Gene action controlling stability and adaptability in maize

Guillermo Eyhérabide[1]*, Teresa Boca[2], César López[3]

[1]Estación Experimental Agropecuaria Pergamino, Instituto Nacional de Tecnología Agropecuaria, Pergamino, Buenos Aires, PO 2700, República Argentina
[2]Instituto de Clima y Agua, Instituto Nacional de Tecnología Agropecuaria, Castelar, Buenos Aires, PO 1686, República Argentina
[3]Facultad de Ciencias Agrarias, Universidad Nacional de Lomas de Zamora, Lavallol, Buenos Aires, PO 1836, República Argentina
*Corresponding author: E-mail: eyherabide.guillermo@inta.gob.ar

Abstract

Limited knowledge about the genetic merit of maize landraces contributes to their little use in breeding, although some reports pointed them as a source of useful alleles. Repeated cultivation of landraces for many generations could make them a useful germplasm source to enhance yield stability. This study pretends to determine if such statement holds, and to analyze stability in terms of gene action involved. Twenty Argentine landraces were testcrossed to three US and two Argentine elite lines, and evaluated in 13 environments. Effects of general and specific combining ability for grain yield and ecovalence, as well as for regression coefficients of response to environments were also predicted. Non-additivity resulted more important than additivity for controlling ecovalence, and frequently resulted detrimental to stability. Although landraces contributed to ecovalence, their importance was less than that of lines. Testcrosses´ adaptability to environments was variable depending on the line tester considered. Relative greater importance of lines´ general combining ability for ecovalence than landraces' general combining ability could be attributed to a successful selection for stability during the development of inbred lines. Sixty percent of landraces appeared more adapted to unfavorable environment, which suggests their higher level of rusticity. Argentine lines provided greater stability to their testcrosses than US lines. Correlation between grain yield and stability was mainly dependent upon non additive effects. More productive testcrosses tend to have greater ecovalence (less stability) due to specific combining ability effects. Inbred lines selected for greater general combining ability effect tend to provide their testcrosses higher stability.

Introduction

Regardless the theoretical efficiency of any maize breeding method, it is the amount of genetic variability which determines the maximum genetic gain attainable. Many authors have pointed out the importance of preserving genetic resources to ensure enough available variability when needed (Ulukan, 2011; Gepts, 2006). It has been estimated that barely 4% of the maize races are used by farmers and breeders (Goodman, 1988). There is a consensus among breeders, geneticists and genetic resource experts regarding the great amount of available genetic variability in the species, although many agree that its usage is still very limited. For example, restriction fragment length polymorphism (RFLP) analysis of nearly one hundred US hybrids revealed little evidence of use of exotic germplasm (Smith et al, 1992). Often, the term «exotic» applied to germplasm is interpreted in a broad sense, in such a way that any germplasm source that has not been previously improved or is not adapted to a target region is included in that category. As the maize cultivated gene pool becomes more genetically homogeneous, little can be done to enhance yields by using existing varieties, and then

it may also become even more vulnerable to stress factors. Global climate change and variability including greater frequencies of severe weather events, and eventually variable patterns of geographical distribution, relative importance and severity of weeds, pathogens an insects (Porter and Semenov, 2005), constitute an additional challenge to plant breeding. Then, the gene pool under cropping should be augmented in order to face present and future biotic and abiotic threats, to satisfy demands of grain quality and to sustain a high rate of yield increase in the medium and long term.

There are several reasons to explain the little usage of landraces for breeding new cultivars. Often landraces exhibit poor performance for agronomic traits when compared with elite germplasm, especially when tested in environments other than their normal habitat. In addition, they could contain dominant favorable alleles not present in elite germplasm, but hindered by linkage to undesirable alleles in other loci, or favorable recessive alleles result masked by unfavorable dominant alleles. Although limited knowledge about the genetic merit of landraces contributes to their little use in breeding new cultivars, previous

results suggest that there is a high probability that landraces constitute a source of useful alleles for improving important traits. Genomics will provide in the future an opportunity for identifying the function of genes and establishing a more precise correspondence between each loci and their effects on the expression of specific traits (Sorrells and Wilson, 1997). According to Bernardo (2001), future major contribution of genomics to maize breeding programs for traits controlled by polygenes will not consist necessarily in a more efficient selection. Instead, genomics would provide a better tool for creating genetic variability and providing criteria for searching for novel alleles in other germplasm sources.

Need for broadening the genetic base of the crop has led breeders to attempt the introgression of tropical and subtropical adapted germplasm into temperate one and viceversa. In this regard, CIMMYT (International Center for Wheat and Maize Improvement), along with NARs (National Agricultural Research Services) and several universities, deserve a major recognition for their commitment. Choice of novel germplasm should be done taking into account the structure and the objectives of breeding programs aimed to detect sources of favorable alleles not present in the currently used gene pool. This is a critical matter, since success of any breeding program relies on an appropriate choice of germplasm source. Besides, it is not an easy task, especially for traits controlled by quantitative genes. Fortunately, several biometrical approaches have been designed, tested and compared (Pfarr and Lamkey, 1992).

Latin American Maize Project (LAMP) evaluated 330 Argentine landraces out of a near 1700 maize accessions from Argentina, Chile, USA and Uruguay using yield per se performance as the criterion for the first and second selection stages. Selected landraces made up a group of almost 70 accessions that was testcrossed to three testers representative of different heterotic groups (Reid Yellow Dent or SSS, Lancaster Sure Crop or non-SSS, and Argentine Flint (Salhuana et al, 1998). Finally, 18 Argentine landraces were selected as elite material and also as basic resources for the Germplasm Enhancement of Maize Project (GEM). Besides these accessions, there are many others that could constitute sources potentially useful to increase yield and grain quality, stability, and tolerance to several kinds of stresses. To profit from these resources, comprehensive assessment of their characteristics is necessary. Results of such studies were reported by López et al (1994), Eyhérabide and Gonzalez (1997), Bertoia (2001), Lorea et al (2006, 2007ab), Delucchi et al (2012), Incógnito et al (2013).

Stability is defined as the ability of certain genotype to perform consistently through a range of environmental conditions. Kang (2002) defined two different concepts of stability. A stable genotype in a biological or static concept of stability does not show differences in performance when exposed to different environments. By the contrary, a stable genotype in an agronomic or dynamic sense exhibits changes in performance under different environments, but the response is parallel to the mean performance of all other tested genotypes. Thus, biological stability is an absolute attribute of a genotype, and agronomic stability is a relative one that varies with the set of genotypes evaluated.

Unintentionally, repeated cultivation of landraces by farmers for a large number of generations may have increased the frequency of alleles for resistance to biotic and non-biotic stress conditions and then contributed to enhance stability for grain yield. The scope of this study is to determine if such statement holds, and to characterize that agronomic stability in terms of gene action involved. Knowledge regarding these matters could be considered in hybrid breeding programs aimed to develop more productive and stable cultivars.

Materials and Methods
Plant Material
Twenty Argentine maize landraces (Table 1) which grain yields in testcrosses were in the upper 5 to 10% of the frequency distribution in a previous study were selected as genetic material for this research. Landraces were collected from 11 Argentine Provinces and previously classified into 15 races. A set of five elite inbred lines, B73, LH195, Mo17, LP612, and LP122-2 («LP» stands for INTA´s proprietary lines) were used as testers of landraces (Olmos et al, 2014). LP 122-2 and LP612 are flint lines. Lines B73 and Mo17 were developed by Iowa State University and The University of Missouri, respectively. Line LH195 is a dent line developed by Holden´s from the same heterotic group as B73 («Stiff Stalk Synthetic»). Eight single crosses among line testers and four commercial hybrids were included as checks.

Experimental procedures
About 100 randomly selected plants from each landrace were pollinated by the five elite line testers. Same amount of kernels were taken from each ear and bulked to represent each landrace x line testcross.

The testcrosses, the hybrids, and check cultivars were accommodated following incomplete block design experiments with two replications. Experimental units consisted of two 6 m long rows, 0.7 m apart. Plant density was adjusted by thinning to about 70,000 plants per hectare.

The experiments were conducted in fourteen environments (combination of 4 to 6 locations within three years (cropping seasons 2003-2004, 2004-2005 and 2005-2006) representative of the Argentine Corn Belt (Northern Buenos Aires Province). One experiment was not considered because of poor experimental conditions and unreliable data. Two locations were planted using non-tillage system. Crop management was adjusted to conventional or non-tillage agricul-

Table 1 - Codes for landraces (1-20), line testers (5) and number of observations (N) for testcrosses evaluated across 13 environments.

| Code | Code Landrace | Line Testers | | | | | N |
		1 LP612	2 LP122-2	3 Mo17	4 B73	5 LH195	
1	ARZM01042	30	30	18	18	18	114
2	ARZM01045	30	30	18	18	18	114
3	ARZM01073	30	30	30	18	18	126
4	ARZM02003	30	30	30	18	18	126
5	ARZM02023	30	30	30	18	18	126
6	ARZM03014	30	30	30	18	18	126
7	ARZM04062	30	30	30	18	18	126
8	ARZM05027	30	30	30	-	18	108
9	ARZM05052	30	30	30	10	10	110
10	ARZM06020	30	30	30	18	18	126
11	ARZM07084	30	30	30	10	18	118
12	ARZM07108	30	30	30	-	18	108
13	ARZM07134	30	30	30	18	18	116
14	ARZM14103	30	30	30	18	18	116
15	ARZM16008	30	30	18	18	18	116
16	ARZM16064	30	30	30	18	18	126
17	ARZM17035	30	30	30	18	18	126
18	ARZM18017	30	30	30	18	18	126
19	ARZM18037	30	30	30	18	18	126
20	ARZM07054	18	18	38	-	8	74

ture, using modern husbandry adopted by farmers.

Statistical procedures

Collected data resulted unbalanced. Since not all genotypes were evaluated in all location and years, unbalanced was reduced considering environment as each combination of location and year. A mixed model was applied and best lineal predictor BLUPs (Henderson, 1985, Bernardo 1996) of grain yield for each genotype (testcrosses) (BLUP_G) across environment and each environment (BLUP_GE) were obtained following Boca and Cantet (2004). Same model was applied to analyze considering genotypes as landraces and lines separately.

Single experiment and across experiment analyses of variance were done using R (R, 2015) and SAS v8 (SAS, 2011).

Genetic models, and stability parameters for the complete (unbalanced) data set

The sum of squares of Genotype x Environment interaction accounted by a particular genotype (W_t) is known as ecovalence (Wricke and Weber, 1986). This phenotypic stability parameter (W_t) is the sum of squares of deviations across l environments between the observed performance of the tth genotype and the expected performance under a regression line with slope b = 1 which origin passes through the intersection of the general mean across both genotypes and locations with the average performance of the tth genotype across locations.

Thus, the sum of squares of Genotype x Environment interaction accounted by a particular genotype is

$$W_t = \sum_j (Y_{tj.} - Y_{t..} - Y_{.j.} + Y_{...})^2$$

where $Y_{tj.}$ is the mean of the tth genotype in the jth environment; $Y_{t..}$ is the mean of the tth genotype across environments; $Y_{.j.}$ is the mean of the jth environment, and $Y_{...}$ is the mean across t genotypes and j locations.

The lower W_t the smaller the ecovalence, and the greater the phenotypic stability of the tth genotype. In other words, the resemblance of the performance of tth genotype with the average performance of all tested genotypes is greater. Kang (2002) has established a perfect correlation between Shukla's stability parameter and ecovalence. Shukla's stability parameter is widely used by breeders and provides an unbiased estimate of the GxE interaction of each genotype. The stability component of a reliability parameter combining yield performance and stability (Kang and Pham, 1991) is based on Shukla's parameter. Ecovalence and Shukla's parameter are relative measures of stability, dependent on the genotypes tested.

In a factorial design, source of variations of crosses is usually partitioned in genetic components attributable to female and male parents and to female x male interactions. In multi-environment trials, same partitioning can be done for the cross x environment interactions. Accordingly, in a diallel experiment, ecovalence of any cross could be splitted in ecovalence due to both parents of a cross (W_i, W_j) and ecovalence due to the interaction between its parents (W_{ij}) as follows:

$$W = W_i + W_j + W_{ij} \qquad [1]$$

The mixed model used allowed to obtain Best Linear Unbiased Predictors of Genotype x Environment interaction for each genotype-environment combinations ($BLUP^{ge}_{tl}$). These predictors are deviations from the mean performance of all genotypes-environment combinations. Consequently an ecovalence predictor

could be defined as:

$$BLUP_t^W = \sum_l (BLUP_{tl}^{ge})^2$$

Thus, for a cross between two parents, equation [1] could be expressed in terms of ecovalence predictors as:

$$BLUP_{ij}^W = BLUP_i^{WG} + BLUP_j^{WG} + BLUP_{ij}^{WS}$$

where each term in the right hand side of the equation are the predictors of ecovalence due to i^{th} parent, to j^{th} parent, and ecovalence to the ith x j^{th} cross, respectively. Three analyses using mixed models were applied, considering as genotype classification criteria to testcrosses, to landraces and to line testers. These allow estimation of $BLUP_{ij}^W$, $BLUP_i^{WG}$, and $BLUP_j^{WG}$, respectively. $BLUP_{ij}^{WS}$ was estimated by the difference between predicted testcross ecovalence and the summation of ecovalence predictors of its parents

Genetic models, and stability parameters for a balanced subset of data

A classical combining ability analyses was carried out following a partial diallel model, in such a way that:

$$Y_{ijl} = \mu + L_l + G_i + G_j + GL_{jl} + SL_{ijl} + e_{ijl}$$

where Y_{ijl} is the mean performance of testcross i^{th} x j^{th} in the lth environment; μ is the general mean across environment and crosses; L_l is the effect of the lth environment; G_i is the general combining ability of the ith female parent; G_j is the general combining ability of the jth male parent; GL_{il} is the general combining ability of the interaction between i^{th} female with the lth environment; GL_{jl} is the general combining ability of the interaction between j^{th} male with the lth environment; SL_{ijl} is the specific combining ability of the interaction between i^{th} female parent crossed to the jth male parent with the lth environment; e_{ijl} is the error term.

Combining ability analyses was made using BLUP estimates as before, but applied to a balanced data set of 15 landraces testcrossed to the five inbred lines and evaluated over eight environments.

Combining ability analyses of testcross ecovalence predictors was made using a 75 x 8 matrix which elements were the $BLUP_{tl}^{ge}$ predictors. Thus

$$BLUP_{tl}^W = \mu + BLUP_i^{WGCA} + BLUP_j^{WGCA} + BLUP_{ij}^{WSCA}$$

The right hand side terms refer to the mean of the BLUPgetl included in the data subset, general combining ability ecovalence predictor of ith female (landrace), general combining ability ecovalence predictor of jth male (line tester) and specific combining ability ecovalence predictor of ith landrace crossed to the jth line tester, respectively.

Combining ability analyses of adaptability, or regression analyses of the grain yield performance over an environmental index followed the approach of Pacheco et al, 1999. Data subset submitted to these analyses was composed by the BLUP predictors of performance of each genotype across environments

and in each environment. Thus

$$\hat{Y}_{ijl} = \mu + BLUP\ G_{ij} + BLUP\ G_{ij}E_l$$

Terms «ecovalence predictors» and «ecovalence» will be referred in the text indistinctly here in after.

Results and Discussion

Estimated variance for grain yield were obtained by mixed model analyses of four unbalanced datasets (genotypes (113), testcrosses (97), line testers across landraces (5) and landraces across testers (20)), all evaluated in 13 environments. An analysis of variance for a balanced data set of 75 testcrosses evaluated in 8 environments was also done for grain yield (Supplementary Table 1).

Variance estimates for Testcrosses and Line Testers were similar to the estimates of their respective interactions with Environments. Landrace x Environment estimate was approximately one third of the estimate of Landraces' variance. It seems as if tester lines would have a buffer effect on the interaction of
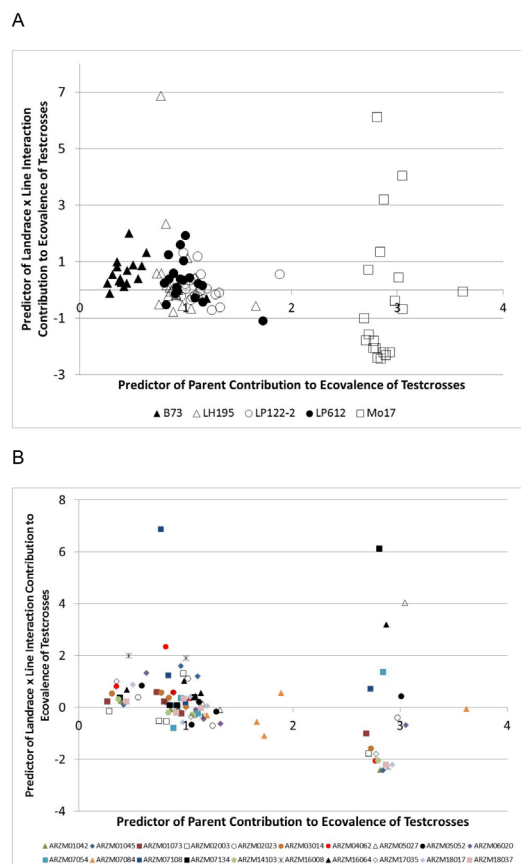
Figure 1 - Predictors of contribution of parental (Landraces + Lines) and Landrace x Line Interaction to testcross ecovalence predictors (x 106) for 97 testcrosses evaluated across thirteen environments. A: classified by line tester parent; B: presented by landrace parent.

each landrace across environment.

Analyses of variance for grain yield of the balanced data subset indicates mean squares significant for testcrosses (p ≤ 0.0001) and testcrosses x environment (p ≤ 0.0001; Supplementary Table 1).

Ecovalence predictors from testcrosses data set (equation [2])

Average predicted genotypic ecovalence of Landrace x Line testcrosses was 1.5×10^6 and the range 0.01×10^6 to 8.9×10^6 kg^2 ha^{-2} (measure units of ecovalence for grain yield will be omitted here in after). The more stable (lower ecovalence) testcrosses were ARZM07054 x LH195, ARZM02003 x B73, ARZM02003 x LH195, ARZM02003 x LP612, and ARZM05052 x LH195. The less stable testcrosses (higher ecovalences) were ARZM07134 x Mo17, ARZM07108 x LH195, ARZM16064 x Mo17, ARZM05027 x Mo17, and ARZM07054 x Mo17 (Supplementary Figure 1B). Testcrosses to ARZM01104 exhibited small scores for ecovalence and also did ARZM14103 no matter the male tester line used. Ecovalences for testcrosses with line Mo17 seem to be greater than those with lines LH195, LP612, LP122-2, and B73 (Supplementary Figure 1A).

Mixed model analyses applied to the complete data set resulted in mean predicted ecovalences contributed by landraces (BLUP$^{WG}_L$) and tester lines (BLUP$^{WG}_T$) of 0.26×10^6 and 0.11×10^6, respectively. Range of BLUP$^{WG}_L$ was 0.06×10^6 to 0.99×10^6 and that of BLUP$^{WG}_T$ was 0.21×10^6 to 2.63×10^6. US dent lines B73 and Mo17, presented the smallest and the largest BLUP$^{WG}_T$, respectively, while LH195, and local lines LP612 and LP122-2 exhibited intermediate values. Landraces ARZM01073 and ARZM02023 presented BLUP$^{WG}_L$ values smaller to 0.1×10^6, and

ARZM06020 and ARZM07084 the two largest values of 0.42 and 0.99×10^6, respectively (data not shown).

Direct comparisons of relative magnitude between BLUP$^{WG}_L$ and BLUP$^{WG}_T$ in terms of their parental contribution to the testcross ecovalence predictors are not correct unless BLUP$^{WG}_T$ is divided by 4 (or BLUP$^{WG}_L$ multiplied by 4), since summation of predictors of BLUP$^{WG}_L$ are made over 20 landraces, and summation of predictors of BLUP$^{WG}_T$ are made over 5 lines. Line tester Mo17 contribution overpassed 50% in most testcrosses. By the contrary, landrace contributions were larger in B73 testcrosses (Supplementary Figure 2).

Contribution of landrace x line tester interaction (non-additive) predicted ecovalences to testcross ecovalences resulted variable (Supplementary Figure 3). Bidirectional non-additive genetic effects to testcross ecovalence were observed, with a range between -0.8×10^6 to 6.9×10^6 and a mean across testcrosses of 0.2×10^6 (considering signs of data) and 0.9×10^6 (in absolute values). Non-additivity seems to be more frequently detrimental to testcross yield stability across environments, since it averaged a positive contribution to ecovalence (negative contribution to stability).

Biplot of the components of testcross ecovalence predictors, parent (both landrace and line) and landrace x line interaction ecovalences, shows a more clearly defined distribution of clusters of parent interaction ecovalences when testcrosses are displayed by line parent than when they are displayed by landrace parent (Figure 1). Testcrosses to line Mo17 showed less grain yield stability (larger ecovalence) in terms of both genetic components of ecovalence. By the contrary, testcrosses to B73 tend to possess greater grain yield stability. Testcrosses to both local

Table 2 - Landraces and line tester ecovalence general combining ability[1] predictors (in italic font) and specific combining ability[2] predictors across eight environments (x10^3).

Landraces	Line Testers	LP612	LP122-2	Mo17	B73	LH195
	GCA	-208	-244	419	-20	53
ARZM01042	-454	233	110	-587	88	156
ARZM01045	63	931	908	-1107	-544	-189
ARZM01073	-332	-82	-185	-111	-184	561
ARZM02003	-425	-205	1716	-644	-440	-428
ARZM02023	55	-252	-510	-118	-116	996
ARZM03014	-214	-40	78	-555	39	478
ARZM04062	260	-341	-106	-1246	-110	1802
ARZM06020	126	-430	-478	308	813	-213
ARZM07134	1361	-1661	-932	5714	-1604	-1517
ARZM14103	-564	-2	284	-628	238	109
ARZM16008	486	1519	-496	-1350	962	-635
ARZM16064	613	-178	-544	2149	-489	-939
ARZM17035	-227	363	-443	-616	565	131
ARZM18017	-331	-184	496	-663	706	-355
ARZM18037	-418	328	102	-549	75	43

[1]standard deviation for Landraces GCA$_i$ = 363.9×10^3, (GCA$_i$ – GCA$_i$') = 532.7×10^3; standard deviation for Line Testers GCA$_j$ = 194.5×10^3, (GCA$_j$ – GCA$_j$') = 532.7×10^3

[2]standard deviation for SCA$_{ij}$ = 727.7×10^3, (SCA$_{ij}$ – SCA$_{ik}$) = 1150.7×10^3; (SCA$_{ij}$ – SCA$_{kj}$) = 1065.3×10^3, (SCA$_{ij}$ – SCA$_{kl}$) = 1020.0×10^3
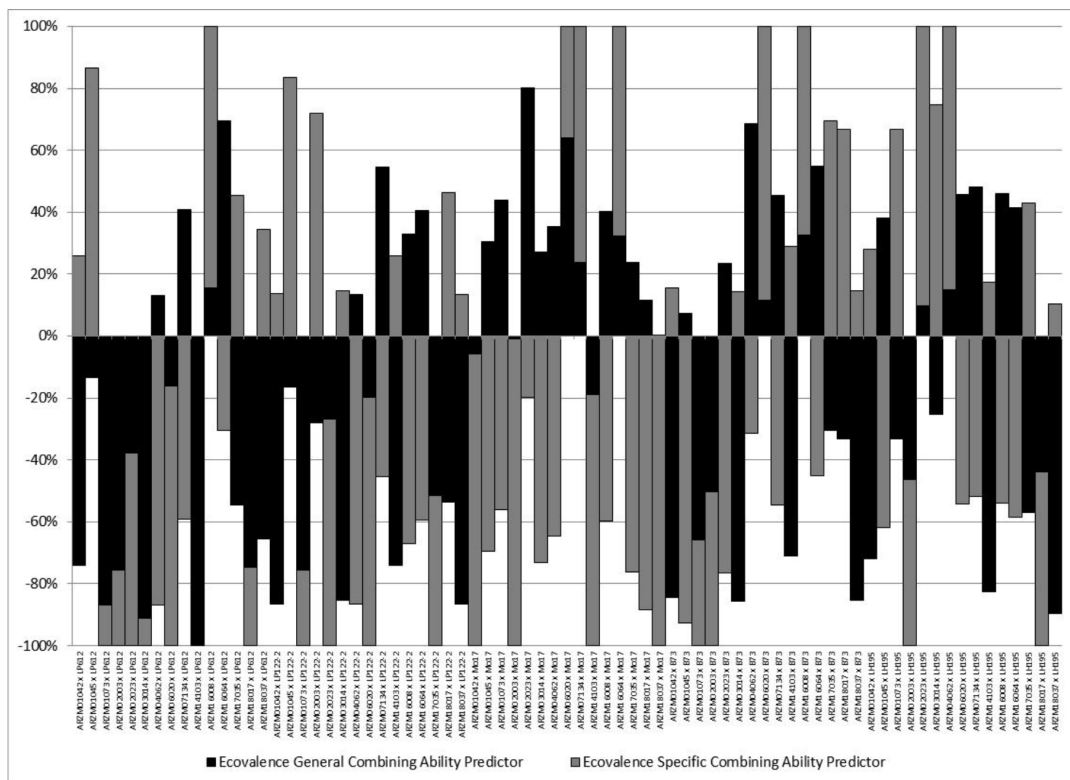
Figure 2 - Relative contribution (%) of predicted ecovalence general combining ability and specific combining ability effects to testcross ecovalence predictors.

flint testers exhibited low dominance ecovalence and intermediate additive ecovalence values in comparison with B73 and Mo17.

Combining ability decomposition of testcross ecovalence from balanced data subset

Testcrosses' ecovalence predictors resulted highly significant, as well as the combining ability sources of variation. General combining ability for landraces and line testers were significant (p ≤ 0.024 and p ≤ 0.203, respectively). Extreme landraces´ general combining ability ecovalence predictors corresponded to ARZM07134, ARZM 16064, ARZM16008 (less stability across environments), and ARZM14103, ARZM01042, and ARZM02003 (greater stability across environments). Local line testers (LP122-2 and LP612) presented smaller general combining ability ecovalence predictors than US lines, especially Mo17 and LH195. Ecovalence specific combining ability predictors presented a wider range of estimates: -1,661 x 10³ (ARZM07134 x LP612) to 5,714 x 10³ (ARZM07134 x Mo17) (Table 2).

In 22 instances out of 75, total parental general combining ability as well as specific combining ability ecovalences effects had both the same sign. For 22 testcrosses, contributions of specific combining ability to testcross ecovalence were larger than 70%. Testcross ecovalences of ARZM02023 x Mo17 and ARZM18037 x Mo17 were determined almost entirely by dominance effects (Figure 2).

Estimates of ecovalence combining ability relative indexes (Baker, 1978) for Landraces and Line Testers were 0.181 and 0.353, respectively (Supplementary Figure 4). Thus, specific combining ability would be equally important than total parent´s general combining ability in order to predict ecovalence of testcrosses. Landraces´ contribution resulted to be less important than that of the line testers. Relatively large importance of non-additive effects for controlling grain yield stability was also found by Eyhérabide et al (2008) and Machado et al (2009) when analyzing genetic control of stability in maize hybrids.

Biplots (Figures 3A and B) of testcross ecovalence vs. general combining ability ecovalence suggest the presence of association between them, but basically determinated by the line testers and barely by landraces, in accordance with estimated combining ability relative indexes (Supplementary Figure 4).

Figure 3A shows that quadrant with negative estimates of both testcross and parent general combining ability predicted ecovalences correspond in a relatively high frequency to crosses with local lines LP612 and LP122-2. This pattern of association is less evident when parental contribution is classified taking into account the landraces (data not shown). Biplot of relationship between specific combining ability ecovalence predictors vs. total general combining ability ecovalence predictors (Figure 3B) shows a pattern of point distribution very resembling
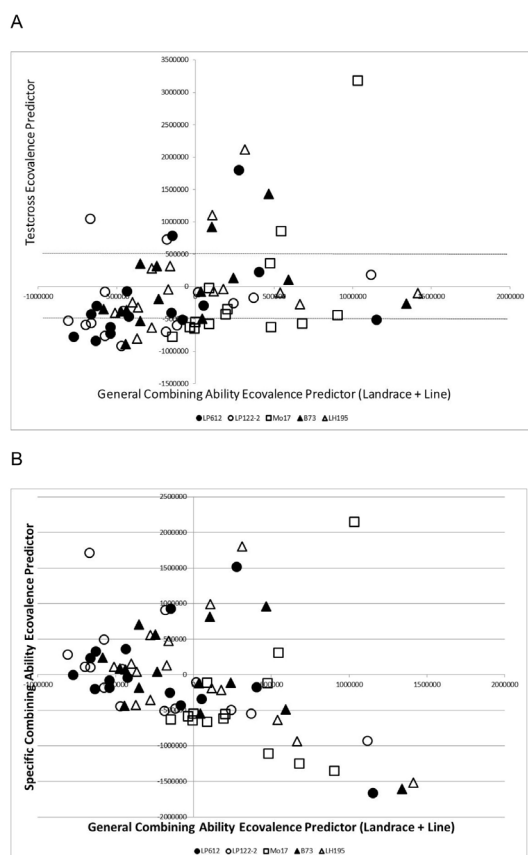
A

B

Figure 3 - Biplots of A) testcross ecovalence predictors vs. predicted ecovalence general combining ability effects (15 landraces + 5 Lines) evaluated across eight environments presented by line tester parent; B) predicted specific combining ability effects for testcrosses vs. predicted general combining ability displayed by line parent.

to that of Figure 3A, suggesting a major contribution of specific combining ability ecovalence effects (non-additive effects) to testcross ecovalence.

Both testcross and specific combining ability ecovalence predictors showed positive and highly significant correlation coefficients with grain yield ($\rho = 0.34$, $p \leq 0.01$ and $\rho = 0.37$, $p \leq 0.01$, respectively; Table 3). In other words, there is a tendency by which more productive testcrosses across environments also exhibited larger genotype x environment predictors (greater ecovalence or less stability across environments). Non-additive or specific combining ability ecovalence effects were positively associated with grain yield. By the contrary, total general combining ability effects presented a weak association with grain yield predictors. Nevertheless, line testers general combining ability ecovalence predictors showed a negative correlation ($\rho = -0.22$, $p \leq 0.05$). Thus, tester lines with lower ecovalence predictors (higher stability) tend to exhibit higher grain yield across locations. Line parental contribution was, in general, towards the desirable direction of greater testcross grain yield stability. Landrace ecovalences would have a smaller

association with grain yield and stability than line ecovalences. Utilization of tester lines with higher stability (smaller line ecovalence predictors) would produce testcrosses with better grain yield performance and stability across environments. In some extent, selection processes followed to develop elite inbred lines would have been very effective in selecting favorable alleles for greater grain yield stability and could explain the difference with landraces which hold a small amount of previous breeding efforts.

Line LP122-2 combined the highest GCA predictor for grain yield with one of the smallest GCA ecovalence predictor (smallest genotype x environment interaction) (Supplementary Figure 5A). By the contrary, line Mo17 presented the smallest GCA predictor for grain yield and the largest GCA ecovalence predictor (largest genotype x environment interaction). Lines B73 and LH195 (SSS lines) presented similar and near zero ecovalence predicted GCA and positive grain yield predicted GCA effect. Flint Line LP612 presented similar ecovalence GCA predicted effect than LP122-2, but smaller grain yield GCA predicted effect. Clearly, local lines made a positive contribution to stability of testcrosses, and Mo17 a negative contribution.

Pattern of distribution of GCA grain yield predicted effects vs GCA ecovalence predicted effects are consistent with the correlation coefficients presented in Table 3: a positive association between the two traits in landraces (although non-significant), and a negative association for tester lines. This last result can be interpreted at the light of successful selection aimed to combine higher yields with higher stability during the line development.

Pattern of distribution of grain yield SCA predicted effects and SCA ecovalence effects (Figure 3B) is also consistent with the correlation coefficient indicated in Table 3. As mentioned above, it means that the highest non additive effects contribution to grain yield tend to be associated with less grain yield stability (large ecovalence).

Only three out of 15 landraces (ARZM01042, ARZM03014 and ARZM18017) presented grain yield and ecovalence GCA predicted effects in the right and low quadrant (Supplementary Figure 5A). Testcrosses between these three landraces crossed to lines LP122-2 and B73 would be those with a highest contribution of GCA effects to grain yield and stability. By the contrary, testcrosses between landraces ARZM02023 and ARZM06020, both testcrossed to Mo17 would have the lowest GCA contribution to grain yield and stability across environments.

Concept of reliability is often used to describe a genotype in terms of its grain yield performance and stability across environments at once. The better grain yield performance and stability has a genotype, the better its reliability. There was detected a small but significant correlation ($\rho = 0.34$; $p \leq 0.01$) between testcross ecovalence and grain yield across environ-

Table 3 - Phenotypic correlation coefficients and significance levels among mean testcross grain yield and testcross ecovalence and its components across eight environments.

Trait	Ecovalence Predictors				
	Testcross	Landrace GCA	Line GCA	Total GCA	SCA
Testcross Grain Yield Predictor	0.34**	0.15ns	-0.22*	0.04ns	0.37**
Landrace GCA Grain Yield		0.24ns	-	-	-
Line GCA Grain Yield		-	-0.50ns	-	-
SCA Testcr.Grain Yield		-	-	-	0.55**
Testcross Ecovalence		0.44**	0.21ns	0.49**	0.87**
Landrace GCA Ecovalence			0.00ns	0.90**	0.00ns
Line GCA Ecovalence				0.43**	0.00ns
Total GCA Ecovalence					0.00ns

**: $P < .01$; *: $P < .05$; ns: not significant

ments (Table 3). There were a few testcrosses which coordinates are in the upper left quadrant of Supplementary Figure 6A that could be selected because of high reliability. By the contrary, the association between general combining ability for grain yield across environments and parent contribution to testcross ecovalence was non-significant (Supplementary Figure 6B).

Combining ability decomposition of adaptability from balanced data subset

In most cases (41 out of 75), signs of slope SCA and slope GCA effects for grain yield of testcrosses were opposite (Supplementary Figure 7). Relative contribution of GCA to "total" slope of testcrosses was very small (less than 10%) in testcrosses ARZM01073 x LP612, ARZM05027 x LP612, ARZM16064 x LP612, ARZM01042 x LP122-2, ARZM02003 x LP122-2, ARZM07134 x LP122-2 and ARZM16064 x B73. By the contrary relative contribution of SCA to «total» slope of testcrosses was very small (less than 10%) in testcrosses ARZM06020 x LP612, ARZM16008 x LP122-2, ARZM16064 x Mo17, ARZM01045 x B73 and ARZM01073 x B73.

Analyses of adaptability indicate that testcrosses to line tester LH195 had the largest frequency of slopes greater than 1 (60%), followed by those to line testers B73 and LP612 (40%). Testcrosses to line tester LP122-2 had the largest frequency of slope smaller than 1 (87%), followed by those to line testers Mo17 (73%) and B73 (53%). Clearly, line testers LH195 and LP612 contribute mostly to adaptation to favorable environments, and LP122-2 and Mo17 to adaptation to less favorable environments. These results were consistent with the slope b_1 GCA predicted effects of line testers (data not shown) and slope b_1 SCA effects (Supplementary Figure 8A and 8B). All crosses of landrace ARZM18037 presented the largest frequency of b_1 slope of testcrosses effects larger than 1 (100%), followed by landraces ARZM01042, ARZM01045 and ARZM06020 (60%). By the contrary, landraces ARZM02003 and ARZM14103 exhibited a 100% frequency of slopes less than 1. These results were consistent with the slope b_1 GCA predicted effects of landraces and SCA effects (Supplementary Figures 8A and 8B). Near 60% of testcrosses showed

adaptation mostly to less favorable environment.

Indexes for relative contribution of general combining ability effects (Supplementary Figure 4) reveal that these made smaller contribution to stability and adaptability than they do to grain yield (near 54% vs 90%) of testcrosses. These results suggest that non-additive effects would be more important to determine stability and adaptability than to grain yield of testcrosses. On the other hand, estimation of the contribution of lines to predicted ecovalence general combining ability doubled that of the landraces (35% vs. 18%). It could be argued that selection for stability during tester line development (average testcross performance across environment) should have been quite effective to profit from both additive and non-additive effects.

Conclusions

Non-additive gene effects were more important than additive effects for controlling agronomic stability estimated by ecovalence predictors. Non-additive effects vary in their sign depending on the testcross considered, but in general they were detrimental to stability. Even though landraces as female parents contributed to ecovalence, their contribution was less important than that of line testers. Testcrosses to line tester Mo17 tend to present less stability across environments than those to LH195, LP612, LP122-2, and especially B73. This line provides to their crosses greater grain yield stability. Adaptability to favorable environment was more frequently found in testcrosses to lines LH195 and LP612. By the contrary, lines LP122-2 and Mo17 were more frequently associated to unfavorable environment. Greater relative importance of general combining ability for inheritance of ecovalence in comparison with landraces general combining ability effect, could be attributed to a successful selection for stability during the development of inbred lines, and negligible amount of breeding effort dedicated to landraces.

Near 60% of landraces appeared more adapted to unfavorable environment. This could be indicative of their higher level of rusticity as could be expected by their origin. As a group, local line testers tend to provide their testcrosses with greater stability across environments than US dent lines do.

Correlation between grain yield and stability, although significant, was mainly dependent upon non additive effects. More productive testcrosses tend to have greater ecovalence (less stability) due to specific combining ability effects. Inbred lines selected for greater general combining ability effect tend to provide their testcrosses a higher stability.

References

Baker RJ, 1978. Issues in diallel analysis. Crop Sci 18: 533-536

Bertoia LM, 2001. Forage yield and quality combining ability of maize composites with different improvements levels. Maydica 46: 87-92

Bernardo R, 1996. Best linear unbiased prediction of maize single-cross performance. Crop Sci 36(1): 50-56

Bernardo R, 2001. What if we knew all the genes for a quantitative trait in hybrid crops? Crop Sci 41(1): 1-4

Boca RT, Cantet RJC, 2004. On the precision of REML estimates of additive and dominance variance components in maize using relationship matrices. Maydica 49: 295-302

Delucchi C, Eyhérabide GH, Lorea RD, Presello DA, Otegui ME, López CG, 2012. Classification of argentine maize landraces in heterotic groups. Maydica 57: 26-33

Eyhérabide GH, Gonzalez AS, 1997. Interactions between testers and Argentine maize landraces. Maydica 42: 29-38

Gepts P, 2006. Plant genetic resources, conservation and utilization: the accomplishments and future of a societal insurance policy. Crop Sci 26: 2278-2292

Goodman MM, 1988. US maize germplasm:origins, limitations, and alternatives, pp. 130-138. In: Recent advances in the conservation and utilization of genetric resources. Proceedings of the Global Maize Germplasm Workshop. CIMMYT, Mexico

Henderson CR, 1975. Best linear unbiased estimation and prediction under a selection model. Biometrics 31: 423-447

Incógnito SJP, Eyhérabide GH, Bertoia LM, López CG, 2013. Breeding potential of elite maize landraces to improve forage yield and quality of two heterotic patterns. Crop Sci 53: 1-11

Kang MS, 2002. Genotype-Environment Interaction: Progress and Prospects. In: Quantitative genetics, genomics, and plant breeding. Kang MS ed. Papers from the Symposium on Quantitative Genetics and Plant Breeding in the 21st Century, Louisiana State University

Kang MS, Pham HN, 1991. Simultaneous selection for high yielding and stable crop genotypes. Agron J 83: 161-165

López CG, Safont J, Ferrer ME, Eyhérabide GH, Solari L,1994. Evaluación de poblaciones locales argentinas de maíz por su comportamiento en cruzas dialélicas. In: Memorias del II Congreso Latinoamericano de Genética y XV Congreso de Fitogenética

Lorea RD, Delucchi C, Eyhérabide GH, López CG, 2006. Identifying argentine maize populations as source of favourable alleles for grain yield. International Plant Breeding Symposium, Mexico

Lorea RD, Eyhérabide GH, Borrás SF, Percibaldi NM, Robutti JL, López CG, Pedrol H, Castellarín JM, Delucchi C, Presello DA, 2007. Argentinian maize landraces (Zea mays L.) as a genetic source for improving physical and chemical composition of grain. In: First Latinoamerican Conference of ICC. New challenges of world demand

Percibaldi NM, Robutti JL, López CG, Pedrol H, Castellarín JM, Delucchi C, Presello DA, 2007. Argentinian maize landraces (Zea mays L.) as a genetic source for improving starch thermal properties. In: First Latinoamerican Conference of ICC. New challenges of world demand

Machado JC, de Souza JC, Patto Ramalho MA, Lima JL, 2009. Stability of combining ability effects in maize hybrids. Sci Agric 66(4): 494-498

Olmos S, Delucchi C, Ravera M, Negri ME, Mandolino C, Eyhérabide GH, 2014. Genetic relatedness and population structure within the public Argentinean collection of maize inbred lines. Maydica 59: 16-31

Pacheco CAP, Cruz CD, dos Santos MX, 1999. Association between Griffing´s diallel and the adaptability and stability analyses of Eberhart and Russell. Genetics and Molecular Biology 22(3): 451-456

Pfarr DG, Lamkey KR, 1992. Comparison of methods for identifying populations for genetic improvement of maize hybrids. Crop Sci 32: 670-677

Porter JR, Semenov MA, 2005. Crop responses to climatic variation. Phil Trans R Soc B 360: 2021-2035

R Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Salhuana W, Pollak LL, Ferrer ME, Paratori O, Vivo G, 1998. Breeding potential of maize accessions from Argentina, Chile, USA, and Uruguay. Crop Sci 38: 866-872

SAS Institute Inc, 2011. Base SAS® 9.3 Procedures Guide. Cary, NC: SAS Institute Inc

Smith JSC, Smith OS, Wright S, Wall SJ, Walton M, 1992. Diversity of US hybrid maize germplasm as revealed by restriction fragment length polymorphisms. Crop Sci 32: 598-604

Ulukan H, 2011. Plant genetic resources and breeding: current scenario and future prospects. Int J Agric Biol 13: 447-454

Wricke G, Weber WE, 1986. Quantitative genetics and selection in plant breeding. Walter de Gruyter, Berlin, New York