

## Assessment of 10 years of maize pedigree breeding for European corn borer tolerance and high-yielding combining ability

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**Abstract** – A multitrait pedigree breeding system including evaluation for European corn borer (*Ostrinia nubilalis* Hbn.) tolerance and other agronomic traits (yield, earliness, stalk lodging) was used for 16 years to create inbred lines from very different temperate germplasms. The ultimate evaluation of the 63 inbred lines was made in comparison with stable known references. The results allowed us to classify this material into three tolerance classes to the insect and demonstrated the efficacy of the method. High-yielding combining ability might be associated with earliness, lodging tolerance and good insect tolerance. The value of some early flint European materials and of Argentinian sources was discussed to improve European corn borer tolerance. (© Inra/Elsevier, Paris.)

*Zea mays* L. / inbred lines / pedigree breeding / corn borer tolerance / high yielding combining ability

**Résumé** – Bilan de dix années d'évaluation de lignées de maïs créées par sélection généalogique multicaractère combinant tolérance à la pyrale et aptitude à la combinaison pour le rendement. Pour associer la tolérance à la pyrale (*O. nubilalis* Hbn.) aux caractères agronomiques habituellement sélectionnés, des programmes de création et d'évaluation de lignées du maïs ont été développés par les laboratoires Inra du Maïs (Montpellier, Saint-Martin de Hinx, Bordeaux). En pépinière et dans les essais d'évaluation, la tolérance est exprimée par une note de dégâts à maturité corrigée pour les différences de précocité du matériel. L'utilisation de lignées étalons éprouvées et reconnues stables permet le classement de lignées en trois groupes de tolérance. La méthode de sélection généalogique repose sur une sélection simultanée par niveaux indépendants pour les deux caractères. Des essais de valeur hybride sur différents testeurs complètent les tris en valeur propre. Du matériel tolérant est obtenu dans les différentes sources utilisées. Toutefois, le

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matériel précoce européen et des sources argentines paraissent plus favorables à l'obtention de lignées tolérantes. Ces programmes ont permis l'obtention d'une soixantaine de lignées à forte aptitude à la combinaison pour le rendement et à bons niveaux de tolérance à la pyrale, avec des gains de précocité et de résistance à la verse. (© Inra/Elsevier, Paris.)

### ***Zea mays* L. / lignées pures / sélection généalogique / tolérance à la pyrale / aptitude à la combinaison**

## **1. INTRODUCTION**

At the beginning of the 1970s the maize acreage in Europe hugely increased, mainly with early varieties in the northern areas. These crops were progressively invaded by European corn borer (E.C.B.), *Ostrinia nubilalis* Hbn., populations which normally develop only one generation per year. In France, the first noticeable occurrence of the borer on new maize crops in the Beauce area was recorded in 1966 [2]. With the lack of natural parasites, both the levels of the E.C.B. population and the damage on the susceptible varieties rose quickly. Control with granulated insecticides was initiated as a temporary alternative measure and management of borer populations using variety resistance began to be considered.

At this time, in Iowa, Dicke and Guthrie developed a laboratory production of E.C.B. egg masses for field infestation and obtained several inbred lines with antibiosis resistance to leaf-feeding [6]. It was shown that the survival rate of the first instar larvae depended on the deterrent and toxic effects of the amount of D.I.M.B.O.A. in the whorl-leaf tissues [11]. Moreover, a late line B52 was found to present a high degree of resistance to sheath-collar feeding after anthesis due to a distinct mechanism [7].

However, in north-European ecological conditions, field observations established that E.C.B. oviposition occurred at the end of the late-whorl stage [8] so that the earlier larvae fed primarily on the tissues of the tassel climbing up in the whorl and the later larvae on sheath and collar tissues. In these conditions, the leaf-feeding resistant North-American lines were of little interest as resource for early material breeding. Moreover, the authors failed in transferring the B52 characters of sheath-

collar resistance to adapted early European lines (unpublished results), probably as the consequence of heavy linkage between these characters and unfavourable characters systematically contra-selected.

Consequently, attention was turned to tolerance, the 'third basis of resistance', defined by Painter [13] as the ability of the plant to withstand, to a marked degree, insect host infestation. On maize, tolerance depends on the role played by the plant in reducing the general boring in the stalk which disturbs the transfer of nutrients to the ear and in the strengthening of tissues which avoids stalk breakage. Tolerance may also be considered as the ability, when the tolerated insect is present, to reduce yield losses due to the borer compared to the losses in a susceptible genotype [3].

Research projects on tolerance were initiated in collaboration with the international working group I.W.G.O./I.O.B.C. Many lines were exchanged among most European countries and evaluated by the same procedures in various environments. Sources of tolerance were discovered. The heritability of tolerance characters was demonstrated [9]. Field experiments showed the efficacy of tolerant lines in reducing in their hybrids the yield losses mainly attributed to a reduction of the weight of individual kernels (unpublished data). Programmes were developed to introduce tolerance into conventional breeding for early and mid-early materials adapted to European conditions. The aim of this paper was: 1) to present the methods used in a pedigree breeding for E.C.B. tolerance and high-yielding combining ability; 2) to summarise and compare in the same way the annual evaluations of more than 60 inbred lines released for 10 years in succession from 1987 to 1996; 3) to compare the value of different germplasm resources to improve E.C.B. tolerance.

## 2. MATERIALS AND METHODS

### 2.1. Basic genetic materials

The pedigree selection programmes successively developed for 16 years used sources covering a large range of maize variability: early European populations and lines, Plata Argentina germplasm, Lancaster and Stiff Stalk dent lines, for instance. These sources were primarily selected for agronomic requirements. The breeding programmes were developed either from single crosses and back-crosses or from composites and open-pollinated populations.

### 2.2. Pedigree breeding

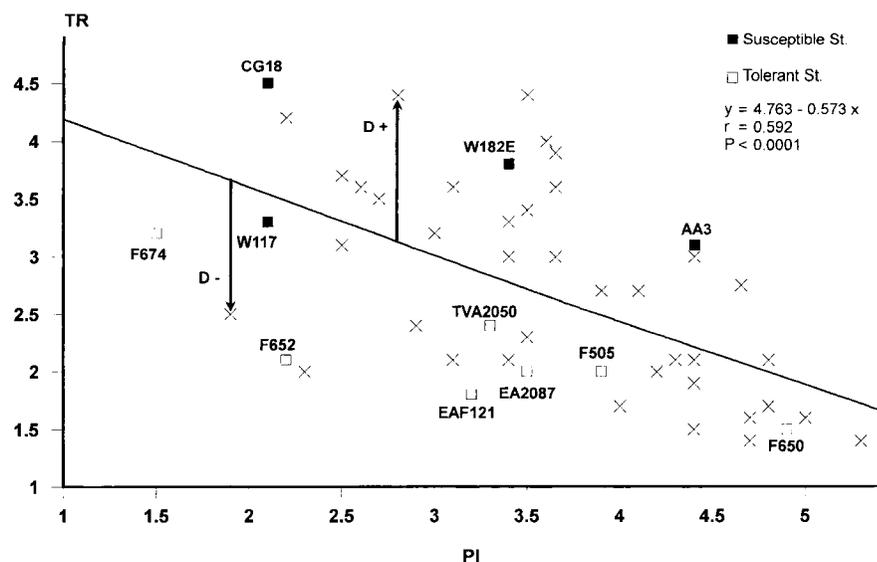
#### 2.2.1. E.C.B. Tolerance evaluation

The plants were artificially infested at the late-whorl stage of plant growth with a low level of 1–2 egg masses per plant only, making estimations of different degrees of tolerance easier. Near physiological maize maturity, plant damage was rated according to a discontinuous rating scale (1 = little damage, 2 = broken tassel, 3 = 2 + broken upper leaves, 4.5 = broken upper stalk, 9 = broken stalk under the ear or dropped ear) [1].

This method was used either for screening in the nursery or for evaluating the lines in experimental trials. For these trials, around 20 to 50 lines were allotted to experimental designs according to earliness with ten plants per plot and four replicates, including 8–10 tolerant and susceptible standards. The plot means of individual tolerance ratings per plant (TR) were calculated and compared by means of variance analysis. Then the regression of TR data on silking dates or on a 1 (early)–6 (late) precocity index (PI) related to the plant growth stage at egg-hatching was studied. *Figure 1* shows, as an example, how the final TR of a line may be estimated by the algebraic value of the difference, D, between observed data and its expected value in the regression. The final TR could also be expressed by adding the D algebraic value to the general mean of the trial. These tests were repeated for 2 years.

#### 2.2.2. Breeding system

To achieve simultaneous breeding for tolerance (TOL) and agronomic conventional traits (AGR), an original breeding system was developed (*table 1*). First, S0 plants were screened for tolerance only. A 25 % selection rate eliminated most of the susceptible plants. The selection in nursery among S1 families used the independent culling level method keeping the best families with ratings above the respective thresholds for both criteria. Then, the advanced generations were developed in nursery without any borer selection pressure. In the



**Figure 1.** Example of presentation of the tolerance ratings obtained in an annual experiment. Regression of the tolerance ratings (TR) on the 1–6 precocity index (PI) related to the plant growth stage at egg hatching. Note the distances (D+ or D-) between the actual data for a given line and its expected value according to the regression.

**Table I.** Schema of pedigree selection including ECB tolerance evaluation.

Years	Generations	Value per se Materials and criteria			Hybrid value Materials and criteria
1	S0 → S1	S0 plants	TOL		
2		S1 lines	TOL + AGR		
3		Repeat			
4	S1 → S2				TC seed production
5					Yield test S1/TC hybrids AGR
6	S2 → S3	S2 bulks test	TOL	S2 nursery AGR	TC seed production
7	S3 → S4	Repeat		S3 nursery AGR	Yield test S2/TC hybrids AGR
8	S4 → S5			S4 nursery AGR	TC seed production
9	S5 → S6	S5 lines test	TOL	S5 nursery AGR	Yield test S4/TC hybrids AGR
10	S6 → S7	Repeat		S6 nursery AGR	Repeat

TOL = European corn borer tolerance evaluation; AGR = evaluation of agronomic traits; TC = test-crosses.

mean time, screenings of S2–S3 families on bulks were independently carried out in distinct field trials for tolerance and for agronomic value in test-crosses. Finally, the performances of the S5 lines were evaluated over 2 years for per se tolerance in experimental plots. On the other hand, the agronomic value on test-crosses (earliness, stalk lodging and yield) was compared over 2 years in an experimental network to reference lines crossed on the same testers. These references (REF) relevant to the concerned germplasm of the line were supposed to

be the best ones of the moment. The lines to be released presented an yield equal or above the reference.

### 2.3. Method for summarising 10 years of results

The results were presented in two ways. First, an attempt was made to draw up a common list of the 63 released lines ordered according to their tolerance level

**Table II.** Characteristics of E.C.B tolerance standards for final evaluation of inbred lines developed in multitrait breeding programmes (1986–1995).

Tolerance classes	Standard lines	Pedigrees or origins	Silking <sup>2</sup>	Tolerance ratings <sup>3</sup>			
				M	CL	FT	VC %
Tolerant	TVA 2050	Trnava/Slovakia	+ 0.5	1.63 ± 0.12	a		8.0
	F 888	Sel/ETO (M) C9 <sup>1</sup>	+ 5.0	1.79 ± 0.24	ab		14.9
	EA 2087	Sel/OP Azpeitia, Spain	– 3.0	2.08 ± 0.16	ab		9.3
	F 652	F2 × BGR 477 <sup>1</sup>	– 4.0	2.24 ± 0.25	b		13.6
Susceptible	F 804	FS14 synthetic <sup>1</sup>	+ 2.0	4.02 ± 0.51	c		15.5
	W 182 E	WD × W 22	0	4.41 ± 0.41	c		11.3
	CG 18	CG7 × CM37	– 4.5	4.59 ± 0.68	c		18.1
Mean/tolerant			– 1.4	1.89 ± 0.12			8.1
Mean/susceptible			0.8	4.33 ± 0.40			12.8

<sup>1</sup> Pedigree selection under ECB infestation at Inra St-Martin de Hinx.

<sup>2</sup> Difference in days with W182E.

<sup>3</sup> Mean ratings (M) for the nine series of 2-year experiments with their confidence limits (CL) for  $P = 0.05$ , the results of the Friedman test (FT) and the variation coefficient (VC).

**Table III.** Mean E.C.B. tolerance performances TR and distribution into three classes of tolerance for the 63 high-yielding and tolerant inbred lines developed in breeding programmes<sup>1</sup> (Bordeaux, Montpellier, St-Martin de Hinx). E.C.B. tolerance is expressed in terms of difference between the TR of the line and the mean TR of the four tolerant standards for the respective years of the test.

Standard lines	TVA 2050	F888	m	EA 2087	F652	
⇐ Highly tolerant ⇒	T1	T2	⇐ Tolerant ⇒	T2	T3	⇐ Moderately tolerant ⇒
				F874		
			F818	F838	F876	F878 F886
			F810 F814 F856	F816	F866	F872 F868
		F692	F806 F812 F844	F668	F880 F864 F830	F850 F698 F858 F820
	F890 F846 F836	F686	F800 F802 F828 F653	F655	F700 F696 F808	F892 F690 F682 F848 F684
F870 F852 F822	F834 F824 F661wx	F659wx F647	F688 F651 F862	F694 F657wx F758 F842	F854 F680 F666 F840 F655	
-0.8 -0.7 -0.6 -0.5 -0.4 -0.3 -0.2 -0.1 0 +0.1 +0.2 +0.3 +0.4 +0.5 +0.6 +0.7 +0.8 +0.9 +1.0 +1.1 +1.2						
E.C.B. tolerance						

<sup>1</sup> The pedigrees of the developed lines are available in the Frasma catalogs, 2, rue du colonel Driant, 75001 Paris.

**Table IV.** Performances of lines originated from North-American dent germplasm.

Release years	Tolerance per se value <sup>1</sup>				Reference × testers hybrid value			Gains lines/ref. on testers <sup>2</sup>			
	Source lines	Tol.	Ref.	Tol.	Ref. × tester	Grain moisture (%)	Grain yield (Mg·ha <sup>-1</sup> )	Stalk lodging (%)	Grain moisture	Grain yield	Stalk lodging
<b>Lancaster</b>											
1990	F682	T3	MO17	T3	MO17 × MBS847	27	100	12			MT
1990	F684	T3	MO17	T3	MO17 × B73	30	117	14	ME		
<b>Stiff Stalk</b>											
1994	F848	T3	F618	S3	F618 × MO17	32	96	19	ME		MT
1995	F876	T3	F618	S3	F618 × MBS847	30	86	9		MHY	
<b>Early dent Wisconsin</b>											
1990	F686	T2	B73	S2	B73 × MO17	30	117	14	ME		MT
1991	F694	T3	F2	T3	F2 × MBS847	29	99	1		HY	
1991	F700	T3	A654	S3	A654 × MBS847	30	104	2	ME		

<sup>1</sup> Tolerance classes: T1 = highly tolerant, T2 = tolerant, T3 = moderately tolerant; susceptibility classes: S3 moderately susceptible, S2 = susceptible, S1 = highly susceptible.

<sup>2</sup> Gains of performances observed in line × tester compared to reference × tester test-crosses: grain moisture: ME = more early (moisture ≤ 120 % of the reference); LE = less early (moisture > 120 %), grain yield: HY = higher yield (≥ 105 % of the reference), MHY = much higher yield (≥ 110 %) stalk lodging: MT = more tolerant (≥ 20 % decreased lodging); LT = less tolerant (≥ 20 % increase lodging).

(table III). To do so, the tolerance of the standards used in the different years of test were studied. In spite of annual variations in the insect-plant relationships (insect survival rate, plant reaction to insect feeding), four tolerant and three susceptible standards presented among them a stability for their ratings and respective rankings, verified by different criteria: confidence limits of the mean, variation coefficient, non-parametric Friedman test (table II). Consequently, tolerance of lines could be expressed (table III) in terms of difference between their own TR and the mean TR of the four tolerant standards for their respective years of test and release.

Second, an analysis was made concerning the responses of different germplasms to breeding. Twelve groups of origins with 44 lines were studied. The lines were arranged according to their genetic origin whatever their years of test. It must be kept in mind that data originate from comparison in individual pairs (the reference line and the tested one) in different years of test. Consequently, the values of the gains obtained by breeding must be considered with caution.

### 3. RESULTS AND DISCUSSION

#### 3.1. Tolerance of the inbred lines

As indicated above, the tolerance data of the lines are given in table III. The statistical parameters observed for the tolerant standards were such that the lines were arranged into three classes: highly tolerant T1 (≥ TVA 2050), tolerant T2 including F888 and EA 2087 and moderately tolerant T3 (≤ F 652).

#### 3.2. Responses of germplasm sources to breeding

The results of analysis are given in the tables IV-VI and VII.

**Table V.** Performances of lines originating from the European (E) and from Argentina–Europe (AE) germplasms and from their crosses with North America dent germplasm (NA).

Release years	Tolerance per se value <sup>1</sup>				Reference × testers hybrid value				Gains lines/ref. on testers <sup>2</sup>		
	Source lines	Tol.	Ref.	Tol.	Ref. × tester	Grain moisture (%)	Grain yield (Mg·ha <sup>-1</sup> )	Stalk lodging (%)	Grain moisture	Grain yield	Stalk lodging
<b>Euskadian population</b>											
1991	F810	T2	F2	T3	F2 × MBS847	29	99	1		MHY	
<b>Early Flint E composite</b>											
1996	F878	T3	F2	T3	F2 × MBS847	32	95	9	LE	HY	MT
1996	F880	T3	F2	T3	F2 × F668	32	83	19		HY	MT
<b>AE Flint composite</b>											
1993	F651	T2	F492	S3	F492 × MBS847	28	84	10		MHY	LT
1993	F653	T2	F2	T3	F2 × Early dent	30	76	31	LE	HY	MT
1992	F822	T1	F2	T3	F2 × MBS847	32	98	8	LE	HY	MT
1992	F828	T2	F2	T3	F2 × MBS847	32	98	8	LE		
1992	F830	T3	F2	T3	F2 × MBS847	32	98	8	LE	HY	MT
1995	F862	T3	F564	T2	F2 × MBS847	37	104	16			MT
1997	F886	T3	F564	T2	F564 × F692	36	92	30		MHY	MT
1997	F659 wx	T2	F651	T2	F651 × F618	29	101	17	LE	HY	MT
<b>E Composite A × Lancaster</b>											
1991	F814	T2	MBS	S3	MBS847 × F816	22	97	6		HY	
1991	F816	T2	MBS	S3	MBS847 × F816	22	97	6	LE	MHY	
1993	F836	T1	F492	S3	F492 × MBS847	28	84	10	ME	MHY	
<b>E Composite B × SSS</b>											
1991	F800	T2	F2	T3	F2 × Early dent	26	89	1		HY	
1993	F834	T1	A632	T3	A632 × Early dent	33	82	29		HY	MT
1994	F846	T1	F618	S3	F618 × MO17	32	96	19	ME		MT
1997	F665	T3	F618	S3	F618 × MO17	30	108	22		HY	MT
1997	F661	T2	F618	S3	F618 × MO17	31	112	16		HY	MT
<b>Pool AE + NA</b>											
1995	F655	T3	F618	S3	F618 × MBS847	30	86	9		HY	
1991	F802	T2	MO17	T3	MO17 × MBS847	24	99	2	ME		
1995	F864	T3	F598	T3	F598 × MBS847	35	100	6			
1995	F866	T3	F611	S1	F611 × MBS847	38	87	19	ME	MHY	MT

<sup>1,2</sup> As in table IV.

### 3.2.1. Global results

For agronomic traits, about 40 and 25 %, respectively, of the lines presented grain yields higher (HY) (105 %) and much higher (MHY) (110 %) than the reference crossed on the same tester. Improvements in stalk lodging tolerance (MT) were observed for 55 % of the lines which exhibit-

ed a 20 % decrease in lodging by comparison to the references. The grain moisture at harvest was higher (LE) or lower (ME) than references, respectively, for 18 and 25 % of the lines. In some cases, high gains were simultaneously obtained for the three agronomic criteria (F 653, F 659 wx, F 822, F 830, F 842, F 850, F 866, F 870, F 878).

**Table VI.** Performances of lines originated from backcrosses and single crosses.

Release years	Tolerance per se value <sup>1</sup>				Reference × testers hybrid value				Gains lines/ref. on testers <sup>2</sup>		
	Source lines	Tol.	Ref.	Tol.	Ref. × tester	Grain moisture (%)	Grain yield (Mg·ha <sup>-1</sup> )	Stalk lodging (%)	Grain moisture	Grain yield	Stalk lodging
Lacaune Flint F2 <sup>2</sup> × Early dent NA											
1992	F818	T2	F2	T3	F2 × MBS847	32	98	8	ME		MT
1992	F820	T3	F2	T3	F2 × MBS847	32	98	8		MHY	MT
1994	F840	T3	F2	T3	F2 × MBS847	35	93	9		HY	
1994	F842	T3	F2	T3	F2 × MBS847	35	93	9	LE	HY	MT
1994	F844	T2	F2	T3	F2 × MBS847	35	93	9		MHY	MT
Lacaune Flint F7 <sup>2</sup> × Early dent NA											
1991	F696	T3	F7	S1	F7 × MBS847	30	99	3		HY	
1991	F698	T3	F7	S1	F7 × MBS847	30	99	3		HY	
F255 (T3) × C0255 (S1)											
1994	F852	T1			CO255 × F618	35	86	23			MT

<sup>1</sup> Tolerance classes: T1 = highly tolerant, T2 = tolerant, T3 = moderately tolerant; susceptibility classes: S3 moderately susceptible, S2 = susceptible, S1 = highly susceptible.

<sup>2</sup> Gains of performances observed in line × tester compared to reference × tester test-crosses: grain moisture: ME = more early (moisture ≤ 120 % of the reference); LE = less early (moisture > 120 %), grain yield: HY = higher yield (≥ 105 % of the reference), MHY = much higher yield (≥ 110 %) stalk lodging: MT = more tolerant (≥ 20 % decreased lodging); LT = less tolerant (≥ 20 % increase lodging).

**Table VII.** Performances of lines originated from ECB tolerant or moderately resistant materials.

Release years	Tolerance per se value <sup>1</sup>				Reference × testers hybrid value				Gains lines/ref. on testers <sup>2</sup>		
	Source lines	Tol.	Ref.	Tol.	Ref. × tester	Grain moisture (%)	Grain yield (Mg·ha <sup>-1</sup> )	Stalk lodging (%)	Grain moisture	Grain yield	Stalk lodging
Tolerant Synthetic FS 12											
1991	F812	T2	A632	T3	A632 × MBS847	24	99	2	ME		
1992	F832	T1	A632	T3	A632 × Early dent	31	94	21			MT
1995	F874	T2	F812	T2	F812 × MO17	29	78	13		MHY	
Polygenic H.T. resistance source											
1994	F850	T3	F566	S2	F566 × Early dent	35	79	27	ME	HY	MT
1995	F868	T3	F566	S2	F566 × F618	31	84	13			
1995	F870	T1	F566	S2	F566 × MBS847	30	79	12	ME	MHY	MT

<sup>1</sup> Tolerance classes: T1 = highly tolerant, T2 = tolerant, T3 = moderately tolerant; susceptibility classes: S3 moderately susceptible, S2 = susceptible, S1 = highly susceptible.

<sup>2</sup> Gains of performances observed in line × tester compared to reference × tester test-crosses: grain moisture: ME = more early (moisture ≤ 120 % of the reference); LE = less early (moisture > 120 %), grain yield: HY = higher yield (≥ 105 % of the reference), MHY = much higher yield (≥ 110 %) stalk lodging: MT = more tolerant (≥ 20 % decreased lodging); LI = less tolerant (≥ 20 % increase lodging).

Globally the E.C.B. tolerance for 68 % of the lines were higher than the tolerance of the references. For about 2/3 of these lines, the higher level of tolerance was correlated with an improvement of their yields when they are crossed on the same tester than the reference: for instance, the lines F 810, F 822, F 844 > F2 in the test crosses with MBS 847; the lines F 655, F 876 and F 665, F 661 WX > F 618 in the test crosses with MBS 847 and MO 17, respectively.

### 3.2.2. Variations according the germplasms

The lines obtained from the North-American dent sources were generally moderately tolerant (*table IV*). On the contrary, a good half of the lines derivated from European (E) and Argentinian-European (AE) composites were tolerant or highly tolerant. Moreover, they are more tolerant to stalk lodging and higher yielding, but generally less early than the references F 2 and F 564 (*table V*).

The progenies of the European composites crossed by the American sources Lancaster and Stiff Stalk Synthetic were as a whole tolerant or highly tolerant and, for the same level of earliness, generally more stalk lodging tolerant and higher yielding than the references MBS 847, F 618 or MO 17 (*table V*).

These results have shown that it is probably easier to obtain T1 and T2 tolerant lines from the generally flint European sources than from the dent N. American material. Is this property linked to the flint type or rather favoured by the more than 450 years of insect selection pressure on the material introduced into the Old World from where the borer originates?

Moreover, back-crosses by well known flint French lines of early dent N. American sources have allowed the obtention of higher yielding lines than F 2 and F 7, with a better tolerance than the highly susceptible F 7 for F 696 and F 698. In the progeny of a susceptible single cross, transgression to tolerance was observed in the F 852 line (*table VI*). In addition, *table VII* exhibited improvements for different criteria in synthetic materials already known for tolerance.

## 4. GENERAL COMMENTS AND CONCLUSION

Before the beginning of our present breeding programme, among the three interrelated bases of insect resistance defined as preference, antibiosis and tolerance [13], American maize breeders set out to discover antibiosis characters increasing young E.C.B. larvae mortality in their leaf and sheath collar feeding. They used high levels of infestation associated with high selection pressure and obtained a large number of leaf-feeding resistant lines. Painter (op. cit.) stated that "the insect must always be the final judge of whether a new variety, selection or hybrid is really resistant". For our part, this idea associated with the concept of tolerance has governed our approach based on the whole insect-plant relationship until maize maturity. In 1976, our breeding project was new and original, first in its objective (developing from European germplasm lines combining E.C.B. tolerance with high agronomic value) and second in its method of evaluating tolerance (low infestation rate in order to appreciate small differences in susceptibility, choice of suitable standards, adjustment of data to earliness) and agronomic value both by breeders and entomologists.

In studies carried out in North America, the criteria of tolerance and yield in breeding for resistance have appeared only recently [10, 12, 17]. However, the present selection for standability and reduction of yield losses for infestations after anthesis belongs mainly to tolerance. The American criteria for cavity counts or length of tunnels are similar to the percentage of damaged internodes correlated with the visual tolerance ratings used in our programmes.

At present, in different countries, the breeding programmes for E.C.B resistance use tropical sources: for instance, development of the MO-2 ECB 2 [4] and of F 888 from ETO (M) C9 in France, CIMMYT programme for multiple borer resistance [5]. Moreover, back-crosses are used in transferring resistance or tolerance characters to susceptible elite lines. For our part, a back-cross breeding programme DE 811 × F 618 is in pro-

gress. The studies of mapping and characterisation of QTLs affecting resistance of lines derived from the cross B73 susceptible × B52 resistant with aid of RFLPs conducted at Ames University (Iowa) and Hohenheim University (Germany) (see for instance Schön et al. [16]) should make it possible to develop inbred lines with high hybrid values and E.C.B. tolerance.

In conclusion, over the course of 16 years, 63 flint and dent inbred lines, adapted to European conditions with high yielding ability and appreciable levels of E.C.B tolerance have been developed and released to maize breeders. They can be considered to contribute to an economical and ecological way of controlling the E.C.B.

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