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Salicylic and succinic acids as inducers of phytoimmunity in winter wheat for the management of powdery mildew (*Blumeria graminis* (DC) Speer f. sp. *tritici*)

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Abstract

Background Growth regulators play an important role in activating the main signal transduction pathways in response to stress, and their activity is key in the general mechanism to understanding the formation of phytoimmunity under biotic stress. The study investigates the specificity of stress-protective reactions in winter wheat varieties with varying degrees of sensitivity to the phytopathogen Blumeria graminis (DC) Speer f. sp. *tritici*, and determined the effectiveness of exogenous salicylic and succinic acids as inducers of resistance to powdery mildew.

Results Exogenous application of 0.1 mM salicylic acid induced stress-protective reactions in the resistant wheat, characterised by increased ethylene release, and phenylalanine amino-lyase and ascorbate peroxidase activity in the flag leaves. These steps help optimize its physiological state and productivity by preserving the integrity of cell membranes and its chlorophyll content. Exogenous succinic acid at a concentration of 0.1 mM also led to the activation of protective antioxidant systems, which did not have a positive effect on plant physiology or productivity during infection. The susceptible variety of winter wheat was unable to mobilize the necessary stress-protective systems, regardless of salicylic or succinic acid treatment, resulting in the spread of infection and reduced productivity.

Conclusions The resistance of winter wheat to phytopathogen damage (*Blumeria graminis* (DC) Speer f. sp. *tritici*) is determined by the capacity of the plant to mobilize stress-protective reactions and optimize its metabolism. Salicylic acid (0.1 mM) effectively enhances plant defence systems, thus improving plant physiology and productivity during the spread of powdery mildew.

Keywords Antioxidant enzymes, Hydrogen peroxide, Ethylene, Phenylalanine-ammonia-lyase, Phytopathogen damage, Powdery mildew, *Triticum aestivum* L.

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Introduction

One of the ongoing challenges faced by agriculture is obtaining high and stable crop yields. Crop production is one of strategic importance for the sustainable development of the world economy; indeed, while cereals have not only been a staple food for millennia, they also increasingly represent a renewable raw material for industrial and energy purposes [1–3]. One of the most profitable agricultural crops is winter wheat (*Triticum aestivum* L.), whose high productivity is determined by a complex combination of external factors [4].

Winter wheat has a vital role in the global human diet. Its high ecological plasticity allows it to be grown in most countries with developed agricultural production, and its wheat growth represents a strategic goal for strengthening the economy of any country [5]. However, in recent years, it has been subject to increasing damage by phytopathogens and pests, which has been exacerbated by climate change [6]. A key factor restricting the productivity of winter wheat is the occurrence of disease, with the most harmful being powdery mildew, septoria leaf spot, brown leaf rust [7].

Powdery mildew of wheat can significantly decrease wheat yield and quality. Its causative agent is the marsupial fungus *Blumeria graminis* (DC) Speer f. sp. *tritici*, an obligate, highly-specialized parasite [8]. Infection with powdery mildew reduces the surface area of leaves available for light assimilation, destroys chlorophyll and thus reduces the intensity of photosynthesis [9]. In turn, this delays the earing and ripening of wheat, and lowers productivity [10]. This is particularly evident in susceptible wheat varieties, where the disease is a major yield limiting factor [11]. It is therefore believed that resistant varieties can be included in breeding programs to prevent yield losses [12–14].

The productive potential of cultivated plants can be increased by activating the plant immune system; this can be done using biologically-active phytohormones, which purposefully affect the endogenous regulatory systems. It has been demonstrated that plant metabolism can be regulated by exogenous analogues of natural growth regulators [15–17]. It has been shown that regulating the metabolism and mobilizing antioxidant properties can increase productivity of winter wheat [18].

Phytohormones play an important role in plant responses to both internal and external factors [19]. Among them, abscisic acid, ethylene, brassinosteroids, salicylates, and jasmonates are produced in response to adverse factors, and are hence recognised as stress phytohormones [20]. Complex functional interactions occur between these phytohormones, the mechanisms of which are still not fully understood.

Salicylic and jasmonic acids and ethylene are involved in the establishment of the immune response of plants, and their transduction pathways are associated with cytokinin, auxin and DELLA protein signalling [21]. In addition, the cross-talk between these transduction pathways modulates the plant response to stress factors, which is primarily of a biotic nature [17]. As their production can be stimulated by exogenous treatment with synthetic analogues, this may be a promising way to enhance the stress response.

Salicylic acid (SA) plays an important role in regulating protective reactions. It can control the synthesis of protective compounds and the formation of systemically acquired resistance (SAR) via receptors in the plasmalemma [22, 23]. SA induces the synthesis of pathogenesis-related (PR) proteins at the transcriptional level: SA-sensitive cis-active elements have been identified in the PR protein gene promotors. SA can hence play an important role in the expression of genes associated with the local and systemic resistance of plants [24–26].

Some physiological reactions induced by SA, such as the increased formation of reactive oxygen species (ROS) and synthesis of some proteins, may also be caused by acids involved in the Krebs cycle, such as succinic acid (SUA) [27, 28]. This acid is able to increase plant resistance to some adverse factors [28]; some authors consider it to be SA mimetic [29]. Despite the use of both acids in plant cultivation in practice, the mechanisms of their effects on plants have not been studied sufficiently, especially those of exogenous SUA.

Research hypothesis: the formation of phytoimmunity of winter wheat to the powdery mildew pathogen *Blumeria graminis* (DC) Speer f. sp. *tritici* is associated with the variety's capacity to implement stress-protective reactions, the components of which are the intensification of ethylene release, the activity of phenylalanine ammonium lyase and antioxidant enzymes, which can be enhanced in response to exogenous growth-regulating substances.

The aim of the research was (i) to investigate the protective reactions of different winter wheat genotypes in response to *Blumeria graminis* (DC) Speer f. sp. *tritici* damage following SA and SUA treatments, (ii) to assess the effectiveness of SA and SUA treatments for increasing the productive potential of different wheat varieties during the development of powdery mildew; (iii) to compare the effects of exogenous SA and SUA as inducers of winter wheat phytoimmunity.

Materials and methods

Conditions of the experiment

Favoritka and Poliska 90, two soft winter wheat varieties (*Triticum aestivum* L.) were selected for the study. Favorite is a resistant and high-intensity type; it was originated by the Institute of Plant Physiology and Genetics, National Academy of Sciences of Ukraine. Poliska 90 is a

susceptible and intensive type, originated by the Institute of Agriculture, Ukrainian Academy of Sciences.

Plants were grown in 10-kilogram vessels on dark gray podzolized soil under optimal water supply and natural lighting. The winter wheat was naturally infected by the phytopathogen *Blumeria graminis* (DC) Speer f. sp. *tritici* during earing– flowering stages. Throughout the course of the ex vivo experiment, the relative humidity of the air and soil, as well as the uniformity of plant illumination, were strictly controlled. This ensured the same conditions for plant growth. When the development of powdery mildew reached 5% of the total natural background of plant damage, the plants were treated with SA and SUA at concentration of 0.1 mM (previously established experimentally) at 27–29˚C and 56–60% relative humidity (Fig. 1). At 14 day after infection, flag leaves were selected for physiological and biochemical analysis. A control group was consisting of plants infected with *Blumeria graminis* (DC) Speer f. sp. *tritici* but not treated with growth regulators (GR).

Determination of hydrogen peroxide (H_2O_2) content

H_2O_2 content was determined by the ferrothiocyanite method [30]. The plant flag leaves was extracted (ratio 1:3) with a cooled solution of 5% trichloroacetic acid. The extract was centrifuged at 14,000 rpm for 5 min (4 °C) and the supernatant was obtained. The concentration of H_2O_2 was determined by a color reaction with potassium thiocyanate spectrophotometrically at a wavelength of 480 nm, and calculated using a calibration curve. The results are presented as μmol per gram of dry matter mass.

Superoxide dismutase (SOD) activity (EC 1.15.1.1)

To obtain the enzyme extract, a 0.2 g of plant material was ground in a mortar with 4 ml of 50 mM phosphate buffer (pH 7.5) containing 2 mM EDTA, 1 mM PMSF, 5 mM β-mercaptoethanol and 1% polyvinylpyrrolidone. The homogenate was centrifuged at 10,000 rpm for 20 min at 4°C. The activity of SOD in the supernatant was determined by its ability to inhibit the photochemical reduction of nitroblue tetrazolium [31]. The reaction mixture contained 50 mM phosphate buffer (pH 7.8), 13 mM methionine, 2 μM riboflavin, 63 μM p-nitroblue tetrazolium, 0.1 mM EDTA, and 100 μL of enzyme extract. The reaction proceeded for 15 min at a light intensity of 70 μmoL quanta/($m^2 \cdot s$) illumination by fluorescent lamps with a power of 15 W. The optical density was measured at 560 nm. The results are presented as units of enzyme activity (U) per mg of protein in the supernatant.

Catalase activity (CAT) (EC 1.11.1.6.)

To obtain the enzyme extract, a 0.2 g of plant material was triturated (ratio 1: 2) with a cooled 0.5 M Tris-HCl

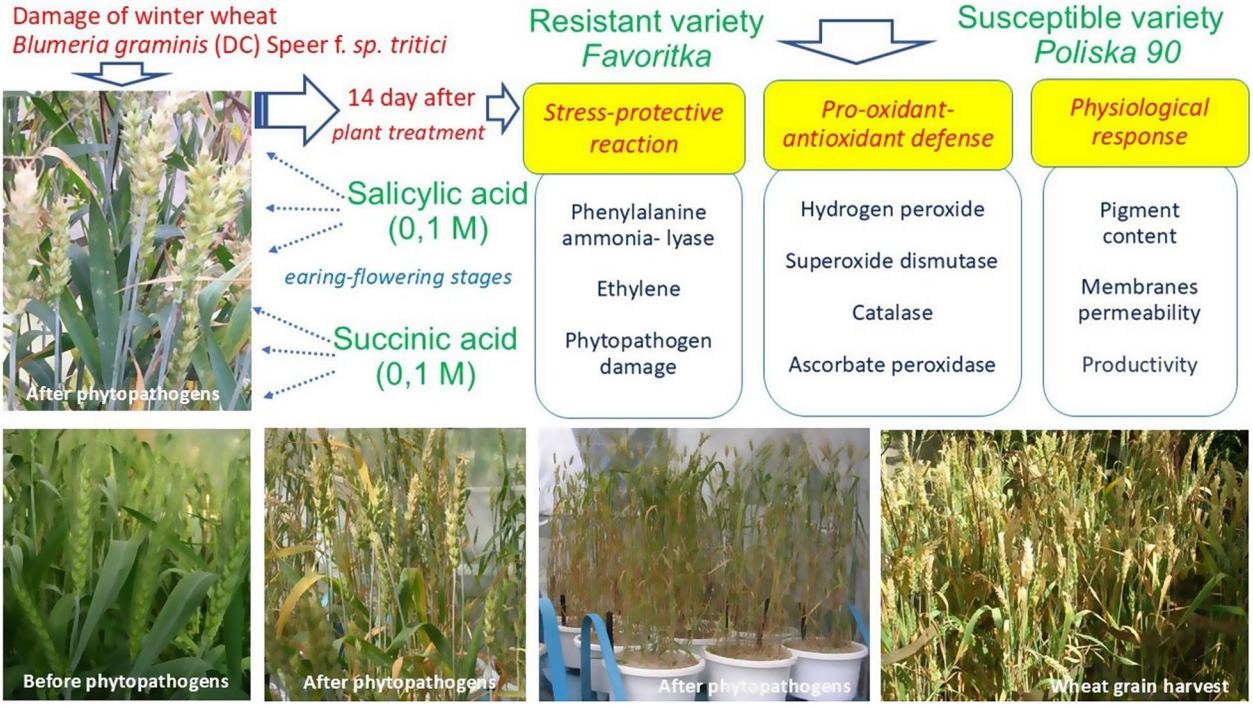

Fig. 1 The main steps of the experiment. The plants were treated with SA or SUA (0.1 mM) in the earing-flowering stages, when the development of powdery mildew reached 5% of the total natural background of plant damage. At 14 day after treatment with GR, flag leaves were selected for physiological and biochemical analysis. The research was conducted at a specially-equipped vegetation site of the Institute of Plant Physiology and Genetics of the National Academy of Sciences of Ukraine

buffer (pH 7.8) containing 5 mM β-mercaptoethanol and 0.1% polyvinylpyrrolidone. The homogenate was centrifuged at 10,000 rpm (4°C) for 20 min. The supernatant was taken and assayed for CAT activity by the development of a color reaction with ammonium molybdate; the concentration was measured at a wavelength of 410 nm [32]. The results are presented as units of enzyme activity (U) per mg of protein in the supernatant.

Ascorbate peroxide (APO) activity (EC 1.11.1.11)

To obtain the enzyme extract, a 0.2 g plant material was ground in a mortar with 4 ml of 50 mM phosphate buffer (pH 7.5), which contained 2 mM EDTA, 1 mM PMSF, 5 mM β-mercaptoethanol and 1% polyvinylpyrrolidone. The homogenate was centrifuged at 10,000 rpm for 20 min at 4°C. APO activity was determined by the decrease in optical density at a wavelength of 290 nm for 2 min as a result of ascorbate oxidation (ε = 2.8 $mM^{-1}cm^{-1}$) [33]. The reaction mixture contained 60 mM potassium phosphate buffer (pH 7.0), 0.1 mM EDTA, 0.2 mM ascorbate, 0.1 mM H_2O_2. The reaction was initiated by adding the supernatant. The results are presented as μmol of oxidized ascorbate in terms of the content (mg) of total soluble protein per minute.

Phenylalanine ammonia-lyase (PAL) activity EC 4.3.1.5)

To obtain the enzyme extract, the plant material was homogenized with a 0.2 M solution of borate buffer (pH 8.8) in a ratio of 1:2 (w/v), which contained 1 mM EDTA, 5 mM β-mercaptoethanol, and 1% polyvinylpyrrolidone (w/v). The homogenate was centrifuged at 12,000 rpm for 20 min at 4°C. The supernatant was used to determine PAL activity spectrophotometrically at 290 nm by the formation of trans-cinnamic acid in 0.1 M borate buffer (pH 8.8) in the presence of 50 mM L-phenylalanine [34]. The reaction mixture was incubated for one hour at 40 °C. The results are presented as units of enzyme activity per protein concentration (mg) in the supernatant.

Total soluble protein measurements

Total soluble protein content was determined according to Bradford [35]. The soluble protein content was measured against a standard curve using bovine serum albumin. The method is based on the reaction of the Coomassie Brilliant Blue G-250 dye. The bound form has a blue color with an absorption maximum at 595 nm. Thus, the increase in light absorption of a solution at a wavelength of 595 nm is proportional to the amount of protein in the solution.

Ethylene emission

One whole wheat flag leaf were placed in 75 mL glass vials, which were immediately sealed and left in the dark for 24 h [36]. After incubation, the gas mixture containing ethylene was analyzed on an Agilent GC system 6850 gas chromatograph (USA). The volume of the analyzed gas mixture sample was 1 ml. Pure ethylene (Sigma-Aldrich, USA) was used as a standard. The amount of ethylene released from the incubated sample was expressed as nmol per plant per hour (nmol C_2H_4/plant · h).

Phytopathogen damage

The degree of damage and infestation is determined by taking into account the affected area of the crop diagonally in two directions, inspecting 10 plants in 10 places [37]. The degree of powdery mildew damage is determined by counting the total number of leaves and stems on a 4-point scale: 0– no damage; 1– up to 25% of the surface is damaged; 2–25–60% of the surface is damaged; 3– more than 50% of the surface is damaged.

Exosmosis of electrolytes (EEL)

Exosmosis electrolytes were evaluated by the electrolyt method [38], i.e. by measuring the resistance of electrolyte solutions washed out of the tissue (exosmosis). Flag leaves (1 g) were immersed for four hours in 100 ml of distilled water. In the resulting solution, the resistance of the washed electrolytes was measured using a rheochord bridge and an X-38 electrolytic cell. The total output of electrolytes was determined by measuring the electrical conductivity after boiling, which destroyed the membranes. The EEL value was calculated as a percentage of total exosmosis.

Chlorophyll content

The wheat flag leaves (0,5 g) was covered with dimethylsulfoxide and placed in a water bath at a temperature of + 63 °C for three hours to ensure complete extraction. The obtained extract was diluted in dimethylsulfoxide (ratio of 1:9). The optical density of the obtained solution was determined at wavelengths of 649 and 665 nm [39].

Productivity

Grain yield was recorded by hand picking and then weighing them [40]. Wheat productivity was determined based on the grain number and 1000-grain mass. This was calculated on the basis of five vessels per variant, 16 plants in each vessel.

Statistical analysis

Basic statistical analyses were conducted using STATISTICA version 13.3 [41]. The significance of differences in physiological parameters between experimental variants (control, SA, SUA) was tested using the nonparametric Kruskal-Wallis ANOVA. Thus, six experimental treatments were created, viz. three treatments for the resistant variety and three for the susceptible variety. Each treatment contained ten vessels, five of which were for

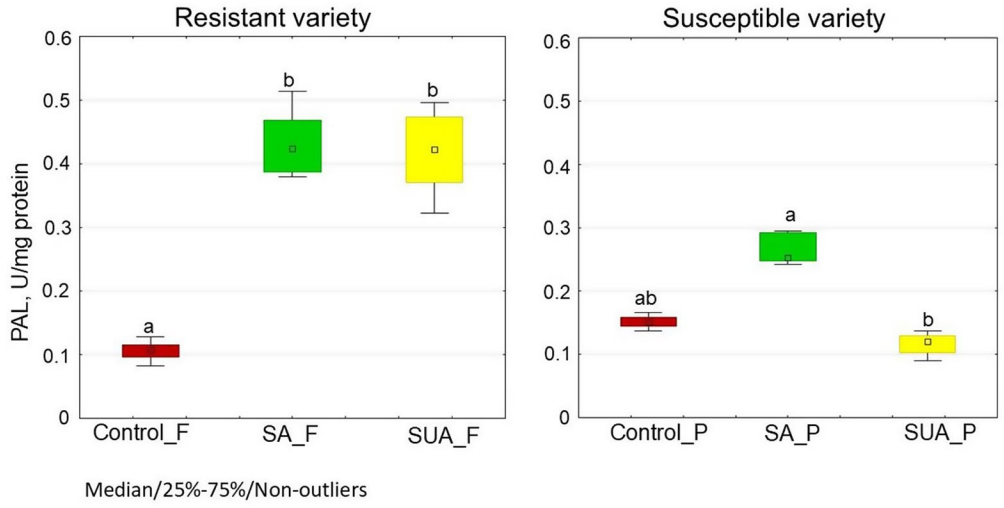

Fig. 2 Effect of treatment with SA and SUA (0.1 mM) on the activity of PAL enzyme in the flag leaves of the resistant (Favoritka_F) and susceptible (Poliska 90_P) wheat variety, on day 14 after treatment following infection with *Blumeria graminis* (DC) Speer f. sp. *tritici*. The letters indicate significant differences between the variants ($p < 0.05$); Kruskal-Wallis test analysis. Experimental treatments, SA: Salicylic Acid, SUA: Succinic Acid, Control: Untreated plants

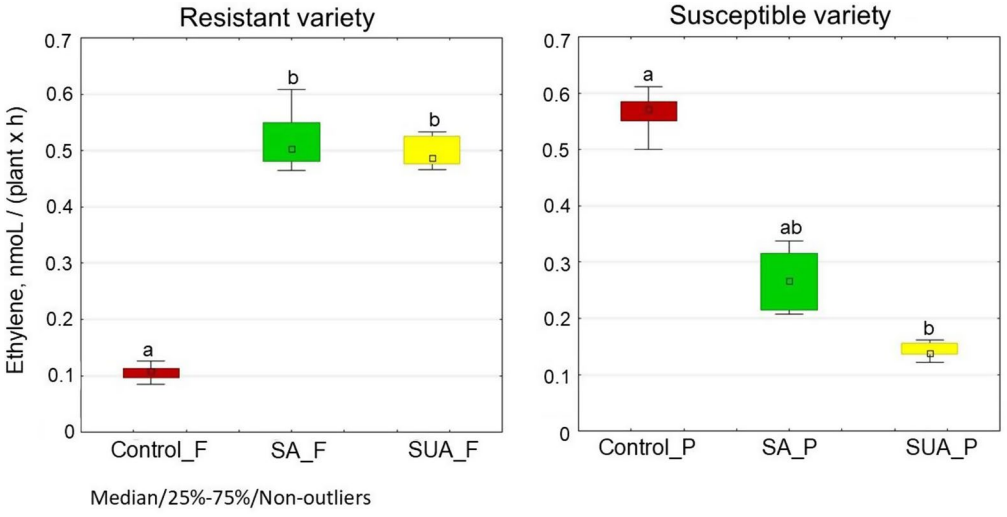

Fig. 3 Effect of treatment with SA and SUA (0.1 mM) on the intensity of ethylene release by flag leaves of the resistant (Favoritka_F) and susceptible (Poliska 90_P) wheat variety, on day 14 after treatment following infection with *Blumeria graminis* (DC) Speer f. sp. *tritici*. The letters indicate significant differences between the variants ($p < 0.05$); Kruskal-Wallis test analysis. Experimental treatments, SA: Salicylic Acid, SUA: Succinic Acid, Control: Untreated plants

productivity, with sixteen plants per vessel. Flag leaves were selected for analysis in six replicates.

An unconstrained ordination using Principal Component Analysis (PCA) was performed in a multidimensional space to visualize the differences and magnitude of plant responses to stress. The analysis included the following three sets of variables: (1) indicators of the plant response to biotic stress and phytopathogen attacks viz. PAL, Ethylene level, and Phytopathogen Damage (Fig. 5); (2) levels of antioxidant enzymes and related compounds, represented by SOD, CAT, APO, and H_2O_2 (Fig. 10); and (3) growth and yield indicators, represented by Exo-electrolytes, Grain Number, 1000-Grain Weight, and Chlorophyll Content (Fig. 15). Multidimensional analysis and ordination plots were performed using the CANOCO 5 package [42].

Results

Stress-protective reaction

In the resistant variety of wheat (Favoritka), PAL activity was significantly higher in plants treated with SA (Me = 0.43 U/mg protein) and SUA (0.42) add as compared to control (0.11) (Fig. 2). The PAL activity in the treated plants were higher by 280–290% respectively (Fig. 2).

On the other hand, in the susceptible variety (Poliska 90) the PAL activity was higher in the treated plants with SA (0.25) than control (0.15) (Fig. 2).

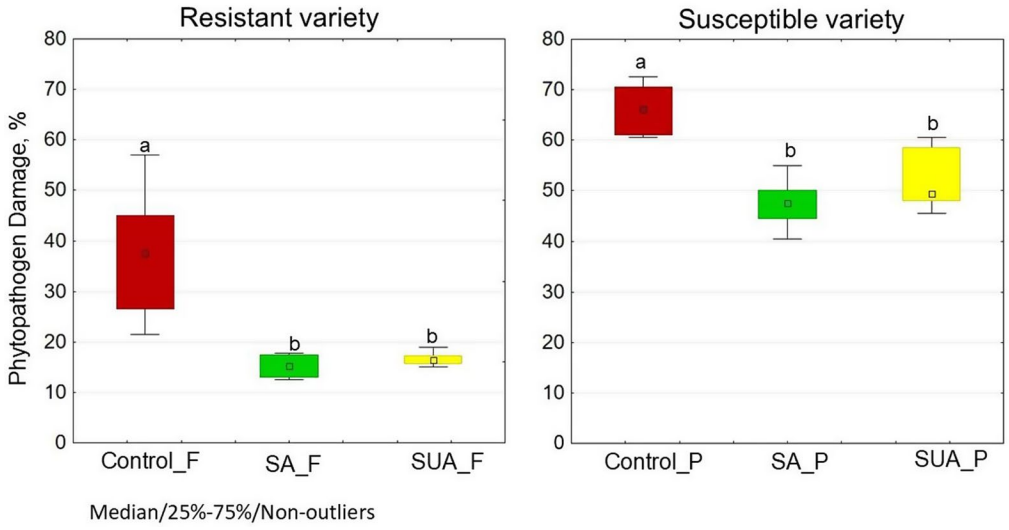

Fig. 4 Effect of treatment with SA and SUA (0.1mM) on the phytopathogen damage by plant to the resistant (Favoritka_F) and susceptible (Poliska 90_P) wheat variety, on day 14 after treatment following infection with *Blumeria graminis* (DC) Speer f. sp. *tritici*. The letters indicate significant differences between the variants ($p < 0.05$); Kruskal-Wallis test analysis. Experimental treatments, SA: Salicylic Acid, SUA: Succinic Acid, Control: Untreated plants

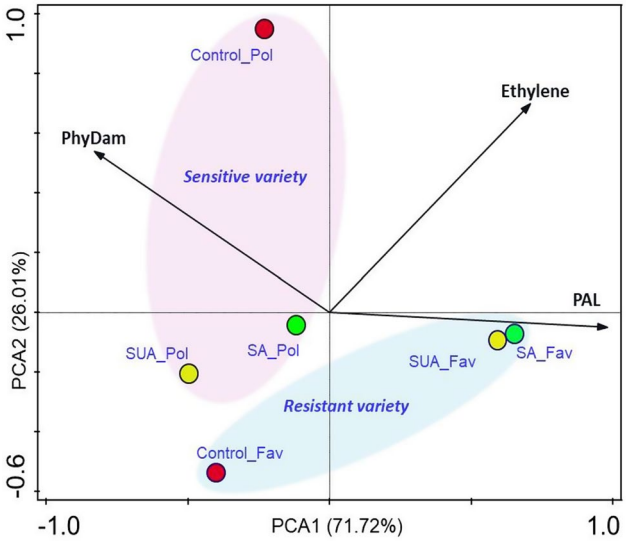

Fig. 5 PCA ordination diagram based on parameters associated with plant mechanisms in response to biotic stress and phytopathogen attacks, represented by PAL, Ethylene, and Phytopathogen Damage (PhyDam). The points represent experimental variants: control (red), SA (green), SUA (yellow) in the susceptible Poliska 90 (Pol) and resistant Favoritka (Fav) wheat varieties. The first PCA axis shows a trend with PAL activity, and the second PCA axis with ethylene and phytopathogen damage. The PCA shows a decrease in ethylene production and an increase in disease spread in susceptible plants under both SA and SUA treatments, while there is no change in PAL activity. In the resistant variety, SA and SUA treatments induced an increase in ethylene and PAL activity and a decrease in pathogen damage

In the resistant variety the release of ethylene was significantly higher in the plants treated with SA (Me = 0.52 nmol C_2H_4/plant · h) and SUA (0.49) as compared to control (0.11) (Fig. 3): the formation of ethylene at 14 day after treatment with GR was higher by 293.2 to 310.0% than control. No statistically significant differences were observed between the SA and SUA variants (Fig. 3).

In the susceptible variety, SUA-treated plants had the lowest ethylene release rate (0.14), as compared to the other treatments; SA-treated plants (0.26) and untreated plants (0.56) (Fig. 3).

In the resistant variety, day 14 after GR treatment, the spread of the disease was found to 59.4% and 55.4% slower in the plants treated with SA and SUA respectively. No statistically significant differences were observed between the SA and SUA variants (Fig. 4).

In the susceptible variety, treatment with SA and SUA resulted in similar disease spread. Less damage was notes on plants treated with SA (47.4) followed by SUA (52.3) as compared to control (66.1) (Fig. 4). No statistically significant differences were observed between the SA and SUA variants (Fig. 4).

The PCA results of the plant factors associated with biotic stress and phytopathogen attacks reveals interesting synthetic patterns, which differ between the susceptible and resistant varieties (Fig. 5). The first PCA axis is connected to PAL activity, the second PCA axis is connected to ethylene, and phytopathogen damage. In the susceptible variety, the addition of SA and SUA resulted in reduced ethylene and pathogen damage but no significant difference in the PAL activity. In the case of the resistant variety, the addition of SA and SUA increased ethylene and PAL activity and decreased pathogen damage (Fig. 5).

Pro-oxidant-antioxidant defense

In the resistant wheat variety, it was found that in the variants with SA and SUA treatments demonstrated

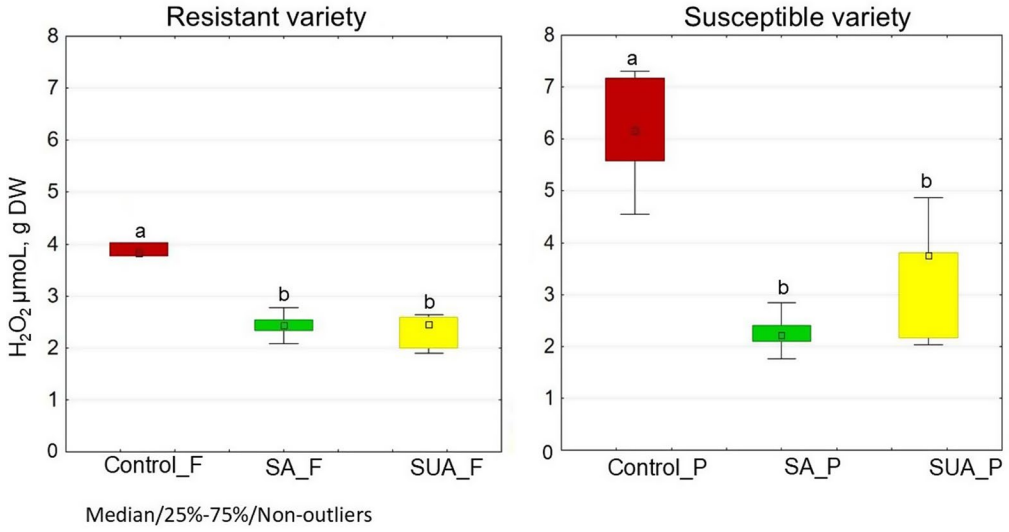

Fig. 6 Effect of treatment with SA and SUA (0.1mM) on the H_2O_2 production in the flag leaves of the resistant (Favoritka_F) and susceptible (Poliska 90_P) wheat variety, on day 14 after treatment following infection with *Blumeria graminis* (DC) Speer f. sp. *tritici*. The letters indicate significant differences between the variants ($p < 0.05$); Kruskal-Wallis test analysis. Experimental treatments, SA: Salicylic Acid, SUA: Succinic Acid, Control: Untreated plants

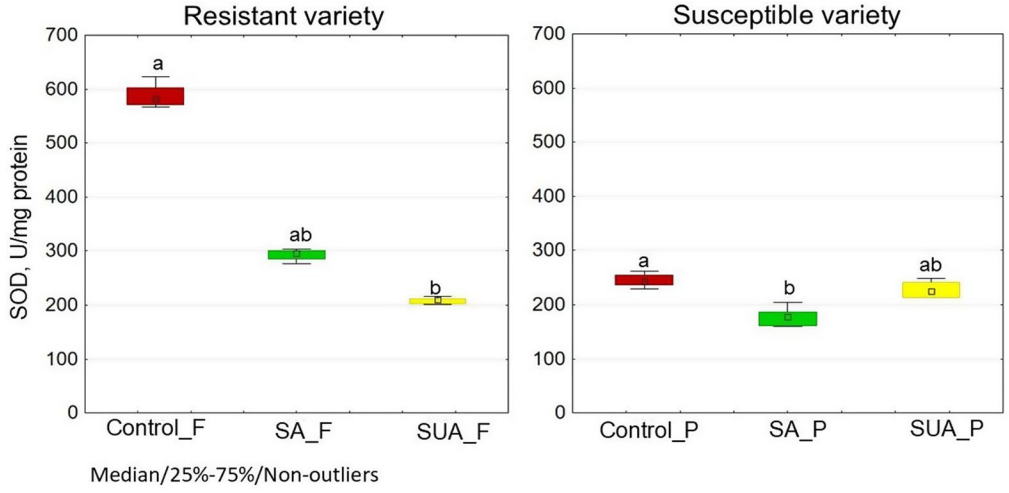

Fig. 7 Effect of treatment with SA and SUA (0.1mM) on the activity of SOD enzyme in the flag leaves of the resistant (Favoritka_F) and susceptible (Poliska 90_P) wheat variety, on day 14 after treatment following infection with *Blumeria graminis* (DC) Speer f. sp. *tritici*. The letters indicate significant differences between the variants ($p < 0.05$); Kruskal-Wallis test analysis. Experimental treatments, SA: Salicylic Acid, SUA: Succinic Acid, Control: Untreated plants

lower H_2O_2 accumulation in flag leaves (respectively Me = 2.43 and 2.31 µmoL/g dry weight) as compared to the control (3.81) (Fig. 6).

In susceptible wheat, the H_2O_2 concentrations were reduced by SA (2.26) and SUA (3.23) treatments: both values were lower than control values (6.15) (Fig. 6).

In the resistant variety, the lowest SOD activity was found in the leaves treated with SA (Me = 292.4 U/mg protein) and SUA (208.21), as compared to the control (588.8) (Fig. 7).

In the susceptible variety, the SOD activity was the lowest in the leaves treated with SA (177.8). Similar SOD activity was noted in the SUA plants (228.2) as controls (245.4) (Fig. 7).

In the resistant wheat variety, CAT activity was lower in the SA (Me = 0.064 U/mg protein · min) and SUA (0.056) variants compared to the control (0.12) (Fig. 8). In the susceptible wheat variety, in contrast to the resistant variety, the SA (0.090) and SUA (0.058) variants yielded greater CAT activity than the control (0.031) (Fig. 8).

In the resistant wheat variety, significantly higher APO activity was noted in the SA (Me = 5.09 µmol ascorbate/mg protein · min) and SUA (3.42) variants than the controls (1.76) (Fig. 9). The SUA (1.67), and SA variants had lower APO activity (2.67) than the control (4.49) (Fig. 9).

PCA ordination based on variables related to antioxidant enzymes and H_2O_2 revealed different patterns for susceptible and resistant varieties (Fig. 10). The SA and

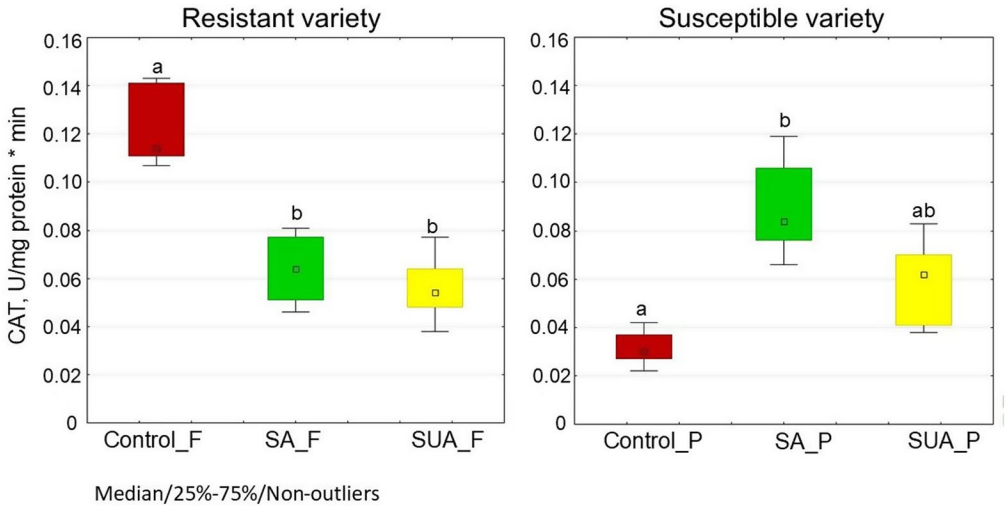

Fig. 8 Effect of treatment with SA and SUA (0.1mM) on the activity CAT enzyme in the flag leaves of the resistant (Favoritka_F) and susceptible (Poliska 90_P) wheat variety, on day 14 after treatment following infection with *Blumeria graminis* (DC) Speer f. sp. *tritici*. The letters indicate significant differences between the variants ($p < 0.05$); Kruskal-Wallis test analysis. Experimental treatments, SA: Salicylic Acid, SUA: Succinic Acid, Control: Untreated plants

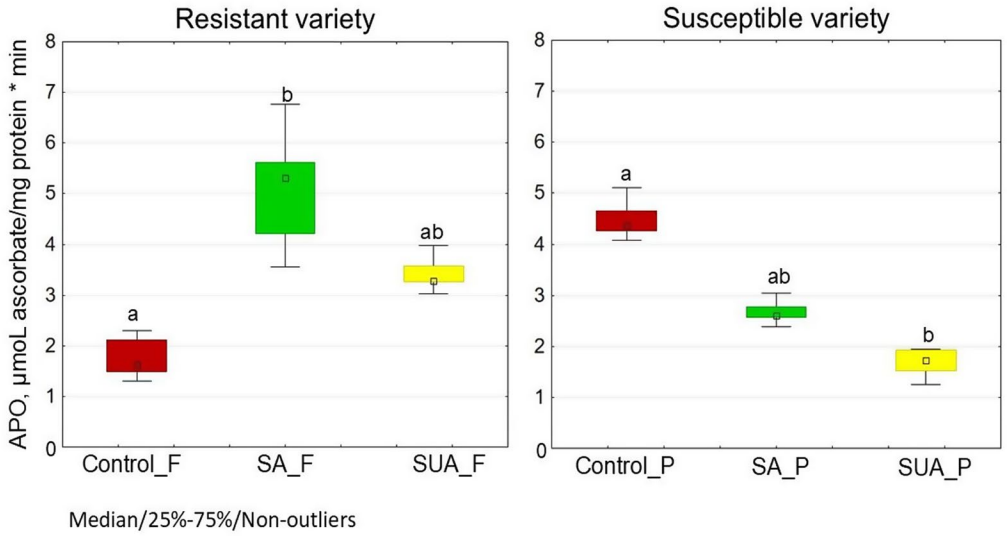

Fig. 9 Effect of treatment with SA and SUA (0.1mM) on the activity APO enzyme in the flag leaves of the resistant (Favoritka_F) and susceptible (Poliska 90_P) wheat variety, on day 14 after treatment following infection with *Blumeria graminis* (DC) Speer f. sp. *tritici*. The letters indicate significant differences between the variants ($p < 0.05$); Kruskal-Wallis test analysis. Experimental treatments, SA: Salicylic Acid, SUA: Succinic Acid, Control: Untreated plants

SUA treatments resulted in a decrease in all parameters, and the points representing both resistant and susceptible varieties are located in the same place in the PCA ordination space. However, differences between the varieties are also evident among the control plants: the susceptible variety showed high H_2O_2 levels, while the resistant variety had high SOD levels (Fig. 10).

Plant physiological response

In resistant wheat, chlorophyll content was significantly higher in leaves treated with SA (Me = 7.32 mg/dm^2) than in the control (4.92) (Fig. 11). No statistically significant differences in chlorophyll content were recorded in control plants and SUA treatment (Fig. 11).

In the susceptible wheat variety, there were no significant differences in chlorophyll content: SA and SUA indices ranged from 4.34 to 4.36 mg/dm^2, while in the control– 3.63 mg/dm^2 (Fig. 11).

Resistant wheat treated with SA showed lower leaf EEL (Me = 32.27%) compared to control (44.9) and SUA (43.1) (Fig. 12). That is, no significant differences were found between control plants and SUA treatments.

In susceptible wheat, lower EEL was found in both SUA (60.9) and SA (50.8) than in control (81.2) (Fig. 12).

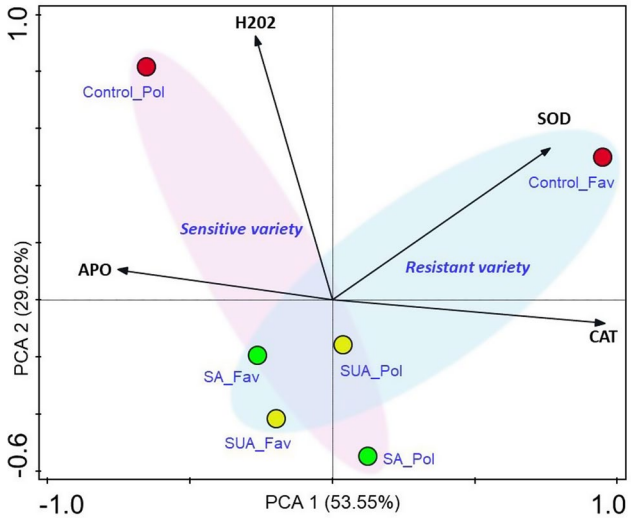

Fig. 10 PCA ordination diagram based on antioxidant enzymes and related compounds, viz. SOD, CAT, APO, and H_2O_2. The points represent experimental variants: control (red), SA (green), SUA (yellow) in the susceptible Poliska 90 (Pol) and resistant Favoritka (Fav) wheat varieties. SA and SUA treatments led to a decrease in all of the above parameters in both resistant and susceptible varieties. At the same time, their points were located in the same space on the PCA ordination. Differences on the PSA ordination were recorded for the controls - a high level of H_2O_2 in the leaves of the susceptible variety and a high activity of SOD in the resistant variety

In both varieties, no significant differences in grain number were observed between SA and SUA treatments and the control (Fig. 13). However, a significant difference was found in the 1000-grain weight index (Fig. 14).

In the resistant variety, the 1000 grain mass was 30% higher when using the SA treatment (Me = 50.9 g) as compared to control (39.2 g) (Fig. 14); However, no statistically significant differences were recorded in this indicator between the control and the SUA treatment.

In the susceptible variety, the SA treatment showed a 17.8% higher 1000 grain mass (32.8 g) than in control (27.8 g). However, no statistically significant differences were observed between the SUA treatment and the control (Fig. 14).

In the PCA ordination, the resistant and sensitive varieties were clearly separated along the first PCA axis based on physiological parameters (EEL and chlorphyll) and yield indicators; these explain 84% of the variance (Fig. 15). The sensitive wheat variety is associated with higher levels of exo-electrolytes and higher grain number, whereas the resistant variety is linked to greater chlorophyll content and grain mass. The highest score along the first PCA axis was achieved by the resistant variety treated with SA.

Discussion

Stress-protective reaction

PAL is a key enzyme in the plant response to biotic stress, and its gene expression and activity are believed to be markers of the defence response [43]. Our findings indicate that both SA and SUA treatments yielded similar increases in PAL activity in the leaves of resistant wheat (Favoritka) 14 days after treatment. In the susceptible wheat (Poliska 90), SA treatment significantly increased activity, while SUA treatment decreased it. This increase in PAL activity after exogenous SA treatment indicates possible changes in plant metabolic pathways to mitigate the effects of phytopathogen-induced stress.

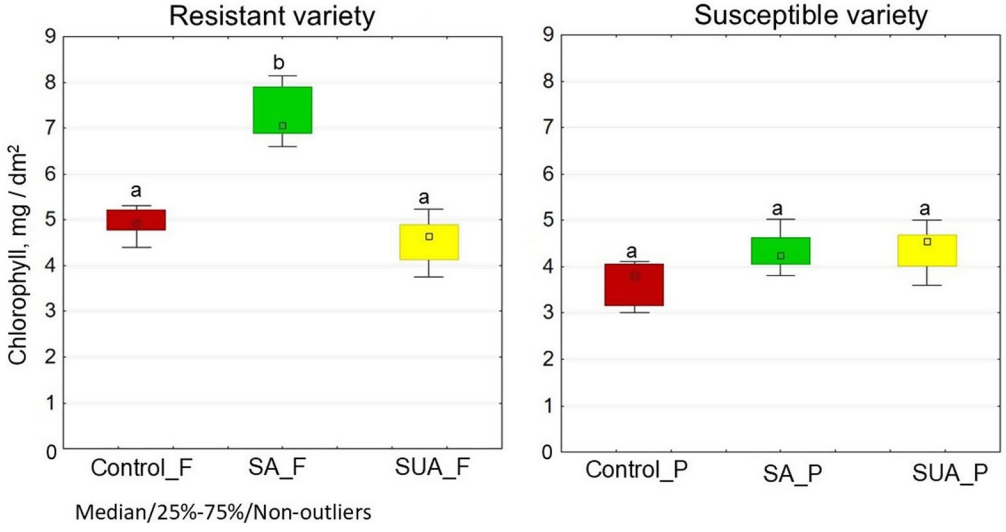

Fig. 11 Effect of treatment with SA and SUA (0.1mM) on the chlorophylls (*a* + *b*) content in the flag leaves of the resistant (Favoritka_F) and susceptible (Poliska 90_P) wheat variety, on day 14 after treatment following infection with *Blumeria graminis* (DC) Speer f. sp. *tritici*. The letters indicate significant differences between the variants ($p < 0.05$); Kruskal-Wallis test analysis. Experimental treatments, SA: Salicylic Acid, SUA: Succinic Acid, Control: Untreated plants

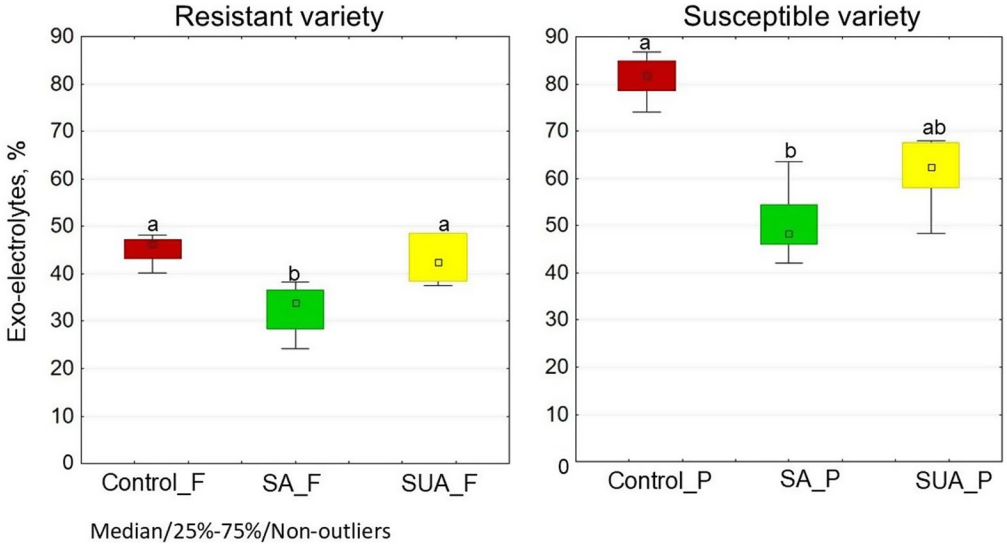

Fig. 12 Effect of treatment with SA and SUA (0.1mM) on the exosmosis of electrolytes by the flag leaves of the resistant (Favoritka_F) and susceptible (Poliska 90_P) wheat variety, on day 14 after treatment following infection with *Blumeria graminis* (DC) Speer f. sp. *tritici*. The letters indicate significant differences between the variants ($p < 0.05$); Kruskal-Wallis test analysis. Experimental treatments, SA: Salicylic Acid, SUA: Succinic Acid, Control: Untreated plants

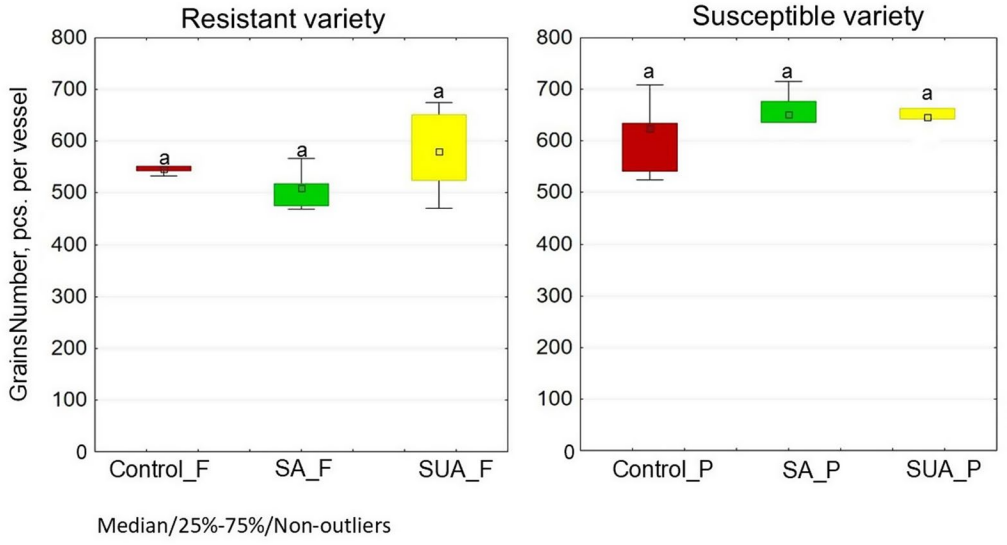

Fig. 13 Effect of treatment with SA and SUA (0.1mM) on the grains number in the resistant (Favoritka_F) and susceptible (Poliska 90_P) wheat variety, on day 14 after treatment following infection with *Blumeria graminis* (DC) Speer f. sp. *tritici*. The letters indicate significant differences between the variants ($p < 0.05$); Kruskal-Wallis test analysis. Experimental treatments, SA: Salicylic Acid, SUA: Succinic Acid, Control: Untreated plants

GR treatment also increased the intensity of ethylene production in the leaves during powdery mildew infection in the resistant variety. No such effect was detected in the susceptible variety; in fact a decrease in ethylene synthesis was noted, especially following SUA treatment.

SA plays a key role in the formation of SAR by facilitating the accumulation of a group of PR proteins. The process has been studied in detail in plants infected by phytopathogens [26, 44]. PAL gene expression is activated by the ethylene/jasmonate signaling pathway, resulting in the development of SAR [45]. Plants respond to phytopathogens by activating pathogen-protective pathways, which are controlled by the interaction between the ethylene, jasmonic acid and SA transduction pathways; these modulate the plant response to infection, resulting in the formation of SAR [45].

Thus, in the resistant variety, GR treatments led to the inclusion of stress-protective reactions, the key components of which are the activation of FAL and ethylene release. This was obviously accompanied by changes in plant metabolism, which slowed down the spread of the powdery mildew pathogen on winter wheat of the resistant variety Favoritka. The susceptible variety Poliska 90, as it turned out, was not able to realise its

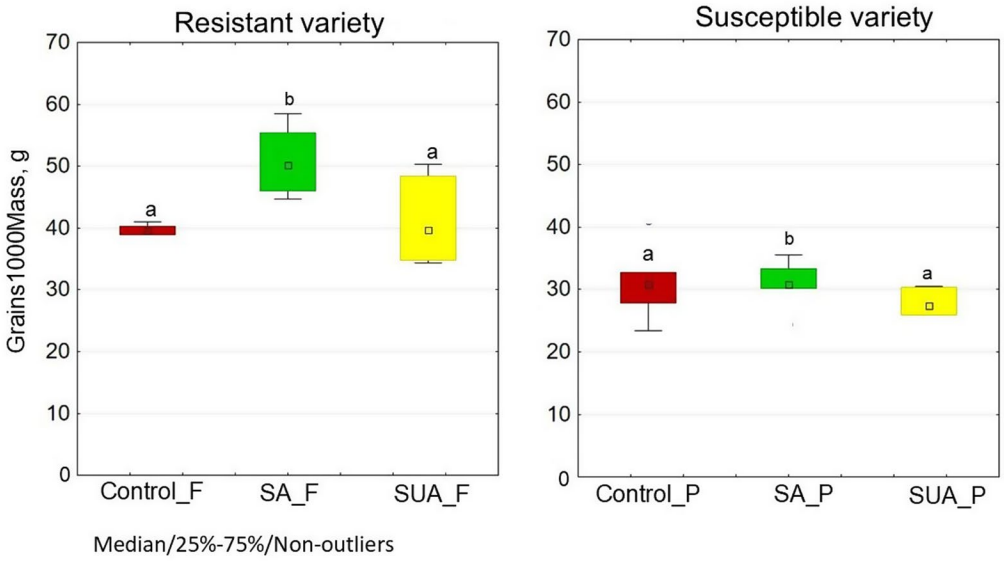

Fig. 14 Effect of treatment with SA and SUA (0.1mM) on the 1000 grains mass in the resistant (Favoritka_F) and susceptible (Poliska 90_P) wheat variety, on day 14 after treatment following infection with *Blumeria graminis* (DC) Speer f. sp. *tritici*. The letters indicate significant differences between the variants ($p < 0.05$); Kruskal-Wallis test analysis. Experimental treatments, SA: Salicylic Acid, SUA: Succinic Acid, Control: Untreated plants

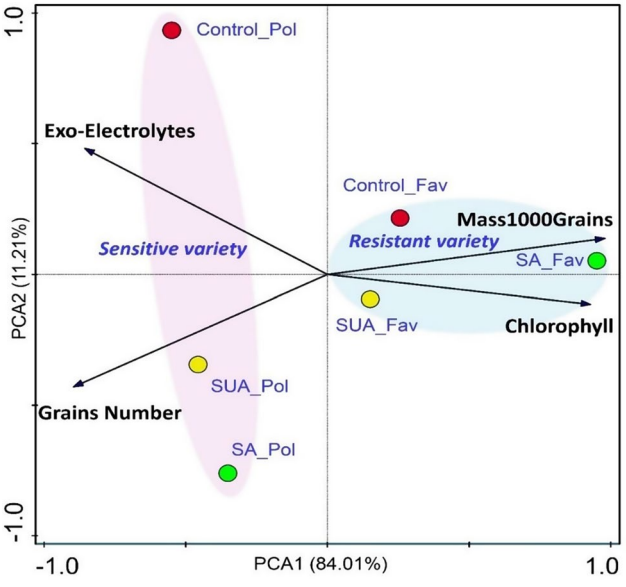

Fig. 15 PCA ordination diagram based on physiological parameters and yield indicators, represented by exo-electrolytes, grain number, 1000 grain mass, and chlorophyll content. The points represent experimental variants: control (red), SA (green), SUA (yellow) in the susceptible Poliska 90 (Pol) and resistant Favoritka (Fav) wheat varieties. The PCA showed that the susceptible wheat variety had higher exoelectrolyte values and grain number. The resistant variety had higher chlorophyll content and 1000 grain mass. PCA showed the highest values of all indicators on the first axis for the resistant variety under SA treatment

stress-protective potential, regardless of the exogenous impact of GR. Thus, the resistant variety achieved a more significant slowdown in disease development when sprayed with SA or SUA as compared to the susceptible variety.

Pro-oxidant-antioxidant defense

Studies indicate that SA affects both ROS generation and the activity of antioxidant enzymes, causing intracellular changes in antioxidant status [46–48]. However, it remains unclear which enzymatic systems are involved in the SA-induced enhancement of ROS generation. It is possible that SA can bind to the active center of CAT and act as a competitive inhibitor in the degradation of hydrogen peroxide [49]. In addition, salicylate-sensitive and salicylate-insensitive forms of CAT have been identified in plants, and these are encoded by independent genes [50].

Exogenous application of GR treatments led to a decrease in the H_2O_2 accumulation and the SOD enzyme activity in the flag leaves of both wheat varieties. Similar trends were recorded in both varieties after SA or SUA treatments.

The exogenous action of GRs were aimed at reducing the development of oxidative stress in both wheat varieties induced by a phytopathogen. This is evidenced by the decrease in the levels of H_2O_2 generation in the leaves of both wheat varieties with SA and SUA treatments. The wheat leaves also demonstrate lower SOD enzyme activity when receiving GR treatments, indicating slower ROS accumulation, since this enzyme is responsible for the utilization of excessive superoxide anion radicals in cells.

Thus, the SOD enzyme, which catalyzes the formation of hydrogen peroxide and oxygen from superoxide anion radicals, is considered a key enzyme in protecting living organisms from oxidative damage [51]. The effective functioning of SOD is largely determined by the functioning of other components of the defense system, in

particular those that utilize excessive amounts of hydrogen peroxide [52]. A whole complex of enzymes and substrates is involved in the removal of hydrogen peroxide. One of the key antioxidant enzymes that protect the aerobic cell from the toxic effects of hydrogen peroxide is APO and CAT [53].

The resistant and susceptible wheat varieties also differed with regard to their response to treatment: SA and SUA treatment increased APO activation and decreased CAT activity in the resistant variety, but increased CAT activity and reduced APO activity in the susceptible variety. It is worth emphasizing that the enzymatic reaction did not depend on the applied exogenous substance, as SA and SUA elicited similar reactions. This suggests that the reaction could be influenced by the genetic characteristics of the variety on the one hand, and the specific reaction of each variety in response to exogenous GRs while experiencing. It is obvious that in both varieties, the enzymatic complexes were activated to counter the excessive production of H_2O_2, and reduce its accumulation.

Plant physiological response

Our previous studies have shown that the use of exogenous GR promotes plant growth, and preserves of tissue hydration and antioxidant status, which improves the resistance of wheat to adverse environmental conditions [18, 53].

In the resistant wheat, the application of SA in the earing-flowering stages led to an increase in the concentration of chlorophylls in the leaves compared with SUA. No similar changes were recorded in the susceptible wheat. This is obviously related to the strong ability of the resistant wheat variety to mobilize defense systems under the influence of SA to protect, or restore, the pigment complexes.

While SA treatment slowed down the release of EEL from the leaves in both varieties, this was not observed for SUA in the resistant variety. This indicates that exogenous SA application has a positive effect on the plant by decreasing the permeability of cell membranes for electrolytes, thus maintaining their integrity during disease development.

SA clearly had a beneficial effect on the physiological state of the resistant wheat plants; in addition to decreasing the permeability of cell membranes for electrolytes, it also improved their integrity against disease and optimized the pigment complex. As a result, SA treatment improved the crop structure in the resistant winter wheat, thus increasing grain yield.

In the susceptible variety, SA treatment resulted in an increase in grain number; the plants tended to produce more small grains, reaching up to 660 pcs. per vessel, and no positive changes were noted in 1000-grain mass. The plants receiving SUA treatment did not demonstrate any significant positive changes in structural yield.

Therefore, exogenous GR application improved the phytoimmunity of winter wheat to phytopathogenic *Blumeria graminis* (DC) Speer f. Sp. *tritici*, the causative agent of powdery mildew. Treatment allowed the activation of stress-protective reactions, such as greater release of the stress hormone ethylene, and increases in PAL, CAT and APO activity. The intensity of these changes depends on the genetic potential of the wheat variety, its capacity to implement stress-protective systems to optimize physiological processes and productivity during phytopathogen spread.

The exogenous application of synthetic SA analogues, or compounds aimed at stimulating endogenous SA, is a promising strategy to increase plant SAR. SAR is a powerful mechanism based on the SA signaling pathway that allows plants to resist a wide range of pathogens. However, to ensure long-term phytoimmunity, is important to consider *inter alia* any possible synergy between SA treatment, other signaling pathways and the use of exogenous stimulants [43].

Our studies have shown that in a resistant winter wheat variety, the use of GR treatments stimulates the development of protective reactions and metabolic changes aimed at the formation of phytoimmunity to powdery mildew. As a result, the resistant variety demonstrated a slower disease development 14 days after SA or SUA treatment. In contrast, the susceptible variety was unable to mobilize protective systems aimed at slowing the spread of powdery mildew regardless of GR treatment (Fig. 16).

The study examines the theoretical basis of the stress-protective reactions demonstrated by various winter wheat varieties with different sensitivity to phytopathogen damage; however, its findings also have practical value, as they can be used to enhance the protective systems employed by plants against phytopathogen damage. More specifically, exogenous treatment with salicylic acid at a concentration of 1 mM effectively supports the immune system. However, this field studies require further detailed study to identify a solution that balances efficiency with economic feasibility.

Conclusions

The formation of phytoimmunity of winter wheat to damage by the phytopathogen *Blumeria graminis* (DC) Speer f. sp. *tritici* depends on its capacity to implement its stress-protective systems during the spread of disease.

The susceptible variety of winter wheat was unable to induce the necessary protective reactions to maintain its functioning regardless of the SA and SUA treatments. However, in the resistant winter wheat, exogenous SA (0.1 mM) induced the formation of phytoimmunity

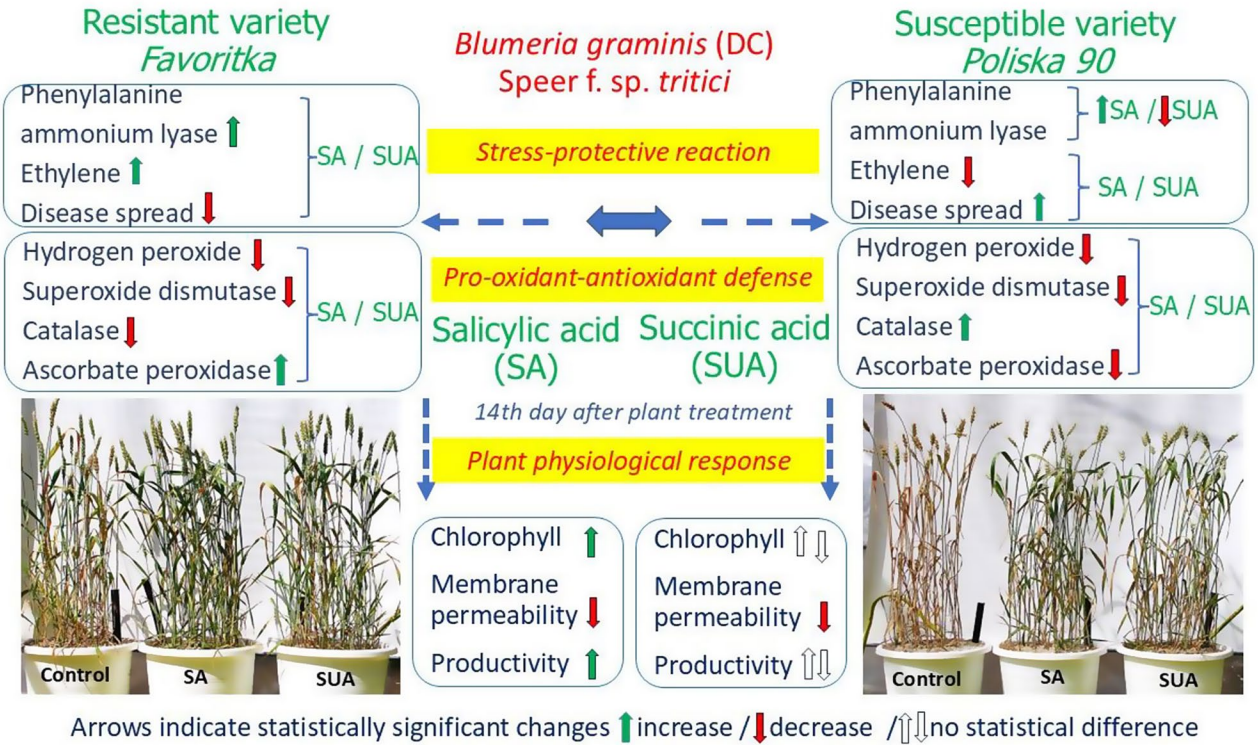

Fig. 16 Schematic representation of the reaction of different winter wheat varieties to damage by the phytopathogen *Blumeria graminis* (DC) Speer f. sp. *tritici* on day 14 after exogenous SA and SUA application. The direction of the arrows indicates a change in the levels of the specified parameter– increase (green) and decrease (red); double white arrows indicate no change relative to control. Experimental treatments, SA: Salicylic Acid, SUA: Succinic Acid, Control: Untreated plants

through the activation of PAL and APO, and intensifying ethylene release in leaves, thus preserving cell membrane integrity and the pigment complex. As a result, the treatment has a positive effect on yield.

Exogenous SUA (0.1 mM) caused similar pro-antioxidant changes in the resistant wheat variety as SA treatment. However, SUA treatment had no positive effect on plants physiological state and grain yield.

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Author contributions
All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by T.N. and M.K. The first draft of the manuscript was written by T.N. and all authors commented on previous versions of the manuscript. Supervision S.K. and E.K. All authors read and approved the final manuscript.

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Data availability
The datasets generated during and/or analyzed during the current study are available from the corresponding author on reason able request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare no competing interests.

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