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SCREENING OF SOYBEAN PLANTS FOR *Rsv1* RESISTANCE GENE AND ANTIOXIDANT ENZYME ISOFORMS UNDER CONDITIONS OF SOYBEAN MOSAIC VIRUS INFECTION

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Soybean mosaic virus (SMV) infection is recognized as the most serious, long-standing problem in soybean producing areas in the world. The Rsv1 locus is a part of resistance genes family involved in plant defense mechanisms against pathogens. Rsv1 and antioxidant enzymes peroxidase and superoxide dismutase are known for their role in providing resistance to the soybean mosaic virus. This work aimed at screening soybean plants both SMV infected and healthy on the presence of Rsv1 locus and peroxidase and superoxide dismutase isozyme patterns. The presence of 3gG2 gene at the Rsv1 locus was detected with PCR in uninfected plants of 17 studied soybean varieties. The presence of 3gG2 gene was also revealed in SMV-infected plants of four varieties indicating that the gene was not expressed in these plants. electrophoresis in PAAG demonstrated that the spectrum of peroxidase and superoxide dismutase isoforms in soybean leaf tissues depends on genotype specificity and the presence/absence of the 3gG2 gene at the Rsv1 locus. The outcome of work will be useful for identification genotypes resistant to SMV and their implementation in soybean breeding programs in Ukraine.

K e y w o r d s: soybean mosaic virus, plant resistance, Rsv1 locus, peroxidase and superoxide dismutase isozymes.

Soybean is one of the most important crops in the world as a source of protein, oil and biologically active substances for humans [1]. In recent years, in Ukraine, damage to soybeans by the Soybean mosaic virus caused a decrease in yield by 20-30% and has a negative effect on seed quality [2, 3]. In various countries around the world, soybean breeding programs successfully select the source material and promising genotypes using biochemical and molecular resistance markers. Four independent loci for Soybean mosaic virus (SMV) resistance have been identified in soybean (*Rsv1*, *Rsv3*, *Rsv4*, and *Rsv5*) [4]. The *Rsv1* locus is located on chromosome 13 of the soybean genome with multiple allelic variants. It is part of a larger family of resistance genes (R-genes) known as NBS-LRR (Nucleotide-binding site-Leucine-rich repeat) genes (NLRs), which are commonly involved in plant defense mechanisms against pathogens, including viruses, and represent a major class of plant immune receptors that greatly affect host–pathogen interactions [5, 6]. When pathogen effectors are detected, NLRs initiate a series of downstream defense responses that activate resistance against the invading viruses, termed effector-triggered immunity (ETI) [7, 8]. When the soybean plant is infected with SMV, the *Rsv1* gene facilitates the recognition of the virus. This triggers a series of defense responses, including the production of antiviral compounds and the activation of signaling pathways that enhance the plant's resistance to the virus.

The *Rsv1* locus in soybean is known for its role in providing resistance to the soybean mosaic virus (SMV). This locus encodes resistance genes that helps the soybean plant recognize and respond to the viral infection, ultimately reducing the severity of symptoms and limiting virus spread within the plant. Research has shown that the *Rsv1* locus is associated with specific alleles that confer different levels of resistance to various SMV strains. To date, several classifications of SMV strains have already used. In the United States, SMV strains were classified into seven strains, namely G1–G7 [9]. In Japan, they were divided into the 5 strains (A-E) [10]. In China SMV isolates were classified into 22 groups (SC1-SC22) [11].

The *Rsv1* locus is associated with the resistance of soybean plants to strains G1, G2, G3, as well as to strains G4-G6 (depending on *Rsv1* alleles).

Breeders often utilize this genetic information to develop soybean varieties that are more resilient to viral infections, enhancing crop yield and quality. Understanding the genetic mechanisms behind this resistance is crucial for improving soybean breeding programs and ensuring sustainable agriculture in regions affected by SMV. By utilizing the *Rsv1* locus in breeding efforts, farmers can cultivate soybean varieties that maintain higher yields and better quality, even in the presence of viral pressure.

Isozymes are one of the most commonly used biochemical markers. Since isozymes are direct gene products, the banding patterns of their electrophoretic spectrum can be effectively correlated to the genetic make-up of the particular genotype [12-14]. Biochemical changes in plants caused by viral infection include activation of antioxidant defense mechanisms through an increase in the number of various antioxidants, including activation of antioxidant enzymes such as peroxidase (EC 1.11.1.7) and superoxide dismutase (EC 1.15.1.11). These enzymes are part of the plant enzymatic antioxidant system and have the ability to respond to any environmental influences by changing the sets of isozymes and/or the expressivity of individual isoforms of these enzymes. It is known that the adaptive role of individual enzyme isoforms of plants is not the same under the influence of adverse environmental factors, including infection by viruses. It was shown that the enhanced activity and expression of some new isoforms of peroxidase involved in lignification, compared with control, highlighted the crucial role of these enzymes against phytopathogen attacks and confirmed their participation in the defense strategy of the resistant tomato genotype against Tobamovirus infection [15]. The effect of PMMoV infection on the antioxidant enzymes of *Nicotiana benthamiana* was studied. It was established that only PMMoV-I stimulated a defense response through up-regulation of different superoxide dismutase (SOD) isozymes. The activity of Fe-SOD and Cu,Zn-SOD I isozymes decreased in PMMoV-S-infected leaves [16]. Our previous results showed an increase in peroxidase activity in wheat plants of the resistant variety upon infection with WSMV [17]. A novel *Rsc15* locus connected with soybean resistance to SMV was identified and mapped to a 95 kb region on chromosome 6. Rsc15-mediated resistance is likely associated with the *GmPEX14* gene, which relative expression was strongly correlated with H_2O_2 accumulation and peroxidase and catalase activation during early stages of soybean plants infection by SMV [18].

This work aims to screen soybean plants for the presence of the *Rsv1* locus conferring resistance to soybean mosaic virus and to investigate their peroxidase and superoxide dismutase isozyme patterns.

The authors believe that the results of this study will be useful for breeding to identify soybean genotypes resistant to SMV using biochemical and molecular markers and will lead to a further understanding of the molecular mechanisms of soybean resistance to SMV.

Materials and Methods

In this study, 30 soybean (*Glycine max* L.) samples were tested (varieties and breeding samples). Soybean plants were selected in fields of the NSC Institute of Agriculture NAAS of Ukraine, Kyiv region. These soybean samples were previously checked for infection with 3 viruses: soybean mosaic virus (SMV), bean yellow mosaic virus (BYMV), and cowpea mild mottle virus (CPMMV) using DAS-ELISA. Seven samples were infected with SMV that was confirmed with PCR [19]. Hence, in this study, 30 soybean samples were involved, both SMV-infected and healthy.

Genomic DNA was extracted from fresh soybean leaves using GeneJET Plant Genomic DNA Purification Kit (K0792, Thermo Fisher Scientific, USA) (https://www.thermofisher.com/order/catalog/product/K0792).

Presence of *3gG2* gene at the *Rsv1* locus was established using PCR with specific primer pair Rsv1-f (TCCTACAAATTCTTTCACGCTC)/

Rsv1-r (GGCACTATAAATTGTTTAACTA) [20]. Polymerase chain reaction amplification was performed as follows: initial denaturation for 3 min at 95°C, followed by 303 cycles of 95°C for 30 s, 53°C for 30 s, and 72°C for 1 min. The final extension was at 72°C for 5 min. The primers are expected to amplify DNA product of 341 bp. PCR products were separated on a 1.5% agarose gel with DNA markers CSL-MDNA-100bp (Cleaver Scientific, UK), and visualized under UV light.

Enzyme electrophoresis. 10% resolving gel and 5% stacking gel were prepared for loading the samples. An equal amount of protein (50 µg) was loaded into each lane. A constant current of 15mA was applied to the gel in the electrophoresis apparatus. The voltage was increased to 35 mA when the dye front reached the resolving gel. The power supply was turned off as the dye front reached the bottom of the resolving gel. Gel was carefully removed and stained to resolve the superoxide dismutase and peroxidase isoenzymes.

For peroxidase, 0.5 g of leaf sample was crushed in liquid nitrogen and homogenized in 0.01 M Tris-glycine, pH 8.3; 15% sucrose, 0.1% DDT, 0.1% ascorbic acid, 0.1g/ml Polyclar AT, centrifuged at 4°C for 20 min at 15 000 g. The obtained supernatant was used to analyze the peroxidase isoenzyme content. The gel was incubated in 80 ml of a 0.2 M Na-acetate buffer (pH 5.2) in the presence of 0.05 M benzidine and 30 mM H_2O_2 [21].

For superoxide dismutase, 0.5 g of leaf sample was crushed in liquid nitrogen and homogenized in 100 mM Na-phosphate (pH 7.8) buffer solution containing 1 mM EDTA, 2 mM PMSF, 1% PVP, and 0.1% Triton X-100, centrifuged at 4°C for 20 min at 15000 g. The obtained supernatant was used to analyze the isoenzyme content of SOD. A solution containing 30 µM of riboflavin, 245 µM of NBT, 28 mM TEMED, and 50 мМ Tris-HCl (pH 7.6) buffer was used to stain the gel. After incubation for 30 min in the dark, the gel was incubated for 15 min in high-intensity light until light-colored spots appeared on a purple-blue background [21].

The developed gels were analyzed using ImageJ 1.53k. The densitograms of the electrophoretic lanes were digitized, and the intensity of spot coloration was evaluated.

The experiments were performed in triple biological and analytical repetitions. Statistical processing of the investigation results was made using the package of programs Analysis of the Data of Electron Tables Microsoft Excel (2000).

Results and Discussion

Detection of 3gG2 gene at the Rsv1 locus. Analysis of PCR results of 30 soybean samples showed amplification product 341 bp in 21 samples that testifies to the presence of *3gG2* gene at the *Rsv1* locus (Fig. 1).

Among SMV-infected varieties, 4 of them have *3gG2* gene at the *Rsv1* locus – varieties 'Sponsor' (#7), 'Sopano' (#12), 'Khvylya' (#16), and breeding sample '10/16' (#24). Infection by SMV of 4 soybean samples carrying the resistance gene may indicate that the gene was not expressed in these plants. This situation may be caused by various factors (e.g., abiotic factors), as a result of which a particular link of ETI immunity, which leads to the expression of defense R-genes, was not activated. In 17 studied soybean varieties without SMV infection,

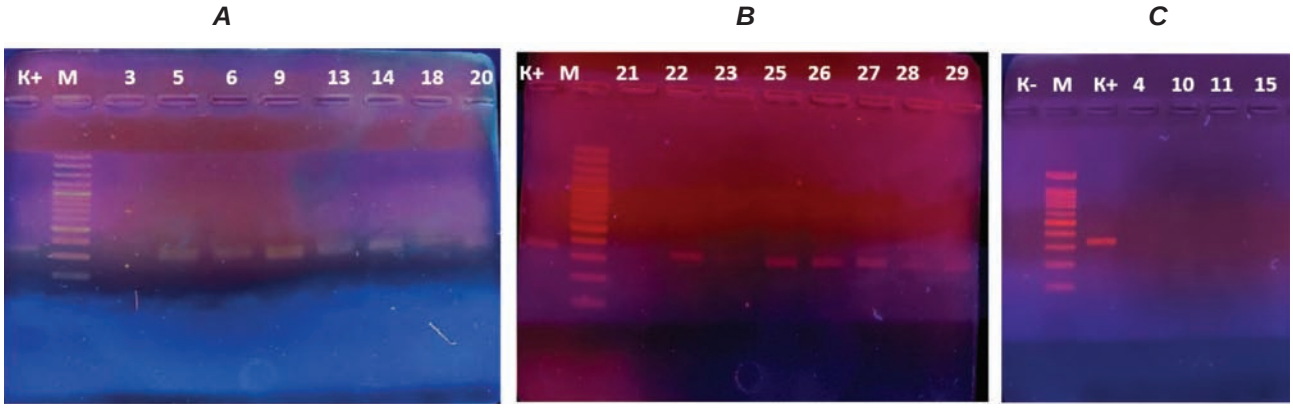

Fig. 1. Electrophoregram of PCR products using primers to 3gG2 gene at the Rsv1 locus (expected product size 341 bp). ***A***, ***B*** *– healthy soybean samples,* ***C*** *– SMV-infected samples: K+– positive control; K- – negative control; M – DNA marker 100 bp*

the resistance *Rsv1* is present. These results may be useful for introducing these varieties into soybean breeding programs in Ukraine. These are the varieties 'Komandor', 'Apika', 'Gladitor', 'Prypyat', Lisabon', 'Vilshanka', 'Elena', 'Arnika', '# 146/15', 'Sultana', 'Diona', 'Anita', 'Legenda', 'Vyshyvanka', 'Hali' (Table 1).

Detection of peroxidase and superoxide dismutase isozymes. Electrophoretic analysis of multiple peroxidase isoforms showed that the number of enzyme isoforms in soybean leaves varies by genotype, ranging from 4 to 13 isoforms with different expressivity (band intensity on electrophoresis) and relative mobility (Fig. 2, 3). The low-mobility iso-

Table 1. Results of soybean screening on the presence of 3gG2 gene at the Rsv1 locus depending on SMV infection

п\п	Name of variety/ sample	Symptoms	SMV	*3gG2* gene at the *Rsv1* locus
1	Komandor	without visual symptoms of infection	–	+
2	Apika	without visual symptoms of infection	–	+
3	Merlin	mild wrinkling on leaves	–	–
4	Niagara	mild wrinkling on young leaves	+	–
5	Gladiator	mild wrinkling on leaves	–	+
6	Prypyat	mild wrinkling on leaves	–	+
7	Sponsor	mild wrinkling on leaves	+	+
8	Muza	leaf deformation	–	–
9	Lisabon	brown mottling	–	+
10	Gentleman	leaf mosaics and mottling	+	–
11	Padua	wrinkling on leaves	+	–
12	Sopano	wrinkling on leaves	+	+
13	Vilshanka	mild wrinkling on leaves	–	+
14	Elena	mild wrinkling on leaves	–	+
15	Yasochka	mild wrinkling on leaves	+	–
16	Khvylya	mosaics and mild wrinkling on leaves	+	+
17	Arnika	severe leaf deformation	–	+
18	Arnika	mosaics and mild wrinkling on leaves	–	+
19	Arnika	brown mottling, wrinkling on leaves	–	+
20	№ 146/15	wrinkling on leaves	–	+
21	Aktor	without visual symptoms of infection	–	–
22	Sultana	leaf deformation	–	+
23	Muza	wrinkling on leaves, leaf deformation	–	–
24	Breeding # 10/16	leaf deformation	+	+
25	Diona	leaf deformation	–	+
26	Anita	mild leaf deformation	–	+
27	Legenda	mild leaf deformation	–	+
28	Vyshyvanka	mild leaf deformation	–	+
29	Hali	mild leaf deformation	–	+
30	Breeding # 105/23	without visual symptoms of infection	–	–

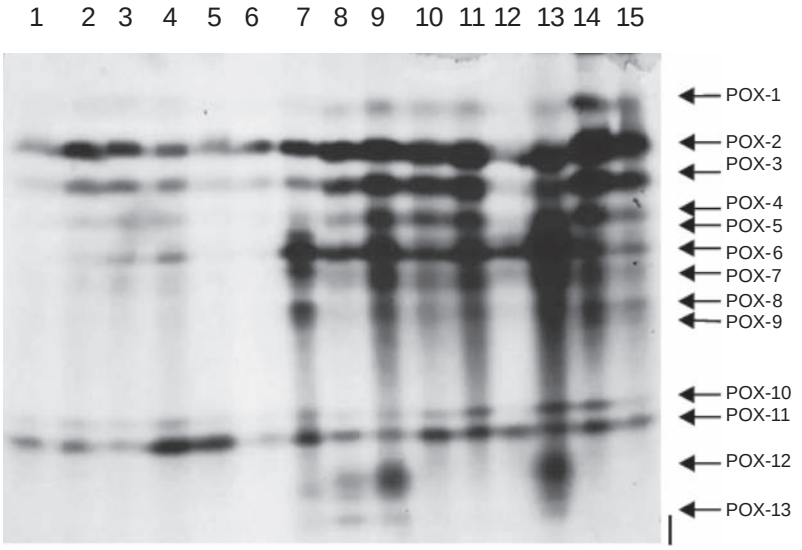

Fig. 2. Peroxidase isozymes in leaves of soybean varieties (No. 1-15): 1 – 'Komandor' ; 2 – 'Apika', 3 – 'Merlin', 4 – 'Niagara', 5– 'Gladiator', 6 – 'Prypyat', 7 – 'Sponsor', 8 – 'Muza', 9 – 'Lisabon', 10 – 'Gentleman', 11 – 'Padua', 12 – 'Sopano', 13 – 'Vilshanka', 14 – 'Elena', 15 – 'Yasochka', POX (1-13) – isoforms of peroxidase

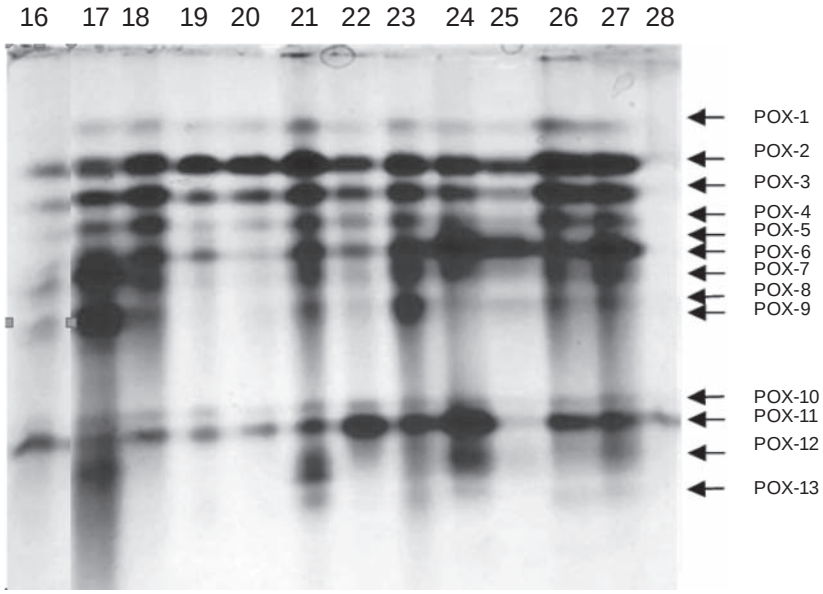

Fig. 3. Peroxidase isozymes in leaves of soybean varieties: 16 – 'Khvylya', 17 – 'Arnika', 18 – '#146/15'; 19 – 'Aktor', 20 – 'Sultana', 21 – 'Muza', 22 – '#10/16', 23 – 'Diona', 24 – 'Anita', 25 – 'Legenda', 26 – 'Vyshyvanka', 27 – 'Hali', 28 – '#105/23', POX (1-13) – isoforms of peroxidase

forms POX-2, POX-3, POX-4, the medium-mobility isoform POX-6 and isoform POX-12 have the highest expressivity. Only varieties 'Sponsor' and 'Anita' (with *3gG2* gene at the *Rsv1* locus) had the isoform POX-5, and its expression in the variety 'Anita' (resistant to SMV) was 2.3 times higher than in the variety 'Sponsor' (susceptible to infection by SMV).

Highly mobile isoforms POX-12 and POX-13 were detected in varieties 'Lisabon', 'Vilshanka', 'Arnika', 'Diona', 'Anita', 'Vyshyvanka', 'Hali' (with *3gG2* gene at the *Rsv1* locus and resistance to SMV), variety 'Sponsor' (with *3gG2* gene at the *Rsv1* locus, susceptible to SMV damage) and variety 'Muza' (without *3gG2* gene at the *Rsv1* locus, but resistant

to SMV). Expressivity of these isoforms in variety 'Sponsor' was 2-12 times lower than in varieties with *3gG2* gene at the *Rsv1* locus and resistance to SMV. The varieties with *3gG2* gene at the *Rsv1* locus and resistance to SMV were characterized by the highest expressivity of the studied peroxidase isoforms: varieties 'Elena', 'Vyshyvanka' (POX-1), varieties 'Elena', 'Vyshyvanka', 'Diona', 'Hali', '#146/15' (POX-2), varieties 'Vilshanka', 'Elena', 'Vyshyvanka', 'Diona', 'Hali', '#146/15' (POX-3), varieties 'Vilshanka', 'Anita', 'Hali' (POX-6), varieties 'Vilshanka', 'Arnika', 'Diona' (POX-7), varieties 'Vilshanka', 'Arnika' (POX-8), varieties 'Arnika', 'Diona' (POX-9), varieties 'Elena', 'Vilshanka' (POX-10) and variety 'Anita' (POX-11).

Electrophoretic analysis of superoxide dismutase showed that the number of isoforms of this enzyme in soybean leaves varies depending on the genotype from 3 to 12 isoforms of different expressivity, relative mobility, genotype resistance to SMV, and the presence of the *3gG2* gene at the *Rsv1* locus (Fig. 4, 5).

The low-mobility isoform Sod 1 was detected in variety 'Merlin' (resistant to SMV but without *3gG2* gene at the *Rsv1* locus). The isoform Sod2 was identified only in 8 studied varieties with *3gG2* gene at the *Rsv1* locus. The correlation coefficient of the presence of the isoform Sod2 with the resistance gene (r = +0.53 at $P < 0.05$). The isoform Sod3 is present only in seven soybean genotypes with *3gG2* gene at the *Rsv1* locus ('Vilshanka', 'Diona', 'Anita', 'Vyshyvanka', 'Hali', 'Legenda' and breeding sample '#146/15') and in two varieties which are resistant to SMV without the presence of the *3gG2* gene at the *Rsv1* locus ('Aktor', 'Muza'). Correlation coefficient of the presence of the isoform Sod3 with the resistance gene (r = +0.50 at $P < 0.05$).

The expressivity of the medium-mobility isoform Sod5 was by 2.4-2.9 times higher in varieties with the *3gG2* gene at the *Rsv1* locus and virus-resistant varieties without resistance gene compared to susceptible to SMV soybean varieties. Other intermediate- and fast-mobility superoxide dismutase isoforms were present in both resistant and susceptible soybean varieties.

Thus, the electrophoretic spectra of peroxidase and superoxide dismutase in soybean leaf tissues are represented by 3 to 13 enzyme isoforms of different mobility and expressivity, depending on the varietal (genotypic) specificity, resistance to SMV, as well as the presence of the *3gG2* gene at the *Rsv1* locus. The obtained results revealed a correlation between the *3gG2* gene at the *Rsv1* locus (r = 0.50-0.53 at $P < 0.05$) and the presence in the electrophoretic spectra of enzymes of the highly mobile isoform of peroxidase (POX-12, POX-13) and the low-mobility isoforms of superoxide dismutase (Sod 2, Sod 3). It should be noted that the same adaptive potential of

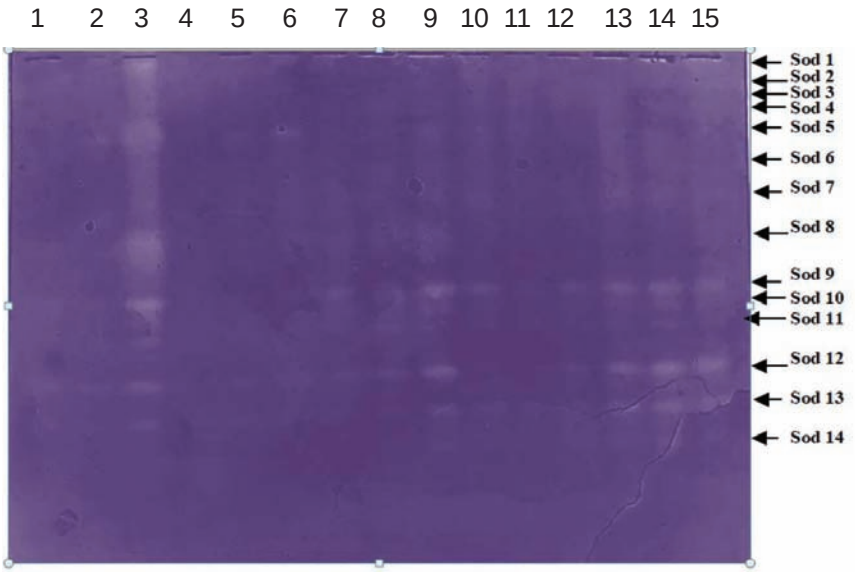

Fig. 4. Superoxide dismutase isozymes in leaves of soybean varieties: 1 – 'Komandor' ; 2 – 'Apika', 3 – 'Merlin', 4 – 'Niagara', 5 – 'Gladiator', 6 – 'Prypyat', 7 – 'Sponsor', 8 – 'Muza', 9 – 'Lisabon', 10 – 'Gentleman', 11 – 'Padua', 12 – 'Sopano', 13 – 'Vilshanka', 14 – 'Elena', 15 – 'Yasochka', Sod (1-14) – isoforms of superoxide dismutase

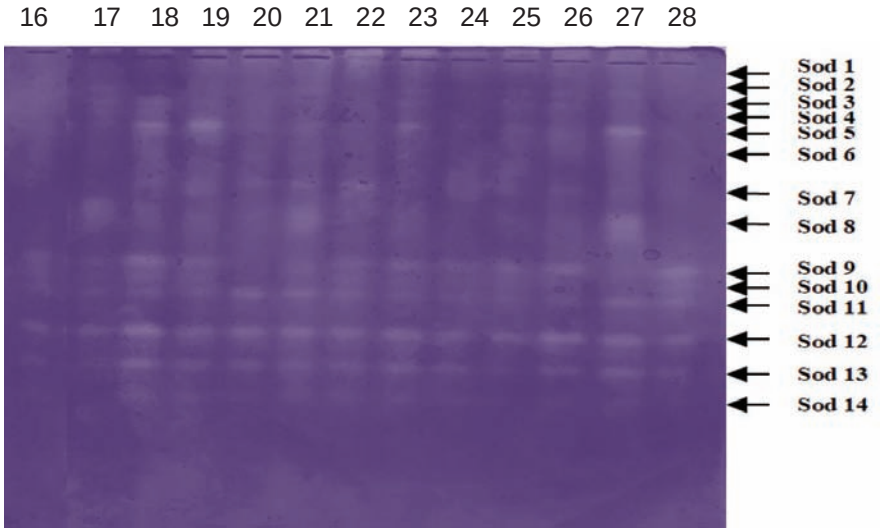

Fig. 5. Superoxide dismutase isozymes in leaves of soybean varieties: 16 – 'Khvylya', 17 – 'Arnika', 18 – '#146/15', 19 – 'Aktor', 20 – 'Sultana', 21 – 'Muza', 22 – '#10/16', 23 – 'Diona', 24 – 'Anita', 25 – 'Legenda', 26 – 'Vyshyvanka', 27 – 'Hali', 28 – '#105/23', Sod (1-14) – isoforms of superoxide dismutase

plants can be provided by different variants of adaptive gene complexes.

Redox homeostasis plays an essential role in plant immunity against viruses [22]. The activity of ROS scavenging enzymes, in particular peroxidase and superoxide dismutase, can be used as a proxy for ROS homeostasis. Through the production of certain isoforms of these enzymes at specific timing and localization, thus by properly and precisely making use of a variety of plant functions of enzymes, the growing plants can respond to and combat a wide variety of stressful challenges with biotic or abiotic nature, including virus infection [14-16, 23-25]. The total peroxidase or superoxide dismutase activity results from the activity of many isoenzymes and only some of them play a role in redox homeostasis. Other isoenzymes (e.g., class III isoperoxidases) contribute to different components of plant immunity, such as strengthening cell walls or biosynthesis of the secondary metabolites [26]. Our research has shown that the electrophoretic spectra of peroxidase and superoxide dismutase in soybean leaf tissues are represented by enzyme isoforms with different mobilities and expressivities. Isozyme patterns depend on genotype specificity, resistance to SMV, and the presence or absence of the *3gG2* gene at the *Rsv1* locus. The obtained results complement field monitoring data and ELISA and RT-PCR analyses for screening soybean varieties for resistance to SMV damage, and can also serve as markers in further studies, allowing for a more detailed assessment of the resistance of soybean varieties to SMV. To our knowledge, this is the first report in Ukraine on the identification of *Rsv1* resistance genes to SMV and the discovery of some biochemical markers of resilience to this virus.

Conflct of interest. Authors have completed the Unified Conflicts of Interest form at http://ukr-biochemjournal.org/wp-content/uploads/2018/12/coi_disclosure.pdf and declare no conflict of interest.

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СКРИНІНГ РОСЛИН СОЇ НА НАЯВНІСТЬ ГЕНА СТІЙКОСТІ *Rsv1* ТА ІЗОФОРМ АНТИОКСИДАНТНИХ ЕНЗИМІВ ЗА ІНФІКУВАННЯ ВІРУСОМ МОЗАЇКИ СОЇ

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Інфекція вірусом мозаїки сої (ВМС) визнана однією з найсерйозніших і тривалих проблем у багатьох регіонах світу, де вирощують сою. Локус *Rsv1* є частиною родини генів стійкості, що беруть участь у захисних механізмах рослин проти фітопатогенів. Відомо, що *Rsv1* та антиоксидантні ензими пероксидаза та супероксиддисмутаза відіграють важливу роль у забезпеченні стійкості до вірусу мозаїки сої. Метою цієї роботи був скринінг рослин сої – як інфікованих, так і здорових – щодо наявності гена *3gG2* у локусі *Rsv1* та ізоформ пероксидази та супероксиддисмутази. Наявність гена *3gG2* у локусі *Rsv1* було виявлено за допомогою ПЛР у неінфікованих рослин 17-ти досліджених сортів сої. Присутність гена *3gG2* також виявлено в інфікованих ВМС рослинах чотирьох сортів, що вказує на те, що цей ген не експресувався у цих рослинах. Електрофорез у ПААГ показав, що ізоензимний спектр пероксидази та супероксиддисмутази в тканинах листків сої залежить від специфіки генотипу та наявності/відсутності гена *3gG2* у локусі *Rsv1*. Результати роботи можуть бути використані для ідентифікації генотипів, стійких до ВМС та їх подальшого залучення до програм селекції сої в Україні.

Ключові слова: вірус мозаїки сої, стійкість рослин, *Rsv1* локус, ізоензими пероксидази та супероксиддисмутази.

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