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Original scientific paper

Antioxidative response of tomato genotypes to late blight infection

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Abstract: Wild species are widely used as potential sources of resistance of tomato to late blight (LB) (causal agent *Phytophthora infestans*). The biochemical response of wild and cultivated tomato genotypes with different levels of resistance to *P. infestans* was assessed through the total phenolic and flavonoid content and antioxidative capacity. In total, six genotypes were included in the research – three cultivated tomato varieties and three wild species. The wild genotypes *Solanum pimpinellifolium* S 220 and *Solanum habrochaites* had a significantly lower infection rate compared to the other tested genotypes. After disease assessment on the leaves, biochemical analyses were performed. Grouping of the wild accessions according to principal component analysis (PCA) analysis indicated similar reaction to LB infection. Furthermore, late blight trait is closer to cultivated genotypes. Although the phenolics and flavonoids have high importance in the reaction of tomato plants to late blight infection, these traits are not closely related to wild species and the disease. According to this study, the antioxidative tests that indicate a response of wild species to late blight infection are total antioxidant activity (TAA), ferric-reducing antioxidant power (FRAP) and radical cation scavenging activity (ABTS).

Keywords: phenolics; flavonoids; *Solanum pimpinellifolium*; antioxidative tests.

INTRODUCTION

Phytophthora infestans (Mont.) de Bary, an oomycete causing late blight, is the primary agent of tomato yield losses,[1–3] and it can cause severe crop damage. Additionally, in locations where sexual reproduction occurs, oospores of the genus *Phytophthora* can survive for months or years in the absence of living hosts.[4] The disease is favoured by cool temperatures and humid conditions.[5,6] This pathogen can spread in a very short period and the entire plant may collapse

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in 5 to 10 days.[7] Chemical treatments can be ineffective under environmental conditions favourable for disease development.[8] Identification of tomato genotypes resistant to late blight is the most efficient manner of disease control.

Plants have developed effective defence mechanisms against pathogenic microorganisms, mostly structural and chemical barriers, in order to prevent pathogen progression.[9] The oxidative burst or rapid and transient production of a large amount of reactive oxygen species (ROS) are the fastest and the earliest active defence responses to a microbial infection known in plants.[10] ROS play an important role in plant response to pathogen attack, but they are also extremely reactive. To overcome ROS toxicity, plants produce enzymatic and non-enzymatic antioxidants that scavenge oxygen species.[11]

Increased levels of ROS, antioxidative activity and content of phenolics indicate an activated plant defence system as a response against pathogens.[12] Defence systems are involved in ROS elimination or prevention of their production. Different phenols are present in the plant before the pathogen infection, providing plants with a certain degree of resistance.[13] On the other hand, phenols are also involved in the first line of defence by their accumulation at the infection site and induction of a hypersensitivity reaction.[14]

Flavonoids also play an important role in plant resistance to pathogenic bacteria and fungi.[13] These bioactive compounds have been related to the mechanisms of cross-linking and inhibition of pathogen enzymes and the formation of crystalline structures as a physical barrier against pathogen attacks.[15] These compounds quench ROS, which are generated both by the pathogens and the plant as a result of an infection.[16]

The antioxidative activity of plants extract is the capability to scavenge free radicals in order to avoid their harmful effects.[14] Different antioxidative tests represent the level of non-enzymatic antioxidative properties of plant species. The antioxidative capacity of infected leaves could show the reaction of tomato genotypes to *P. infestans*.

The aim of this study was to screen the intensity of ROS formation and non-enzymatic antioxidative activity in leaves of different tomato genotypes (wild and cultivated) against the oomycete *P. infestans*.

EXPERIMENTAL

Field trial. A field trial was conducted at the experimental field of the Institute of Field and Vegetable Crops, Vegetable Crops Department at Rimski Šančevi, Vojvodina, Serbia, in 2014. The trial was designed in three replicates with ten plants in each replicate. A list of the genotypes (from the collection of Vegetable Crops Department) included in the trial is given in Table I. Sowing for seedlings production in a glass house was performed on 3rd of April and the plants were transplanted on 27th of May into the open field. The between-row spacing was 140 cm, and within-row spacing was 50 cm. There was no fungicide application and *Phytophthora infestans* natural infection was evaluated.

The first evaluation of the early blight on leaves was performed on 4th of August, the second on 18th of August and the last assessment was realized on 8th of September. Per each sampling date, ten fully expanded leaves per replicate were taken from the top of different plants and the intensity of the late blight infection was assessed. Evaluation of the disease intensity on leaves was performed according to the EPPO modified scale: 0 - without infection, 1 – less than 5 % of leaf affected, 2 – spots covering 5–10 %, 3 – spots covering 10––25 %, 4 – spots covering 25–50 %, 5 – spots covering more than 50 % of the leaf.[17]

TABLE I. List of tested tomato genotypes; plant growth type according to UPOV descriptors: 1 –determinate, 2 – indeterminate

Collection number	Genotype	Origin	Plant growth type	Time to maturity, days
S 340	Rutgers	USA	2	130
S 468	AT-70/11	Denmark	1	120
S 32	Bull's heart[a]	Serbia	2	140
S 120	*Solanum pimpinellifolium*	–	2	110
S 220	*Solanum pimpinellifolium*	–	2	112
S 214	*Solanum habrochaites*	–	2	130

[a]Local population

Analysis of biochemical parameters. After disease assessment, the biochemical parameters were determined in the Laboratory for Biochemistry, Faculty of Agriculture, Novi Sad, Serbia, during 2015. The measurements were performed per each genotype and sampling date in triplicate. The average values of each repetition were statistically analysed. Plant material (200 mg) was extracted with 70 % aqueous acetone solution (50 ml) by sonication for 20 min in an ultrasonic bath at ambient temperature. The extracts were rapidly vacuum-filtered through a sintered glass funnel and kept refrigerated until assayed.

The total phenolic content was determined using the Folin–Ciocalteu colorimetric method.[18] The results are expressed in milligrams of quercetin equivalents per 1 g of dry leaf weight (mg GA equivalents (g DW)$^{-1}$).

The total flavonoid content was determined spectrophotometrically.[19] The amount of flavonoids was calculated as a quercetin equivalent (*QE*) from the calibration curve of quercetin standard solutions.

Measurement of antioxidative activity. Scavenging of free radicals was tested in a 2,2-diphenyl-1-picrylhydrazyl (DPPH) acetone solution.[20] The scavenging efficiency of the added substance is indicated by the degree of decolouration of the solution. The ferric-reducing antioxidant power (*FRAP*) assay was performed according to the standard procedure.[21] The results are expressed as mg Trolox equivalents per g of leaf dry weight (mg TE (g DW)$^{-1}$). The 2,2′-azinobis-(3-ethylbenzothiazoline-6-sulfonic acid) (ABTS) assay was based on a method developed by Miller.[22] A methanolic solution of known Trolox concentrations was used for calibration and the results are expressed as mg Trolox equivalents per g of dry leaf weight (mg TE (g DW)$^{-1}$). The total antioxidant activity of the leaf extracts was evaluated by the phosphormolybdenum method.[23] The standard curve for total antioxidant activity was plotted using Trolox solution. A reducing power assay (total reduction capacity) was performed by the method of Saha *et al.*[19] Trolox was used as a standard. The superoxide free radical scavenging activity was performed by the NBT (Nitroblue tetrazolium) test.[23] The percent inhibition of the superoxide anion generated was calculated using the formula:

Scavenging activity, % = 100(1 – absorbance of sample/absorbance of control)

Statistical analysis. The obtained data were analysed using Statistica 13.2 (Dell Inc., USA). The values for leaf tomato infection were analysed by the nonparametric statistics Kruskal–Wallis test. The results for biochemical parameters were tested by analysis of variance followed by a comparison of means by the Bonferroni test ($P < 0.01$). Correlation coefficients were calculated according to Spearman. Principal component analysis (PCA) was used to identify the most significant traits. All data per genotype, sampling date and replication were used for the PCA with non-linear iterative partial least squares (NIPALS) algorithm and the components over eigenvalues 1 were interpreted.

RESULTS AND DISCUSSION

The first assessment of late blight on leaves was performed at the beginning of August. The average infection rate (medians) varied from 0–3. The infection rate was the lowest on the wild genotypes: *S. pimpinellifolium* S 120, *S. pimpinellifolium* S 220 and *S. habrochaites*, while the other examined genotypes had a significantly higher intensity of infection on the leaves (Fig. 1A). In the second assessment, the disease intensity varied from 0–2. On the wild species, a lower disease intensity was registered. However, only *S. habrochaites* showed lower susceptibility compared to all tested genotypes, except for the local population (Bull's heart, Fig. 1B).

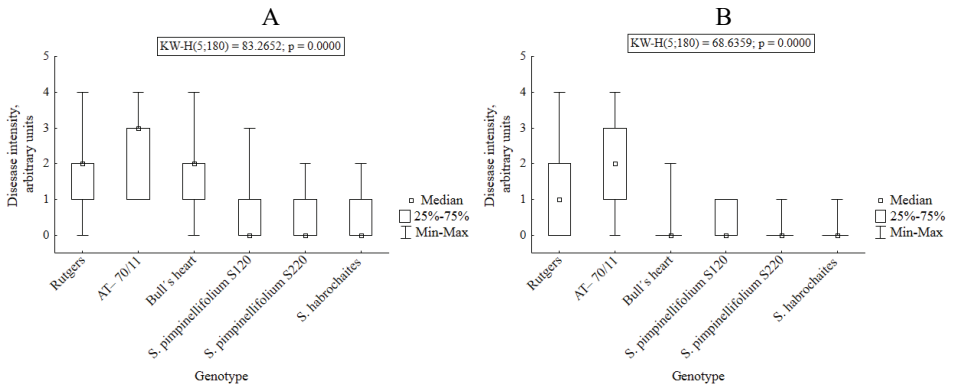

Fig. 1. The first (A) and the second (B) assessment of late blight intensity.

A similar situation was observed in the final assessment, but the infection rate was higher, which was expected (Fig. 2). Wild genotypes *S. pimpinellifolium* S 220 and *S. habrochaites* had a significantly lower infection rate compared to the other tested genotypes. The median values for the genotypes with higher susceptibility were from 3 to 4, which mean that the infection intensity varied from 25–50 %.

So far, genetic resources for resistance to late blight have been identified within the tomato wild species – in particular, *S. pimpinellifolium* and *S. habrochaites.*[24] However, the inconsistency between data in the literature about resist-

ance to *P. infestans* even in lines of *S. pimpinellifolium* and *S. habrochaites*, make it difficult for tomato breeders to use resistant germplasms.[25] The lines derived from *L. pimpinellifolium L3708 (syn. S. pimpinellifolium)* have stronger resistance than those derived from *L. hirsutum LA 1033-2 (syn. S. habrochaites*).[26] *S. pimpinellifolium* is more closely related and highly cross-compatible to the cultivated tomato.[27] Furthermore, recent late blight resistance research[28] (including *S. pimpinellifolium* and *S. habrochaites*) resulted in only one resistant line of *S. arcanum*. The findings in this study showed almost the same level of resistance for *S. pimpinellifolium* S 220 and *S. habrochaites* accessions.

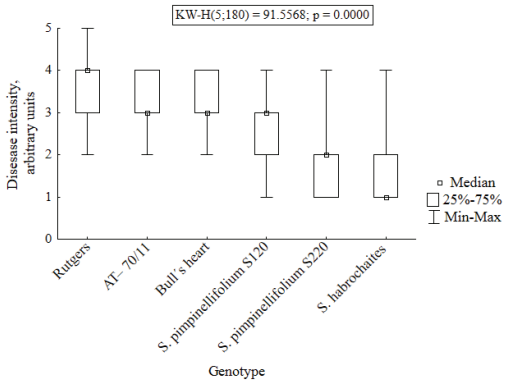

Fig. 2. The final assessment of late blight.

Differences between the intensity of late blight in tomato genotypes indicate that there could be variability in the biochemical response of these genotypes to late blight infection. The antioxidant activity of the plant was measured through several tests and the linkage between the level of infection and antioxidant activity is shown in Table II. According to ANOVA, genotype, sampling date and interaction of these two factors have a significant influence on all measured biochemical parameters in the leaves (Table II).

TABLE II. *F* values for the biochemical parameters in tomato leaves; *d.f.* – degree of freedom; all data are significant at 1 % level, $n = 3$; QE – quercetin; *DW* – dry weight; *TP*– total phenolic content; *TF* – total flavonoid content; *DPPH* – radical cation scavenging activity; *ABTS* – radical cation scavenging activity; *FRAP* – ferric-reducing antioxidant power; *NBT* test – Nitroblue tetrazolium test; *TRC* – total reduction capacity; *TAA* – total antioxidant activity

Parameter	*d.f.*	*TP*	*TF*	*DPPH*	*ABTS*	*FRAP*	Scavenging activity (NBT test), %	*TRC*	*TAA*
		mg QE (g DW)$^{-1}$		mg Trolox (g DW)$^{-1}$				mg Trolox (g DW)$^{-1}$	
Genotype (G)	5	1043.1	479.4	1593.2	516.0	648.2	658.4	476.9	161.8
Sampling date (S)	2	8405.9	12111.8	8340.8	3996.8	864.7	2294.5	27.7	630.4
G×S	10	291.3	170.3	625.9	638.8	1603.7	184.0	200.6	35.7

Generally, half of the measured biochemical parameters (*TP*, *TF*, *DPPH*, and *NBT*) had the highest values in the second sampling date, then in the first and in the third sampling date (Fig. 3). Wild species and local population of Bull's heart had the highest phenolic and flavonoid content in the second sampling date when the lowest level of infection was observed.

The Bull's heart population had the highest level of *TP*, *TF* and *DPPH*, although, when comparing its susceptibility to late blight, this genotype is placed between wild species and other cultivated genotypes tested in this trial.

Spearman coefficient for three sampling dates jointly showed that six out of eight biochemical parameters are in strong negative correlation with late blight infection (Table III).

However, the situation is different for the correlation for each sampling date separately. In the first two sampling dates, *DPPH*, *FRAP* and *TRC* are in significant positive correlation with late blight infection, while *TP* is in positive correlation with disease infection in the first sampling date (Table IV). This indicates that at the beginning of the infection, the plants defend themselves by increasing the antioxidative activity measured by selected assays. However, a strong negative correlation between disease intensity and biochemical parameters in the third sampling date implies that the disease progression throughout the vegetation period leads to a decrease in the scavenging activity.

According to the obtained results, *DPPH* positively correlates with all phenolic compounds. Similar results were obtained when the reaction of tomato fruits against early blight was tested.[29]

ABTS and *FRAP* tests are in correlation with the content of flavonoids in the samples. Although flavonoids are a subclass of phenols, these tests are not in the correlation with total phenols (Table III). Flavonoids have an important role in many biological processes, particularly in plant response to biotic and abiotic stress. The antioxidative activity of flavonoids, as widespread polyphenolic secondary metabolites, depends on their structure.[30,31] The hypersensitive reaction in the site of infection can also be induced by accumulation of flavonoid compounds, which is the earliest defence mechanism in infected plants.[14]

A non-enzymatic defence system in plants beside phenolics includes other hydro and liposoluble compounds as strong scavengers of free radicals. Vitamin C, vitamin E, plant polyphenols, carotenoids and glutathione are a few examples of non-enzymatic antioxidants.[32,33] According to correlation coefficient results (Tables III and IV), the antioxidative capacity of the samples depends not only on the total phenolic content but also on other bioactive components in the essay.

Synthesis of phenolics in the cell wall, besides rapid cell collapse and death, accumulation of antimicrobial compounds and the synthesis of hydrolytic enzymes, is one of the early responses of the plant defence system.[34] Phenolic compounds play an important role in the defence of potato and tomato plants against *P. infestans* by inhibition of pathogen hyphal penetration.[7,35]

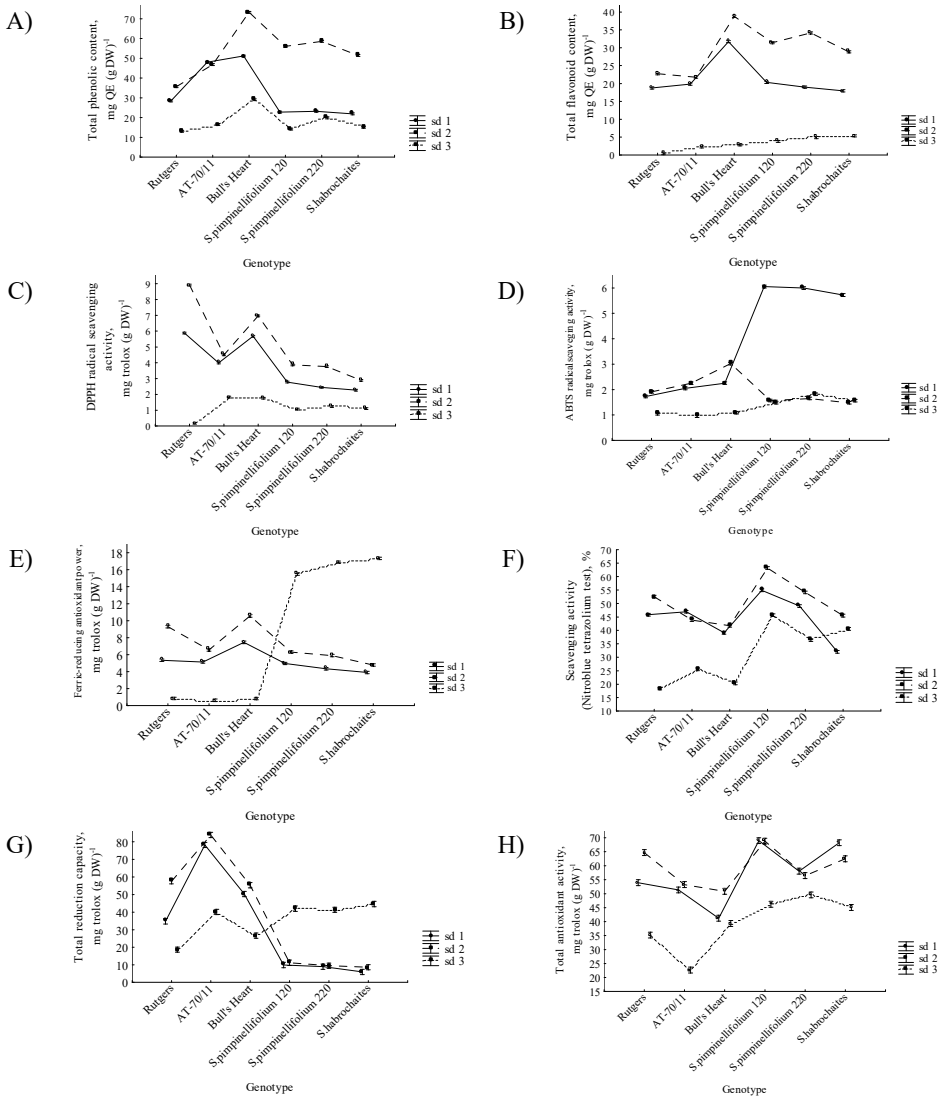

Fig. 3. A) Total polyphenol content in tomato leaves; B) total flavonoid content in tomato leaves; antioxidant activity in tomato leaves measured by: C) radical cation scavenging activity (DPPH test); D) radical cation scavenging activity (*ABTS*); E) ferric-reducing antioxidant power (*FRAP*); F) Nitroblue tetrazolium test (NBT test); G) total reduction capacity (*TRC*); H) total antioxidant activity (*TAA*). Means of three independent experiments with three replicates; the bars represent standard errors. *sd* 1 – sampling date 1; *sd*-2 – sampling date 2; *sd*-3 – sampling date 3.

Different authors observed a direct link between the availability of phenolics and the strength of the cell walls of potato tubers.[36,37] Although under stress con-

ditions, the biosynthesis of phenolic compounds that are precursors of lignin intensifies, and lignin provides a physical barrier against initial pathogen colonization.[38,39] The accumulation of lignin to a higher level in resistant potato cultivars does not necessarily mean that these compounds are involved in disease resistance.[35] The oxidative burst triggered by the infection that results in an increase of total phenolic content sometimes is not strong enough to hinder pathogen penetration into the host tissue.[10,40] This can be the explanation for the highest level of *TP* and *TF* in local population Bull's heart, although the disease infection was much higher than in wild species.

TABLE III. The correlation coefficient between biochemical parameters and leaf infection for three sampling dates jointly; QE – quercetin; DW – dry weight; *DI* – disease intensity; *TP* – total phenolic content; *TF* – total flavonoid content; *DPPH* – radical cation scavenging activity; *ABTS* – radical cation scavenging activity; *FRAP* – ferric-reducing antioxidant power; NBT test – Nitroblue tetrazolium test; *TRC* – total reduction capacity; *TAA* – total antioxidant activity; ** – significant at 1 % level

Variable	*TP*	*TF*	*DPPH*	*ABTS*	*FRAP*	Scavenging activity (NBT test), %	*TRC*	*TAA*
	mg QE (g DW)$^{-1}$		mg Trolox (g DW)$^{-1}$				mg Trolox (g DW)$^{-1}$	
DI a.u.	–0.57**	–0.73**	–0.42**	–0.46**	–0.18	–0.57**	0.42**	–0.76**
TP mg QE (g DW)$^{-1}$		0.90**	0.79**	0.27	0.14	0.46**	0.11	0.37**
TF mg QE (g DW)$^{-1}$			0.80**	0.46**	0.35**	0.61**	0.09	0.53**

TABLE IV. The correlation coefficients between biochemical parameters and intensity of late blight leaf infection (LB) for different sampling dates; QE – quercetin; DW – dry weight; *sd*-1: 4th of August; *sd*-2: 18th of August; *sd*-3: 8th of September; * – significant at 5 % level, ** – significant at 1 % level

Biochemical parameter	*DI* / a.u.		
	sd-1	*sd*-2	*sd*-3
Total phenolic content, mg QE (g DW)$^{-1}$	0.81**	–0.52*	–0.15
Total flavonoid content, mg QE (g DW)$^{-1}$	0.37	–0.60**	–0.90**
DPPH Radical scavenging activity, mg Trolox (g DW)$^{-1}$	0.68**	0.65**	0.07
ABTS Radical scavenging activity, mg Trolox (g DW)$^{-1}$	–0.69**	0.51*	–0.82**
Ferric-reducing antioxidant power, mg Trolox (g DW)$^{-1}$	0.69**	0.51*	–0.83**
Scavenging activity (Nitroblue tetrazolium test), %	–0.19	–0.04	–0.68**
Total reduction capacity, mg Trolox (g DW)$^{-1}$	0.84**	0.78**	–0.73**
Total antioxidant activity, mg Trolox (g DW)$^{-1}$	–0.77**	0.09	–0.86**

Even though phenolics and flavonoids are highly important in the variability of the evaluated genotypes (Fig. 4), these traits are not closely related to late blight response detected in wild species. The PCA analysis confirmed the fact that in the reaction of tomato wild species to late blight, beside *TP* and *TF*, other

compounds also play an important role. Recent findings[41] provide evidence that different preformed flavonoids and terpenoids in potato may play important roles in its defence or susceptibility to *P. infestans*. According to these authors, the accumulation of phenolic compounds, such as flavonone P3 and rutin, in susceptible potato genotypes does not help the plant to stop the development of the late blight infection process. On the other hand, accumulation of terpenoids (T1) helps a moderately resistant cultivar to keep its resistance. If the primary defence system fails, plants activate the second system of resistance that leads to programmed cell death and pathogen growth restriction.[42,43]

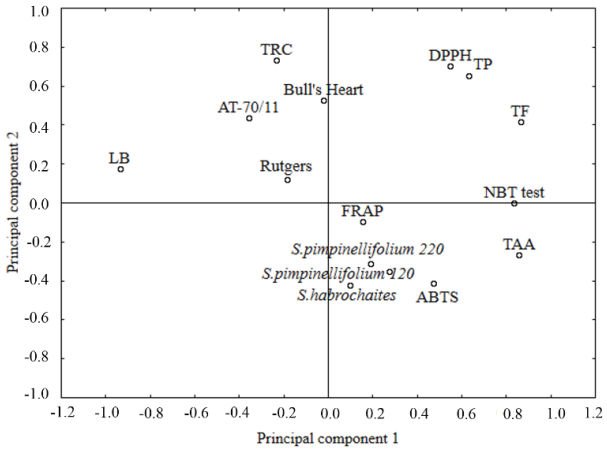

Fig. 4. PCA biplot of tested tomato genotypes and evaluated parameters.

According to the PCA, wild genotypes have more similarities between each other than the cultivated ones. It could be noted that 3 wild accessions grouped closely, showing a clear distinction from cultivated genotypes (Fig. 4). Such grouping of the wild accessions indicates a similar reaction to LB infection. The traits which express the related response of wild genotypes are *TAA*, *FRAP*, and *ABTS* (Fig. 4). Furthermore, late blight trait is on the distal side of the graph, closer to cultivated tomatoes (Fig. 4).

Since the first four principal components (PC) were over eigenvalue 1, only those were interpreted (Table V). The principal component analysis found two major PCs explaining 47.51 % of the total variance. The most important positive variables-traits (over 0.40) in the first two PC were *TF*, NBT test, *TAA*, *DPPH* and *TRC* while the negative was late blight leaf infection (Table VI). Although *TF*, NBT test, *DPPH* and *TRC* had high influence on the first two main components (PC1 and PC2), these traits are not close to the evaluated genotypes on the PCA graph. However, only *TAA* is close to the wild species, which means its higher influence in their reaction to leaf blight infection.

TABLE V. Eigenvalues and variance of the first four principal components

Component	Eigenvalue	Total variance	Cumulative eigenvalue, %	Cumulative variance, %
1	4.33	28.89	4.33	28.89
2	2.79	18.63	7.13	47.51
3	1.60	10.64	8.72	58.16
4	1.45	9.64	10.17	67.79

TABLE VI. Principal component analysis of evaluated parameters and tomato genotypes; QE – quercetin; DW – dry weight

Variable	PC 1	PC 2	PC 3	PC 4
Total phenolic content, mg QE (g DW)$^{-1}$	0.30	0.39	–0.13	–0.16
Total flavonoid content, mg QE (g DW)$^{-1}$	**0.42**	0.25	–0.14	–0.03
DPPH Radical scavenging activity, mg Trolox (g DW)$^{-1}$	0.20	**0.42**	0.01	0.28
ABTS Radical scavenging activity, mg Trolox (g DW)$^{-1}$	0.23	–0.25	–0.13	–0.05
Ferric-reducing antioxidant power, mg Trolox (g DW)$^{-1}$	0.07	–0.06	0.40	–0.28
Scavenging activity (Nitroblue tetrazolium test), %	**0.40**	0.00	0.38	0.04
Total reduction capacity, mg Trolox (g DW)$^{-1}$	–0.11	**0.44**	0.36	–0.14
Total antioxidant activity, mg Trolox (g DW)$^{-1}$	**0.41**	–0.16	0.08	0.16
Late blight leaf infection, a.u.	**–0.45**	0.10	0.10	0.06
Rutgers	–0.09	0.07	–0.00	0.77
AT-70/11	–0.17	0.26	0.29	–0.21
Bull's Heart	–0.01	0.31	–0.44	–0.21
Solanum pimpinellifolium 120	0.13	–0.21	0.40	0.05
S. pimpinellifolium 220	0.09	–0.19	–0.03	–0.23
S. habrochaites	0.05	–0.25	–0.22	–0.15

CONCLUSIONS

Wild genotypes *Solanum pimpinellifolium* S 220 and *Solanum habrochaites* had a significantly lower infection rate compared to other tested genotypes. Genotype, sampling date, and interaction of these two factors had a significant influence on the biochemical parameters measured in the leaves. The Spearman coefficient for the three sampling dates together showed that six out of eight biochemical parameters are in a strong negative correlation with late blight infection. Based on the analysis performed, total antioxidant activity (*TAA*), ferric-reducing antioxidant power (*FRAP*) and radical cation scavenging activity (*ABTS*) were discriminate for less susceptible wild tomato species.

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ИЗВОД

БИОХЕМИЈСКИ ОДГОВОР РАЗЛИЧИТИХ ГЕНОТИПОВА ПАРАДАЈЗА НА ИНФЕКЦИЈУ ПЛАМЕЊАЧОМ

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Дивље врсте се широко користе као потенцијални извори отпорности парадајза према пламењачи. Биохемијски одговор дивљих и гајених генотипова парадајза са различитим нивоом отпорности према *P. infestans* процењен је кроз укупан садржај фенола, флавоноидна и антиоксидативни капацитет. Дивљи генотипови *Solanum pimpinellifolium* S 220 и *Solanum habrochaites* су имали значајно нижи степен инфекције у поређењу са другим тестираним генотиповима. Груписање дивљих врста према PCA анализи указује на сличну реакцију ових генотипова према пламењачи. Иако су феноли и флавоноиди од велике важности у реакцији биљака парадајза заражених пламењачом, ове особине нису кључне у реакцији дивљих врста према пламењачи. Према разултатима добијеним у овом истраживању, најважнији антиоксидативни тестови који указују на реакцију дивљих врста парадајза према пламењачи су укупна антиоксидативна активност (*TAA*), ferric-reducing antioxidant power (*FRAP*) и 2,2'-азинобис-(3-етилбензотиазолин-6-сулфонска киселина) (*ABTS*).

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