

ARTICLE

Genetic variability and breeding potential of Flintisa Composite of maize in two levels of technology

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Abstract: The purpose this study was to verify the breeding potential of Flintisa Composite for low (LT) and high (HT) technology of cultivation, and the best selection strategy to be adopted. For this reason half-sib progenies were evaluated in the two technological levels. In HT, it was used basic fertilization, two top dressing and supplementary irrigation. In LT, these practices were suppressed, and less fertile soil was used. Except for grain yield (GY), heritability was high at plant level and at progenies mean level. With mass selection, estimated gains ranged from 3.3% (GY in LT) to 41.8% (tassel branches number in LT). For half-sib selection, estimated gains ranged from 4.7% (plant height in HT) to 23.6% (erect plants in HT). For ear height, stratified mass selection in just one environment should be valid for both. Half-sib selection, with S_1 recombination should be adopted in specific selection programs for LT and HT.

Keywords: heritability, genetic additive variance, selection, genotype x environment interaction.

INTRODUCTION

Obtaining cultivars with good agronomic potential requires continuous selection programs. In these breeding programs, the knowledge of the genetic variability in the population is of great interest for breeders, since variability is fundamental for the success of a selection work. Once every observation that is made on a quantitative trait consists of a genetic and a non-genetic (environmental) component, the variance of this trait is also composed of genetic and environmental variances. The former is used in selection, and the latter is not, and it goes against the breeder's interest (Vencovsky 1987).

The decision on the best improvement method, on the proper selection intensity, and on the traits to be considered in the selection is based on the knowledge of the genetic structure of the population. Therefore, the estimate of genetic parameters, such as additive genetic variance, variance of the progeny x environment interaction, heritability, and expected progress with selection is one of the first steps to be taken in a breeding program (Singh et al. 2018), and it should be carried out in various environments, if possible. The genotype x environment interaction may hinder selection in breeding for various environments. Its magnitude will indicate if it is necessary to use separate selection programs. In the case where the environment differs on technology levels, it is possible to obtain important information on the breeding potential of populations, in order to obtain more responsive and/or more rustic varieties.

Crop Breeding and Applied Biotechnology 19: 145-152, 2019 Brazilian Society of Plant Breeding. Printed in Brazil http://dx.doi.org/10.1590/1984-70332019v19n2a21

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> Received: 28 August 2014 Accepted: 12 August 2015

¹ Universidade Estadual Paulista, Departamento de Biologia e Zootecnia, Campus de Ilha Solteira, 15.385-000, SP, Brazil For the second case, the efforts are justified in studies aimed to obtain cultivars with greater ability to take advantage of the naturally available resources, or that are offered in insufficient amount, such as soil nutrients.

The process of genetic parameter estimation was made feasible, developed and widely used for several schemes of genetic mating and genetic-statistical procedures (Falconer and Mackay 1996, Hallauer et al. 2010, Khan et al. 2018). Over the selection cycles, this procedure helps in the checking, from time to time, of the evolution of genetic variability and the need for changes in the selection process (Freitas Júnior et al. 2009). Large ranges of values in the genetic parameter estimates are reported for the traits studied in this work, as well as other traits that make part of yield components in Brazilian maize populations (Candido and Andrade 2008, Andrade and Miranda Filho 2008, Faluba et al. 2010, Reis et al. 2014) and semi-exotic populations (Oliveira et al. 2015, Souza et al. 2018).

This study aimed to verify the genetic variability and the potential of Flintisa Composite for breeding in high and low cultivation technology environments, and the best selection strategy to be adopted.

MATERIAL AND METHODS

Flintisa Composite was obtained by the recombination of the populations Esalq - VF 1, Suwan and Cateto Colombia. It was subjected to six selection cycles for yield. The first, the second, the fourth and sixth cycles were carried out based on stratified mass selection. The third selection cycle was carried out between half-sib, and the fifth cycle was carried out between half-sib progenies with S₁ progenies recombination. All selection cycles were carried out without any fertilizer, and were considered as low technology environment.

In this study, it was used 223 half-sib progenies with their respective S_1 progenies, taken from prolific plants of the population obtained after the sixth selection cycle in Flintisa Composite. Half-sib progenies were evaluated in eight experiments set in high-tech environment (soil of average fertility, with fertilizer according to soil analysis, and under supplementary irrigation). Of this total, 191 progenies were also evaluated in eight experiments in low-tech environment (less fertile soil, without fertilization and without irrigation), as shown in Table 1. The S_1 progenies were stored as remnant seed, aiming at the recombination of progenies selected by the method of selection between half-sib, with recombination of inbred progenies.

All experiments were carried out in a randomized block design with three replications, in the agricultural year of 2010/11, in Selvíria-MS (lat 20° 20′ S, long 51° 21′ W, and alt 335 m asl). The high-tech environment experimental plot consisted of a 4m row with 20 plants, spaced 20 cm apart. In the low-tech environment, plots consisted of a 4.28 m row, with 20 plants spaced 21.4 cm apart. In both cases, the spacing between rows (plot) was 85 cm. The commercial hybrids, P30F80 and C 929, were used as controls in the high-tech experiments, and the hybrids AG519 and Master were used as control in the low-tech experiments. The change in the controls was due to their different adaptability. The hybrids P30F80 and C929 are recommended for high-tech farms, whereas the hybrids AG 519 and Master are more rustic, and thus are recommended for low-tech farms.

In the high-tech environment it was used a fertilization of 250 kg ha⁻¹ of the formula 8-28-16, at sowing, and two top dressings. In the first (at the stage of 4 to 5 developed leaves), it was applied 300 kg ha⁻¹ of the formula 20-00-15, and in the second (at the stage of 6 to 7 developed leaves), 140 kg ha⁻¹ of urea. The population of 58,800 plants ha⁻¹ was used since most commercial cultivars recommended for high technology adopt population around 60,000 plants ha⁻¹. This is also because fertilization was carried out aiming at a yield of about 8 t ha⁻¹, and because the experiment was set under the central pivot. The low-tech environment was primarily characterized by a little less fertile soil (Table 1), and by the absence of fertilization, which also led to the use of a smaller plant population (55,000 plants ha⁻¹).

Table 1. Chemical analysis of the soil where the experiments of maize progenies were carried out

Tachnalagulaval	P-resin	O.M.	pH in	K ⁺	Ca⁺⁺	Mg ⁺⁺	(H⁺+AI***)	V
Technology level	mg cm ⁻³	(%)	CaCl ₂		Med	cm ⁻³		(%)
High-tech	16	2.8	4.8	0.23	2.1	1.6	3.8	51
Low-tech	09	2.4	4.9	0.12	1.4	1.7	3.4	49

The following variables were analyzed in the trials: Plant height (PH) - measured in m, from the ground level to the bottom of the flag leaf sheath (mean of five competitive plants in the plot); Ear height (EH) - measured in m, from the ground level to the insertion of the upper ear (mean of five competitive plants in the plot); Tassel branches number (TB) - obtained by simple counting, as the mean of five competitive plants in the plot; Erect plants (EP) - percentage of plants that did not fall in relation to the final stand of the plot; Grain yield (GY) - measured in kg as the total of the plot, adjusted to 13% moisture, and to ideal stand of 20 plants per plot, by analysis of covariance (Vencovsky and Barriga 1992).

The experiments were analyzed individually, grouped for each technology level and jointly, involving both technology levels. Data from individual plants were used to calculate separately the mean square within plots, whereas the plots means were used to calculate the other mean squares of the analysis of variance, except for GY, for which total plots were used. Analysis of covariance was carried out between variables in order to obtain estimates of phenotypic and additive covariance, and the coefficients of phenotypic and genetic additive correlations. For this purpose, all variables, except for GY, were considered as plot means. For the estimates, the environment factor was considered as fixed, and the progenies factor was considered as random, according to Vencovsky and Barriga (1992).

Based on the expectations of mean squares and mean products, the following parameters were estimated for each technology level and/or joint analysis (Vencovsky and Barriga 1992): a) Phenotypic variance within progenies for PH, EH and TB. For GY, the within phenotypic variance was considered to be 10 times the environmental variance between plots, as suggested by Gardner (1961); b) Environmental variance between plots; c) Genetic variance between progenies; d) Variance of the progenies x technology levels interaction; e) Phenotypic variance at plant level; f) Mean phenotypic variance; g) Additive genetic variance; h) Coefficient of heritability for selection based on individual plants; i) Coefficient of heritability for selection based on progeny means; j) Expected gain with mass selection for one sex; k) Expected gain with selection between and within half-sib progenies, for two and one sex, respectively; l) Environmental covariance; m) Covariance between progenies; n) Additive genetic covariance; o) Mean phenotypic covariance; p) Coefficient of phenotypic correlation; q) Coefficient of additive genetic correlation; r) Correlated response with mass selection in one sex; s) Correlated response with selection between and within half-sib progenies, for two and one sex, respectively.

RESULTS AND DISCUSSION

Most of the coefficients of variation of the experiments were below 20%, except for EP in high-tech environment. This suggests good accuracy of the results for progeny trials, which is in accordance with the literature (Scapim et al. 1995). EP is related to lodged plants, and in this sense, the high coefficients of variation are also in agreement with the literature. Also, the ratio between the highest and lowest residual mean square was lower than 7 for all traits, indicating the possibility of carrying out grouped and joint analyses of variance for each environment (Pimentel-Gomes and Garcia 2002).

The first evidence of genetic variability is noticed by significant F test for progenies (p<0.01) for all traits in the grouped analyses in both environments and in joint analysis (Table 2). In high-tech environments, plants had higher means for PH and EH, and lower means for EP (higher incidence of lodging), compared to low-tech environment. Compared to the controls, progenies means were 7.8 and 16.4% higher for plant and ear height, respectively (18.9 and 22.4 cm higher). On the other hand, EP in progenies was 41.1% lower than in controls. This is normally associated with plant and ear heights, since, in most populations, there is positive correlation between these traits and lodging (Candido and Andrade 2008), and it is also associated to the fact that controls are selected for less lodging and breakage. Thus, it would be expected that the correlation of PH and EH with EP is negative. This did not occur in the present study, since correlations were close to zero (Table 4). In this case, poor quality of stem and high density of plants might have contributed to the difference between progenies and controls. In low-tech environment, EP difference was not so high, and progenies presented 12.5% less EP than controls. Although correlations were not high, plants were shorter in low-tech than in high-tech environment.

For GY, progenies mean was below the controls mean in both environments. Differences were 31.6% and 34.8%, in high and low-tech environments, respectively (Table 2). However, in both environments, it was observed that the best progenies were similar to controls.

Estimates of additive variance (Table 3) were high for PH (279.8 and 355.1 (cm pl $^{-1}$)²), and EH (207.9 and 209 (cm pl $^{-1}$)²),

when compared with data presented by Candido and Andrade (2008), Andrade and Miranda Filho (2008), Hallauer et al. (2010) and Faluba et al. (2010) and similar to estimates by Souza et al. (2018). For GY, the estimate of 588.1 (g pl⁻¹)² (hightech environment) was superior to the mean found by Hallauer et al. (2010) and Reis et al. (2014), similar to estimates by Souza et al. (2018) for the populations CRE-1 and CRE-2, but lower than the estimate found by Faluba et al. (2010) for UFV 7 population (622.7 (g pl⁻¹)²). For TB, the additive variances were 21.9 (high-tech) and 34.7 (branches pl⁻¹)² (low-tech), close to that obtained by Souza Júnior et al. (1985) (28.55), Souza et al. (2018) (19.29 and 18.9) and higher than that obtained by Andrade and Miranda Filho (2008) (13.57 (branches pl⁻¹)²).

Heritability coefficients (Table 3) were high both at individuals level and means level, for PH, EH, TB and EP. For GY, heritability at mean level (56% in high-tech and 41.7% in low-tech) was 3.8 and 4.9 times higher than at plant level. Heritability of these magnitudes was also found by Andrade and Miranda Filho (2008), Candido and Andrade (2008), Faluba et al. (2010) and Souza et al (2018). Araújo et al. (2005) also obtained similar estimate for the population CMS 39, evaluated at 0.9 m spacing (44.6%), and lower estimates at 0.5 m spacing (29.5%). For PH, EH and GY, Shahrokhi et al. (2013) and Carvalho et al. (2003) obtained similar estimates in populations ksc 704, CMS 47, BR 5011, CMS 35 and CPATC-3. Under nitrogen stress conditions, Soares et al. (2011) found heritability of 82%, 72% and 83%, respectively, for PH, EH and GY, in a population originated from the crossing between two tropical inbred lines.

In low-tech environment, EP also presented high heritability at mean level. However, the expected gain was 44.7% lower when compared to high-tech environment (Table 3), although, in absolute terms, gains were similar in both environments. This is because the mean was 53.3% higher, and the heritabilities were similar.

According to the expected gains (Table 3), it appears that PH, EH and TB may be easily modified with mass selection. Even using the S_1 progenies recombination, in which it is expected that gain with selection between half-sibs are duplicated (Vencovsky 1987), mass selection should still be preferred. The expected gains with mass selection in EH were 12.6%

Table 2. Means, coefficients of variation and means squares (MS) of the grouped and joint analyses of variance for plant height (PH), ear height (EH), tassel branches number (TB), percentage of erect plants (EP) and grain yield (GY) of maize

S.V.	df	PH (cm)	EH (cm)	ТВ	EP (%)	GY (kg plot ⁻¹)
		MS of gro	ouped analysis in high	tech environment		
Progenies/Exp.	222	301.479 **	229.873 **	22.633 **	516.019 **	0.315 **
Controls x Exp.	7	31.417	20.783	0.823	57.420	0.060
Mean error	476	91.655	73.929	6.213	228.098	0.139
Within progenies	2758	312.886	254.792	25.385	-	-
Progenies mean	-	261.19	158.77	22.67	54.36	2.14
Controls mean	-	242.30	136.40	14.89	92.26	3.13
CV (%)	-	3.66	5.42	10.99	29.08	17.37
		MS of gr	ouped analysis in low-	tech environment		
Progenies/Exp.	190	383.744 **	230.189 **	32.274 **	345.483 **	0.101 **
Controls x Exp.	7	143.502	42.606	3.265	36.324	0.105
Mean error	412	117.404	73.407	6.245	145.683	0.039
Within progenies	2568	335.526	237.496	28.462	-	-
Progenies mean	-	243.59	139.56	21.21	83.36	1.49
Controls mean	-	234.60	132.15	18.25	95.23	2.29
CV (%)	-	4.45	6.14	11.78	14.48	13.28
		MS of jo	oint analysis for both t	echnology levels		
Tech. Level (TL)	1	12159.153 **	13343.951 **	35.182 **	39850.602 **	1.492 **
Progenies/Exp	190	580.859 **	373.842 **	47.051 **	585.017 **	0.231 **
Progenies/Exp x TL	190	109.935	80.645	7.872	197.298	0.184 **
Mean error	824	106.900	74.324	6.939	194.928	0.093
Progenies mean	-	251.75	148.48	23.24	68.69	1.84
CV (%)	-	4.11	5.81	11.34	20.33	16.53

^{** -} Significant at 1% probability level.

and 14.8%/cycle, respectively, for high and low-tech environments. For PH, the expected gains with selection between half-sibs (4.6% for high, and 5.6% for low-tech environments) were similar to those reported by Kist et al. (2010) for the population MPA1.

For GY, the expected gain with mass selection in high-tech environment was 7.7%, which is equivalent to the gain of 7.9% reported by Souza et al. (2018) in three semi-exotic populations, and higher than that reported by Andrade and Miranda Filho (2008) (4.17%). In low-tech environment, it was calculated a 50% lower expected gain. In selection between progenies, it is expected a gain twice as the mass selection gain, both for high and low-tech environments. In this type of selection, gain in low-tech environment (7.3%) is equivalent to that obtained by Andrade and Miranda Filho (2008) (6.98%), and the gain in high-tech environment (14.8%) is close to that obtained by Candido and Andrade (2008) for a dwarf population, in densities of 57,800 and 80,000 plants/ha (16.0 and 19.2%, respectively). Araújo et al. (2005) estimated lower gains (8.1 and 9.0%) for the population CMS 39, at 0.5 m and 0.9 m spacing, as well as Kist et al. (2010), with estimates of 3.9%, 5.7% and 5.0% for the population MPA1, in a convergent-divergent selection scheme. In this study, gains with mass and selection between progenies are practically the same, when considering the time and labor required to carry out a selection cycle by both methods. In this case, it is expected that the use of half-sib

Table 3. Genetic parameter estimates for each technology level, and for joint analysis for plant height (PH), ear height (EH), tassel branches number (TB), erect plants (EP), and grain yield (GY) for Flintisa Composite of maize

Parameters	PH	EH	ТВ	EP	GY
	High-te	ech			
Variance within progenies	312.89	254.79	25.38		3464.02
Environmental variance	29.08	22.97	1.14	228.10	346.40
Variance between progenies	69.94	51.98	5.47	95.97	147.02
Additive genetic variance	279.76	207.93	21.89	383.89	588.09
Individual phenotypic variance	411.90	329.74	31.99		3957.44
Mean phenotypic variance	100.49	76.62	7.54	172.01	262.49
Heritability at plant level	0.68	0.63	0.68		0.15
Heritability at mean level	0.697	0.68	0.72	0.56	0.56
Gain with mass selection (%)*	9.26	12.66	29.99		7.65
Gains with selection between HS1 (%)*	4.69	6.56	15.42	23.62	14.85
Gains w/ sel. betw. and within HS (%)*	8.37	11.56	28.10		16.54
	Low-te	ch			
Variance within progenies	335.52	237.50	28.46		2168.30
Environmental variance	50.30	25.91	0.55	145.68	216.83
/ariance between progenies	88.78	52.26	8.68	66.60	51.75
Additive genetic variance	355.12	209.04	34.70	266.40	207.00
ndividual phenotypic variance	474.60	315.66	37.69		2436.88
Mean phenotypic variance	127.91	76.73	10.76	115.16	124.03
Heritability at plant level	0.75	0.66	0.92		0.085
Heritability at mean level	0.69	0.68	0.81	0.58	0.42
Gain with mass selection (%)*	11.74	14.79	41.84		3.32
Gains with selection between HS1(%)*	5.65	7.50	19.58	13.06	7.36
Gains w/ sel. betw. and within HS (%)*	10.49	13.42	36.26		8.27
	Joint Ana	alysis			
Environmental Variance	106.90	74.32	6.94	194.93	288.75
Variance between progenies	78.99	49.92	6.68	65.01	115.25
Additive genetic variance	315.97	199.68	26.74	260.06	460.75
/ariance of progeny x TL² interaction	0.50	1.05	0.15	0.39	28.50
Mean phenotypic variance	96.81	62.31	7.84	97.50	163.25
Heritability at mean level	0.82	0.80	0.85	0.67	0.70
Gain with selection between HS (%)*	5.60	7.47	18.03	16.82	15.02

¹ Half-sib; ² Technological level; * Intensity of 10% for all selection modalities; Selection for both sexes between progenies, and one sex within progenies and in mass selection.

selection with S_1 recombination surpasses mass selection in efficiency, which usually occurs for traits of low heritability. In low-tech environment, the expected gain with selection between progeny was lower than high-tec (3.3%). However, with selection between and within half-sib progenies, it is expected a gain of 8.3%/cycle, showing that, in this case, it will be the best method to be used, as suggested by Candido and Andrade (2008). In the most stressful conditions, the discrimination between superior and inferior genotypes is less accurate, probably due to the limitation of the expression of many genes with additive effects, which requires more accurate techniques for selection. Thus, it is noted that obtaining considerable gains in yield depends on the use of inbreeding in the selection unit, in the evaluation unit, or in both, as in the case of the selection between S_1 progenies, when all the additive variance is exploited.

The expected gain with mass selection for TB in low-tech environment (41.8%) was 1.4 times higher than in high-tech, and also higher than expected for the varieties Centralmex (23.2%), Dentado composite (10.9%), Flint composite (13.4%) (Geraldi et al. 1985), Esalq-PB1 (27.4%) (Andrade and Miranda Filho 2008) and three semi-exotic populations (1.4, 0.03 and 0.22%) (Souza et al. 2018).

The correlation coefficients (Table 4) and the correlated responses (Table 5) indicated genetic independence of PH and EH in relation to TB and EP. This indicates that although the high lodging may be due to PH and EH, this is an environmental relationship. Thus, the high population would have caused some etiolating, making the stems more fragile.

Due to the high correlation between PH and EP, selection for lower ear height is sufficient, in this population, to assist in the improvement of plant architecture, as indicated by Tengan et al. (2012) in backcross populations between not opaque and opaque-2 maize and Izzam et al. (2017). On the other hand, under high-tech environment, correlations of TB with EP and with GY are negative, indicating that selection for less tassel branches will provide a decrease in lodging and an increase in GY. As TB has high heritability, it can be an excellent selection trait to increase yield, especially in more advanced selection cycles, when the genetic variance for yield is lower. With mass selection, this possibility of gains with indirect selection is in agreement with the studies of Falconer and Mackay (1996), since there is high additive genetic correlation between traits, low heritability in the main trait (GY), and high heritability in the secondary trait (TB). Sohail et al. (2018) also found favorable correlations between physiological traits and GY in the CZP-132011 population.

Selection based on EP is also a good possibility to bring about positive correlated response in yield, almost equal to the expected gain with direct selection. This is done indirectly, since lodged and/or broken plants are rejected at any selective process, helping to maximize the gain in GY.

There was significance at 1% probability for the technology level variation source in all the traits. However, only GY had significant interaction between progeny and technology levels. Vencovsky and Barriga (1992) consider that, in any population with genetic variability, there will be genotype x environment interaction. The relative magnitude of this interaction subsidizes the breeder in relation to the strategy of choosing genotypes of broad adaptation or of restricted

Table 4. Estimates of the coefficients of additive genetic correlation (above the diagonal) and phenotypic correlation at mean level (below the diagonal), between plant height (PH), ear height (EH), tassel branches number (TB), erect plants (EP) and grain yield (GY) for Flintisa Composite in high and low technology environments

	PH	EH	ТВ	EP	GY
			High-tech		
PH		0.73	0.02	0.04	0.21
EH	0.73		0.07	0.02	0.31
TB	0.04	0.02		-0.35	-0.32
EP	0.02	0.02	-0.25		0.50
GY	0.17	0.26	-0.24	0.37	
			Low-tech		
PH		0.93	0.09	0.02	0.38
EH	0.87		0.18	-0.03	0.33
TB	0.08	0.16		-0.11	0.08
EP	-0.02	-0.05	-0.08		-0.06
GY	0.28	0.23	0.07	0.04	

Table 5. Estimates of correlated responses in plant height (PH), ear height (EH), tassel branches number (TB), erect plants (EP), and grain yield (GY), with selection between and within half-sib progenies and mass selection (10% intensity) in Flintisa Composite, in high and low-tech environments

Correlated	Selected trait						
Response ¹	AP (%)	AE (%)	NR (%)	PP (%)	RG (%)		
	High-tec	h environment – Select	ion between and within				
PH		5.891	0.174	0.178	0.899		
EH	8.582		0.846	0.103	1.868		
ТВ	0.558	1.864		-5.198	-4.305		
EP	1.121	0.450	-10.352		11.818		
GY	3.537	5.117	-5.368	7.400			
	H	ligh-tech environment -	– Mass Selection				
PH		6.561	0.196				
EH	9.658		0.951				
ТВ	0.628	2.075					
	Low-tec	h environment – Selecti	ion between and within				
PH		12.887	3.153	0.321	3.573		
EH	9.191		5.682	-0.381	3.084		
ТВ	1.056	2.669		-1.758	0.878		
EP	0.116	-0.186	-1.889		-0.561		
GY	1.652	1.927	1.209	-0.718			
	l	ow-tech environment -	- Mass Selection				
PH		14.678	3.591				
EH	10.312		6.375				
ТВ	1.240	3.134					

¹ Selection for both sexes between progenies and one sex within progenies and in mass selection.

adaptation to specific environments. Although the influence of the interaction in high heritability traits is usually lower, Carvalho and Souza (2007) and Aci et al. (2018) state the importance of evaluating yield in various environments, in order to improve the efficiency of the selection process, and to obtain more accurate estimates of variance components.

The expected gain with selection between half-sib, taking into account the means of the two environments, is equivalent to that expected with the specific selection for each environment (Table 3) for PH, EH and TB. For EP, the expected gain with joint selection is 28.8% lower than that expected with selection in high-tech, and 28.7% higher than that expected in low-tech environment. These results and the non-significance of the progenies x technology levels interaction indicate that in the traits related to plant architecture (PH, EH and TB) and EP, selection may be carried out in any of the environments, with valid results for both. The comparison between the estimates of the progenies variance and the progenies x technology levels interaction (Table 2) shows that the latter is lower than the former for PH, EH, TB and EP. For GY, progenies variance was four times higher than the interaction variance. However, since the interaction variance was significant, it is suggested that separate programs are carried out for better adaptation to specific environments. This does not exclude the possibility of achieving progeny that adapt to both environment (Table 3). However, the evaluation in both environments is still required, so there is no divergence between the progenies selected in each environment. Thus, it is recommended to carry out separate programs for GY, since the selection process by grouping the two environments does not reduce costs. Moreover, there is the possibility of having sharp decrease in gain with joint program, as genetic variability decreases over the selection cycles.

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