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Genetic divergence among wild and hybrid tomato accessions based on morphoagronomic and physiological traits

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ABSTRACT

The objective of this study was to evaluate the genetic divergence among accessions of wild tomato species and interspecific F_1 hybrids. Six wild accessions were characterized (*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’), the commercial cultivar Redenção, and the respective interspecific F_1 hybrids: ‘Redenção’ x ‘AF 26970’, ‘Redenção’ x ‘LA-1401’, ‘Redenção’ x ‘AF 19684’, ‘Redenção’ x ‘PI-127826’, ‘Redenção’ x ‘PI-134417’, and ‘Redenção’ x ‘LA-716’. Thirty-five quantitative traits were evaluated, encompassing 29 morphoagronomic and six physiological characteristics. Principal component analysis (PCA) was performed. Tocher’s optimization method was used based on the Mahalanobis distance and the graphic dispersion of canonical variables, which followed the same trend of genotype clustering, forming three distinct groups. The PCA indicated some genetic divergences not shown by the other methods. A high divergence was observed among the species accessions and interspecific hybrids. The cultivar Redenção had the greatest genetic dissimilarity, and the interspecific hybrids of *S. lycopersicum* with wild accessions showed the greatest morphoagronomic and physiological similarity with the wild parents.

Keywords: *Solanum lycopersicum*, wild species, multivariate analysis, genetic dissimilarity.

RESUMO

Divergência genética entre acessos silvestres e híbridos de tomateiro baseada em caracteres morfoagronômicos e fisiológicos

O objetivo foi avaliar a divergência genética entre acessos de espécies silvestres e híbridos interespecíficos F_1 de tomateiro. Caracterizou-se seis acessos silvestres (*Solanum pimpinellifolium* ‘AF 26970’, *S. galapagense* ‘LA-1401’, *S. peruvianum* ‘AF 19684’, *S. habrochaites* var. *hirsutum* ‘PI-127826’, *S. habrochaites* var. *glabratum* ‘PI-134417’ e *S. pennellii* ‘LA-716’), a cultivar comercial Redenção e os respectivos híbridos interespecíficos F_1: ‘Redenção’ x ‘AF 26970’, ‘Redenção’ x ‘LA-1401’, ‘Redenção’ x ‘AF 19684’, ‘Redenção’ x ‘PI-127826’, ‘Redenção’ x ‘PI-134417’ e ‘Redenção’ x ‘LA-716’. Foram avaliados 35 caracteres quantitativos, sendo 29 morfoagronômicos e seis fisiológicos. Realizou-se análises de componentes principais (ACP). Utilizou-se os métodos de otimização de Tocher, baseado na distância de Mahalanobis e a dispersão gráfica das variáveis canônicas, que seguiram a mesma tendência de agrupamento dos genótipos, formando três grupos distintos. As ACP permitiram observar algumas divergências genéticas não observadas pelos demais métodos. Ocorreu alta divergência entre os acessos das espécies e híbridos interespecíficos. A cultivar Redenção teve a maior dissimilaridade genética e os híbridos interespecíficos de *S. lycopersicum* com acessos silvestres, apresentaram maior similaridade morfoagronômica e fisiológica com os genitores silvestres.

Palavras-chave: *Solanum lycopersicum*, espécies silvestres, análise multivariada, dissimilaridade genética.

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Tomato (*Solanum lycopersicum*) is one of the most economically important vegetable crops. It is widely cultivated, and the fruits are consumed fresh or processed (Bedinger *et al.*, 2011; Zhou *et al.*; 2015). Brazil occupies the 8th place in the world ranking of tomato production, with approximately 3.75 million tons produced in 52 thousand hectares. China is the largest producer in the world, followed by India, Turkey, the United States, Egypt, Italy, Iran, and Mexico (FAO 2020). In turn, when referring specifically to tomatoes for processing, Brazil has an estimated production of approximately 1.35 million tons.

The tomato *Solanum lycopersicum*, compared to its wild ancestor *Solanum pimpinellifolium*, had an increase in fruit size and has undergone many other morphological, phenological, and genetic changes throughout the domestication and evolution process (Peralta *et al.*, 2008).

The first variability source used by tomato genetic improvement programs was the intraspecific one, which provided great advances in developing cultivars. In turn, selection processes aimed at improving traits of interest to human needs, such as the yield-related ones, narrowed the tomato genetic base (Wang *et al.*, 2016) and caused cultivated tomato plants to lose many biological functions that confer resistance to damaging factors (Zhou *et al.*, 2015). Nevertheless, despite having disappeared from cultivated tomato plants, these biological functions are present in wild species accessions, thus motivating the search for variation sources in interspecific variability (Zeist *et al.*, 2021).

The cultivated tomato plant, in addition to its direct ancestor and the cerasiforme variety, has several wild species native to the Andean region of western South America, with which it shows greater or lesser compatibility in interspecific crosses: *Solanum cheesmaniae*, *Solanum galapagense*, *Solanum pennellii*, *Solanum habrochaites*, *Solanum huaylasense*, *Solanum corneliomulleri*, *Solanum peruvianum*, *Solanum chilense*, *Solanum arcanum*, *Solanum chmielewskii*, *Solanum neorickii*, *Solanum lycopersicoides*, *Solanum sitiens*, *Solanum juglandifolium*, and *Solanum ochranthum* (Peralta *et al.*, 2008; Bedinger *et al.*, 2011). Similar to the cultivated tomato, wild species are diploid, with their genes distributed in 12 chromosome pairs (2n=24) (Anderson *et al.*, 2010).

Currently, the vegetable germplasm bank at Midwest State University and Londrina State University have accessions of some wild tomato species. These accessions are currently being used to introduce genes that confer tolerance and/or resistance to cultivated tomato plants against arthropod pests, such as *Ralstonia solanacearum*, low temperatures, and that improve photosynthetic efficiency. Nevertheless, knowledge of the genetic diversity of these materials is crucial for breeders to exploit their genetic variability for various other traits. In general, in-depth diversity studies are essential to define the most efficient strategies for exploring interspecific resources (Zhou *et al.*, 2015; Wang *et al.*, 2016).

Genetic diversity can be assessed using morphoagronomic traits or DNA markers (Vargas *et al.*, 2015; Figueiredo *et al.*, 2016; Wang *et al.*, 2016). However, morphoagronomic characteristics are the most economical and simplest way to investigate diversity (Zhou *et al.*, 2015), yet they show good efficiency when suitable characters are used to assess genetic divergence.

Assessing genetic divergence based on the variability of physiological traits represents an important alternative, despite being rarely used (Sun *et al.*, 2015; Vasanthi *et al.*, 2015). These characteristics have advantages, as they make it possible to analyze diversity based on attributes that provide information that allows the identification of genotypes that may achieve higher yields under certain soil and climate conditions (Vasanthi *et al.*, 2015).

Considering the above information, this work aimed to analyze the genetic divergence among wild tomato species and interspecific F_1 hybrids through morphoagronomic and physiological traits.

MATERIAL AND METHODS

The experiment was carried out in a greenhouse at the Vegetable Research Center of the Department of Agronomy of the Midwest State University, UNICENTRO, located in the municipality of Guarapuava-PR (25°38'S, 51°48'W, 1100 meters altitude).

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'), the commercial cultivar Redenção (*S. lycopersicum* line suitable for processing) and the interspecific hybrids F_1 ('Redenção' x 'AF 26970'), F_1 ('Redençao' x 'LA-1401'), F_1 ('Redenção' x 'AF 19684'), F_1 ('Redenção' x 'PI-127826'), F_1 ('Redenção' x 'PI-134417'), and F_1 ('Redenção' x 'LA-716') were characterized. The genotypes were evaluated in a randomized block design, with three replications and each plot consisting of eight plants.

The genotypes were sown in 200 cells trays of expanded polystyrene (Isopor®), containing commercial substrate based on biostabilized pine bark. Seedlings were transplanted with 4 to 5 expanded leaves in 8-dm^3 pots containing sieved soil and cured bovine manure at 3:2 proportion. Irrigation was carried out as needed by the plants using microdrippers. The plants were staked using vertical strings. Phytosanitary control was carried out with preventive spraying of commercial products according to technical recommendations, using thiamethoxam (Actara®) and azoxystrobin + difenoconazole (Amistar Top®).

Twenty-nine morphoagronomic traits (Table 1) were evaluated during full flowering (flower-related traits) and setting periods (root and flower-related traits), development (plant-related traits), and fruit maturation (fruit-related traits). The characteristics root dry mass (RDM), stem dry mass (SDM), leaf dry mass (LDM), and fruit dry mass (FDM) (1, 5, 18, and 29) were assessed by collecting two plants per plot and separating the plant fractions related to each trait. Soon after collection, the roots were washed in running water. Then, the different parts of the plants were placed in an oven with forced air circulation at 65°C until constant weight. Following that, the mass was weighed on a 0.001 g precision scale. Before the leaves were placed in the greenhouse, leaf area (LA) (17) was obtained using the bench-top leaf area meter (cm) (Area Meter) LI-COR®, model LI 3100C.

The main stem diameter (MSD), leaf length (LL), leaf width (LW), central leaflet length (CLL), central leaflet width (CLW), secondary leaflet number (2°LN), secondary leaflet width

(2°LW), tertiary leaflet length (3°LL), and tertiary leaflet width (3°LW) (2, 7, 8, 9, 10, 12, 13, 15, and 16) were assessed using a digital caliper (mm) or measuring tape (cm). Lateral stem number (LSN), node number (NN), leaf number (LN), secondary leaflet number (2°LN), tertiary leaflet number (3°LN), and fruit number (FN) (3, 4, 6, 11, 14, and 23) were counted directly on the plants. To evaluate petal number (PN), sepal number (SN), anther number (AN), and stigma length (SL) (19 to 22), the flowers were collected from the 2nd to the 7th bunches, placed in plastic trays duly identified and sent to the Laboratory of Plant Physiology/Horticulture. There, using sharp tweezers, the flowers were fractionated into petals, sepals, anthers, and stigma, and then the PN, SN, and AN were counted, and CE was measured with a digital caliper (mm).

To evaluate fruit number (FN), horizontal diameter (FHD), vertical diameter (FVD), locus number (LN), and number of seeds per fruit (NSF) (24 to 28), the fruits of a plant per plot were collected weekly, placed in properly identified plastic trays, and sent to the Plant Physiology/Horticulture laboratory, where the NF was counted, and the FHD and FVD were measured with a digital caliper (mm). The fruits were cut horizontally to obtain the LN. Then, the seeds were separated from the pulp, and the NSF was counted.

For the physiological traits (Table 2), net photosynthesis (*A*), internal CO_2 concentration (*Ci*), transpiration (*E*), water use efficiency (*WUE*), and carboxylation efficiency of Rubisco (CER) (30 to 34) (all related to gas exchange) were measured using a portable photosynthesis measurement system (IRGA, Infrared Gas Analyzer, Li-cor, LI6400XT) when the plants were in full bloom, according to Zeist *et al.* (2017). Stomata density on the abaxial face (SD) (35), related to photosynthetic morphology, was obtained when the plants were in full bloom by analyzing the abaxial faces of the leaflets in a scanning electron microscope (Tescan® Vega3) with an attached camera.

The data obtained from the morphoagronomic and physiological traits were subjected to analysis of variance according to a randomized block design, through which the means and the matrix of variance and residual covariances were obtained. Means were grouped using the Scott-Knott test at 5% probability. However, traits whose genotype effect was not significant ($p<0.05$) were eliminated. Thus, only the traits 1 to 10, 12, 13, 15 to 18, 22 to 26, and 28 to 35 remained (Tables 1 and 2). In addition, 2°LN, 3°LN, PN, SN, AN, and LN (11, 14, 19, 20, 21, and 27) did not present residual variance. Nevertheless, they were maintained and, together with the means of the traits that had a significant effect, were subjected to principal component analysis (PCA). Two principal component analyses were carried out, one for the morphoagronomic traits (Table 1) and the other for the physiological traits (Table 2), arranging species and interspecific hybrids in the plane (x,y), which was formed by the first two principal components, where the PCA was used for the correlation matrix.

Of the traits 1 to 10, 12, 13, 15 to 18, 22 to 26, and 28 to 35, nine were selected based on the diagnosis of multicollinearity to study genetic divergence: LSN, LW, CLW, CLL, SL, FHD, FVD, NSF, FDM, *A*, *E*, *WUE*, and SD.

The genetic divergence among the accessions was assessed based on the evaluated traits. To estimate the dissimilarity between treatments, Mahalanobis' generalized distance ($D^2_{ii'}$) was used, standardizing the data by the standard deviation (Z value). Then, the genetic divergence among the genotypes (based on morphoagronomic and physiological traits) was determined by cluster analysis using Tocher's optimization method. The diversity among genotypes was also presented in a scatter plot based on the scores of the first two canonical variables, as described by Cruz *et al.* (2012). Genetic divergence analyses were performed using the computer program GENES (Cruz, 2013).

RESULTS AND DISCUSSION

For the genetic divergence study, the morphoagronomic and physiological traits were selected based on their significance for the effect of genotypes in the analysis of variance ($p<0.05$) and a weak multicollinearity value between the selected response variables. According to Figueiredo *et al.* (2016), the phenotypic traits used to study genetic divergence must not be redundant (correlated with each other) and invariant (absence of variation between genotypes); they must preserve the fundamental structure of the biological system being studied.

The average Mahalanobis' generalized distance between the tomato genotypes was 796, with a range of 53 [between F_1 ('Redenção' x 'PI-134417') and F_1 ('Redenção' x 'PI-127826')] to 2,941 (between 'LA-1401' and 'Redenção'). When analyzing only the combinations between 'Redenção', 'AF 26970', 'LA-1401', 'AF 19684', 'PI-127826', 'PI-134417', and 'LA-716', the average distance of Mahalanobis was even higher (1,266) (Table 3), indicating the presence of wide genetic variability among wild accessions or between them and the cultivated tomato *S. lycopersicum*.

The interspecific combinations of the most divergent pairs of genotypes were between the cultivar Redenção and the wild accessions, whose Mahalanobis distances were 1,776, 2,241, 2,319, 2,617, 2,843, and 2,941 for the combinations with 'AF 26970', 'AF 19684', 'PI-134417', 'LA-716', 'PI-127826', and 'LA-1401', respectively (Table 3). These values contributed to the isolation of 'Redenção' from the other genotypes by Tocher's optimization method, reflecting the considerable genetic dissimilarity of *S. lycopersicum* with its wild parents (Figure 1).

Although *S. lycopersicum* comes from the same region as the other tomato species, it was domesticated outside the center of origin, far from interspecific variability, and was selected and improved from a few individuals and with a very restricted number of alleles (Bergougnoux, 2014; Zeist *et al.*, 2021). The high genetic dissimilarity between the cultivar Redenção and the wild accessions, based on morphoagronomic and physiological traits, may be due to the various morphological changes the cultivated tomato has undergone throughout the domestication and evolution processes. During domestication and improvement, a set of characteristics began to distinguish the improved plant from the wild ancestors (Bai & Lindhout, 2007).

It is necessary to emphasize that the existence of divergence between *S. lycopersicum* and wild accessions based on quantitative morphoagronomic and physiological traits is of great importance, considering that the characteristics evaluated, in addition to morphological differences, also showed the intensity of phenotypic expressions. Remarkable phenotypic differences between the parents and the cultivated tomato, evaluated under the same conditions, demonstrate that wild accessions show behaviors that are not present or not expressed in the cultivated tomato. Thus, depending on the characteristic that is only present or more expressed in the wild species, it may be useful to be incorporated into the cultivated tomato in genetic improvement programs.

In addition to having a high Mahalanobis distance with wild accessions, 'Redenção' showed greater dissimilarity with the progenies than the respective male parents. While 'Redenção' had an average distance of 1,613 and a range of 1,017 to 2,086 with the interspecific hybrids, the wild accessions had an average distance of 344 and a range of 102 to 700 in relation to the respective hybrids (Table 3). This result demonstrates that when interspecific crosses are carried out between the cultivated tomato and wild species, several backcross cycles with the recurrent parent will be necessary to recover the characteristics present in the plant of commercial interest.

In general, in traditional genetic improvement, when a wild accession is used as a donor parent, it takes between 5 and 10 years to carry out the stages of interspecific crossing, backcrossing with the recurrent parent, and selections. An example is the commercial cultivar Redenção, which was developed by Ferraz *et al.* (2003) through six selection cycles from the cross between the cultivar Viradouro (*S. lycopersicum* line suitable for processing) and the accession 'LA 3473' (carrier of the *TY-1* gene that confers tolerance to the tomato yellow leaf curl virus, obtained from crossing *S. chilense* and *S. lycopersicum* with subsequent backcrossing to *S. lycopersicum*).

The wild accession and the interspecific hybrid that showed the smallest Mahalanobis distances with 'Redenção' were 'AF 26970' (*S. pimpinellifolium*) and F$_1$ ('Redenção' x 'AF 26970'), respectively (Table 3). It was verified that of the 13 quantitative traits used for the divergence study, in approximately half of them, there was a significant difference ($p<0.05$) between 'Redenção' and 'AF 26970' and/or F$_1$ ('Redenção' x 'AF 26970 '). These results are possibly due to the fact that

Table 1. Morphoagronomic traits analyzed in the cultivar Redenção (female parent), wild accessions (male parents), and the respective interspecific hybrids of tomato. Guarapuava, UNICENTRO, 2016.

Trait's Nº	Morphoagronomic traits	Evaluation stage
	Root	
1	Root dry mass (RDM)	Fruit set
	Plant	
2	Main stem diameter (MSD)	Fruit development
3	Lateral stem number (LSN)	Fruit development
4	Node number (NN)	Fruit development
5	Stem dry mass (SDM)	Fruit development
	Leaves	
6	Leaf number (LN)	Fruit set
7	Leaf width (LW)	Fruit set
8	Leaf length (LL)	Fruit set
9	Central leaflet length (CLL)	Fruit set
10	Central leaflet width (CLW)	Fruit set
11	Secondary leaflet number (2^0LN)	Fruit set
12	Secondary leaflet length (2^0LN)	Fruit set
13	Secondary leaflet width (2^0LW)	Fruit set
14	Tertiary leaflet number (3^0LN)	Fruit set
15	Tertiary leaflet length (3^0LL)	Fruit set
16	Tertiary leaflet width (3^0LW)	Fruit set
17	Leaf area (LA)	Fruit set
18	Leaf dry mass (LDM)	Fruit set
	Flowers	
19	Petal number (PN)	Full bloom
20	Sepal number (SN)	Full bloom
21	Anther number (AN)	Full bloom
22	Stigma length (SL)	Full bloom
23	Flower number per bunch (FNB)	Full bloom
	Fruits	
24	Fruit number (FN)	Fruit maturation
25	Fruit horizontal diameter (FHD)	Fruit maturation
26	Fruit vertical diameter (FVD)	Fruit maturation
27	Locus number (LN)	Fruit maturation
28	Seed number per fruit (NSF)	Fruit maturation
29	Fruit dry mass (FDM)	Fruit maturation

Solanum pimpinellifolium is the main ancestor of *S. lycopersicum*, with both species belonging to the Licopersicon group (Peralta *et al*., 2008).

Although the species *S. galapagense* accession 'LA-1401' is also phylogenetically classified as belonging to the same group as *S. lycopersicum* and *S. pimpinellifolium*, based on the morphoagronomic and physiological characters used for the dissimilarity analysis, the Mahalanobis distance between 'LA-1401' and 'Redenção' was higher. In turn, there was less dissimilarity between the accessions 'LA-1401' and 'AF 26970' (Table 3). This fact can be explained by Darwin *et al*. (2003). The authors reported that although *S. galapagense* is autogamous and produces reddish fruits like the other species of Licopersicon (*S. lycopersicum*, *S. pimpinellifolium*, and *S. cheesmaniae*), it presents great variation when compared to other species.

When observing the average Mahalanobis distance of each genotype in relation to the others, the highest averages of dissimilarity were found for 'Redenção' (2,036) and the accession 'PI-127826' (1,250), while for the other genotypes, the dissimilarities ranged from 461 to 897 (Table 3). It is possible to consider that these distances allowed the formation of three groups by Tocher's optimization method, with group I formed by 'AF 26970', 'LA-1401', 'AF 19684', 'PI-134417', 'LA- 716', F1 ('Redenção x AF 26970'), F_1 ('Redenção x LA-1401'), F_1 ('Redenção' x 'AF 19684'), F_1 ('Redenção' x 'PI-127826'), F_1 ('Redenção' x 'PI-134417'), and F_1 ('Redenção' x 'LA-716'). Group II was formed by 'PI-127826' and group III by 'Redenção' (Figure 1).

Although 'PI-127826' from *S. habrochaites* var. *hirsutum* was allocated as the only member of a group, when observing the arrangement in the graph concerning the scores of the first two canonical variables (in which individuals who are nearer are less dissimilar than those who are more distanced). This group was allocated close to the accession 'PI-134417' from the var. *glabratum* and to the interspecific hybrids F_1 ('Redenção' x 'PI-134417') and F_1 (Redenção' x 'PI-127826') (Figure 1). Some characteristics of the accession 'PI-127826', with emphasis

Table 2. Physiological traits analyzed in the cultivar Redenção (female parent), wild accessions (male parents), and the respective interspecific hybrids of tomato. Guarapuava, UNICENTRO, 2016.

Trait's Nº	Physiological traits	Evaluation stage
	Gas exchange	
30	Net photosynthesis (*A*)	Full bloom
31	Internal CO_2 concentration (*Ci*)	Full bloom
32	Transpiration rate (*E*)	Full bloom
33	Water use efficiency (*WUE*)	Full bloom
34	Carboxylation efficiency of Rubisco (CER)	Full bloom
	Photosynthetic morphology	
35	Stomatal density on the abaxial face (DE)	Fruit development

Table 3. Mahalanobis' generalized distance between cultivar Redenção (female parent), wild accessions (male parents), and the respective interspecific hybrids of tomato based on data of morphoagronomic and physiological traits. Guarapuava, UNICENTRO, 2016.

Genotype	Red.	AF 26970	LA 1401	AF 19684	PI 127826	PI 134417	LA 716	Red. X AF 26970	Red. X LA-1401	Red. X AF 19684	Red. X PI-127826	Red. X PI-134417
AF 26970	1.776											
La-1401	2.941	339										
AF 19684	2.242	395	478									
PI-127826	2.844	1.315	2.019	1.311								
PI-134417	2.320	593	947	404	283							
LA-716	2.618	607	369	131	1.893	765						
Red. X AF 26970	1.018	368	1.097	522	1.027	530	886					
Red. X LA-1401	1.591	355	700	320	661	199	611	203				
Red. X AF 19684	1.767	489	419	207	1.523	550	248	606	345			
Red. X PI-127826	1.514	620	998	396	527	147	709	345	118	359		
Red. X PI-134417	1.708	653	1.064	537	379	103	882	406	156	455	53	
Red. X LA-716	2.086	544	513	258	1.221	459	219	520	278	264	344	428
Mean	2.036	671	897	600	1.250	608	828	627	461	602	569	594

Red: *S. lycopersicum* commercial cultivar Redenção; AF 26970: *S. pimpinellifolium* accession 'AF 26970'; LA-1401: *S. galapagense* accession 'LA-1401'; AF 19684: *S. peruvianum* accession 'AF-19684'; PI-127826: *S. chilense* accession 'LA-1967'; PI-127826: *S. habrochaites* var. *hirsutum* accession 'PI-127826'; PI-134417: *S. habrochaites* var. *glabratum* accession 'PI-134417'; LA-716: *S. pennellii* accession 'LA-716'.

on LSN, *A*, and *E* and the lower FDM, may have contributed to the genotype being the only individual in group II.

The commercial cultivar Redenção presented high values for LW, FHD, FVD, and LDM and the smallest LSN. These are the traits related to the morphoagronomic changes that *S. lycopersicum* suffered throughout its evolution and that contributed the most to distance the cultivated plant from wild accessions and interspecific hybrids and form a group with only one individual using Tocher's optimization method (Figure 1).

In general, regarding the genotypes that formed group II, even with significant differences ($p<0.05$) for the traits that constituted the genetic divergence study, there were low Mahalanobis distances between the genotype pairs in this group (Table 3). These genotypes showed low dispersion when observing the arrangement in the graph in relation to the scores of the first two canonical variables (Figure 1).

According to Benitez *et al*. (2011), several other studies with varied species estimated genetic divergence through multivariate techniques, such as Mahalanobis' generalized distance, Tocher's optimization clustering method, and the graphic dispersion of the canonical variables. However, considering that 35 traits were described and that seven of them did not present residual variance and another fifteen were not used for the study of genetic divergence based on the diagnosis of multicollinearity, principal component analysis (PCA) was applied to observe divergences yet undisclosed, in the same way as performed by Vargas *et al*. (2015).

Regarding the morphoagronomic traits, the PCA revealed that the plant- and fruit-related traits were the main ones responsible for the highest variance (76.70%), followed by the leaf-related characteristics (9.11%), which were correlated with components 1 and 2, respectively. According to these two components, three clusters were formed. Group I was composed of the interspecific hybrids F_1 ('Redenção' x 'PI-127826'), F_1 ('Redenção' x 'PI-134417'), and F_1 (Redenção' x 'LA-716'). Group III comprised the accessions 'AF 26970', 'LA-1401', 'AF 19684', 'PI-127826', 'PI-134417', and 'LA-716', and the hybrid F_1 ('Redenção' x 'AF 19684'). Group II was formed by the cultivar Redenção and the interspecific hybrids F_1 ('Redenção'x

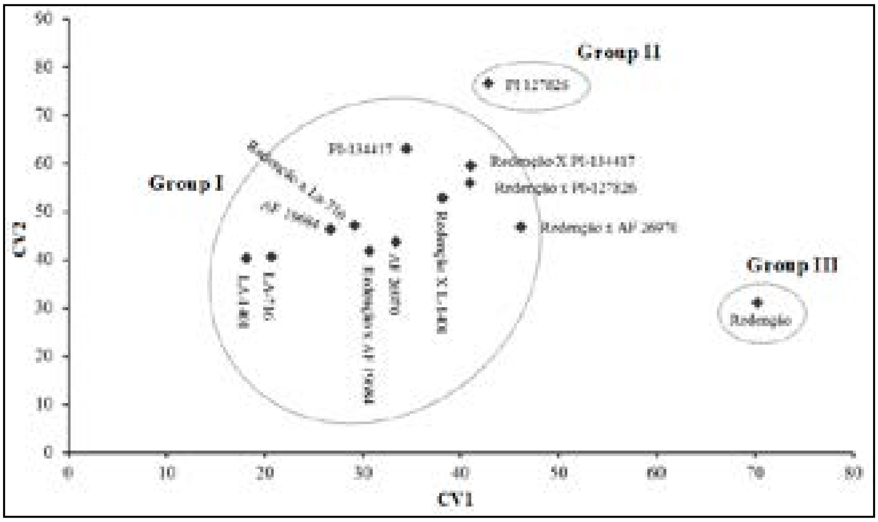

Figure 1. Graphic dispersion of the cultivar Redenção (female parent), wild accessions (male parents), and the respective interspecific hybrids of tomato in relation to the scores of the first two canonical variables (CV1 and CV2) and grouping with Tocher's method based on the Mahalanobis' generalized distance (D2) from morphoagronomic and physiological traits. Guarapuava, UNICENTRO, 2016.

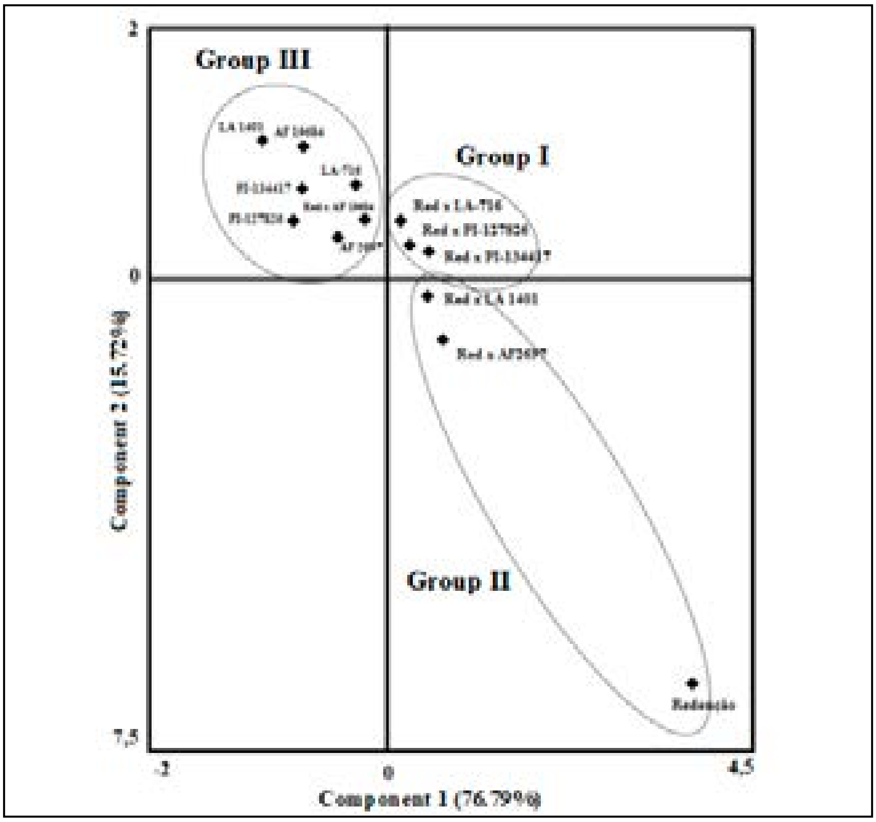

Figure 2. Result of the principal component analysis for the cultivar Redenção (female parent), wild accessions (male parents), and the respective interspecific tomato hybrids based on morphoagronomic traits. Guarapuava, UNICENTRO, 2016.

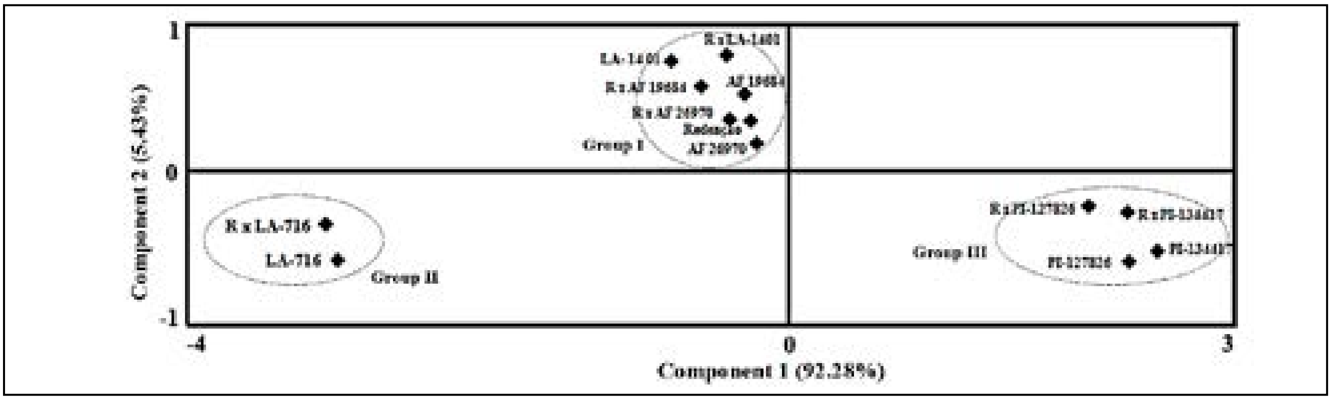

Figure 3. Result of principal component analysis for cultivar Redenção (female parent), wild accessions (male parents), and the respective interspecific hybrids of tomato based on data on physiological traits. Guarapuava, UNICENTRO, 2016.

'AF 26970') and F_1 ('Redenção' x 'LA-1401') (Figure 2).

It is worth noting that in the divergence study using Mahalanobis' generalized distance, Tocher's optimization clustering method, and the graphic dispersion of the canonical variables, only nine of the 29 morphoagronomic characteristics and four of the six physiological traits were used. In contrast, using PCA for the correlation matrix, all traits described in Tables 1 and 2 were used. In addition, two matrices were obtained, allowing the grouping of genotypes according to morphoagronomic or physiological specificities (Figures 2 and 3).

For the physiological traits, PCA revealed that SD and *A* were the main ones responsible for the highest variance (92.8%) and correlated with component 1. According to components 1 and 2, three clusters were formed. Group I comprised the cultivar Redenção, the accessions 'AF 26970', 'LA-1401', and 'AF 19684' and the interspecific hybrids F_1 ('Redenção' x 'AF 26970'), F_1 ('Redenção' x 'LA-1401 '), and F_1 ('Redenção' x 'AF 19684') for presenting similar results for all the characteristics evaluated. Group II was formed by accession 'LA-716' and the hybrid F_1 ('Redenção' x 'LA-716'), as they have lower *A* and SD, in addition to high *WUE* and *Ci* and low *E* and CER. Group III was composed of the accessions 'PI-127826' and 'PI-134417' and the hybrids F_1 ('Redenção' x 'PI-127826') and F_1 ('Redenção' x 'PI-134417'), which were highlighted for *A* and SD, in addition to higher *E* and lower *WUE* (Figure 3).

Based on the physiological traits, the accessions 'PI-127826' and 'PI-134417' from the species *S. habrochaites* and the respective hybrids with the cultivar Redenção presented higher *A* and SD and were clustered into a single group. Thus, it is very likely that *S. habrochaites* is an interesting alternative allele donor for genetic improvement programs that wish to make advances in obtaining genotypes with improved photosynthetic characteristics. Furthermore, some works have already reported that *S. habrochaites*, which is adapted to a wide range of latitudinal distributions, presents physiological characteristics that allow development, even when conditions during the day or throughout the cycle are unfavorable for the development of other tomato species (Venema *et al*., 2008; Poudyala *et al*., 2015).

Unlike accessions of *S. habrohaites*, 'LA-716' from *S. pennellii* and the respective hybrid with 'Redenção' showed low *A* and SD, contributing to the isolation of the genotypes as single members of a group. However, it should be noted that 'LA-716' and F_1 ('Redenção' x 'LA-716') also showed high *WUE* and low *E*, thus demonstrating that *S. pennellii* is an interesting alternative for allele introgression for tolerance to water deficit into *S. lycopersicum*. Furthermore, it is commonly reported that *S. pennellii* has the east of the Peruvian Andes to the west of the Pacific Coast as its natural habitat, which are hot and dry regions (Dariva *et al*., 2020), thus providing superior performance in relation to water use efficiency when compared to other tomato species.

Unlike the results obtained using Tocher's optimization clustering method, 'Redenção' was allocated to clusters containing other genotypes when PCA was applied to morphoagronomic and/or physiological traits. On the other hand, it is important to emphasize that, regarding the physiological characteristics, they did not quantify the evolutionary morphological changes of *S. lycopersicum* compared to its wild parents. In relation to morphoagronomic characters, despite 'Redenção' having integrated the same group of the interspecific hybrids F_1 ('Redenção' x 'AF 26970') and F_1 ('Redenção' x 'LA-1401'), it was the one that showed the greatest dispersion in relation to all genotypes in the matrix correlation.

The greater proximity of 'Redenção' with the hybrids F_1 ('Redenção' x 'AF 26970') and F_1 ('Redenção' x 'LA-1401') in the PCA regarding morphoagronomic traits possibly occurred because the interspecific hybrids were obtained from crosses of *S. lycopersicum* with two species that constitute the same phylogenetic group. In contrast, the crosses of 'Redenção' with species belonging to other phylogenetic groups generated hybrids closer to the wild accessions. This aspect can be observed even more clearly in the PCA of the physiological characters (Figure 3), in which the interspecific hybrids of 'Redenção' with the accessions 'PI-127826', 'PI-134417', and 'LA-716', belonging to phylogenetically distinct groups of *S. lycopersicum*, were grouped with the wild parents.

Analyses based on morphoagronomic and physiological traits revealed the existence of high divergence between wild tomato accessions and interspecific hybrids. Of the tomato species evaluated, *S. lycopersicum* has the greatest genetic dissimilarity, and the interspecific crosses of *S. lycopersicum* with wild accessions generate offspring with morphoagronomic and physiological traits closer to those of the wild parents. This highlights the need for successive cycles of backcrosses and selections after interspecific hybridization in tomato so that the traits of the recurrent parent are recovered, and traits of interest to the wild donor parent are introduced.

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