DIALLEL CROSSING AMONG MAIZE POPULATIONS FOR RESISTANCE TO FALL ARMYWORM

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ABSTRACT: Among the insects infecting the maize (*Zea mays* L.) crop in Brazil, the fall armyworm (*Spodoptera frugiperda* Smith, 1797, *Lepdoptera: Noctuidae*) is considered one of the most important because it causes the highest damage to yield. Genetic resistance to the fall armyworm has be an effective control strategy. The main objective of this work was to evaluate new germplasm sources for resistance to the fall armyworm, the key pest for the maize crop in Brazil. A partial diallel design between 20 varieties of Brazilian germplasm and nine exotic and semi-exotic varieties of different origin was used. The 180 crosses and 29 parental varieties along with two commercial checks were evaluated in three locations in the State of *São Paulo* State (Brasil). Fall armyworm resistance (FAWR) under artificial and natural infestations, grain yield (GY), and plant height (PH) were analyzed. The populations CMS14C and MIRT, and hybrid São José x MIRT showed the highest resistance, with values of 1.8, 1.7 and 1.4, respectively. Populations PMI9401 and PR91B, and the hybrid CMS14C x (B97xITU) had best yields, with 4893, 3858 and 5677 kg ha^{-1}, respectively. Heterosis ranged from –28% to 47% for FAWR and from –21% to 125% for GY, with mean values of –0,43% and 31%, respectively. Genotype by environment interaction was not significant for FAWR. The effects of varieties and heterosis were significant for all traits, showing that both additive and dominance effects may be important as sources of variation. For FAWR, only specific heterosis presented significance, suggesting strong genetic divergence between specific pairs of parental populations. Brasilian populations PMI9302 and São José, and the exotic population PR91B presented high performance *per se,* and also in croses for FAWR and GY. Crosses PMI9401 x (Cuba110 x EsalqPB1) and São José x MIRT presented high specific heterosis effects for both characters. These populations can be useful to be introgressed in maize breeding programs.
Key words: genetic resistance, partial diallel, germplasm

CRUZAMENTO DIALÉLICO ENTRE POPULAÇÕES DE MILHO PARA RESISTÊNCIA À LAGARTA DO CARTUCHO

RESUMO: Dentre as pragas que infestam a cultura de milho (*Zea mays* L.) no Brasil, destaca-se a lagarta do cartucho (*Spodoptera frugiperda* Smith, 1797, *Lepdoptera:* Noctuidae), considerada como a praga chave por ser a que produz o maior dano. A utilização de cultivares resistentes constitui um método de controle eficiente. O principal objetivo deste trabalho foi a avaliação de novas fontes de germoplasma para resistência à lagarta do cartucho, praga chave da cultura de milho no Brasil. Foi utilizado um esquema dialélico parcial entre 20 populações representantes de germoplasma brasileiro e nove populações exóticas e semi-exóticas de diferentes origens. Os 180 híbridos e as 29 variedades genitoras, junto com duas testemunhas comerciais, foram avaliados em três locais no Estado de São Paulo (Brasil). Foram analizados os caracteres resistência à lagarta do cartucho (RLC), sob infestação artificial e natural, produtividade de grãos (PG) e altura de planta (AP). As populações CMS14C e MIRT, e o híbrido São José x MIRT apresentaram a maior resistência, com valores de 1,8 , 1,7 e 1,4, respectivamente. As populações PMI9401 e PR91B, e o híbrido CMS14C x (B97 x ITU) tiveram a maior produtividade, com 4893, 3858 e 5677 kg ha^{-1}, respectivamente. Os valores de heterose foram de –28% a 47% para RLC e de –21% a 125% para PG, com valores médios de –0,43% e 31%, respectivamente. O caráter RLC não apresentou interação genótipo x ambiente significativa. Os efeitos de variedades e de heterose foram significativos para os três caracteres, indicando que tanto os efeitos aditivos quanto os de dominância podem ser importantes como fontes de variação. Para FAWR, somente a heterose específica foi significativa, sugerindo uma forte divergência genética entre pares específicos de populações parentais. As populações brasileiras PMI9302 e São José, e a população exótica PR91B apresentaram boa performance *per se* e em cruzamentos para resistência e produtividade. Os híbridos PMI9401 x (Cuba110 x ESALQ-PB1) e (São José x MIRT) apresentaram altos efeitos de heterose específica para ambos caracteres. Estes materiais podem ser promissores para sua incorporação em programas de melhoramento.
Palavras-chave: resistência genética, dialelo parcial, germoplasma

INTRODUCTION

Among the insects infecting the maize crop in Brazil, the fall armyworm (*Spodoptera frugiperda* Smith, 1797) is considered one of the most important because it causes the highest economic damage. Larvae feed mainly on leaves, reducing the photosynthetic area of the plant and affecting indirectly the grain production. Losses of the order of 15% to 34% have been reported, depending on the phase of the plant development (Cruz, 1995).

The use of resistant cultivars has been suggested by several authors (Sprague & Dahms, 1972; Wiseman & Widstrom, 1992) as an efficient and feasible method to control armyworm infestation, either by decreasing the population of insects or by increasing the efficiency of insecticide application, thus reducing the amount of chemical products and also reducing the negative impact on environment.

In spite of the great genetic variability of the maize germplasm in Brazil, little is known in relation to the genetic potential of different materials as sources of resistance to insect infestations. The characterization of germplasm and the identification of new sources of resistance to be used in the development of new commercial varieties become more important when faced to the presence or the increase of insects attacks.

Breeding for resistance to fall armyworm has had a slow development until the advent of techniques for artificial infestation that allowed uniform evaluations of large number of plants in the field. Such techniques were developed by Ortega et al. (1980) and modified by Wiseman & Widstrom (1980). Artificial infestation has the advantage to provide more uniform levels of attack, with approximately the same number of larvae per plant. The evaluation under such conditions are really necessary when the high natural infestation does not occur in the experiment. On the other hand, there are environments where the population of insects remain at a high level every year, so that natural infestation is sufficient to assure evaluation with the desired precision. In the evaluation under field conditions, visual scales are used, which take into account the type of damage (size and number of lesions) and the damaged tissues (leaves and/or whorl) (Carvalho, 1970; Davis et al., 1992).

The genetic base of the resistance to fall armyworm has been demonstrated to be of quantitative nature and the variation is due mainly to additive genetic effects although the presence of dominant gene action cannot be ruled out (Williams et al., 1989; Widstrom et al., 1992; Widstrom et al., 1993; Guimarães e Viana, 1994 e Williams et al., 1995). The identification of new sources of resistance must be a continuous process in any breeding program for resistance to insects aiming the introgression of new genes into the genetic base of the commercial cultivars. The incorporation of new genotypes, either local or exotic, in the evaluations increase the chances for identification of mechanisms and/or genes for resistance that were not previously available. In Brazil, several studies have been conducted for the evaluation of resistance to fall armyworm, either under natural infestation (Fornasieri Filho et al., 1980; Lara et al., 1984; Marques et al., 1988) or under artificial infestation (Viana & Potenza, 1991; Viana & Guimarães, 1994; Nishikawa, 1999).

The genetic potential of different materials are usually studied in controlled crosses; in this sense, the diallel mating scheme has been useful and largely used to estimate the potential value of genotypes *per se*, their combining ability and heterosis effects (Hallauer & Miranda Filho, 1995). Miranda Filho & Geraldi (1984) suggested the partial diallel cross between two fixed sets of varieties or lines, as an adaptation of the complete diallel model of Gardner & Eberhart (1966). Geraldi & Miranda Filho (1988) concluded that the adapted model of Gardner & Eberhart (1966) is more informative than the partial diallel adapted from Griffing's (1956) model. The objectives of the present work were to evaluate maize germplasm from Brazil and exotic or semi-exotic germplasm for their agronomic traits and resistance to fall armyworm; to estimate genetic parameters for agronomic traits and resistance to fall armyworm using the partial diallel scheme (Miranda Filho & Geraldi, 1984); and to select populations with high level of resistance and desirable agronomic traits to be indicated for their use in breeding programs.

MATERIAL AND METHODS

Germplasm

The identification of populations used in this work is shown in Table 1, divided in two groups: Group I, comprising 20 Brazilian populations previously introduced in the NAP (*Núcleo de Apoio à Pesquisa*) Project; and Group II, represented by nine exotic and semi-exotic populations of diverse origins. The 20 populations of Group I were selected for fall armyworm resistance, from 113 populations of the NAP Project, under artificial infestation (data not shown).

Exotic populations were introduced on the basis of their pattern of resistance to *S. frugiperda* or other corn borer species in their sites of origin. Some of the exotics (MIRT and PR91B) were used directly and others were previously crossed with local populations to develop semi-exotics better adapted to local conditions. Two commercial hybrids (MASTER: resistant; and P3041: susceptible) were used as checks, which were chosen as the extremes for resistant pattern from a set of 12 cultivars previously evaluated under artificial and natural infestation (data not shown).

Experiments

Populations of Group I were crossed with Group II, under partial diallel scheme suggested by Miranda Filho & Geraldi (1984). The 211 entries (29 parental populations, 180 crosses and 2 hybrid checks) were evaluated in two locations representing three environments: [1] Piracicaba (SP), under artificial infestation; [2] Anhembi (SP), under natural infestation; and [3] Piracicaba (SP), under no infestation. The geographical coordinates, represented by latitude, longitude and altitude of the two locations are: 22°42'South, 47°38' West and 546 m for Piracicaba; and 22°48'South, 48°07' West and 469 m for Anhembi,

Table 1 - Designation and origin of populations from the NAP Project (Group I) and exotic and semi-exotic populations (Group II).

Code	Population	Origin
	Population of the NAP Project	
N1	BAIII Tusón	CNPMS[1]
N2	Caribeño DMR	IAC[2]
N3	CMS 14C	CNPMS
N4	CMS 23	CNPMS
N5	CMS 454	CNPMS
N6	CMS 55 PH4	CNPMS
N7	CMS 61	CNPMS
N8	ESALQPB2 x ESALQPB3 Amarelo	ESALQ/USP[3]
N9	ESALQPB2 x ESALQPB3 Branco	ESALQ/USP
N10	GUATEMALA	IAC
N11	IUBATÃ	IAC
N12	MEB	IAC
N13	Philippine DMR 4	IAC
N14	PIRANÃO	ESALQ/USP
N15	PMI 9302	IAPAR[4]
N16	PMI 9306	IAPAR
N17	PMI 9401	IAPAR
N18	São José	CNPMS
N19	Tuxpeño amarillo	IAC
N20	WP 12	IAC
	Exotic and semi-exotic population	
E1	MIRT(Multiple Insect Resistance Tropical Population)	CIMMYT
E2	PR91B	CIMMYT
E3	B95 x ITU	US Corn Belt x Local
E4	B97xITU	US Corn Belt x Local
E5	Population 58	CIMMYT
E6	PI571676 (Madre de Dios 47) x ESALQ PB1	Cuba x Local
E7	PI489360 (Cuba 113) x ESALQ PB1	Cuba x Local
E8	PI489357 (Cuba 110) x ESALQ PB1	Cuba x Local
E9	Pi571833 (Libertad 179) x ESALQ PB1	Cuba x Local

[1]CNPMS: Centro Nacional de Pesquisa de Milho e Sorgo (EMBRAPA) – Sete Lagoas, [2]IAC: Instituto Agronômico de Campinas, Estado de São Paulo. [3]ESALQ/USP: Escola Superior de Agricultura “Luiz de Queiroz” (Universidade de São Paulo) – Piracicaba, Estado de São Paulo. [4]IAPAR: Instituto Agronômico do Estado de Paraná. Londrina, Estado de Paraná.

respectively. The three environments will be here designated as experiments, symbolized by EXP [1], EXP [2] and EXP [3], respectively. A completely randomized block design was used, with one-row plots, 5 m long with spaces of 0.9 m between rows and 0.2 m between plants within rows; with an expected stand of 25 plants per plot after thinning. Number of replications were three in EXP [1] and EXP [3] and four in EXP [2]. Planting dates were September 23, September 22 and November 20 for EXP [1], EXP [2] and EXP [3], respectively, in 1998. Plots of the susceptible check were intercalated each 15 rows in EXP [1] and EXP [2], for observation on the uniformity of infestations and for calculating the correlation between traits.

Evaluated traits

The resistance to the fall armyworm (RFA) was evaluated in EXP [1] under artificial infestation and in EXP [2] under natural infestation. Artificial infestation in the field was made by application of young larvae mixed with corn cob grits using a manual dispenser “bazooka” (Wiseman et al., 1980). Infestations were made in eight plants per plot in the stages V6 to V8, with approximately 15 larvae per plant. In EXP [1] visual evaluation of the damage was at 7 and 14 days after infestation. In EXP [2] the first evaluation was 7 days after the stages V6-V8, following another evaluation one week later. In both experiments a scale of notes (0: non-damaged plant to 5: plant whorl completely destroyed) was used (Carvalho, 1970). Data for statistical analysis was represented by the average of two measurements, as suggested by Davis et al. (1992). Grain yield (GY: total grain weight of the plot, in kg ha^{-1}) and plant height (PH: mean of ten plants per plot, in cm) were also included for analysis of EXP [2] and EXP [3].

Statistical analysis

Preliminary analysis of variance for each experiment and combined analysis over experiments were performed for all traits. The analysis of variance of the partial diallel tables combined over experiments followed the model (Miranda Filho & Geraldi, 1984; Belluci, 1994):

$$Y_{ijk} = \mu + \alpha\,[d + (ld)_k] + \tfrac{1}{2}\,[v_i + v_j + (lv)_{ik} + (lv)_{jk}] + l_k$$
$$+\ \theta\,[\,\bar{h} + h_i + h_j + s_{ij} + (1\,\bar{h})_k + (lh)_{ik} + (lh)_{jk} + (ls)_{ijk} + \bar{e}_{ijk}$$

where Y_{ijk} is the mean of the cross between i^{th} population (Group I) and j^{th} population (Group II) in the k^{th} experiment; μ is the mean of the two groups; $\alpha = 1$, $\alpha = -1$ and $\alpha = 0$ for parental varieties of groups I and II and crosses, respectively; d is a measure of the difference between group means; v_i and v_j are the effects of populations for Groups I and II, respectively; l_k is the fixed effect of experiments; $\theta = 0$ for parental populations (Y_{ii} and Y_{jj}) and $\theta = 1$ for crosses (Y_{ij}); $\bar{h}$ is the average heterosis over experiments; h_i and h_j are the effects of heterosis of populations for Groups I and II, respectively; s_{ij} is the specific heterosis of the cross i x j; $\bar{e}_{ijk}$ is the error term associated to the observed mean (Y_{ii} , Y_{jj} or Y_{ij}) in the k^{th} experiment; all other terms in the model refer to the interaction of the respective effects with experiments (environments).

RESULTS AND DISCUSSION

Observed means are presented for three traits: RFA, combined for EXP. [1] and EXP. [2]; GY for EXP. [2] and EXP. [3] and PH combined for EXP. [2] and EXP. [3] (Table 2).

Preliminary analyses of variance

The preliminary analysis of variance, combined over experiments (data not shown), revealed differences between the hybrid checks for the variable RFA, indicating the effectiveness of the conditions of infestation for the discrimination between genotypes. Also, the non-significance of the interaction checks x experiments indicated that the reaction of the hybrid checks was relatively stable, even though the level of incidence of *S. frugiperda* was different between experiments. The non significance of the treatment x experiment interaction also reinforce the stable response of genotypes under the two different conditions of infestation.

For the variable GY significance was detected for both treatments and treatment x experiment interaction, indicating results should be interpreted for each experiment representing different environments. A similar pattern of significance was observed for the variable PH, but the mean square for treatments was 6.6 times greater than for the interaction treatment x experiment; although significant, the later showed a lower level of variation, as indicated by the F test (F = 1.4). For that reason, all parameters for PH were calculated with the mean over experiments.

Analysis of the diallel tables

Table 3 shows the analyses of variance for the three variables for the partial diallel table, represented by observed means of parental populations and their crosses. Differences were observed between groups for RFA ($P < 0.01$) and PH ($P < 0.05$). For RFA the difference was for advantage of Group II (lower mean) with an estimated parameter of d = 0.162. This result is explained by the fact that the NAP populations (Group I) were chosen for their pattern of resistance to *S. frugiperda* but, except for CMS14C, CMS23 and São José, all other were never submitted to selection for resistance. On the other hand, the exotic populations (Group II) were released for their high pattern of resistance to *S. frugiperda* and other *Lepdoptera* species.

Populations N3 (CMS14C) and E1 (MIRT), and the cross N18 (São José) x E1 (MIRT) presented highest resistance, with values of 1.8, 1.7 and 1.4, respectively. Populations PMI9401 and PR91B, and hybrid CMS14C x (B97xITU) had best yields, with 4893, 3858 and 5677 kg ha^{-1}, respectively (Table 2). Genotype by environment interaction was not significant for FAWR (Table 3).

Heterosis showed significance ($P < 0.01$) for all traits. For RFA the significant components of heterosis were population heterosis in Group I and specific heterosis; $\bar{h}$ = - 1.04%) indicated non unidirectional dominance effects (Vencovsky & Barriga, 1992), which can be explained by the presence of different mechanisms of resistance, under the control of different genetic systems. In fact, the heterosis effects in crosses varied from negative (-28%) to positive (47%) in the crosses N14 x E3 and N3 x E3, respectively (Table 4). For GY and PH all the heterosis components showed significance.

The significance for GY heterosis variation is explained by the wide range of estimates, which varied from -20.0% (N12 x E6) to 138.3% (N14 x E5) and from –23.0% (N12 x E6) to 114.1% (N14 x E3) in EXP 2 and EXP 3, respectively (Table 5). Mid-parent heterosis higher than 20% was represented by 64% and 68% of the crosses in EXP 2 and EXP 3, respectively. Hallauer & Miranda Filho (1995) reported heterosis of 19.5% on the average of crosses involving 611 different parental varieties. High heterosis suggests a high concentration of homozygotes, as expected in races or populations continuously maintained through small population size (Miranda Filho, 1999). However, the lack of adaptation also may result in a low performance of the parental population and, if the other parent allows the recovery of an acceptable pattern of adaptation, the final result may be the expression of a high heterosis (Regitano Neto & Miranda Filho, 1999). Heterosis for PH is of lesser interest for a breeding programs and it has shown low expresion in population crosses (Hallauer & Miranda Filho, 1995). Observations (data not shown) indicated heterosis varying from –11.8% to 26.4% and only 16% of the crosses showed mid-parent heterosis higher than 10%.

Table 2 - Observed means for resistance to fall armyworm (RFA), grain yield (GY) and plant height (PH) for populations and crosses.

CODE	RFA	GY_{E2}	GY_{E3}	PH	CODE	RFA	GY_{E2}	GY_{E3}	PH
N1	2.5	1847	2015	179	N1xE8	2.4	4544	4333	200
N2	2.6	3081	3307	180	N1xE9	2.1	3378	2359	189
N3	1.8	4236	3111	189	N2xE1	1.9	4089	4356	179
N4	2.1	3656	2811	173	N2xE2	2.1	4292	3326	179
N5	2.3	5031	3896	181	N2xE3	1.8	3603	3859	188
N6	2.7	3374	3033	194	N2xE4	2.1	5142	4026	189
N7	3	3558	3363	180	N2xE5	2.2	3169	3493	175
N8	2.1	4011	3700	181	N2xE6	2.4	3236	2619	202
N9	1.9	4769	3437	186	N2xE7	2	3389	3093	201
N10	2.3	3814	2670	180	N2xE8	2.4	4258	3222	199
N11	2.5	3714	3304	188	N2xE9	2.6	3372	2593	187
N12	2.4	4603	3126	235	N3xE1	1.7	4925	4485	186
N13	2.1	2894	2170	182	N3xE2	1.6	5125	3352	189
N14	2.9	2239	1989	160	N3xE3	2.7	4961	3304	187
N15	1.8	4111	3156	188	N3xE4	2.3	6769	4585	202
N16	2.3	4469	2848	186	N3xE5	1.8	4081	2574	182
N17	2	5217	4570	198	N3xE6	2.3	4922	4206	228
N18	2.3	4756	4304	209	N3xE7	1.7	4847	3604	210
N19	2.5	4114	3356	163	N3xE8	2.2	5450	3737	205
N20	2.1	4350	3378	195	N3xE9	2.3	5131	3844	200
E1	1.7	2953	2433	165	N4xE1	2.4	4208	3422	178
E2	1.7	4050	3667	186	N4xE2	1.5	4525	4533	192
E3	2	2333	1519	165	N4xE3	1.7	5194	3593	200
E4	1.9	4342	3089	181	N4xE4	2	5131	3541	193
E5	2	1697	1826	148	N4xE5	1.8	3404	3226	180
E6	2	4042	2515	216	N4xE6	1.9	3992	3141	213
E7	2.1	3489	3256	221	N4xE7	1.6	4408	4333	208
E8	2.4	3864	3722	207	N4xE8	1.8	3956	3196	192
E9	2.1	3056	1874	185	N4xE9	2.1	3825	3522	176
N1xE1	2.3	4003	3104	188	N5xE1	1.7	4547	3970	178
N1xE2	1.8	4081	2459	186	N5xE2	2.1	4561	4030	175
N1xE3	1.7	4772	3215	191	N5xE3	1.6	5203	3844	182
N1xE4	2.3	4244	3778	186	N5xE4	2	5331	4374	185
N1xE5	2.4	3550	2933	181	N5xE5	2	4947	3915	192
N1xE6	2.1	4242	3433	220	N5xE6	2.5	4817	4467	215
N1xE7	1.8	3861	3389	214	N5xE7	1.8	4414	3933	191
N5xE8	2.4	5492	5133	204	N9xE8	2	5192	4033	203
N5xE9	2.3	4592	3726	179	N9xE9	2.8	4689	2996	184
N6xE1	2.1	3969	3019	173	N10xE1	2.6	4683	3330	180
N6xE2	2	4628	3633	179	N10xE2	2	5183	4130	185
N6xE3	2.2	4700	4085	198	N10xE3	2	4575	3315	183
N6xE4	2.5	5558	3974	191	N10xE4	2.4	5564	4867	193
N6xE5	2.6	4814	3400	186	N10xE5	2.1	3150	3615	165
N6xE6	2.3	4339	4244	216	N10xE6	2.3	4108	4174	204
N6xE7	1.9	4283	4230	204	N10xE7	1.8	4294	3763	191
N6xE8	1.91	4830	3974	195	N10xE8	1.9	3914	3944	194
N6xE9	2.57	3800	3589	189	N10xE9	2.2	4183	3648	180
N7xE1	2.15	4589	3567	181	N11xE1	2.2	4756	4096	171
N7xE2	2.25	4436	4089	179	N11xE2	2.4	5406	4496	193
N7xE3	2.07	4800	3300	192	N11xE3	1.7	4703	3056	185
N7xE4	2.34	5031	3874	189	N11xE4	2	5078	4019	181
N7xE5	1.99	4308	3252	170	N11xE5	1.8	4686	4204	179
N7xE6	2.1	4481	4452	207	N11xE6	2	4833	4370	221
N7xE7	2.47	4585	4693	202	N11xE7	2.5	5419	3326	210
N7xE8	2.52	4556	4270	210	N11xE8	2.2	5072	3374	211
N7xE9	2.29	3537	3833	179	N11xE9	2.1	4231	3352	191

N8xE1	2.15	4308	4044	182	N12xE1	1.6	4706	2885	211
N8xE2	1.84	5133	4578	176	N12xE2	1.9	5614	3200	200
N8xE3	2.26	5272	2963	188	N12xE3	1.9	5208	3293	207
N8xE4	2.35	5108	4867	186	N12xE4	2.1	5306	3652	211
N8xE5	1.71	3767	3981	185	N12xE5	1.7	5042	3378	212
N8xE6	2.1	4628	3178	225	N12xE6	2.7	3456	2170	252
N8xE7	2.81	4275	3804	198	N12xE7	2.1	4433	4363	239
N8xE8	2.12	5069	3930	190	N12xE8	2.1	4756	4185	217
N8xE9	2.69	4164	3374	186	N12xE9	2.8	4556	3174	205
N9xE1	2.12	5019	3948	186	N13xE1	2.2	4472	2893	176
N9xE2	2.35	5186	4489	188	N13xE2	2.2	4419	3578	183
N9xE3	1.55	3967	3133	187	N13xE3	2.2	3567	3015	175
N9xE4	2	5625	3493	193	N13xE4	2	5250	3893	201
N9xE5	2.02	4486	3256	185	N13xE5	1.9	4003	3593	174
N9xE6	2.24	4733	3344	212	N13xE6	2.4	3792	3607	216
N9xE7	1.71	4239	3659	201	N13xE7	2.8	3669	4230	203
N13xE8	2.1	4408	4122	205	N17xE8	2	4556	4270	218
N13xE9	2.7	4608	2907	193	N17xE9	2.7	3537	3833	196
N14xE1	2	5136	4544	201	N18xE1	1.4	4308	4044	195
N14xE2	2	4350	2611	196	N18xE2	2.1	5133	4578	202
N14xE3	1.8	5319	3756	198	N18xE3	2.1	5272	2963	185
N14xE4	2.1	4472	3789	189	N18xE4	2	5108	4867	200
N14xE5	2.3	4689	3037	195	N18xE5	1.8	3767	3981	197
N14xE6	2.6	4250	2741	230	N18xE6	2.5	4628	3178	209
N14xE7	2.3	3644	3526	213	N18xE7	2	4275	3804	222
N14xE8	2.3	5569	4407	219	N18xE8	1.95	5031	4556	219
N14xE9	2.3	4908	3081	196	N18xE9	2.2	4211	3326	181
N15xE1	1.5	4314	4056	178	N19xE1	1.96	3803	4074	171
N15xE2	2.1	5225	3800	177	N19xE2	2.13	5264	3504	170
N15xE3	2.2	5508	4048	188	N19xE3	1.82	5003	3448	175
N15xE4	2.2	5589	3085	174	N19xE4	2.48	6006	4693	179
N15xE5	1.8	4094	3304	187	N19xE5	2.04	4256	3441	172
N15xE6	2.2	4464	4752	215	N19xE6	2.14	4111	4263	204
N15xE7	1.6	4836	3819	202	N19xE7	1.81	3953	3556	195
N15xE8	2.1	5492	5133	206	N19xE8	2.3	5011	3800	190
N15xE9	1.9	4592	3726	189	N19xE9	2.46	3200	2626	177
N16xE1	1.8	3969	3019	183	N20xE1	2.11	5636	4367	182
N16xE2	2.1	4628	3633	172	N20xE2	2.17	5167	3944	168
N16xE3	2.4	4700	4085	191	N20xE3	2.19	5553	3533	189
N16xE4	2	5558	3974	183	N20xE4	1.94	6050	4374	203
N16xE5	1.6	4814	3400	175	N20xE5	1.83	4831	3552	191
N16xE6	2.4	4339	4244	218	N20xE6	2.83	4728	3770	220
N16xE7	1.7	4283	4230	201	N20xE7	2.53	4969	3996	196
N16xE8	2.5	4830	3974	205	N20xE8	2.09	6086	4841	202
N16xE9	2.1	3800	3589	178	N20xE9	2.15	5733	3333	188
N17xE1	2.2	4589	3567	166	Mean	2.14	4486	3634	192.7
N17xE2	2.7	4436	4089	191	Max	3.00	6769	5133	251.7
N17xE3	2.7	4800	3300	191	Min	1.40	1697	1519	147.7
N17xE4	1.8	5031	3874	194	H_R	1.97	5706	4567	186.8
N17xE5	2.2	4308	3252	179	H_S	3.00	6847	4774	197.3
N17xE6	2.3	4481	4452	226	---	---	---	---	---
N17xE7	2.4	4585	4693	207	---	---	---	---	---

RFA – means of two experiments (environments) in notes from 0 to 5 (see text).
GY_{E1} and GY_{E3} : means in kg ha^{-1} for EXP 2 and EXP 3, respectively.
PH : mean of two experiments (EXP 2 and EXP 3).

Interactions of effects with experiments were non-significant for RFA and AP (except populations I x experiments); for GY all the effects presented interaction with experiments.

Dominance effects can be an important source of variation for all traits. The relative contribution of each source of variation to the total sum of squares shows that dominance effects are differentiated among the studied traits. For RFA 32% of the total sum of squares are due to the variation of populations while 68% are attributed to the total heterosis; specific heterosis is responsible for 84% of the total variation of heterosis. For similar situations, Miranda Filho & Vencovsky (1984) considered that even if the additive and dominance effects are confounded in the effects of populations (v_i and v_j), it is reasonable to suppose that the dominance effects are more expressive at the interpopulation (population cross) level. The detection of dominance effects in the control of the resistance to *S. frugiperda* was already reported by Williams et al. (1978), Widstrom et al. (1993), Guimarães & Viana (1994), and Williams et al. (1995). For GY and PH, the proportion of the variation due to populations and heterosis were 46.9 : 53.1 and 77.8 : 22.2, indicating that the dominance at the interpopulation level is more expressive for GY than for PH. Similar results were reported by Miranda Filho & Vencovsky (1984) and Santos et al. (1994). Low heterotic response for PH has also been reported by many authors (Castro et al. 1968; Barriga e Vencovsky, 1973; Souza, Jr., 1981; Miranda Filho & Vencovsky, 1984).

The estimates of the effects (μ, d, v_i, v_j, $\bar{h}$, h_i, h_j; except s_{ij}) in the partial diallel model are presented in Table 6 for RFA and PH and in Table 7 for GY for both experiments. The effect of general combining ability (GCA) was estimated by $g_i = \frac{1}{2} v_i + h_i$ and $g_j = \frac{1}{2} v_j + h_j$ (Geraldi & Miranda Filho, 1988). Outstanding populations in Group I for GCA (negative g_i) of RFA were N4 (CMS23), N15 (PMI9302) and N18 (Tuxpeño Amarelo). CMS23 is a population that had undergone selection at EMBRAPA under artificial selection and was released for its good level of resistance to *S. frugiperda*. Results observed in the present work allowed the identification of populations, as mentioned above, to be used as source of resistance at levels similar to CMS23.

In Group II, two populations from CIMMYT (E1 – MIRT and E2- PR91B) exhibited the best values for resistance (negative v_j). The use of v_j instead of g_j (Table 4) for discriminating the best populations is explained by the non significance of population heterosis effects. MIRT (*Multiple Insect Resistance for Tropical Regions*) was selected at CIMMYT (Smith et al., 1989) and released for its high resistance to several species of the family *Lepdoptera* (*Ostrinia nubilalis*, *Diatraea saccharalis*, *D. grandiosella*, and *S. frugiperda*). PR91B is a population selected at CIMMYT (Colombia) for resistance to *S. frugiperda.*

For GY the highest GCA effects in EXP 2 were observed for N20 (WP12), N3 (CMS14C) and N17 (PMI9401) in Group I and for E4 (B97 x ITU), E8 (Cuba 110 x ESALQ PB1), E2 (PR91B) and E3 (B95 x ITU) in Group II. In EXP 3 the highest GCA effects were for N17 (PMI9401), N5 (CMS454), N18 (São José) and N20 (WP12) in Group I and E8 (Cuba110 x ESALQPB1), E4 (B97 x ITU), E2 (PR91B) and E7 (Cuba113 x ESALQPB1) in Group II.

Regarding PH, low estimates are desired if the objective is to identify populations with lower plant height and ear height, as generally occur with tropical germplasm. Lower estimates of GCA were obtained for N19 (Tuxpeño amarillo), N10 (Guatemala), N2 (Caribeño DMR), N5 (CMS454) and N16 (PMI9306) in Group I; and for populations E1 (MIRT), E5 (Pop. 58), E2(PR91B) and E9(Libertad179 x ESALQPB1) in Group II.

Selection of populations

Heterosis in variety crosses can be used directly in the first generation of the cross between two parental varieties. The parental populations of heterotic crosses also can be used for the development of inbred lines to be used in hybrid crosses. On the other hand, the synthesis of composites by intercrossing *n* parental varieties is a mean to retain heterosis in the population, because *(n-1)/n* of the heterosis component remain as part of the expected mean of the new population (Miranda Filho & Vencovsky, 1984).

In the present work, expressive heterosis effects were detected for both RFA and GY, which can be utilized by selecting the outstanding crosses. The effects of varieties or populations also were detected in both groups of populations and selection based on this parameter leads to the identification of the most appropriate populations for intrapopulation recurrent selection.

The correlation coefficients between RFA and GY, calculated from measurements of the hybrid check, planted every fifteen rows in the experiments, were non significant: r = -11%, P = 0.46 under artificial infestation; and r = -1,4%, P = 0.92 under natural infestation. For this reason, selection of populations based only on GY is not recommended and, both traits (RFA and GY) must be taken into account.

Populations N4 (CMS23), N15 (PMI9302) and N18 (São José) from Group I, and E1 (MIRT) and E2 (PR91B), from Group II, showed the best performance for RFA in crosses. The good resistance level of crosses between these two selected groups is explained by the fact that N4, N15 and N18 exhibited the best estimates of g_i in Group I and E1 and E2 showed the best level of resistance per se (v_j) in Group II.

For GY an analysis for each experiment (environment) was necessary because the existence of genotype x experiment interaction. In EXP 2, N4 did not presented a good performance in relation to GCA effect (g_i), while N15 and N18 showed good levels for GCA. In

Table 3 - Mean squares and their significance in the analyses of diallel tables for the variables RFA, GY and PH combined over experiments.

Source of variation	GL	RFA	GY^1	PH
		Mean square		
Dialelll	208	0.6753 **	28.660 **	1762.47 **
Groups	1	5.7230 **	2.760 ns	1107.04 *
Populations (I)	19	1.0460 **	76.979 **	4506.65 **
Populations (II)	8	2.4401 **	166.534 **	24799.49 **
Heterosis	180	0.5297 **	17.575 **	452.58 **
Average heterosis	1	0.0756 ns	134.009 **	8671.46 **
Population heterosis (I)	19	0.5745 **	12.509 **	762.61 **
Population heterosis (II)	8	0.4804 ns	18.475 **	1034.06 **
Specific heterosis	152	0.5297 **	9.460 **	329.15 **
Dialell x Experiments (E)	208	0.2999 ns	8.080 **	265.17 **
Between experiments	1	---	16.229 ns	74.89 ns
Populations (I) x E	19	---	2787.904 **	872.83 **
Populations (II) x E	8	---	6692.450 **	357.51 ns
Heterosis x E	180	---	5.647 **	197.98 ns
Avg. heterosis x E	1	---	43841.062 **	608.33 ns
Pop. heterosis (I) x E	19	---	412.727 **	239.83 ns
Pop. heterosis (II) x E	8	---	403.075 **	284.72 ns
Specific heterosis x E	152	---	5.127 ns	185.48 ns
Pooled error	1050	0.2917	4.372	183.84

**, *, ns - significance levels for the F test: $P < 0.01$, $P < 0.05$ and non significant, respectively. [1]Mean squares multiplied by 10^{-5}

Table 4 - Estimates of total heterosis (h_{ij}: upper valuer) and specific heterosis (s_{ij}: lower values) for RFA in population crosses.

	E1	E2	E3	E4	E5	E6	E7	E8	E9
N1	9.5	-14.3	-24.4	4.5	6.7	-6.7	-21.7	-2.0	-8.7
	0.35	-0.21	-0.27	0.18	0.42	-0.23	-0.26	0.29	-0.27
N2	-11.6	-2.3	-21.7	-6.7	-4.3	4.3	-14.9	-4.0	10.6
	-0.13	-0.04	-0.29	-0.12	0.15	0.06	-0.06	0.19	0.24
N3	-2.9	-8.6	42.1	24.3	-5.3	21.1	-12.8	4.8	17.9
	-0.24	-0.37	0.77	0.21	-0.07	0.05	-0.34	0.05	-0.05
N4	26.3	-21.1	-17.1	0.0	-12.2	-7.3	-23.8	-20.0	0.0
	0.63	-0.3	-0.04	0.16	0.03	-0.15	-0.21	-0.15	0.04
N5	-15.0	5.0	-25.6	-4.8	-7.0	16.3	-18.2	2.1	4.5
	-0.25	0.1	-0.31	-0.1	0.07	0.3	-0.16	0.32	0.02
N6	-4.5	-9.1	-6.4	8.7	10.6	-2.1	-20.8	-25.1	7.1
	-0.02	-0.14	0.05	0.26	0.5	-0.13	-0.28	-0.35	0.12
N7	-8.5	-4.3	-17.2	-4.5	-20.4	-16.0	-3.1	-6.7	-10.2
	0.02	0.06	-0.08	0.08	-0.11	-0.34	0.3	0.24	-0.19
N8	13.2	-3.2	10.2	17.5	-16.6	2.4	33.8	-5.8	28.1
	0.04	-0.33	0.13	0.1	-0.37	-0.32	0.65	-0.14	0.23
N9	17.8	30.6	-20.5	5.3	3.6	14.9	-14.5	-7.0	40.0
	0.15	0.32	-0.45	-0.11	0.08	-0.04	-0.31	-0.11	0.47
N10	30.0	0.0	-7.0	14.3	-2.3	7.0	-18.2	-19.1	0.0
	0.59	-0.11	-0.06	0.24	0.08	0.02	-0.3	-0.27	-0.19
N11	4.8	14.3	-24.4	-9.1	-20.0	-11.1	8.7	-10.2	-8.7
	0.24	0.38	-0.29	-0.1	-0.18	-0.3	0.46	0.08	-0.29
N12	-22.0	-7.3	-13.6	-2.3	-22.7	22.7	-6.7	-12.5	24.4
	-0.42	-0.11	-0.13	-0.02	-0.25	0.37	0.07	0	0.49
N13	15.8	15.8	7.3	0.0	-7.3	17.1	33.3	-6.7	28.6
	0.05	-0.06	0.02	-0.25	-0.24	-0.04	0.56	-0.23	0.18
N14	-13.0	-13.0	-26.5	-12.5	-6.1	6.1	-8.0	-13.2	-8.0
	-0.06	-0.11	-0.32	-0.13	0.28	0.26	0.14	0.06	-0.11
N15	-14.3	20.0	15.8	18.9	-5.3	15.8	-17.9	0.0	-2.6
	-0.37	0.23	0.32	0.22	0.05	0.02	-0.3	0.11	-0.28
N16	-10.0	5.0	11.6	-4.8	-25.6	11.6	-22.7	6.4	-4.5
	-0.11	0.07	0.45	-0.05	-0.28	0.12	-0.34	0.38	-0.24
N17	18.9	45.9	35.0	-7.7	10.0	15.0	17.1	-9.1	31.7
	0.01	0.39	0.46	-0.55	0.03	-0.23	0.15	-0.35	0.1
N18	-30.0	5.0	-2.3	-4.8	-16.3	16.3	-9.1	-17.0	0.0
	-0.47	0.18	0.16	-0.08	-0.04	0.32	0.08	-0.1	-0.05
N19	-6.7	1.4	-19.1	12.7	-9.3	-4.9	-21.3	-6.1	7.0
	-0.05	0.05	-0.2	0.33	0.06	-0.18	-0.25	0.14	0.1
N20	11.1	14.2	6.8	-3.0	-10.7	38.0	20.5	-7.1	2.4
	0.03	0.02	0.08	-0.28	-0.23	0.43	0.39	-0.16	-0.29

Table 5 – Estimates of total heterosis (h_{ij}) for GY in two experiments (EXP 2: upper values; and EXP 3: lower values).

	E1	E2	E3	E4	E5	E6	E7	E8	E9
N1	66.8	38.4	128.3	37.1	100.3	44.1	44.7	59.1	37.8
	39.6	-13.4	81.9	48.0	52.7	51.6	28.6	51.1	21.3
N2	35.5	20.4	33.1	38.5	32.6	-9.1	3.2	22.6	9.9
	51.8	-4.6	59.9	25.9	36.1	-10.0	-5.7	-8.3	0.1
N3	37.0	23.7	51.0	57.8	37.6	18.9	25.5	34.6	40.7
	61.8	-1.1	42.7	47.9	4.3	49.5	13.2	9.4	54.2
N4	27.3	17.4	73.5	28.3	27.2	3.7	23.4	5.2	14.0
	30.5	40.0	66.0	20.0	39.1	17.9	42.8	-2.2	50.4
N5	13.9	0.5	41.3	13.8	47.1	6.2	3.6	23.5	13.6
	25.5	6.6	42.0	25.2	36.8	39.4	10.0	34.8	29.2
N6	25.5	24.7	64.7	44.1	89.9	17.0	24.8	33.5	18.2
	10.5	8.4	79.5	29.8	39.9	53.0	34.5	17.7	46.3
N7	41.0	16.6	63.0	27.4	64.0	17.9	30.1	22.8	7.0
	23.1	16.3	35.2	20.1	25.3	51.5	41.8	20.5	46.4
N8	23.7	27.4	66.2	22.3	32.0	14.9	14.0	28.7	17.8
	31.9	24.3	13.5	43.4	44.1	2.3	9.4	5.9	21.1
N9	30.0	17.6	11.7	23.5	38.8	7.4	2.7	20.3	19.8
	34.5	26.4	26.4	7.0	23.7	12.4	9.3	12.7	12.8
N10	38.4	31.8	48.9	36.4	14.3	4.6	17.6	2.0	21.8
	30.5	30.3	58.3	69.0	60.8	61.0	27.0	23.4	60.6
N11	42.7	39.3	55.5	26.1	73.2	24.6	50.5	33.9	25.0
	42.8	29.0	26.7	25.7	63.9	50.2	1.4	-4.0	29.5
N12	24.6	29.8	50.2	18.6	60.1	-20.0	9.6	12.3	19.0
	3.8	-5.8	41.8	17.5	36.4	-23.1	36.7	22.2	27.0
N13	53.0	27.3	36.5	45.1	74.4	9.3	15.0	30.5	54.9
	25.7	22.6	63.5	48.1	79.8	54.0	55.9	39.9	43.8
N14	97.8	38.3	132.7	35.9	138.3	35.3	27.2	82.5	85.4
	105.5	-7.7	114.1	49.2	59.2	21.7	34.5	54.3	59.5
N15	22.1	28.0	70.9	32.2	41.0	9.5	27.3	37.7	28.1
	45.1	11.4	73.2	-1.2	32.6	67.6	19.1	49.3	48.2
N16	7.0	8.7	38.2	26.2	56.1	2.0	7.6	15.9	1.0
	14.3	11.5	87.1	33.9	45.5	58.3	38.6	21.0	52.0
N17	12.3	-4.3	27.2	5.3	24.6	-3.2	5.3	0.3	-14.5
	1.9	-0.7	8.4	1.2	1.7	25.7	19.9	3.0	19.0
N18	11.8	16.6	48.7	12.3	16.8	5.2	3.7	16.7	7.8
	20.1	14.9	1.8	31.7	29.9	-6.8	0.6	13.5	7.7
N19	7.6	29.0	55.2	42.1	46.5	0.8	4.0	25.6	-10.7
	40.7	-0.2	41.5	45.6	32.8	45.2	7.6	7.4	0.4
N20	54.3	23.0	66.2	39.2	59.8	12.7	26.8	48.2	54.8
	50.3	12.0	44.3	35.3	36.5	27.9	20.5	36.4	26.9

h_{ij}: expressed in percent of mid-parent.

Group 2, E1 showed a low performance for GCA while E2 were among the best ones for this effect. In EXP 3, N18 and E2 were oustanding for GCA, while N4 and E1 were among the poorest ones.

Finally, when considering the general performance for GY in crosses, N4 and E1 should be discarded among the populations selected for RFA. Therefore, N15, N18 and E2 are recommended as the most promising for incorporation in breeding programs, as indicated by their good level of resistance to *S. frugiperda* and acceptable agronomic traits. For plant height, N15 and E2 showed negative values for GCA and should be indicated as source of genotypes to lower plant architecture.

Selection of specific crosses also can be done from the presented results. High specific heterosis for both RFA and GY were shown by crosses N17 (PMI9401) x E8 (Cuba 110 x ESALQ PB1) and N18 (São José) x E1 (MIRT). Total heterosis in percent of mid-parent in these crosses were 9% and 27% for RLC and 26% and 24% for GY, respectively, the indicated crosses for their properties can be used directly for the exploitation of heterosis in reciprocal recurrent selection programs, or as base for the development of inbred lines to be used in crosses.

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Table 6 - Estimates of components of the diallel model and their variances and estimates of general combining ability (g_i and g_j) for RFA, and PH.

	Resistance to fall armyworm			Plant height		
Group I	v_i	h_i	g_i	v_i	h_i	g_i
N1	0.181	-0.126	-0.036	-7.23	4.93	1.32
N2	0.304	-0.117	0.035	-5.98	-1.93	-4.92
N3	-0.543	0.216	-0.056	2.94	3.68	5.14
N4	-0.212	-0.150	-0.256	-13.48	5.35	-1.39
N5	-0.049	-0.050	-0.075	-5.48	-1.83	-4.57
N6	0.346	-0.083	0.090	7.81	-5.50	-1.59
N7	0.706	-0.237	0.116	-6.61	-0.54	-3.85
N8	-0.214	0.204	0.097	-5.48	-0.26	-3.00
N9	-0.403	0.165	-0.036	0.10	-0.68	-0.63
N10	-0.058	0.027	-0.003	-6.48	-4.29	-7.53
N11	0.175	-0.099	-0.012	1.35	-0.87	-0.20
N12	0.117	-0.077	-0.019	48.19	-0.72	23.37
N13	-0.195	0.245	0.148	-4.40	0.23	-1.97
N14	0.634	-0.253	0.064	-25.98	23.22	10.23
N15	-0.526	0.078	-0.185	1.77	-4.21	-3.32
N16	0.003	-0.063	-0.061	-0.44	-4.05	-4.27
N17	-0.274	0.361	0.224	11.94	-3.25	2.72
N18	-0.039	-0.094	-0.114	22.69	-4.11	7.23
N19	0.225	-0.113	0.000	-23.82	-0.45	-12.36
N20	-0.179	0.167	0.077	8.60	-4.72	-0.42
Variance	0.0395	0.0143	---	24.95	9.01	---
Group II	v_j	h_j	g_j	v_j	h_j	g_j
E1	-0.332	0.049	-0.116	-21.26	-0.85	-11.48
E2	-0.267	0.081	-0.052	0.08	-9.83	-9.79
E3	-0.006	-0.094	-0.097	-21.17	5.79	-4.79
E4	-0.044	0.040	0.018	-4.63	-0.38	-2.70
E5	0.001	-0.150	-0.149	-38.38	8.57	-10.62
E6	0.018	0.182	0.191	30.28	8.74	23.88
E7	0.112	-0.125	-0.069	35.12	-5.92	11.64
E8	0.448	-0.184	0.040	20.66	0.07	10.40
E9	0.070	0.201	0.236	-0.67	-6.21	-6.55
	0.037	0.011	---	23.34	7.00	---
μ		2.145			186.16	
d		0.162			0.15	
$\bar{h}$		-0.022	(1.03%)		7.53	(4.0%)

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Table 7 - Estimates of components of the diallel model and their variances and estimates of general combining ability (g_i and g_j) for GY in two experiments.

	Exp 2			Exp 3		
Group I	v_i	h_i	g_i	v_i	h_i	g_i
N1	-2044	442	-579	-1162	65	-515
N2	-811	-409	-815	130	-405	-339
N3	343	308	480	-66	38	5
N4	-236	-242	-360	-366	56	-126
N5	1138	-345	223	719	56	416
N6	-518	151	-107	-143	127	55
N7	-333	-7	-174	185	94	187
N8	118	-77	-18	522	-142	119
N9	877	-300	138	259	-273	-143
N10	-78	-209	-248	-506	380	126
N11	-178	343	254	126	8	72
N12	710	-223	131	-51	-345	-371
N13	-997	87	-411	-1006	302	-200
N14	-1653	876	49	-1188	355	-239
N15	218	118	227	-21	55	44
N16	577	-279	9	-329	84	-80
N17	1324	-277	384	1393	-161	534
N18	863	-234	197	1126	-311	252
N19	221	-253	-142	178	-115	-26
N20	457	533	762	200	129	229
Variance	105826	38215	---	134501	48570	---
Group II	v_j	h_j	g_j	v_j	h_j	g_j
E1	-361	79	-101	-222	113	2
E2	736	-123	244	1011	-314	191
E3	-980	674	184	-1137	354	-213
E4	1027	254	768	433	66	282
E5	-1616	409	-399	-829	139	-275
E6	727	-704	-340	-140	44	-25
E7	175	-381	-294	600	-118	181
E8	550	44	319	1066	-158	374
E9	-258	-251	-380	-781	-127	-517
Variance	99018	29705	---	125849	37755	---
μ		3603			2916	
d		289			261	
$\bar{h}$		1051	(29.2%)		822	(28.2%)

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