Claude Welcker – INRA Guadeloupe

Summary

Research activities at INRA – Guadeloupe concentrated on three main aspects:

- Assessment of genetic progress in maize for tolerance to soil acidity and identification of superior source germplasm compared to local adapted germplasm to develop cultivars for acid soils
- Characterization of genotypical responses to soil acidity and identification of target or secondary traits for adaptation to be used as selection criteria
- Analysis of the genetic variation in maize for tolerance to soil acidity, evaluation of the breeding value of tolerant source germplasm and determination of common breeding strategy for adaptation.

Agronomical, variety and diallel trials were sown in Guadeloupe on ferralitic acid soils during the four project years. Shoot and root characteristics correlated responses on acid soils were assessed. Germplasm was extensively exchanged between the groups and evaluated across acid locations of the network. A common set of maize source populations derived from the different breeding programs and CIMMYT, and their crosses forming a diallel was evaluated. INRA Guadeloupe took actually initiative to enhance collaboration between breeders including CIMMYT in the frame of the project and a joint breeding approach established for which we took the main co-ordinating responsibility.

Our results clearly show that effective progress has been achieved in breeding for tolerance to soil acidity the last decades and that different combinations of adaptation traits lead to higher yielding capacity in acid soil environments and better tolerance to soil acidity. Progress concerned hybrids and open pollinated populations as well enhancing the chance of appropriation by farmers. Improved materials from CIMMYT (Columbia) appeared to be the most tolerant ones exhibiting low grain losses under acid soils and showed more stable grain yields across locations. Some brasilian materials were classified as P efficient whereas Cameroun materials appeared more specifically tolerant to Al toxicity. These different materials constituted valuable source germplasm for breeding programs. Some experimental varieties out-yielding 20% more than cultivars could be immediately released to farmers.

Adaptation to acid soils appears to be based on expression of vigor during young stage allowing the development of an homogenous and efficient crop canopy and on realization of a complete life cycle in a short period allowing the harvest of clean and fulfilled ears. Plant vigor at young stage, plant height, silking, prolificacy constitute easy assessible phenotypic plant parameters and heritable traits to be used in breeding for adaptation. Callose formation was confirmed as relevant trait however its genetic parameters will be estimated by screening the complete diallel in nutrient solution. Target criteria of root adaptation should be considered more extensively by the breeders. The use of root electrical capacitance to assess the root system appears promising; thus characterization of rooting patterns of maize genotypes in field conditions will be pursuited within the next INCO project and compared with shoot characteristics correlated responses.

Diallel analysis helps breeders to determine heterotic patterns among their populations and choose appropriate materials and methods for their breeding program. Importance of both additive and non-additive gene effects for yield and secondary traits and high heterosis value suggested that reciprocal recurrent selection would be effective for development of superior open-pollinated populations and hybrids for acid soils. The best cross combining SA7 and CMS36 out-yielded for about 22% the best known experimental hybrid still selected. Heterosis observed between tolerant populations indicated that original combinations of favorable alleles occured and new progress should be expected in breeding within the studied germplasm. Based on specific adaptation traits provided by some tolerant source populations, the GCA effects of the populations and heterosis, recurrent selection that exploits both GCA and SCA effects would include, for sustainable improvement, the white populations SA7, ATPW, SA6 and TUXP and the yellow populations SA3, ATPY, CMS36 and SA4. Moreover, recombinations between these two pools should provide significant progress. Besides lines can be extracted from the tolerant populations and crossed with lines of heterotic populations to produce superior hybrids. These lines should constitute good candidates for mapping genes of adaptation to soil acidity. Diallel analysis will be completed by results of current field trials in Brasil and future laboratory screenings at Hannover. Then, we will be able to define a common breeding strategy thanks to a better understanding of genetic of adaptation and combining abilities between the studied source germplasm. Besides, we plan to develop experimental varieties to be released as soon as possible to farmers.

Visiting scientist and Pre-doctoral fellows

Dr Thé from IRAD Cameroun spent some time at INRA Guadeloupe in 1998 and 2000 in order to elaborate common genetic studies: mating designs, standardization of the measurement of plant parameters, statistical analysis of common data sets. A diploma student from the University of Dresden, supervised by the co-ordinator, jointed our program for five months in 1998 in order to compare field and laboratory screenings. The INRA program hosted four other students in agronomy from ENSAIA Nancy and ESA Purpan for their training. They contributed by working on each INCO trials to the analysis of genetic variation in maize for adaptation to soil acidity.

Introduction

Maize is grown on approximately eight million hectares of acidic soils, where yields are low because of Al and Mn toxicity and mineral deficiencies. Acid-tolerant cultivars would be an environmentally friendly and relatively inexpensive tool for sustaining maize cropping system in acid tropics. Information that would assist the breeders selecting suitable germplasms for their breeding programs and choosing appropriate breeding methodology is still limited.

During the four project years, research activities at INRA Guadeloupe concentrated on three main aspects:

- Assessment of genetic progress in maize for tolerance to soil acidity and identification of superior source germplasm compared to local adapted germplasm to develop cultivars for acid soils
- Characterization of genotypical responses to soil acidity and identification of target or secondary traits for adaptation to be used as selection criteria
- Analysis of the genetic variation in maize for tolerance to soil acidity, evaluation of the breeding value of tolerant source germplasm and determination of breeding strategy for adaptation.

Agronomical, variety and diallel trials were sown in Guadeloupe on ferralitic acid soils; sets of genotypes were distributed to each member of the INCO network. INRA Guadeloupe took actually initiative to enhance collaboration between breeders included CIMMYT in the frame of the project. Germplasm was extensively exchanged and a joint breeding approach established for which we had taken the main co-ordinating responsability.

Dr Thé from Cameroun spent some time at INRA Guadeloupe on 1998 and 2000. A diploma student from the University of Dresden, supervised by the coordinator jointed our program for five months in 1998; the INRA program hosted four other students in agronomy for their training.

A Evaluation of tolerant source germplasm and assessment of progress in breeding for adaptation to soil acidity

A 3 Introduction

Over the past 20 years, breeding efforts lead to the identification of source germplasm with tolerance to aluminium toxicity and to the development of maize cultivars better adapted to soil acidity. This constraint is an important cause of low fertility of tropical soils. It is generally characterized by low pH, Aluminium and Manganese toxicity and minerals deficiencies inhibiting root development and reducing nutrients and water uptake, therefore it limits dramatically yield of eight millions hectares of maize in the tropics (Edmeades & Deutsch, 1994, Sanchez, 1977). There is a wide agreement that additional progress sustaining maize cropping system in the acid tropics, would be related to breeding for multiple stress in maize.

The INCO collaborative program aims at enhancing breeding of maize for tolerance to soil acidity. Identification and utilization of source germplasms with tolerance to different components of soil acidity or essential genes would make the development of otherwise well adapted and high yielding cultivars much more efficient. Therefore, genetic material selected by each breeder's team was extensively exchanged, evaluated in the fields of the network covering a wide and interesting range of acid soil environments and screened for short term response in nutrient solution supplied with Al. Expected results would be i) evaluation of genetic progress accumulated for tolerance to acid soils, ii), characterization of tolerance, iii) analysis of genetic variance for yield in acid soils, estimation of the importance of genetic by environment interaction effects on tolerance component, iv) utilization of tolerant germplasms, and v) valorisation of tolerant cultivars.

We report here main results from trials conducted in Guadeloupe during the main growing season on 1998 and from trials sown across locations of the INCO network in 1998 and 1999.

A 2 Material and Methods

Experimental varieties i.e. populations, double-cross hybrids and single-cross hybrids selected for adaptation to acid soil environments in Brazil (EMBRAPA), Columbia (CIAT/CIMMYT International Network), Cameroun (IRAD) and Guadeloupe (INRA) and high yielding varieties have been evaluated across environments (Tab. 1). Different stages of recurrent breeding schemes provide the studied materials coming from different genetic backgrounds and covering different adaptation abilities (Parentoni et al, 1996, Pandey et al, 1994, Ceballos et al, 1998, Magnavac et al, 1987, The, 1996, Welcker, 1996).

Tab 1 : Description of the genetic material evaluated within the network - Guadeloupe 1998.

Genotype	Origin	Type	Characteristics
BR201M	EMBRAPA, Brasil	HS	Al Tolerant
HS64x1143	EMBRAPA, Brasil	HS	Al Tolerant- P inefficient
BR201F	EMBRAPA, Brasil	HS	Al suceptible - P efficient
BR201	EMBRAPA, Brasil	HD	P efficient

HS20x724	EMBRAPA, Brasil	HS	N efficient
HD91102	EMBRAPA, Brasil	HD	Al Tolerant - High yielding
HD9176	EMBRAPA, Brasil	HD	Al Tolerant - High yielding
HD9481	EMBRAPA, Brasil	HD	Al Tolerant - High yielding
HS11x723	EMBRAPA, Brasil	HS	Al sensitive - P&N inefficient
CMS36	EMBRAPA, Brasil	POP	Al Tolerant
CMS30	EMBRAPA, Brasil	POP	Al Tolerant
CMS14C	EMBRAPA, Brasil	POP	Al Tolerant
96SA3	CIMMYT, Colombia	POP	Acid Tolerant
96SA4	CIMMYT, Colombia	POP	Acid Tolerant
96SA6	CIMMYT, Colombia	POP	Acid Tolerant
96SA7	CIMMYT, Colombia	POP	Acid Tolerant
Hyb8x3	CIMMYT, Colombia	HS	Acid Tolerant
Hyb8x6	CIMMYT, Colombia	HS	Acid Tolerant
Sikuani	CIMMYT, Colombia	POP	Acid Tolerant
93SA8	CIMMYT, Colombia	POP	Acid Tolerant
ATP.SR.Y	IRAD, Cameroun	POP	Al & Mn Tolerant
ATP.SynI.Y	IRAD, Cameroun	POP	Mn Tolerant
ATP.SynI.W	IRAD, Cameroun	POP	Al Tolerant
CMS9213	IRAD, Cameroun	POP	Al moderated Tolerant
Spectral	INRA, Guadeloupe	POP	Acid moderated Tolerant
Natal	INRA, Guadeloupe	POP	Acid susceptible
Kristal27	INRA, Guadeloupe	POP	unknown
PX304C	INRA, Guadeloupe	HS	Acid moderated Tolerant
HD9148	EMBRAPA, Brasil	HD	Al suceptible
HD9153	EMBRAPA, Brasil	HD	Al Tolerant
91SA3	CIMMYT, Colombia	POP	Acid Tolerant
93SA3	CIMMYT, Colombia	POP	Acid Tolerant
Clavito	CORPOÏCA, Colombia	POP	moderated acid susceptible
ICA V.109	CORPOÏCA, Colombia	POP	Acid suceptible
ATP.SR.W	IRAD, Cameroun	POP	Al Tolerant
ATP.Syn.S4.Y	IRAD, Cameroun	POP	Al Tolerant
ATP.SynII.Y	IRAD, Cameroun	POP	Al Tolerant
ATP.Syn.S3.W	IRAD, Cameroun	POP	Al Tolerant
ATP.Syn.S5.Y	IRAD, Cameroun	POP	Al Tolerant
ATP.Syn.S5.W	IRAD, Cameroun	POP	Al Tolerant
ICTA farm	UWI, Trinidad	POP	Al moderated Tolerant
POPG-C2	INRA, Guadeloupe	POP	unknown
T2A	CIMMYT, Mexico	POP	unknown
T4A	CIMMYT, Mexico	POP	unknown
MpSWCB4	USDA, Mississipi	POP	unknown
ANTIGUA	CIMMYT, Mexico	POP	unknown

HS : Simple-Cross Hybrid, HD : Double-Cross Hybrid, POP : Open pollinated Variety & Population.

Trials were sown during the main growing season of 1998 in Guadeloupe (INRA) on a preserved and stable ferralitic glacy at « La Providence ». Two main-plots of different levels of acidity have been delimitated: normal acidic soil (Acid soil environment) and limed soil to lower Al saturation and soil acidity (Non Acid soil environment). Data were recorded at different stages: seedling, whorl stage, flowering and maturity; grain yield and yield components have been measured - see Welcker, 1998 for complete description of the tested materials, the experimental design, cultivation practices, the observed parameters and the statistical procedures.
Trials were also sown in 1998 in Cameroun (IRAD) at Ebolowa, in 1999 in Columbia (CIMMYT) at Matazul and at Vilavicienco and partially sown in 1999 in Brazil (EMBRAPA).

A 3 Results

A 3.1 Characterization of the experimental sites

In Guadeloupe, the soil of the nursery « La Providence » is a ferralitic soil resulting from the alteration of volcanic material as many of the caribbean soils. The proportion of clay is high (nearly 90%), mainly of Halloïsyte (1:1) and Smectite (2:1) type with a low CEC. Thus the CEC of the guadeloupean ferralitic soils mainly depend on the organic matter. Under the humid tropical climate of the nursery (over 3500 mm a year), the alteration of this soil results in an excess supply of free exchangeable aluminium. During the project years, characterisation of this soil was realized by CIRAD at Montpellier and INRA in Guadeloupe. Al saturation was high (61%) and appeared quite similar to those from the other acid sites of the network (Tab. 2). However, the guadeloupean acid soil is characterized by a high P-fixing capacity. We observed pH differences of nearly one unit for the top soil, less than 0.3 unit for the sub-soil between the acid environment and the non-acid environment (limed plot) when no differences were observed under 40 cm (KCl pH = 4.01).
In Columbia, Matazul was described as more critical than Vilavicienco which is rather more fertile. Soil data from Cameroun seemed less stable over the years but the acidity also appeared dramatic (Tab. 2).

Soil parameters	Guadeloupe-INRA		Colombia-CIMMYT		Cameroon-IRAD
	Non Acid	Acid	Villavicencio	Matazul	Ebolowa
pH	5.5	4.6	4.5	4.7	4.7
Al saturation (%)	2.6	61	65	70	62
CEC (meq)	8.1	5.6	3.4	3	3.7
O.M. (%)	2.6	3.1	3.4	3.4	-
Fertilizers	135 kg/ha N	135 kg/ha N	120 kg/ha N	92 kg/ha N	100 kg/ha N
	85 kg/ha P2O5	65 kg/ha P2O5	0 kg/ha P2O5	25 kg/ha P2O5	20 kg/ha P2O5
	110 kg/ha K2O	110 kg/ha K2O	35 kg/ha K2O	110 kg/ha K2O	20 kg/ha K2O

Table 2: Environments where maize trials were grown during the INCO project years 1998 and 1999

A 3.2 Identification of superior maize genotypes for adaptation to guadeloupean acid soils

There were considerable genotypic variations for yield on acid soil environment (from 2.9 t/ha to 7.2 t/ha) and tolerance expressed as the ratio ((Yield in Non Acid env.- Yield in Acid env.) / Yield in Non Acid env.), (from 55% to 6%). The results emphasis effective gains in breeding for adaptation to soil acidity. Distribution for yield on acid and non acid soils were reported in Fig 1.
Single-cross hybrid HybSA8xSA6_from CIMMYT shows the highest yield on acid soil (7.24 t/ha). Experimental open pollinated varieties issued from the same genetic background

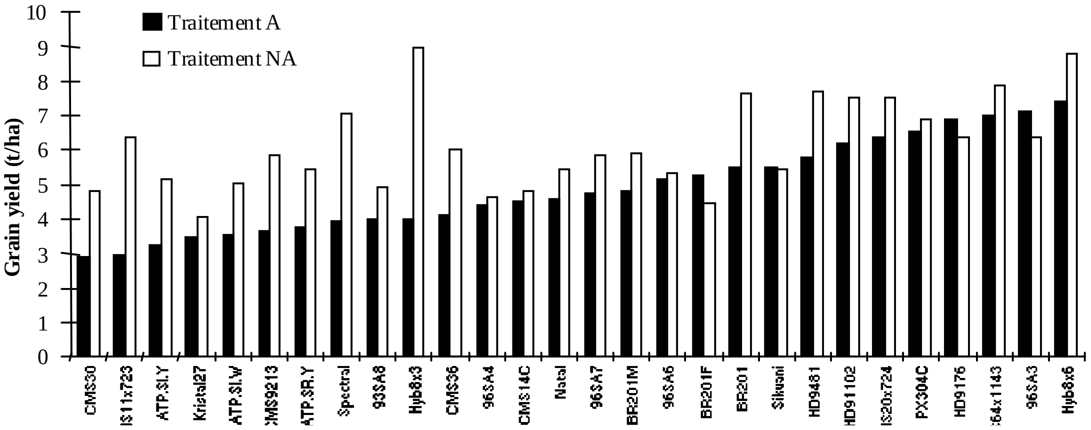


Fig 1: Genotypes by environment interaction effects for Grain yield among 28 tropical maize genotypes grown under acid (A) and non acid (NA) soil - Guadeloupe 1998.

yielded an average of 4.92 t/ha. Nevertheless, the more recent variety selected in the population SA3 which has been found as the best CIMMYT population adapted to Guadeloupe environment (Welcker, 1996) reached 6 t/ha. Moreover, SA improved populations appear as the most tolerant ones (6% of grain yield losses from non acid to acid env.). Those results underline the interest of this material as tolerant source germplasm and the importance of heterosis for grain yield on acid soil.

The most recent brasilian selected material, yielded the most; improved tolerant source populations (composed in 1976), hybrid from the last decade (Magnavaca *et al*,1987), double cross hybrid from the beginning of the 90's and recent experimental single cross hybrids (Parentoni *et al*, 1996, Bahia Filho *et al*, 1997) averaged 4.08 t/ha, 4.80 t/ha, 6.23 t/ha and 6.48 t/ha respectively. The gain between the last ones mainly concerns earliness (4 days less to silking); grain production per hectare per day should be an objective of breeding particulary in tropical regions (Evans, 1993).

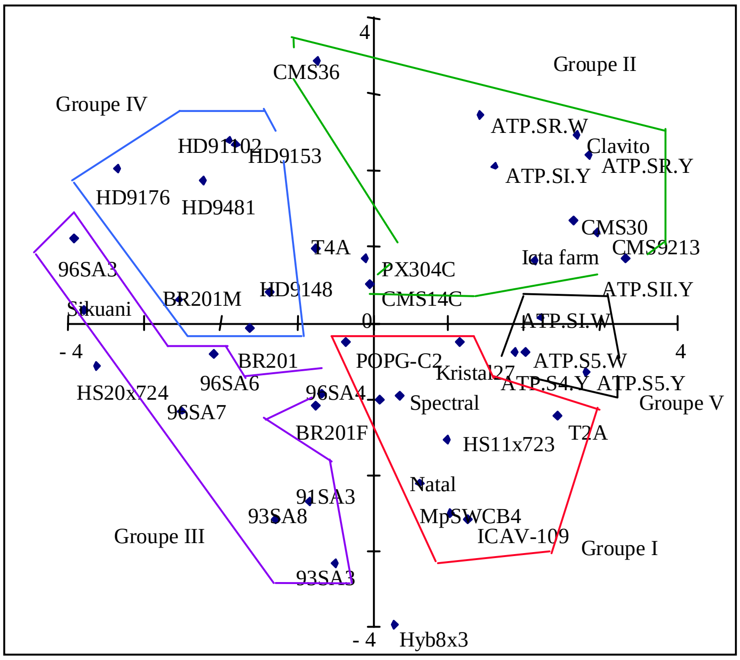
Grain losses from non-acid to acid soil environments was the highest for HS11x723 (2t/ha), known as N and P inefficient. This results agree with the general knowledge on the importance for a genotype to use as efficiently as possible the mineral ressources especially when acidity reduces availability of N et P.

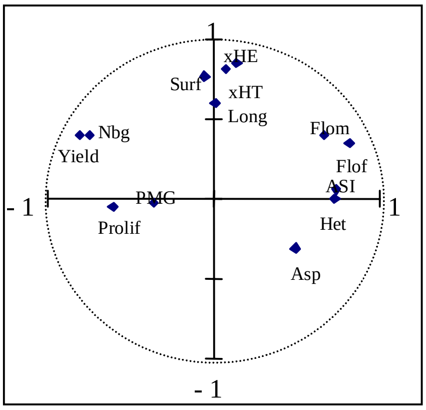
Yield and yield stability of CMS14C improved population from EMBRAPA confirms its interest in Guadeloupe (Welcker, 1996).

The open pollinated populations selected for yield across environments by INRA within pools adapted to lowland tropics showed low tolerance to soil acidity. However, Spectral which yields 7.1 t/ha on non-acid soil, yields 4.4 t/ha on acid soil , as much as some improved populations, but seems to be not so tolerant as usual (Welcker, 1996, The, 1996).

Yields of selected material from Cameroun appear lower than expected from observation realized at young stages. The usual delay observed during flowering suggests that an other factor of adaptation is playing a major role, limiting the expression of the tolerance to Al identified in Cameroun.

Finally, several genotypes issued from different genetic background and from different breeding strategies showed better adaptation to soil acidity (Fig. 2). Tolerance appears clearly to be quantitatively inherited. Different combinations of traits lead to higher yielding capacity and better tolerance, within these materials (Fig. 2). The use of SA experimental varieties and HD9176 should be promoted. More useful to a farmer in increasing maize production and food output is a variety that has been improved to overcome the most significant constraint of the ecosystem, while still performing as well as or better than the farmer's current variety for secondary stresses. The crops of maize farmers in Central America and the Caribbean suffer from insects pests. Our trials revealed a low variation for insect tolerance within acid tolerant genotypes, showing relative advantages of Spectral and SA7. Thus, further progress could be expected by breeding for multiple stress tolerance within those adapted germplasms.





PCA-Factor patterns - acid soil - Guadeloupe 1998

Fig 2: Principal components analysis ordination of 40 experimental maize populations and hybrids evaluated on acid soils in Guadeloupe INRA 1998

A 3.3 Assessment of genetic progress for adaptation to acid soils of the tropics

Based on average grain yields, Columbian acid soils appeared the most stressing (Tab.3). Across location analysis revealed significant high progress for adaptation of maize to acid soils of the tropics (Tab. 4). The best experimental open pollinated varieties (OPV's) or the best experimental hybrids out-yielded the respective check from more than 20 % to almost 40%.

	cameroun	guadeloupe	colombieV	colombieM
Mean	4.36	4.3	2.88	3.06
Mean square	3.12	1.6	0.19	0.62
I.C. (95%)	0.59	0.4	0.15	0.26
Min	1.23	2.09	2.12	0.94
Max	7.83	7.24	3.82	4.88

Tab 3 : statistical data for yield (t/ha) evaluated within INCO acid

Within the OPV's, SA7 and SA3 experimental varieties from CIMMYT showed the highest yield across acid soil environments. Moreover, several selected materials from Cameroun confirmed their abilities, particularly the tolerant population ATP-W (tab. 4). These OPV's constituted key materials for release to farmers.

Within hybrids, three way hybrids selected at CIMMYT showed high yielding capacity on acid soils (Tab. 4). However, recent double hybrids selected in Brasil expressed significant progress compared to the performance of the brasilian commercial hybrid BR201.

As a conclusion, our results clearly reveal that effective progress has been achieved in breeding for tolerance to soil acidity the last decades, different phenotypes providing good performances on acid soils. These adaptation abilities should precisely be described in order to facilitate their utilization in breeding and to maximise further progress.

number	Populations	tol.moy
17	ATP.S3.Y	-56.89
16	ATP.S3.W	-30.87
20	ATP.S5.Y	-29.85
19	ATP.S5.W	-29.26
1	91SA3	-17.59
15	ATP.II.Y	-15.09
14	ANTIGUA	-13.37
52	MpSWCB4	-13.13
2	93SA3	-12.82
54	POPG-C2	-11.56
58	Spectral	-11.13
53	Natal	-9.58
28	clavito	-7.39
49	ICAV.109	-6.88
5	93SA8	-5.38
50	ICTAfarm	-2.97
24	ATP.SR.Y	-2.64
34	CMS14C	-0.91
18	ATP.S4.Y	0.00
61	Tuxpeño Sequia	0.00
38	CMS9213	0.53
51	Kristal	1.06
21	ATP.SI.W	1.10
22	ATP.SI.Y	2.16
8	96SA6	2.91
35	CMS30	4.11
36	CMS36	7.59
7	96SA4	18.28
57	Sikuani ICA V-110	19.08
56	Sikuani	21.40
23	ATP.SR.W	22.40
9	96SA7	28.15
6	96SA3	29.35

number	Hybrids	tol.moy
37	CMS85O1	-50.42
10	8321xE1.	-29.67
47	HS701B	-24.37
59	T2A	-22.58
11	88094x87036	-21.88
13	89301x91*	-17.53
12	88094xNC	-7.64
26	BR201F	-5.98
27	BR201M	-3.71
60	T4A	-3.31
44	HS11x723	-3.03
31	CLA20 x CLA24	-2.90
40	HD9148	-1.64
55	PX304C	-0.88
25	BR201	0.00
30	CLA18 x CLA17	6.35
46	HS64x1143	7.45
45	HS20x724	10.58
43	HD9481	10.94
41	HD9153	15.34
39	HD91102	15.62
29	CLA16 x (LASP2XLASP3)	21.66
42	HD9176	28.88
48	hyb SA8*SA6	31.04
33	CLA44 x (LASP2xLASP3)	36.78
32	CLA41 x (LASP2xLASP3)	39.15

Tab 4: Ranking of maize experimental populations and hybrids for yield evaluated across acid soil environments (Guadeloupe, Cameroun, Colombie). Yield is expressed as percentage of the performance of maize cultivars used during the 1990's. Performances of recent released variety (Sikuani) and hybrid (HD9176) were also underlined. INRA Guadeloupe INCO. Results presented at Yaounde July 2000.

B Characterization of genotypical response to soil acidity and identification of secondary traits for adpatation to acid soil environments

B 1 Introduction

The use of secondary traits (the primary trait is usually grain yield) as selection criteria in plant breeding has often been suggested, yet the contribution of these traits to increased grain yield under stress has generally been poorly quantified. We focussed our study on putative secondary traits associated with acidity tolerance such as those affecting seedling survival, plant growth, ear formation and grain filling. Results presented here were issued from different experiments conducted in Guadeloupe within the breeding trials.

B. 2 Materials and methods

We conducted our investigations in all the trials sown in Guadeloupe during the project years: first, when studying the response to soil acidity at young and flowering stages of 12 genotypes covering a range of adaptation - see Welcker et al 1997 -; second, when evaluating genetic progress for adaptation to acid soil environments as reported in part A of the present paper - see Welcker 1998 -, and third, when analysing the diallel of maize populations as developed in part C of the present report - see Welcker 1999 and Welcker 2000 -. Interactions between plant and soil were studied at different integrative levels: the crop, the plant, the roots and at different stages. Maize germplasm was evaluated in Guadeloupe on both acidic and limed soils i.e. stressed and non-stressed environments.

B. 3 Results

B.3.1 Acid stress main effects on plant growth and development

In every trials, the plants yielded about two times lower, silked later (6 days), were about one half shorter in acid soil plots than in non-acid soil plots (Welcker 1998, 1999, 2000). These results agreed with those reported by Granados et al (1993), Duque- Vargas et al (1994), Pandey *et al* (1994), Welcker (1996) and Salazar et al (1997).

Stress effects could be seen from young stage, reducing dramatically plant vigor, leading sometimes to plant death and resulting in poor crop density and in heterogeneous canopy hardly compensated by individual plant production adjustments (Welcker, 1998). For the trial sown in 2000, leaf area was reduced of a half and photosynthetic rate reduced of 20 %. Moreover delaying of flowering and lengthening of the life cycle may contribute to reducing plant fertility and ear quality. Consequently, they did not only decrease yield but also nutritive value and quality of the seeds, reducing the chance to observe good plant emergence of the following generation seeds in farmers' fields.

Grain yield in acid soil environment showed highly significant negative correlations with silking (-0,51**,-0.78**, -0,82** in 1998, 1999 and 2000 respectively), with Anthesis to Silking Interval-ASI (-0,65** in 1999 and -0.66** in 2000) and positive correlations with plant vigor at young stage (0.81% in 2000), with plant height (0,65** in 1999, 0.71** in 2000), with ears per plant (0,50**, 0,74**, 0.74**) and with ears aspect (0.79% in 2000).

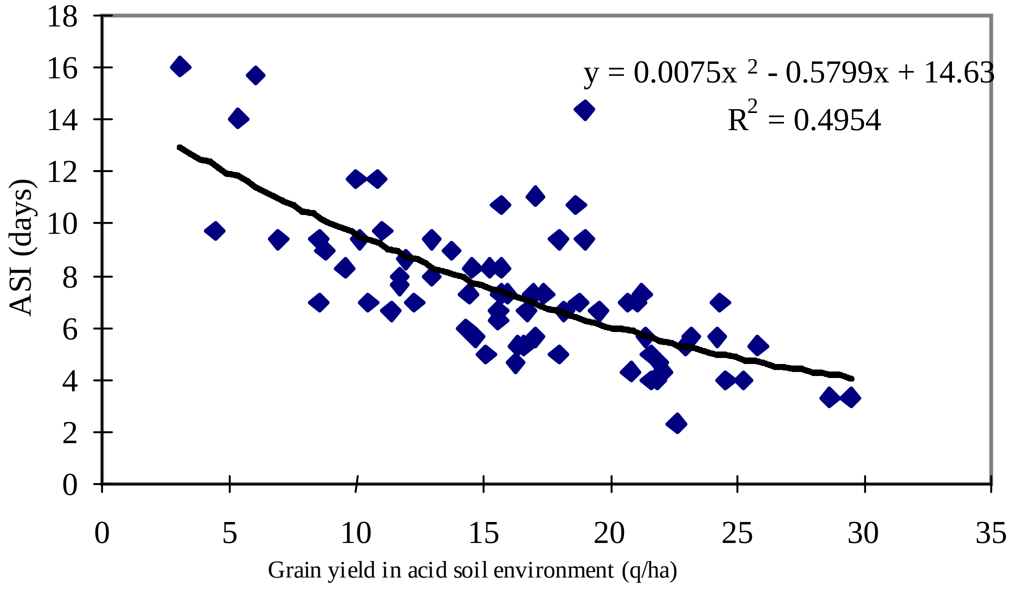


Fig 3: Description of relationships between grain yield and ASI for 11 maize populations, their crosses and hybrid checks crosses and 6 hybrids evaluated in Guadeloupe, 1999.

These relationships were consistent with those reported by Granados *et al* (1993), Duque-Vargas *et al* (1994), Welcker (1996) and Salazar *et al* (1997). ASI and ears per plant observed in acid soil environment appeared strongly related to yield under stress. In Figures 3 and 4 variations for ASI and ear per plant in acid soil environment appear predictive of variation for

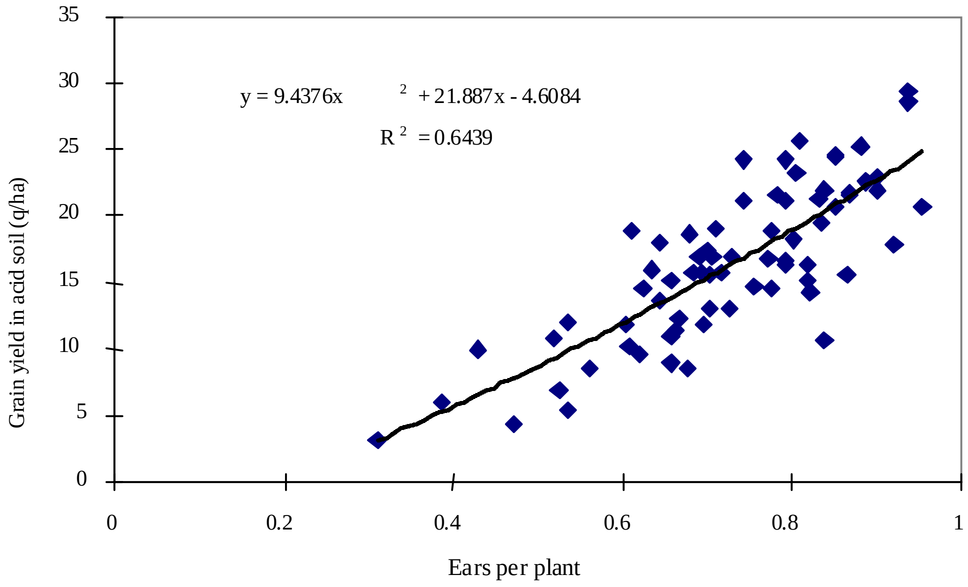


Fig 4: description of relationships between grain yield and ear per plant for 11 maize populations, their crosses and cheks evaluated in acid soil environment in Guadeloupe, 1999.

grain yield in acid soil environment. Those two traits are strongly related to yield under stress including drought, soil low in N and P, excess moisture, iron deficiency and low soil pH (Vasal *et al*, 1996). Moreover heritability of these secondary traits were often higher than heritability of grain yield, the complex trait to be predicted (Welcker 1999, 2000). They should constitute useful selection criteria for adaptation of maize to soil acidity. Nevertheless, earlier adaptation traits specifically related to acidity stress components such as Al toxicity, P availability, should be identified.

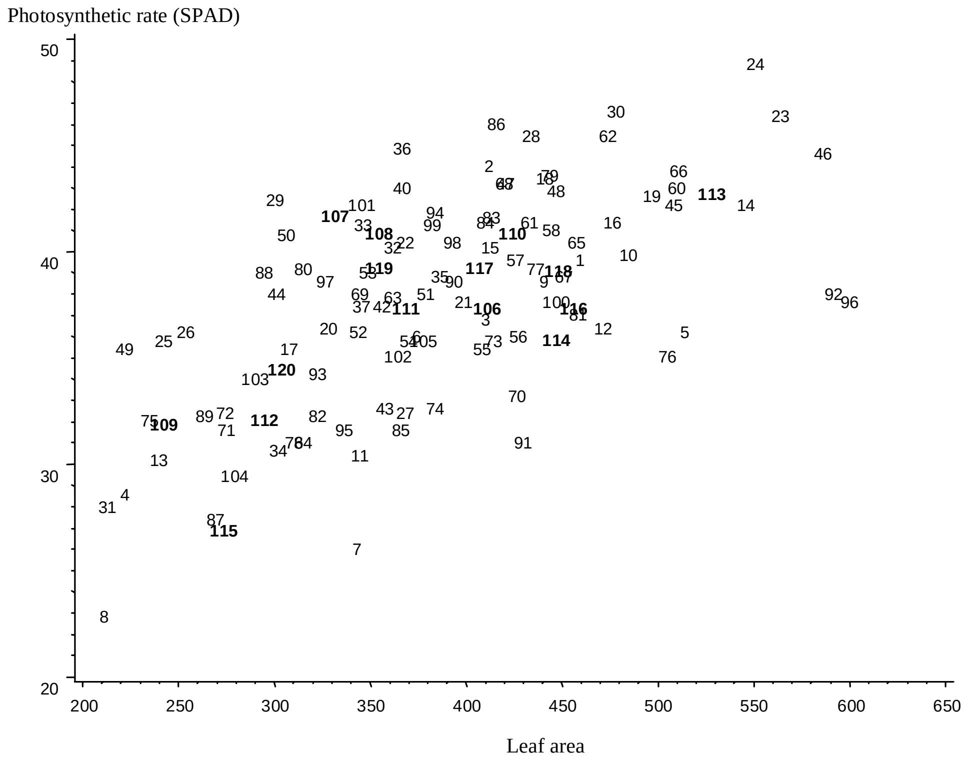


Figure 5: Relation between leaf area and photosynthetic rate for 15 maize populations and their 105 crosses evaluated in acid soil of Guadeloupe in 2000

Plant vigor at young stage reflected the first visible response of the plant to stress. Distribution of plant vigor showed a consistent classification of the parents of the diallel and a continuous variation between the crosses with a high heritability (0.75) (Welcker, 2000). This trait is easy to observe and consistent with detailed observations of seedlings of contrasted genotypes for adaptation to soil acidity, done in 1997 (Welcker *et al*, 1997). It should be used extensively in screening for adaptation to acid soils.

Grain yield in acid soil environment also showed highly significant positive correlations with leaf area (0.75**) and photosynthetic rate (0.78**). These criteria could be used with the usual ones to characterize genotypic responses and to situate stress events and effects. Relationships between these two criteria showed that the best performances for yield in acid soil environment were often realized by genotypes which associated high photosynthetic rate and high leaf area or at least, high level of one of them (Fig. 5).

B 3.2 Root system responses to acid stress

Numerous descriptions of root growth and architecture have been done during the project years in Guadeloupe. Among root parameters, the seminal root length measured at 4 leaves stage appeared to be the most sensitive trait (Welcker, 1997), Al toxicity inducing inhibition of root elongation as shown by Horst in laboratory screenings. However, this measurement is destructive and time consuming when performed in the field. Measurement in rhyzotron allowed us to distinguish some genotypic responses to acidity for root growth and root colonization of the substrat (Lorenz, 2000). Nevertheless, breeding program optimization is still mainly dependent on the possibility to easily characterize the ability of the plant root system to colonize the soil layers in field conditions. Root electrical capacitance has been shown as good predictor of the root size of maize by Chloupeck (1972). Root electrical capacitance measured at flowering time within the trial sown in 2000 appeared highly affected by soil acidity (-70%). This non-destructive method permitted us also to observe differences between contrasted genotypes such as for one susceptible (1.45) and for one tolerant (2.88), corresponding to a root mass for the tolerant genotype four times larger than for the susceptible one. However, an in depth evaluation of this parameter as suitable indicator for genotypic grain yielding capacity on acid soil is still worth. Dr Ozier-Lafontaine (INRA-APC) and us will keep on with such investigations in Guadeloupe during the next INCO project.

Previous results clearly indicated that the induction of callose formation in the root tips by Al can be used as a sensitive indicator of genotypic Al sensitivity (Horst *et al*, 1997). Data collected on one sample of the diallel showed a consistent classification of the parents and an interesting relation between *per se* and combining ability values for this trait; SA4 showed the most favorable GCA effect when CMS9213 whereas TUXP the most undesirable one. However, digitonine induced callose formation appeared higher heritable (0.42) than Al (0.17) at this step of the study. Furthermore yield in acid soil of Guadeloupe (2000) was rather well related to Al induced callose formation (Fig. 6). These results will be confirmed during the next INCO project by screening of the complete diallel mating design in nutrient solutions for Al tolerance and P efficiency.

Classification of maize populations and hybrids evaluated in acid soil environments the INCO network appeared consistent with clusters derived from staining with hematoxilyn (Barcelo, 1997, 1999, Welcker,1997, 2000). This technic should help the breeders to screen large germplasm collections for Al tolerance.

As a conclusion, genetic analysis of these adaptation traits will be pursued within the next INCO project. In any case, our results clearly indicated that selection of adapted maize genotypes is possible using root and shoot growth and development phenotypic characteristics.

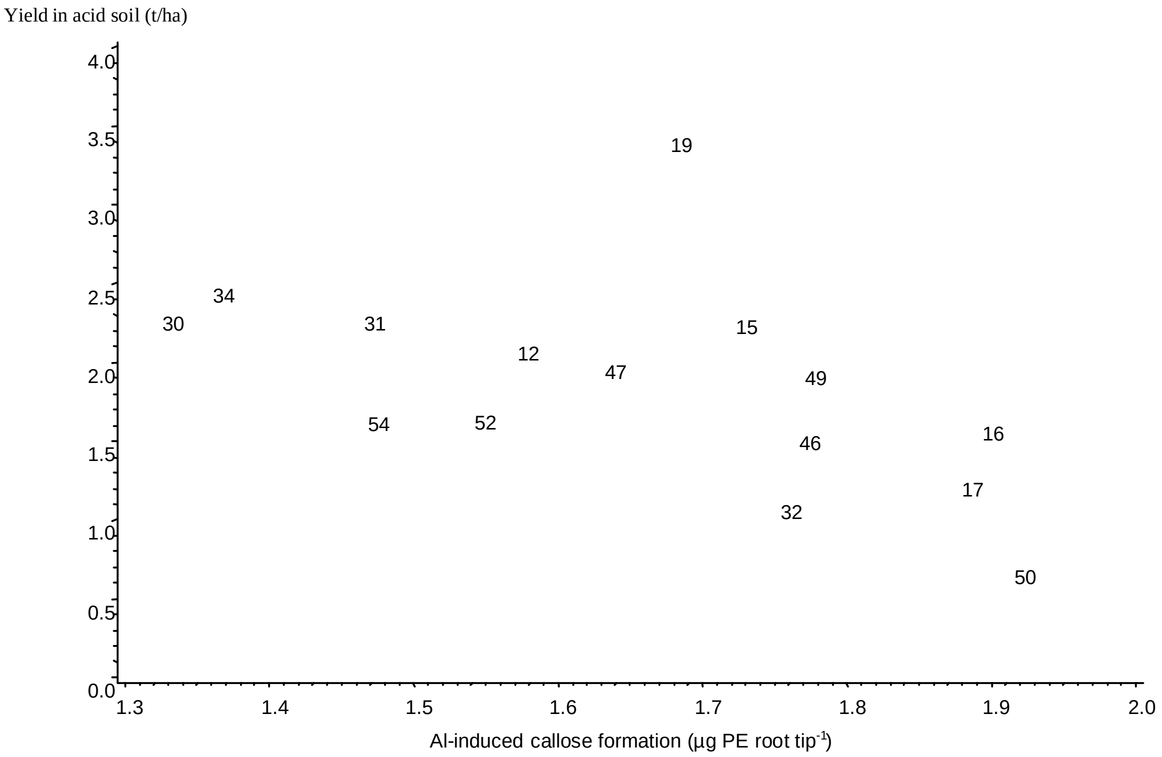


Fig 6: Relation between Al-induced callose formation and yield in acid soil of Guadeloupe for the F1 of a partial maize diallel

C Combining ability in tropical maize for adaptation to acid soils and breeding strategy for stress tolerance

C 1 Introduction

Genetic variation for adaptation of maize to acid soils has been clearly reported. Both qualitative and quantitative inheritance have been reported. Significant genetic progress has been achieved in developing acid tolerant germplasm these last decades. Recurrent selection has been effective in improving maize for yield in acid soil environments. Besides several populations were selected by the breeders from Brazil, Columbia, Cameroon and Guadeloupe in their respective environments. Although gain for yield or specific plant characters of adaptation clearly appeared, identification of stable genotypes were not extensive. More information on the breeding value of the available tolerant source germplasms and on the genetic of the adaptation to soil acidity would help the breeders to choose appropriated plant materials and efficient methods for their breeding program. Moreover selection based on performances evaluated across a range of acid soil environments would lead to broader adaptation of the selected germplasm.

We mainly report here results of the diallel trials conducted in Guadeloupe during the main growing season of 1999 and 2000 compared with some results getting from a first regrouping of data collected over the network.

1. C 2 Materials and methods

In a joint breeding effort within INCO project, eleven tropical maize populations from different genetic origins and covering a wide range of acid-soil adaptation abilities were

crossed. The diallel was evaluated in Guadeloupe and Cameroon acid and non acid soil environments in 1999.
The working group proposed to use extensively this original genetic mating design in order i) to complete the study of the genetic of adaptation and ii) to verify effectiveness of using secondary traits in breeding for yield in acid soil environments and the relative importance of specific adaptation factors to stress components. Therefore new crosses were made in Cameroon, source germplasms from Brazil and Guadeloupe were added, new set of trials were prepared in Guadeloupe for multilocal evaluation. The diallel trials were sown in Guadeloupe (INRA), Cameroon (IRAD) and Columbia (CIMMYT and CORPOICA) in April 2000. Two sets were sent to Brazil in September 2000 for sowing this current growing season both in Al toxic and P deficient acid soils. The diallel was partly tested at the University of Hanover and will be sent to University of Barcelona and again to Hanover for new lab screenings.
Diallel crosses were made among the fifteen populations by plant to plant crossing in Cameroon during winter season of 1998 and 1999 (Tab. 5). 110 F (11*10) following by 210 F1 (15*14) populations were generated. Seeds from ears resulting from reciprocal crosses were bulked to represent each cross because of lack of significant reciprocal effects (Salazar *et al* 1997) - see Welcker C.,1999 and Welcker C., 2000 for complete description of the tested materials, the experimental designs, cultivation practices, the observed parameters and the statistical procedures and genetic models.

Genotype	Code	Color	Origin	Characteristics
Parents:				
ATP.S4.Syn.Y	ATPY	Y	IRAD, Cameroun	Al tolerant
Tuxpeño Sequía	TUXP	W	CIMMYT, Columbia/Mexique	Acid soil susceptible
96SA7	SA7	W	CIMMYT, Columbia	Acid soil tolerant
96SA6	SA6	W	CIMMYT, Columbia	Acid soil tolerant
96SA4	SA4	Y	CIMMYT, Columbia	Acid soil tolerant
96SA3	SA3	Y	CIMMYT, Columbia	Acid soil tolerant
BR106	BR 106	Y	EMBRAPA, Brasil	Acid soil susceptible
Spectral	SPEC	W-Y-R	INRA, Guadeloupe	Acid soil moderately tolerant
Kristal27	KRIS	Y	INRA, Guadeloupe	Acid soil susceptible
CMS9213	CMS92	W	IRAD, Cameroun	Acid soil susceptible
ATP.Syn.I.W	ATPW	W	IRAD, Cameroun	Al tolerant
CMS36*	CMS36	Y	EMBRAPA, Brasil	Al tolerant
CMS14C*	CMS14C	Y	EMBRAPA, Brasil	Al tolerant
Antigua Gpo2*	ANTIG	Y	CIMMYT, Mexique	unknown
Natal*	NAT	Y	INRA, Guadeloupe	Acid soil susceptible
Checks:				(- : inefficient)
PX304C	PXC	Y	INRA, Guadeloupe	Acid soil moderately tolerant
HS64x1143	HS64	Y	EMBRAPA, Brasil	Al, P tolerant
HS11x723	HS11	Y	EMBRAPA, Brasil	Al, P-, N susceptible
CLA20xCLA24	CLA	Y	CIMMYT, Columbia	Acid soil tolerant (SA3xSA4)
CLA16x(LASP2xLASP3)	H3V	Y	CIMMYT, Columbia	Acid soil tolerant (SA3xhybSA5)
87036x88094	HYBC	W	IRAD, Cameroun	Acid soil susceptible

Tab 5: Germplasm description of the maize populations used in the diallel study and of the hybrids used as chek in trial in Guadeloupe in 1999 (except *) and 2000.

C 3 Results

C 3.1 Performances of the parental populations in Guadeloupe and characterization of tolerant source germplasm

The first set of materials was sown in Guadeloupe (La Providence – Basse-Terre, Guadeloupe; 16°17’ N, 61°43’ W, 252mas) in 1999 on two contrasted plots (Welcker, 1999).

Genotype	Grain yield Acid soil	Yield losses (%)	Ears aspect Acid soil	Ears per plant Acid soil	Silking Acid soil	ASI Acid soil	Plant height Acid soil
SA7	2.18	44.5	3.2	0.87	70.3	4	106.4
SA3	1.67	53.7	3.3	0.77	79.3	6.7	96.3
SA4	1.7	54.7	3.3	0.73	79.3	5.7	97.4
SA6	2.26	57.7	3.2	0.89	74.7	2.3	97.9
KRIS	1.3	67.7	3.6	0.73	80.7	8	104.5
ATPW	1.08	73.8	3.5	0.52	92.7	11.7	105.5
SPEC	0.88	80.6	4.4	0.66	80	9	88.5
ATPY	0.44	82.1	4.8	0.47	95	9.7	97.8
TUXP	0.69	87.3	4.7	0.52	89.7	9.3	75.8
CMS	0.31	92.3	4.9	0.31	99	16	99
Means A	1.25	69.4	3.9	0.65	84.07	8.2	96.91
Means NA	4.45	.	2.5	0.93	65.6	2	174.6

Tab 6: Means for grain yield (t/ha), yield losses (%), ears quality (1=good to 5=bad), ears per plant, silking (days), ASI (days) and plant height (cm) of parental populations and hybrid checks evaluated in acid soil in Guadeloupe during 1999.

The second set *i.e.* 15 parental populations, their 105 crosses and 6 hybrid checks, was sown in Guadeloupe (same site) on two main plots with different levels of acidity. As characterized in collaboration with agronomists from INRA (Montpellier and Guadeloupe) and CIRAD (Montpellier), the plots appeared contrasted for water pH (5.5 for non-acid soil or liming soil *vs* 4.6 for the native acid soil) and therefore for Al saturation (3% *vs* 61%) and P deficiency (P is highly fixed in this soil and available P is always less than 15 ppm).

Maize parental populations ranged from 0.31 to 2.26 t/ha for yield in acid soil environment in 1999 (Tab. 6) and from 0.78 to 3.22 t/ha, in 2000 (Tab. 7). Grain yield losses from non-acid to acid soil environments varied from 92% to 44% in 1999 and from 39 to 80% in 2000.

Genotype	Grain yield Acid soil	Yield losses (%)	Ears aspect Acid soil	Ears per plant Acid soil	Silking Acid soil	ASI Acid soil	Plant height Acid soil
SA4	3.22	39.61	3	0.95	67.0	5	115
SA3	2.79	49.21	3.3	0.91	70	6	105
SA7	2.44	54.01	4	0.98	65	4	96
KRIS	2.34	58.85	3.6	0.86	77	8	110
SPEC	2.16	47.81	3.8	0.92	76	10	94
ATPW	1.98	54.78	4.2	0.84	80	9	114
TUXP	1.81	49.11	3.7	0.93	79	7	85
NAT	1.78	66.94	4	0.75	79	9	86
ATPY	1.75	51.82	4	0.76	78	9	117
CMS14C	1.70	39.36	4.2	0.83	79	9	115
CMS36	1.53	64.68	3.5	1.03	75	7	130
SA6	1.29	75.69	4.3	0.93	79	8	80
CMS92	1.09	42.17	5.2	0.71	89	13	81
BR 106	0.82	80.01	4.8	0.77	84	10	74
ANTIG	0.78	61.99	5	0.74	84	12	75
Means A	1.83	55.74	4	0.86	77	8	98
Means NA	4.23	.	3.2	1.06	65	3	184

Tab 7: Means for grain yield (t/ha), yield losses (%), ears aspect (1=good to 5=bad), ears per plant, silking (days), ASI (days), plant height (cm) and plant vigor of parental populations evaluated in acid soil in Guadeloupe during 2000

The tolerant maize populations averaged greater yield in acid soil environment than the unselected populations revealing effective progress in breeding for adaptation of maize to acid soil of the tropics.

Among the tolerant populations, 96SA6 and 96SA4 out-yielded all other populations in 1999 and 2000 respectively and showed the lowest yield losses from non-acid to acid soil environments. Within the tolerant CIMMYT populations, 96SA7 was the earliest over the two years. Globally, the tolerant source germplasms from CIMMYT had the highest number of ears per plant and the lowest ASI (Tables 6 & 7). Fewer number of days to silk for these tolerant genotypes is probably not due to their early maturity *per se* but because their tolerance to soil acidity permits them to flower and complete their life cycle earlier than susceptible early populations (Salazar *et al*, 1997).

The lowest yield measured in acid soil environment concerned the acid susceptible parent, CMS9213 (CMS) as well as two unknown populations largely used in breeding in lowland tropics, BR106 and ANTIGUA, (Tab. 7). Population CMS showed the lowest vigor at young stage, flowered extremely late, had the lowest number of ears per plant and the highest ASI in acid soil environment confirming previous observations. Population TUXP expressed medium performances in 2000 as compared to the ones from 1999. However, its vigor and plant height in acid soil environments remained within the lowest ones. Populations Spectral (SPEC) and ATP Syn S4 Y (ATPY) showed better performances in 2000 than in 1999.

Within the populations from Cameroon, the tolerant population ATPW appeared the most adapted to guadeloupean acid soil environments. However ATPY known as tolerant to Al toxic soils showed a better plant vigor at young stage.

Population CMS36 from Brazil showed very interesting adaptation traits such as plant vigor, plant height even if it yielded less than expected. Moreover even if it flowered quite late in Guadeloupe, its flowering was not delayed in stress conditions as susceptible late populations.

The studied germplasm covered a wide spectrum of plant adaptation traits to soil acidity complex.

C 3.2 Performances of the crosses in Guadeloupe, heterosis and combining ability

Crosses ranged from 0.85 to 2.94 t/ha for yield in acid soil environment in 1999 and from 0.50 to 4.19 t/ha in 2000 when yield losses varied from 84% to 37% and from 91% to 24% respectively. Crosses had significantly greater mean yield in acid soil environment than the parental populations (1.72 vs 1.34t/ha in 1999, 2.2 *vs* 1.7 t/ha in 2000) indicating significant heterosis.

The crosses between tolerant populations tended to yield higher in acid soil environment than those between tolerant and susceptible populations and those between susceptible populations (Welcker 1999, 2000). More than the third of the crosses out-yielded the tolerant parent SA7. The best cross out-yielded the best parent from about 30% (Welcker, 2000). Moreover, some of the tolerant crosses showed also good performances in non-acid soil environment.

During the year 2000, crosses did not flower earlier than their parents but their flowering were much more concentrated allowing a better fertilization. They were more vigorous at young stage and were higher about 10%. They formed longer and more filled ears with the same number of rows but with kernels rather larger (+7%). That reveals heterosis for most of the traits, particularly high for yield in acid soil environment (+ 37%). Heterosis has been reported by several authors (Pandey *et al*, 1994, Borrero *et al*, 1995, Salazar *et al,* 1997, Welcker, 1999). 'Hybrid' vigor, increase in size or rate of growth of crosses over parents should certainly contribute to enhance plant capacity to tolerate stress.

However, under a quantitative viewpoint, heterosis may occur whenever there is genetic divergence between parents and some level of dominance controlling the traits (differences in alleles distribution frequencies). That would be obviously the case within this tested germplasm including improved varieties and based populations from different genetic origin.

The highest-yielding crosses, SA7xSA6 (1999) and SA4xSA3 (2000) involved heterotic tolerant populations as developed by CIMMYT (Pandey *et al*, 1994). The tolerant source populations the most often present in the good combinations for yield were firstly from CIMMYT origin (Columbia): SA4, SA3, SA7, secondly from Brazil (EMBRAPA): CMS36 and then from Cameroon (IRAD): ATPW. However as for SA6, Kristal (KRIS) from Guadeloupe provided very good F1 progenies in 1999. Introduction of new genetic variability within the diallel mating design of the year 2000 reveals several promising combinations for adaptation of maize to soil acidity. Thus the best crosses combined the parental populations SA7 and CMS36, yielding 4.19 t/ha in acid soil environment. It out-yielded for about 22% the best experimental single hybrid still selected at CIMMYT and evaluated in Guadeloupe. Six other crosses expressed also better yield than this check. Crosses involving the parental population CMS36 from Brazil generally exhibited relatively high heterosis in 2000 whereas that was the case with SA7 in 1999.

The cross ATPY by ATPW appeared within the ten best combinations in 2000. It involved two populations segregated from ATP-SR pool for kernels color and uses (The, personal com.). The high performance of this cross could argue for difference in allele distribution frequencies for the target trait between the two breeding populations.

The significant increase of the potential yield in acid soil environment measured in 2000 trial compared to 1999 might be due both to original combinations derived from the studied material and to better management of the fertility of the plots by small application of phosphorus at sowing. In any case, results demonstrated that original combinations of favorable alleles occurred and new progress should be expected in breeding within the studied source germplasm.

Source	**df**	**Yield**	**Ears aspect**	**Prolificacy**	**Silking**	**ASI**	**Plt height**	**Plant vigor**
Replications	1	0.002^{ns}	10.43^{***}	0.0203^{ns}	36.2^{*}	17.9^{ns}	2.20^{ns}	0.504^{ns}
Genotypes	101	1.208^{**}	0.501^{**}	0.0182^{*}	50.2^{***}	16.2^{***}	399.1^{***}	2.073^{**}
AGC	14	2.306^{**}	0.441^{ns}	0.0529^{**}	0^{ns}	20.0^{**}	352.3^{ns}	2.678^{**}
ASC	87	1.032^{*}	0.511^{*}	0.0126^{ns}	63.5^{**}	15.6^{**}	406.6^{*}	1.975^{**}
Error	101	0.687	0.314	0.0129	21.3	7.5	212.9	1.186
Model	102	1.209^{**}	0.609^{***}	0.0181^{*}	50.7^{***}	16.2^{***}	392.6^{***}	2.117^{**}

Tab 8: Means squares for yield, ear aspect, prolificacy, silking, plant height and plant vigor for 105 (diallel with 15 parental populations) evaluated in acid soil of Guadeloupe 2000.

In 2000, general combining ability (GCA) mean squares were significant for all traits excepted for ear aspect and silking when specific combining ability (SCA) mean squares were significant for all traits excepted for prolificacy (Tab. 8). General combining ability (GCA) accounted for 27% of the total sum of squares among crosses for yield, 32% for ear size, 40% for prolificacy, 18% for plant vigor at young stage and 17% for ASI. Those values differed from those of Duque-Vargas *et al* (1994) and Pandey *et al* (1994) and were quite similar to those of Borrero *et al* (1995) and Salazar *et al* (1997) and those obtained in 1999 by Welcker. Thus, heterosis for yield appeared primarily due to dominance gene effects and may be partially explained by high genetic distance between the populations included in the design. However these results demonstrate importance of both additive and non-additive gene effects for yield and yield components in acid soil environment Thus performances of hybrids could be partially predicted on the basis of GCA effects of the parents *i.e.* parents with high GCA effects provide high-yielding crosses.

Population SA7 showed the highest general combining ability for yield in acid soil environment over the two years (Fig. 7). GCA effects for yield were also high or positive for CMS36, SA3 and SA4 even if they were not stable from year to year. At the opposite, population CMS9213 showed significant undesirable GCA effects for all traits. KRIS had

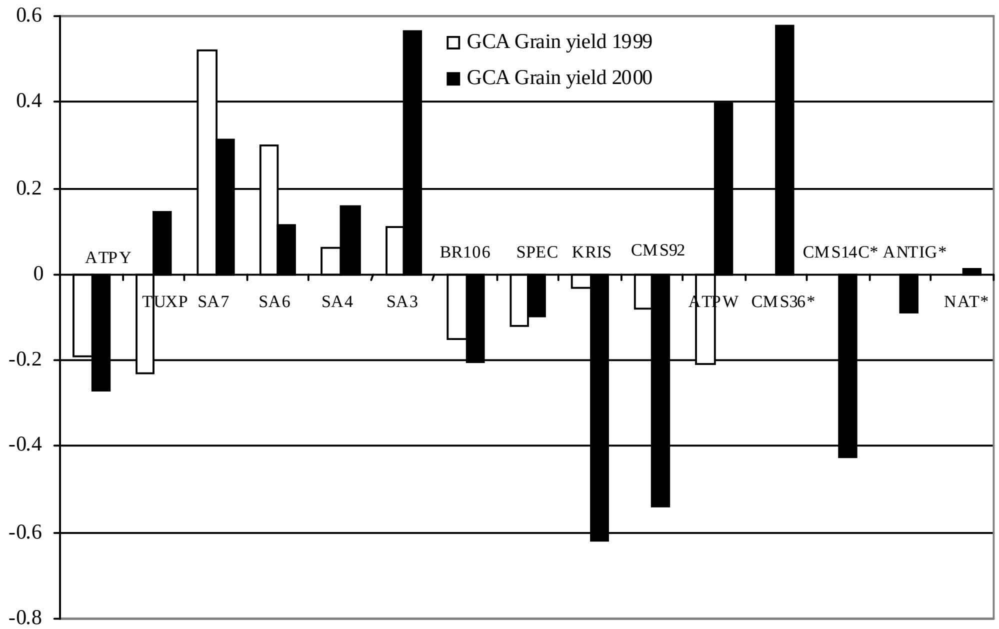


Figure 7: Estimates of general combining abilities of the eleven maize populations evaluated in the diallel crosses in Guadeloupe in 1999 (exept *) and in 2000.

significant desirable effects for secondary traits in 1999 as for SA3 and SA4 when it showed undesirable GCA effects for all traits in 2000. However KRIS expressed the highest combining ability for potential yield mesured on limed soil. ATW showed significant undesirable GCA effects for all traits in 1999 whereas it showed high positive combining ability for yield on acid soil in 2000. These results underlined the interest to estimate GCA by environments interaction effects before to define a breeding strategy. GCA effects for days to silk, silking duration and ASI were generally negative for the tolerant parents and positive for the most susceptible ones. However the susceptible populations SPEC and TUXP showed rather positive GCA effects for these traits when the tolerant parents SA6 and ATPY showed rather negative effects.

The tolerant populations from Cameroon ATPY and ATPW even if quite similar for *per se* performances were highly different for combining abilities (Tab. 6, 7). In 2000, ATPW showed favorable effects for plant vigor, earliness, silking duration and yield in acid soil environment.

C 3.3 Across acid locations analysis of the diallel

Across locations analysis based on available data from Guadeloupe (1999 and 2000), Cameroun (1999, at Ebolowa and N'Kolbisson) and Columbia (2000, Matazul) showed

Source	df	Plant height	Silking	ASI	Prolificacy	Yield
Environment (E)	8	447572 ***	8582.6 ***	960.9 ***	2.84 ***	715 ***
Replications/E	16	13082 ***	238.3 ***	36.6 ***	0.10 ***	27 ***
Genotypes (G)	65	1920 ***	112.5 ***	15.7 ***	0.06 ***	5.6 ***
G*E	520	407 **	27.8 **	5.5 ***	0.03 ***	2.2 ***
Error	1039	348	21.6	3.4	0.02	1.4
Model	609	6789 ***	154.3 ***	19.8 ***	0.07 ***	12.7 ***

Table 9: Mean squares for plant height, silking ASI, prolificacy, and yield for eleven populations of maize and their 55 crosses evaluated in nine non-acid and acid environments during 1999 and 2000

highly significant effects for environments, genotypes and environment by genotype interaction for all traits (Tab. 9). Plant yielded to times lower (2.9 t/ha *vs* 5.6 t/ha), silked later (70 *vs* 63 days) and were shorter (140 *vs* 205 cm) in acid soil environments than in non-acid soil environments, respectively (Tab. 10). Based on mean genotypic performances, the experimental sites were classified as stressing or non-stressing environments for further analysis (Tab. 10).

location	Plant height	Silking	ASI	Prolificacy	Yield	Environment
nkNA99	207	63.0	2.82	1.09	5.49	normal
nkA99	212	61.9	2.71	1.08	6.82	normal
guNA00	200	63.8	2.26	0.99	5.38	normal
ebNA99	247	62.2	2.72	1.06	5.33	normal
guNA99	181	66.2	1.91	0.94	4.92	normal
mtz00	133	63.7	1.59	0.89	2.18	stressed
guA00	105	78.2	8.38	0.86	2.16	stressed
ebA99	167	68.8	3.79	1.04	2.01	stressed
guA99	104	80.4	7.26	0.73	1.66	stressed

Table 10: Means for plant height (cm), silking (days), ASI (days), prolificacy and grain yield (t/ha) for eleven populations of maize and their 55 crosses evaluated in nine environments during 1999 and 2000

Highly significant differences occurred among the parents (not communicated) and the F1 crosses evaluated across stressing environments for all traits (Tab.11). Environments and genotype by environment interaction effects were also significant indicating pertinence of the network.

Source	df	Plant height	Silking	ASI	Prolificacy	Yield
Environment (E)	3	137229 ***	9891.4 ***	1391.8 ***	2.69 ***	10.5 ***
Replications/E	7	3686 ***	107.4 **	52.9 ***	0.04 **	9.53 ***
Genotypes (G)	54	728 ***	102.1 ***	14.7 ***	0.03 **	4.41 **
G*E	162	282 *	44.9 **	9.6 ***	0.02 *	0.96 **
Error	378	238	33.3	5.56	0.02	0.63
Model	226	2316 ***	190.4 ***	29.9 ***	0.06 ***	1.44 ***

Table 11: Mean sqares for plant height (cm), silking (days), ASI (days), prolificacy and grain yield (t/ha) for 55 crosses evaluated in four acid soil environments during 1999 and 2000 (guA99, ebA00,guA00, mtz00)

Crosses ranged from 0.84 to 2.92 t/ha for yield in acid soil environments. Twenty five crosses out-yielded the best tolerant population SA4 (2.1 t/ha) and were issued from tolerant by tolerant or tolerant by susceptible as well and same times from susceptible by susceptible *i.e.* TUXPxSPEC and BR106xSPEC. The ten percent best crosses out-yielded this parent from about 35 %. These best crosses involved SA7, SA4, SA3 from CIMMYT, ATW from Cameroon and KRIS from Guadeloupe. These results confirmed that heterosis was playing a major role for acid soil tolerance.

The best combiners for grain yield on acid soils were SA7, SA4, SA3 and ATP-W maize populations. Within these populations, SA7 provided the most stable and positive GCA effects for yield across locations, whereas TUXP, KRIS and SA3 showed high GCA by location interaction effects for yield (Fig. 8).

Results assessed genetic progress for adaptation to soil acidity and permitted us to identify traits of interest within the parental populations. Heterosis appeared higher than expected. Both additive and non-additive gene actions with predominance of non-additive effects were

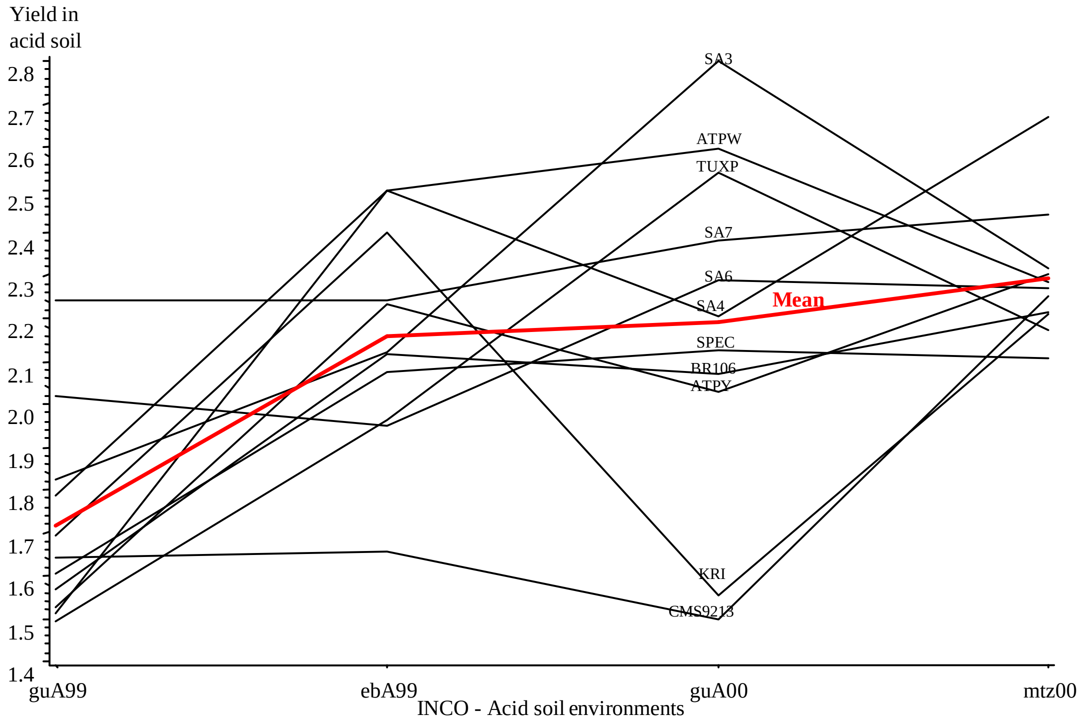


Figure 8: Mean yields of the F1 progenies of each parental population evaluated in four acid soil environments during 1999.

observed, suggesting to develop heterotic pools as starting point of a common breeding methodology (The and Welcker, 3rd progress reports, 1999 and oral communication at Yaounde in July 2000). These pools should included the tolerant populations SA7, SA4, SA3 from CIMMYT, ATP-W from Cameroun and CMS36 from Brasil and, depending on breeding and agronomical targets, KRIS from Guadeloupe or TUXP from CIMMYT. The development and improvement of original heterotic pools within the next INCO project has been discussed at Yaoundé on August 2000. A common breeding methodology could be define since the diallel analysis is achieved.

Conclusions

Our results clearly show that effective progress has been achieved in breeding for tolerance to soil acidity the last decades and that differents combinations of adaptation traits lead to higher yielding in acid soil environments and better tolerance to soil acidity. Progress concerned hybrids and open pollinated populations as well enhancing the chance of appropriation by farmers. Improved materials from CIMMYT (Columbia) appeared to be the most tolerant exhibiting low grain losses under acid soils. This material show more stable grain yields across locations accomplishing its life cycle in the shortest time. Some brasilian materials were classified as P efficient when Cameroun materials appeared more specifically tolerant to Al toxicity as revealed in nutrient solution. These different materials constituted valuable source germplasm for breeding programs. Combination of these different source germplasms i.e. plant adaptation abilities if factors of tolerance could be determined within the next project, could allowed significant genetic progress. In any case, some populations could be immediately released to farmers.

Adaptation to acid soils appears to be based on expression of vigor during young stage allowing the development of an homogenous and efficient crop canopy and on realization of a complete life cycle in a short period allowing the harvest of clean and fulfilled ears. Plant vigor at young stage, plant height, silking, prolificacy constitute easy to measure and heritable traits to be use in breeding for adaptation. Callose formation was confirmed as relevant trait however its genetic parameters will be estimate by screening the completed diallel in nutrient solution. Target criteria of root adaptation should be considered more extensively by the breeders. The use of root electrical capacitance to assess the root system appears promising; thus characterization of rooting patterns of maize genotypes in field conditions will be pursuit within the next inco project and compared with shoot characteristics correlated responses.

Diallel analysis helps breeders to determine heterotic patterns among their populations and choose appropriate materials and methods for their breeding program. Importance of both additive and non-additive gene effects for yield and secondary traits and high heterosis value suggested that reciprocal recurrent selection would be effective for development of superior open-pollinated populations and hybrids for acid soils. Heterosis observed between tolerant populations should convinced the breeders to exploit this complementarity in a common breeding program. Based on specific adaptation traits provided by some tolerant source populations, the GCA effects of the populations and heterosis, recurrent selection that exploits both GCA and SCA effects would include, for sustainable improvement, the white populations SA7, ATPW, SA6 and TUXP and the yellow populations SA3, ATPY, CMS36 and SA4. Moreover, recombinations between these two pools should provide significant progress. From the tolerant populations, however, lines can be extracted and crossed with lines of heterotic populations to produce superior hybrids. These lines should constituted good candidates for mapping genes of adptation to soil acidity. Diallel analysis will be completed by results of current field trials in Brasil and future laboratory screenings at Hannover. Then, we will be able to define a common breeding strategy thanks to a better understanding of genetic of adaptation and combining abilities between the studied source germplasms. Besides, we plan to develop experimental varieties to be released as soon as possible to farmers.

Acknowledgments

The author would like to thank the co-ordinator and partners for the trust they have put in him after it’s initiative for a common breeding approach. He would like to express his sincere appreciation to Charles The for his always relevant remarks, his courage and the interesting and constructive discussions we had friendly. He would like to express his sincere appreciation to partners for they constant and truly support of the work and especially Walter Horst, the coordinator, Carlos de Leon from CIMMYT Columbia and Henry Calba from CIRAD. He is thankful to Luc Chauvin student in agronomy from ESAP-Toulouse, Claudia Lorenz student in biology from the University of Hanover, Benoit L’Hôte and Mehdi Alrifaï students in agronomy from ENSAIA-Nancy and to colleagues from INRA Guadeloupe, especially Raymond Bonhomme, Yves-Marie Cabidoche, Maurice Clairon, Harry Ozier-Lafontaine (INRA-Agronomy) and J. Félicité, Jean-Pierre Cinna, Pierre Renac, Olivier Loudet, Benoit Defrenne (INRA-Plant Breeding) for their scientific and technical contributions.

References

Bahia Filho A.F.C., Magnavaca R., Schaffer R.E., Alves V.M., 1997. Identification, utlization, and economic impact of maize germplasm tolerant to low levels of phosphorus and toxic levels of exchangeable aluminium in Brazilian soils, in Plant-Soil Interactions at low pH. Brazilian Soil Science Society, pp 59-70.

Borrero J.C., S. Pandey, H. Ceballos, R. Magnavaca, A.F.C. Bahia-Fihlo, 1995: Genetic variances for tolerance to soil acidity in a tropical maize population; Maydica 40: 283-288

Cabidoche Y.M., C. Feller, P. Larque, O. Sobesky, 1987: Sur un double mécanisme d'acidification des sols sous l'influence de cendres volcaniques récentes. Le cas de la Soufrière de Guadeloupe après les éruptions de 1976-1977, C.R. Acad. Sc. Paris, 304 II (15): 935-93

Ceballos H., Pandey S., Narro L., Perez-Velazquez J.C., 1998. Additive, dominant, and epistatic effects for maize grain yield in acid and non-acid soils. Theor Appl Genet 96, pp 662-668.

Duque-Vargas J., S. Pandey, G. Granados, H. Ceballos, E. Knapp, 1994: Inheritance of tolerance to soil acidity intropical maize; Crop Sci. 34: 50-54

Edmeades G.E., J.A. Deutsch, 1994: Stress tolerance breeding: maize that resists insects, drought, low nitrogen, and acid soils, Mexico, DF; CIMMYT:21-92

Granados G.,S. Pandey, H. Ceballos, 1993: Response to selection for tolerance to acid soils in a tropical maize population; Crop Sci. 33: 936-940

Horst W.J., A.-K. Püschel, N. Schmohl, 1997: Induction of callose formation is a sensitive marker for genotypic aluminium sensitivity in maize; Plant and Soil 192: 23-30

Magnavaca R., C.O. Gardner, R.B. Clark, 1987: Inheritance of aluminium tolerance in maize; H.W. Gabelman and B.C. Loughman (ed) Genetic aspects of plant mineral nutrition Martinus Nijhoff Publ., Dordrecht, the Netherlands: 201-212

Parentoni S.N., Bahia Filho A.F.C, Gama E.E.G., Lopez M.A. Guimares P.E.O., Santos M.X., 1996. Diallel analysis in acid fertile doil of maize inbred lines differing in their levels of aluminium tolerance and phosphorus efficeincy, in maize; IV Internat. Symp. on Plant - Soil Interactions at low pH, march 17-24, 1996, Belo Horizonte, Minas Gerais, Brasil

Pandey S., H. Ceballos, R. Magnavaca, A.F.C. Bahia-Filho, J. Duque-Vargas, L.E. Vinasco, 1994: Genetics of tolerance to soil acidity in tropical maize; Crop Sci. 34:1511-1514

Salazar F.S., Pandey S., Narro L., Perez J.C., Ceballos H., Parentoni S.N.et Bahia Filho A.F.C., 1997. Diallel Analisis of acid-soil tolerant and intolerant tropical maize populations. Crop Sci.37, pp 1457-1462.

Sanchez P.A., 1977: Advances in management of Oxisols and Ultisols in tropical South America; K. Kawaguchi (ed) Int. sem. on soil, environment and fertility management in intensive agriculture, Tokyo, Soc. of Soil Sci. and Manure, Japan: 535-566

The C., 1996. Adaptation of maize to acid soils of the tropics, in Final scientific report STD3 n°TS3*-CT92-0071, European Communities Program Life Sciences and Technologies for Developing Countries. pp 1-11

The C., 1999: Fitting maize into cropping systems on acid soils of the tropics, in 3rd Scientific Progress Report INCO-DC-ERBIC 18CT9600063: 17p

Vasal S.K., Cordova H., Beck D.L., and Edmeades G.O., 1996. Choices among Breeding Procedures and Strategies for Developing Stress Tolerant Maize Germplasm, in Developing Drought and low N Tolerant Maize. Proceedings of a symposium, march 25-29,1996, CIMMYT, El Batàn, Mexico.

Welcker C., 1996. Adaptation of maize to acid soils of the tropics, in Final scientific report STD3 n°TS3*-CT92-0071, European Communities Program Life Sciences and Technologies for Developing Countries. pp 1-9

Welcker C., Loudet O., Félicité J., 1997. Fitting maize into cropping systems on acid soils of the tropics, in 1st Scientific Progress Report INCO-DC-ERBIC 18CT9600063: 9p

Welcker C., 1998. Fitting maize into cropping systems on acid soils of the tropics, in 2nd Scientific Progress Report INCO-DC-ERBIC 18CT9600063: 8p

Welcker C., 1999. Fitting maize into cropping systems on acid soils of the tropics, in 3rd Scientific Progress Report INCO-DC-ERBIC 18CT9600063: 14p

Welcker C., 2000. Fitting maize into cropping systems on acid soils of the tropics, in 4th Scientific Progress Report INCO-DC-ERBIC 18CT9600063: 9p

Diploma thesis

Chauvin Luc, 1998 : Evaluation du progrès génétique pour la tolérance du maïs aux sols acides tropicaux, ESA Purpan, France – stage de fin d'étude d'ingénieur en agriculture – INRA Guadeloupe : mai-décembre 1998 (mémoire : 71 pp)

L'Hôte Benoît, 1999 : Analyse de la variabilité génétique pour l'adaptation du maïs aux sols acides tropicaux à partir d'un diallèle de populations, ENSAIA Nancy, France – stage de fin d'étude supérieure, INRA Guadeloupe : mars- septembre 1999 (mémoire : 39pp)

Lorenz Claudia, 2000 : Field and laboratoty screening of maize cultivars for adaptation to an acid-Al-toxic soil in Guadeloupe, University of Dresden, University of Hannover and INRA – Guadeloupe : avril – septembre 1999 (diploma thesis: 71 pp)

Al Rifaï Mehdi, 2000 : Etude de l'intérêt en sélection de populations de maïs source de tolérance à l'acidité à partir d'un plan de croisement diallèle, ENSAIA Nancy, France – stage de fin d'étude supérieure, INRA Guadeloupe : mars- septembre 2000 (mémoire : 57pp)