Combining abilities for maize stem antibiosis, yield loss and yield under infestation and no infestation with pink stem borer

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Abstract

The pink stem borer (*Sesamia nonagrioides* Lef.) is the main pest of maize (*Zea mays* L.) in northwestern Spain. Little is known about combining ability for antibiosis and tolerance to this pest. Therefore, the objectives of this work was the estimation of general combining ability (GCA), specific combining ability (SCA) and reciprocal effects (R) for stem damage traits, yield and yield loss, using a complete diallel of ten inbreds, and to determine the most useful trait for evaluating the level of defense to pink stem borer. The diallel design was evaluated for two years for stem damage traits, yield loss, and for yield under two conditions, infestation with *Sesamia nonagrioides* and no infestation. For all stem damage traits, general combining ability was significant, while specific combining ability and reciprocal effects were not significant. This indicated that, for this set of inbreds, only additive effects were important for stem antibiosis. GCA and SCA effects were significant, in at least a trial, for yield under both infestation conditions and for yield loss. R effects were significant for yield of infested and no infested plants in 1995. The lack of concordance among lines that exhibited the most favorable GCA effects for stem antibiosis, yield loss, and yield under infestation conditions and the low correlation coefficient between SCA effects for yield under infestation and no infestation conditions showed that yield under infestation conditions is the best trait for evaluating the level of defense against pink stem borer attack. A interpopulational recurrent selection program for yield under infestation conditions appears as the most efficient program to improve the defense level against pink stem borer attack.

Key words: *Sesamia nonagriodes*, stem borer, antibiosis, yield loss, combining ability.

Introduction

Insect pests can cause high yield losses at different fenological stages of maize. The most important pest of maize in temperate areas of the northern hemisphere is the European corn borer (*Ostrinia nubilalis* Hbn), but in southern Europe the pink stem borer also causes significant damage to maize. Specifically, in the northwest of Spain, the pink stem borer is the main pest of maize (Cordero et al., 1998).

Sesamia nonagrioides is a tropical moth (Fam. *Noctuidae*) and temperatures below 0ºC limit the population levels (Galichet, 1982). In most of its area it has two generations per year, but it can reach even four generations per year. Most of the larvae development takes places into the maize plant and it can provoke lodging stem, ear drop and direct yield losses, but *Sesamia nonagrioides* prefers attacking stems rather than ears (Cordero et al., 1998). The yield losses could reach up to 30% of yield (Larue, 1984).

One of the most promising methods for controlling an insect pest in the overall context of integrated pest control is to grow insect resistant cultivars (Ortega et al., 1980; Pathak, 1991). To start a breeding program to increase the level of defense of maize to *Sesamia nonagrioides* it is necessary to know the different mechanisms of defense against this insect and to determine the transmission of each mechanism from the original plants to cultivars (Pathak, 1991). The mechanisms of defense have been classified into three groups, namely antixenosis, antibiosis, and tolerance (Painter, 1951). Antixenosis reduces the probability of contact between parasites and plants. Antibiosis is the ability of the plant to reduce or stop the growth and/or development of the parasite. Tolerance is the mechanism by which plants reduce the extent of damage per unit parasite present. Therefore, to detect differences in tolerance among genotypes it is necessary to determine the amount of yield reduction per unit of infection. A tolerant plant could present an elevated injury without showing a proportional yield loss.

The first step in a breeding program for increasing the level of plant defense to insect attack is to identify sources of defense mechanisms. Several authors have evaluated stem and ear antibiosis of maize to the pink stem borer (Anglade, 1961a; Anglade and Bertin, 1968; Malvar et al*.,* 1993; Cartea et al*.,* 1994; Butrón et al., 1998a, b; Butrón et al., 199-). After identifying the sources of defense mechanisms, it is necessary to study how they are transmitted from the original varieties to improved cultivars to design an efficient breeding program (Pathak, 1991). A study has been carried out to estimate general and specific combining abilities and reciprocal effects for antibiotic resistance of the ear. It has showed that specific combining ability (SCA) effects were not important for grain antibiosis to the pink stem borer (Butrón et al*.,* 1998a). However, there is only one study about transmittability of stem antibiosis (Anglade and Bertin, 1968). They evaluated the antibiotic resistance to pink stem borer of inbred lines and their hybrids and concluded that antibiotic resistant lines transmitted antibiosis to their hybrids.

There is only a work about the three mechanisms of defense against *Sesamia nonagrioides* (Butrón et al*.,* 1998b). In this work tolerance was an important mechanism of defense, since only a small part of the variation of yield loss could be predicted from the level of antibiosis. This indicated the need of selecting genotypes by a comprehensive measure such as yield loss that combines antibiosis and tolerance. However, Lynch (1980) showed that the high yield losses of certain hybrids were compensated by their high potential yield. So, the evaluation of yield under infestation conditions appears as an important way to estimate the defense level against insect attack. Therefore, the knowledge about combining ability effects for yield loss and yield under infestation conditions and about relationship between combining ability effects for both traits would allow determine the best strategy to improve tolerance to pink stem borer

So, the objectives of this work were: i) to estimate GCA, SCA, and R effects for antibiotic resistance of stem, yield and yield loss, using a complete diallel of ten inbreds, and ii) to check the relationships among antibiotic resistance, yield loss, and yield under infestation and no infestation conditions to choose the most useful traits for evaluating the defense against pink stem borer attack.

Materials and methods

Ten maize inbred lines that showed different degrees of resistance to the pink stem borer attack in a previous study (Butrón et al*.,* 199-) were used as parents of a diallel set of crosses with reciprocals (Table 1). In 1994, the 90 hybrids were obtained from the diallel design. The 90 F_1 single crosses were evaluated with 10 checks in a split-plot where plots were sorted according to a 10 × 10 simple lattice. The whole plots were genotypes and the subplots were treatments, namely either infestation with *Sesamia nonagrioides* or no infestation. The experiment was carried out in 1995 and 1996 in Pontevedra, in the Atlantic coast of Spain (42º 25' N, 4º 57' W and 20 m above sea level). In 1996, successive granular insecticide (triclorfon 2.5%) treatments were applied on the no infested subplots to guarantee protection against pink stem borer attack. Whole plot consisted of two rows and each of them received randomly one different treatment (infestation or no infestation).

At silking, corresponding subplots were infested with eggs of the pink stem borer. Each one of five plants per subplot received a mass of about 40 eggs of *Sesamia nonagrioides*. The infestation was made according to Anglade's technique (Anglade, 1961) with a modification, eggs were placed between the shank of main ear and the stem, instead of placing them at the third leaf below the main ear. The rearing method of eggs was described by Eizaguirre (1989).

At harvest, yields of infested plants and no infested plants at 140 g Kg^{-1} moisture content were calculated from the ears of infested and no infested plants, respectively. On the basis of these yields, the percentage of yield loss was computed as:

%yield loss = (1 - yield of infested plants/yield of no infested plants) * 100

Stems of infested plants in each plot were dissected. Data were recorded on number of entry holes, number and length of tunnels, and number of larvae of *Sesamia nonagrioides*. Individual analyses of variance were made for stem damage traits and yield loss according to a lattice design. Repetitions were considered as a random factor and hybrids as a fixed factor. If the efficiency of the lattice design was not at least 110% of the randomized complete block, the combined analysis of variance was analyzed as a randomized complete block design. Combined analysis of variance for yield was computed according to a split-plot design.

In the combined analysis of variance for each trait, the variation due to genotypes was orthogonally divided into checks, hybrids of diallel, and checks *versus* hybrids of diallel. Variation among hybrids of diallel was further partitioned into GCA, SCA, and R effects. Griffing's Method 3, Model I (fixed effects) (Griffing, 1956) was used to determine combining ability and reciprocal effects for antibiotic resistance of stem, yield, and yield loss. The analyses of the diallel design was made using the program DIALLEL Analysis and simulation (Burow and Coors, 1994).

The comparisons of means for GCA, SCA, and R effects were carried out by the Fisher's least significant difference method. The standard errors for GCA, SCA, R, and differences among GCA and SCA effects were calculated according to Griffing (1956).

The simple correlation coefficients between GCA and SCA effects for yield under infestation conditions and yield loss, and between GCA and SCA effects for yield under infestation and no infestation conditions were calculated. Analysis of variance and simple correlation coefficients were made with the SAS package (SAS Institute, 1989).

Results and discussion

The combined analyses of variance for stem damage traits were made according to a randomized complete block design because the lattice analyses did not show a significantly higher efficiency (108, 99, 102 and 109 % for number of holes, number of tunnels, tunnel length and number of larvae of *Sesamia*, respectively).

The combined analyses of variance showed significant differences among hybrids of diallel for number and length of tunnels, and number of larvae of *Sesamia* (Table 2). For stem damage traits, there were significant differences among GCA effects and there were not among SCA and R effects. Then, for stem antibiosis only additive effects were important for this set of lines as it was already pointed out for grain antibiosis (Butrón et al., 1998a). Besides, Anglade and Bertin (1968) showed that resistance to *Sesamia nonagrioides* is transmitted from inbreds to hybrids. On the other hand, most studies carried out for determining the genic control of the antibiotic resistance of maize to other pests showed that it was mainly additive, but with a dominant component (Scott *et al.*, 1964; Chiang *et al.*, 1978; Jennings *et al.*, 1974; Ortega *et al.*, 1980; Kaan *et al.*, 1983; Pathak and Otieno, 1990; Thome *et al.*, 1992). In general, the diallel designs made to determine the inheritance of insect resistance showed significant differences among GCA and SCA (Jennings *et al.*, 1974; Ajala, 1993; Widstrom *et al.*, 1992; Thome *et al.*, 1994) in disagreement with our results, since we showed that GCA effects were the only significant for stem antibiosis to pink stem borer. For all stem damage traits, there were neither significant reciprocal effects nor significant interaction year x reciprocal effects. This means that for the genotypes studied, the cytoplasmic effects were not important in the inheritance of stem resistance to the pink stem borer as it has been already pointed out by other authors for the inheritance of corn earworm resistance (Widstrom, 1972). However, there are other studies that show the existence of reciprocal effects for pest resistance (Khalifa and Drolsom, 1988; Widstrom *et al.*, 1992; Ajala, 1993) and that reciprocal effects are large enough to influence decisions in a breeding program for corn borer resistance (Khalifa and Drolsom, 1988). There was not any significant interaction with years, so the genotypes in these trials had a similar behavior across different environments as it was expected since the evaluations were made in both years under artificial infestation. Since GCA effects were the only significant, a intrapopulational recurrent selection program for stem antibiosis would be useful for reducing the stem damage made by the pink stem borer.

The split-plot combined analysis of variance for yield showed significant differences between treatments (data not shown), average yield under infestation conditions (7.65 t ha^{-1}) being lower than under no infestation conditions (8.96 t ha^{-1}). The existence of significant interactions hybrids of diallel × treatments and GCA × treatments for yield (data not shown) was the cause of carrying out the analysis of variance for yield under infestation and no infestation conditions separately.

The combined analyses of variance for yield under infestation and no infestation conditions, and yield loss showed significant differences among GCA effects (Table 2). There were also significant differences among SCA effects for yield of no infested plants, but not for yield under infestation conditions and yield loss. The existence of significant interactions SCA × year for both traits could have masked the differences among SCA effects for yield of infested plants and yield loss. Reciprocal effects were not significant for both traits. However, the significant interaction R × year for yield under infestation conditions could be the cause of the lack of differences among R effects for this trait. Individual analyses for yield under infestation and no infestation were computed on account of the significance of these interactions.

Individual analysis showed significant differences among GCA effects for yield under infestation and no infestation conditions in both years and for yield loss in 1995 (data not shown). There were also significant differences among SCA effects for yield of no infested plants in both years and for yield of infested plants and yield loss in 1996. Reciprocal effects for yield under infestation and no infestation conditions were only significant in 1995. Then, additive and dominant effects were present in the inheritance of yield loss and yield under infestation and no infestation conditions for this set of inbreds. Thome *et al.* (1994) obtained similar results studying yield under infestation with Southwestern corn borer (*Diatraea frugiperda* Dyar) and protected conditions in a diallel set of crosses among maize inbreds. Besides, cytoplasmic effects should be considered to improve yield under infestation and no infestation conditions.

The expression of yield under infestation conditions and yield loss have had an important environmental component since the interactions SCA × year and R × year were significant for yield under infestation conditions and the interaction SCA × year was significant for yield loss. Therefore, in a breeding program to improve the yield under infestation conditions or reduce yield loss caused by the pink stem borer evaluations should be made in several environments.

The inbreds A509 and F7 showed the best GCA effects for number of holes and tunnel length (Table 3). EP28 and F7 exhibited the most favorable GCA effects for number of tunnels. Finally, the lines A509, EP28, and F7 showed the most negatives values for the GCA for the number of larvae of *Sesamia*. EP42 had significant positive GCA effects for all traits. The lines A661, CM105, EP28, and PB60 had, in general, GCA effects that did not significantly differ from zero. A637 showed unfavorable GCA effects for number of holes and tunnel length and the hybrids of the line EP31 performed worse than the hybrid mean for tunnel length. Therefore, the inbreds A509 and F7 were the best general combiners for stem resistance and EP42 was the worst.

Under both infestation conditions inbreds A637, A661 and CM105 showed favorable GCA effects for yield, while A509 and EP31 exhibited unfavorable GCA effects (Table 3). The line A637 did not show favorable GCA effects for the antibiosis of the stem, as it was pointed out, and of the ear (Butrón et al*.,* 1998a), but its hybrids were as productive under infestation conditions as those derived from the inbreds A661 and CM105. On the other hand, the line A509, that transmitted antibiotic resistance to stem attack by the pink stem borer to its hybrids and that did not show unfavorable GCA effects for yield loss, exhibited a significant unfavorable GCA effect for yield under infestation and no infestation conditions. Inbred F7 showed good GCA effects for stem antibiosis and yield loss, but did not have significant favorable GCA effects for yield under infestation conditions because its hybrids, in general, showed a low yield under no infestation conditions. The low yield loss suffered by these hybrids did not compensate their low yield under no infestation. So, there were not a good concordance between stem antibiosis and yield under infestation conditions as it was already showed between stem antibiosis and yield loss (Butrón et al., 1998b).

The no convenience of using yield loss instead of yield under infestation conditions for evaluating the defense level against pink stem borer attack was supported by the low simple correlation coefficient between GCA effects for yield under infestation conditions and those for yield loss (r = 0.12). Inbreds A661 and CM105, in spite of not showing favorable GCA effects for yield loss, had good GCA effects for yield under infestation conditions (Table 3). There was a lack of concordance between the lines that exhibited the most favorable GCA effects for yield under infestation conditions and yield loss and a good concordance between inbreds that showed the best GCA effects for yield of infested plants and no infested plants (r = 0.90*). These results supported the proposals made by Lynch (1980), since the high yield under no infestation conditions of certain hybrids compensated the higher yield loss experimented by them than by others such as those derived from the lines EP28 and F7. Therefore, it is important to consider yield under infestation conditions for breeding maize performance to pink stem borer attack as it has already been proposed for other pests (Klenke et al., 1986; Thome et al., 1994; Anglade et al., 1996).

The hybrid A637 × EP42 had significant favorable SCA effects for yield under infestation and no infestation conditions in 1995 (Table 4). Besides, we have already pointed out that the inbred A637 showed a good GCA for yield; then this cross could be used directly by maize growers due to its high yield under infestation and no infestation conditions. This hybrid responds to the heterotic pattern "American dent × European flint" suggested as a interesting heterotic pattern for northwestern Spain conditions (Moreno-González, 1988). The crosses A637 × PB60 and A661 × F7 exhibited significant favorable SCA effects for yield under infestation conditions, but their yield performance under no infestation conditions were not as good as that exhibited by A637 × EP42. There were significant correlation coefficients between SCA effects for yield under infestation conditions and yield loss (r = -0.75 in 1995 and r = -0.56 in 1996). Therefore, SCA effects for yield under infestation conditions and yield loss were related. The hybrid A637 × EP42 showed favorable significant SCA effects for both traits, yield and yield loss under infestation conditions. However, SCA effects for yield under high infestation conditions were little related with SCA effects for yield under no infestation conditions (in 1996 the correlation coefficient between SCA effects for yield of infested and no infested plants was r = 0.34*). Then, it would no be adequate to use the yield of no infested plants as a estimation of yield under infestation conditions.

Hybrids A509 × A637, A509 × CM105, A637 × EP31, EP42 × A661, EP28 × CM105, and Z77016 × CM105 showed values for yield under infestation conditions better than those of their corresponding reciprocal crosses (Table 4). Therefore, if these crosses are directly used by maize growers, it will be necessary to use the first line of each cross as the female parent.

Based on the evidence that additive gene action is the only component of inheritance of stem antibiosis to *Sesamia nonagrioides* for this set of inbreds, the lines mentioned by their good GCA effects could be used as donors of resistance to make a synthetic population that would respond positively to an intrapopulational recurrent selection program for stem antibiosis. However, from this study it appears that the high level of yield under no infestation conditions conferred a better yield performance under infestation conditions, though high yielding hybrids can suffer higher yield loss and/or higher plant damage. Therefore, breeding for antibiosis could increase the level of maize defense to *Sesamia nonagrioides* attack, but at the end the main criterion of selection to develop genotypes with high level of defense mechanisms should be yield under infestation conditions (Thome et al., 1994). Since GCA, SCA, and R effects were significant for yield under infestation conditions, a interpopulational recurrent selection program for yield under infestation conditions appears as the most efficient program to take advantage of both additive and dominant genetic effects.

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References

Ajala, S.O. 1993. Population cross diallel among maize genotypes with varying levels of resistance to the spotted stem-borer *Chilo partellus* (Swinhoe). Maydica 38: 39-45.

Anglade, P. 1961. Essai de mise au point d'une méthode de mesure de la sensibilité des lignées de maïs aux chenilles de la génération estivale de la Sésamie (*Sesamia nonagrioides* Lef.). Ann. Epiph. 12: 413-422.

Anglade, P., and C. Bertin. 1968. Mise en évidence d’une résistance à la Sésamie des lignées de maïs et de sa transmission aux hybrides. Ann. Epiph. 19: 579-587.

Anglade, P., B. Gouesnard, A. Boyat, and A. Panouillé. 1996. Effects of multitrait recurrent selection for European corn borer tolerance and for agronomic traits in FS12 synthetic. Maydica 41: 97-104.

Barry, D., M.S. Zuber, A.Q. Antonio, and L.L. Darrah. 1983. Selection for resistance to the second generation of the European corn borer (Lepidoptera: Pyralidae) in maize. J. Econ. Entomol. 76: 392-394.

Burow, M.D., and J.G. Coors. 1994. Diallel: A microcomputer program for the simulation and analysis of diallel crosses. Agron. J. 86: 154-158.

Butrón, A., R.A. Malvar, M.E. Cartea, A. Ordás, and P. Velasco. 199-. Resistance of maize inbreds to pink stem borer. Crop Sci. (accepted).

Butrón, A., R.A. Malvar, P. Velasco, M.E. Cartea, and A. Ordás. 1998a. Combining abilities and reciprocal effects for maize ear resistance to pink stem borer. Maydica (in press).

Butrón, A, R.A. Malvar, P. Velasco, P. Revilla, and A. Ordás. 1998b. Defense mechanisms of maize against pink stem borer. Crop Sci. (in press).

Cartea, M.E., R.A. Malvar, P. Revilla, A. Ordás, and A. Alvarez. 1994. Seasonal ocurrence and response of maize inbred lines to pink stem borer in the northwest of Spain. Maydica 39: 191-196.

Chiang, M.S., A.C. Hudon, and D. Chez. 1978. Improving short-season maize. Canada Agriculture 23: 3-5.

Cordero, A., R.A. Malvar, A. Butrón, P. Velasco, P. Revilla, and A. Ordás. 1998. Life-cycle of *Sesamia nonagrioides* and *Ostrinia nubilalis* in maize cultivars of NW Spain (Lepidoptera, Noctuidae, Pyralidae). Maydica (in press).

Eizaguirre, M. 1989: Inducción de la diapausa en *Sesamia nonagrioides* Lef. (Lepidoptera: Noctuidae) y su papel en el ciclo biológico de las comarcas de Lérida. Thesis doctoral. Universidad Politécnica de Catalunya. Spain.

Galichet, P.F. 1982. Hibernation d'une population de *Sesamia nonagrioides* Lef. (*Lép. Noctuidae*) en France méridionale. Agronomie 2: 561-566.

Griffing, B. 1956. Concept of general and specific combining ability in relation to diallel crossing systems. Aust. J. Biol. Sci. 9: 463-493.

Jennings, C.W., W.A. Russell, and W.D. Guthrie. 1974. Genetics of resistance in maize to first- and second-brood of European corn borer. Crop Sci. 14: 394-398.

Khalifa, I., and N. Drolsom. 1988. Combining ability for European corn borer resistance and three agronomic traits in maize. Maydica 33: 247-259.

Kaan, F., P. Anglade, A. Boyat, and A. Panouille. 1983. La résistance à la pyrale, *Ostrinia nubilalis* Lef. (Lep. *Pyralidae*) dans un diallèle de 14 lignées précoces de maïs, *Zea mays* L. Agronomie 3: 507-512.

Klenke, J.R., W.A. Russell, and W.D. Guthrie. 1986. Recurrent selection for resistance to European corn borer in a corn synthetic and correlated effects on agronomic traits. Crop Sci. 26: 864-868.

Larue, P. 1984. La Sésamie du maïs (*Sesamia nonagrioides* Lef.) dégâts et actualisation de la lutte. La Défense des Végétaux 227: 163-179.

Lynch, R.E. 1980. European corn borer: yield loss in relation to hybrid and stage of corn development. J. Econ. Entomol. 73: 159-164.

Malvar, R.A., M.E. Cartea, P. Revilla, A. Ordás, A. Alvarez, J.P., and Mansilla. 1993. Sources of resistance to pink stem borer and European corn borer in maize. Maydica 38: 313-319.

Moreno-González, J. 1988. Variétés de maïs adaptées au nord-ouest de l'Espagne. Phosphore et Agriculture 80: 55-62.

Ortega, A., S.K. Vasal, J. Mihm, and C. Hersheand. 1980. Breeding for insect resistance in maize. pp. 372-419. In: F.G. Maxwell and P.R. Jennings (eds.). Breeding Plants Resistant to Insects. J. Wileand. New York.

Painter, R.H. 1951. Insect resistance in crop plants. McMillan (ed.). New York. 520 p.

Pathak, R.S. 1991. Plant genetics in pest management. Insect Sci. Applic. 12: 553-564.

Pathak, R.S., and S.M. Othieno. 1990. Inheritance of resistance to the spotted stem-borer, *Chilo partellus* (Swinhoe), in maize. Maydica 35: 247-252.

SAS Institute Inc. 1989. SAS/STAT user's guide, version 6, 4th ed., vols.1 and 2. SAS Institute Inc., Cary, North Carolina, USA.

Scott, G.E, A.R. Hallauer, and F.F. Dicke. 1964. Types of gene action conditioning resistance to European corn borer leaf feeding. Crop Sci. 4: 603-604.

Thome, C.R., M.E. Smith, and J.A. Mihm. 1994. Yield reduction in a maize diallel under infestation with southwestern corn borer. Crop Sci. 6: 1431-1435.

Widstrom, N.W. 1972. Reciprocal differences and combining ability for corn earworm injury among maize single crosses. Crop Sci. 12: 245-247.

Widstrom, N.W., K. Bondari, and W.W. McMilian. 1992. Hybrid performance among maize populations selected for resistance to insects. Crop Sci. 32: 85-89.

Table 1. Germplasm description of ten parental inbred lines used for a diallel crossing design with reciprocals.

Inbred lines	Pedigree	Type of germplasm
A509	A78 x A109	American dent
A637	CO106 x A321	American dent
A661	AS-A	American dent
CM105	V3 x B14^2	American dent
EP28	AS-D	American dent
EP31	Silleda	European flint
EP42	Tomiño	European flint
F7	Lacaune	European flint
PB60	Nostrano dell'Isola	European flint
Z77016	Z27 x Z36	European flint

Table 2. Mean squares combined over years of the pertinent sources of variation for four stem damage traits, yield under infestation (I) and no infestation (N) with pink stem borer, and yield loss from a diallel with reciprocals of ten inbred lines tested in two years.

Sources of		Number	Number of	Tunnel	Number of	Yield		Yield
variation	df	of holes	tunnels	length	larvae of *Sesamia*	I	N	loss
Hybrids of diallel (H)	89	15,66	1,03 **	413,61 **	1,92 **	4.12	5.90**	254.06
GCA	9	56,30 **	3,61 **	2067,11 **	8,73 **	16.29**	32.42**	586.68**
SCA	35	12,20	0,68	262,24	1,23	4.11	4.68**	295.58
R	45	10,21	0,79	200,65	1,09	1.70	1.53	155.24
Years x H	89	12,40	0,64	230,76	1,17	3.16**	1.70*	300.19*
Years x GCA	9	6,80	0,81	405,00	1,18	2.34	2.32	229.82
Years x SCA	35	11,25	0,45	153,94	0,91	3.35*	1.39	387.02**
Years x R	45	14,41	0,75	255,65	1,38	3.20*	1.82	246.74
Error	198[†]	12,92	0,67	270,38	1,36	2.01	1.22	214.35

*,** Significant at the 5 and 1% level of probability, respectively.

† For yield under no infestation conditions and yield loss, freedom degrees were 178 and, for yield under infestation conditions, they were 177.

Table 3. GCA estimates for four stem damage traits, yield of infested and no infested plants, and yield loss from a diallel with reciprocals of ten inbred lines tested in two years.

Inbred line	Number of holes	Number of tunnels	Tunnel length	Number of larvae of *Sesamia*	Yield of infested plants	Yield of no infested plants	Yield loss
A509	-1.2*	-0.2	-5.3*	-0.4*	-0.5*	-0.8*	-0.9
A637	1.0*	0.0	7.2*	-0.1	0.5*	0.6*	0.7
A661	0.4	0.2	-3.0	0.2	0.6*	0.8*	1.3
CM105	-0.7	0.1	-2.5	0.0	0.7*	1.1*	2.5
EP28	-0.5	-0.3*	-0.9	-0.5*	0.3	0.0	-3.7*
EP31	0.7	0.2	4.1*	0.2	-0.8*	-0.9*	0.1
EP42	1.5*	0.4*	10.0*	0.7*	0.1	0.2	1.1
F7	-1.2*	-0.3*	-8.2*	-0.3*	-0.1	-0.7*	-6.4*

PB60	0.5	0.0	1.5	0.3*	-0.1	0.4*	4.1*
Z77016	-0.5	-0.1	-2.9	-0.1	-0.6*	-0.6*	1.3
LSD (5%)	1.2	0.2	5.7	0.4	0.5	0.4	5.1

* GCA estimate differed significantly from zero.

Table 4. Specific combining ability (SCA) and reciprocal effects (R) of diallel crosses among ten inbred lines for maize yield under infestation (I) and no infestation (N) conditions and for yield loss in 1995 and 1996.

	1995					1996				
	SCA			R		SCA			R	
	Yield		Yield	Yield		Yield		Yield	Yield	
	I	N	loss	I	N	I	N	loss	I	N
A509 × A637	-0.10	0.10	3.2	2.32*	1.82*	0.56	-0.43	-9.8	-0.41	-0.19
A509 × A661	-0.13	0.04	2.0	-0.09	-0.25	-0.75	-1.34*	-4.2	0.25	0.18
A509 × CM105	0.81	0.47	-4.7	1.53*	0.43	-0.60	0.19	8.9	-0.91	-0.48
A509 × EP28	-0.49	-0.10	5.2	0.78	0.59	-0.04	0.31	2.0	0.28	-0.85
A509 × EP31	0.66	0.00	-10.4	0.94	0.24	0.18	0.19	-1.5	-0.39	0.25
A509 × EP42	0.36	0.47	1.1	-1.49	-1.03	-0.51	-0.21	4.0	0.79	0.36
A509 × F7	-0.97	0.02	12.3	0.77	0.69	1.02	0.94	-2.8	-0.32	0.28
A509 × PB60	-0.37	-0.68	-2.2	0.40	0.65	0.00	-0.42	-1.5	-0.43	-0.81
A509 × Z77016	0.22	-0.32	-6.4	-1.41	-0.72	0.14	0.77	4.9	-0.16	0.38
A637 × A661	-0.36	0.00	2.7	-1.07	0.27	-0.37	0.27	5.0	0.12	-0.22
A637 × CM105	-2.70*	-0.98	20.8	-0.37	-0.71	-0.03	-0.22	-1.0	0.15	0.69
A637 × EP28	-0.32	-0.65	-4.7	-0.37	0.36	-1.15	-1.03*	2.6	1.04	0.46
A637 × EP31	-0.79	-0.31	10.7	1.74*	0.77	0.04	-0.01	2.0	-1.42	-1.30
A637 × EP42	2.66*	1.65*	-13.1	0.14	-0.13	0.97	-0.59	-14.5*	-0.78	-0.09

1	A637 × F7	-0.17	0.41	6.7	1.06	0.13	-0.14	0.51	6.2	0.55	0.38
2	A637 × PB60	1.39*	0.49	-12.1	1.07	-0.30	-0.26	0.86	7.7	0.68	-0.54
3	A637 × Z77016	0.40	-0.72	-14.2	0.57	0.20	0.36	0.65	1.7	0.98	0.09
4	A661 × CM105	1.02	0.15	-10.1	0.62	0.18	-0.15	-0.64	-3.0	-0.11	0.72
5	A661 × EP28	-1.02	-1.79*	-8.3	0.45	0.95	-0.04	-1.17*	-10.3	-0.06	-0.56
6	A661 × EP31	-1.27	-1.21*	6.5	-0.59	-0.52	0.58	-0.58	-10.0	-0.16	0.01
7	A661 × EP42	-0.45	0.44	8.7	-1.89*	-1.37*	-0.25	1.36*	13.4*	-0.09	-0.23
8	A661 × F7	1.51*	1.26*	-3.6	-0.67	-0.62	0.88	0.88	-0.2	0.30	0.09
9	A661 × PB60	0.72	1.00*	-0.1	0.06	0.94	-0.45	0.78	10.7	0.44	0.89
10	A661 × Z77016	-0.01	0.10	2.3	0.65	-0.17	0.55	0.45	1.5	-0.26	0.25
11	CM105 × EP28	0.55	0.27	-1.6	-2.13*	-1.07	0.51	-0.08	-7.1	0.63	0.17
12	CM105 × EP31	-0.92	-0.48	5.7	-0.34	-0.55	0.32	-1.72*	-22.4*	-0.14	-0.75
13	CM105 × EP42	0.04	-0.23	-3.9	0.39	0.66	-0.93	0.69	15.1*	0.16	0.24
14	CM105 × F7	1.16	0.76	-5.3	-0.59	-0.22	0.74	1.15*	3.3	0.33	0.60
15	CM105 × PB60	-0.44	-0.63	-1.9	1.18	1.05	-0.23	0.33	6.3	-0.75	0.12
16	CM105 × Z77016	0.48	0.67	0.9	-2.03*	-1.51*	0.38	0.31	-0.2	0.56	0.64
17	EP28 × EP31	-0.55	-0.03	8.6	0.53	0.49	0.13	0.44	3.1	-0.06	0.09
18	EP28 × EP42	0.22	0.76	4.9	-0.09	-0.28	0.61	0.52	-1.1	-0.23	-0.57
19	EP28 × F7	-0.22	-0.09	1.2	-0.09	0.58	0.47	0.58	0.1	0.25	0.08
20	EP28 × PB60	0.89	0.43	-6.3	-0.35	0.05	-1.10	-0.51	8.7	0.80	0.26
21	EP28 × Z77016	0.94	1.20*	1.1	0.56	0.97	0.61	0.93	1.9	0.76	0.50
22	EP31 × EP42	0.01	-0.35	-4.6	-0.47	0.58	0.82	0.44	-4.2	-0.37	0.10
23	EP31 × F7	0.89	0.44	-8.0	-0.15	-0.19	-0.83	0.37	14.3*	0.36	0.09

EP31 × PB60	0.71	1.06*	2.3	-0.80	-0.41	-0.49	0.63	7.1	0.72	-2.19
EP31 × Z77016	1.27	0.89	-10.8	0.49	0.75	-0.76	0.24	11.7*	0.18	-0.04
EP42 × F7	-0.30	-0.91	-7.7	0.27	-0.23	-0.67	-1.25*	-5.9	-0.50	-0.32
EP42 × PB60	-1.95*	-1.22*	13.2	0.21	0.56	0.23	-0.40	-4.0	0.25	-0.30
EP42 × Z77016	-0.58	-0.62	1.5	-1.04	-0.27	-0.27	-0.57	-2.7	-0.57	-0.52
F7 × PB60	-0.06	-0.56	-7.1	-0.34	0.29	0.92	-0.83	-17.0*	0.16	-0.29
F7 × Z77016	-1.83*	-1.32*	11.5	0.33	0.04	-2.40	-2.36*	2.1	-0.80	-0.42
PB60 × Z77016	-0.89	0.12	14.2	-1.20	-1.59*	1.38	-0.43	-18.0*	-0.37	0.08
LSD (SCA_{ij} - SCA_{ik})	2.01	1.48					1.44	17.5		
LSD (SCA_{ij} - SCA_{kl})	1.86	1.37					1.34	16.2		

* Estimate differed significantly from zero.