PLANTA DANINHA

SOCIEDADE BRASILEIRA DA CIÊNCIA DAS PLANTAS DANINHAS

SBCPD

<http://www.sbcpd.org>

ISSN 0100-8358 (print)
1806-9681 (online)

Article

Does the Interference of GR® Volunteer Corn Alters Stress Metabolism on Soybean?

A Interferência de Milho Voluntário RR® Altera o Metabolismo do Estresse na Soja?

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Received: Novewmber 15, 2016
Approved: January 6, 2017

Planta Daninha 2018; v36:e018171955

ABSTRACT - The cultivation of GR® corn prior to soybean favors the occurrence of GR® volunteer corn plants interfering in soybean crops. The interference of volunteer corn causes the soybean yield losses, and the magnitude of losses varies with the corn density. The soybean yield losses can be partially explained by the occurrence of oxidative stress, which occurs by the higher content of reactive oxygen species (ROS), such as hydrogen peroxide (H_2O_2). The objective of this study was to quantify H_2O_2 content and the activity of superoxide dismutase (SOD), catalase (CAT) and ascorbate peroxidase (APX) on soybean as a function of interference of populations of GR® volunteer corn originated from individual plants and clumps (clumps are seven corn plants emerged at the same point) in different times, as well as to determine wheter this interference alters stress metabolism on soybean. Quantification was performed at 20, 35 and 46 days after emergence (DAE) of soybean. The mean volunteer corn populations were 0, 0.5, 1, 2, 4, 8, 10 and 12 plants or clumps m^{-2}. The results show changes in H_2O_2 content and SOD, CAT and APX activity as a response to interference with volunteer corn populations and origins. The higher activity was observed for SOD. Soybean yield reduce with the increase of populations of volunteer corn originated from individual plants and clumps.

Keywords: *Glycine max*, *Zea mays,* volunteer plants, competition, oxidative stress.

RESUMO - O cultivo de milho RR® antecedendo a soja favorece a ocorrência de plantas voluntárias de milho RR® interferindo em lavouras de soja. A interferência de plantas voluntárias de milho reduz a produtividade da soja, sendo mais intensa quanto maior for a população. A intensa redução na produtividade da soja sob inteferência de milho voluntário pode estar relacionada com o estresse oxidativo decorrente da maior produção de espécies reativas de oxigênio (EROs), como o peróxido de hidrogênio (H_2O_2). O objetivo deste estudo foi quantificar os teores de H_2O_2 e a atividade das enzimas superóxido dismutase (SOD), catalase (CAT) e ascorbato peroxidase (APX) na soja em competição com populações de milho voluntário RR®, originado de plantas individuais e/ou touceiras (sete plantas de milho emergidas no mesmo ponto) em diferentes épocas, bem como, determinar se a interferência de milho voluntário altera o metabolismo do estresse em soja. As quantificações foram realizadas aos 20, 35 e 46 dias após a emergência (DAE) da soja. As populações médias de milho utilizadas foram de 0, 0,5, 1, 2, 4, 8, 10 e 12 plantas ou touceiras m^{-2}. Os resultados demonstram alterações nos teores de H_2O_2 e na atividade das enzimas SOD, CAT e APX com o aumento das populações de ambas as origens do milho. A maior atividade enzimática foi observada para a SOD. A produtividade da soja reduz com o aumento nas populações de plantas individuais e touceiras de milho voluntário.

Palavras-chave: *Glycine max*, *Zea mays*, plantas voluntárias, competição, estresse oxidativo.

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Doi: 10.1590/S0100-83582018360100018

INTRODUCTION

The cultivation of soybean after glyphosate-resistant (GR®) corn favors the occurrence of GR® volunteer corn (VC) plants, interfering with soybean (Marquardt et al., 2013). Also referred to as "*tigueras*" or "*plantas guachas*", VC originate from unharvested seeds or those lost during harvest. These seeds occur individually, producing individual plants, or as whole ears or rachis segments, resulting in clumps derived from several seeds present at a single point (Beckett and Stoller, 1988; Bernards et al., 2010). VC has a high competitive capacity in relation to soybean and reduce soybean yield even in populations less than one plant per square meter (Piasecki et al., 2015).

In agricultural ecosystems, the competition between plants is established when environmental resources are limited for crop and weed development (Radosevich et al., 1997). Among the factors that affect the competition degree of the community infesting the culture, it is possible to highlight aspects related to weed species, distribution and population (Pitelli, 1985), period of coexistence and edaphoclimatic conditions (Silva et al., 2009).

In plants, biotic, abiotic or xenobiotic factors trigger the production of reactive oxygen species (ROS) (Caverzan et al., 2016). The high ROS production causes oxidative stress in plant tissues (Tripathy et al., 2007); this results in damages to the cell structures, which can lead to cell death (Caverzan et al., 2016). In plants under oxidative stress, important changes in the metabolism occur, especially the increase in membrane peroxidation, which affects the photosynthetic system of plants and inactivates the reaction centers of the photosystems (Tripathy et al., 2007). The lipid peroxidation process forms hydroperoxides, which are then converted into side products, such as ROS, free radicals, aldehydes, alkanes, oxyacids, jasmonic acid and methyl jasmonates (Vick and Zimmerman, 1987).

ROS such as the hydroxyl radical ($HO^{\bullet -}$), the superoxide radical ($O_2^{\bullet -}$), the singlet oxygen ($^1O_2$), and the hydrogen peroxide (H_2O_2) are highly reactive and may cause cellular damage, such as changes in the DNA, protein oxidation and lipid peroxidation (Gill and Tuteja, 2010). In addition, ROS are involved in processes such as growth, development, response to biotic and abiotic stresses, programmed cell death (Caverzan et al., 2016) and stomatal regulation (Xiao et al., 2001).

Plants have enzymatic and non-enzymatic antioxidant defense systems in order to prevent potential damages caused by ROS, as well as to maintain their growth, metabolism, development and productivity. The balance between ROS production and elimination at the intracellular level should be finely regulated and/or efficiently metabolized. Thus, the balance between ROS production and detoxification is supported by enzymatic and non-enzymatic antioxidants (Mittler, 2002).

Defense mechanisms against oxidative stress include enzymes such as glutathione-S-transferase (GST), ascorbate peroxidase (APX), superoxide dismutase (SOD), catalase (CAT), guaiacol peroxidase (POX), peroxidases (POD) and peroxiredoxins (Prxs). These enzymes, along with others from the ascorbate-glutathione cycle, which is the main disposal route for ROS in plants acting on chloroplast, cytosol, mitochondria, apoplast and peroxisomes, detoxify these toxic molecules (Cavalcanti et al., 2004).

In addition, the synthesis of other non-enzymatic substances, such as anthocyanins, tocopherols, phenolic components, glutathione and ascorbate (Gill and Tuteja, 2010; Sharma et al., 2012), act in controlling ROS levels. The level of oxidative stress in cells is determined by the quantity of hydrogen peroxide, superoxide radical, singlet oxygen and hydroxyl radicals. Thus, the balance of SOD, APX and CAT enzyme activities is fundamental to minimize the toxic levels of ROS in the cells (Apel and Hirt, 2004).

The objective of this study was to quantify H_2O_2 content and the activity of the enzymes SOD, CAT and APX in soybean in interference with populations of GR® VC originated from individual plants and clumps in different periods, as well as to determine whether this interference alters stress metabolism on soybean.

MATERIAL AND METHODS

In order to establish the interference/competition of soybean with the populations of GR® VC originated from individual plants or clumps, in the 2013/2014 season two experiments were carried out at the Centro de Pesquisa e Extensão Agropecuária (CEPAGRO) of the Universidade de Passo Fundo (UPF), Passo Fundo - Rio Grande do Sul, Brazil. Both experiments were conducted using a randomized block experimental design with four replications. In experiment 1, individual seeds originated individual VC plants, while in experiment 2 VC was originated from clumps. Each clump were adjusted to have seven plants of corn. In the two experiments, the mean studied VC populations were 0, 0.5, 1, 2, 4, 8, 10 and 12 individual plants or clumps m^{-2}.

The experiments were implemented in the no-tillage system, in an area with cultural remains of black oat and ryegrass that were previously controlled with 76.2 g ha^{-1} of clethodim and 720 g a.e. ha^{-1} of glyphosate. In the two experiments, corn and soybean were sown on the same day, but VC emergence occurred one day before soybean. Soybean was fertilized with 5.6 ha^{-1} N, 78.4 kg ha^{-1} P_2O_5 and 50.4 kg ha^{-1} K_2O. Soybean seeds were inoculated with *Bradyrhizobium japonicum*, and treated with insecticides and fungicides recommended for the culture (Embrapa, 2012).

GR® VC used in the experiments was originate from ears of the corn hybrid AG 8088 PRO_2® that were collected in the F_2 generation during the previous harvest (2012/2013). According each treatment, kernels of VC plants or clumps were manually aleatory distributed and buried at a depth of approximately 3.5 cm, in 17.5 m^2 (3.5 x 5 m) plots. VC density and number of plant per clump were manually adjusted twice according each treatment: three days after corn emergence and readjusted seven days after emergence, trough rip out plants. Immediately after corn sowing, the soybean cultivar BMX Turbo RR® was sowed mechanically at a density that provided the establishment of 30 soybean plants m^{-2}, spaced 50 cm apart. In order to avoid the interference of other weeds, as well as the attack of insects and diseases, glyphosate, insecticides and fungicides were applied according to the recommendations for soybean (Embrapa, 2012).

In the two experiments, H_2O_2 levels and the activity of SOD, CAT and APX enzymes were quantified in soybean on 20, 35 and 46 days after the emergence (DAE) of soybean, at the stages V_4, V_6 and R_2 (full flowering), respectively. In laboratory were determined soybean H_2O_2 content, and SOD, CAT, and APX activities. Analyses were performed at the Laboratory of Plant Virology, School of Agronomy, UPF. For the determination of H_2O_2 concentrations and SOD, CAT, and APX activities, the last fully expanded trifoliate leaf was collected from five plants (composite sample) aleatory selected from of useful area in each experimental unit. The material was stored at -18 °C until its analysis.

The H_2O_2 content were determined according to Sergier et al. (1997), with the following adaptation: the samples were centrifuged at 5600 rpm for 25 min. A standard curve generated with known H_2O_2 concentrations was used to measure the leaf H_2O_2 concentrations, which are expressed in millimoles per gram of fresh weight (mmol g^{-1} FW).

For the determination of the SOD, CAT, and APX activities, 0.2 g samples were ground in a porcelain mortar with liquid nitrogen and 0.02 g of polyvinylpyrrolidone (PVP); extracted in 900 µL of 200 mM phosphate buffer (pH 7.8), 18 µL of 10 mM EDTA, 180 µL of 200 mM ascorbic acid, and 702 µL of ultrapure water; and centrifuged for 25 min at 5600 rpm and 4 °C. The results were expressed in enzyme active units (U), specifically U mg^{-1} FW min^{-1}.

The SOD activity was determined according to Peixoto (1999), with adaptations, by calculating the amount of enzyme extract that inhibited by 50% the photoreduction of ρ-nitro blue tetrazolium chloride (NBT). This method measures the inhibition of NBT photoreduction by the enzyme extract, preventing chromophore formation. One U of SOD was defined as the amount of enzyme that inhibits NBT photoreduction by 50%. Two types of blank without extract were prepared: one exposed to light and one not exposed to light.

The CAT and APX activities were determined according to Azevedo et al. (1998), by following the consumption of H_2O_2 (APX extinction coefficient: 2.9 mM cm^{-1}; CAT extinction coefficient: 39.4 mM cm^{-1}). Both for CAT activity and APX activity, for calculation purposes, it was considered that the decrease of one absorbance unit is equivalent to one active unit (AU). The activities of total extract were determined by calculating the amount of extract that reduced the absorbance reading by one AU expressed in AU mg^{-1} of FW min^{-1}.

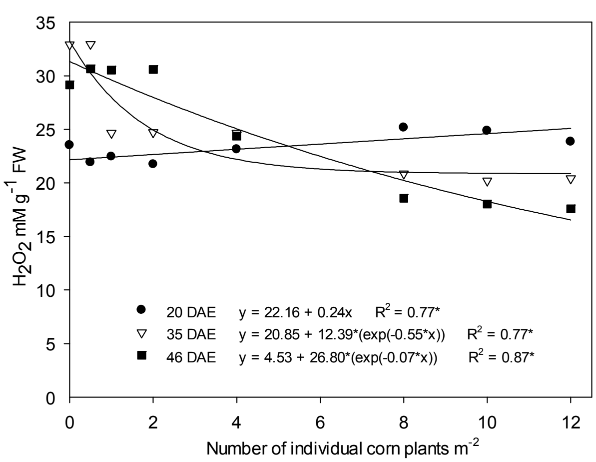
In order to determine the soybean grain yield, soybean plants were collected on 7.5 m^2 from useful area in each experimental unit. After harvesting, the material was tracked, weighed and grain humidity determined. After correcting humidity to 13%, the grain yield per hectare was estimated.

The obtained data were analyzed as for normality by Shapiro-Wilk test and homoscedasticity was analyzed by Hartley's test and, subsequently, they were submitted to analysis of variance (ANOVA) ($p<0.05$). The effect of the populations was evaluated by regression analysis, testing the linear, quadratic polynomial and exponential adjustment models, at 5% significance.

RESULTS AND DISCUSSION

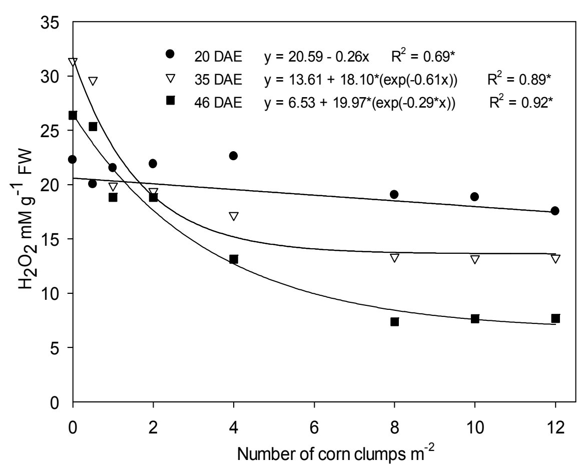
The H_2O_2 content in soybean plants, analyzed on day 20 DAE (days after emergence), increased linearly according to a larger population of individual corn plants. On 35 and 46 DAE, H_2O_2 levels decreased as the corn population increased (Figure 1). For soybeans in interference with VC originated from clumps, H_2O_2 levels decreased in the three evaluated periods, although the most severe reduction was observed on 35 and 46 DAE (Figure 2). In general, H_2O_2 levels decreased with the increase of VC populations, with a tendency to stabilize the effects from the population of eight plants or clumps m^{-2} (Figures 1 and 2). In this case, the factors that would be contributing to the highest levels of H_2O_2 in soybean under low interference would be high light intensity and temperature. Thus, the lower radiation incident on soybean interfering with the largest VC populations may have resulted in the establishment of milder microclimates at the plant canopy.

Factors such as radiation (ultraviolet-B - UV-B - is an exogenous source of ROS), heat, hydric stress, cold, heavy metals, pathogen attack, salinity, herbicides and reactions caused by normal plant processes, like photosynthesis and respiration, are potential sources of H_2O_2 production (Alexieva et al., 2001; Mittler, 2002; Caverzan et al., 2016). H_2O_2 acts as a messenger of stress, spreading oxidative damages over plant cells (Barbosa et al., 2014). As a way to avoid oxidative damages to tissues, even with low H_2O_2 levels, there is an increase in the activity of antioxidant enzymes in plant cells (Oliveira, 2013).



* Significant at p<0.05.

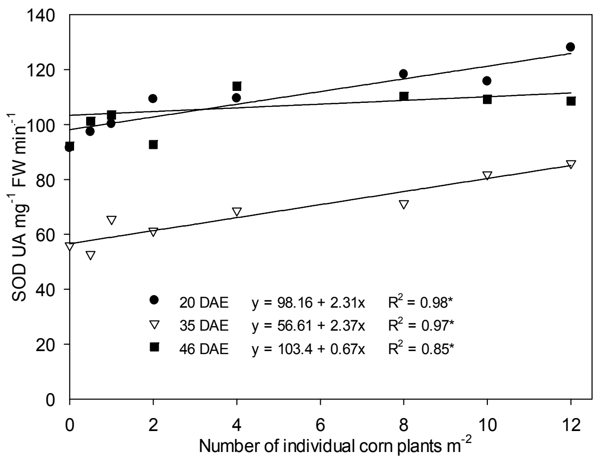
Figure 1 **-** Hydrogen peroxide (H_2O_2) contents (mM g^{-1} FW) extracted from soybean leaves, cultivar BMX Turbo GR®, according to the interference with individual plant populations of GR® F_2 volunteer corn, analyzed on day 20, 35 and 46 DAE (days after emergence).



* Significant at p<0.05.

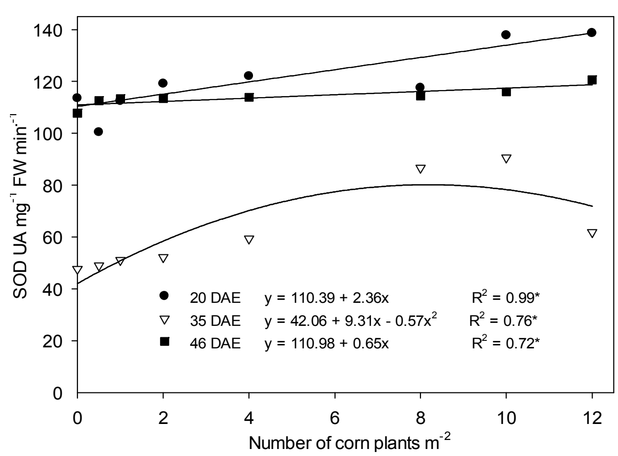
Figure 2 **-** Hydrogen peroxide (H_2O_2) contents (mM g^{-1} FW) extracted from soybean leaves, cultivar BMX Turbo GR®, according to the interference with clump populations of GR® F_2 volunteer corn, analyzed on day 20, 35 and 46 DAE (days after emergence).

On 20 and 35 DAE, the activity of SOD increased according to the major population of VC originated from individual plants and clumps. On 46 DAE, there was no SOD level increase in soybean in interference with corn, in the studied populations (Figures 3 and 4).



* Significant at p<0.05.

Figure 3 **-** Activity of superoxide dismutase enzyme (SOD) (UA mg^{-1} FW $min.^{-1}$), extracted from soybean leaves, cultivar BMX Turbo GR®, according to the interference with individual plant populations of GR® F_2 volunteer corn, analyzed on day 20, 35 and 46 DAE (days after emergence).



* Significant at p<0.05.

Figure 4 **-** Activity of superoxide dismutase enzyme (SOD) (UA mg^{-1} FW $min.^{-1}$), extracted from soybean leaves, cultivar BMX Turbo GR®, according to the interference with clump populations of GR® F_2 volunteer corn, analyzed on day 20, 35 and 46 DAE (days after emergence).

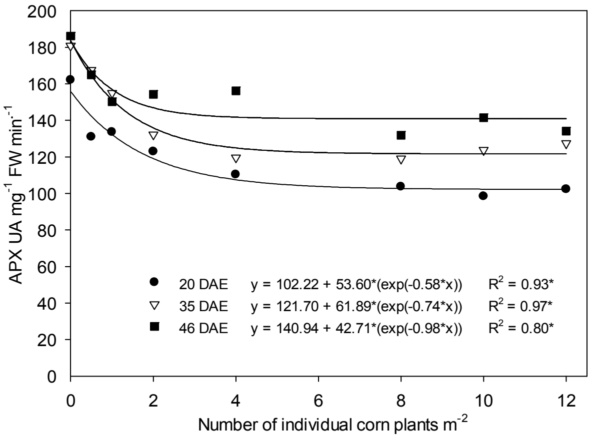
SOD participates in the modulation of the H_2O_2 level in chloroplasts, mitochondria, cytosol and peroxisomes (Mittler, 2002); it is the first enzyme to act in the detoxification process, catalyzing the dismutation of O^{2-} to H_2O_2 and O_2 (Gill and Tuteja, 2010). The produced H_2O_2 is converted to H_2O and O_2 by the enzymes APX and CAT (Wang et al., 2004). Thus, it is expected that, when SOD activity increased, also increase the activity of CAT and APX enzymes that metabolize H_2O_2 (Oliveira, 2013), but this increase was not observed in this study. In this work there was a greater action of the SOD enzyme in the detoxification of ROS in soybean plants.

The possible action of non-enzymatic factors or non-evaluated enzymes that are capable of eliminating the H_2O_2 produced by the action of SOD has probably acted over the control of H_2O_2 levels, specifically under the studied soybean conditions. In addition to CAT and APX, the H_2O_2 formed by the action of SOD can be converted to H_2O and O_2 by the action of POD enzymes (Locato et al., 2010), Prxs and GPXs (Barbosa et al., 2014). Another possibility is that the action of SOD on $O_2^{\bullet-}$ produced higher contents of $^1O_2$; therefore, H_2O_2 levels did not increase as the interference of VC populations with soybean increased.

In spite of being less reactive than $OH^{\bullet}$, $^1O_2$ is more reactive than H_2O_2 and $O_2^{\bullet-}$, being considered a highly toxic molecule (Barbosa et al., 2014). $^1O_2$ spreads over significant distances from its production site, and lipid peroxidation in chloroplasts is almost exclusively due to its action (Triantaphylides and Havaux, 2009).

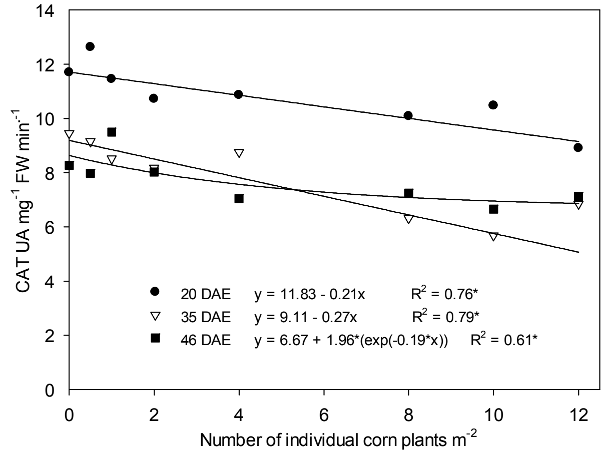
The activity of APX and CAT enzymes decreased due to the increase of the VC population during the evaluated periods (Figures 5 to 8). Since H_2O_2 levels in soybean also decreased with the increased corn interference, this may be a possible explanation for the reduction in APX and CAT activity (Figures 5 to 8). Furthermore, APX and CAT are not enzymes that act on the front line in the process of $^1O_2$ extinction that was probably generated in greater quantity from the action of SOD over $O_2^{\bullet-}$ (Triantaphylides and Havaux, 2009). As a result, there was probably no greater production of APX and CAT enzymes (Figures 5 to 8).

APX are found in cytosol, mitochondria, peroxisomes and chloroplasts (Dabrowska et al., 2007). In chloroplasts and mitochondria, APX reduces the H_2O_2 formed by the action of SOD to



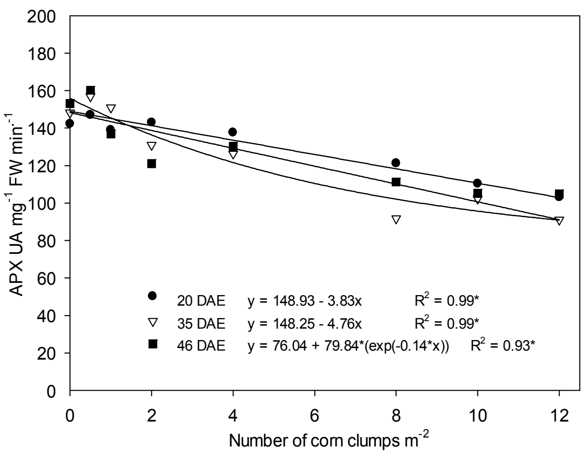
* Significant at $p<0.05$.

Figure 5 - Activity of ascorbate peroxidase enzyme (APX) (UA mg-1 FW min.-1), extracted from soybean leaves, cultivar BMX Turbo GR®, according to the interference with individual plant populations of GR® F_2 volunteer corn, analyzed on day 20, 35 and 46 DAE (days after emergence).



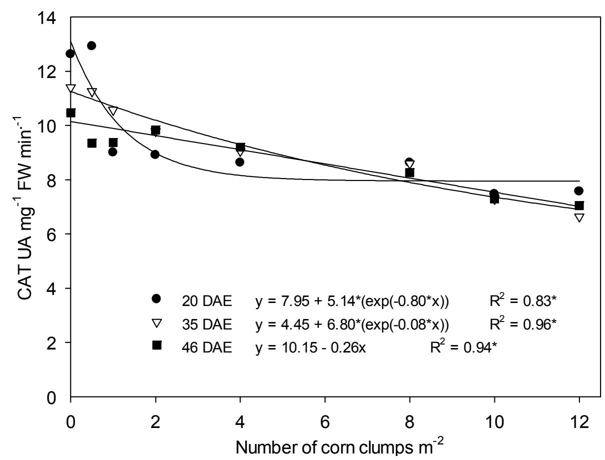
* Significant at $p<0.05$.

Figure 7 - Activity of the catalase enzyme (CAT) (UA mg-1 FW min.-1), extracted from soybean leaves, cultivar BMX Turbo GR®, according to the interference with individual plant populations of GR® F_2 volunteer corn, analyzed on day 20, 35 and 46 DAE (days after emergence).



* Significant at $p<0.05$.

Figure 6 - Activity of ascorbate peroxidase enzyme (APX) (UA mg-1 FW min.-1), extracted from soybean leaves, cultivar BMX Turbo GR®, according to the interference with clump populations of GR® F_2 volunteer corn, analyzed on day 20, 35 and 46 DAE (days after emergence).



* Significant at $p<0.05$.

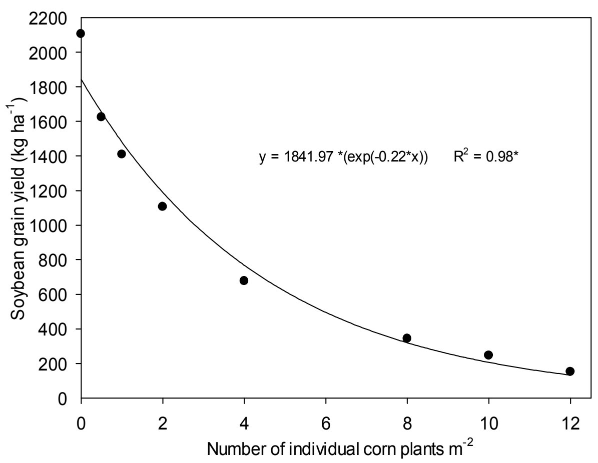
Figure 8 - Activity of the catalase enzyme (CAT) (UA mg-1 FW min.-1), extracted from soybean leaves, cultivar BMX Turbo GR®, according to the interference with clump populations of GR® F_2 volunteer corn, analyzed on day 20, 35 and 46 DAE (days after emergence).

water through the use of ascorbate as an electron donor (Locato et al., 2010). CAT acts on glyoxysomes and peroxisomes, and can be found in mitochondria (Barbosa et al., 2014). It converts two molecules of H_2O_2 into water and molecular oxygen (Dubey, 2011).

APX and CAT enzymes work together against the excessive accumulation of H_2O_2: APX performs the fine modulation of the reactive species, while the CAT removes the excess (Mittler, 2002; Gill and Tuteja, 2010). APX has a great affinity for H_2O_2 (Locato et al., 2010), higher than CAT (Gill and Tuteja, 2010).

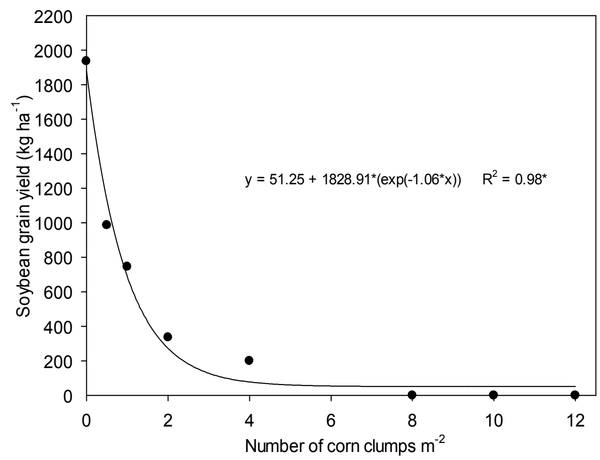
Thus, the results obtained in this research indicate that the interference exerted by VC populations and origins alters the stress metabolism of soybean plants by increasing the activity of antioxidant enzymes, such as SOD, and by the reduction in the activity of CAT and APX enzymes.

The soybean yield in interference with VC populations decreased significantly in both experiments (Figures 9 and 10). For population of 0.5, 1 and 2 m^{-2}, soybean yield decreased 481, 696 and 998 kg ha^{-1}, and 1,118, 1,359 and 1,768 kg ha^{-1} when interfering with indivual plants and clumps of VC, respectively, in relation to the interference-free control sample (Figure 10). From eight individual plants or clumps m^{-2}, there was a tendency to stabilize the effects of the interference on soybean yield, with no grain production from that population when interfering with clumps (Figures 9 and 10). A similar behavior was observed for most of the evaluated metabolic variables.



* Significant at p<0.05.

Figure 9 - Grain yield (kg ha^{-1}) of the soybean cultivar BMX Turbo GR®, according to the interference with individual plant populations of GR® F_2 volunteer corn.



* Significant at p<0.05.

Figure 10 - Grain yield (kg ha^{-1}) of the soybean cultivar BMX Turbo GR®, according to the interference with clump populations of GR® F_2 volunteer corn.

ACKNOWLEDGEMENTS

The authors are grateful to Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for financial support. PNPD/CAPES for scholarship of Andréia Caverzan and Prosup/CAPES for scholarship Cristiano Piasecki.

These results show the high competitive capacity of VC originated from individual plants and clumps on soybean. Probably, the high losses on soybean yield resulted from environmental resources limiting as a function of VC population interferences and not to the stress metabolism alteration.

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