Article

Combinatorial aptitude and resistance to leaf damage of *Spodoptera rugiperda* (J. E. Smith) in maize germplasm native to Tamaulipas

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Abstract

An agricultural pest of economic importance is *Spodoptera frugiperda*, in Tamaulipas it is common the incidence in corn, causing foliar damage which reduces the yield of grain, a solution to this problem is to use resistant cultivars; the native germplasm of Tamaulipas co-evolved with this insect, causing resistance to it. In order to evaluate the genetic effects and resistance of maize cultivars derived from native germplasm, foliar damage caused by S. frugiperda was determined in six inbred lines and their 30 crosses, under application conditions and non-application of insecticide in the Location of Güemez, Tamaulipas (spring-summer, 2015), a dialelic analysis was carried out with Griffing's design I. For foliar damage, there were significant effects of general combinatorial aptitude (ACG), specific (ACE) and ACG interaction×insecticide treatment; there were only significant effects of ACG in the non-application treatment. The genetic expression of this germplasm determined by the mean values of the leaf damage showed a wide variation, the line LlHL₅S₃ had significant and negative effects of ACG and the crosses TGL₂S₃×LlHL₅S₃ the greater effects of negative ACE and less leaf damage (1.12), the crosses $PWL_1S_3 \times TGL_2S_3$, PWL₁S₃×LlNL₄S₃, TML₃S₃×LlNL₄S₃ and TML₃S₃×PWL₆S₃ excelled with leaf damage greater than 1.70; however, they had a reduction of less than 15.5% of grain yield. The variation of leaf damage depended on additive and non-additive effects and there was resistance to S. frugiperda, both due to non-preference and tolerance to leaf damage.

Keywords: Zea mays, armyworm, combinatorial ability, diallelic.

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Introduction

The agricultural regions of the center and south of Tamaulipas, present environmental conditions of dry tropics, humid and High Valleys (Castro *et al.*, 2013) and varied and extreme climate, for which, the maize is established under diverse systems of production (Resendiz *et al.*, 2014), in some of these we use native germplasm with high variability, resistance to environmental stress conditions and grain yield potential, among other desirable characteristics (Pecina *et al.*, 2011).

Most of these production systems are established in favorable environments for the development of *S. frugiperda* or cogollero worm (Blanco *et al.*, 2014, Loera and Castillo, 2015), therefore, their presence is common in agroecosystems dedicated to the production of corn in these regions, mainly in the spring-summer agricultural cycle, presents favorable conditions of temperature and humidity for the growth and development of this insect (Resendiz *et al.*, 2016), reaching to develop more than four generations during a same agricultural cycle (Blanco *et al.*, 2014).

Feeding mainly of foliar tissues in development, causing decrease of the foliar area of the corn plant, in extreme cases up to 70% of this, which can reduce the yield of grain (Hruska and Gould, 1997); This insect also feeds on other developing tissues such as stems, inflorescences, bracts and grain (Valdez-Torres *et al.*, 2012; Loera and Castillo, 2015), which favors the infestation by microcoleoptera and fungi such as *Asperguillus* spp. (Rodríguez-del-Bosque *et al.*, 2010) and *Fusarium* spp, microorganisms that produce mycotoxins (García-Aguirre and Martínez-Flores, 2010, Martínez *et al.*, 2013), this in addition to diminishing grain yield, affects the quality of it (Resendiz *et al.*, 2016), is a plague of economic importance in corn.

Its control is often carried out through the application of chemical insecticides, increasing production costs (Barrientos-Gutiérrez *et al.*, 2013) and the development of resistance of the insect is induced (Ahmad and Arif, 2010), besides, it can be a source of environmental pollution (Devine *et al.*, 2008). On the other hand, many corn production systems in the center and south of Tamaulipas are established on a small scale and for self-consumption, where the cost represented by the use of hybrid cultivars is unviable and the low adaptation of these to these specific environments increases this problematic (Turrent *et al.*, 2012; García-Salazar and Ramírez-Jaspeado, 2014). A viable solution is to form and release cultivars that can be used in the specific environmental conditions of each region and resistant to *S. frugiperda* and that do not increase production costs.

In this sense, in a program of genetic improvement, the choice of germplasm to use is a decisive decision for the success of it, therefore, the use of native germplasm as a base population for the development of cultivars resistant to *S. frugiperda* is a viable alternative, since this germplasm has high adaptation to the environmental conditions of these regions (Castro *et al.*, 2013), wide variability (Pecina *et al.*, 2011; Castro *et al.*, 2013), it has also developed under the constant presence of this lepidopteran, which is a source of characteristics that provide resistance to attack (Cantú *et al.*, 2012, Loera and Castillo, 2015). The use of this germplasm in breeding programs allows the conservation, management and exploitation of this phytogenetic resource, contributing to the reduction of genetic loss and erosion (González *et al.*, 2014).

The planning of a plant breeding program is based on knowing the genetic component of the base germplasm used (Gutiérrez *et al.*, 2004); that is, to understand the gene action that controls the characters of interest; In this sense, the combinatorial aptitude of the parents allows selecting those with an outstanding average behavior in a series of crosses (Luna-Ortega *et al.*, 2013) and identifying specific combinations with a behavior higher than expected based on the average of the parents that intervene in the crossing and in this way, define heterotic patterns (Guillén-de la Cruz *et al.*, 2009), which constitute a source of germplasm for the generation of elite lines of great utility in a breeding program dynamic; the above can be achieved through the evaluation of diallel crosses (Antuna *et al.*, 2003).

The evaluation of general combinatorial aptitude (ACG) and specific (ACE) by diallel crosses, allows efficient classification of parents based on the behavior of their progeny (Antuna *et al.*, 2003), is considered effective in identifying useful sources of germplasm for maize breeding programs (Ávila *et al.*, 2009) in this sense, the ACG determines the additive portion of the genetic effects that control the expression of the phenotypic characteristics of interest, while the ACE non-additive effects, this is the gene action of dominance and epistasis (Camposeco *et al.*, 2015).

In this way, when there are greater effects of ACG, it is feasible to take advantage of the additive portion of the available genetic variance, through any recurrent selection methodology; while the existence of a greater ACE favors the exploitation of the non-additive variance, through the implementation of a reciprocal recurrent selection or hybridization program (Preciado *et al.*, 2005). The objective of the present work was to evaluate the genetic effects of leaf damage caused by *Spodoptera frugiperda* and the resistance to it of lines derived from maize germplasm native to Tamaulipas and its crosses.

Materials and methods

The experiment was carried out during the spring-summer 2015 cycle, in the Experimental Field "Ing. Herminio García González" of the Autonomous University of Tamaulipas located in the municipality of Güemez, Tamaulipas, at 23° 56' 26" north latitude and 99° 05' 59" west longitude, at an altitude of 193 meters above sea level. With a subtropical, semi-dry and warm extreme climate, average annual temperature of 23.8 °C, with an annual rainfall of 721.1 mm.

They were evaluated six maize S_3 inbred lines, PWL₁S₃ and PWL₆S₃ derived from a native population of Padilla C-3001, TGL₂S₃ and TML₃S₃ derived from populations C-3007 and C-3012 from Tula and LlNL₄S₃ and LlHL₅S₃ from populations C-3033 and C-3040 of Llera, Tam. and its direct and reciprocal crosses, giving a total of 36 cultivars; were established in two treatments, the first with insecticide for the control of *S. frugiperda* with three applications of Denim[®] 19 CE (emamectin benzoate) at a dose of 200 ml ha⁻¹ in each application; the first application was made at the time of the complete expansion of sheet 5, second to sheet 9 and third to leaf flag and the second without insecticide.

The planting was done manually on September 11, 2015, the cultivars were established at a population density of 50 000 plants ha⁻¹ under irrigation conditions, the fertilizer dose of 120N-60P-00K, 50% was applied of N and 100% of P in the sowing and the rest of the N in the first weeding, 32 days after sowing; weed control was performed manually at the time of complete

expansion of leaves 8 and 14. The experimental plot was a furrow of 5 m in length and a separation of 0.80 m between rows, the experiment was established under a block design complete at random, with an arrangement of divided plots, where the large plot was the treatments with and without insecticide to control *S. frugiperda* and the small plot the cultivars, with three repetitions.

Foliar damage was determined by *S. frugiperda*, using the modified damage scale of Fernandez and Exposito (2000) (Table 1), at the moment of male flowering by individual plant in all the plants of the experimental plot, to later obtain the average per floor.

 Table 1. Modified visual scale of leaf damage caused by S. frugiperda in cultivars derived from germplasm native corn of Tamaulipas.

Grade	Damage characteristics
0	No visible damage
1	Perforations in the shape of a window, circular, elongated small smaller than 5 mm in less than 20% of the leaf area of the plant
2	Circular or elongated perforations between 5 to 10 mm, affecting between 20 and 40% of the foliar area of the plant
3	Circular or elongated perforations greater than 10 mm, affecting 40 to 60% of the foliar area of the plant with less than 20% destruction of the whorl
4	Circular or elongated perforations greater than 10 mm, affecting between 60 to 80% of the foliar area of the plant with the verticil destroyed more than 50%
5	Circular or elongated perforations greater than 10 mm, affecting between 80 to 100% of the leaf area of the plant with the whorl completely destroyed

The yield of grain per plant (RGP), was calculated as the product of the weight of ear per experimental plot at harvest, by the content of dry matter of the grain, standardized to 14% of humidity of the grain, by the proportion of the weight of grain with respect to the total weight of ear and averaged by the total number of plants per plot. By means of the difference between treatments with and without insecticide the decrease of the RGP was calculated because of the foliar damage of *S. frugiperda* in grams and percentage.

An analysis of variance and a diallyl analysis were carried out under Griffing method I and model I (fixed effects), to determine general combinatorial aptitude (ACG) and specific (ACE), maternal (EM) and reciprocal effects (ER) using the DIALLEL-SAS05 program proposed by Zhang and Kang (2005). On the other hand, we considered as low preference cultivars for *S. frugiperda*, those that had a foliar damage inferior to the value of the mean minus the variance ($\mu - \sigma$) and cultivars of high preference, to those that had a superior foliar damage to the value of the mean plus the variance ($\mu + \sigma$) (De la Cruz-Lazaro *et al.*, 2010).

Results and discussion

The analysis of variance detected significant statistical differences ($p \le 0.01$) between the insecticide application treatments for the variable leaf damage of *S. frugiperda* (Table 2), with an average foliar damage of 0.14 in the insecticide treatment, lower than the treatment without insecticide with an average leaf damage of 1.64.

Source of variation	Leaf damage of S. frugiperda			
Source of variation	Combined	TCI	TSI	
Trat	< 0.001	-	-	
Cruza	0.018	0.903	0.044	
Cruza×trat	0.03	-	-	
Acg	0.012	0.813	0.012	
Ace	0.042	0.51	0.137	
Acg×trat	0.035	-	-	
Ace×trat	0.45	-	-	
Rec	0.349	0.954	0.42	
Rec×trat	0.676	-	-	
Mat	0.128	0.754	0.227	
Mat×trat	0.631	-	-	
Nomat	0.536	0.932	0.573	
Nomat×trat	0.639	-	-	

 Table 2. Statistical significance of genetic effects of 6 lines S₃ progenitor of corn and their crosses for foliar damage of S. frugiperda with and without insecticide.

TCI = treatment with insecticide; TSI = treatment without insecticide; ACG = general combinatorial aptitude; ACE = specific combinatorial aptitude; TRAT = insecticide treatment; REC = reciprocal effects; MAT = maternal effects; NoMAT = non-maternal effects.

We also detected significant differences between the crosses evaluated for this same variable, this is indicative of the existence of genetic variability for this variable between the parents; since according to Guillen-de la Cruz *et al.* (2009) and De la Cruz-Lazaro *et al.* (2010) as the genetic diversity of the parents increases, the differences between their crosses are increased, both in agronomic and physiological characteristics, it can cause differences in the tolerance to a pest and its preference (Zavala, 2010). *S. frugiperda* (Camarena, 2009). Statistical significance ($p \le 0.05$) was found for the genetic effects of ACG of foliar damage of *S. frugiperda*, similarly occurred for ACE (Table 2).

This indicates that the variation between the crosses evaluated for foliar damage of *S. frugiperda*, is due to both additive and non-additive gene action (Camposeco *et al.*, 2015). In this sense, the sum of squares of crosses (data not shown) shows that, the variation corresponding to the effects of ACG for foliar damage of *S. frugiperda* was 25.9%, while for the effects of ACE the results were 45.7 % and for reciprocal effects of 28.4% which shows that the variation of leaf damage was controlled to a greater extent by non-additive effects (Widstrom *et al.*, 1972).

On the other hand, for the interaction of Cruza×Trat in this variable, significant effects were present $(p \le 0.05)$, this shows evidence of different foliar damage of *S. frugiperda* among the crosses within each of the evaluated treatments, which it could be indicative of genetic variability among these cultivars for the preference of this insect, as mentioned by Medina *et al.* (2001) and González *et al.* (2008). Similarly, the significance in the ACG×TRAT interaction demonstrates that the additive effects for this variable were expressed according to the environmental condition in which the plant was developed is necessary, that the evaluation and selection of cultivars be carried out in different

environmental conditions, in order to know the interactions between these and the various factors involved in their behavior, both biotic and abiotic (Callejas and Ochando, 2005) and in this way, to be able to identify with greater precision the effects of ACG and thus then choose the parents according to the specific needs of the improvement program (Yan and Hunt, 2002).

On the other hand, there was no significance (p > 0.05) for the reciprocal effects, nor for the interaction with insecticide treatment and therefore, neither for maternal, not maternal effects and their respective interactions with the insecticide treatment, so it can be considered that there were no cytoplasmic or extranuclear factors, or interaction of these with nuclear factors involved in the expression of this variable (Ávila *et al.*, 2009).

Taking into account the significant interaction of ACG×TRAT (Table 2), a diallel analysis was performed within each of the treatments, not finding significant effects of ACG in the treatment with insecticide; conversely, significant effects of ACG were observed in the treatment without insecticide (Table 2); in this treatment for the variable foliar damage by *S. frugiperda*, the PWL₁S₃ line presented significant effects of ACG with a positive value (Table 3).

Table 3. Estimated effects of general combinatorial aptitude on the diagonal and specific
combinatorial ability on the diagonal of 30 crosses and 6 maize lines progenitor for
foliar damage of S. frugiperda.

Progenitor	PWL_1S_3	TGL_2S_3	TML ₃ S ₃	$LINL_4S_3$	LIHL ₅ S ₃	PWL ₆ S ₃
PWL_1S_3	0.146 *	0.134	-0.166	-0.03	-0.009	-0.022
TGL_2S_3		-0.042	-0.099	-0.171	-0.2 *	0.022
TML ₃ S ₃			0.108	0.002	-0.067	0.074
LINL ₄ S ₃				0.101	0.026	-0.032
LIHL ₅ S ₃					-0.177 *	-0.023
PWL ₆ S ₃						-0.137

*= significance a $p \le 0.05$.

Conversely, the LlHL₅S₃ line had significant and negative ACG effects; these results indicate that both lines have a high contribution in the expression of the variation of this characteristic, positively and negatively, in their respective progenies and that the additive effects are important, so it is feasible to exploit the additive proportion of the variance genetic available in these lines, by any variant of recurrent selection (Guillén-de la Cruz *et al.*, 2009; Coutiño *et al.*, 2010) to modify the resistance to damage of *S. frugiperda* (Widstrom *et al.*, 1992) in the rest of the lines evaluated did not show significance for this effect (Table 3).

The positive correlation (r=0.62) of the foliar damage of *S. frugiperda* of the progenitors with the average damage of the F₁ crosses that form their respective progenies, corroborates that the resistance to damage caused by this insect within these inbred lines, is controlled by additive effects (Figure 1). In this sense, the susceptibility of the PWL₁S₃ line is demonstrated with a high level of damage when evaluated as line *per se* (2.17) and with the average damage of all its progeny (1.71); conversely, a lower level of susceptibility was observed in the LlHL₅S₃line, both when evaluated as line *per se* (1.74), and when its progeny was evaluated (1.41); the above, also demonstrates the amplitude of the phenotypic and genotypic variability of the parents evaluated.

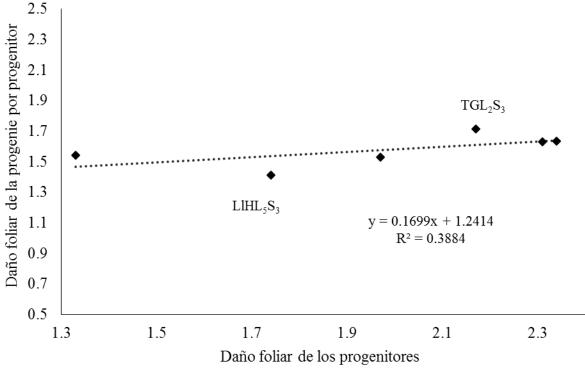


Figure 1. Relationship between foliar damage of S. frugiperda of the progenitors and their progeny.

For the same variable there were only significant ($p \le 0.05$) and negative effects of ACE in the cross TGL₂S₃×LIHL₅S₃ (Cuadro 3), if we consider the absence of reciprocal effects (Table 2) this indicates that the direct and reciprocal crosses of the lines TGL₂S₃ and LIHL₅S₃ present a leaf damage less than that of their parents; from the above it is suggested that the non-additive gene action is involved in the level of foliar damage by *S. frugiperda* in the indicated crosses and that the non-preference of this insect for this germplasm can be increased by hybridization processes, according to a Preciado *et al.* (2005), who mention that characteristics of corn, controlled by non-additive effects can be modified by hybridization methods.

The LlHL₅S₃line presented significance for negative ACG effects and is also one of the progenitors of the higher ACE cross (TGL₂S₃×LlHL₅S₃) (Table 3). These results corroborate that at higher ACE crosses there is at least one high ACG line (Reyes *et al.*, 2004; Escorcia-Gutiérrez *et al.*, 2010) it can be inferred that the high ACG of at least one parent is an indicator of greater ACE in their progeny, on the other hand, if the low ACG of the progenitor is considered. line TGL₂S₃ (Table 3), we can deduce the existence of genetic divergence between it and the line LlHL₅S₃ according to what was mentioned by Romero *et al.* (2002), who found that differential levels of ACG indicate genetic divergence between parents; which explains the high ACE in the crosses that these two parents participate (Table 3).

The regression analysis between leaf damage values of F_1 crosses and the average of their parents (Figure 2), shows relative dominance exhibited by these crosses, as a function of heterosis. All F_1 crosses had lower leaf damage of *S. frugiperda*, compared to the average values of their parents (Figure 2) and except for four crosses (PWL₁S₃×PWL₆S₃, TGL₂S₃×PWL₆S₃, TML₃S₃×PWL₆S₃,

 $LlNL_4S_3 \times PWL_6S_3$) they showed less damage than the less preferred parent (Table 4), due to the fact that the PWL_6S_3 line participates in these crosses, which presented the lowest level of leaf damage (1.33) by *S. frugiperda* (Table 4).

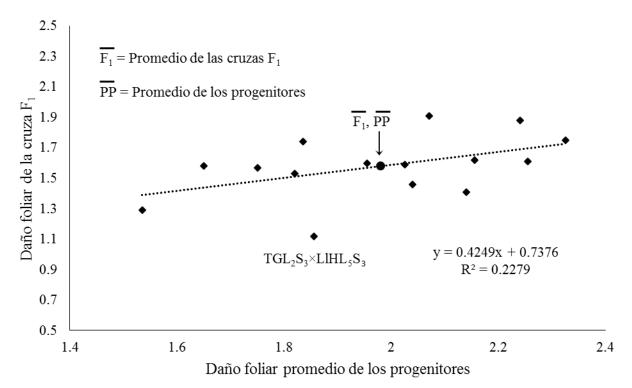


Figure 2. Relation of the foliar damage of *S. frugiperda* of the F₁ crosses of maize and the average progenitor in conditions without insecticidal application.

All the points that were distributed uniformly and closely along the trend line, indicate that the variation in leaf damage of the F_1 crosses, depended mainly on additive gene action, in a contrary way, the non-additive effects (dominance and epistasis), are identified in points that deviate considerably from this line (Figure 2). The negative non-additive effects are found in points farther below the trend line, for the case of the direct and reciprocal crosses of the lines TGL_2S_3 and $LlHL_5S_3$, this is corroborated in Table 3, where estimated effects of ACE negative in the crossing of these two lines.

In Figure 2, the dispersion of most of the points was established along the regression line, corroborating the results of the diallel analysis, which showed significant effects of ACG that favor less leaf damage in the progeny of these lines, established in conditions without insecticide. Likewise, there are points that deviate considerably from the regression line and lower damage values predominate in the F_1 crosses, compared to their parents (negative non-additive effects), such as in the TGL₂S₃×LIHL₅S₃, cross, which suggests positive dominance for the resistance to the attack of *S. frugiperda*.

The genetic expression of the crosses and progenitors, determined by the mean values of the foliar damage by *S. frugiperda* in the treatment without insecticide, showed a wide variation, the crosses $TGL_2S_3 \times LIHL_5S_3$ and $LIHL_5S_3 \times PWL_6S_3$ and the parent PWL_6S_3 had a foliar damage inferior to

1.35, within which the cross stands out $TGL_2S_3 \times LlHL_5S_3$, with the lowest level of leaf damage (1.12) (Table 4) and with greater estimated effects of ACE (Table 3), therefore, it can be considered that these cultivars have low preference on the part of *S. frugiperda* (Casmuz *et al.*, 2010). Therefore, the line $LlHL_5S_3$ is a good option to be used in breeding programs, especially for the derivation of lines of higher inbreeding with high ACG for low preference of *S. frugiperda* or in a hybridization program taking advantage of the high ACE that showed with the TGL_2S_3 line (Table 3).

Cultivor	DEsCI	Decrease in the RGP		
Cultivar	DFoSI	(g)	(%)	
PWL ₁ S ₃	2.17 ^S *	36.08	39.9	
TGL_2S_3	1.97 ^S *	-	-	
TML ₃ S ₃	2.34 ^S **	24.39	34.2	
LINL ₄ S ₃	2.31 ^S **	20.4	24.6	
LIHL ₅ S ₃	1.74	7.23	6.7	
PWL ₆ S ₃	1.33 ^R *	19.09	18.5	
$PWL_1S_3 \times TGL_2S_3$	1.91	11.92	6.9	
PWL ₁ S ₃ ×TML ₃ S ₃	1.61	38.04	32.7	
$PWL_1S_3 \times LINL_4S_3$	1.88	18.53	15.1	
PWL1S3×LlHL5S3	1.6	29.8	28.2	
$PWL_1S_3 \times PWL_6S_3$	1.57	-	-	
$TGL_2S_3\!\!\times\!\!TML_3S_3$	1.62	15.29	16.7	
$TGL_2S_3 \times LINL_4S_3$	1.41	17.54	9.1	
$TGL_2S_3 \times LlHL_5S_3$	1.12 ^R *	19.05	15.8	
$TGL_2S_3 \times PWL_6S_3$	1.58	30.14	24.5	
TML ₃ S ₃ ×LlNL ₄ S ₃	1.75	-	-	
TML ₃ S ₃ ×LlHL ₅ S ₃	1.46	25.98	24.8	
TML ₃ S ₃ ×PWL ₆ S ₃	1.74	15.76	12.8	
LINL ₄ S ₃ ×LIHL ₅ S ₃	1.59	26.12	23.2	
LINL ₄ S ₃ ×PWL ₆ S ₃	1.53	26.32	21.6	
LlHL ₅ S ₃ ×PWL ₆ S ₃	1.29 ^R *	40.37	32.1	

 Table 4. Leaf damage by S. frugiperda and decrease in grain yield per plant, of maize progenitor lines and their crosses.

DFoSI = foliar damage of *S. frugiperda* in treatment without insecticide; RGP = grain yield per plant; S** = values greater than $\mu + 2\sigma$; S* = values greater than $\mu + \sigma$; R* = values less than μ - σ .

On the other hand, for the foliar damage of *S. frugiperda* in the treatment without insecticide, it was observed that the lines PWL_1S_3 , TML_3S_3 and $LINL_4S_3$ presented an average superior to 2 with a decrease in the average grain yield of 32.9% (Table 4), these lines can be considered with high preference on the part of *S. frugiperda* and susceptible to leaf damage caused by this pest, while the TGL₂S₃ line, despite having a damage greater than 1.9, did not register a decrease in grain yield, can be considered with high preference on the part of *S. frugiperda*, but with tolerance to leaf damage caused by this insect; finally, the PWL₆S₃ line presented the least leaf damage (1.33), consequently the decrease in grain yield due to this damage was only 18.5% (Table 4).

Within the crosses evaluated, the PWL₁S₃×TGL₂S₃, PWL₁S₃×LlNL₄S₃, TML₃S₃×LlNL₄S₃ andTML₃S₃×PWL₆S₃ showed an average leaf damage greater than 1.7, but a low level of grain yield reduction, lower than 15.5% (Table 4), so it can be inferred that these crosses have tolerance to foliar damage caused by *S. frugiperda* (Casmuz *et al.*, 2010) in a contrary manner, crosses PWL₁S₃×TML₃S₃, LlHL₅S₃×PWL₆S₃ and PWL₁S₃×LlHL₅S₃ had lower leaf damage to 1.62, but had a decrease in grain yield of 32.7, 32.1 and 28.2% respectively and can be considered to have a low tolerance to leaf damage; finally, the cross TGL₂S₃×LlHL₅S₃ had a low leaf damage (1.29) of *S. frugiperda* and consequently a reduction in grain yield of only 15.8% (Table 4).

Conclusions

Within the evaluated germplasm there is resistance to *S. frugiperda*, both due to non-preference and tolerance to leaf damage, which caused a smaller decrease in grain yield due to the incidence of this pest; In general, there was heterosis for the non-preference of this pest, so this germplasm can be considered as a source of characteristics that provide resistance to *S. frugiperda*.

The variation of the foliar damage of *S. frugiperda* in the germplasm evaluated, depended as much on additive as non-additive effects, and the additive effects depended on the application condition or without insecticide, considering that it is feasible the inclusion of this germplasm in programs of selection or hybridization for the improvement of resistance to *S. frugiperda*.

The effects of non-additive type were of greater importance for foliar damage caused by *S*. *frugiperda* in the germplasm evaluated, so that processes of improvement through reciprocal recurrent selection or hybridization are viable.

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