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Phenotypic diversity in Argentinian populations of *Bromus catharticus* (Poaceae). Genetic and environmental components of quantitative traits

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Abstract Genetic and environmental components were analysed in 32 Argentinian populations of *Bromus catharticus*. The research was based on 39 vegetative and reproductive characters. Constancy (r_c) and heritability (h^2) ratios were calculated. ANOVAS showed differences between populations for 14 traits, most of them reproductive. Total phenotypic variation was mostly due to the environmental component. Microfloral attributes showed the highest values of r_c and h^2. The traits average length of the spikelets (LS), average number of florets per spikelet (NFS), and lemma length (LL), which simultaneously reach r_c values higher than 1 and h^2 values higher than 0.60, could be considered useful in systematic studies. Leaf, stem, and some reproductive characters, linked to propagule production, had plastic responses. However, traits associated with size and shape of propagules and spikelets remained constant. Results suggest that a double strategy is operating: plasticity in some traits (to give greater adaptability), and constancy in other traits related to species stability that are of systematic significance.

Keywords *Bromus catharticus*; genetic variation; environmental variation; phenotypic plasticity; constancy; heritability

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INTRODUCTION

Praire grass or rescue grass (*Bromus catharticus* Vahl.; syn. *B. willdenowii* Kunth. or *B. unioloides* Kunth.) is an annual species that grows naturally in the Argentine pampas and is widely distributed in divergent ecological conditions. It shows two types of flowering, cleistogamic and chasmogamic, so it is considered a facultative autogamous species, with a low rate of allogamy (Cladera & Pahlen 1984; Naranjo 1985; Pahlen 1986; Morant 1990). Flowering periods are conditioned by the photoperiod and soil humidity (Ragonese & Marcó 1941, 1943). The chasmogamic flowering usually occurs at the beginning of spring and the cleistogamic one at the end of spring and during the summer (Perez López 1975).

Several authors have found a high phenotypic variability in this species not only among populations, as expected, but also within them (Perez López 1975; Pahlen et al. 1980; Arturi et al. 1983; Pahlen 1986; Garcia & Arturi 1992; Szpiniak et al. 1995; Wolff et al. 1996; Pistorale et al. 1999). Most of that research has been aimed at the analysis of the variability in traits of forage importance, and, in a few cases, the heritability ratios were estimated (Perez López 1975; Arturi et al. 1983).

In other species of *Bromus* a high amount of phenotypic variation (Harlan 1945; Jain et al. 1970) and a remarkable plasticity for quantitative variables (Jain 1978; Esnault 1984) have been found. Phenotypic plasticity studies suggested that it is strongly conditioned by genes and, as a result, it is highly heritable (Bradshaw 1965; Jain 1978; Scheiner & Lyman 1989). Plasticity has its own genic control, so it must be considered as an adaptative trait in itself (Schlichting & Levin 1986; Sultan 1987; Thompson 1991; Jasiensky et al. 1997). Plasticity in a trait may decrease the likelihood of selection for genetic differentiation (Sultan 1987).

The objectives of this research, carried out on Argentinian populations of *B. catharticus*, were: a) to study the phenotypic variability of morphological traits, both reproductive and vegetative; b) to estimate the genetic and environmental components;

c) to calculate genetic parameters; and d) to identify a variable or group of variables that can differentiate populations.

MATERIALS AND METHODS

Collection method

Wild populations of *B. catharticus* were sampled from 31 locations in Buenos Aires Province (Fig. 1). All geomorphologic subregions of the Pampa ("Sandy pampas", "Interhills pampas", "Wavy pampas", "Depressed pampas") were sampled. Original information (accession no., collecting place, date of collection, identification, and geographic location) is presented in Table 1. Following the suggestions made by Marshall & Brown (1975) for self-pollinated species, a minimum of 50 matured reproductive tillers were sampled from an ecological homogeneous area of 100 to 1000 m^2. It was ensured that each tiller belonged to a different individual.

From each panicle, 10 caryopses were taken out to make a genetic pool for each population. In this way each genotype was equally represented. Pools were used to set the first trial.

Design of the experiment

The study was conducted in a randomised complete block design with 4 replications. Plots were four rows (0.40 m row spacing) wide and 2.25 m long, with a total of 64 plants per plot (0.15 m plant spacing). The trials were conducted in the Instituto Fitotécnico Santa Catalina of Llavallol, Buenos

Table 1 Collection details of specimens from 32 natural populations. n.d., no data.

No.	Collection date	Location name	Identification	Location site	Nearest town	
					City name	Dist.(km)
1	21 Dec 1988	San Vicente	SVICEN	Crossroad no. 6 & 210	San Vicente	25
2	21 Dec 1988	Cañuelas	CAÑUE	Route no. 6	Cañuelas	11
3	21 Dec 1988	Gral. Las Heras	GHERAS	Route no. 6	Marcos Paz	10
4	01 Dec 1988	Gral. Rodríguez	GRODRI	Crossroad no. 6 & 7	Luján	8
5	21 Dec 1988	Pilar	PILAR	Route no. 6	Pilar	4
6	21 Dec 1988	Belén de Escobar	BESCO	Way to Luján River	B. de Escobar	5
7	15 Dec 1988	Balcarce	BALCA	Route no. 77, km 65	Balcarce	15
8	26 Dec 1988	Mercedes	MERCE	Route no. 5	Mercedes	20
9	26 Dec 1988	Chivilcoy	CHIVI	Route no. 5, km 23	Suipacha	6
10	26 Dec 1988	Bragado	BRAGA	Route no. 5, km 196	Larrea	5
11	26 Dec 1988	Nueve de Julio	NJUILO	Route no. 5, km 238	Dennely	11
12	26 Dec 1988	Carlos Casares C	CCASC	Route no. 5, km 291	Cambaceres	4
13	26 Dec 1988	Carlos Casares B	CCASB	Route no. 5, km 291	Cambaceres	4
14	26 Dec 1988	Pehuajó	PEHUA	Route no. 5, km 361	Pehuajó	7
15	26 Dec 1988	Trenque Lauquen	TLAUQ	Route no. 5, km 441	T. Lauquen	5
16	26 Dec 1988	Girondo	GIRON	Route no. 226, km 450	Girondo	3
17	26 Dec 1988	Bolivar	BOLIV	Route no. 226, km 577	Bolivar	19
18	26 Dec 1988	Olavarría	OLAVA	Route no. 226	Blanca	13
19	26 Dec 1988	Azul	AZUL	Route no. 226	Azul	25
20	26 Dec 1988	Tapalqué	TAPAL	Route no. 51	Tapalqué	2
21	30 Dec 1988	Lomas de Zamora	SCATA	Route no. 4	Llavallol	1
22	31 Dec 1988	Lezama	LEZAM	Route no. 2, km 152	Lezama	4
23	31 Dec 1988	Maipú	MAIPU	Route no. 2, km 294	Las Armas	6
24	01 Feb 1989	Mar del Plata	MPLATA	Route no. 88	Mar del Plata	7
25	10 Dec 1988	Magdalena	MAGDA	Route no. 11	Magdalena	13
26	11 Dec 1988	Pipinas	PIPIN	Route no. 36	Pipinas	5
27	11 Dec 1988	Castellí	CASTE	Route no. 11	C. de la Gloria	5
28	11 Dec 1988	San Clemente	SCLEM	Route no. 11	San Clemente	1
29	04 Jan 1989	Henderson	HENDER	n.d.	Henderson	15
30	n.d.	Las Flores	LFLORE	n.d.	n.d.	n.d.
31	n.d.	Parque Pereyra	PPEREY	n.d.	Berazategui	15
32	n.d.	Punta Lara	PLARA	n.d.	La Plata	n.d.

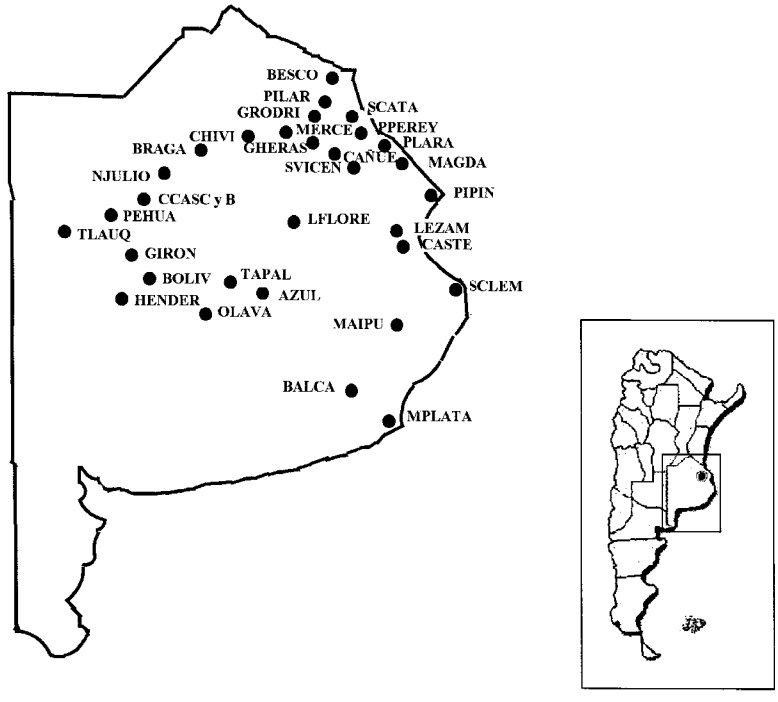

Fig. 1 Geographic distribution of the 32 sampled localities in the province of Buenos Aires, Argentina. Abbreviations as in Table 1.

Aires (34°47′S, 58°27′W) on an Argiudoll typical soil in two years (1989 and 1990). Planting date and location of the two trials in the experimental field were different. The first (1989) was planted on 30 March (early season) and the second (1990) on 25 June (late season). Harvests were made in each trial, in spring (September) and in summer (January). Ten reproductive tillers per plot were cut in the first harvest. Because of the natural dehiscence of the caryopses, inflorescences on the tillers were cut completely developed but immature, to measure floral attributes which could not be studied on the mature tillers. A second harvest was scheduled late in the season (summer) with the additional purpose of collecting seeds produced by cleistogamous florets. These seeds from the first trial were then used to plant the second trial, in 1990. All harvested cuttings were dried and mounted on herbarium sheets.

Vegetative and reproductive traits

On the dried specimens from herbarium material, 39 quantitative traits were measured in each population and environment. These traits and abbreviations used are shown in Table 2.

The DFSPN was determined by averaging the distance between the first and second nodes and between the third and fourth nodes of the panicle. FGL, SGL, LL, FGW, SGW, LW, NNFG, NNSG, and NNL were calculated by averaging two glumes and lemmas per panicle. NFS and LS were obtained by averaging the measurements of four spikelets per panicle. LBFN, LBSN, LFBFN, LFBSN, NSFN, and NSSN were estimated by averaging two primary branches per node and per panicle. DSFN was then estimated as a ratio between LFBFN and NSFN. DSSN was calculated with the same last procedure.

Statistical analysis

A combined analysis model (McIntosh 1983) was applied to the 39 traits over the 32 populations. Environments were assumed to sample year effects. A random model was used:

$$X_{ijm} = \mu + \alpha_i + \beta_{im} + \delta_m + \gamma\delta_{im} + \varepsilon_{ijm}$$

where: X_{ijm} = ijm-th phenotypic variation; $i = 1,..., g$; $j = 1,..., r$; $m = 1,..., e$; g = number of populations; r = number of blocks per experiment; e = number of environments; μ = the parametric mean, α_i = the i-th population effect; β_{im} = the j-th block effect within the m-th experiment; δ_m = the m-th environment

effect; $\gamma\delta_{im}$ = the *im*-th genetic-environment interaction; ε_{ijm} = the *ijm*-th residual error effect.

Expected mean squares were performed as shown below:

Environments (E): $\hat{\sigma}_e^2 + g\,\hat{\sigma}_{R\subset E}^2 + r\,\hat{\sigma}_{GE}^2 + r\,g\hat{\sigma}_E^2$

Blocks in environments (Rep/E): $\hat{\sigma} + g\,\hat{\sigma}_{R\subset E}^2$

Populations (G): $\hat{\sigma}_e^2 + r\,\hat{\sigma}_{GE}^2 + r\,e_{GE}^2$

Population × Environment (G×E): $\hat{\sigma}_e^2 + r\,\hat{\sigma}_{GE}^2$

Error: $\hat{\sigma}_e^2$

where: $\hat{\sigma}_G^2$ = variance among populations; $\hat{\sigma}_E^2$ = variance among environments, $\hat{\sigma}_{GE}^2$ = variance due to population by environmental interactions. $\hat{\sigma}_e^2$ = variance due to error; g = number of populations, e = number of environments; r = the number of blocks per experiment.

Variance components were estimated from the expected mean squares. The total variance was calculated as the sum of their components $(V_T = \hat{\sigma}_e^2 + \hat{\sigma}_G^2 + \hat{\sigma}_{R\subset E}^2 + \hat{\sigma}_E^2 + \hat{\sigma}_{GE}^2)$. The relative

Table 2 Quantitative traits measured on morphologic and reproductive organs. All measurements in cm.

No.	Quantitative traits	Abbreviation
1	Flag leaf length	FLL
2	Flag leaf width	FLW
3	Flag leaf sheath length	FSL
4	Penultimate leaf length	PLL
5	Penultimate leaf width	PLW
6	Penultimate leaf sheath length	PSL
7	Number of nodes per reproductive tiller	NNRT
8	Reproductive tiller length	RTL
9	Internode length (down the flag leaf node)	IL
10	Panicle length (from insertion to tip)	PL
11	Length of panicle pedunculus (from insertion to first node)	PPL
12	Average distance between the first and the second panicle nodes	DFSPN
13	Number of nodes per panicle	NNP
14	Total number of primary branches per panicle	NPB
15	Total number of spikelets per panicle	NSP
16	Average number of florets per spikelet	NFS
17	Average length of the spikelets	LS
18	Average number of existing primary branches at the first and second panicle nodes	NBFSN
19	Average number of existing primary branches at third and fourth panicle nodes	NBTFN
20	Average number existing spikelets at the branches of the first and second panicle nodes	NSFSN
21	Average number existing spikelets at the branches of the third and fourth panicle nodes	NSTFN
22	Average length of panicle primary branches at the first node	LBFN
23	Average length of panicle primary branches at the second node	LBSN
24	Average length of the portion with flowers of the branches at the first node	LFBFN
25	Average length of the portion with flowers of the branches at the second node	LFBSN
26	Average number of spikelets of the panicle branches at the first node	NSFN
27	Number of average spikelets of the panicle branches at the second node	NSSN
28	Distance between spikelets of the branches at the first node	DSFN
29	Distance between spikelets of the branches at the second node	DSSN
30	First glume length	FGL
31	First glume width	FGW
32	Nervation number in the first glume	NNFG
33	Second glume length	SGL
34	Second glume width	SGW
35	Nervation number in the second glume	NNSG
36	Lemma length	LL
37	Lemma width	LW
38	Nerves number in lemma	NNL
39	Lemma awn length	LAL

magnitudes of the variance components V_e, V_G, V_R, V_E, and V_{GE} were expressed as percentages of V_T. *F* test was used to compare environments. The contrasts were considered only when their effects were significant.

Genetic parameters

With the components of the phenotypic variance, two ratios were calculated:

a) Constancy ratio as $r_c = \hat{\sigma}^2_G / (\hat{\sigma}^2_E + \hat{\sigma}^2_{GE})$ following Ron & Ordás (1989);

b) Broad-sense heritability ratio (Hanson et al. 1956) as

$$h^2 = \frac{\hat{\sigma}^2_G}{\hat{\sigma}^2_G + \frac{\hat{\sigma}^2_{GE}}{e} + \frac{\hat{\sigma}^2_e}{er}}$$

The genetic variance would contain both the additive and non-additive effects. Due to sampling error, some negative variance components were obtained. In making ratios, these negative estimates were equated to zero (Robinson et al. 1955).

Table 3 Randomised complete block experiments combined over years for 39 quantitative traits. Abbreviations as in Table 2. Mean squares (MS) and *F* test significances: ns, not significant; *, $P < 0.05$; **, $P < 0.01$.

Traits	Environment (E)	Rep/(E)	Populations (G)	G×E	Error × 10^{-2}
FLL	571.22ns	83.50**	9.63ns	7.25**	316.9
FLW	0.51**	0.01**	0.01**	0.00ns	0.47
FSL	22.00ns	4.54**	2.20ns	1.69**	35.2
PLL	2960.97**	70.74**	16.01ns	9.51**	513.0
PLW	1.07**	0.02**	0.004ns	0.00**	0.5
PSL	124.87**	5.18**	2.00ns	1.59**	41.2
NNRT	419.68**	2.78**	0.42ns	0.34**	14.9
RTL	40850.10**	631.36**	87.96ns	83.96**	39.92
IL	184.08ns	31.36**	5.11ns	4.51*	282.3
PL	23.43ns	163.43**	27.07*	22.63ns	1600.8
PPL	3509.45**	85.29**	11.42ns	8.89ns	972.37
DFSPN	0.41ns	2.45**	0.86ns	0.71**	19.89
NNP	353.24**	9.18**	0.31ns	0.22ns	23.69
NPB	3.245.21**	36.91**	18.56*	4.44*	172.43
NSP	56107.87**	470.13**	65.53**	36.72ns	2715.0
NFS	9.87ns	7.22**	0.83**	0.28*	17.0
LS	0.26ns	0.74**	0.10**	0.03ns	2.72
NBFSN	58.18**	0.25**	0.48ns	0.27**	7.0
NBTFN	17.82**	0.10ns	0.17ns	0.11**	5.16
NSFSN	3047.23**	13.32**	4.96ns	3.23*	204.5
NSTFN	1132.62**	13.39**	1.58**	0.63ns	63.54
LBFN	230.47**	5.09**	2.60ns	2.47**	110.24
LBSN	940.57**	5.97**	2.12ns	1.83**	87.3
LFBFN	252.50**	1.58*	0.78ns	1.26**	61.01
LFBSN	288.74**	1.60**	0.59ns	0.76**	42.03
NSFN	332.97**	2.00*	1.17ns	1.29*	75.07
NSSN	248.19**	2.22**	0.88ns	0.78**	42.91
DSFN	0.07ns	0.16**	0.01ns	0.01ns	0.98
DSSN	0.27ns	0.17**	0.02*	0.01ns	0.87
FGL	0.01ns	0.05**	0.01ns	0.01**	0.26
FGW	15.72**	0.45*	0.48**	0.11ns	10.75
NNFG	1.04**	0.01ns	0.02ns	0.01ns	1.53
SGL	0.01ns	0.05**	0.01ns	0.01**	0.25
SGW	10.70**	0.46**	0.26**	0.10ns	7.77
NNSG	45.16**	2.07**	0.48ns	0.29*	17.37
LL	0.06ns	0.10**	0.03**	0.01*	0.48
LW	57.93*	4.29**	0.55**	0.24ns	22.79
NNL	4.76*	0.54**	0.16**	0.11ns	7.79
LAL	642.40**	4.07**	3.41**	0.86ns	67.33

Table 4 Mean values of 27 traits in Year 1 (1989) and Year 2 (1990). Different letters in a trait indicate a significant difference between years using *F* test. Abbreviations as in Table 2.

Traits	Year 1	Year 2
FLW	0.5967 a	0.5072 b
PLL	29.1280 a	22.3260 b
PLW	0.7051 a	0.5757 b
PSL	13.5390 a	12.1420 b
NNRT	7.9346 a	5.3738 b
RTL	115.2300 a	89.9690 b
PPL	23.0500 a	30.4560 b
NNP	10.5700 a	8.2203 b
NSP	61.6630 a	32.0540 b
NPB	21.8560 a	14.7350 b
NBFSN	3.1681 a	2.2147 b
NBTFN	2.6311 a	2.1034 b
NSFSN	15.0110 a	8.1104 b
NSTFN	8.7661 a	4.5593 b
LBFN	11.1840 a	9.2859 b
LBSN	10.2730 a	6.4396 b
LFBFN	6.0104 a	4.0241 b
LFBSN	5.1946 a	3.0706 b
NSFN	6.3883 a	4.1074 b
NSSN	5.3356 a	3.3663 b
FGW	0.7767 a	0.8262 b
NNFG	8.9298 a	9.0571 b
SGW	0.5492 a	0.5901 b
NNSG	5.8958 a	6.7359 b
LW	1.1433 a	1.2384 b
NNL	10.8760 a	11.1490 b
LAL	0.6355 a	0.3187 b

RESULTS

Populations showed significant differences for 13 reproductive characters (PL, NSP, NSTFN, NPB, DSSN, LS, NFS, FGW, SGW, LL, LW, NNL, and LAL) and only one morphologic character (FLW) (Table 3).

The model revealed a significant environmental effect for most of the characters except for three morphological traits (FLL, FSL, and IL) and nine reproductive traits (PL, DFSPN, NFS, LS, DSFN, DSSN, FGL, SGL, and LL). The G×E interaction effect was significant for all the morphological traits except FLW, and non-significant for some reproductive variables (PL, PPL, NNP, NSP, NSTFN, LS, DSFN, DSSN, FGW, NNFG, SGW, LW, NNL, and LAL). The repetition within environment effect was significant for all studied traits except NNFG and NBTFN.

At first year (Environment 1), leaf, tiller, and some reproductive attributes presented scores higher than for the second year (Environment 2) (Table 4). The traits that showed this behaviour were presumably responding better to early growing conditions. The traits that showed inverse behaviour (average of the second year being higher than the first year) were the reproductive variables related to the number of nerves, width of the lemma and glumes, and length of the lemma and of the panicle peduncule. They apparently did not respond to better growing conditions.

Environmental variation (V_E) was higher than 50% of the total variation for 19 of the 39 studied traits (Table 5). The error variation (V_e) occupied a second place of relative importance and 15 attributes reached amounts of more than 30%. However, none of them reached 70% of the V_E. The V_R component explained the development conditions of the trials and only four traits (NFS, LS, DSFN, DSSN) exceeded 30% of the total variation.

The genetic (V_G) and the genetic-environmental variation (V_{GE}) had a relative low weight. Only some

Table 5 Relative magnitudes of the variance components expressed as percentages of the total variances. Population parameters: constancy ratio (r_c) and heritability ratio (h^2). Abbreviations as in Table 2.

Traits	V_A	V_R	V_G	V_{GA}	V_E	r_c	h^2
FLL	35.08	23.31	2.77	9.50	29.36	0.06	0.25
FLW	65.11	5.76	2.96	1.56	24.57	0.14	0.44
FSL	12.48	12.97	6.39	33.06	35.09	0.04	0.23
PLL	71.27	6.48	2.57	3.46	16.22	0.03	0.41
PLW	75.09	6.59	0.83	3.36	14.12	0.01	0.19
PSL	50.43	8.10	2.82	15.93	22.72	0.04	0.21
NNRT	91.94	2.33	0.26	1.40	4.06	0.003	0.18
RTL	81.78	4.82	0.13	2.87	10.40	0.002	0.04
IL	21.89	16.55	1.39	0	52.33	0.05	0
PL	0	20.18	2.44	7.25	70.14	0.34	0.16
PPL	68.51	6.05	0.54	0	24.90	0.004	0.15
DFSPN	0	17.02	4.71	30.32	47.90	0.16	0.18
NNP	91.94	8.69	0.26	0	4.06	0.002	0.34
NPB	86.20	3.79	1.82	2.25	5.94	0.02	0.49
NSP	90.24	2.87	0.75	0.50	5.60	0.01	0.44
NFS	13.93	43.56	13.45	5.55	33.51	1.41	0.66
LS	0	37.89	15.60	0.49	46.01	31.81	0.71
NBFSN	74.88	0.95	4.29	8.25	11.63	0.05	0.43
NBTFN	64.97	0.74	3.61	6.41	24.26	0.05	0.37
NSFSN	89.06	1.32	0.81	1.11	7.69	0.01	0.35
NSTFN	88.36	4.03	1.19	0	6.42	0.01	0.60
LBFN	52.46	3.73	0.42	10.26	33.05	0.01	0.04
LBSN	84.80	1.85	0.42	2.78	10.15	0.01	0.14
NSFN	73.61	1.12	0	3.86	21.41	0	0
NSSN	76.60	2.24	0.49	3.54	17.13	0.01	0.11
LFBFN	70.88	1.09	0	5.91	22.12	0	0
LFBSN	80.51	1.32	0	3.06	15.10	0	0
DSFN	0	31.18	3.68	0.08	65.05	42.75	0.31
DSSN	4.77	32.70	3.45	3.19	55.89	0.43	0.29
FGL	0	29.55	8.06	14.97	47.42	0.54	0.38
FGW	41.97	3.67	0.16	0.55	37.80	0.38	0.76
NNFG	33.23	0	3.02	0	63.76	0.09	0.27
SGL	0	26.49	7.79	18.14	47.57	0.43	0.34
SGW	40.65	6.09	10.11	3.58	39.56	0.23	0.60
NNSG	54.04	9.53	3.78	4.69	27.95	0.06	0.39
LL	0	25.40	23.85	7.49	43.26	3.18	0.72
LW	51.41	15.58	4.73	0.31	27.97	0.09	0.56
NNL	23.34	10.41	4.12	6.48	55.65	0.14	0.29
LAL	81.31	1.73	5.19	0.78	10.98	0.06	0.75

attributes related with spikelets (NFS, LS), glumes (FGW, SGW, NNSG), and lemmas (LL) reached a V_G ratio of 10%. The G×E variation explained more than 30% of the total variation only for two morphological traits (FSL and DFSPN).

A low constancy ratio showed that the phenotypic variation was highly associated with the environment and the interaction. A heritability ratio above 0.5% indicated a medium to high genetic control (Falconer 1981).

DISCUSSION

Analysis of variation

ANOVAS showed differences between genotypes for 14 attributes. Most of these attributes were reproductive, except for the vegetative variable FLW. For the morphologic traits of the leaf and stem and some reproductive ones, the effects "environment" and "G×E" were higher than the genotypic effect. These results did not show differences among

populations and pointed out an important environmental component, which explains the phenotypic variation.

Systematic implications

The use of characters calculated indirectly from other variables could be the cause of contradictory results to those obtained with the original variables (Goodman & Paterniani 1969). A clear example of this is the distance calculated between spikelets (DSFN and DSSN) obtained as a ratio. The "genotypic" effect was not significant for the original variables, but the environmental and interaction G×E effects were. However, the derivative ratios (DSFN and DSSN) reached no significant effects for the last two variation sources and the genotypic effect was only significant ($P < 0.05$) for DSSN. A character (ratios or direct measurements) will be useful in systematics if it fulfills two main conditions: 1) To be highly repeatable (mainly in studies based on herbarium specimens), 2) to be effective in taxon (race, population, species) discrimination. Thus, it is very important to select traits with higher constancy values and significant genetic variances.

The lemma and its awn have been repeatedly used in taxonomic studies of *Bromus* and have usually been used for intrageneric classification by various authors (Raven 1960; Melderis 1968; Maw 1974; Hill & Kirby 1985; Planchuelo 1991; Gutiérrez & Pensiero 1998; Peterson & Planchuelo 1998; Kosina 1999). The present results showed that lemma awn length (LAL) and nervation number in the lemma (NNL) differentiated populations significantly, but they were not classified in the group of variables with a higher constancy ratio because of their high environmental variation. This finding suggests that neither attribute should be used in systematics research, which includes herbarium material because the environmental contribution cannot be quantified. NFS, LS, and LL simultaneously reached the values $r_c > 1$ and $h^2 > 0.60$. These three variables shared a high genetic component and a non-significant environmental effect. LL showed the highest variation between populations (23.8%). However, LL and NFS showed a significant G×E effect ($P < 0.05$). In conclusion, the three traits kept a standard phenotype in spite of environmental disturbance (Mayr 1963), so they would be the attributes that contribute better to identify groups of populations and should be used to measure morphologic similitude or evolutive divergence. However, LS and NFS cannot be measured in dried material, due to the natural dehiscence of the spikelets. Possibly, LL would be the most appropriate variable to use in systematic studies, because it is an attribute of good conservation during specimen preparation, with great discriminative power and low fluctuation to environmental changes.

Genotypic and environmental variations

Heritability is a measure of genetic variation. A significant genetic variation would predicate a high heritability (Falconer 1981). Nevertheless, for the constancy concept, the relative magnitude of the environmental variation is relevant. A low constancy ratio would indicate that the differences between populations are due to the environmental and interaction effects more than to the real (genetic) differences between them. Considering the whole number of tested traits, 23% of them (9 of 39) showed $r_c > 0.30$, from which only 11% reached values of $r_c > 1$ and 40% had a significant genetic component. The rest showed phenotypic plasticity, because they responded vaguely or greatly to environmental variations. Low genetic variance and high phenotypic plasticity are consistent with those expected for inbreeding populations (Carr & Fenster 1994; Charlesworth & Charlesworth 1995). Inbreeding taxa increased their plasticity to compensate the lower levels of genetic variation associated with homozygosity (Marshall & Jain 1968; Jain 1979).

Most of the stable variables shared high heritability. However, there were traits with a low r_c but with a high h^2 and vice versa. For example, DSFN showed stable behaviour but low heritability, due to non-significant genotypic, environmental, and G×E effects. Contrary to this, LAL reached a high heritability ($h^2 > 0.70$) but a low constancy ratio. This was a consequence of a highly significant environmental variation, which explained 80% of the total variation.

Most of the stable attributes were related to floral structures. On the other hand, the morphologic, vegetative, and some reproductive variables (related to seed production) had plastic responses.

The environments (years) were different in planting date (early and late) and in the location of the experimental field, which possibly determined different experimental non-controlled conditions, but which obviously showed different growing responses. The first year, being early, gave advantage to the vegetative development of the leaf and tiller and other reproductive traits, as was shown by the results of the comparison among environments. Anderson & Shaw (1994) demonstrated in *Crepis*

tectorum that "early" characters such as leaf variables influence fitness traits (as total flower number) through "late" characters (such as plant architecture and floral variables) by correlation. Berg (1960) predicted for grass species with diminutive wind-pollinated flowers strong coupling between vegetative and floral traits. Our findings, in contrast with that prediction, pointed out a partial decoupling model because plants increased leaf and tiller size, number of nodes per tiller and per panicle, length and number of the panicle branches, spikelet number, and lemma length. However, other variables showed contrasting behaviour such as those related to the width and number of nerves in glumes and lemmas, and the length of the panicle peduncle. Ambruster et al. (1999) reported similar results in Poaceae.

Environmental variation (V_E) reached a relatively high proportion for most of the traits. Our findings demonstrated that populations had the ability to respond amply to environmental changes, which can only be explained by a great phenotypic plasticity. Many authors have pointed out this ability for other annual species of *Bromus* (e.g., Jain 1978; Smith 1981; Esnault 1984) and other Gramineae species (e.g., Marshall & Jain 1968; Scheiner & Teeri 1986).

Stebbins (1950) implied that traits which are formed by long periods of meristematic activity (especially size and number of leaves) would be subjected to environmental influence and, as a result, they would be more plastic than those formed faster, such as reproductive structures. Sultan & Bazzaz (1993) found that characters that are under stronger selection pressures might show less genetic variation and a larger plastic response than those that receive less concentrated selection pressure. Scheiner & Teeri (1986) found in the grass *Danthonia spicata* that traits closely associated with fitness will be more plastic. Our results demonstrated that some reproductive variables such as the number of nodes (NNP), branches (NPB), and spikelets per panicle (NSP) had the higher environmental responses although, in some cases, populations could control the production of spikelets or branches per panicle. However, it could be concluded that the environment could influence seed production, while the traits linked to size and shape of the propagules and spikelets would remain constant. Maybe this tendency is related to energy saving. This behaviour was reported for other species by several authors quoted by Bradshaw (1965).

Morphological traits associated with panicle and stem architecture had the lowest heritabilities because of low genetic variances and significant G×E interactions. Wu & Stettler (1997) cited similar results in *Populus*. On the other hand, traits related to flower production showed moderate heritabilities (0.34–0.60). As we pointed out above, this pattern was not due to their lower level of genetic variance but to their higher environmental variance. Similarly, other experimental evidence from animal and plant populations showed a negative relationship between heritability values and reproductive success (Gustafsson 1986; Mousseau & Roff 1987; Houle 1992; Anderson 1996; Merilä & Sheldon 1999). Traits closely associated with fitness would have low heritabilities because stabilising selection has acted on them over time reducing their genetic variation (Stearns 1980).

In term of adaptative implications, phenotypic plasticity allows a population to dampen the effect of short-term environmental variation and to respond to the range of environmental conditions that the organisms have experienced in recent evolutionary time (Takebayashi & Morrell 2001). However, the ability to respond to novel selective challenges is proportional to additive genetic variance (Falconer 1981). We have not calculated the additive effects but spikelet and flower traits (glume width, lemma length and width, number of florets, and spikelet length) reached the most important genetic variances. Therefore, it is possible that these variances were explained by a high additive component. Other authors have mentioned moderate to high levels of genetic variation associated with floral size and shape in out-crossing or partially selfing species (Schoen 1982; Mazer & Schick 1991; Campbell et al. 1994; Carr & Fenster 1994; Robertson et al. 1994; Young et al. 1994; Anderson 1996; Ashman 1999; Vogle et al. 1999) and in self-fertilising species (Lawrence 1972; Carr & Fenster 1994). Consequently, floral structures, especially those related to the mating system, would be capable of responding to selection in natural populations (Young et al. 1994), and so they would have evolutionary importance.

In conclusion, prairie grass shows a double strategy: on one hand, ability to respond to changing environments with some plastic traits, and on the other hand, constancy in those under major genic control and related to speciation and species stability. Perhaps both processes are responsible for the reproductive success and the good adaptation that this autogamous species has in the great region of the humid Pampas.

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