Genotypic variability and response to selection in foxtail millet (*Setaria italica* (L.) P. Beauv.)

Variabilidad genotípica y respuesta a la selección en moha (*Setaria itálica* (L.) P. Beauv.)

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Abstract

Foxtail millet (*Setaria italica*) is a summer annual C4 short-season crop used as cereal and forage. The aim of this study was to estimate genetic parameters useful for genetic improvement of traits related to grain and forage yield in populations adapted to Argentina. Genotypic variation, genotypic correlations and the expected genetic gain in pure lines selection were estimated in cultivars Carapé INTA y Yaguané INTA. The cultivars differed mainly in number of tillers, plant height and panicle size. Yaguané INTA showed higher levels of genotypic variation than Carapé INTA in all traits. The number of tillers had strong negative correlations with the rest of morphological traits in Yaguané INTA while these correlations were less marked in Carapé INTA. The expected genetic gains in Yaguané INTA were higher than those obtained in Carapé INTA for all traits with greater gains in panicle size and number of tillers. The estimated parameters suggest that Yaguané INTA has the greatest potential for genetic improvement.

Key words: Biomass yield, genotypic correlations, heritability, inbred lines.

Resumen

La moha (*Setaria italica*) es un cultivo de verano, anual, tipo C_4, utilizado como cereal o forraje. El objetivo de este estudio fue estimar parámetros genéticos de utilidad para el mejoramiento en caracteres relacionados con rendimiento de grano y forraje en las poblaciones de la especie adaptadas de Argentina. Se estimaron la variabilidad y las correlaciones genotípicas, y la ganancia genética esperada por selección de líneas puras en los cultivares Carapé INTA y Yaguané INTA. Los cultivares se diferenciaron principalmente en número de macollos, altura de planta y tamao de panoja. En todos los caracteres evaluados, Yaguané INTA mostró mayores niveles de variabilidad genotípica que Carapé INTA. En Yaguané INTA el número de macollos presentó una fuerte correlación negativa con el resto de caracteres morfológicos, mientras que en Carapé INTA esta asociación fue menos marcada. Las ganancias genéticas esperadas en Yaguané INTA fueron superiores que las obtenidas en Carapé INTA sobre todos los caracteres, con las mayores ganancias en el tamao de panoja y número de macollos. Los parámetros estimados sugieren que Yaguané INTA posee el mayor potencial para mejoramiento.

Palabras clave: Correlaciones genotípicas, heredabilidad, líneas puras, rendimiento de biomasa.

Introduction

The foxtail millet (*Setaria italica* (L.) P. Beauv.) is a C4 annual Poaceae with a very short stationary growth cycle. It is self-pollinating species with estimated rates of outcrossing between 0.0 – 1.4% (Till-Bottraud *et al.* 1992). The reduced size of its genome ($2n = 2x = 18$, 1C = 490 Mb) with a highly conserved structure has determined the foxtail millet as a model for genetic and phylogenetic studies related with other C4 species used for bioenergy, deriving in the full sequencing of its genome (Zhang *et al.*, 2012). Foxtail millet is adapted to subtropical, temperate-humid, subhumids and semiarids climates. It is cultivated above 2000 masl, mainly in regions with annual precipitations between 400 and 700 mm. It is a crop that can tolerate water deficit due to its short cycle (60-100 days) and its high water use efficiency (Brink, 2006). This species is used as cereal in Asia, mainly in China and India, Africa and eastern Europe; in North and South America, Europe, South Africa and Australia is used as forage crop as hay and silage (Baltensperger, 1996). In Argentina, the existing cultivars were obtained between 1965 and 1968 by individual selection on introduced populations from China in 1960 that have some variability (Larreguy, 1982). The high degree of autogamy in this species determined relatively stable populations composed by a mix of homozygous genotypes. Thus, available cultivars nowadays shall constitute local varieties or landraces, with low maintenance and affected by diverse processes in the environments where they were multiplied during almost 50 years since their introduction. Among these cultivars maintained and multiplied by commercial businesses, the only ones conserved today are Carapé INTA and Yaguané INTA. Both are used as forages and represent all the existent variability in the country. However, they have not been characterized according to population genetic parameters in traits associated with grain production and total biomass. This prevents the correct valuation of strengths and weaknesses of the available germplasm. The objective of the present study was to estimate useful genetic parameters for breeding and to define selection criteria in adapted populations of foxtail millet.

Materials and methods

From a commercial multiplication batch of Carapé INTA and Yaguané INTA cultivars panicles from individual plants were harvested. Then the progeny of each was obtained, they were composed of highly homozygous and genetically identical individuals, in order to get pure lines (Cubero, 2003). In this way, two groups of lines were derived, one from each landrace, and for this study a sample with 32 representative pure lines was taken. The experiment was performed in summer 2008-09 in the Pergamino Station of INTA in Buenos Aires (33° 54' S and 60° 35' W), Argentina, on a typic Argiudol soil with silt loam texture. The experimental design used was a quadruple lattice 8 x 8, with plots of 14 plants in line spaced 0.4 x 0.4 m. The experiment was done under a rainfed and no fertilization regime. Number of says to 50% of the plot in anthesis were registered. On six plants of each plot it was measured the lamina length and width of the leaf before the flag leaf; plant height; tillers number; length, width and weight of the main panicle and weight of 100 seeds. On four plants of each plot it was determined the neutral detergent fiber content (NDF) and the acid one (ADF) and, the in vitro dry matter digestibility (IVDMD), according to the Ankom Technology technique (ANKOM Corp., 2009). To analyse variability between and among populations it was used a mixed linear model with nested factors, with population effects fixed and the line effects within the population random. Equations of mixed model and expected mean squares were used to determine the effect significance and to estimate the components of the variance by the GLM procedure with the software SAS (SAS Institute Inc., 2009). Heritability on a wide sense, based on the line means, was calculated according to: $H^2 = s^2_G / s^2_G + s^2_{amb}$, where s^2_G is the genotypic variance (pure lines) and s^2_{amb} is the environmental variance (residual). Standard errors and confidence intervals of H^2 and the genotypic correlation coefficients (r_G) between traits were evaluated according to Bernardo (2002). The expected response when pure lines are selected by plot means was estimated according to Bernardo (2002): $R = i.\ H^2.\ s_F$, where i=selection strength and s_F is the phenotypical standard deviation. The expected correlated response in the Y trait (RC_Y) by indirect selection on the X traits was calculated according to Simmonds and Smartt (1999): $RC_Y = i.\ H_X.\ H_Y.s_{F(Y)}.\ r_{G(XY)}$.

Results

Mean values, ranges and coefficients of variations for each population are shown in Table 1. Yaguané population had less number of tillers, it was taller, laminas were bigger and panicles were larger and heavier than Carapé. This last one was, in average, earlier and with heavier seeds. Parameters related with forage quality (NDF, ADF and IVDMD) were similar in both populations. Ranges and coefficients of variation of Yaguané were higher in the twelve studied traits.

In Table 2 is observed that the largest proportion of variability between populations was in tiller number, panicle length and weight. In contrast, there was a larger variability among the lines within the populations for the characters of lamina width, days to flowering, weight of 1000 seeds, NDF, ADF and IVDMD. When the variation of each population is considered, there is a higher variability within the lines of Yaguané population for all the characters. Comparison between population means showed differences (P <0.05) for all the characters except NDF and IVDMD. Similarly, there were significant differences between the total per line for all the characters. Differences between the Yaguané lines were highly significant (P <0.01) for all the characters, whereas for Carapé lines there were no significant differences for tiller number, panicle width and weight and fiber content.

As a result of the analysis of variability among and within the lines, the genotypic component of the phenotypic variance for both populations was estimated (Table 3). Genotypic variance of Yaguané was larger than in Carapé for all the characters, mainly in tiller number, lamina width and panicle size and weight. The coefficients of genotypic variance (CVG) of Carapé population were limited and smaller than in Yaguané for all the characters (1.1 - 7.5% vs. 2.7 - 32.8%, respectively). In this last population, CVGs were higher for tiller number and in characters associated to panicle.

In Table 4 are displayed the broad-sense heritability (H2), the standard error and interval of confidence estimated (α=0.95) and, expected response after a cycle of selection (R). Heritability for all characters was higher in Yaguané and to highlight are the characters associated with tillage, precocity and panicle size (0.89, 0.87 y 0.85, respectively), whereas for Carapé the highlights were lamina length and days to flowering. In both populations

Table 1. Mean, standard error, maximum and minimum values and coefficient of variation in the observations of the Carapé (C) and Yaguané (*Y*) populations of foxtail millet (*Setaria italica*) for all the evaluated characters.

Character	Mean ± S.E.		Range (min.-max.)		Coefficient of Variation (%)	
	C	*Y*	*C*	*Y*	*C*	*Y*
Tiller number	24.7 ± 0.3	11.1 ± 0.5	15.5 – 35.3	2.8 – 32.5	15.9	55.2
Lamina length (cm)	46.6 ± 0.3	49.7 ± 0.5	38.1 – 53.9	36.3 – 61.0	6.8	10.7
Lamina width (cm)	2.17 ± 0.1	2.55 ± 0.1	1.80 – 2.50	1.75 – 3.30	6.7	13.4
Days to flowering	70.2 ± 0.3	73.3 ± 0.7	61.0 – 78.0	62.0 – 96.0	4.9	10.3
Plant height (cm)	102.3 ± 1.0	118.6 ± 1.4	68.5 – 128.8	87.0 – 164.5	11.4	13.0
Panicle length (cm)	18.4 ± 0.1	26.4 ± 0.3	14.9 – 21.8	16.3 – 34.5	6.6	14.7
Panicle width (cm)	1.53 ± 0.0	2.35 ± 0.1	1.20 – 2.00	1.30 – 4.90	11.0	26.4
Seed weight (g)	2.87 ± 0.01	2.79 ± 0.02	2.48 – 3.12	2.19 – 3.27	4.6	6.
Panicle weight (g)	5.7 ± 0.09	13.0 ± 0.42	3.6 – 8.3	5.2 – 24.0	16.9	36.2
NDF (%)	59.7 ± 0.2	59.4 ± 0.3	55.4 – 62.9	55.0 – 66.5	2.8	3.
ADF (%)	30.1 ± 0.2	29.2 ± 0.3	26.8 – 32.4	25.8 – 33.5	4.4	5.
IVDMD (%)	83.0 ± 0.3	83.5 ± 0.4	74.3 – 88.3	73.9 – 89.4	3.3	3.

Table 2. Sums of squares for the variation between populations and among the total lines within the populations expressed as percentage of total variability and percentages of the sum of squares of each foxtail millet (*Setaria italica*) population.

Character	Populations		Lines within populations		Carapé lines		Yaguané lines	
	%SS	***t***	**%SS**	***F***	**%SS**	***F***	**%SS**	***F***
Tiller number	61	18.6***	39	19.0***	13	1.2 ^{ns}	87	36.8***
Lamina length (cm)	15	-5.7***	85	7.5***	21	3.2***	79	11.8***
Lamina width (cm)	42	-11.7***	58	9.6***	10	1.9**	90	17.3***
Days to flowering	8	-4.2***	92	21.4***	14	6.0***	86	36.7***
Plant height (cm)	43	-9.5***	57	3.9***	25	2.0**	75	5.9**
Panicle length (cm)	69	-22.2***	31	17.2***	5	1.6*	95	32.8***
Panicle width (cm)	50	-14.3***	50	13.3***	3	0.9 ^{ns}	97	25.7***
Seed weight (g)	7	3.6***	93	4.6***	25	2.3***	75	6.9***
Panicle weight (g)	58	-16.9***	42	15.6***	2	0.5 ^{ns}	98	30.6***
NDF (%)	1	0.9 ns	99	2.6***	31	1.6 ^{ns}	69	3.6***
ADF (%)	12	3.4***	88	2.5***	31	1.6 ^{ns}	69	3.5***
IVDMD (%)	1	-1.0 ns	99	2.4***	39	1.9*	61	2.9***

ns: no significant; *: P < 0.05; **: P < 0.01; ***: P < 0.001.

Table 3. Components of variance and coefficients of phenotypic and genotypic variation for Carapé (C) and Yaguané (Y) populations of foxtail millet (*Setaria italica*).

Character	σ^2_F		σ^2_G		CV_F		CV_G	
	C	***Y***	***C***	***Y***	***C***	***Y***	***C***	***Y***
Tiller number	0.04	0.56	0.01	0.48	4.8	24.0	1.8	21.1
Lamina length (cm)	9.9	28.3	4.40	19.4	6.8	10.7	4.5	8.9
Lamina width (cm)	0.21	1.18	0.07	0.88	6.7	13.5	3.9	11.6
Days to flowering	11.8	58.6	8.10	50.9	4.9	10.5	4.1	9.7
Plant height (cm)	115	221	26.00	114.0	10.5	12.5	5.0	9.0
Panicle length (cm)	1.5	15.5	0.40	13.2	6.6	14.9	3.5	13.8
Panicle width (cm)	0.26	3.87	0.06	3.05	10.6	26.5	5.2	23.6
Seed weight (g)	17	36.0	5.00	21.0	4.6	6.8	2.4	5.2
Panicle weight (g)	0.8	22.4	0.20	18.2	15.4	36.4	7.5	32.8
NDF (%)	2.8	4.5	0.40	2.8	2.8	3.6	1.1	2.8
ADF (%)	1.8	2.6	0.20	1.7	4.4	5.6	1.4	4.5
IVDMD (%)	7.7	8.6	1.30	5.3	3.3	3.5	1.4	2.7

quality parameters for forage showed less heritability. Expected values after a cycle of selection were higher in Yaguané population for all the evaluated characters.

Genotypic correlations among all the characters are included in Table 5. Among them, characters linked to lamina size, plant height and panicle size have significant and negative correlations with tiller number in Yaguané, whereas in Carapé these correlations were smaller in magnitude and positive for panicle width. The least correlated characters were tiller number in Carapé population and seed weight in Yaguané. In both populations forage quality parameters showed significant genetic correlations with plant height and days to flowering and, IVDMD was highly correlated with ADF.

Table 4. Broad-sense heritability (H^2), standard error (S.E.) and interval of confidence of heritability (I.C.) and, response to selection (R) on the corresponding measurement units for Carapé (C) and Yaguané (Y) populations of foxtail millet (*Setaria italica*).

Character	**H^2 ± S.E.**		**I.C. H^2 (α = 0.95)**		**R***	
	C	***Y***	***C***	***Y***	***C***	***Y***
Tiller number	0.33 ± 0.10	0.89 ± 0.03	0.15 - 0.53	0.80 - 0.93	0.03	0.33
Lamina length (cm)	0.44 ± 0.09	0.68 ± 0.07	0.26 - 0.63	0.54 - 0.81	2.2	5.6
Lamina width (cm)	0.33 ± 0.10	0.74 ± 0.06	0.16 - 0.53	0.61 - 0.85	0.08	0.40
Days to flowering	0.68 ± 0.07	0.87 ± 0.03	0.53 - 0.86	0.79 - 0.93	3.7	10.3
Plant height (cm)	0.23 ± 0.09	0.52 ± 0.09	0.06 - 0.44	0.34 - 0.69	3.8	12.0
Panicle length (cm)	0.29 ± 0.10	0.85 ± 0.04	0.11 - 0.49	0.76 - 0.91	0.5	5.2
Panicle width (cm)	0.24 ± 0.10	0.79 ± 0.05	0.07 - 0.44	0.67 - 0.88	0.06	0.77
Seed weight (g)	0.29 ± 0.10	0.58 ± 0.08	0.13 - 0.51	0.41 - 0.73	0.06	0.17
Panicle weight (g)	0.24 ± 0.09	0.81 ± 0.05	0.06 - 0.44	0.70 - 0.89	0.3	6.0
NDF (%)	0.15 ± 0.17	0.63 ± 0.10	-0.20 - 0.47	0.36 - 0.80	0.4	2.1
ADF (%)	0.11 ± 0.17	0.64 ± 0.10	-0.24 - 0.43	0.38 - 0.81	0.2	1.6
IVDMD (%)	0.17 ± 0.16	0.61 ± 0.11	-0.18 - 0.49	0.34 - 0.79	0.8	2.8

* Response considering a selective strength i=1.554 (15% of the selected individuals).

Table 5. Genotypic correlations of Carapé populations (under the diagonal) and Yaguané (above the diagonal) of foxtail millet (*Setaria italica*).

r_G		**Yaguané**											
		TN	**LL**	**LW**	**DF**	**PH**	**PL**	**PA**	**SW**	**PW**	**NDF**	**ADF**	**IVDMD**
Carapé	Tiller number (TN)		-0.84[Q]	-0.78[Q]	0.09	-0.53[r]	-0.74[Q]	-0.68[Q]	0.06	-0.79[Q]	-0.12	0.05	-0.15
	Lamina length (LL)	-0.50[r]		0.73[Q]	0.06	0.58[r]	0.77[Q]	0.51[r]	-0.01	0.77[Q]	-0.16	-0.30	0.16
	Lamina width (LW)	-0.33	0.64[Q]		-0.24	0.36*	0.52[r]	0.65[Q]	-0.10	0.76[Q]	-0.13	-0.26	0.22
	Days to flowering (DF)	-0.01	0.84[Q]	0.72[Q]		0.66[Q]	0.18	0.02	0.08	0.18	0.58[Q]	0.55[r]	-0.73[Q]
	Plant height (PH)	-0.03	1.00[Q]	0.71[Q]	1.00[Q]		0.76[Q]	0.26	0.12	0.70[Q]	0.50[r]	0.37*	-0.51[r]
	Panicle length (PL)	-0.39*	1.00[Q]	0.75[Q]	0.84[Q]	0.82[Q]		0.49 [r]	0.19	0.80[Q]	0.13	0.05	-0.02
	Panicle width (PW)	0.23	0.70[Q]	0.98[Q]	0.72[Q]	0.78[Q]	0.69[Q]		-0.38*	0.79[Q]	0.00	-0.05	0.02
	Seed weight (SW)	-0.56r	0.89[Q]	0.77[Q]	0.61[Q]	0.78[Q]	0.98[Q]	0.66[Q]		-0.04	0.03	0.23	-0.14
	Panicle weight (PW)	-0.13	0.91[Q]	0.59[Q]	0.63[Q]	0.77[Q]	0.78[Q]	0.51r	0.65[Q]		0.14	0.03	-0.13
	NDF	-0.30	0.71[Q]	0.58r	0.50r	1.00[Q]	0.48r	0.11	0.38*	0.52r		0.92[Q]	-0.71[Q]
	ADF	-0.16	0.70[Q]	0.66[Q]	0.66[Q]	1.00[Q]	0.57r	0.42*	0.43*	0.50r	0.88[Q]		-0.76[Q]
	IVDMD	0.09	-0.57r	-0.75[Q]	-0.57[Q]	-0.90[Q]	-0.47r	-0.66[Q]	-0.69[Q]	-0.40*	-0.62[Q]	-0.80[Q]	

*: $P < 0.05$; [r]: $P < 0.01$; [Q]: $P < 0.001$.

Expected responses by direct or indirect selection for each simple criterion of selection on the populations are included as percentages on Table 6. Responses to direct selection (%R) in Carapé were relatively low for all the considered characters (0.7 – 5.2%). It is possible that when selecting for later lines the response could be the same for lamina length, as the one obtained by direct selection, in order to increase lamina width and plant height. %R levels in Yaguané were higher than in Carapé mainly for panicle width, length and

Table 6, a-b. Direct (%*R*) (shadow) and correlated (%RC_Y) response expressed as percentage of the corresponding character mean to the Carapé (a) and Yaguané (b) populations of foxtail millet (*Setaria italica*).

Criterio de selección	NM	LL	AL	DF	AT	LP	AP	PS	PP	FDN	FDA	DIVMS
(a) Direct and correlated response (%) i Carapé												
NM	2.1	-2.0	-1.1	-0.1	-0.1	-1.2	1.1	-1.2	-0.9	-0.3	-0.2	0.1
LL	-1.2	4.7	2.5	3.5	5.2	3.7	3.8	2.3	7.1	0.8	1.1	-0.8
AL	-0.7	2.6	3.4	2.6	3.2	2.4	4.6	1.7	3.9	0.6	0.8	-0.9
DF	0.0	4.8	3.5	5.2	6.4	3.8	4.8	1.9	6.1	0.7	0.9	-0.7
AT	-0.1	3.3	2.0	3.0	3.8	2.2	3.0	1.4	4.3	0.8	1.1	-0.9
LP	-0.8	3.8	2.4	2.8	3.5	2.9	3.0	2.0	4.9	0.4	0.7	-0.5
AP	0.4	2.4	2.9	2.2	3.0	1.9	3.9	1.2	2.9	0.1	0.5	-0.7
PS	-1.1	3.3	2.5	2.1	3.3	2.9	2.9	2.0	4.1	0.3	0.5	-0.8
PP	-0.2	3.1	1.7	1.9	2.9	2.1	2.0	1.2	5.6	0.3	0.6	-0.4
FDN	-0.4	1.9	1.3	1.2	3.0	1.0	0.3	0.6	2.4	0.7	0.8	-0.5
FDA	-0.2	1.6	1.3	1.4	2.6	1.0	1.1	0.5	1.9	0.5	0.7	-0.6
DIVMS	0.1	-1.6	-1.2	-1.5	-2.9	-1.1	-2.2	-1.1	-1.9	-0.4	-0.8	0.9
(b) Direct and correlated response (%) in Yaguané												
NM	33.5	-10.9	-13.3	1.3	-7.0	-14.9	-23.6	0.5	-38.0	-0.5	0.3	-0.6
LL	-24.7	11.4	10.9	0.7	6.8	13.6	15.5	-0.1	32.5	-0.6	-1.7	0.6
AL	-10.1	8.6	15.5	-3.1	4.4	9.6	20.6	-0.7	33.4	-0.5	-1.5	0.8
DF	3.0	0.8	-4.0	14.1	8.6	3.6	0.7	0.6	8.6	2.4	3.6	-2.9
AT	-13.6	5.8	4.7	7.2	10.1	11.7	6.9	0.7	25.8	1.5	1.8	-1.6
LP	-24.2	9.8	8.7	2.5	9.9	19.7	13.6	1.4	37.6	0.5	0.3	-0.1
AP	-21.5	6.2	10.4	0.3	3.2	9.3	32.5	-2.7	35.8	0.0	-0.2	0.1
PS	1.6	-0.1	-1.4	0.9	1.3	0.8	-10.1	6.1	-1.6	0.1	0.8	-0.5
PP	-25.3	9.5	12.4	2.5	8.9	15.4	26.2	-0.3	45.9	0.6	0.2	-0.5
FDN	-3.4	-0.5	-1.9	7.0	5.6	2.2	0.0	0.2	5.7	3.5	5.1	-2.4
FDA	1.4	-3.3	-3.8	6.7	4.2	0.8	-1.5	1.5	1.2	2.1	5.5	-2.6
DIVMS	-4.2	0.2	3.1	-8.7	-5.6	-0.3	0.6	-0.9	-5.2	-2.4	-4.1	3.3

weight and in tiller number. Although, when selecting for the later character there is a reduction in the other characters associated with forage biomass production and seed production. The highest % RCY in Yaguané were obtained on panicle weight, being an inverse response when selecting by tiller number (-38.0%).

Discussion

Inter and intra population variability

Mean values for the morphological characters of both populations showed contrasting characteristics and agreed with the findings of Josifovich and Echeverría (1971), who described Carapé as a plant population with higher capacity for tilling, shorter and earlier, with smaller lamina and panicles than Yaguané population. Differences observed between these populations support those reported by other authors that for the same characters highlight the high variability within the local varieties of foxtail millet in other parts of the world (Ochiai 1996; Kawase *et al.*, 1997; Reddy *et al.*, 2006). These differences could be associated with the degree of domestication of the populations that could include an increase in apical dominance (Ichitani *et al.*, 2003; Doust *et al.*, 2004). This suggests that Carapé might be associated with earlier stages of domestication, while the strong apical dominance of Yaguané might reflect a more advanced stage towards a domesticated phenotype.

It is important to highlight that Yaguané population dominated the actual foxtail millet market and has a considerably larger geographical diffusion than Carapé. This could be a consequence of the high genetic variation of Yaguané which can give it a better environmental tolerance (broad adaptation). Contrastingly, the limited genetic variability for Carapé population could explain its smaller geographic diffusion and indicates a trend to local adaptation of few multilocus genotypes (Dekker, 2003). The different levels of genotypic variability in these populations are the result of a history of events happening on each population. One first factor to consider is the variability on the populations brought from China in which selection was done; then, the resultant variability on the new populations obtained in Argentina. According to Saxena and Singh (2006) the lack of maintenance of varietal purity, as is the case for these cultivars, would have led to evolve into new landraces. This process would involve events that differentially affected each population like mutations, recombinations, natural selection by fertility on the growing conditions and even specific factors of the multiplication facilities (Berg, 2009).

Heritability and response to selection

Since the foxtail millet populations studied constitute pure line groups, the most useful estimator is the broad-sense heritability (H2), because in this case it will be possible to exploit all the genetic variability (Bernardo, 2002). The genetic variability exposed by Yaguané in all the characters is the determinant factor for the high expected heritability in this population in relation to Carapé.

The high heritability of the character days to flowering in both populations agrees with the findings of Basheeruddin and Sahib (2004) who estimated its heritability in 0.96. Rathod *et al.* (2002) found high H2 for tiller number and panicle length, similar to what was estimated in Yaguané. These authors worked on populations from Eurasia. However, heritability information for foxtail millet grown in Argentina was not available. Highest responses for direct selection in Yaguané were due to its larger phenotypic variability and to its higher H2 values in comparison to Carapé. These differences were more evident in characters with contrasting genetic variability, for example, tiller number and length, panicle width and weight. Rathod *et al.* (2002) estimated the larger responses when selecting on tiller number and panicle length in genotypes from India, that is in the same sense as the estimated responses for Yaguané.

Genotypic correlations and correlated responses

The high negative genotypic correlations of tiller number with the rest of the morphological characters in Yaguané might be conditioned by the apical dominance. The low or null genetic correlation between tilling and the other characters in Carapé might be explained by the low variability in loci that define the apical dominance degree in this population. Relation between days to flowering and the rest of the characters is different in both populations. In Carapé, the same genes that delay flowering favored vegetative and reproductive growth. This pleiotropic effect was suggested in foxtail millet (Ichitani *et al.*, 2003; Siles *et al.*, 2004) and in the Poaceae in general (Lin *et al.*, 1995). Opposite, in Yaguané population it was only found a significant genotypic association between days to flowering and plant height, which might indicate higher genetic independence between both characters and the rest of the morphological characters associated with biomass production. The high genotypic correlation between plant height and panicle length agrees with the results of Siles *et al.* (2004) who studied heterosis crossing foxtail millet lines and suggested that both characters could be controlled by the same genes or that could be ligated in the linkage phase.

The minor expected responses to selection, both direct (%R) as indirect (%RCY), in Carapé could be explained by the low heritability and few variability in all the characters. Even though a larger sample size might allow more reliable parameters on the populations, these first estimations done in Carapé and Yaguané represent an important advance on the genetic characterization for the future germplasm breeding adapted to Argentina. Publications on responses to selection in foxtail millet are limited, however, it can be found in literature two reports on this topic with graniferous genotypes from India (Rathod *et al.*, 2002; Basheeruddin and Sahib 2004) but, there are no studies specifically related with forage use.

Conclusions

- Strong morphological differences between the populations and diverse variability levels within each population were detected.
- Yaguané population showed a higher genotypic variability than Carapé population in all the studied characters and showed a higher potential for breeding on the characters of agronomic interest considered in the study.

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