Entomology/ Original Article

Interrelationship between potassium rates and the efficiency of *Bt* genes in the control of *Spodoptera frugiperda*

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Abstract – The objective of this work was to identify the effect of potassium rates on *Bt* transgenic resistance and damage caused by *Spodoptera frugiperda* in corn plants at different developmental stages. The experimental design was a randomized complete block in a 3x6 factorial arrangement, with three potassium rates (0, 45, and 90 kg ha^{-1}) and six corn hybrids (20A55Hx, 30A77PW, AG1051, MG652PW, NS90VTPro2, and NS92VTPro), with three replicates. The hybrids were evaluated through the analysis of canonical variables. With low potassium rates, the effectiveness of the corn hybrids in controlling the *S. frugiperda* caterpillar decreases in the different phenological stages. The use of the *Bt* technology is more efficient under an adequate potassium rate of 90 kg ha^{-1} KCl.

Index terms: *Zea mays*, caterpillar, damage, pest, transgenics.

Inter-relação entre doses de potássio e a eficiência de genes *Bt* no controle de *Spodoptera frugiperda*

Resumo – O objetivo deste trabalho foi identificar o efeito de doses de potássio sobre a resistência transgênica *Bt* e os danos causados por *Spodoptera frugiperda* em plantas de milho, em diferentes estádios de desenvolvimento. O delineamento experimental foi de blocos ao acaso, em arranjo fatorial 3x6, com três doses de potássio (0, 45 e 90 kg ha^{-1}) e seis híbridos de milho (20A55Hx, 30A77PW, AG1051, MG652PW, NS90VTPro2 e NS92VTPro), com três repetições. Os híbridos foram avaliados por meio de análise de variáveis canônicas. Com doses baixas de potássio, a eficácia dos híbridos de milho no controle da lagarta *S. frugiperda* diminui nos diferentes estádios fenológicos. O uso da tecnologia *Bt* é mais eficiente quando sob dosagem adequada de potássio de 90 kg ha^{-1} KCl.

Termos para indexação: *Zea mays*, lagarta, danos, praga, transgênicos.

Introduction

Genetically modified plants can encode proteins with insecticidal activity, being the main alternative for controlling target pests and maintaining their natural enemies in the corn (*Zea mays* L.) crop (Santana et al., 2017; Xing et al., 2019). Currently, the Cry-origin proteins produced by *Bacillus thuringiensis* (*Bt*) are the most frequently used for pest control, as they are poisonous to defoliating caterpillars and stem borers (Ferrerira-Agüero et al., 2021).

Corn plants with *Bt* technology, specifically containing *Bt* events MON 810, MON 89034, and MON 89034 × NK603 × TC1507 for the control of *Spodoptera frugiperda* and *Diatraea saccharalis*, showed higher grain yields, ranging from 750 to 900 kg ha^{-1}, than commercial cultivars without the technology (Vertuan et al., 2017). In *Bt* corn, Bernardi et al. (2016) found that the YieldGard VTPRO (expressing Cry1A.105/Cry2Ab2) and PowerCore (Cry1A.105/Cry2Ab2/Cry1F) technologies caused the complete mortality of *S. frugiperda*. However, the performance of *Bt* plants regarding pest control varies according to the expression of the *Bt* protein during the plant developmental cycle and to its variations in different plant structures (Huang et al., 2014). In addition, *Bt* technologies need to be correctly managed in order to avoid risks due to the selection of resistant insects and, consequently, the development of populations capable of causing economic damage to crops (Cao et al., 2014).

In this scenario, the ability of the plants to resist pest attacks could also be associated with fertilizer use, considering that the chemical and physical defense patterns of genotypes are interrelated with plant access to nutrients and can be critical for the ideal functioning of resistance mechanisms against insects (Mason et al., 2022). When evaluating fertilizers, Singh et al. (2021) concluded that the growth and development of *S. frugiperda* larvae on bermudagrass [*Cynodon dactylon* (L.)] was favored by nitrogen rates but discouraged by those of potassium. Likewise, Bala et al. (2018) observed that potassium plays a crucial role in activating defense mechanisms and enhancing resistance against insect pests by increasing the metabolism of secondary compounds and reducing the accumulation of carbohydrates, which leads to a decrease in the insect population, particularly of orders Coleoptera, Lepidoptera, and Hemiptera. Therefore, joint strategies, in the field, are fundamental to maintain yield, resulting in cultivars efficient in pest control, as well as in reduced production costs.

However, there are few known studies about the role of potassium and its effect on the performance of genetically modified plants with the *Bt* event and on the interaction between the events present in the cultivars and the damage caused to corn yield.

The objective of this work was to identify the effect of potassium rates on *Bt* transgenic resistance and damage caused by *Spodoptera frugiperda* in corn plants at different developmental stages.

Materials and Methods

Two experiments were conducted during the summer harvests of 2014/2015 and 2015/2016 at the Ipameri unit of Universidade Estadual de Goiás, in the state of Goiás, Brazil (170°43'19"S, 480°09'35"W, at an altitude of 773 m). The soil of the area was classified as a Latossolo Vermelho-Amarelo (Santos et al., 2018) i.e., a Typic Hapludox. According to Köppen's classification, the local climate is Aw, characterized by tropical wet conditions with a dry winter (Figure 1).

The experimental design was a randomized complete block with three replicates, in a 3x6 factorial arrangement, consisting of three K rates (0, 45, and 90 kg ha^{-1}) and six commercial corn hybrids (20A55Hx, 30A77PW, AG1051, MG652PW, NS90VTPro2, and NS92VTPro). The experimental plots consisted of two 3.0 m long rows, spaced at 0.5 m, with a useful area of 3.0 m^2.

The *Bt* genes of the commercial corn hybrids were: Cry1F in 20A55Hx, Cry1A.105/Cry2Ab2/Cry1F in 30A77PW, Cry1A.105/Cry2Ab2/Cry1F in MG652PW, Cry1A.105/Cry2Ab2/CP4-EPSPS in NS90VTPro2, and Cry1A.105/Cry2Ab2 in NS92VTPro; AG1051, with no resistance genes (conventional), was used as the control. The applied potassium rates of 0, 45, and 90 kg ha^{-1} represented a low, intermediate, and adequate availability of potassium chloride (KCl), respectively.

Before the corn crop was sown, the soil was prepared with one plowing and two harrowing operations. Fertilization followed the guidelines of Alvarez V. et al. (1999), based on the soil analysis (Table 1), for an expected grain yield of 8.0 Mg ha^{-1}. At sowing, 120 kg ha^{-1} P$_2$O$_5$ and 32 kg ha^{-1} N (urea) were applied, as well as the varying KCl rates of 0, 45, and 90 kg ha^{-1}. At the V$_6$ stage, 124 kg ha^{-1} N (urea) were applied as topdressing and distributed manually next to the sowing furrow. Corn was sown manually in November, with five seeds per meter and subsequent thinning at the V$_3$ stage, resulting in a final stand of 55,000 plants per hectare. Irrigation was not used during cultivation. At the V$_4$ stage, weed control was conducted with benzoyl cyclohexanedione at a rate of 240 mL ha^{-1}, applied with a backpack sprayer, combined with manual weeding in the following months. The control of the caterpillars

was performed only in the conventional hybrid, at the V5 stage, by a single application of 150 mL ha^{-1} flubendiamide after monitoring.

The damage caused by *S. frugiperda* to corn whorl and leaves in each plot was determined using a visual rating scale, ranging from 0 to 9, adapted from the one proposed by Davis et al. (1992) to estimate damage at different plant stages, i.e., at 30, 70, and 110 days after sowing (DAS). Three plants were used randomly in

each evaluation, and the plot's average was estimated. At 70 DAS, photosynthetic rates were determined in five plants per plot using the CFL1030 chlorophyll meter (Falker, Porto Alegre, RS, Brazil); after measurements, the obtained values were transformed into average per plot, called leaf chlorophyll index, in Falker units.

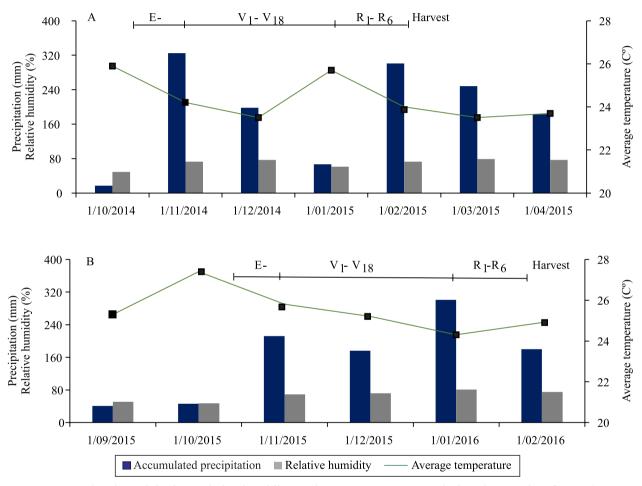All ears from the plots were harvested manually when they reached the point of physiological

Figure 1. Accumulated precipitation, relative humidity, and average temperature during the months of corn (*Zea mays*) cultivation in 2014/2015 and 2015/2016 crop seasons. Source: Inmet (2019).

Table 1. Soil chemical attributes at a 0 to 20 cm depth after limestone application in the 2014/2015 and 2015/2016 harvests[1].

Harvest	pH CaCl$_2$	OM (g dm^{-3})	P$_{resin}$ (mg dm^{-3})	H+Al	Al^{3+}	K$^+$	Ca^{2+}	Mg	CEC	BS (%)
				------------------------------(cmol$_c$ dm^{-3})------------------------------						
2014/2015	5.60	29.70	29.90	1.50	0.00	0.64	4.00	1.20	7.34	79.56
2015/2016	5.40	25.60	31.50	0.98	0.00	0.79	5.00	1.00	7.77	87.38

[1]pH, active acidity; OM, organic matter; P, available phosphorus; H+Al, potential acidity; Al, exchangeable acidity; K, available potassium; Ca, exchangeable calcium; Mg, exchangeable magnesium; CEC, effective cation exchange capacity; and BS%, base saturation at pH$_{7.0}$.

maturation, with humidity around 30%. Subsequently, for each plot, five random ears were used to obtain average ear diameter (in millimeters) with the aid of a graduated caliper and average ear length (in centimeters) with a graduated ruler. To determine the percentage of ears without damage, the ears without injuries caused by the caterpillars were counted, then transformed into percentage based on the total number of ears of the plot. Grain yield was obtained from grain mass (in kilograms) after threshing all ears of each plot, corrected to 13% moisture, and, then, transformed to kg ha^{-1}. Grain samples separated randomly from each plot were used to determine 1,000-grain weight, corrected to 13% moisture, in grams.

The univariate analysis of variance was performed, and the significance of the F-test was verified, followed by the multivariate analysis of variance, in which the set of evaluated variables was grouped according to their characteristics and in coordinate axes (biplot) through the analysis of canonical discriminant variables (Hair Jr. et al., 2005). The results of these analyzes were represented in graphs, together with the 95% confidence ellipses for the treatments, which inferred about the equality of the treatments from the superposition of their confidence ellipses, using the R software (R Core Team, 2022) and the candisc package (Friendly & Fox, 2021).

Results and Discussion

Considering the multivariate analysis, for the KCl rate of 0 kg ha^{-1}, the average variation explained by canonical variables 1 and 2 was 72.3 and 19% of total variance, respectively, in the 2014/2015 and 2015/2016 harvests (Figure 2). In comparison, the average variation explained by each canonical variable was 61.5 and 25.2% of total variance for the rate of 45 kg ha^{-1} (Figure 3) and 65.5 and 28% for that of 90 kg ha^{-1} (Figure 4), also in 2014/2015 and 2015/2016, respectively. Therefore, the eigenvectors and eigenvalues were able to explain the obtained results, in line with Hair Jr. et al. (2005), who concluded that the objective of the analysis of canonical variables is reached when a relatively small number of extracted variables can explain most of the variability from the original data.

According to Crubelati-Mulati et al. (2019), the multivariate analysis allows of a better discrimination
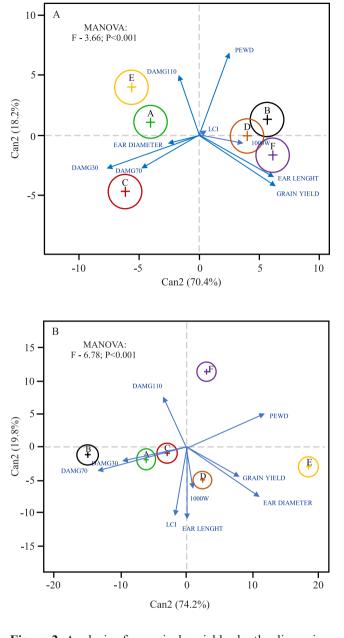

Figure 2. Analysis of canonical variables by the dispersion of corn (*Zea mays*) hybrids, without the application of potassium (0 kg ha^{-1} KCl), in the 2014/2015 (A) and 2015/2016 (B) harvests. The evaluated hybrids and respective proteins between parenthesis were: A, 20A55Hx (Cry1F); B, 30A77PW (Cry1A.105/Cry2Ab2/Cry1F); C, AG1051 (conventional, without Cry proteins, used as the control); D, MG652PW (Cry1A.105/Cry2Ab2/Cry1F); E, NS90VTPro2 (Cry1A.105/Cry2Ab2/CP4-EPSPS); and F, NS92VTPro (Cry1A.105/Cry2Ab2). DAMG30, damage at 30 days after sowing; DAMG70, damage at 70 days after sowing; DAMG110, damage at 110 days after sowing; LCI, leaf chlorophyll index; 1000W, 1,000-grain weight; and PEWD, percentage of ears without damage.

of different genotypes in a breeding program, aiming at resistance to *S. frugiperda*, based on a subset of traits that do not have a great collinearity or correlation with each other. In the present work, this analysis helped to identify possible mechanisms of resistance and/or susceptibility in each group of genotypes, based on the vectors and eigenvalues regarding the efficiency of the Cry protein.

The damage caused by *S. frugiperda* at 30 and 70 DAS was highly correlated and associated with the axis of greater explanation (abscissa) in both harvests. Therefore, the percentage of ears without damage showed a low correlation with damage at 30 and 70 DAS, but a partial and less important one (axis of coordinates) with damage at 110 DAS (Figure 2). The damage caused to AG1051, the conventional hybrid, was similar to that observed in 20A55Hx, which has only one Cry protein. Although the conventional hybrid presented higher initial damages at 30 and 70 DAS, its ears were not affected and damages at 110 DAS were low.

In the case of hybrids 30A77PW and NS90VTPro2, contrasting damages were observed in the different evaluated stages, which highlights the importance of analyzing different harvests and determining the effect of other stresses, abiotic and biotic, on corn plants (Figure 2). In 2014/2015, the damage caused by *S. frugiperda* was more severe in hybrid NS90VTPro2, which showed a lower resistance/tolerance and greater susceptibility to the attacks of this pest, possibly related to the drought during the end of the vegetative cycle and beginning of the reproductive one (Figure 1 A and B). In this harvest, precipitation, humidity, and temperature had a greater variation, despite the higher rainfall of ±921 mm, which was poorly distributed in the growing season when compared with the ±869 mm in 2015/2016. Similarly, Llano & Vargas (2016) linked the high variation in the average Brazilian grain yield to the climatic conditions during the corn cultivation cycle, concluding that the average precipitation required by each stage impacted flowering and accounted for 44% of the expected variations in grain yield.

In 2015/2016, climate had a lower influence on grain yield due to the high damage caused by a low K availability even with the presence of up to three different Cry proteins (Figure 2), as observed for the 30A77PW hybrid, which was not efficient in controlling the caterpillar, as well as for MG652PW
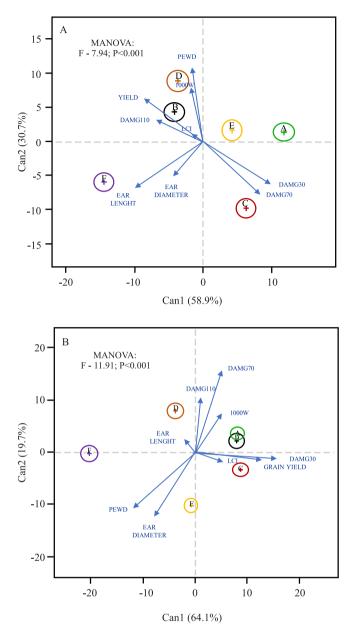

Figure 3. Analysis of canonical variables by the dispersion of corn (*Zea mays*) hybrids, with the application of potassium at a rate of 45 kg ha^{-1} KCl, in the 2014/2015 (A) and 2015/2016 (B) harvests. The evaluated hybrids and respective proteins between parenthesis were: A, 20A55Hx (Cry1F); B, 30A77PW (Cry1A.105/Cry2Ab2/Cry1F); C, AG1051 (conventional, without Cry proteins, used as the control); D, MG652PW (Cry1A.105/Cry2Ab2/Cry1F); E, NS90VTPro2 (Cry1A.105/Cry2Ab2/CP4-EPSPS); and F, NS92VTPro (Cry1A.105/Cry2Ab2). DAMG30, damage at 30 days after sowing; DAMG70, damage at 70 days after sowing; DAMG110, damage at 110 days after sowing; LCI, leaf chlorophyll index; 1000W, 1,000-grain weight; and PEWD, percentage of ears without damage.

and NS90VTPro2. A low K availability can also lead to the generation of resistant insects, as it does not prevent the population growth of *S. frugiperda*, with the possibility of resistance outbreaks, including simultaneous ones. According to Storer et al. (2012), there are already insects resistant to the Cry1F protein (Herculex), a technology present in hybrids 20A55Hx, 30A77PW, and MG652PW, and populations that survive in higher numbers are more likely to form in tropical countries, as detected in several regions of Puerto Rico.

The chances of the plants to tolerate the attack of *S. frugiperda* and, possibly, the effectiveness of their genes increased with the application of 45 kg ha^{-1} KCl. In the 2014/2015 harvest, damage at 30 and 70 DAS presented an opposite behavior and explained most of the variation (axis of abscissa), whereas damage at 110 DAS and on the ear had little influence on grain yield (axis of coordinates) (Figure 3). In the 2015/2016 harvest, the plants showed an increased tolerance and greater efficiency, as damage at 70 and 110 DAS and on the ears was less important for the observed variation and damage at 30 DAS presented a low interference on grain yield. In this line, Sampaio et al. (2007) reported that higher K rates induce or increase plant tolerance to *S. frugiperda* through several mechanisms, such as the accumulation of phenolic compounds and their derivatives, considered toxic to insects. These authors also found that the caused damage showed a decreasing linear performance, was reduced at the different phenological stages, and decreased with increasing K$_2$O rates, from 0 to 40 kg ha^{-1}.

At the highest KCl rate of 90 kg ha^{-1}, *S. frugiperda* caused a greater damage on the AG1051 conventional hybrid (control) when compared with all others containing transgenic genes, except NS92VTPro, in the 2015/2016 harvest, with two Cry proteins (Cry1A.105/Cry2Ab2) (Figure 4). Although, according to Storer et al. (2012), hybrid 20A55Hx, with Cry1F, is not effective in caterpillar control due to the long time the technology has been on the market (17 years), in the present study, the opposite was observed with an increased K rate, as well as a higher plant tolerance and gene efficiency. Barcelos et al. (2018) researched the behavior of different hybrids with *Bt* technology in the control of *S. frugiperda*, finding that 2B587HX and 30F53YH, with the Cry1F technology, were less effective, also showing a higher frequency of small
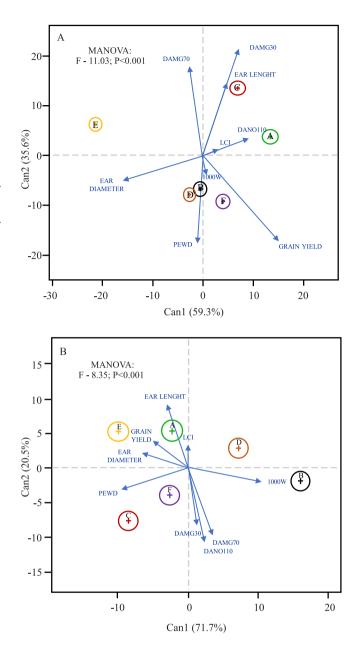

Figure 4. Analysis of canonical variables by the dispersion of corn (*Zea mays*) hybrids, with the application of potassium at a rate of 90 kg ha^{-1} KCl, in the 2014/2015 (A) and 2015/2016 (B) harvests. The evaluated hybrids and respective proteins between parenthesis were: A, 20A55Hx (Cry1F); B, 30A77PW (Cry1A.105/Cry2Ab2/Cry1F); C, AG1051 (conventional, without Cry proteins, used as the control); D, MG652PW (Cry1A.105/Cry2Ab2/Cry1F); E, NS90VTPro2 (Cry1A.105/Cry2Ab2/CP4-EPSPS); and F, NS92VTPro (Cry1A.105/Cry2Ab2). DAMG30, damage at 30 days after sowing; DAMG70, damage at 70 days after sowing; DAMG110, damage at 110 days after sowing; LCI, leaf chlorophyll index; 1000W, 1,000-grain weight; and PEWD, percentage of ears without damage.

(< 1.5 cm) and large (> 1.5 cm) caterpillars, requiring two chemical applications, which may be related to the low K rate used. In a conventional corn crop, Roel et al. (2017) compared the effects of organic fertilization, no fertilization, and chemical fertilization (using K and N) on *S. frugiperda* control, concluding that chemical fertilization lead to a shorter larval and pulpal development period and to pupae with a lower weight, causing less damage to the plants.

As to the effect of water deficit, plant performance under 0 and 45 kg ha^{-1} KCl was similar. However, when comparing harvests, that of 2014/2015 differed significantly from that of 2015/2016 (Figure 1) and showed a lower correlation with future harvests (Figures 1 and 2). In 2015/2016, when there was no water deficit, the damage caused by *S. frugiperda* at 30 and 70 DAS had less influence on grain yield and the ears were less damaged; in addition, ear diameter was more important than length, increasing the photosynthetic rate. Possibly, K does not favor the survival or development of *S. frugiperda* larvae, and maintaining a higher level of this nutrient in plant tissues can help reduce feeding damage, increasing the mortality and reducing the weight of the larvae (Singh et al., 2021). Although this result was observed at the rates of 0 and 45 kg ha^{-1} KCl, they were more visible at 90 kg ha^{-1} KCl through the damages located in opposite directions, indicating their influence on grain yield (Figures 2, 3, and 4).

Regarding yield, in 2014/2015, the highest values were obtained for hybrids NS92VTPro, 30A77PW, and MG652PW at the highest KCl rate due to the lower damage to their ears, with heavier grains, showing a low correlation with the other secondary components (Figure 4). Although ear damage and 1,000-grain weight were less important, they are variables that tend to be more similar in commercial hybrids and that, most evidently, do not show damage in the different phenological stages. Amanullah et al. (2016), studying corn crop growth and grain yield in the field and under water deficit conditions, found better results for plant height, leaf area, ear length, 1,000-grain weight, and grain yield in the plots that received 90 kg ha^{-1} K and that had a better rainfall distribution during cultivation.

In the 2015/2016 harvest, hybrids 20A55Hx and NS90VTPro2 were more productive due to ear diameter and length, as well as to a higher chlorophyll content. NS90VTPro2 showed the best performance

in this year, at the rate of 45 kg ha^{-1} KCl, with ears with a longer length, greater diameter, and less damage (Figure 3). According to Paiva et al. (2016), this same hybrid provokes an aversion to feeding and/ or antibiosis reaction in *S. frugiperda*, controlling satisfactorily this pest by causing 100% larval mortality in less than ten days. These findings confirm the hybrid's resistance potential, the efficiency of the used protein, and the importance of the K rate for the technology to work. Contrastingly, the 20A55Hx hybrid presented a moderate resistance, and AG1051 was highly susceptible, similarly to the other studied hybrids.

Therefore, the obtained results show an interaction between KCl rates, corn phenological stages, and the environment, with harvests presenting divergent performances and the studied variables showing effects sometimes opposite to damage (Figures 2, 3, and 4). However, the relationship between defense mechanisms and fertilization are not yet clear, although there could be benefits related to the access to nutrients, such as K, which would nullify the selection of host plants by herbivores (Mason et al., 2022). Moreover, since the *Bt* technology works efficiently in the different phenological stages only at the rate of 90 kg ha^{-1} KCl (Figure 4) and under a better rainfall distribution (in the 2015/2016 harvest), further researches on K application are fundamental.

Regarding the importance of K, Peter et al. (2016) reported increased K contents in the corn leaves and a longer ear length with increasing K rates, as well as a reduction in chlorophyll content, which was not observed in the present study. The chlorophyll index was higher in the 2015/2016 harvest, but with little explanation for yield (Figures 2, 3, and 4), being more important at the rate of 45 kg ha^{-1} KCl (Figure 2). Zhao et al. (2016) added that K plays a key role in the function of stomata and the electron transport chain, reducing the photosynthetic rate under water deficit conditions. Therefore, K is important for photosynthesis, especially for Rubisco activity and nutrient assimilation and translocation related to enzymatic activity, which are all affected simultaneously, generating a series of consequences to which each hybrid will respond in a specific way.

According to the data obtained in the present study, K plays a fundamental role in the maintenance of the *Bt* technology, meaning that reductions in K

rates must be planned and monitored. This way, the technology will have a greater viability and increase the tolerance of hybrids to the attack of *S. frugiperda* caterpillars for a longer time, while maintaining an effective resistance (Figures 2, 3, and 4). Despite these findings, there are still several interactions that were not measured here, including genetic factors linked to the tolerance of each hybrid and their relationship with environmental conditions (crops in the field), as well as to the allocation of resources for the induction of defenses, highlighting the need for a deeper analysis of resistance/tolerance characteristics in different contexts to achieve more consistent and predictable results.

Conclusions

1. At low potassium rates, the effectiveness of corn (*Zea mays*) hybrids in controlling *Spodoptera frugiperda* caterpillars decreases.

2. The presence of more Cry proteins does not prevent the attack of *Spodoptera frugiperda* at low potassium rates.

3. The use of the *Bt* technology is more efficient under an adequate potassium rate of 90 kg ha^{-1} KCl.

Acknowledgments

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