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ANTIOXIDATIVE DEFENSE RESPONSE TO APHID-INDUCED OXIDATIVE STRESS IN *Glycine max* (L.) Merr. cv. "Nam Dan"

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ABSTRACT

Infestation of cowpea aphid (*Aphis craccivora* Koch) induced oxidative stress in leaves of soybean (*Glycine max* (L.) Merr. cv. "Nam Dan") with a burst in generation of reactive oxygen species (ROS) products such as superoxide anion radical ($O_2^{\cdot-}$) and hydrogen peroxide (H_2O_2) recorded around 24 hours after aphid feeding. A continuous increase in content of thiobarbituric acid reactive substances (TBARS) in lipid peroxidation and a defined percentage of injury in aphid-infested leaves (2.20 - 8.79 %) were resulted from the cellular oxidative damage. An enhanced activity of the antioxidant enzymes such as superoxide dismutase (SOD, EC 1.15.1.1) and catalase (CAT, EC 1.11.1.6) was recorded in leaves of soybean "Nam Dan" from 24 to 48 hours post-infestation (hpi). The enhancement of these enzymes function as the antioxidative response that controlled both ROS-accumulation playing as defensive element and ROS-detoxifying, therefore, reduce the oxidative damage within 48-96 hpi. Activity of SOD and CAT also can improve the tolerance of soybean "Nam Dan" to infestation from *A. craccivora*.

Keywords. soybean "Nam Dan", cowpea aphid, oxidative stress, antioxidative, defense response.

1. INTRODUCTION

Oxidative stress, resulting from the strong release of reactive oxygen species (ROS), including superoxide anion radical ($O_2^{\cdot-}$) and hydrogen peroxide (H_2O_2), is a common phenomenon in plants under effect of the environmental stresses. Being induced by infestation of aphids (Hemiptera: Aphididae), generation of ROS often played both positive and negative impacts to plant cells. The increase of $O_2^{\cdot-}$ and H_2O_2 levels, together with induction of cell death in the infested areas, is an important response in plant defense mechanism against aphid herbivores. Contrary, the high content of ROS can exert toxic effects, and their uncontrolled productions can result in cellular oxidative damage of proteins, lipids, and nucleic acids [1]. To maintain a balance of two those antagonistic roles of ROS, plant cells produce a number of antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), peroxidases (POX), etc., which are able to control the ROS-generation as a defensive element and ROS-detoxifying to reduce oxidative damage [2]. However, these antioxidative defense mechanisms are not

uniformly regulated in plant response to aphids [3]. Within a single plant species, aphid feeding can enhance expression of certain antioxidant enzymes while suppressing others.

Although oxidative responses of plants have been mentioned in several plant-aphid interactions [4,5], no comparable studies were reported for soybean (*Glycine max* (L.) Merr. cv. "Nam Dan")-a valuable crop in agricultural production in Nghe An province (Vietnam). Furthermore, cowpea aphid (*Aphis craccivora* Koch), one of the most important pests of leguminous plants, can feed soybean from the germination stage until harvest, therefore, cause serious damages to this crops [6]. In this study, we investigated the antioxidative responses in defense mechanism of *G. max* cv. "Nam Dan" against infestation of *A. craccivora*, in which, the changes in levels of H_2O_2, $O_2^{\cdot-}$ as well as changes in activity of antioxidant enzymes, SOD (EC 1.15.1.1) and CAT (EC 1.11.1.6) were assessed. As an additional objective, the degree of cellular damage was estimated on the basis of electrolyte leakage measurement and levels of thiobarbituric acid reactive substances (TBARS)-product of lipid peroxidation.

2. MATERIALS AND METHODS

2.1. Materials

2.1.1. Plant

Plant used in this study was cultivar "Nam Dan" of soybean (*Glycine max* (L.) Merr.).

Soybean seeds have been exclusively provided by Nam Dan Agricultural Extension Center (Nghe An province, Vietnam). Seeds were surface-sterilized for 10 minutes in 0.01 % $HgCl_2$ solution and imbibed in the incubator at 22 – 23 ^oC for 48 hours. The germinated seeds were cultured in 20-cm-diameter plastic pots containing Hoagland medium placed in the phytotron with temperature of 23 – 25 ^oC, related humidity of 70 – 75 %, light intensity of 110 - 130 μM photons.m^{-2}.s^{-1} and light period of 12 light/12 dark hours. Soybean plants in the V3 stage (with first two trifoliate leaves fully developed, third trifoliate leaf unrolled) were used to establish experiments.

2.1.2. Aphid infestation

Cowpea aphid (*Aphis craccivora* Koch) is cultured and supported by Department of Applied Entomology (Institute of Ecology and Biological Resources, Vietnam Academy of Science and Technology, Vietnam).

Each soybean plant in stage V3 was treated by 10, or 20, or 30 wingless adults of *A. craccivora*. Aphid individuals were carefully transferred to the estimated leaves with a fine paintbrush. Control was soybean plants without aphid infestation. All control and aphid-infested variants were separately put in clear glass boxes (50 cm × 50 cm × 50 cm) covered by nylon gauze and placed in the phytotron, in which, the environmental factors such as temperature, relative humidity, light intensity and light period were strictly controlled.

Leaves of soybean plants were collected after 0, 24, 48, 72 and 96 hours post-infestation (hpi) of cowpea aphid. Leaves were carefully taken and weighed, then frozen in nitrogen liquid and kept at -70 ^oC for subsequent analyses. Content of superoxide anion radical ($O_2^{\cdot-}$) and hydrogen peroxide (H_2O_2) was determined in fresh materials at particular time points.

2.2. Analyses

2.2.1. Chemicals

All analytical chemicals were purchased from Singapore supplier of Sigma-Aldrich (USA).

2.2.2. Determination of superoxide anion radical content

Determination of superoxide anion radical ($O_2^{\cdot-}$) content in biological samples was based on its ability to reduce nitro blue tetrazolium (NBT) [7]. Soybean leaves (0.30 g fresh materials-FW) were immersed in 10 mM potassium phosphate buffer (pH 7.8) containing 0.05 % NBT and 10 mM NaN_3 in a final volume of 3 mL and incubated for an hour at room temperature. After incubation, 2 mL of the reaction solution was heated at 85 ^oC for 15 min and rapidly cooled. Levels of $O_2^{\cdot-}$ in soybean leaves were expressed as absorbance at 580 nm per 1 gram of fresh materials ($A_{580}.g^{-1}$ FW). The measurement was carried out in the UV-Vis CARY 60 spectrophotometer (Agilent, USA) connected a computer; the spectral data was analyzed by using the UV-Win 5.0 application software.

2.2.3. Determination of hydrogen peroxide content

Content of hydrogen peroxide (H_2O_2) was determined following the spectrophotometric method [8]. Leaves of soybean (0.50 g FW) were homogenized with 3 mL of 5 % trichloroacetic acid (TCA) and 0.10 g of activated charcoal. The homogenate was centrifuged at 12,000×*g* for 30 min at 4 °C. The reaction mixture contained extracted solution, 100 mM potassium phosphate buffer (pH 8.4), and reagent (0.6 mM 4-(-2 pyridylazo)resorcinol : 0.6 mM potassium-titanium oxalate, 1 : 1 in proportion). The decrease of absorbance was measured at a wavelength of 508 nm in the UV-Vis CARY 60 spectrophotometer. Blanks were obtained by using 5% TCA to replace extracted solution in the mixture. Content of H_2O_2 was determined from the difference of A_{508} between each sample and blank. The amount of hydrogen peroxide in soybean leaves was expressed as $\mu M.g^{-1}$ FW.

2.2.4. Enzyme assay

The frozen leaves (0.50 g) were homogenized at 4 ^oC in 2.0 mL of 50 mM sodium phosphate buffer (pH 7.0), containing 1.0 mM EDTA, 2 % NaCl and 1 % PVP (polyvinyl pyrrolidone) and centrifuged at 10,000 × g for 30 min.

The activity of SOD (EC 1.15.1.1) was spectrophotometrically assayed by measuring its ability to inhibit the photochemical reduction of NBT [9]. The 3 mL reaction mixture contained 50 mM phosphate buffer (pH 7.8), 13 mM methionine, 75 mM NBT, 0.1 mM EDTA and 30 µL of enzyme extract and 2 mM riboflavin. The test tubes were placed 30 cm below the light of two 15 W fluorescent lamps and proceeded for 15 min. After that, the measurement was carried out with the UV-Vis CARY 60 spectrophotometer. The amount of the enzyme that caused the inhibition of NBT reduction by 50 % was taken as a unit of SOD activity. The enzyme activity was expressed as nanokatal per 1 mg of protein ($nkat.mg^{-1}$ protein).

The activity of CAT (EC 1.11.1.6) was determined by measuring H_2O_2 consumption [10]. The reaction mixture contained 100 mM phosphate buffer (pH 7.0), 3 % H_2O_2 and plant extract. The reaction was started by introducing H_2O_2 to the reaction mixture. The absorbance activity

was assessed by measuring at 240 nm against a calibration curve using the UV-Vis CARY 60 spectrophotometer. The activity of CAT was expressed as nkat.mg^{-1} protein.

2.2.5. Electrolyte leakage

Electrolyte leakage was conductometrically measured to assess the injury percentage of plasma membrane [11]. Five fresh leaves of each sample were placed in test-tubes containing 20 mL of deionized water and incubated on a shaking platform at room temperature for 3 hours. The electrical conductivity of samples was measured with a conductivity meter (Orion Star A320, Thermo Scientific, USA). After the first measurement, leaves were autoclaved at 100 ^{o}C for 20 min to completely rupture the membranes; the second measurement was done after cooling the solution to room temperature. The membrane damage in aphid-infested leaves was evaluated as the injury percentage compared with control (%).

2.2.6. Lipid peroxidation

Level of lipid peroxidation was determined by thiobarbituric acid reactive substances (TBARS) assay [12]. 0.50 g of leaves was homogenized in 3 mL of 0.5 % thiobarbituric acid (TBA) in 20 % trichloroacetic acid (TCA) and centrifuged at 12,000×g for 20 min at 4 ^{o}C. A reacted mixture consists of 0.5 mL of potassium phosphate buffer (pH 7.0) and 1 mL of reagent (0.5 % TBA in 20 % TCA, w/v) and 0.5 mL aliquot of the supernatant. A blank consisted of 0.5 mL buffer and 1 mL reagent. The test-tubes were incubated at 95^{o}C for 30 min and then quickly cooled in an ice bath. After cooling mixes were centrifuged at 10,000×g for 10 min to give a clear supernatant. The absorbance of supernatant was measured at 532 nm in the UV-Vis CARY 60 spectrophotometer after subtracting the non-specific absorbance at 600 nm. Results are presented as μM TBARS. g^{-1} FW.

2.3. Statistical analysis

All analyses were performed in three replicates in three independent experiments. Analysis of variance (ANOVA) was applied to verify whether means from the given experimental variants were significantly different with the level of significance as P-value < 0.05. Data shown in the figures are means of triplicates for each variant and standard errors (s.e.).

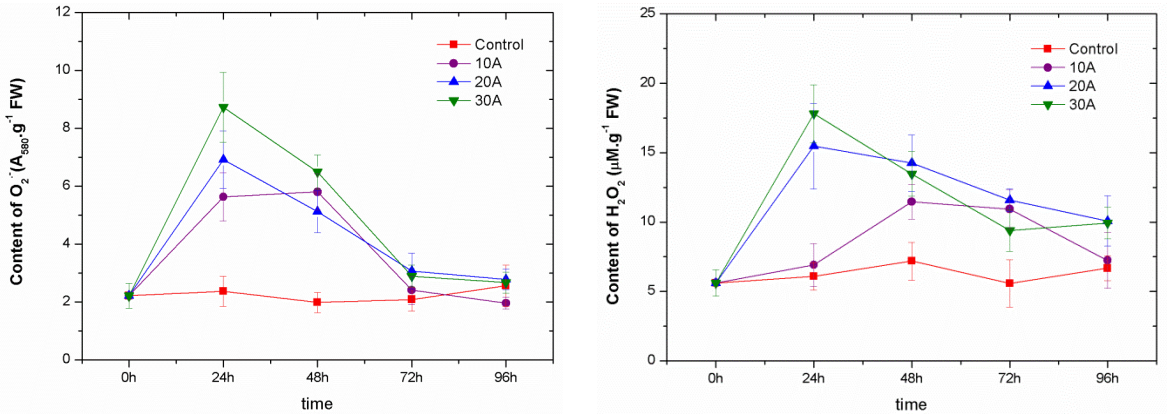
3. RESULTS AND DISCUSSION

3.1. Aphid-accumulated reactive oxygen species

An accumulation of reactive oxygen species (ROS) such as superoxide anion radical ($O_2^{\cdot-}$) and hydrogen peroxide (H_2O_2) in leaves of soybean (*G. max* cv. "Nam Dan") was revealed to induce by infestation of cowpea aphid (*A. craccivora* Koch).

A strong generation of $O_2^{\cdot-}$ was observed from 0-24 hpi in soybean leaves infested by 20 and 30 aphids, whereas infestation of 10 aphids caused an increased content of $O_2^{\cdot-}$ within 0-48 hpi. The highest amount of $O_2^{\cdot-}$ obtained at 24 hpi in leaves infested by 30 aphids was 8.73 A_{580}.g^{-1} FW, having by 3.68- and 3.94-fold higher than in control and in the beginning, respectively. The most remarkable differences between $O_2^{\cdot-}$ content in the aphid-treated and in control plants were recorded within 24-48 hpi, however, levels of that free radical in the infested leaves were not significantly different from that observed in control within 72-96 hpi (Fig. 1a).

A limited available studies regarding the involvement of $O_2^{\cdot-}$ in plant defense against insect herbivores documented that, $O_2^{\cdot-}$ played as a feeding deterrent against the infestation of aphid [8], or converted into H_2O_2 via catalyzing by enzyme superoxide dismutase (SOD), and then H_2O_2 functions as a signal molecule to initiate responses [13]. A large amount of $O_2^{\cdot-}$ in the cell wall also contributed to limit the invasion of viral pathogens that can be directly transmitted from aphid saliva during its penetration into plant tissues [6].



a b

Figure 1. Content of $O_2^{\cdot-}$ (a) and H_2O_2 (b) in leaves of *G. max* cv. "Nam Dan" control and *A. craccivora* infested plants.

In soybean leaves, H_2O_2 showed a remarkable accumulation to the highest content at 24 hours after infestation of 20 or 30 aphids, having 2.54-, and 2.92-fold higher than at the beginning, respectively. This ROS molecule then continuously decreased to lower levels within 48-96 hpi. In control, H_2O_2 remained at low levels throughout experiment (Fig. 1b). ANOVA results showed that the differences in content of H_2O_2 in 20 and 30 aphid-infested variants and control in all estimated time were highly significant; whereas, that in 10 aphid-infested leaves obtained within 48-72 hpi ($P < 0.05$).

H_2O_2 is a relatively stable partially-reduced form of ROS and its ability to diffuse freely allows H_2O_2 to play a control role in the generation of the defense response in plants [13, 14]. An early accumulation of H_2O_2 to high levels in soybean "Nam Dan" at 24 hpi could be the beginning of a cascade of events that triggers physiological and molecular responses to prevent or minimize cowpea aphid attack.

3.2. Cellular membrane damage

The burst of $O_2^{\cdot-}$ and H_2O_2 generation often causes "oxidative damage" in living cell. The induction of damaged cellular components often associates to leakage of cellular content and lipid peroxidation, and leads to cell death in herbivore-effected areas.

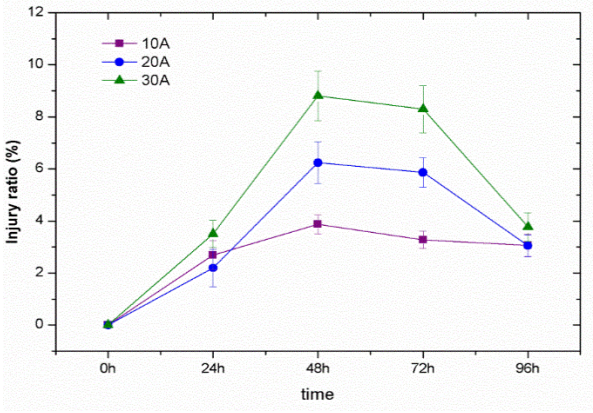


Figure 2. The percentage of injury (based on electrolyte leakage) in leaves of *G. max* cv. "Nam Dan" infested by *A. craccivora* compared with control plants.

The percentage of injury (based on electrolyte leakage) in soybean "Nam Dan" leaves' cells caused by *A. craccivora* infestation compared with control is shown in Figure 2. An increase in the electrolyte leakage in all aphid-infested leaves from 0 to 48 hpi was followed by a decrease within 72-96 hpi. The highest percentages of injury were recorded at 48 hpi, having by 3.87 %, 6.24 %, and 8.79 % (in proportion to infestation of 10, 20 and 30 aphids, respectively) higher than in control plants. ANOVA showed the significant differences between the injury ratio in 20 and 30 aphid-treated variants compared with control within 48-72 hpi ($P < 0.05$).

Increased electrolyte leakage is used to monitor loss of membrane integrity, and hence can indicate damage in leaf cells caused by feeding activities. The maximum injury percentage in soybean leaves after cowpea aphid infestation was only 8.79 %. Therefore, it can be assumed that the components of aphid sheath and watery saliva can play a pivotal role in establishing physical and chemical constraints on electrolyte leakage. *A. craccivora* has probably developed a range of physical and chemical properties to minimize wounding area and to limit electrolyte leakage, therefore, reduce plant response to stylet penetration.

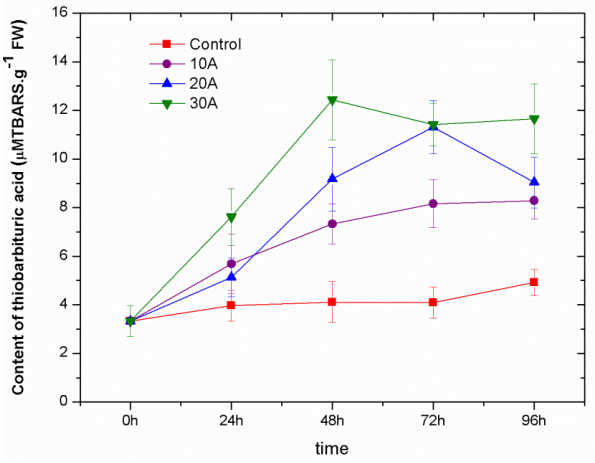


Figure 3. Lipid peroxidation in leaf tissues of *G. max* cv. "Nam Dan" control and *A. craccivora* infested plants.

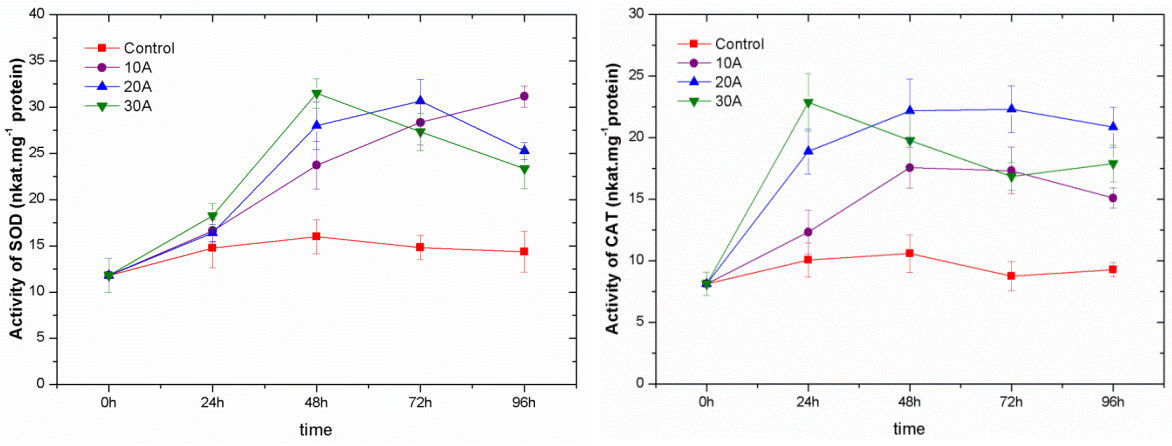
A well-established mechanism of cellular injury in plants and is used as an indicator of oxidative stress is lipid peroxidation that was measured as the amount of thiobarbituric acid

reactive substances (TBARS). A progressive increase in content of TBARS was recorded in leaves of *G. max* cv. "Nam Dan" in the duration of *A. craccivora* infestation and reached to various maximum levels under the influence of different numbers of cowpea aphid (Fig. 3). The highest level of TBARS in 30 aphid-infested leaves (12.44 μM.g^{-1} FW) was obtained at 48 hpi; a respective value in 20 aphid-infested variant (11.31 μM.g^{-1} FW) was recorded at 72 hpi, whereas that in 10 aphid-infested soybean was continuously increased till 96 hpi. However, in all analyzed point time, TBARS content in aphid-infested leaves was significant higher than in control ($P < 0.05$).

Results of our study in soybean "Nam Dan" were in agreement with previous reports, which all confirmed that the increase in lipid peroxidation in crops, e.g., pea plants, was directly induced by aphids' feeding [6]. Therefore, we can conclude that, infestation of *A. craccivora* stimulated a strong generation of $O_2^{\cdot-}$ and H_2O_2 in leaves' cells of *G. max* cv. "Nam Dan", which caused oxidative damage of membrane integrity due to the increase in percentage injury of cell membrane and activation of lipid peroxidation processes.

3.3. Activity of antioxidant enzymes

The spectrophotometric analyses showed an enhancement of enzyme SOD in *G. max* cv. "Nam Dan" infested by *A. craccivora*. Activity of this enzyme in aphid-infested leaves increased in most of estimated time points, and was much higher than in control (Fig. 4a). In the case of soybean plants infested by 30 aphids, activity of SOD increased remarkably and reached the highest value at 48 hpi (31.49 nkat.mg^{-1} protein), having by 197.12 % and 266.86 % higher than that observed in control and at the beginning, respectively. In turn, SOD activity in leaves infested by 10 and 20 aphids increased up to 72 hpi and was higher than in 30 aphid-infested leaves within 72-96 hpi. ANOVA analyses showed significant differences between the SOD activities in all aphid-infested leaves and control from 48 to 96 hpi ($P < 0.05$).



a b

Figure 4. Activity of SOD (a) and CAT (b) in leaves of *G. max* cv. "Nam Dan" control and *A. craccivora* infested plants.

Within the living cells, SOD constitutes the first line of defense against ROS, because this enzyme can counteract oxidative damage caused by over-accumulation of superoxide anion radical. As enzyme engaged in the dismutation of $O_2^{\cdot-}$, the remarkably increased activity of SOD in the aphid-infested leaves of soybean "Nam Dan" caused for a strong decrease in level of $O_2^{\cdot-}$

in the period time of 48-96 hours (Fig. 1a). It was suggested that an enhancement of SOD activity was directly involved the resistance of soybean "Nam Dan" to cowpea aphid.

Similar to SOD, activity of CAT in soybean leaves was also induced by *A. craccivora* infestation. The large contents of CAT in aphid-infested leaves were noted at 24 hpi and maintained in high levels until ending of experiment (Fig. 4b). ANOVA analyses revealed a significant difference between activities of CAT in aphid-infested leaves and control during the experimental time ($P < 0.05$).

Our study supported that CAT may contribute to the defense mechanisms of *G. max* cv. "Nam Dan" against *A. craccivora* infestation by regulating levels of H_2O_2. The activation of CAT was disproportionately higher than H_2O_2 generation in soybean leaves. High activity of CAT within 24-96 hpi strongly catalyzes H_2O_2 breakdown into H_2O and O_2, therefore, reduced level of this ROS product, and the relatively low accumulation of H_2O_2 from 48 to 96 hpi was probably due to the high activation of CAT (Fig. 1b). A strong enhancement of CAT protects soybean leaf cells against an excess of H_2O_2 and thus against considerable membrane damage.

The high efficiency of the antioxidative enzymes such as SOD and CAT observed in soybean "Nam Dan" is one of the most important elements of the defense mechanisms to oxidative stress. SOD and CAT regulated to generate $O_2^{\cdot-}$ and H_2O_2 to function as defensive element but detoxify the excess of ROS to reduce oxidative damage. In addition, the enhanced activity of SOD and CAT in soybean leaves under *A. craccivora* attack also plays an important role in the stress tolerance of *G. max* cv. "Nam Dan".

4. CONCLUSION

Cowpea aphid infestation induced the oxidative stress in leaves of soybean (*Glycine max* (L.) Merr. cv. "Nam Dan") with a burst of $O_2^{\cdot-}$ and H_2O_2 released in 24 hours after aphid attack. The cellular damage resulted from oxidative stress were obviously confirmed by a continuous increase in content of TBARS, product of membrane lipid peroxidation, and a defined percentage of injury (2.20 - 8.79 %) in soybean leaves' cells. The accumulation in activity of antioxidant enzymes SOD and CAT since 24 hours following cowpea aphid infestation played as the antioxidative defense response of soybean "Nam Dan" via the mode, in which, these enzymes catalyzed to reduce content of $O_2^{\cdot-}$ and H_2O_2, therefore, contributing to control oxidative stress in soybean leaves.

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TÓM TẮT

PHẢN ỨNG BẢO VỆ CỦA GIỐNG ĐẬU TƯƠNG NAM ĐÀN ĐỐI VỚI STRESS "ÔXY HÓA" GÂY RA BỞI RỆP MUỘI ĐEN

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Tác động của rệp muội đen (*Aphis craccivora* Koch) đã cảm ứng stress "ôxy hóa" ở lá cây đậu tương Nam Đàn (*Glycine max* (L.) Merr.) với sự bùng nổ sinh tổng hợp các dạng ôxy hoạt hóa như gốc tự do superoxide ($O_2^{\cdot-}$) và hydrogen peroxide (H_2O_2) sau 24 giờ gây hại. Stress "ôxy hóa" đã gia tăng liên tục quá trình peroxide hóa lipid, làm thay đổi cấu trúc, chức năng của màng sinh chất, gây thiệt hại ở các tế bào lá đậu tương Nam Đàn với tỉ lệ tổn thương 2,20 - 8,79 %. Trong những lá bị stress đã có sự cảm ứng tăng cường hoạt độ các enzyme chống ôxy hóa như superoxide dismutase (SOD, EC 1.15.1.1) and catalase (CAT, EC 1.11.1.6) sau khi rệp phá hại 24 - 48 giờ. Các enzyme này kiểm soát sinh tổng hợp $O_2^{\cdot-}$ và H_2O_2, góp phần giảm thiểu thiệt hại do stress "ôxy hóa" trong 48 - 96 giờ, đồng thời duy trì lượng ôxy hoạt hóa cần thiết để tham gia các phản ứng bảo vệ, tăng cường khả năng chống chịu của đậu tương Nam Đàn đối với sự phá hại của rệp.

Từ khóa: đậu tương Nam Đàn, rệp muội đen, stress "ôxy hóa", enzyme chống ôxy hóa.