



Biomass association in specimens and interspecific hybrids of tomatoes

André Ricardo Zeist¹ , Marcos Ventura Faria², Juliano Tadeu Vilela de Resende³, André Gabriel², Julio José Nonato² and Matheus Hermann dos Santos²

¹Universidade do Oeste Paulista, Rodovia Raposo Tavares, km 572, 19067-175, Presidente Prudente, São Paulo, Brazil. ²Departamento de Agronomia, Setor de Ciências Agrárias e Ambientais, Universidade Estadual do Centro-Oeste, Guarapuava, Paraná, Brazil. ³Universidade Estadual de Londrina, Londrina, Paraná, Brazil. *Author for correspondence. E-mail: andre.zeist@bol.com.br

ABSTRACT. The objective of this study is to analyze the growth of wild species of tomato, of the cultivar Redenção and of the respective F₁ hybrids of interspecific crossings. We evaluated six wild-type accessions (*Solanum pimpinellifolium* 'AF 26970', *S. galapagense* 'LA-1401', *S. peruvianum* 'AF 19684', *S. habrochaites* var. *hirsutum* 'PI-127826', *S. habrochaites* var. *glabratum* 'PI-134417', and *S. pennellii* 'LA-716') and the commercial cultivar Redenção (*S. lycopersicum*) together with their respective interspecific hybrids. In completely randomized blocks and plots subdivided by time (16, 28, 42, 56, 70, and 84 days after transplanting), we evaluated leaf area (LA), total dry matter (TDM), absolute growth rate (AGR), relative growth rate (RGR) and net assimilation rate (NAR). The distribution of assimilates in the different organs followed different patterns according to genotype. There was a greater accumulation of LA and TDM in the accessions 'PI-127826' and 'PI-134417' and in the hybrids 'Redenção' x 'PI-127826' and 'Redenção' x 'PI-134417'. Due to a heterotrophic effect provided by the crossings, there were higher LA, TDM, AGR, RGR and NAR in hybrids than in parent plants. The accessions 'PI-127826' and 'PI-134417' presented a potential to be donor parents for obtaining tomatoes with a greater capacity of net assimilation and biomass accumulation.

Keywords: *Solanum lycopersicum*; wild accessions; growth analysis; pre-breeding.

Received on December 27, 2017.

Accepted on March 12, 2018

Introduction

Tomato, in addition to the domesticated and cultivated species *Solanum lycopersicum* L. and the cerasiform variety, presents several wild species with which there is some interspecific compatibility between crosses (Peralta, Spooner, & Knapp, 2008; Bedinger et al., 2011). The main consequence of the *S. lycopersicum* domestication process is genetic erosion, that is, the loss of important characteristics that provide tolerance or resistance, which began to distinguish improved plants from their wild ancestors (Bai & Lindhout, 2007; Veasey et al., 2011).

The species *S. lycopersicum* was domesticated and selected outside its center of origin in South America in an intentional way aiming to improve the productive characteristics of interest for human needs, thus suffering several genetic and morphological changes (Bergougnoux, 2014; Blanca et al., 2015). On the other hand, by natural selection, populations of wild species have undergone a selection pressure to guarantee their reproduction and survival under the conditions of their origin. They developed mechanisms against the most adverse variations in the natural environment, such as adaptations to certain edaphoclimatic conditions and resistance to pests and diseases.

Together with crops such as coffee and cotton, tomato stands out as one of the main species that underwent a genetic drift due to the selection process carried out by humans outside its center of origin (Bai & Lindhout, 2007; Veasey et al., 2011; Bergougnoux, 2014). However, even on a small scale, the opposite has been happening. Researchers seek alleles in wild accessions that provide resistance or tolerance and can be reintroduced by crossing and backcrossing (Albrecht, Escobar, & Chetelat, 2010). Among such alleles are those that provide resistance to phytopathogens (Hurtado et al., 2012), insects and pest-arachnids (Lucini, Faria, Rohde, Resende, & Oliveira, 2015; Dias et al., 2016) and to abiotic stresses (Morales, Resende, Bordini, Galvão, & Resende, 2015), as well as those that present improvements in nutritional quality.

However, studies are still needed to identify alleles in wild species and the effects of interspecific crosses on tomato development and growth.

There are several studies based on physiological indexes reporting the growth and productivity of tomatoes cultivated under the most diverse management conditions (Fayad, Fontes, Cardoso, Finger, & Ferreira, 2001; Andriolo, Espindola, Godoi, Bortolotto, & Luz, 2004; Lopes et al., 2011; Soares, Negreiros, Lopes, Dombroski, & Lucena, 2013; Martinazzo, Perboni, Posso, Aumonde, & Bacarin, 2015; Pedó, Aumonde, Lopes, & Mauch, 2015). In contrast, little is known about the detailed quantitative physiological indexes of the growth of wild species and interspecific hybrids of tomatoes in comparison to cultivated tomatoes.

Indexes determined by a physiological analysis of plant growth measure the ability of plants to synthesize and allocate carbohydrates to various organs that depend on photosynthesis, thus quantifying the performance of net assimilation during a certain period (Lopes et al., 2011). Basic studies on the quantitative growth of tomato species and interspecific hybrids in different environments may contribute to the understanding of the interactions between genotypes and environments and, consequently, contribute to the development and selection of cultivars with high yields under certain growing conditions.

Considering the information above, the objective of this study is to analyze the growth of wild tomato species, of the cultivar Redenção and of the respective F₁ hybrids of interspecific crossings cultivated in two environments.

Material and methods

The experiments were conducted during the agricultural year 2015/2016 in the Center for Research on Vegetables of the Department of Agronomy of the State University of the Center-West (Unicentro), located in the municipality of Guarapuava, Paraná State, latitude 25° 38' S, longitude 51° 48' W, and altitude of 1,100 meters.

The experiment was conducted in a protected external environment, where we used a greenhouse with evaporative air cooling provided by an air extractor installed on opposite sides and running water in expanded clay. Within this environment, the seedlings were transplanted to pots with a capacity of 10 dm³ containing sieved soil and cattle manure at a 3:2 ratio. For the external environment, a field 110 m distant from the protected-environment experiment site was used. In it, plowing was performed, and then a rotation waver was used for the preparation of 1.0 m-wide beds.

In the protected environment, we evaluated six wild accessions (*Solanum pimpinellifolium* accession 'AF 26970', *Solanum galapagense* accession 'LA-1401', *Solanum peruvianum* accession 'AF 19684', *Solanum habrochaites* var. *hirsutum* accession 'PI-127826', *Solanum habrochaites* var. *glabratum* accession 'PI-134417' and *Solanum pennellii* accession 'LA-716') and the commercial cultivar Redenção (strain of *Solanum lycopersicum* with characteristics for processing), along with their interspecific hybrids ('Redenção' x 'AF 26970'), ('Redenção' x 'LA-1401'), ('Redenção' x 'AA-1961'), ('Redenção' x 'PI-127826'), ('Redenção' x 'PI-134417'), and ('Redenção' x 'LA-716'). In the external environment, we evaluated all the genotypes of the protected environment, except for the *S. pennellii* accession, because the plants died. Interspecific parents and hybrids were arranged in a block design with random plots subdivided into time, with three replications. Each plot consisted of eight genotypes, and the subplots were divided by sample collection times.

The sowing was performed in expanded polystyrene trays with 200 cells containing commercial substrate based on bio-stabilized pine bark and incubated in a hydroponic floating system inside a greenhouse. The sowing of the accessions 'AF 26970' and 'AF 19684' and the interspecific hybrids was performed together with that of the Redenção strain. The sowing of the accessions 'LA-1401', 'PI-127826', 'PI-134417', and 'LA-716' was performed ten days earlier due to differences in germination, emergence and initial development. The seedlings were transplanted 27 days after the emergence of the female parent plant, when they had 4 to 5 expanded leaves (December 22, 2015).

In the experimental units of the protected environment, the pots containing plants were organized in four rows spaced 0.40 m apart at 0.40 m between plants. In the external environment, each experimental unit consisted of a bed with two continuous rows spaced 0.90 m apart and 0.40 m between plants.

In both environments, the soil classified as a Brown Latosol, with a very clayey texture (*Empresa Brasileira de Pesquisa Agropecuária* [Embrapa], 2013), was corrected early, according to the needs indicated by soil chemical analysis, by applying calcitic limestone to increase the base saturation to 80% and maintain

a 4:1 ratio between Ca and Mg. To carry out basic fertilization, 15 g of NPK (4-20-20) and 7.0 g of simple superphosphate were used per plant. Irrigation was carried out using micro-drippers according to the needs of the crop and based on the criteria established for tomatoes in each environment.

During the experimental period, the daily minimum and maximum air temperature data for the external environment were collected at the automatic meteorological station of the Central-Western State University, *campus* Cedeteg, located 180 m from the experiment site. In the protected environment, data collection was performed daily using maximum and minimum temperature thermometers.

To obtain primary growth data, successive samplings were performed in the morning at fourteen-day intervals up to 84 days after transplanting (DAT). The leaf area of green leaves (LA) was obtained using a bench leaf area meter (Area Meter, LI-COR®, LI 3100C) and expressed in square centimeters per plant ($\text{cm}^2 \text{ plant}^{-1}$). At each collection, the plants were fractionated into roots, stems, leaves and fruits; then, the roots were washed under running water. To obtain dry matter, the material was placed in a forced-air circulation oven at 65°C until constant weight, and, in sequence, we determined the dry matter of roots, stems, leaves and fruits using a 0.001 g precision scale. The total dry matter (TDM) was obtained by summing the dry matter accumulations of the different plant parts (g): $\text{TDM} = \text{roots} + \text{stems} + \text{leaves} + \text{fruits}$.

According to studies on the quantitative analysis of tomato growth (Lopes et al., 2011; Soares et al., 2013), we determined the following functions of LA and dry matter: absolute growth rate (AGR) = $(\text{TDM}_2 - \text{TDM}_1)/(\text{T}_2 - \text{T}_1)$ ($\text{g plant}^{-1} \text{ day}^{-1}$); relative growth rate (RGR) = $[\ln(\text{TDM}_2) - \ln(\text{TDM}_1)]/(\text{T}_2 - \text{T}_1)$ ($\text{g g}^{-1} \text{ day}^{-1}$), where $\ln(\text{TDM}_2)$ and $\ln(\text{TDM}_1)$ are natural logarithms of the TDM of two successive samplings; net assimilation rate (NAR) = $[(\text{TDM}_2 - \text{TDM}_1)/(\text{T}_2 - \text{T}_1)] \times [\ln(\text{LA}_2) - \ln(\text{LA}_1)]/(\text{LA}_2 - \text{LA}_1)$ ($\text{g cm}^{-2} \text{ day}^{-1}$), where $\ln(\text{LA}_2)$ and $\ln(\text{LA}_1)$ are natural logarithms of LA of two successive samplings. In all equations, TDM_2 and TDM_1 and LA_2 and LA_1 corresponded to the TDM and LA of two successive samplings, respectively, and T_2 and T_1 represent the times of sampling.

The data of the evaluated characteristics were tested for normality and homogeneity of residual variances by Lilliefors and Bartlett tests, respectively, and later submitted to analysis of variance. When the F test was significant, the averages were submitted to Scott-Knott test at 5% probability for the genotypes and polynomial regression for sampling times, as analyzed by ASSISTAT statistical software version 7.7 (Silva & Azevedo, 2016).

Results and discussion

We observed that in the protected environment, the minimum temperature ranged between 13.3 (03/07/2016) and 21.8°C (12/31/2015), and the maximum temperature ranged between 24.0 (03/04/2016) and 33.9°C (01/09/2016); in the external environment, the minimum temperature ranged between 9.8 (03/12/2016) and 21.0°C (12/22/2015), and the maximum temperature ranged between 22.0 (03/04/2016) and 30.0°C (02/15/2016).

For leaf area (LA), we observed an intensified increase at 42 and 56 DAT for the protected cultivars, except for the accessions 'PI-127826' (*S. habrochaites* var. *hirsutum*), PI-134417 (*S. habrochaites* var. *glabratum*), and 'AF 26790' and the interspecific hybrids 'Redenção' x 'PI-127826' and 'Redenção' x 'AF 19684', which increased up to 70 DAT (Table 1). In the external environment, the hybrid 'Redenção' x 'PI-134417' stood out because it presented the highest values for LA at all collection times.

The stabilization and decrease of leaf area when approaching 84 DAT (Table 1) possibly occurred due to senescence suppressing the emergence of new leaves in most genotypes, as was also observed for tomatoes cultivated by Lopes et al. (2011), Soares et al. (2013), and Martinazzo et al. (2015).

For total dry matter (TDM), the hybrids 'Redenção' x 'LA-1401', 'Redenção' x 'AF 19684', 'Redenção' x 'PI-134417', and 'Redenção' x 'LA-716' obtained the greatest accumulations at 56 DAT in the protected environment. In the external environment, the hybrid 'Redenção' x 'PI-134417' was highlighted with the highest values of TDM in all collections (Table 2).

In both environments, the lowest TDM accumulations were observed for the cultivar Redenção and the wild accessions 'AF 26970', 'LA-1401', 'AF 19684', and 'LA-716'. In contrast, there were higher TDM values for their interspecific descendants 'Redenção' x 'AF 26970', 'Redenção' x 'LA-1401', 'Redenção' x 'AF 19684', and 'Redenção' x 'LA-716' (Table 2).

This is possibly related to the expression of the heterotic effect of such crossings, increasing the carbohydrate accumulation of hybrids in relation to the average of parent plants. In general, similar

performances have also been verified for the hybrids 'Redenção' x 'PI-127826' and 'Redenção' x 'PI-134417' (Table 2).

As occurred for LA, there was a greater accumulation of TDM in the accessions 'PI-127826' and 'PI-134417', related to the species *S. habrochaites*, and in the interspecific hybrids of those accessions related to the 'Redenção' cultivar. The species *S. habrochaites*, because it is adapted to a wide range of latitudinal distributions, presents characteristics that allow development and growth even when conditions are not favorable for the development of other tomato species (Liu & Heins, 2002; Venema, Boukelien, Bax, Hasselt, & Elzenga, 2008; Poudyala, Khatria, & Uptmoora, 2015).

Studies report that the use of *S. habrochaites* as rootstock, in comparison with other tomato species, provided an increase in shoot and root dry matter (Zeist, Resende, Giacobbo, Faria, & Dias, 2017) and presented higher values for photosynthetic yield, water use efficiency and fruit production (Zeist et al., 2017), corroborating this study, where *S. habrochaites* was an interesting alternative to promote increases in biomass accumulation.

The distribution of assimilates to the different tomato plant organs followed different patterns according to genotype (Figure 1). When entering the reproductive phase, more precisely with the beginning of fruiting, there was a greater orientation of photoassimilates toward fruits of the cultivar 'Redenção', the accession 'AF 26970' and the hybrid 'Redenção' x 'AF 26970' (Figure 1A to C).

The species *S. pimpinellifolium*, related to the accession 'AF 26970', is a direct ancestor of the cultivated tomato, which could have migrated from an Andean center of origin to the north of South America, been domesticated by the Indians and been taken to other continents (Peralta et al., 2008). The highest percentage of dry matter of fruits in *S. pimpinellifolium* and *S. lycopersicum* and their respective interspecific hybrids are due to the characteristics related to fruit production.

Table 1. Leaf area (LA), in cm² plant⁻¹, of the cultivar Redenção (female parent), wild accessions (male parent) and the respective interspecific hybrids of tomatoes cultivated in a protected and an external environment at 14, 28, 42, 56, 70 and 84 days after transplanting (DAT).

Genotype	Protected						
	14 DAT	28 DAT	42 DAT	56 DAT	70 DAT	84 DAT	Média
Redenção	1061.8 a	3187.6 c	5769.7 b	4186.5 c	3609.6 d	3233.1 c	3508.1 f
AF 26970	919.9 a*	4465.8 b	4959.3 c	4928.7 c	6872.8 c	3306.5 c	4242.1 e
LA-1401	462.4 a	3962.4 c	4890.0 c	6009.4 b	5182.9 c	3944.8 c	4075.3 e
AF 19684	366.7 a	2176.5 c	4983.3 c	3752.4 c	3743.5 d	3530.1 c	3092.0 f
PI-127826	700.8 a	3063.0 c	6545.2 b	6730.5 b	12287.9 a	8107.9 a	6239.2 c
PI-134417	872.9 a	8109.4 a	11187.3 a	12348.0 a	13177.4 a	9510.7 a	9201.1 a
LA-716	145.2 a	529.0 c	2680.4 c	2859.3 c	2540.7 d	1660.7 c	1735.9 g
Redenção x AF 26970	2650.1 a	5265.5 b	6190.0 b	5258.9 c	4720.6 d	4478.6 c	4760.6 e
Redenção x LA-1401	1747.6 a	4982.4 b	6742.5 b	7879.5 b	6493.6 c	6104.2 b	5658.3 d
Redenção x AF 19684	1631.6 a	5782.5 b	7407.2 b	7645.8 b	8722.7 b	6912.4 b	6350.4 c
Redenção x PI-127826	862.2 a	2497.9 c	6545.2 b	8123.8 b	12141.0 a	9706.6 a	6646.2 c
Redenção x PI-134417	2338.9 a	7634.2 a	7517.4 b	13140.8 a	9866.4 b	9133.0 a	8271.6 b
Redenção x LA-716	1019.2 a	4668.0 b	6767.6 b	6931.3 b	6623.5 c	6158.9 b	5361.4 d
Média	1136.8	4332.6	6321.9	6907.4	7383.3	5829.5	
CV (%)				26.0			
Genotype	External						
	14 DAT	28 DAT	42 DAT	56 DAT	70 DAT	84 DAT	Média
Redenção	61.9 a	1111.0 b	2720.6 d	5571.0 d	3685.2 e	3507.4 e	2776 f
AF 26970	56.9 a*	1243.7 b	12225.4 c	12862.5 c	8810.0 e	6257.4 e	6909.3 e
LA-1401	25.0 a	282.4 b	4440.1 d	4577.1 d	5889.5 e	4482.7 e	3282.8 f
AF 19684	11.3 a	1049.2 b	4221.2 d	5354.58 d	4920.6 e	4154.0 e	3285.1 f
PI-127826	119.8 a	2633.4 b	8321.6 d	21862.1 b	22370.8 c	23360.0 c	13113.1 c
PI-134417	66.5 a	1855.8 b	13358.6 c	15199.5 c	15869.2 d	15910.5 d	10386.5 d
Redenção x AF 26970	118.6 a	5983.5 a	19621.7 b	20891.4 b	21697.6 c	20756.0 c	14844.8 b
Redenção x LA-1401	110.0 a	3592.9 b	13979.7 c	13486.7 c	14045.8 d	6936.6 e	8691.9 e
Redenção x AF 19684	122.8 a	2456.0 b	13888.6 c	12033.9 c	9912.1 e	7855.0 e	7711.4 e
Redenção x PI-127826	40.1 a	2235.2 b	13339.5 c	18006.1 b	30463.8 b	31330.2 b	15902.4 b
Redenção x PI-134417	147.2 a	9997.3 a	36144.3 a	47538.6 a	51211.8 a	57133.5 a	33695.4 a
Redenção x LA-716	73.3 a	2340.8 b	12655.1 c	9302.2 d	7526.7 e	6998.8 e	6482.8 e
Média	79.5	2898.4	12909.7	15557.1	16366.9	15729.3	
CV (%)				26.9			

*Means followed by the same lowercase letters in rows belong to the same group by Scott Knott test at 5%. For the lines, the treatments are quantitative, and the means comparison test does not apply.

Table 2. Total dry matter, in grams, of the cultivar Redenção (female parent), wild accessions (male parent) and the respective interspecific hybrids of tomatoes cultivated in a protected and an external environment at 14, 28, 42, 56, 70 and 84 days after transplanting (DAT).

Genotype	Protected						
	14 DAT	28 DAT	42 DAT	56 DAT	70 DAT	84 DAT	Average
Redenção	5.70 a*	35.63 b	106.77 b	125.69 c	134.09 c	145.12 c	93.83 d
AF 26970	5.22 a	43.86 b	89.32 c	127.79 c	177.54 b	161.68 c	100.89 d
LA-1401	1.83 a	36.88 b	67.79 c	104.07 c	127.49 c	123.97 d	77.00 e
AF 19684	1.78 a	20.61 b	70.04 c	88.29 d	92.40 d	99.42 e	62.09 f
PI-127826	4.93 a	42.08 b	115.18 b	155.36 b	231.79 a	211.30 b	126.77 b
PI-134417	4.25 a	60.75 a	132.76 a	195.88 a	237.03 a	253.93 a	147.43 a
LA-716	0.93 a	9.44 b	53.49 c	53.79 e	95.71 d	86.91 e	50.04 f
Redenção x AF 26970	13.75 a	59.46 a	135.83 a	158.82 b	149.03 c	158.47 c	112.56 c
Redenção x LA-1401	6.93 a	63.80 a	106.93 b	200.33 a	200.72 b	206.14 b	130.80 b
Redenção x AF 19684	6.31 a	52.02 a	154.00 a	194.33 a	255.98 a	245.67 a	151.38 a
Redenção x PI-127826	8.24 a	34.06 b	105.13 b	162.18 b	212.29 b	196.44 b	119.72 c
Redenção x PI-134417	9.60 a	75.12 a	135.05 a	210.06 a	263.34 a	263.07 a	159.37 a
Redenção x LA-716	4.83 a	56.51 a	137.18 a	212.64 a	207.37 b	204.05 b	137.09 b
Average	5.71	45.40	108.42	153.78	183.44	181.24	
CV (%)				16.28			

Genotype	External						
	14 DAT	28 DAT	42 DAT	56 DAT	70 DAT	84 DAT	Average
Redenção	1.13 a*	12.23 a	42.97 d	90.90 f	126.72 e	121.76 g	65.95 g
AF 26970	1.23 a	8.98 a	110.04 c	177.64 e	174.71 e	172.26 g	107.47 f
LA-1401	0.58 a	2.36 a	32.57 d	38.29 e	115.22 e	115.79 g	50.79 g
AF 19684	0.80 a	7.90 a	37.94 d	68.81 e	91.68 e	96.48 g	50.60 g
PI-127826	2.53 a	23.10 a	180.90 b	337.5 d	391.15 c	421.60 e	226.12 d
PI-134417	1.90 a	14.25 a	119.48 c	182.31 e	421.78 c	517.62 d	209.55 d
Redenção x AF 26970	0.87 a	65.43 a	244.44 b	687.22 b	588.47 b	588.27 c	362.44 b
Redenção x LA-1401	0.94 a	26.94 a	204.43 b	491.01 c	527.73 b	504.92 d	292.66 c
Redenção x AF 19684	0.80 a	25.32 a	179.15 b	300.62 d	333.34 e	362.90 e	200.35 d
Redenção x PI-127826	0.40 a	17.44 a	155.44 b	198.82 e	594.46 b	803.12 b	295.33 c
Redenção x PI-134417	1.08 a	72.50 a	398.49 a	803.61 a	893.97 a	904.03 a	512.28 a
Redenção x LA-716	0.68 a	31.22 a	199.04 b	237.65 e	273.76 d	282.58 f	169.15 e
Average	1.07	25.00	158.73	301.19	377.74	407.60	
CV (%)				18.62			

*Means followed by the same lowercase letters in rows belong to the same group by Scott Knott test at 5%. For the lines, the treatments are quantitative, and the means comparison test does not apply.

Unlike 'Redenção' and its ancestor *S. pimpinellifolium*, the species *S. galapagense* ('LA-1401'), *S. peruvianum* ('AF 19684'), *S. habrochaites* var. *hirsutum* ('PI-127826') and var. *glabratum* ('PI-134417'), and *S. pennellii* ('LA-716'), as well as their interspecific hybrids, showed a low photoassimilate targeting to fruits (Figure 1D to M). This aspect is possibly because such wild species present characteristics unfavorable to fruit production, which, in addition to being pubescent, are very small (Peralta & Spooner, 2005; Peralta et al., 2008).

In both environments, at 14 and 28 DAT, the leaves were source drains since they were responsible for the production of photoassimilates. They also accumulated most of the TDM, which, from then on, was redistributed to organs not self-sufficient photosynthetically. In contrast, the stems, from the beginning until 84 DAT, were similar to drains, with a continuous accumulation of dry matter (Figure 1).

From the beginning of the formation of the first fruits, we observed that there was a higher orientation of assimilates of leaves to fruits and stems. This was more evident for the commercial cultivar 'Redenção', the wild accessions 'AF 26970', 'LA-1401', 'AF 19684' and 'LA-716', and the hybrids 'Redenção' x 'AF 26970' and 'Redenção' x 'LA-1401' (Figure 1A to E).

In general, the roots in all samples were source drains (Figure 1). While leaves provide carbon, roots provide the other organs with water and minerals and, at the same time as the accumulation of dry matter in shoots, new roots are emitted for absorbing essential elements that will promote growth, flowering and fruiting (Xu, Yang, & Yang, 2001).

For all genotypes, in both environments, the net assimilation rate (NAR) presented a cubic fit, reaching the maximum estimated values at approximately 34 DAT and decreasing from then on until presenting a slight increase at 84 DAT (Figure 2). As reported by Lopes et al. (2011) and Soares et al. (2013) for cultivated tomatoes, it is possible to state that, in this study, from 28 to 42 DAT, due to an increase in the growth of

genotypes, specifically leaf area, there was a self-shading of the vegetative canopy, thus causing a decrease in NAR.

In general, between 28 and 56 DAT, higher values of NAR were observed in relation to the protected environment (Figure 2). In relation to the characteristics absolute growth rate (AGR) and relative growth (RGR), similar performances were observed between cultivation environments (Figures 3 and 4). These results are because, from 42 to 72 DAT, the accumulation of dry matter in the external environment was higher than in the protected environment (Table 2).

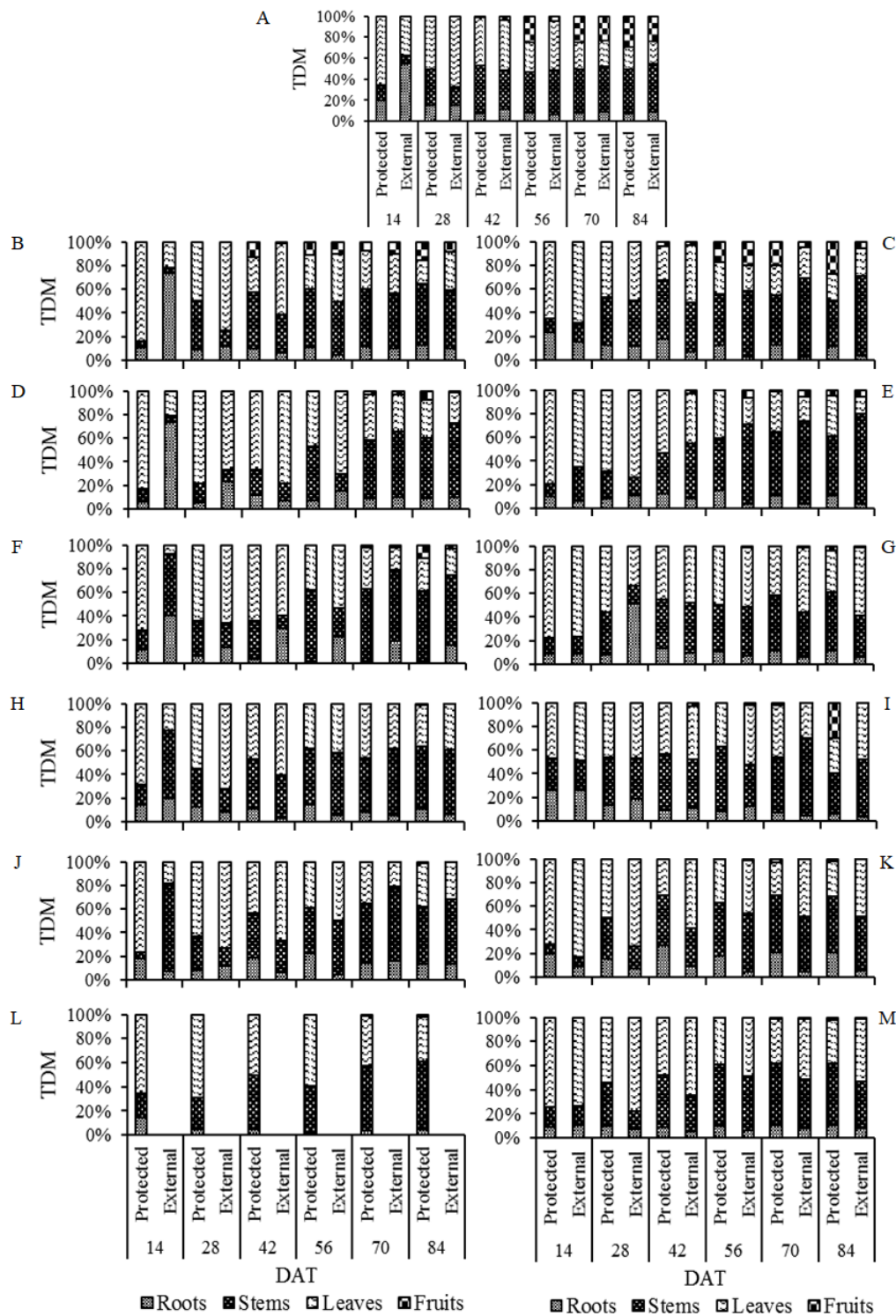


Figure 1. Participation of assimilates of ‘Redenção’ (A), ‘AF 26970’ (B), ‘Redenção’ x ‘AF 26970’ (C), ‘LA-1401’ (D), ‘Redenção’ x ‘LA-1401’ (E), ‘AF 19684’ (F), ‘Redenção’ x ‘AF 19684’ (G), ‘PI-127826’ (H), ‘Redenção’ x ‘PI-127826’ (I), ‘PI-134417’ (J), ‘Redenção’ x ‘PI-134417’ (K), ‘LA-716’ (L) and ‘Redenção’ x ‘LA-716’ (M) cultivated in protected and external environments at 14, 28, 42, 56, 70 and 84 days after transplanting (DAT).

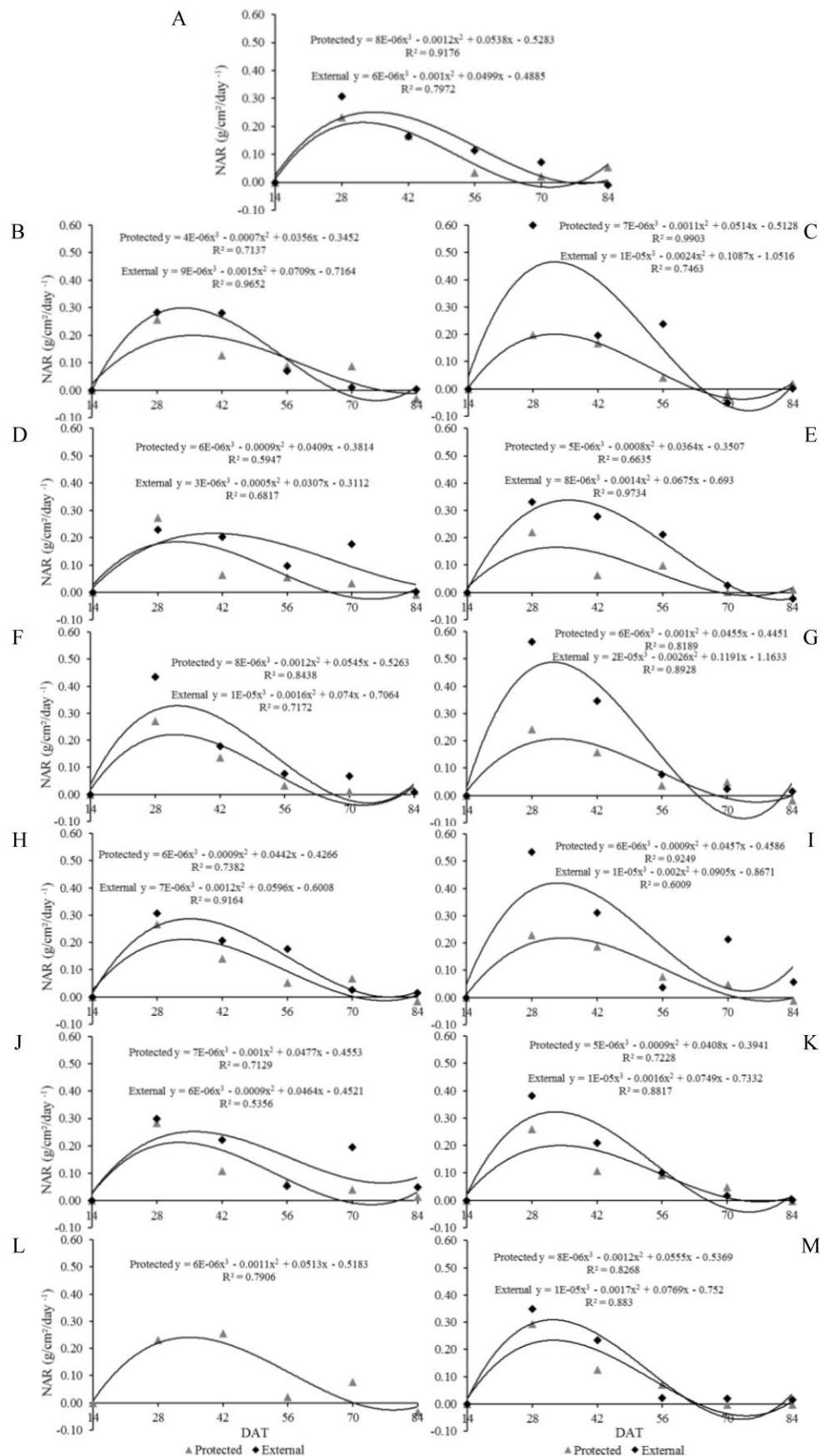


Figure 2. Net assimilation rate (NAR) of 'Redenção' (A), 'AF 26970' (B), 'Redenção' x 'AF 26970' (C), 'LA-1401' (D), 'Redenção' x 'LA-1401' (E), 'AF 19684' (F), 'Redenção' x 'AF 19684' (G), 'PI-127826' (H), 'Redenção' x 'PI-127826' (I), 'PI-134417' (J), 'Redenção' x 'PI-134417' (K), 'LA-716' (L) and 'Redenção' x 'LA-716' (M) cultivated in protected and external environments at 14, 28, 42, 56, 70 and 84 days after transplanting (DAT).

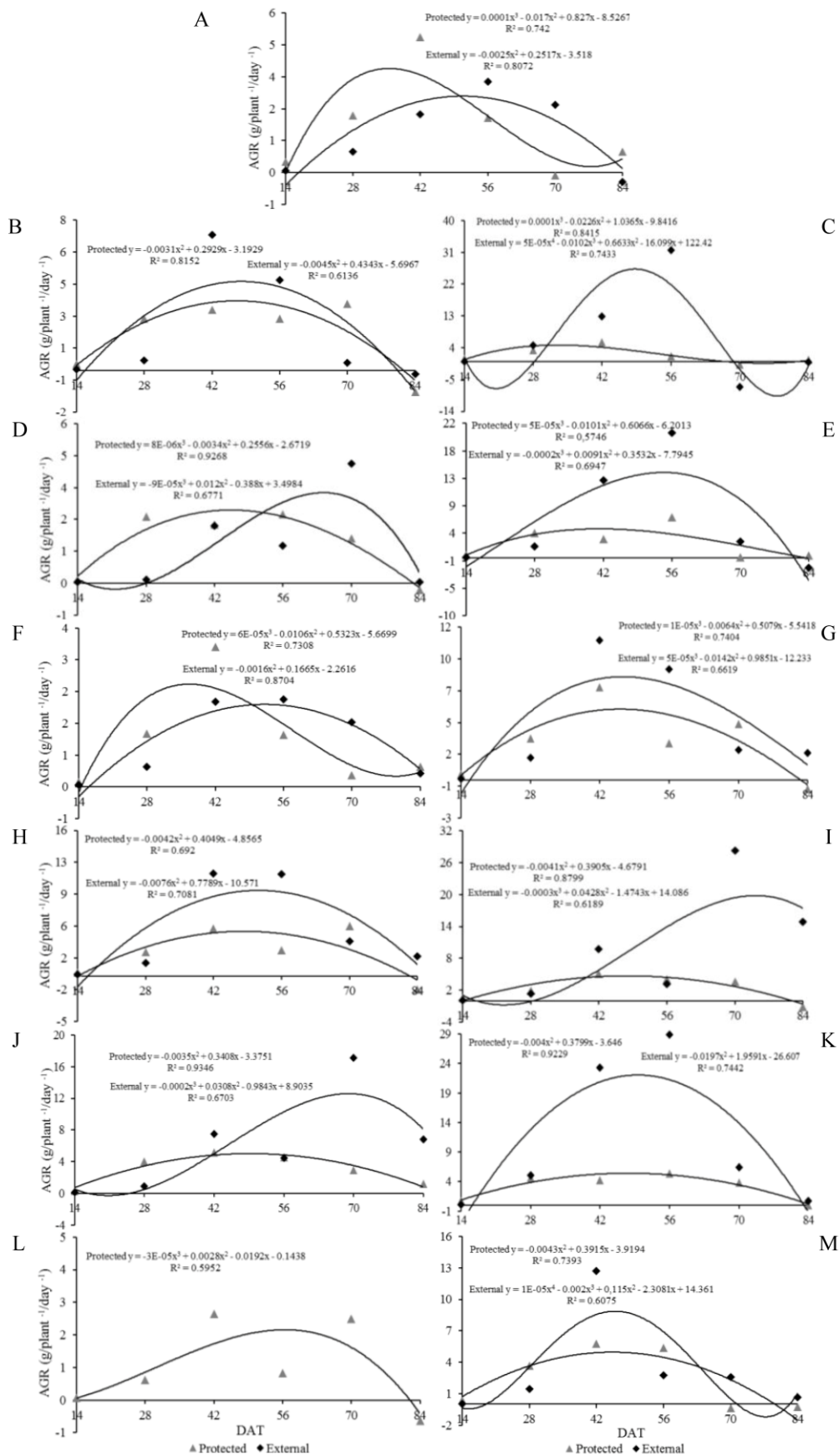


Figure 3. Absolute growth rate (AGR) of 'Redenção' (A), 'AF 26970' (B), 'Redenção' x 'AF 26970' (C), 'LA-1401' (D), 'Redenção' x 'LA-1401' (E), 'AF 19684' (F), 'Redenção' x 'AF 19684' (G), 'PI-127826' (H), 'Redenção' x 'PI-127826' (I), 'PI-134417' (J), 'Redenção' x 'PI-134417' (K), 'LA-716' (L) and 'Redenção' x 'LA-716' (M) cultivated in protected and external environments at 14, 28, 42, 56, 70 and 84 days after transplanting (DAT).

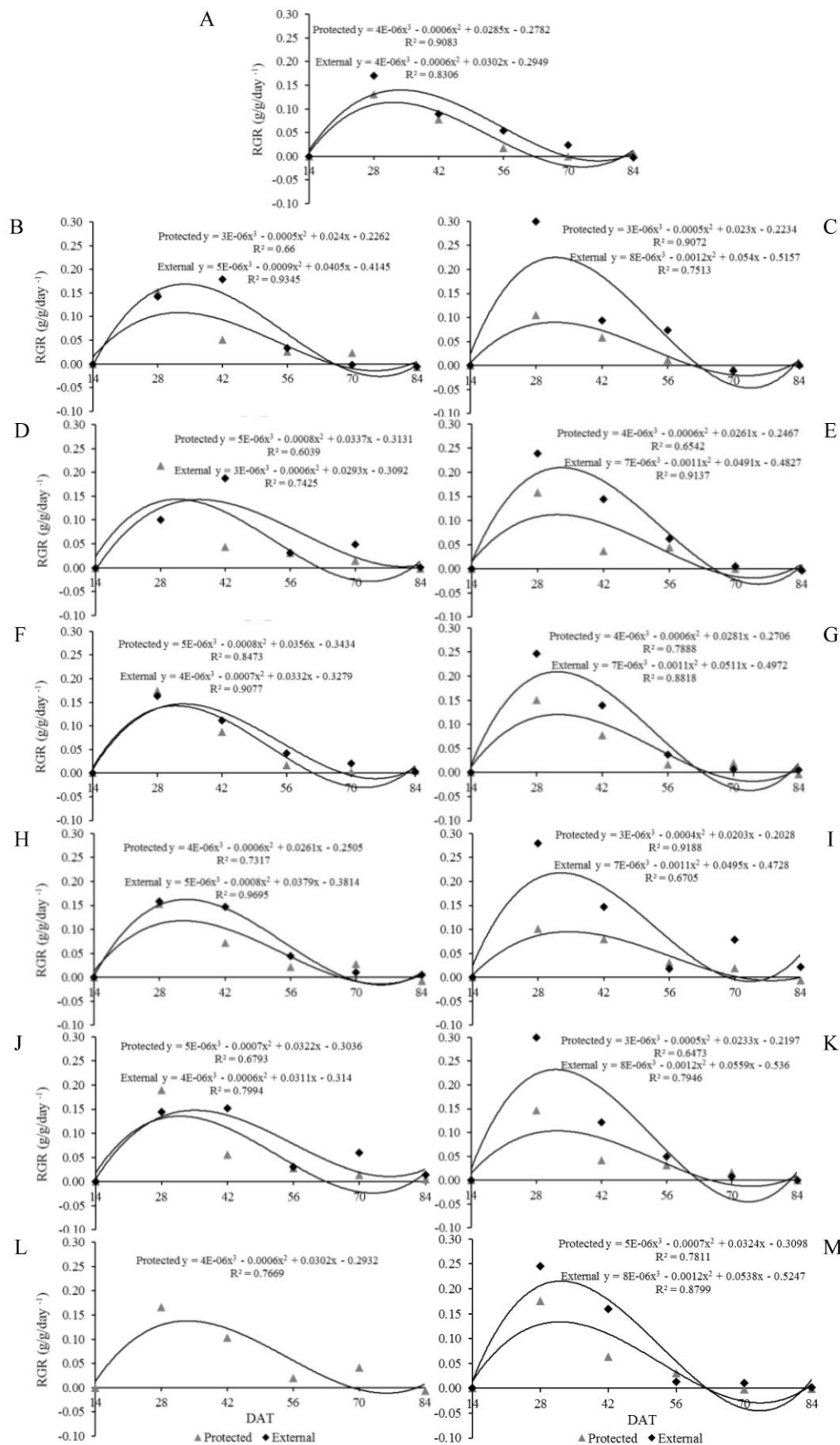


Figure 4. Relative growth rate (RGR) of 'Redenção' (A), 'AF 26970' (B), 'Redenção' x 'AF 26970' (C), 'LA-1401' (D), 'Redenção' x 'LA-1401' (E), 'AF 19684' (F), 'Redenção' x 'AF 19684' (G), 'PI-127826' (H), 'Redenção' x 'PI-127826' (I), 'PI-134417' (J), 'Redenção' x 'PI-134417' (K), 'LA-716' (L) and 'Redenção' x 'LA-716' (M) cultivated in protected and external environments at 14, 28, 42, 56, 70 and 84 days after transplanting (DAT).

As for AGR, interspecific parents and hybrids presented different results explained by quadratic, cubic and fourth-degree regression equations. The estimated absolute growth rates were different from one genotype to another, with the maximum growth occurring in the protected environment between 33 and 54 DAT and in the external environment between 44 and 76 DAT (Figure 3). It can be stated that the difference in absolute growth is due to the genetic diversity of the studied genotypes.

Regarding RGR, as also observed for NAR, all genotypes presented a cubic fit. The maximum estimated growth data occurred at approximately 34 DAT, decreasing thereafter, and slightly increasing at 84 DAT (Figure 4). In studies conducting analyses of tomato growth, decreases in the values of RGR along the cycle are commonly reported. They are related to decreases in the net assimilation rate and in the ratio between leaf area and total dry matter (Fayad et al., 2001; Soares et al., 2013).

Biomass accumulation and growth rates may be due to a balance between plant availability and carbon demand. For Aumonde, Lopes, Moraes, Peil, and Pedó (2011), this phenomenon presents a logistic behavior because at the beginning of development the growth is slow, and from then on, there is an exponential phase in which there are increases in rates until growth becomes slow again. Thus, growth is characterized as limited.

Although the accessions referring to wild species presented NAR, AGR, and RGR similar to 'Redenção', we observed higher NAR and RGR for interspecific hybrids in the external environment when compared to their parent plants (Figure 2B to K and Figure 4B to K) and increased AGR in both growing environments (Figures 3B to 4K). As also verified for the accumulation of total dry matter, it can be considered that the heterotic effect of interspecific crossings resulted in an increase in net assimilation rates and absolute and relative growth in comparison to parent plants.

Due to low fruit production, wild tomato species have a low commercial value (Peralta et al., 2008), as shown in Figure 1. However, the crossings of wild accessions with 'Redenção' were promising for breeding programs, as they provided interspecific hybrids with increased NAR, AGR, and RGR (Figures 2 to 4). Among them, 'PI-127826' and 'PI-134417', related to the species *S. habrochaites* var. *hirsutum* and *glabratum*, stood out. They also provided the greatest increase in leaf area accumulation and total dry matter.

Although the accessions 'PI-127826' and 'PI-134417' are commonly used by means of interspecific variability to incorporate features that confer resistance to pests into the tomato species *S. lycopersicum*, no interspecific cross-breeding information is available for the species *S. habrochaites* for maximizing biomass accumulation.

Based on the evaluated characteristics of quantitative growth, it is possible to state that the tomato species and interspecific hybrids studied presented a diversity of behaviors regarding the synthesis and allocation of carbohydrates. Until then, there was no information in the literature addressing the quantitative growth of interspecific species and tomato hybrids, and this type of analysis, in addition to allowing growth evaluation, also allows measuring vegetative behavior based on different physiological processes, adaptation under cultivation conditions and fruit yield.

The results obtained by the growth analysis could be used by breeding programs of tomatoes aiming to develop genotypes with increased biomass accumulation.

Conclusion

The tomato species *Solanum habrochaites* var. *hirsutum* accession 'PI-127826' and *Solanum habrochaites* var. *glabratum* accession 'PI-134417' have the potential to be used as donor parents for the development of lineages with a greater capacity for net assimilation and biomass accumulation.

References

- Albrecht, E., Escobar, M., & Chetelat, R. T. (2010). Genetic diversity and population structure in the tomato-like nightshades *Solanum lycopersicoides* and *S. sitiens*. *Annals of Botany*, 105(4), 535-554. DOI: 10.1093/aob/mcq009
- Andriolo, J. L., Espindola, M. C. G., Godoi, R., Bortolotto, O. C., & Luz, G. L. (2004). Crescimento e produtividade de plantas de tomateiro em cultivo protegido sob alta densidade e desfolhamento. *Ciência Rural*, 34(4), 1251-1253. DOI: 10.1590/S0103-84782004000400047
- Aumonde, T. Z., Lopes, N. F., Moraes, D. M., Peil, R. M. N., & Pedó, T. (2011). Análise de Crescimento do híbrido de mini melancia Smile® enxertada e não enxertada. *Interciencia*, 36(9), 1-5.

- Bai, Y., & Lindhout, P. (2007). Domestication and breeding of tomatoes: what have we gained and what can we gain in the future?. *Annals of Botany*, 100(5), p.1085-1094. DOI:10.1093/aob/mcm150
- Bedinger, P. A., Chetelat, R. T., McClure, B., Moyle, L. C., Rose, J. K. C., Stack, S. M., ... Royer, S. (2011). Interspecific reproductive barriers in the tomato clade: Opportunities to decipher mechanisms of reproductive isolation. *Sexual Plant Reproduction*, 24(3), 171-187. DOI: 10.1007/s00497-010-0155-7
- Bergougnoux, V. (2014). The history of tomato: from domestication to biopharming. *Biotechnology Advances*, 32(1), 170-189. DOI: 10.1016/j.biotechadv.2013.11.003
- Blanca, J., Montero-Pau, J., Sauvage, C., Bauchet, G., Illa, E., Díez, M. J., ... Cañizares, J. (2015). Genomic variation in tomato, from wild ancestors to contemporary breeding accessions. *BMC Genomics*, 16(1), 1-19. DOI: 10.1186/s12864-015-1444-1
- Dias, D. M., Resende, J. T. V., Marodin, J. C., Matos, R., Lustosa, I. F., & Resende, N. C. (2016). Acyl sugars and whitefly (*Bemisia tabaci*) resistance in segregating populations of tomato genotypes. *Genetics and Molecular Research*, 15(2), 1-11. DOI: 10.4238/gmr.15027788
- Empresa Brasileira de Pesquisa Agropecuária [Embrapa]. (2013). *Centro Nacional de Pesquisa de Solos. Sistema Brasileiro de classificação de solos* (3 ed.). Rio de Janeiro, RJ: Embrapa/CNPQ.
- Fayad, J. A., Fontes, P. C. R., Cardoso, A. A., Finger, L. F., & Ferreira, F. A. (2001). Crescimento e produção do tomateiro cultivado sob condições de campo e de ambiente protegido. *Horticultura Brasileira*, 19(3), 232-237. DOI: 10.1590/s0102-05362001000300016
- Hurtado, F. D., Gil, M. A., Zubiaur, Y. M., Aguilera, J. G., Xavier, C. A. D., Zerbini, J. F. M., & Silva, D. J. H. (2012). Fontes de resistência em tomateiro aos begomovírus bissegmentados Tomato yellow spot virus e Tomato severe rugose virus. *Horticultura Brasileira*, 30(4), 639-644. DOI: 10.1590/s0102-05362012000400013
- Liu, B., & Heins, D. (2002). Photothermal ratio affects plant quality in 'Freedom' Poinsettia. *Journal of the American Society for Horticultural Science*, 127(1), 20-26. DOI: 10.21273/JASHS.127.1.20
- Lopes, W. A. R., Negreiros, M. Z., Dombroski, J. L. D., Rodrigues, G. S. O., Soares, A. M., & Araújo, A. P. (2011). Análise do crescimento de tomate 'SM-16' cultivado sob diferentes coberturas de solo. *Horticultura Brasileira*, 29(4), 554-561. DOI: 10.1590/s0102-05362011000400019
- Lucini, T., Faria, M. V., Rohde, C., Resende, J. T. V., & Oliveira, J. R. F. (2015). Acylsugar and the role of trichomes in tomato genotypes resistance to *Tetranychus urticae*. *Arthropod-Plant Interactions*, 9(1), 45-53. DOI: 10.1007/s11829-014-9347-7
- Martinazzo, E. G., Perboni, A. T., Posso, D. A., Aumonde, T. Z., & Bacarin, M. A. (2015). Análise de crescimento e partição de assimilados em plantas de tomateiro cv. Micro-Tom submetidas ao nitrogênio e piraclostrobina. *Semina: Ciências Agrárias*, 36(5), 3001-3012. DOI: 10.5433/1679-0359.2015v36n5p3001
- Morales, R. G. F., Resende, L. V., Bordini, I. C., Galvão, A. G., & Resende, F. C. (2015). Caracterização do tomateiro submetido ao déficit hídrico. *Scientia Agraria*, 16(1), 9-17. DOI: 10.5380/rsa.v16i1.41042
- Pedó, T., Aumonde, T. Z., Lopes, N. F., & Mauch, C. R. (2015). Crescimento e conversão de energia solar em tomateiro enxertado sob cultivo protegido. *Semina: Ciências Agrárias*, 36(3), 1927-1934. DOI: 10.5433/1679-0359.2015v36n3supl1p1927
- Peralta, I. E., & Spooner, D. M. (2005). Morphological characterization and relationships of wild tomatoes (*Solanum* L. Section *Lycopersicon*). *Systematic Botany Monographs*, 104, 227-257.
- Peralta, I. E., Spooner, D. M., & Knapp, S. (2008). Taxonomy of wild tomatoes and their relatives (*Solanum* sect. *Lycopersicoides*, sect. *Juglandifolia*, sect. *Lycopersicon*; *Solanaceae*). *Systematic Botany Monographs*, 8, 1-186. DOI: 10.2307/25027972
- Poudyala, D., Khatri, L., & Uptmoora, R. (2015). An introgression of *Solanum habrochaites* in the rootstock improves stomatal regulation and leaf area development of grafted tomatoes under drought and low root-zone-temperatures. *Advances in Crop Science and Technology*, 3(3), 1-11. DOI: 10.4172/2329-8863.1000175
- Silva, F. A. S., & Azevedo, C. A. V. (2016). The assistat software version 7.7 and its use in the analysis of experimental data. *African Journal of Agricultural Research*, 11(39), 3733-3740. DOI: 10.5897/ajar2016.11522
- Soares, A. M., Negreiros, M. Z., Lopes, W. A. R., Dombroski, J. L. D., & Lucena, R. R. M. (2013). Crescimento do tomateiro cultivado em solo coberto com polipropileno preto. *Revista Ciência Agronômica*, 44(4), 790-797. DOI: 10.1590/s1806-66902013000400016

- Veasey, E. A., Piotto, F. A., Nascimento, W. F., Rodrigues, J. F., Mezette, T. F., Borges, A., & Mistro, J. C. (2011). Processos evolutivos e a origem das plantas cultivadas. *Ciência Rural*, 41(7), 1218-1228. DOI: 10.1590/s0103-84782011000700018
- Venema, J. H., Boukelien, E. D., Bax, J. E. M., Hasselt, P. R. V., & Elzenga, J. T. M. (2008). Grafting tomato (*Solanum lycopersicum*) onto the rootstock of a high-altitude accession of *Solanum habrochaites* improves suboptimal-temperature tolerance. *Environmental and Experimental Botany*, 63(1), 359-367. DOI: 10.1016/j.envexpbot.2007.12.015
- Xu, X., Yang, X., & Yang, Y. (2001). Effect of HCO_3^- on root growth and nutrient absorption of different rice genotypes. *Ying Yong Sheng Tai Xue Bao*, 12(4), 557-560.
- Zeist, A. R., Resende, J. T. V., Giacobbo, C. L., Faria, C. M. D. R., & Dias, D. M. (2017). Graft takes of tomato on other solanaceous plants. *Revista Caatinga*, 30(2), 513-520. DOI: 10.1590/1983-21252017v30n227r
- Zeist, A. R., Resende, J. T. V., Silva, I. F. L., Oliveira, J. R. F., Faria, C. M. D. R., & Giacobbo, C. L. (2017). Agronomic characteristics of tomato plant cultivar Santa Cruz Kada grafted on species of the genus *Solanum*. *Horticultura Brasileira*, 35(3), 419-424. DOI: 10.1590/s0102-053620170317