During the reproductive stage, the CGR decreased slowly from the beginning to the end of this evaluation period. This growth trend was a consequence of time and the linear

and negative quadratic form of the response to the DAT (as a result of the senescence of photosynthetic machinery and the competition by reproductive structures) and with minimal effects of K (Table III). In contrast, N had no effect on the CGR during the reproductive stage because, during this period, the plant received only residual effects of the additional N supplied during the vegetative crop period. In this context, the maximum values of CGR of 6.6, 6.7, 6.8, 6.9, and 7g/day were observed at the beginning (69 DAT) of this period, with minimal differences (1, 3, 4, and 6%) associated with the concentration of K from 5 to 13mol_c·m⁻³, and thereafter the CGR gradually decreased until reaching values of 1.67, 1.77, 1.86, 1.96, and 2.05g/day at 170 DAT (Figure 4c). The most notable effects of K on the CGR were observed at 170 DAT, with increases of 6, 11, 17, and 23% attributed to increasing the concentration of K from 5 to 13mol_c·m⁻³ (Figure 4d).

The CGR was slow early in the vegetative stage but subsequently increased gradually to a maximum (Figure 3c). During the reproductive stage, the CGR gradually decreased, with the lowest values occurring at the end of this period (Figure 4c). Azofeifa and Moreira (2004) observed that at the start of plant growth, the leaf area is small, the photosynthetic rate is low, and the photoassimilates produced are continuously reinvested into the formation of new vegetative structures, which favors an increase in leaf area. An adequate supply of N to C3 plants grown in hydroponics increases foliar area, N, chlorophyll, soluble proteins and RuBisCO contents (Li *et al.*, 2013). This condition triggers an increase in the light interception, which in turn may improve photosynthesis (Heuvelink and Dorais, 2005). As a result of these dynamics, the rate of photoassimilate production initially increases rapidly. Subsequently, with the formation and development of reproductive

structures, these organs become the principal demand of the plant, and vegetative growth decreases. During the life cycle, each leaf changes from a sink to a source transition for both nutrients (N and K) and photosynthates; this transition occurs in dicotyledons species when the leaves are 30-60% expanded. Afterwards, photosynthetic activity decreases because senescence starts (Engels *et al.*, 2012), and lower leaves are under more shadow, which interrupts light interception (Mengel and Kirkby, 2001). At the end of the crop cycle, the aggregate weight of all of the fruit accounts for between 52 and 72% of the total dry weight of the tomato plant (Peil and Galvez, 2005).

Of all of the essential elements, nitrogen exerts a very strong influence on plant growth; the optimal range for growth varies with the growth stage (high in the initial stages and decreasing with age). In tomato, the content of foliar N that is sufficient for growth ranges from 2.7 to 5% of dry matter (Jones, 2008). In the present study, the nitrogen concentrations of the nutrient solutions used in the vegetative stage had a significant and positive direct relationship with the CGR for the concentrations of N from 10 to 16mol_c·m⁻³ (Figure 3d). However, there was no effect of N on the CGR during the reproductive stage.

Potassium affects physiological and biochemical processes that influence plant growth and metabolism (Wang *et al.*, 2013). On one hand, K participates in loading of sucrose and solute transport in the floem; and thus, the transport of photosynthates from source to sink (Hawkesford *et al.*, 2012). On the other hand, this element plays a central role in maintenance of photosynthesis and related process among which are stomatal conductance, mesophyll resistance and RuBisCO activity (photosynthetic CO₂ fixation; Cakmak, 2005). In tomato crops, reductions in K uptake have been reported to reduce growth rates

(Colpan *et al.*, 2013). In contrast, our results indicate that the CGR increased as the concentration of K in the nutrient solution increased, most notably at the end of the reproductive stage, when the CGR increased by 23% in response to the highest concentration of K (13mol_c·m⁻³) (Figure 4d).

The results obtained and analyzed for the reproductive stage of the hydroponic tomato crop in this study were limited by the apical pruning of the plants, as indicated in the materials and methods (108 DAT). Although the Charleston tomato cultivar is of indeterminate habit, the apical pruning imposed certain limitations on the behavior of the response variables. According to Schwarz *et al.* (2014), in order to have sufficient and balanced fruit setting and yield, particularly during the first 2-3 months, a good balance between vegetative and reproductive growth is necessary, which can be obtained by fruit pruning. Indeed, pruning is necessary when an indeterminate tomato type is tested in experiments with a longer cultivation period (more than ~5 weeks). Consequently, the VDB exhibited increases up to constant or insignificant values from 152 DAT until the end of the experiment. In the case of the NAR, RGR, and CGR, these variables exhibited typical behaviors for cultivars with a determinate growth habit given the reported reductions to negligible values caused by crop senescence at the end of the evaluation period. Accordingly, Monte *et al.* (2013) reported that the indeterminate hybrid Debora tends to keep growing and compete with the fruit reproductive growth. Because the final height growth is determined by crop management, when the apical yolk is eliminated, growth should not continue after a determined height to avoid competition between vegetative and reproductive organs.

Conclusions

Our results demonstrate that both N and K affect tomato metabolism and these effects

induce different responses on biomass production and growth, depending on the phenological stage of the plant.

During the vegetative stage, the N concentration varied from 10 to 16 mol_c·m⁻³, which resulted in increases in vegetation dry biomass. The highest values were obtained for the treatments with 14 and 16 mol_c·m⁻³ of N applied in the nutrient solution. The crop growth during this period fitted to quadratic models for net assimilation, relative growth, and crop growth rates, which varied in terms of the positive effects imposed by N.

Positive effects on vegetation dry biomass were observed with an increase in the concentration of K in the nutrient solution during the reproductive stage. These effects resulted in significant increases when the concentration of this nutrient was increased from 5 to 11 mol_c·m⁻³. The net assimilation and relative growth rates were fit to models of the negative asymptotic type, while the crop growth rate was fit to a positive quadratic model; this latter growth rate was the only index that demonstrated a direct relationship with the concentrations of K evaluated for this final stage of a hydroponic tomato crop.

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