horticultura brasileira

Research

ZEIST, AR; RESENDE, JTV; FARIA, MV; GABRIEL, A; ADRIANO, E; LIMA FILHO, RB. 2018. Photosynthetic characteristics in species and interspecific hybrids of tomato. *Horticultura Brasileira* 36:362-370.DOI - http://dx.doi.org/10.1590/S0102-053620180313

Photosynthetic characteristics in species and interspecific hybrids of tomato

André R Zeist; Juliano TV Resende; Marcos V Faria; André Gabriel; Elisa Adriano; Renato B Lima Filho[1]

[1]Universidade Estadual do Centro-Oeste (UNICENTRO), Guarapuava-PR, Brazil; andre.zeist@bol.com.br; jvresende@uol.com.br; mfaria@unicentro.br; andre.gb85@hotmail.com; elisaadrianojd@gmail.com; delimafilho.renato@yahoo.com

ABSTRACT

Gas exchanges in species and interspecific hybrids of tomato in different environments may contribute to the development and selection of genotypes with a higher tolerance to adverse cultivation conditions. This study aimed to assess the photosynthetic characteristics of wild tomato species and the cultivar Redenção, as well as the respective F_1 hybrids of interspecific crosses cultivated under two environments. The experimental design was a randomized block design with three replications and the assessment of six wild accessions, one cultivar, and the respective interspecific hybrids under two environments. At 14, 28, 42, 56, and 70 days after transplanting (DAT), gas exchange characteristics were assessed by means of a portable photosynthesis measurement system. The stomatal density of abaxial and adaxial surfaces of first-order leaflets was estimated under a protected cultivation at 56 DAT. We observed a higher influence of wild tomato species and interspecific hybrids on the assessed characteristics when compared to the cultivation environments. The accession 'LA-716' and the hybrid 'Redenção' × 'LA-716' presented the highest water use efficiency and the accessions 'PI-127826' and 'PI-134417' and the interspecific hybrids 'Redenção' × 'PI-127826' and 'Redenção' × 'PI-134417' presented the highest values of CO_2 assimilation, transpiration, instantaneous in vivo carboxylation efficiency of Rubisco, and number of stomata on the abaxial leaflet surface. Thus, the descendants of *Solanum habrochaites* are an interesting alternative to breeding programs that aim to make advances in obtaining strains that exhibit improvement in their photosynthetic characteristics.

Keywords: *Solanum lycopersicum*, wild accessions, pre-breeding, gas exchange.

RESUMO

Características fotossintéticas em espécies e híbridos interespecíficos de tomateiro

As trocas gasosas em espécies e híbridos interespecíficos de tomateiro em diferentes ambientes podem contribuir para o desenvolvimento e seleção de genótipos com maior tolerância às condições adversas de cultivo. O objetivo deste trabalho foi avaliar características fotossintéticas em espécies silvestres de tomateiro e na cultivar Redenção, bem como dos respectivos híbridos F1 de cruzamentos interespecíficos cultivados em dois ambientes. Na condução do experimento utilizou-se delineamento de blocos ao acaso, com três repetições, avaliando-se seis acessos silvestres, uma cultivar e os respectivos híbridos interespecíficos em dois ambientes. Aos 14, 28, 42, 56 e 70 dias após o transplantio (DAT), avaliaram-se características de trocas gasosas por meio do sistema portátil de medidas de fotossíntese. No cultivo protegido, aos 56 DAT, foi estimada a densidade de estômatos das faces abaxial e adaxial dos folíolos de primeira ordem. Foi observada maior influência das espécies silvestres de tomateiro e híbridos interespecíficos do que dos ambientes de cultivo nas características avaliadas. O acesso 'LA-716' e o híbrido 'Redenção' × 'LA-716' apresentaram a maior eficiência do uso da água e os acessos 'PI-127826' e 'PI-134417' e os híbridos interespecíficos 'Redenção' × 'PI-127826' e 'Redenção' × 'PI-134417', apresentaram os maiores resultados de assimilação de CO2, transpiração, eficiência instantânea de carboxilação in vivo da Rubisco e número de estômatos na superfície abaxial dos folíolos. Demonstrou-se assim, que os descendentes da espécie *S. habrochaites* são uma interessante alternativa para os programas de melhoramento genético, que desejarem realizar avanços na obtenção de linhagens e que apresentem melhoria nas características fotossintéticas.

Palavras-chave: *Solanum lycopersicum*, acessos silvestres, pré-melhoramento genético, trocas gasosas.

Received on June 13, 2017; accepted on April 6, 2018

Research and teaching institutions have increasingly invested in characterizing plant genetic resources (Hilsdorf & Hallerman, 2017). Activities related to plant pre-breeding are of paramount importance considering their proposal to solve problems arising from the narrowing of the genetic base of cultivated species and promote an increase in the efficiency of breeding programs.

In addition to the variety cerasiforme, tomato (*Solanum lycopersicum*) has several wild species that have higher or lower interspecific compatibility of crosses (Peralta *et al.*, 2008). These wild species do not present commercial characteristics since they have small and usually pubescent fruits. However, these wild species are promising for use in breeding programs because they possess resistance genes, which, when properly studied and known, can be introduced into the cultivated tomato (Lucini *et al.*, 2015).

Several tomato species have characteristics that enable the development and vegetative growth under diverse soil and climatic conditions because they are native to regions that comprise a wide range of habitats located along the west coast of South America, encompassing mainly the Andes of Ecuador, Peru, northern Chile, and the Galapagos Islands (Peralta *et al.*, 2008; Bergougnoux, 2014).

These characteristics are due to some biological functions present in wild species, which can be incorporated into the cultivated tomato. Among these functions, there are those that confer resistance to phytopathogens (Hurtado *et al.*, 2012), arthropod-pests (Lucini *et al.*, 2015), abiotic stresses (Morales *et al.*, 2015), and improvements in nutritional quality. However, studies are still needed to identify new characteristics that may be of interest to tomato breeding programs.

Several studies have reported the photosynthetic performance of tomato cultivated under the most diverse management conditions (Soares *et al.*, 2012; Ramos *et al.*, 2015, Zeist *et al.*, 2017a). However, little is known about the photosynthetic characteristics of wild species and interspecific hybrids in comparison to the cultivated tomato. Even for plants of the same species, photosynthesis rate may vary between cultivars (Driever *et al.*, 2014). Thus, gas exchange rates may have great variations among tomato species.

The qualitative and quantitative photosynthetic performance of plants is an important indicator of productivity (Zeist *et al.*, 2017a,b) and mainly of tolerance to biotic (Bilgin *et al.*, 2010) and abiotic stress (Saibo *et al.*, 2009; Gururani *et al.*, 2015; Morales *et al.*, 2015). Thus, basic studies on the behavior of gas exchanges of species and interspecific hybrids of tomato plants under different environments can contribute to the understanding of genotype-environment interactions and, consequently, collaborate for the development and selection of cultivars with a higher tolerance to adverse conditions of cultivation.

Considering that, the aim of this study was to assess photosynthetic characteristics of wild tomato species and the cultivar Redenção, as well as the respective F_1 hybrids of interspecific crosses cultivated under two environments.

MATERIAL AND METHODS

The experiments were carried out in the agricultural season 2015/2016 at the Center for Research in Vegetables of the Department of Agronomy of the State University of Midwest (UNICENTRO), located in Guarapuava, PR, Brazil (25°38′S, 51°48′W). The soil of Guarapuava is classified as a very clayey Oxisol (Latossolo Bruno, Brazilian System of Soil Classification).

Six wild accessions (*S. pimpinellifolium* accession ‘AF 26970’, *S. galapagense* accession ‘LA-1401’, *S. peruvianum* accession ‘AF 19684’, *S. habrochaites* var. *hirsutum* accession ‘PI-127826’, *S. habrochaites* var. *glabratum* accession ‘PI-134417’, and *S. pennellii* accession ‘LA-716’) and the commercial cultivar Redenção (strain of *S. lycopersicum* with processing characteristics), together with the respective interspecific hybrids obtained from crosses between ‘Redenção’ (female parent) and wild accessions (male parents) (‘Redenção’ × ‘AF 26970’, ‘Redenção’ × ‘LA-1401’, ‘Redenção’ × ‘PI-127826’, ‘Redenção’ × ‘PI-134417’, and ‘Redenção’ × ‘LA-716’) were assessed. The genotypes were assessed in a randomized block design with three replications and under protected (greenhouse) and external (field) environments. Each plot consisted of eight plants.

In order to obtain interspecific hybrid seeds, fruits developed from the crosses between ‘Redenção’ and wild accessions were collected and had their seeds taken. The sowing of these seeds and their parents was carried out in 200-cell expanded polystyrene trays containing bio-stabilized pine bark-based commercial substrates and maintained in a floating hydroponic system in a greenhouse.

Sowing of the accessions ‘AF 26970’ and ‘AF 19684’ and interspecific hybrids was carried out together with the ‘Redenção’ strain. In addition, sowing of the accessions ‘LA-1401’, ‘PI-127826’, ‘PI-134417’, and ‘LA-716’ was performed ten days earlier due to their difference regarding germination, emergence, and development. Seedlings were transplanted 27 days after emergence of the female parent when they presented 4 to 5 expanded leaves (December 22, 2015).

The experiment conducted in the protected environment used a compartment inside the greenhouse with evaporative air cooling by means of an exhaust fan and running water in expanded clay installed in opposite sides. In this environment, seedlings were transplanted into 8-dm^3 capacity pots containing sieved soil mixed with decomposed bovine manure in the proportion 3:2. For the experiment in the external environment, an area 110 m far from the greenhouse was used. This area was plowed and 1.0 m wide seedbeds were prepared with a rotary tiller.

In the experimental units of the protected environment, the pots containing the plants were placed in four rows spaced 0.40 m from each other and 0.40 m between plants. In the external environment, each experimental unit consisted of two continuous rows of transplanted plants spaced 0.90 m from each other and 0.40 m between plants.

In both environments, the soil was corrected according to soil chemical analysis by applying calcitic limestone to raise base saturation to 80% and maintain the 4:1 ratio between Ca and Mg. Planting fertilization was carried out with 15 g NPK fertilizer (04-20-20) and 7.0 g simple superphosphate per plant. Micro-drippers were used to irrigate plants, according to crop needs and based on the criteria established for tomato in each environment.

During experimental period, daily minimum and maximum air temperature data for the external environment were collected at an automatic meteorological station of the State University of Midwest, Campus Cedeteg, located 180 m from the experiment. In the protected environment, data were collected daily using thermometers of maximum and minimum temperatures. Minimum temperatures ranged from 13.7 (March 1, 2016) to 21.8°C (December 31, 2015) and maximum temperatures from 26.3 (February 27, 2016) to 33.9°C (January 9, 2016). In the external environment, minimum temperatures ranged between 13.2 (March 1, 2016) and 21.0°C (December 22, 2015) and maximum temperatures between 22.6 (January 1, 2016) and 30.0°C (February 15, 2016).

Gas exchange was assessed by means of a portable photosynthesis measurement system (IRGA, Infrared Gas Analyzer, LI-COR, LI6400XT) with 1000 μmol photons $m^{-2}s^{-1}$, 400 μmol mol^{-1} CO_2, and $\Delta CO_2 + \Delta H_2O$ lower than 1%, by determining net CO_2 assimilation (*A*, μmol $CO_2 m^{-2}s^{-1}$), internal CO_2 concentration (*Ci*, μmol mol^{-1}), and transpiration rate (*E*, mmol H_2O $m^{-2}s^{-1}$). From these data, we quantified water use efficiency (*WUE*, mmol H_2O^{-1}) and the instantaneous in vivo carboxylation efficiency of Rubisco (*EiC*), estimated by the relation between net CO_2 assimilation and transpiration rate (*A*/*E*) and the relation between net CO_2 assimilation and internal CO_2 concentration in the leaf (*A*/*Ci*), respectively.

In the protected environment, stomatal density (SD) was estimated at 56 days after transplanting in the two central plants of each plot by collecting leaf discs of 1 cm in diameter from the primary leaflets and fixed with carbon tape on a metal support, with subsequent analysis of 300 μm^2 of the abaxial and adaxial surfaces in a Tescan® Vega3 scanning electron microscope (SEM) with coupled camera. In order to facilitate stomata counting, leaflet surfaces were photographed.

Data of evaluated characteristics were tested for normality and homogeneity of residual variances by the Lilliefors and Bartlett tests, respectively, and later submitted to individual and joint analysis of variance. When F-test was significant, means were submitted to Scott-Knott cluster test at 5% probability and analyzed by ASSISTAT statistical program version 7.7 (Silva & Azevedo, 2016).

RESULTS AND DISCUSSION

In general, we observed a much higher influence of genotypes on gas exchange characteristics assessed at different days after transplanting when compared to cultivation environments, thus demonstrating the existence of a diversity of photosynthetic behaviors among the studied tomato species.

In the five assessment dates, the highest values of net CO_2 assimilation (*A*) and instantaneous in vivo carboxylation efficiency of Rubisco (*EiC*) were observed for the wild species *S. habrochaites* var. *hirsutum* accession 'PI-127826' and *S. habrochaites* var. *glabratum* accession 'PI-134417' and the interspecific hybrids 'Redenção' × 'PI-127826' and 'Redenção' × 'PI-134417'. In general, the highest transpiration values (*E*) and lowest internal CO_2 concentrations (*Ci*) were also observed for these wild species and respective interspecific hybrids (Tables 1 to 4). These results showed that the F_1 hybrids 'Redenção' × 'PI-127826' and 'Redenção' × 'PI-134417' inherited characteristics related to the photosynthetic behavior of the male parents 'PI-134417' and 'PI-127826'.

For the parents 'PI-127826' and 'PI-134417' and hybrids 'Redenção' × 'PI-127826' and 'Redenção' × 'PI-134417', higher values of *A*, *E*, and *EiC* were inversely related to *Ci* (Tables 1 to 4). It is assumed that the lower CO_2 concentration in the substomatal chamber of these plants is related to a higher use of CO_2 by ribulose-1,5-bisphosphate carboxylase oxygenase (Rubisco) in the Calvin cycle for the synthesis of P-trioses. The lower *Ci* in plants tends to stimulate stomatal opening and transpiration, thus allowing a higher CO_2 entry into the substomatal spaces, which, consequently, promotes a higher net CO_2 assimilation (Zeist *et al.*, 2017b), as observed for 'PI-127826' and 'PI-134417' and hybrids 'Redenção' × 'PI-127826' and 'Redenção' × 'PI-134417'.

Gas exchange rates for the accessions 'PI-127826' and 'PI-134417' of the species *S. habrochaites* and the respective hybrids with the cultivar Redenção stood out, which is in accordance with several studies in the literature (Liu *et al.*, 2012; Ealson *et al.*, 2014; Poudyala *et al.*, 2015). These authors have observed that this species, because it is adapted to a wide range of latitudinal distribution, presents characteristics that allow better photosynthetic behavior even when conditions during the day or along the cycle are not favorable for the development of other tomato species.

Regarding the interaction genotype × environment, 14 days after transplanting (beginning of plant development), the cultivar 'Redenção' (female genitor), the wild accessions' LA-1401', 'AF 19684', 'PI-127826', and 'PI-134417' (male parents), and the respective hybrids presented a higher transpiration rate when cultivated under protected environment. This result is possibly due to a higher net CO_2 assimilation observed in the protected environment when compared to the external environment (Table 1).

According to Ferraz *et al.* (2012), the increase or decrease of photosynthetic yield may be directly related to the transpiration rate. This occurs because the lower the gas diffusion of H_2O is, the more limiting the net CO_2 assimilation (Adams *et al.*, 2016). In addition, the male parent 'LA-716' of the species *S. pennellii* and the hybrid 'Redenção' × 'LA-716' presented both lower transpiration rates and net CO_2 assimilation at the same time in all assessment days.

In general, the wild accessions 'AF 26970', 'LA-1401', and 'AF 19684', as well as cultivar 'Redenção' and the respective interspecific hybrids 'Redenção' × 'AF 26970', 'Redenção' × 'LA-1401', and 'Redenção' × 'AF 19684' presented a similar performance for gas exchange characteristics in all assessments (Tables 1 to 4). In addition, the values of net CO_2 assimilation obtained for the strain 'Redenção'' are close to those reported for the species *S. lycopersicum* (Soares *et al.*, 2012; Ramos *et al.*, 2015; Zeist *et al.*, 2017a).

At 14 days after transplanting, the genotypes cultivated in protected environment presented higher transpiration rate, which reflected in lower water use efficiency (Table 3). At 56 days after transplanting, the lowest internal CO_2 concentration without increment of net CO_2 assimilation in the protected environment in relation to the external environment (Table 4) for the wild accessions 'AF 19684', 'PI-134417', and 'LA-716', the cultivar Redenção, and the interspecific hybrids 'Redenção' × 'LA-1401', 'Redenção' × 'AF 19684', 'Redenção' × 'PI-127826', and 'Redenção' × 'PI-134417' is possibly due to the lower carbon dioxide availability in the protected

Table 1. Net CO_2 assimilation (*A*), internal CO_2 concentration (*Ci*), and transpiration rate (*E*) for species and interspecific hybrids of tomato cultivated under protected (P) and external (E) environments at 14, 28, and 42 days after transplanting. Guarapuava, UNICENTRO, 2015/2016.

Genotype	*A* (µmol CO_2 m^{-2} s^{-1})			*Ci* (µmol mol^{-1})			*E* (µmol H_2O m^{-2} s^{-1})		
	P	E	Average	P	E	Average	P	E	Average
				14 days					
Redenção	17.6[ns]	14.6	16.1c	160.2[ns]	159.6	159.9a	2.3Ac	1.7Bc	2.0d
AF 26970	17.7	16.2	16.9b	152.4	153.7	152.1a	1.3Ad	1.2Ad	1.3e
LA-1401	15.4	15.8	15.6c	156.6	166.1	161.4a	2.3Ac	1.6Bc	2.0d
AF 19684	15.7	12.5	14.1c	155.8	164.2	160.0a	2.4Ac	1.7Bc	2.0d
PI-127826	20.1	19.4	19.7a	106.3	113.3	109.8b	3.5Ab	2.6Bb	3.0b
PI-134417	20.2	20.9	20.6a	107.0	107.6	107.3b	3.5Ab	2.2Bb	30.b
LA-716	17.2	17.2	17.2b	156.5	165.4	160.9a	1.0Ad	0.9Ad	0.9e
Redenção x AF 26970	18.0	17.8	17.9b	163.5	163.6	163.5a	2.5Ac	2.4Ab	2.5c
Redenção x LA-1401	18.0	17.0	17.51b	162.5	162.6	162.5a	2.8Ac	1.9Bc	2.3c
Redenção x AF 19684	16.6	14.5	15.6c	161.1	161.4	161.3a	2.6Ac	1.8Bc	2.2d
Redenção x PI-127826	20.5	20.2	20.4a	127.5	120.5	124.0b	4.2Aa	3.5Ba	3.8a
Redenção x PI-134417	21.3	20.0	20.7a	121.7	127.3	124.5b	3.3Ab	3.3Aa	3.3b
Redenção x LA-716	15.8	15.4	15.6c	170.1	161.3	165.7a	1.3Ad	1.1Ad	1.2e
Average	18.0A	17.0B		146.3A	148.2A		2.5A	2.0B	
CV (%)		8.4			13.7			13.4	
				28 days					
Redenção	15.1[ns]	17.2	16.1c	176.1[ns]	169.3	172.7a	3.8[ns]	3.7	3.8b
AF 26970	17.4	16.9	17.2c	178.9	150.1	164.5a	3.8	4.1	4.0b
LA-1401	19.5	20.4	20.0b	157.3	152.4	154.8a	3.9	3.7	3.8b
AF 19684	17.5	17.6	17.5c	174.5	155.1	164.8a	3.7	4.1	3.9b
PI-127826	22.3	22.6	22.4a	77.8	64.2	71.0c	4.0	4.5	4.3a
PI-134417	23.0	23.6	23.3a	66.0	115.0	90.5c	4.4	4.1	4.2a
LA-716	19.2	18.9	19.0c	167.2	159.9	163.1a	3.2	3.1	3.1c
Redenção x AF 26970	15.1	15.5	15.3c	125.4	112.9	119.1b	3.3	4.2	3.8b
Redenção x LA-1401	17.1	17.6	17.4c	168.5	153.6	161.0a	4.0	4.0	4.0b
Redenção x AF 19684	15.7	18.2	16.9c	143.4	154.4	148.9a	3.9	3.9	3.9b
Redenção x PI-127826	22.1	21.8	21.9a	97.7	113.5	105.6b	4.3	4.6	4.4a
Redenção x PI-134417	23.0	22.6	22.7a	82.3	74.3	78.3c	4.6	4.3	4.4a
Redenção x LA-716	17.6	18.9	18.2c	130.0	146.9	138.4a	2.9	3.1	3.0c
Average	18.8A	19.4A		134.2A	132.3A		3.8A	3.9A	
CV (%)		8.9			19.6			10.2	
				42 days					
Redenção	17.2[ns]	15.1	16.1b	69.8[ns]	59.6	64.7a	2.8[ns]	1.7	2.2c
AF 26970	16.5	16.5	16.5b	63.4	66.5	64.9a	3.2	3.3	3.3b
LA-1401	20.7	19.9	20.3a	71.6	70.0	70.8a	2.5	2.2	2.4c
AF 19684	15.5	14.8	15.1b	70.3	69.4	69.9a	2.4	2.2	2.3c
PI-127826	21.1	20.2	20.6a	49.7	55.8	52.7a	3.8	4.3	4.1a
PI-134417	21.4	21.7	21.5a	56.7	55.5	56.1a	4.0	3.8	3.9a
LA-716	13.6	17.2	15.4a	63.4	62.1	62.8a	1.2	1.6	1.4c
Redenção x AF 26970	18.1	18.1	18.1b	62.5	68.8	65.7a	2.7	2.9	2.8c
Redenção x LA-1401	18.2	17.0	17.6b	64.3	63.4	63.9a	2.7	2.4	2.5c
Redenção x AF 19684	16.6	16.7	16.6b	69.7	65.8	67.8a	2.9	2.1	2.5c
Redenção x PI-127826	21.3	21.3	21.3a	66.2	66.2	66.2a	4.4	4.4	4.4a
Redenção x PI-134417	21.8	21.1	21.4a	61.8	67.8	64.8a	4.7	4.5	4.6a
Redenção x LA-716	15.2	14.3	14.7b	64.0	60.0	62.0a	1.1	1.1	1.1d
Average	18.2A	18.0A		64.1A	63.9A		2.9A	2.8A	
CV (%)		13.1			17.2			16.5	

*Means followed by same uppercase letters in the rows and lowercase letters in the columns belong to the same group by Scott-Knott test at 5%; [ns]No significant interaction.

environment when compared to open field areas.

The wild species *S. pennellii* 'LA-716' and hybrid 'Redenção' × 'LA-716' were more efficient regarding water use in all assessment dates (Tables 3 and 4). The highest *WUE* for these genotypes is possibly due to their lowest transpiration rates (Tables 1 and 2). In fact, the species *S. pennellii* has as natural habitat the region belonging to the eastern Peruvian Andes to the western Pacific Coast (Peralta *et al*., 2008), which is warm and dry, providing a superior performance in relation to the water efficiency use when compared to the cultivated tomato (Ealson & Richards, 2009). Thus, the accession 'LA-716' proves to be an interesting alternative for the introgression of resistance genes to water deficit in *S. lycopersicum*.

The accessions 'PI-127826' and 'PI-134417' and the hybrids 'Redenção' × 'PI-127826' and 'Redenção' × 'PI-134417' showed a higher *EiC* in all assessment dates (Tables 4 and 5). These results are probably due to the close relation of the instantaneous carboxylation efficiency with the increments in net CO_2 assimilation, as also observed by Machado *et al.* (2005) in citrus and Ferraz *et al.* (2012) in common beans ecotypes.

Table 2. Net CO_2 assimilation (*A*), internal CO_2 concentration (*Ci*), and transpiration rate (*E*) for species and interspecific hybrids of tomato cultivated under protected (P) and external (E) environments at 56, and 70 days after transplanting. Guarapuava, UNICENTRO, 2015/2016.

Genotype	***A*** **(μmol CO_2 m^{-2} s^{-1})**			***Ci*** **(μmol mol^{-1})**			***E*** **(μmol H_2O m^{-2} s^{-1})**		
	P	**E**	**Average**	**P**	**E**	**Average**	**P**	**E**	**Average**
				56 days					
Redenção	17.8^{ns}	17.8	17.8b	56,5Bd	82.9Ac	69.7d	3.8^{ns}	3.7	3.7c
AF 26970	16.2	16.5	16.4c	66.9Ac	767.6Ac	77.2d	3.7	3.4	3.6c
LA-1401	20.7	17.3	19.0a	71.6Ac	64.8Ad	68.2d	2.5	3.5	3.0c
AF 19684	15.5	15.8	15.6c	73.6Bc	102.8Aa	88.2c	3.5	3.5	3.5c
PI-127826	21.1	20.9	21.0a	67.3Ac	79.6Ac	73.5d	4.5	4.3	4.4b
PI-134417	20.7	21.0	21.0a	63.4Bd	89.2Ac	76.3d	4.0	4.5	4.3b
LA-716	15.0	15.0	15.0c	72.5Bc	94.3Ab	83.4c	2.2	2.5	2.3d
Redenção x AF 26970	17.8	18.5	18.2b	71.9Ac	79.6Ac	75.7d	3.4	3.2	3.3c
Redenção x LA-1401	18.2	17.0	17.6b	83.3Bb	107.2Aa	95.3b	3.4	3.4	3.4c
Redenção x AF 19684	17.4	17.4	17.4b	66.4Bc	105.3Aa	86.1c	3.7	3.4	3.5c
Redenção x PI-127826	21.4	21.6	21.5a	59.3Bd	78.6Ac	69.0d	4.3	4.7	4.5b
Redenção x PI-134417	20.7	21.0	20.8a	58.7Bd	92.6Ab	75.6d	5.5	4.6	5.0a
Redenção x LA-716	15.0	15.2	15.1c	104.2Aa	105.7Aa	104.9a	2.3	2.3	2.3d
Average	18.0A	18.1A		70.4B	89.3A		3.6A	3.6A	
CV (%)		11.1			9.4			11.8	
				70 days					
Redenção	15.0^{ns}	16.3	15.7b	99.8^{ns}	82.9	91.4a	3.7^{ns}	3.9	3.8c
AF 26970	13.3	13.1	13.2c	103.5	101.7	102.6a	3.9	3.8	3.8c
LA-1401	13.4	14.0	13.7c	104.1	105.1	104.6a	3.6	3.7	3.7c
AF 19684	12.9	12.0	12.5d	117.9	109.2	113.6a	4.1	4.0	4.0c
PI-127826	20.0	19.3	19.7a	90.3	102.9	96.6a	5.1	4.7	4.9b
PI-134417	19.3	19.3	19.3a	98.9	110.7	104.8a	5.4	5.6	5.5a
LA-716	10.0	10.8	10.4d	104.2	107.6	105.9a	3.0	2.9	3.0d
Redenção x AF 26970	13.6	13.4	13.5c	104.5	109.7	107.1a	3.7	3.8	2.6c
Redenção x LA-1401	12.9	12.7	12.8d	96.7	107.2	101.9a	3.4	3.5	3.5c
Redenção x AF 19684	12.3	12.1	12.2d	112.3	109.2	110.7a	3.6	3.7	3.7c
Redenção x PI-127826	19.5	19.5	19.5a	105.2	95.3	100.3a	4.3	4.7	4.5b
Redenção x PI-134417	20.3	18.7	19.5a	106.7	106.1	106.4a	5.5	5.3	5.4a
Redenção x LA-716	11.2	12.0	11.5d	104.2	106.4	105.3a	2.5	2.3	2.4d
Average	14.9A	14.9A		103.7A	104.2A		4.0A	4.0A	
CV (%)		10.6			10.3			13.0	

*Means followed by same uppercase letters in the rows and lowercase letters in the columns belong to the same group by Scott-Knott test at 5%; ^{ns}No significant interaction.

Table 3. Water use efficiency (*WUE*) and in vivo carboxylation efficiency of Rubisco (*EiC*) for species and interspecific hybrids of tomato cultivated under protected (P) and external (E) environments at 14, 28, and 42 days after transplanting. Guarapuava, UNICENTRO, 2015/2016.

Genotype	***WUE* (mmol H_2O m^{-2} s^{-1})**			***EiC***		
	P	**E**	**Average**	**P**	**E**	**Average**
			14 days			
Redenção	7.9^{ns}	8.7	8.3c	0.11^{ns}	0.09	0.10b
AF 26970	13.8	13.4	13.6b	0.12	0.11	0.11b
LA-1401	6.5	10.5	8.5c	0.10	0.10	0.10b
AF 19684	6.6	7.6	7.1c	0.10	0.08	0.09b
PI-127826	5.9	7.8	6.8c	0.19	0.17	0.18a
PI-134417	5.8	8.4	7.1c	0.19	0.20	0.19a
LA-716	19.7	19.5	19.6a	0.11	0.10	0.11b
Redenção x AF 26970	7.1	7.5	7.3c	0.11	0.11	0.11b
Redenção x LA-1401	6.5	9.2	7.8c	0.11	0.10	0.11b
Redenção x AF 19684	6.6	8.3	7.4c	0.11	0.09	0.10b
Redenção x PI-127826	5.0	5.9	5.5c	0.16	0.17	0.17a
Redenção x PI-134417	6.5	6.0	6.3c	0.18	0.17	0.17a
Redenção x LA-716	12.4	13.9	13.1b	0.09	0.09	0.09b
Average	8.5A	9.7A		0.13A	0.12A	
CV (%)		25.8			17.4	
			28 days			
Redenção	3.9^{ns}	4.6	4.3c	0.09^{ns}	0.12	0.10c
AF 26970	4,5	4.2	4.3c	0.10	0.12	0.11c
LA-1401	5.1	5.5	5.3b	0.13	0.14	0.13c
AF 19684	4.8	4.4	4.6c	0.10	0.12	0.11c
PI-127826	5.8	5.1	5.4b	0.31	0.36	0.31a
PI-134417	5.3	5.8	5.5b	0.35	0.21	0.28a
LA-716	6.0	6.2	6.1a	0.11	0.12	0.12c
Redenção x AF 26970	5.7	3.7	4.2c	0.12	0.14	0.13c
Redenção x LA-1401	4.3	4.4	4.3c	0.10	0.16	0.10c
Redenção x AF 19684	4.1	4.7	4.4c	0.12	0.12	0.12c
Redenção x PI-127826	5.3	4.8	5.0b	0.23	0.19	0.21b
Redenção x PI-134417	5.1	5.2	5.1b	0.30	0.35	0.33a
Redenção x LA-716	6.0	6.4	6.2a	0.14	0.14	0.14c
Average	5.0A	5.0A		0.17A	0.17A	
CV (%)		15.1			30.1	
			42 days			
Redenção	6.1^{ns}	9.0	7.5c	0.27^{ns}	0.27	0.27c
AF 26970	5.2	4.9	5.1d	0.26	0.25	0.26c
LA-1401	8.2	10.8	9.5b	0.29	0.31	0.30c
AF 19684	6.7	6.7	6.7c	0.23	0.21	0.22c
PI-127826	5.7	4.7	5.2d	0.43	0.37	0.40a
PI-134417	5.3	5.7	5.5d	0.39	0.40	0.40a
LA-716	11.8	11.9	11.9a	0.22	0.28	0.25c
Redenção x AF 26970	7.0	6.3	6.6c	0.29	0.27	0.28c
Redenção x LA-1401	6.7	7.3	7.0c	0.29	0.27	0.28c
Redenção x AF 19684	5.8	8.4	7.1c	0.24	0.26	0.25c
Redenção x PI-127826	4.8	4.8	4.8d	0.32	0.32	0.32b
Redenção x PI-134417	4.7	4.7	4.7d	0.35	0.31	0.33b
Redenção x LA-716	14.4	12.6	13.5a	0.24	0.24	0.24c
Average	7.1A	7.5A		0.29A	0.29A	
CV (%)		23.0			20.2	

*Means followed by same uppercase letters in the rows and lowercase letters in the columns belong to the same group by Scott-Knott test at 5%; ^{ns}No significant interaction.

Regarding stomatal density (SD), measured only in the protected environment, the highest number of stomata on the abaxial surface of leaflets was observed in the accession 'PI-127826', followed by the accession 'PI-134417' and the hybrids 'Redenção' × 'PI- 127826' and 'Redenção' × 'PI-134417', with values of 67.00, 49.00, 45.66, and 47.00 stomata per 300 μm^2, respectively (Table 5). On the contrary, the highest number of stomata on the adaxial surface of leaflets was observed in the hybrid 'Redenção' × 'AF 19684', with a value of 30.00 stomata per 300 μm^2. Similarly, other studies have reported higher number of stomata in the epidermis of the abaxial surface of leaflets when compared to the adaxial surface (Tari, 2003; Cunha *et al.*, 2013).

The basic function of a stomata is to control the entry and exit of gases and those of the abaxial surface is the main responsible for controlling transpiration, photosynthesis, and respiration in plants (Lucas & Renzaglia, 2002). The increased number of stomata on

Table 4. Water use efficiency (*WUE*) and in vivo carboxylation efficiency of Rubisco (*EiC*) for species and interspecific hybrids of tomato cultivated under protected (P) and external (E) environments at 56, and 70 days after transplanting. Guarapuava, UNICENTRO, 2015/2016.

Genotype	*WUE* (mmol H_2O m^{-2} s^{-1})			*EiC*		
	P	E	Average	P	E	Average
			56 days			
Redenção	4.7Ab	4.8Ab4.8b	4.8b	0.32Ab	0.22Ba	0.27b
AF 26970	4.4Ab	4.9Ab	4.6b	0.24Ac	0.21Aa	0.23c
LA-1401	8.2Aa	4.9Bb	6.6a	0.29Ab	0.27Aa	0.28b
AF 19684	4.5Ab	4.5Ab	4.5b	0.21Ac	0.15Bb	0.18d
PI-127826	4.7Ab	4.9Ab	4.8b	0.31Ab	0.26Aa	0.23a
PI-134417	5.2Ab	4.7Ab	4.9b	0.33Ab	0.24Ba	0.28a
LA-716	7.0Aa	6.0Aa	6.5a	0.21Ac	0.16Ab	0.18d
Redenção x AF 26970	5.3Ab	5.8Aa	5.5b	0.25Ac	0.24Aa	0.24b
Redenção x LA-1401	5.4Ab	5.1Ab	5.3b	0.22Ac	0.16Bb	0.19d
Redenção x AF 19684	5.8Ab	5.3Ab	5.0b	0.26Ac	0.16Bb	0.21c
Redenção x PI-127826	5.0Ab	5,7Ab	4.8b	0.37Aa	0.28Ba	0.32a
Redenção x PI-134417	3.9Ab	4.6Ab	4.3b	0.36Aa	0.23Ba	0.29a
Redenção x LA-716	6.8Aa	6.6Aa	6.7a	0.14Ad	0.14Ab	0.14c
Average	5.4A	5.1A		0.27A	0.21B	
CV (%)		16.0			12.6	
			70 days			
Redenção	4.0^{ns}	4.1	4.1a	0.15^{ns}	0.20	0.18a
AF 26970	3.4	3.5	3.4b	0.13	0.13	0.13b
LA-1401	3.7	3.8	3.8b	0.13	0.13	0.13b
AF 19684	3.2	3.1	3.1b	0.11	0.11	0.11c
PI-127826	4.1	4.2	4.1a	0.22	0.19	0.21a
PI-134417	3.6	3.5	3.5b	0.20	0.18	0.19a
LA-716	3.5	4.0	3.7b	0.10	0.10	0.10c
Redenção x AF 26970	3.7	3.8	3.8b	0.13	0.13	0.13b
Redenção x LA-1401	3.8	3.6	3.7b	0.13	0.12	0.13b
Redenção x AF 19684	3.4	3.2	3.3b	0.11	0.11	0.11c
Redenção x PI-127826	3.6	4.2	3.9b	0.19	0.21	0.20a
Redenção x PI-134417	3.7	3.5	3.6b	0.19	0.18	0.18a
Redenção x LA-716	4.7	5.3	5.0a	0.11	0.11	0.11c
Average	3.8A	3.8A		0.15A	0.15A	
CV (%)		19.7			14.5	

*Means followed by same uppercase letters in the rows and lowercase letters in the columns belong to the same group by Scott-Knott test at 5%; ^{ns}No significant interaction.

Table 5. Stomatal density (SD) on the abaxial and adaxial surfaces in first-order leaflets for species and interspecific hybrids of tomato cultivated under protected environment. Guarapuava, UNICENTRO, 2015/2016.

Genotype	SD (300 μm²)	
	Abaxial	Adaxial
Redenção	33.5d	11.0c
AF 26970	34.7d	14.7b
LA-1401	26.7e	4.7d
AF 19684	20.0f	5.7d
PI-127826	67.0a	6.7d
PI-134417	49.0b	1.7e
LA-716	11.0g	6.7d
Redenção x AF 26970	33.0d	7.7d
Redenção x LA-1401	40.0c	17.7b
Redenção x AF 19684	42.0c	30.0a
Redenção x PI-127826	45.7b	16.7b
Redenção x PI-134417	47.0b	13.0c
Redenção x LA-716	24.7e	10.3c
Average	36.2	11.3
CV (%)	9.9	16.4

*Means followed by same lowercase letters in the columns belong to the same group by Scott-Knott test at 5%.

the abaxial surface of the genotypes ‘PI-127826’, ‘PI-134417’, ‘Redenção’ × ‘PI-127826’, and ‘Redenção’ × ‘PI-134417’ is possibly the main factor that provided higher net CO_2 assimilation, transpiration, and instantaneous in vivo carboxylation efficiency of Rubisco.

Depending on the characteristics, we can consider the existence of a diversity of physiological responses between tomato species. The results of photosynthetic behavior observed in our study may collaborate with breeding programs, providing practical information that allows developing and selecting genotypes that best adapt to certain growing conditions.

The importance of qualitative and quantitative photosynthetic behavior in the development and plant growth is commonly reported in the literature. Considering this and that the accessions ‘PI-127826’ and ‘PI-134417’ and the respective interspecific F_1 hybrids ‘Redenção’ × ‘PI-127826’ and ‘Redenção’ × ‘PI-134417’ presented higher net CO_2 assimilation, instantaneous in vivo carboxylation efficiency of Rubisco, and stomatal density on the abaxial surface, the descendants of the varieties *hirsutum* and *glabratum* proved to be an interesting alternative for breeding programs that aim to make advances in obtaining genotypes that present improvement in their photosynthetic characteristics. Due to the higher water use efficiency, the accession ‘LA-716’ and the hybrid ‘LA-716’ × ‘Redenção’ proved to be an interesting genetic resource for tomato breeding programs, aiming at tolerance to water deficit.

REFERENCES

ADAMS, WW; STEWART, JJ; COHU, CM; MULLER, O; DEMMIG-ADAMS, B. 2016. Habitat temperature and precipitation of *Arabidopsis thaliana* ecotypes determine the response of foliar vasculature, photosynthesis, and transpiration to growth temperature. *Frontiers in Plant Science* 7: 1-18.

BERGOUGNOUX, V. 2014. The history of tomato: From domestication to biopharming. *Biotechnology Advances* 32:170-189.

BILGIN, DD; AVALA, JA; ZHU, J; CLOUGH, SJ; ORT DR; DELUCIA, EH. 2010. Biotic stress globally downregulates photosynthesis genes. *Plant, Cell & Environment* 33: 1597-613.

CUNHA, VC; SANTOS, JB; FERREIRA, EA; CABRAL, CM; SILVA, DV; GANDINI, EM. 2013. Anatomia foliar comparativa em espécies de guanxuma. *Planta Daninha* 31: 341-349.

DRIEVER, SM; LAWSON, T; ANDRALOJC, PJ; RAINES, CA; PARRY, MAJ. 2014. Natural variation in photosynthetic capacity, growth, and yield in 64 field-grown wheat genotypes. *Journal of Experimental Botany* 65: 4959-4973.

EALSON, HM; RICHARDS, JH. 2009. Drought response in self-compatible species of tomato (*Solanaceae*). *American Journal of Botany* 96: 605-611.

EASLON, HM; ST.CLAIR, DA; BLOOM, AJ. 2014. An introgression from wild tomato (*Solanum habrochaites*) affects tomato photosynthesis and water relations. *Crop Science* 54: 779-784.

FERRAZ, RLS; MELO, AS; SUASSUNA, JF; BRITO, MEB; FERNANDES, PD; NUNES JUNIOR, ES. 2012. Trocas gasosas e eficiência fotossintética em ecotipos de feijoeiro cultivados no semiárido. *Pesquisa Agropecuária Tropical* 42: 181-188.

GURURANI, M; MOHANTA, T; BAE, H. 2015. Current understanding of the interplay between phytohormones and photosynthesis under environmental stress. *International Journal of Molecular Sciences* 16: 19055-19085.

HILSDORF, AWS; HALLERMAN, EM. 2017. *Genetic resources of neotropical fishes*. Berlim: Springer. 258p.

HURTADO, FD; GIL, MA; ZUBIAUR, YM; AGUILERA, JG; XAVIER, CAD; ZERBINI JUNIOR, FM; SILVA, DJH. 2012. Fontes de resistência em tomateiro aos begomovírus bissegmentados tomato yellow spot virus e tomato severe rugose virus. *Horticultura Brasileira* 30: 639-644.

LIU, H; OUYANG, B; ZHANG, J; WANG, T; LI, H; ZHANG, Y; YU, C; YE, Z. 2012. Differential modulation of photosynthesis, signaling, and transcriptional regulation between tolerant and sensitive tomato genotypes under cold stress. *PLoS One* 7: 1-16.

LUCAS, JR; RENZAGLIA, KS. 2002. Structure and function of hornwort stomata. *Microscopy and Microanalysis* 8: 1090-1092.

LUCINI, T; FARIA, MV; ROHDE, C; RESENDE, JTV; OLIVEIRA, JRF. 2015. Acylsugar and the role of tricomes in tomato genotypes resistance to *Tetranychus urticae. Arthropod-Plant Interactions* 9: 45-53.

MACHADO, EC; SCHMIDT, PT; MEDINA, CL; RIBEIRO, RV.2005. Respostas da fotossíntese a fatores ambientais em três espécies de citros. *Pesquisa Agropecuária Brasileira* 40: 1161-1170.

MORALES, RGF; RESENDE, LV; BORDINI, IC; GALVAO, AG; RESENDE, FC. 2015. Caracterização do tomateiro submetido ao déficit hídrico. *Scientia Agraria* 16: 9-17.

PERALTA, IE; SPOONER, DM; KNAPP, S. 2008. Taxonomy of wild tomatoes and their relatives (*Solanum* sect. *Lycopersicoides*, sect. *Juglandifolia*, sect. *Lycopersicon*; *Solanaceae*). *Systematic Botany Monographs* 8: 1-186.

POUDYALA, D; KHATRIA, 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: 1-11.

RAMOS, ARP; AMARO, ACE; MACEDO, AC; SOUZA, ER; RODRIGUES, JD; ONO, EO. 2015. Acúmulo de carboidratos no desenvolvimento de tomateiro tratado com produtos químicos. *Semina. Ciências Agrárias* 36: 705-718.

SAIBO, NJM; LOURENCO, T; OLIVEIRA, MM. 2009. Transcription factors and regulation of photosynthetic and related metabolism under environmental stresses. *Annals of Botany* 103: 609-623.

SILVA, FAS; AZEVEDO, CAV. 2016. The assistat software version 7.7 and its use in the analysis of experimental data. *African Journal of Agricultural Research* 11: 3733-3740.

SOARES, LAA; SOUSA, JRM; BRITO, MEB; ANDRADE, EMG; SÁ, FVS; SILVA, ECB. 2012. Influência de diferentes lâminas de irrigação nas trocas gasosas do tomateiro na fase vegetativa. *Agropecuária Científica no Semi-Árido* 8: 118-122.

TARI, I. 2003. Abaxial and adaxial stomatal density, stomatal conductances and water status of bean primary leaves as affected by paclobutrazol. *Biologia Plantarum* 47: 215-220.

WREGE, MS; STEINMETZ, S; REISSER JUNIOR, C; ALMEIDA, IR. 2011. *Atlas climático da região sul do Brasil: Estados do Paraná, Santa Catarina e Rio Grande do Sul*. Pelotas: Embrapa Clima Temperado, Colombo: Embrapa Florestas. 336p.

ZEIST, AR; RESENDE, JTV; SILVA, IFL; OLIVEIRA, JRF; FARIA, CMDR; GIACOBBO, CL. 2017a. Agronomic characteristics of tomato plant cultivar Santa Cruz Kada grafted on species of the genus *Solanum*. *HorticulturaBrasileira* 35: 419-424.

ZEIST, AR; PIVA, R; RESENDE, JTV; SILVA, IFL; ATHANAZIO, JC; RODRIGUES, JD. 2017b. Physiological and agronomic traits of cabbage plants hybrid Fuyutoyo® sprayed with plant growth regulators. *Horticultura Brasileira* 35: 210-215.