Contribution of autochthonous maize populations for adaptation to European conditions

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Abstract

Early vigor, earliness and cold tolerance are the main potential contributions of European maize (*Zea mays* L.) for breeding programs for adaptation to areas with short growing seasons and cold springs. The objective of this research was to determine the potential contributions of populations from different European regions to breeding for adaptation. Six Spanish and six French maize populations differing on variability for earliness, vigor and cold tolerance were crossed in a complete diallel without reciprocals. The populations and their crosses were evaluated in the field and in a cold chamber. Minimum temperatures were the main environmental trait affecting genotype × environment interaction, probably due to the cold sensitivity of the genotypes with the best performance in the field. The best population cross, based on specific heterosis for adaptation-related traits in the field, was Viana × Rastrojero, but this cross was cold sensitive. Tuy × Lazcano should be the best choice for a breeding program based on adaptation, based on performance in the field and cold tolerance. There was variability for earliness, vigor and cold tolerance among the populations and crosses involved in this study, and the highest yielding crosses were cold sensitive. These genotypic factors, along with cold temperatures, were identified by Malvar et al. (2005) as the main factors affecting genotype × environment interaction.

Introduction

Maize has been introduced into Europe during the last five centuries, from various American origins (Rebourgh et al. 2003 and Revilla et al., 2003). Although European maize comes from almost any American latitude and has adapted to a broad range of environments, diversity within European maize is necessarily narrower than within the American sources because adaptation involves reduction of variability. However a substantial amount of variability is still available, particularly for the main keys for maize adaptation to European conditions, which are cold tolerance, early vigor and short growing cycles. Spain has the maize germplasm with largest variability among European countries, followed by France (Rebourgh et al., 2003; Revilla et al., 2003), that has the largest production in Europe.

American maize is widely used in Europe in hybrid combinations, following the well-known heterotic pattern European flint × U.S. dent (Moreno-González, 1988; Ordás, 1991). Even though European germplasm has lower yield than American varieties, European maize is being used as a source of adaptation, in order to allow proper grow under cold springs and short growing periods, to avoid summer drought, pests and diseases, and to reduce the costs of chemical treatments and labor.

The main contributions of European germplasm, emergence under cold conditions, vigor and early silking, are required for adaptation of maize to regions with cold humid springs (Ordás et al., 1994; Revilla et al., 1999). Early vigor, earliness, and minimum temperatures were identified by Malvar et al. (2005) as the main effects explaining genotype × environment interaction on yield for the French and Spanish populations and their hybrids analyzed in this work.

The objective of this research was to determine the potential contributions of populations from different European regions to breeding for adaptation.

Materials and methods

Plant material

Six Spanish and six French maize populations were crossed in a complete diallel without reciprocals in 1999 in Pontevedra (northwest of Spain). The Spanish populations were Tuy (ESP0090205, Galicia N4205, W00865, 30 m a.s.l.), Viana (ESP0090214, Galicia N4218, W00710, 700 m a.s.l.), Lazcano (ESP0070892, the Basque Country N4303, W00210, 630 m a.s.l.), Basto/Rastrojero (ESP0090338, Andalucía), Rastrojero (ESP0090032, the Ebro River Valley), and Enano levantino/Hembrilla (ESP0090025, the South East). The French populations were Bade (FRA0410006, from Alsace), Lacaune (FRA0410015, Midi-Pyrenées N4333, E00235, 813 m a.s.l.), Esterre (FRA0410022, Midi-Pyrenées N4252, E00000, 1087 m a.s.l.), Ain (FRA0410474, Rhône-Alpes), Millette du Lauragais (FRA0410639, Languedoc Roussillon), and Millette Montagne Noire (FRA0410668, Languedoc Roussillon N4323, E00216, 741 m a.s.l.).

Crosses between each pair of varieties were made in five sets of paired rows with 15 plants per row, and each plant was used only as male or female, in order to obtain about 50 ears per cross. Similarly, each variety was multiplied to obtain seed in the same environmental conditions. Entries were the 12 parental varieties, their 66 crosses, and three check varieties, which were evaluated in a 9 × 9 triple partially balanced lattice design in the field and in a cold chamber.

Field trials

Field trials were planted in Pontevedra (northwest of Spain 42°24’N, 8°38’W, 20 m a.s.l.), Zaragoza (eastern Spain 41°44’N, 0°47’W, 250 m a.s.l.), Mauguio (southeast of France 43°37’N, 4°0’W, 13 m a.s.l.), and Saint Martin de Hinx (southwest of France 43°34’N, 1°16’WW, 65 m a.s.l.) in 2000 and

2001. Two rows-plots were used. Rows, spaced 0.80 m apart, had 25 two-plant hills spaced 0.21 m apart. The final density was approximately 60000 plants ha^{-1}. Data taken were early vigor (from 1 = poor, to 9 = high), silking date (days from sowing to 50% of plants silking), adult plant appearance after flowering was completed (from 1 = poor, to 9 = excellent), and plant height (cm from ground to top of tassel). Early vigor and adult plant appearance were recorded only in the two Spanish locations. Plant height was estimated from a sample of 10 random plants from each plot.

Cold chamber trial

The cold chamber trial was planted in trays filled with sterilized peat at 14 h with light at 14 ºC and 10 h without light at 8 ºC. Each experimental plot consisted of two 13-kernel rows spaced 4 cm. Sowing depth was 2 cm and the distance between consecutive kernels was 2 cm as well. Traits were emergence proportion (%), days from planting to 50% emergence, survival of emerged plants, vigor (1 = weak to 9 = vigorous), and color (1 = white to 9 = dark green).

Statistical analyses

Individual analyses of variance were carried out for each lattice design (Cochran and Cox, 1957). If the relative effectiveness of the lattice design was smaller than 105% for a trait, data were analyzed as randomized complete blocks design. The cold chamber trial was analyzed as a randomized complete block design. Analyses were computed with PROC LATTICE (SAS, 2000). Combined analyses of lattice design were made with adjusted treatment means, using the PROC GLM (SAS, 2000). Treatments mean squares were ortogonally partitioned into diallel populations (parental varieties and crosses), check varieties, and among groups. Diallel populations were divided, according to the Analysis II of Gardner and Eberhart (1966), using PROC IML of SAS (2000). Standard errors were calculated following Moreno-González et al. (1997). The standard error of heterosis was calculated as the square root of 1.5 times the variance of combining error, following Keeratinijakal and Lamkey (1993).

Results and discussion

Field trials

Populations were significantly different for all traits, as well as the environment × population interaction (Table 1). Variety heterosis was not significant for early vigor, while average and specific heterosis were significant. Accordingly, previous reports have shown that the inheritance of early vigor involves additive and dominance effects (Revilla et al., 1999). All effects except variety heterosis were significant for silking date. For plant height, all sources of variation were significant.

Plant appearance, a measure of overall vegetative development, was best for Millette du Lauragais, which did not differ from Millette Montagne Noire, Rastrojero, and Lazcano (Table 2). The growing cycle was shortest for Viana, followed by Lacaune, Esterre, and Bade. The populations with the tallest plants and significant positive variety effects were Rastrojero and Millette du Lauragais. Considering together growing cycle and early vigor at early and adult stages, the population Lazcano had the best performance. Early vigor was highest for Lazcano × Tuy, although several crosses did not differ significantly from this one (Table 3). Hybrids involving Lazcano and most crosses of Tuy were among the most vigorous crosses.

These results match with expectations because Lazcano and Tuy are mid maturing populations from the humid area of Spain, where early vigor is required. Early vigor of early populations from areas with short growing cycles was similar to that of populations from other regions. The reason may be that early populations can be sown late in regions with short growing seasons, avoiding the cold humid conditions that would require early vigor (Revilla et al., 1998). The largest positive specific heterosis for early vigor was for crosses between populations with low vigor *per se* as Viana × Rastrojero, Lacaune × Basto/Rastrojero, Ain × Esterre, and Lacaune ×

Enano levantino/Hembrilla. Therefore, the highest specific heterosis for early vigor was shown by crosses that corresponded with the heterotic patterns based on specific heterosis for yield. Those crosses followed the patterns dry Spain × humid Spain (Ordás, 1991) and dry Spain × southern France (Revilla et al., 2005).

Growing cycle was shortest for hybrids involving Viana, particularly when crossed to the early populations Lacaune and Esterre (Table 4). Two crosses among early populations, Viana × Bade and Esterre × Lacaune had early silking and the largest significant specific heterosis for earliness. However, the early heterotic pattern suggested by Revilla et al. (2005), based on grain moisture and yield, was Bade × Esterre, which had mid-early silking date and non-significant specific heterosis. Other crosses with high negative specific heterosis, Viana × Basto/Rastrojero and Lazcano × Bade, had relatively early flowering (Table 4). The population Rastrojero, with late silking, produced late hybrids with non significant specific heterosis except when crossed to Esterre.

Cold chamber trial

In the cold chamber trial, differences among populations were significant for all traits except days to emergence (Table 1). The variety effect was significant for emergence proportion, vigor and color, average heterosis for vigor, variety heterosis for color, and specific heterosis was significant for emergence proportion.

Emergence proportion was above 90 % for Bade, Lazcano, and Millette du Lauragais, but the only populations that had significantly lower emergence were Rastrojero (58 %), Lacaune (67 %) and Millette Montagne Noire (67%). Variety effects were not significant for emergence proportion except for Rastrojero (-20.9). Bade had high vigor (5.3), but only Rastrojero, Lacaune, Millette Montagne Noire, and Millette du Lauragais had significantly lower vigor. Bade had also a significant positive variety effect for vigor. The populations with the best color and variety effect for color were Basto/Rastrojero, Viana, Enano levantino/Hembrilla, Bade and Lacaune. Altogether, the populations Bade, Basto/Rastrojero and Viana were the most cold tolerant and had the best variety effects in the cold chamber.

Fifty five population and crosses had a germination proportion not significantly different from Enano levantino/Hebrilla × Millette Montagne Noire, which was the population cross with largest germination and specific heterosis effect (Table 5). Enano levantino/Hebrilla had a significant positive specific heterosis effect also with Lacaune. Enano levantino/Hembrilla was among the cold tolerant populations, albeit with an insignificant variety effect for early vigor, while Millette Montagne Noire was cold sensitive and Lacaune had low mean and variety heterosis for emergence and vigor. Among the remaining crosses, the best combination was Basto/Rastrojero × Bade, and Viana × Bade was not significantly different from that one (Table 5). These two crosses involve three cold tolerant parents (Table 2). None of the cold tolerant combinations correspond to the heterotic patterns defined by Revilla et al. (2005), although they could fit the north-central Europe × southern Europe heterotic pattern suggested by Revilla et al. (2002), based on inbred lines. None of the heterotic patterns defined previously by Ordás (1991), Malvar et al. (2005) and Revilla et al. (2005) was cold tolerant when considering the parental populations and their hybrid.

Conclusions

Overall adaptation in the field was highest for Lazcano, which produced the most vigorous hybrids when crossed to Tuy, significant negative specific heterosis for silking date when crossed to Bade, and medium size plants across crosses. The best cross, based on specific heterosis for adaptation-related traits in the field, was Viana × Rastrojero, with relatively high early vigor and medium performance for most traits, but this cross was cold sensitive and had significantly lower yield and higher kernel moisture than Tuy × Lazcano (Revilla et al., 2005). Tuy × Lazcano had the best performance in the field, particularly the highest early vigor and high plant appearance, therefore should be the best choice for a breeding program for adaptation. However, Tuy × Lazcano had negative, though no significant, specific heterosis effect for germination and light green color, although was among the crosses with high germination and had an average vigor under cold conditions.

There was variability for earliness, vigor and cold tolerance among the populations and crosses involved in this study, and the highest yielding crosses were cold sensitive. These genotypic factors, along with cold temperatures, were identified by Malvar et al. (2005) as the main factors affecting genotype × environment interaction.

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References

Cochran, W.G. & G.M. Cox. 1957. Experimental designs. 2nd ed. John Wiley and Sons, New York.

Gardner, C.O. & S.A. Eberhart. 1966. Analysis and interpretation of the variety cross diallel and related populations. Biometrics 22:439-452.

Keeratinijakal, V. & K.R. Lamkey. 1993. Responses to reciprocal recurrent selection in BSSS and BSCB1 maize populations. Crop Sci. 33: 73-77.

Malvar, R.A., P. Revilla, A. Butrón, B. Gouesnard, A. Boyat, P. Soengas, A. Álvarez & A. Ordás. 2005. Performance of crosses among French and Spanish maize populations across environments. Crop Sci. 45:1052-1057.

Moreno-González, J. 1988. Diallel crossing system in sets of flint and dent inbred lines of maize (*Zea mays* L.). Maydica 33:37-49.

Moreno-González, J., F. Ramos-Gourcy & E. Losada. 1997. Breeding potential of European flint and earliness-selected U.S. Corn Belt dent maize populations. Crop Sci 37:1475-1481.

Ordás, A. 1991. Heterosis in crosses between American and Spanish populations of maize. Crop Sci. 31:931-935.

Ordás, A., P. Revilla, R.A. Malvar & M.E. Cartea. 1994. Development of sweet corn hybrids adapted to the environmental conditions of the northwest of Spain. Maydica 39:171-175.

Rebourg, C., M. Chastanet, B. Gouesnard, C. Welcker, P. Dubreuil & A. Charcosset. 2003. Maize introduction in Europe : the history reviewed in the light of molecular data, Theoretical and Applied Genetics. 106:895-903.

Revilla, P., A. Boyat, A. Álvarez, B. Gouesnard, P. Soengas, A. Ordás & R.A. Malvar. 2005. Heterotic patterns among French and Spanish maize populations. Maydica: (in press).

Revilla, P., A. Butrón, R.A. Malvar & A. Ordás. 1999. Relationships among kernel weight, early vigor, and growth in maize. Crop Sci. 39:654-658.

Revilla, P., A. Butrón, R.A. Malvar & A. Ordás. 1998. Identifying open-pollinated populations of field corn as sources of cold tolerance for improving sweet corn. Euphytica 101:239-247.

Revilla, P., P. Soengas, M.E. Cartea, R.A. Malvar & A. Ordás. 2003. Isozyme variability among European maize populations and the introduction of maize in Europe. Maydica: 48:141-152.

SAS. 2000. The SAS System. SAS OnlineDoc.HTML Format. Version eight. SAS Institute, Cary, North Carolina.

Table 1. Mean squares from the analysis of variance of yield and yield components for a diallel of twelve French and Spanish populations grown in two Spanish locations and two French locations in 2000 and 2001 and in a cold chamber.

	Field trials					Cold chamber trial				
Source of variation	Degrees of freedom[a]	Early vigor	Adult plant appearance	Silking date	Plant height	Emergence proportion	Days to emergence	Survival	Early vigor	Color
Environments	7 (3)	15.73**	3.94**	717.47*	91470.51**					
Populations	77	1.38**	6.15**	103.46**	1410.33**	320.13**	9.76	58.93*	1.52*	1.19**
Varieties (v_j)	11	4.93	32.52**	707.87**	8693.90**	589.43**		37.60	2.38**	2.28**
Heterosis (h_{ij})	66	0.79**	1.75**	2.72**	196.40**	275.24*		27.48	1.37*	1.01
Average (h)	1	17.76**	10.49	14.20*	6362.20**	262.84		34.18	13.35**	0.26
Variety (h_j)	11	0.43	2.64**	1.14	172.31**	221.49		28.65	1.35	1.57*
Specific (s_{ij})	54	0.54**	1.41	2.83**	87.13**	286.42*		27.12	1.15	0.91
Environments × populations	539 (231)	0.81**	1.57**	1.62**	70.49**					
Environments × v_j	77 (33)	3.64**	4.30**	5.91**	217.05**					

Environments × h_{ij}	462 (198)	0.34**	1.11**	0.90**	46.06*					
Environments × h	7 (3)	0.24	2.08**	1.99**	121.19**					
Environments × h_j	77 (33)	0.41**	0.77*7	0.85	43.24					
Environments × s_{ij}	378 (162)	0.33**	1.64**8	0.89**	45.24					
Error	[b]	0.19	0.24	0.64	39.28	194.91	8.58	20.45	0.98	0.73

*,** Significant at P= 0.05 and 0.01, respectively.

[a] Degrees of freedom for early vigor and adult plant appearance are between parenthesis and were different than for the other traits because these traits were recorded only in both Spanish locations.

[b] The degrees of freedom for the error term were 1184 for silking date, 955 for plant height, 592 for early vigor, and 616 for adult plant appearance. And 154 for the cold chamber trial

Table 2. Mean and variety effects (v_j) for twelve parental maize populations of a diallel evaluated in 2000 and 2001 in two locations of Spain and two locations of France and in a cold chamber.

	Field trials								Cold chamber trial					
	Early vigor		Adult plant appearance		Silking date		Plant height		Emergence proportion		Early vigor		Color	
Population	mean	v_j	mean	v_j	mean	v_j	mean	v_j	mean	v_j	mean	v_j	mean	v_j
	(1-9)[a]		(1-9)[a]		days		cm		%		(1-9)[a]		(1-9)[a]	
Tuy	6.5	1.29*	5.5	0.15	69	2.29*	187	11.53*	76	-3.0	4.0	0.14	2.7	-0.53
Viana	4.7	-0.48	3.5	-1.86*	58	-8.70*	146	-29.67*	81	2.2	4.3	0.47	4.3	1.14*
Lazcano	6.2	0.99*	6.3	1.02	66	-1.04	174	-0.92	91	12.4	4.0	0.13	2.0	-1.19*
Basto/Rastrojero	4.4	-0.86*	4.8	-0.52	68	1.62	167	-8.15	88	9.9	4.7	0.81	4.7	1.47*
Rastrojero	5.1	-0.14	6.9	1.58*	74	7.35*	206	30.52*	58	-20.9*	2.7	-1.19*	3.0	-0.19
Enano levantino/Hembrilla	4.9	-0.35	6.0	0.67	70	3.88*	180	4.79	81	2.2	3.7	-0.19	3.7	0.47
Bade	5.3	0.10	4.8	-0.52	63	-3.59*	170	-5.37	92	13.7	5.3	1.47*	3.3	0.14
Lacaune	4.7	-0.50	3.7	-1.61*	61	-5.54*	154	-21.02*	67	-11.9	3.3	-0.53	3.3	0.14

Esterre	5.1	-0.08	4.4	-0.88	61	-5.36*	172	-2.87	74	-4.3	3.7	-0.19	2.7	-0.53
Ain	4.0	-1.22*	2.9	-2.43*	65	-1.71	153	-22.19*	79	0.6	4.0	0.14	2.7	-0.52
Millette du Lauragais	5.7	0.49	7.7	2.37*	72	5.67*	199	24.08*	90	11.1	3.3	-0.53	3.0	-0.19
Millette Montagne Noire	6.0	0.75*	7.3	2.03	72	5.13*	195	19.28*	67	-11.9	3.3	-0.53	3.0	-0.19
LSD (0.05)	1.3		1.7	1.77			9	15.75	23	23	1.6	1.62	1.4	1.39

* Exceeded twice the standard error.

[a] Using a scale from 1 = poor to 9 = high.

Table 3. Mean early vigor[a] (above the diagonal) and specific heterosis (below the diagonal) for a diallel of twelve maize populations[b] evaluated in 2000 and 2001 in two locations of Spain.

	Tuy	Viana	Lazcano	Ba/Ra	Rastrojero	El/He	Bade	Lacaune	Esterre	Ain	MdL	MMN
Tuy		6.2	7.2	6.1	6.7	6.2	5.6	6.2	5.9	5.8	6.3	6.5
Viana	0.08		6.3	5.3	6.6	5.6	5.3	5.2	5.4	5.0	5.5	6.2
Lazcano	0.33	0.09		6.4	6.5	6.2	6.6	5.9	6.1	6.2	6.4	6.6
Ba/Ra	-0.07	-0.24	0.06		5.3	5.8	6.2	6.2	4.9	5.4	6.0	5.8
Rastrojero	0.26	0.80*	-0.11	-0.55*		5.6	6.0	5.9	6.3	5.6	5.7	5.7
El/He	0.16	0.14	0.01	0.27	-0.13		5.8	5.9	5.6	4.3	5.5	5.8
Bade	-0.63*	-0.35	0.19	0.44	0.03	0.19		5.5	5.8	5.9	5.7	6.1
Lacaune	0.19	-0.24	-0.32	0.68*	0.13	0.54*	-0.14		5.2	5.5	4.9	5.7
Esterre	-0.25	-0.11	-0.25	-0.69*	0.43	0.08	0.08	-0.33		6.1	6.1	6.0
Ain	-0.18	-0.39	0.02	-0.09	-0.13	-1.09*	0.31	0.22	0.63*		5.8	6.2
MdL	0.09	-0.07	0.04	0.36	-0.23	-0.14	-0.10	-0.62*	0.30	0.25		6.1
MMN	0.02	0.29	-0.04	-0.17	-0.50	-0.04	-0.01	-0.10	-0.02	0.44	0.06	

LSD (0.05) = 1.3 for means. For specific heterosis LSD = 0.77 for hybrid sharing a common parent, and 0.72 for unrelated hybrids.

* Exceeded twice the standard error. [a] Using a scale from 1 = poor to 9 = high.

[b] Ba/Ra=Basto/Rastrojero, El/He=Enano levantino/Hembrilla, MdL=Millette du Lauragais, and MMN=Millette Montagne Noire.

Table 4. Mean silking date (above the diagonal, days) and specific heterosis (below the diagonal) for a diallel of twelve maize populations[a] evaluated in 2000 and 2001 in two locations of Spain and two locations of France.

	Tuy	Viana	Lazcano	Ba/Ra	Rastrojero	El/He	Bade	Lacaune	Esterre	Ain	MdL	MMN
Tuy		64	67	68	71	68	65	65	64	66	70	70
Viana	0.65*		62	62	66	64	60	59	59	60	64	64
Lazcano	-0.38	0.50		67	70	68	64	63	63	65	68	68
Ba/Ra	0.36	-0.94*	0.61*		71	68	67	64	64	66	69	69
Rastrojero	-0.21	0.02	0.77	0.21		72	69	67	66	69	73	72
El/He	-1.06*	0.43	0.14	-0.64*	0.12		68	66	65	68	70	70
Bade	-0.36	-0.67*	-0.91*	1.58*	0.13	1.01*		62	62	63	67	67
Lacaune	0.66*	-0.17	-0.55	-0.06	0.09	0.17	-0.06		60	62	66	67
Esterre	-0.03	0.54	0.14	-0.30	-1.18*	-0.10	0.50	-0.78*		62	67	66
Ain	0.24	-0.37	-0.13	0.03	-0.12	1.04*	-0.52	-0.01	0.21		67	67
MdL	-0.14	-0.02	-0.11	-0.62*	0.30	-0.87*	0.06	-0.16	0.76*	-0.10		72
MMN	0.26	0.03	-0.06	-0.22	-0.14	-0.23	-0.76*	0.88*	-0.39	-0.28	0.61*	

LSD (0.05) = 1.2 for means. For specific heterosis LSD = 0.9 for hybrid sharing a common parent, and 0.8 for unrelated hybrids.

* Exceeded twice the standard error.

[a] Ba/Ra=Basto/Rastrojero, El/He=Enano levantino/Hembrilla, MdL=Millette du Lauragais, and MMN=Millette Montagne Noire.

Table 5. Mean emergence proportion (above the diagonal, %) and specific heterosis (below the diagonal) for a diallel of twelve maize populations[a] evaluated in a cold chamber.

	Tuy	Viana	Lazcano	Ba/Ra	Rastrojero	El/He	Bade	Lacaune	Esterre	Ain	MdL	MMN
Tuy		72	87	94	83	68	88	96	87	90	87	82
Viana	-8.81		90	78	65	74	88	65	68	74	87	87
Lazcano	-2.13	8.89		92	82	91	95	90	79	73	83	74
Ba/Ra	6.71	-0.21	5.18		72	82	96	83	82	87	64	82
Rastrojero	3.42	-6.06	1.79	-5.93		50	87	78	78	76	83	88
El/He	-10.56	4.31	12.27	5.72	-19.77*		73	91	62	71	71	97
Bade	-1.63	6.83	4.54	8.25	6.24	-6.46		76	87	86	79	88
Lacaune	9.32	-12.98	2.67	-1.31	0.53	14.75*	-12.21		95	92	85	61
Esterre	4.14	-6.63	-3.80	1.20	4.31	-10.95	3.11	14.07		85	87	64
Ain	3.24	-3.68	-13.67	2.86	-1.71	-5.43	-1.63	8.04	4.14		92	83
MdL	0.17	8.63	-3.93	-20.73*	5.47	-5.95	-8.55	-0.16	-1.44	7.86		95
MMN	-3.88	9.71	-11.81	-1.74	11.69	22.06*	1.51	-22.72*	-23.43*	-0.03	11.00	

LSD (0.05) = 23 for means. For specific heterosis LSD = 22 for hybrid sharing a common parent, and 20 for unrelated hybrids.

* Exceeded twice the standard error.

[a] Ba/Ra=Basto/Rastrojero, El/He=Enano levantino/Hembrilla, MdL=Millette du Lauragais, and MMN=Millette Montagne Noire.