

1 **Defense mechanisms of maize against pink stem borer**

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Abstract

The pink stem borer (*Sesamia nonagrioides* Lef.) is the most important pest of maize (*Zea mays* L.) in northwestern Spain. The objective of this work was to evaluate defense mechanisms against *Sesamia* in ten inbred lines and the 10-parent diallel among these inbreds. Hybrids and inbred lines were tested over two years in northwestern Spain under natural and artificial infestations. Yield of infested and no infested plants per plot were computed to calculate yield loss caused by the pink stem borer attack. Principal component analyses for stem damage traits and for ear damage traits were made for each infestation condition. From the principal component analysis an index was computed to measure stem damage and ear damage. Damage index under artificial infestation was used to evaluate antibiosis while antixenosis was detected comparing for each genotype between damage index under artificial and natural infestation. The regressions of yield loss on the damage index were used to separate the genotypes into four groups according to the possession of antibiosis and/or tolerance mechanisms. A509, A661, EP31, F7, PB60, and Z77016 showed stem antibiosis. A637, A661, EP31, F7, and PB60 exhibited stem tolerance. A509, A661, and EP31 stood out by their ear antibiosis. A637, A661, F7, and PB60 were tolerant to ear damage. We conclude that the three mechanisms of defense to the pink stem borer attack (antixenosis, antibiosis and tolerance) were found among inbred lines and hybrids. A multitrait selection scheme using damage traits and yield could improve the defense level against pink stem borer.

Key words: *Sesamia nonagrioides*, antixenosis, tolerance, antibiosis.

1 The most important maize pest in North America as well as in Central Europe is the
2 European corn borer (*Ostrinia nubilalis* Hübner). However, in the South of Europe the pink stem
3 borer (*Sesamia nonagrioides* Lef.) also causes significant damage to maize. *S. nonagrioides* is the main
4 borer in Northwestern Spain especially in coastal areas (Cordero *et al.*, 1998).

5 Plants have a great diversity of strategies and mechanisms of defense against pests. The
6 mechanisms of defense may be classified into three groups, namely antixenosis, antibiosis and
7 tolerance (Painter, 1951). Antixenosis reduces the probability of contact between potential
8 consumers and plants and has been described in some genotypes against the European corn
9 borer (Barry and Darrah, 1988). Dicke and Guthrie (1988) proposed that late maturity corn is
10 more attractive than early corn to the moths of the second generation of European corn borer.
11 The same results were found for the second generation of *Sesamia nonagrioides* (Malvar *et al.*,
12 1993).

13 Antibiosis is the ability of the plant to reduce the growth and/or development of the
14 larvae after contact has been initiated. The search for maize genotypes resistant to the European
15 corn borer has been in progress for over 60 years in inbreds (Guthrie and Dicke, 1972; Hudon
16 and Chiang, 1985; Hudon and Chiang, 1991) and populations (Reid *et al.*, 1991). Also, sources of
17 antibiotal resistance to the pink stem borer have been detected among populations and inbred
18 lines (Anglade and Bertin, 1968; Malvar *et al.*, 1993; Cartea *et al.*, 1994; Malvar *et al.*, 1995).

19 Tolerance is the mechanism by which plants maintain similar levels of production under
20 vastly different levels of infestation. Tolerance does not reduce the levels of infection in contrast
21 with antibiosis or antixenosis. It is very difficult to detect the differences in tolerance among
22 plant genotypes because it is necessary to determine the amount of yield reduction per unit of
23 infection. This means that yield under protected conditions has to be compared with the yield of
24 an infected crop. This is a complicated work with large experimental errors so few studies have
25 been conducted on true tolerance (Niks *et al.*, 1993).

1 The use of resistant varieties produces selection pressure on the insect populations and
2 there is some possibility of breakdown of the resistance. The tolerance effect is on the plant itself
3 without affecting the populations of insects. The presence of several types of defense
4 mechanisms in plants would allow not only a reduction in insect numbers on the plants, but also
5 recovery from damage caused by the few surviving larvae. Kumar and Mihm (1995) found
6 resistant varieties that exhibited either tolerance or antibiosis against fall armyworm (*Spodoptera*
7 *frugiperda* J.E. Smith), sugarcane borer (*Diatrea saccharalis* Fabricius) and southwestern corn borer
8 (*D. grandiosella* Dyar). Both types of defense mechanisms were detected against *Chilo partellus*
9 Swinhoe (Kumar, 1994).

10 The objective of this study was to detect antixenosis, antibiosis, and/or tolerance against
11 *Sesamia nonagrioides* in ten inbred lines of maize and their single crosses in a diallel to evaluate
12 their potential use for a breeding program against this pest.

13

Materials and methods

Ten inbreds with different degrees of antibiosis to stem tunneling by *S. nonagrioides* (A509, A661, A637, CM105, EP28, EP31, EP42, F7, PB60 and Z77016) were selected as parents of a diallel. In 1994, the 10 inbred lines were crossed to produce a complete diallel set with reciprocals.

The 90 F₁ single crosses with reciprocals were evaluated along with 10 checks in a 10 x 10 simple lattice design under artificial infestation conditions. Experiments were carried out in 1995 and 1996 in Pontevedra, in Northwestern Spain (42°42'N, 8°39'W, 20 m above sea level). Each two-row experimental plot consisted of 15 hills with two kernels per hill. The rows were spaced 0.80 m apart and the hills were spaced 0.21 m apart. Hills were thinned to one plant after emergence, obtaining a final plant density of 60 000 plants ha⁻¹. The 10 inbred parents were evaluated in a randomized complete block design with four replications. The experimental plot was identical to the hybrid trial except that 13 kernels were planted in each row in the inbred trial. Both trials (hybrids and inbreds) were separated by border rows to limit competition, but they were managed under the same conditions.

At silking, the first five plants in each plot were artificially infested with one egg mass of about 40 eggs. The infestation technique has been described by Anglade (1961), but the eggs were placed between the shank of the main ear and the stem instead of placing them on the third leaf below the main ear. Egg masses were obtained according to Eizaguirre's rearing method (Eizaguirre, 1989). The other plants in the plot grew under natural infestation. In 1996, in the hybrid trial, one row per plot was protected with granular insecticide (Triclorfon 2.5%) at a rate of 30 kg ha⁻¹. In the inbred trial insecticide was not used because inbred genotypes are more susceptible to stress factors than the hybrids and insecticide treatment could reduce or stop the development of determined lines.

In 1995 and 1996 the inbred lines and the F₁ single crosses without reciprocals were also evaluated in an adjacent plot in the same environment as the other trials but under natural

1 infestation conditions. A 7 x 7 triple lattice design was used for the hybrid evaluation while the
2 inbreds were evaluated in a randomized complete block design with four replications. The
3 experimental plot was identical to that of the trials under artificial infestation.

4 At harvest, five plants were harvested in each plot. In the artificial infestation trials
5 infested plants were harvested, while in the trials carried out under natural infestation normal and
6 competitive plants were harvested. Stems were dissected and number of entry holes, number and
7 length of tunnels, and number of larvae were recorded. The general appearance of the ear was
8 rated on a five point scale from 1 (ear without damage) to 5 (wholly damaged ear) (Velasco,
9 1997). Data on the number and length of tunnels per ear, number of larvae in the ear, and the
10 percentages of ears without damage (neither in grain nor in cob), with damaged grain, with
11 damaged cob, and with damage in both grain and cob were also taken.

12 At harvest, in the trials carried out under artificial infestation, five ears from infested and
13 other five from uninfested plants in each plot were weighed and shelled. Grain weight was later
14 adjusted at 140 g Kg⁻¹ moisture content. On the basis of yield of infested and uninfested plants,
15 the percentage of yield loss was computed as:

16

$$17 \quad \% \text{ Yield loss} = (1 - \text{yield of infested plants} / \text{yield of uninfested plants}) * 100$$

18

19 Hybrids and inbred lines were analyzed separately. The reciprocal crosses were not considered
20 because reciprocal effects were not significant for damage traits (Butrón *et al.*, 1997). Therefore,
21 the mean for each F₁ was calculated. Check hybrids were also removed for the analysis.

22 Principal component analyses was conducted with all stem (number of entry holes,
23 number and length of tunnels, and number of larvae) and ear (general appearance number and
24 length of tunnels per ear, number of larvae in the ear, and the percentages of ears without
25 damage, with damaged grain, with damaged cob, and with damage in both grain and cob)
26 damage traits separately. Principal component analyses were made in individual trials and in

1 combined trials over years. From each of these principal component analysis, two new variables
2 that are a linear combination of the stem and ear original traits, respectively, were computed and
3 can be used in place of the original variables as indexes to measure stem and ear damage.

4 The average damage index obtained from principal component analysis of pooled data
5 over two years under artificial infestation was used to evaluate antibiosis. To detect non-
6 preference for oviposition, that is a kind of antixenosis mechanism, the comparison for each
7 genotype between the mean of damage indexes showed in 1995 and 1996 under artificial
8 infestation and the mean of those exhibited under natural infestation in the same years were
9 computed. The comparisons were made using Student's "t". Stem and ear indexes were analyzed
10 separately.

11 Regressions of yield loss on the index for stem and ear damage traits were computed for
12 pooled data of all genotypes in the hybrid and inbred trials with artificial infestation. Following
13 the method of Ortega *et al.* (1980), the quadrants created by the intersection of the line for the
14 mean of damage index and the regression line were used to separate the genotypes into four
15 groups: with antibiosis and tolerance, with antibiosis and without tolerance, with tolerance and
16 without antibiosis, and without antibiosis and tolerance.

17 For each inbred line we computed its general combining ability (Falconer, 1981) for the
18 index of stem and ear damage traits and for the yield loss. For the same traits, the simple
19 correlation coefficients between general combining ability and the performance of the inbred
20 lines were estimated.

21

Results and discussion

For the hybrids, the principal component analysis of pooled data over two years for stem damage traits showed a first principal component (PC1) that explained the 73% of the total variation under artificial infestation. The PC1 was the only component whose eigenvalue was higher than 1. The coefficients of all stem damage traits for the PC1 were positive, therefore the PC1 could be considered as a stem index of susceptibility. Resistant genotypes showed high negative values for this component. The coefficients of the original traits on the PC1 were about 0.50 for number of entry holes, number and tunnel length, and number of larvae.

For inbreds, the PC1 for the principal component analysis of pooled data over two years for stem damage traits explained the 60% of the total variation under artificial infestation. The coefficients of PC1 also were positive for all stem damage traits and this PC1 could be considered as a stem damage index. The inbred line CM105 was removed from the inbred analysis because it grew poorly in both years. The stem damage index under artificial infestation from pooled data over years was used to evaluate the stem antibiosis of the genotypes (Table 1). The inbreds A509, A661, EP31, F7, PB60 and Z77016 showed stem antibiosis (stem damage index < 0). A509 had also exhibited antibiosis in a previous study (Malvar *et al.*, 1995). F7 and A509 showed the best general combining ability for the stem damage index under artificial infestation (Table 2).

The correlation coefficient between inbred performance and general combining ability for stem antibiosis was 0.77. This means that the performance of hybrids for stem attack could be predicted from the performance of the inbred parents. This is in agreement with the idea that the additive effects are the most important for resistance to insects (Jennings *et al.*, 1974; Soon-Kwon *et al.*, 1989; Ajala, 1992). General combining ability was more important than specific combining ability for damage traits caused by *S. nonagrioides* (Butrón *et al.*, 1997). The most antibiotal resistant hybrid combination was A509 x F7 (Table 1). This hybrid could be used

1 directly by farmers in areas with heavy attacks of *S. nonagrioides* or used by breeders as a source of
2 new antibiotal resistant inbreds.

3 Stem resistance did not correlate with ear resistance (Malvar *et al.*, 1996). Therefore, the
4 analyses for stem and ear damage were made independently. The PC1 for hybrids under artificial
5 infestation for pooled ear damage traits over two years explained 46% of total variation. The
6 PC1 had positive coefficients for all damage traits except for percentage of ears without damage.
7 Hence a genotype with a high negative value for PC1 was considered to have ear antibiosis.
8 General appearance, number and length of tunnels, and proportions of ears with damaged grain
9 and without damage had the highest coefficients in absolute value (about 0.40). The percentages
10 of ears with damaged cob and with damaged cob and grain, and number of larvae in the ear had
11 coefficients less than 0.15. The second component explained approximately 30% of the total
12 variation, but some coefficients for this component were negative and other positive, so it is
13 difficult to explain its meaning in a biological sense. Therefore, the PC1 for hybrid ear damage
14 traits could be considered as a index of ear damage.

15 In the analyses of pooled inbred data over two years, the total variation of all ear damage
16 traits explained by the PC1 was 55%. The results of the principal component analysis for inbred
17 ear traits were similar to those for hybrid ear traits. Therefore, PC1 for inbred ear damage traits
18 could also be used as a index of inbred ear damage.

19 A509, A661, and EP31 had ear antibiosis (Table 1). A509 had shown ear antibiosis in a
20 previous study (Malvar *et al.*, 1996). The correlation coefficient between performance *per se* and
21 general combining ability for ear damage index was lower than the correlation coefficient for
22 stem traits ($r=0.40$). A reason for this could be that for ear traits the PC1 explained a lower
23 proportion of the total variation than for stem traits. A661 and CM105 showed the best general
24 combining ability (Table 2) and the most antibiotal resistant hybrid were A661 x CM105.

1 As it had already say, the PC1 for stem damage traits explained a higher percentage of
2 total variability than the PC1 for ear damage traits. This could be caused by the fact of ear attack
3 distribution was at random since *S. nonagrioides* prefers stem attack than ear attack.

4 The comparison for each genotype between damage index under artificial and natural
5 infestation conditions was used to detect non-preference for the oviposition by *S. nonagrioides*.
6 The population pressure under natural infestation in both years were high enough since, in a
7 adjacent plot to the trial, the percentage of damaged plants at harvest were about 100% and the
8 number of larvae per plant was higher than 1 (Cordero *et al.*, 1998). The inbred line Z77016
9 showed less damage in the stem under natural infestation than under artificial infestation
10 although the difference was not significant (-2.07 and -0.75 under natural and artificial
11 infestation, respectively) (data not shown). This line exhibited also significantly less ear damage
12 under natural conditions (-2.16 and 1.33 under natural and artificial infestation, respectively).
13 Hybrids from the inbred Z77016, in general, had better stem and ear damage index under natural
14 infestation than under artificial infestation, although the differences there were not significant in
15 all cases. Therefore, non-preference for oviposition could be a defense mechanism of the inbred
16 Z77016. Malvar *et al.* (1993) proposed that late maturity maize was more attractive than early
17 maize to the moths of the second generation of *S. nonagrioides*. However the inbred Z77016 and
18 its hybrids had intermediary flowering among the evaluated genotypes. Several substances have
19 been shown to attract or repel *Ostrinia nubilalis* (Udayagiri and Mason, 1995). Z77016 is a glossy
20 mutant and perhaps the wax on the leaf could influence the ovipositional behavior of the moths
21 of *S. nonagrioides*.

22 This study was only a preliminary evaluation of non-preference for oviposition
23 mechanisms because the damage level under natural infestation conditions could be random. To
24 study all antixenosis mechanisms it is necessary to evaluate all genotypes in a enclosed
25 environment and to control the number of moths in the environment (Barry and Darrah, 1988).
26 This is not feasible when evaluating large numbers of genotypes.

1 Antibiosis and antixenosis are not the only defense mechanisms present in plants.
2 Tolerance can also be considered in a breeding scheme. Determining yield loss allows us
3 determination of the relative contribution of tolerance in the defense against the pest. The
4 relative contribution of antibiosis can be estimated as the part of yield loss which can be
5 predicted from damage traits (regression of the yield loss due to corn borer attack). The
6 deviation from the regression line reflects the tolerance component (Ortega *et al.* 1980).

7 The regression coefficient between yield loss and index of stem damage was $b=1.01$
8 ($r^2=0.07$) for hybrids and $b=2.48$ ($r^2=0.31$) for inbreds. The regression coefficients between yield
9 loss and index of ear damage were $b=1.19$ ($r^2=0.12$) for hybrids and $b=1.34$ ($r^2=0.17$) for
10 inbreds. These lack of fit for the regressions of yield loss on damage indexes indicated that, in
11 addition to resistance components, tolerance to *S. nonagrioides* was also present in these plants.
12 Kumar and Mihm (1995) also found both defense mechanisms (antibiosis and tolerance)
13 operating in maize hybrids against fall armyworm, southwestern corn borer, and sugarcane borer
14 attack.

15 The inbreds A637, A661, F7, and PB60 showed stem (fig. 1) and ear tolerance (fig. 2).
16 The antibiosis of hybrids could be predicted from the performance of the inbred parents, but the
17 correlation between inbred performance and general combining ability for yield loss was low
18 ($r=0.13$). Thus, tolerance does not depend only on the tolerance of the inbreds parents.

19 Some genotypes had antibiosis and others had tolerance. Antibiosis and tolerance did not
20 always occur in the same genotype and seem to be unrelated. Jarvis *et al.* (1991) found the same
21 result for the attack of the second generation of the European corn borer.

22 Yield loss depends on tolerance and antibiosis of genotypes. Only a small part of the
23 variation of yield loss can be predicted from stem or ear antibiosis. This indicates the need for
24 selecting genotypes by a comprehensive measure such as yield loss (Ortega *et al.*, 1980). Thome *et*
25 *al.* (1994) studied the yield reduction in maize under infestation with southwestern corn borer.
26 They found that selecting directly for combining ability for yield across environments may be

1 more useful than selecting directly for antibiosis without selecting for yield. Similar conclusions
2 were reached by Klenke *et al.* (1986), Jarvis *et al.* (1991), and Anglade *et al.* (1996). F7 showed the
3 best general combining ability for yield loss the best specific combination being F7 x PB60. The
4 inbred line F7 could be used in breeding programs to improve stem antibiosis to *Sesamia*
5 *nonagrioides* and thus, to reduce yield losses.

6 In conclusion we can say that antixenosis, antibiosis and tolerance are operating in maize
7 against *Sesamia nonagrioides*. A multitrait selection scheme using damage traits and yield could
8 improve the mechanisms of defense against the pink stem borer.

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1 Table 1. Stem (SDI) and ear damage index (EDI) under artificial infestation and yield loss (YL)
 2 for inbreds (in the diagonal)and hybrids (above the diagonal).

		A509	A637	A661	CM105	EP28	EP31	EP42	F7	PB60	Z77016
6	A509	SDI-2.00	-0.25	-2.71	-0.32	-1.73	-1.35	0.80	-2.97	0.20	-2.29
7		EDI-1.38	-3.63	-2.46	-1.85	-1.30	-1.92	2.44	-2.11	1.80	1.62
8		YL 14.22	10.92	13.69	18.05	13.40	7.56	17.07	11.87	15.79	13.99
10	A637	SDI	0.89	2.78	0.00	-1.49	0.66	3.00	-2.91	2.38	1.55
11		EDI	0.67	1.44	-0.56	-1.33	2.08	-1.63	1.36	1.18	2.22
12		YL	11.70	20.30	27.56	10.45	21.53	2.40	15.22	17.05	10.19
14	A661	SDI		-0.01	-0.65	-0.73	0.89	4.09	-0.73	-0.06	0.15
15		EDI		-3.65	-5.78	-1.19	-2.18	0.96	-2.06	0.38	0.87
16		YL		10.07	11.72	2.76	14.05	27.80	7.51	25.15	17.40
18	CM105	SDI			-	-0.68	0.09	2.23	-0.44	-0.65	-1.69
19		EDI			-	-0.31	-0.95	-0.78	0.08	0.53	-1.72
20		YL			-	8.91	8.64	23.54	9.59	23.21	18.49
22	EP28	SDI				0.67	0.34	0.74	-2.82	-0.75	-1.02
23		EDI				0.63	1.87	0.29	-1.06	0.89	0.97
24		YL				18.32	16.68	13.69	5.06	16.09	13.51
26	EP31	SDI					-0.81	2.07	0.26	2.54	1.18
27		EDI					-2.76	-0.20	-0.71	0.48	2.22
28		YL					11.57	11.13	12.98	23.24	16.20
30	EP42	SDI						3.36	2.18	0.93	1.18
31		EDI						1.40	1.50	1.40	1.17
32		YL						29.33	2.32	24.17	16.13
34	F7	SDI							-0.92	-0.91	-2.81
35		EDI							2.37	-1.29	4.17
36		YL							12.37	0.14	16.13
38	PB60	SDI								-0.12	-0.27
39		EDI								0.94	3.11
40		YL								7.14	17.86
42	Z77016	SDI									-1.07
43		EDI									1.78
44		YL									22.05

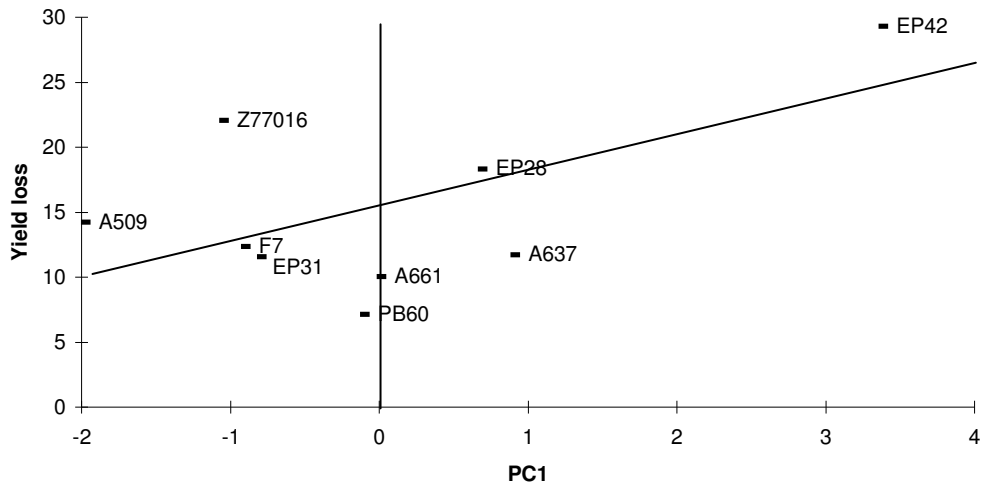
1 Table 2. General combining ability of inbred parents for stem and ear damage index under
2 artificial infestation and for yield loss.

4 Inbred line	Stem damage index	Ear damage index	Yield loss
6 A509	-1.33	-0.93	-0.94
7 A637	0.71	0.14	0.72
8 A661	0.38	-1.25	1.31
9 CM105	-0.26	-1.42	2.48
10 EP28	-1.02	-0.15	-3.67
11 EP31	0.83	0.09	0.05
12 EP42	2.15	0.64	1.05
13 F7	-1.39	-0.02	-6.35
14 PB60	0.43	1.06	4.10
15 Z77016	-0.50	1.83	1.25

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1 Fig. 1. Relationship between stem damage index for inbreds and percentage of yield loss.

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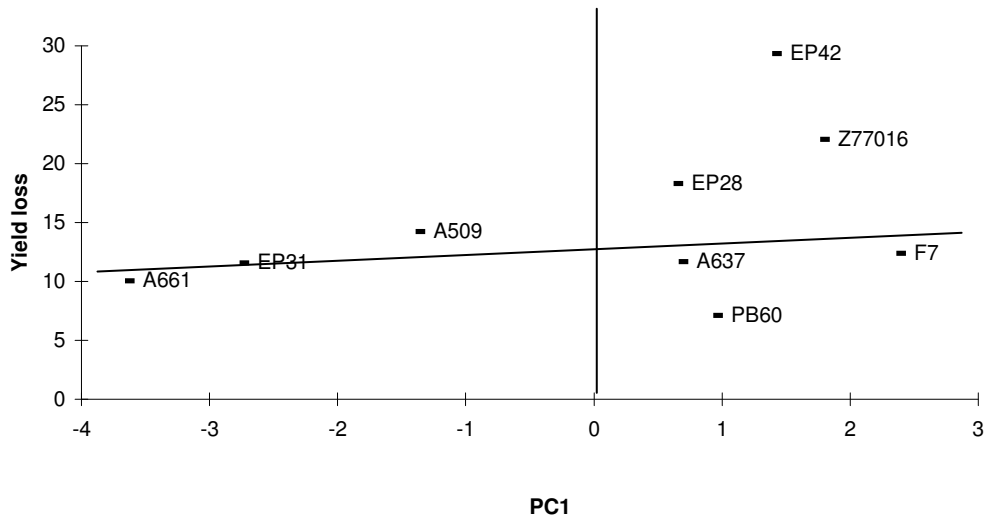


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5 Fig. 2. Relationship between ear damage index for inbreds and percentage of yield loss.

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