Effect of three environments on the efficiency of indirect selection in *Eragrostis curvula* (lovegrass) genotypes

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SUMMARY

A significant genotype–environment interaction can limit gains in selecting superior genotypes since the best genotype in one locality may not be the best one in another locality. The efficiency of indirect selection is related to the heritability of the trait and to the genetic correlation between localities. Since a major objective of *Eragrostis curvula* (lovegrass) breeding programmes in Argentina is to select superior genotypes from new cultivar introductions, research on the relative effectiveness of direct and indirect selection is necessary in order to identify localities under which the efficiency of indirect selection could be maximized. To do this, experiments using a set of 18 hybrids were carried out in three localities from the semi-arid region of Argentina. Aerial biomass yield, leaf length, crown diameter, panicle number and panicle length were measured and an analysis of variance and covariance were performed. The high genetic correlation obtained suggests that the genetic mechanisms involved in the expression of these traits would be the same, or at least very similar, in Río Cuarto, Villa Mercedes and Bahía Blanca environments where the hybrids showed a stable performance. In general, the heritability obtained was higher in Villa Mercedes and Bahía Blanca than in Río Cuarto. For a given selection intensity the expected correlated response in Villa Mercedes and Bahía Blanca to indirect selection was compared with the expected gain with direct response to selection in Río Cuarto. For dry matter yield, indirect selection in Bahía Blanca did not differ from selection done in Río Cuarto (-3%). However, for performance in Villa Mercedes indirect selection was shown to be less efficient (-29%). For the other traits considered, indirect selection was variable and less efficient, ranging from -18 to -34%. The estimated decrease in efficiency of selection for all the traits considered in the locality of Río Cuarto was higher than in the other localities, suggesting that this place was not a good choice for carrying out indirect selection. Conversely, genetic progress would be faster if selection was carried out in Villa Mercedes, because the evaluations provide higher and more accurate estimates of the heritabilities than in the other localities.

INTRODUCTION

Eragrostis curvula (Schrad.) Nees (lovegrass) is a very variable grass native to Southern Africa. Its several forms are known as lovegrasses and were introduced and spread in Australia, the USA and Argentina as fodder grasses. In Argentina *E. curvula* is the most extensively cultivated warm season perennial grass, especially well adapted to the light-textured soils of the semi-arid regions. Most strains are polyploid

apomicts, but diploids and some tetraploid strains are sexual (Voigt 1971; Voigt & Bashaw 1972, 1976). Sexual and apomictic reproduction allow recombination of desirable agronomic traits from different strains, and promising forage genotypes have been obtained through hybridization (Voigt 1984). The main objective of lovegrass breeding programmes in Argentina is to select superior genotypes from existing cultivars that perform well in a wide range of environments.

The conditions for perennial forage crop production change extensively among the different areas of the central semi-arid region and among different

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growing seasons, causing considerable variation in the development and growth patterns of crops as well as in forage yield. Studies on hybrids of *E. curvula* in relation to permanent and temporary environmental effects and phenotypic correlations indicated high values of repeatability and absence of genotype-harvest interaction for the crown diameter, leaf length and dry matter yield (Di Renzo *et al.* 2000). Estimates of repeatability, which are related to broad sense heritability of traits among a group of fixed entities such as clones, indicated that two measurements were sufficient to evaluate the germplasm. Ibañez *et al.* (1998) reported that genotype–environment interactions affected the germination capacity and the initial growth of ten apomictic lovegrass cultivars of *E. curvula*. Significant genotype–environment interaction was shown to affect genotypic responses and the stability of forage yield across two growing seasons and three localities in the semi-arid region of Argentina (Ibañez *et al.* 2001). Information obtained in the present study suggested a dependable year-to-year reproducibility but differential responses of genotypes associated with localities. Mean values and variances of most of the traits can be affected by climate and soil characteristics and by different growing conditions. A significant genotype–environment interaction for a quantitative trait such as forage yield can seriously limit selection gains since the best genotype in one locality may not be the best one in another locality. The results for the semi-arid region indicate the need to study the relative effectiveness of direct and indirect selection for yield and other agronomic traits in different localities in order to determine the environment in which an advantage for direct selection might exist. Breeders can evaluate the relative efficiency of direct and indirect selection if heritabilities of the measured trait in different environments and the estimates of genetic correlations between environments are available. Genetic correlation is an inverse measurement of genotype–environment interaction (Yamada 1962; Atlin & Frey 1990). Therefore, when varieties are selected in one locality, the relative efficiency of indirect selection is expected to decrease if the genotype–environment interaction is high. Falconer & Mackay (1996) indicated that a trait measured in two different environments could be considered as separate characteristics, controlled by different genes. In consequence, selection in one environment to improve performance in a second environment may produce little or no gain in the second environment (Rowe & Brink 1993). Therefore, identifying appropriate localities where the selection should be carried out is an important aspect of a plant-breeding programme in order to maximize the efficiency of selection. However, as far as is known, there is no published information about the relative efficiency of indirect selection for productive and reproductive traits in lovegrasses. In order to provide this information for lovegrass breeding programmes, the aim of the present research work was to estimate population parameters involved in forage yield and other different traits in lovegrass hybrids and to predict the gain with indirect selection in terms of selection efficiency in three different localities.

MATERIALS AND METHODS

Germplasm and observations

The experiments were carried out in three localities from the temperate semi-arid region of Argentina. Río Cuarto (33°8′S 64°20′W, 334 m a.s.l., 630 mm average rainfall, typic Hapludolls soil) was the locality where direct selection was carried out. Villa Mercedes (33°43′S 65°29′W, 515 m a.s.l., 607 mm average rainfall, typic Ustorthent soil) and Bahía Blanca (38°44′S 62°10′W, 83 m a.s.l., 624 mm average rainfall, typic Ustipsamment soil) were the target localities in which selected genotypes are destined to grow. The study comprised a set of 18 hybrids taken at random from a progeny obtained by Dr P. W. Voigt at Temple, Texas, USA. These experimental hybrids involved five different sexual, tetraploid hybrids as female parents and nine apomictic selections as male parents (Voigt *et al.* 1996).

The plants were sown in March 1994 and were evaluated during the growing seasons of 1996 and 1997. Genotypes were germinated in a greenhouse and seedlings transplanted to a trial field in a randomized complete-block design with three replications of 12 plants per plot in the three localities. All plants were planted with a spacing of 1 m between rows and 0·5 m between plants. The experimental field was surrounded by a guard row of Tanganyika plants, a variety locally well adapted, and the experimental area was maintained in weed-free conditions by mechanical cultivation and hand weeding.

Vegetative characteristics, such as yield of aerial biomass, leaf length and crown diameter and reproductive characteristics such as panicle number and panicle length were measured in four cuts. Three regrowths were harvested at arbitrarily fixed intervals of 30–40 days. The data were recorded as the average of the four cuts and expressed on a plot mean basis. Forage was harvested at the beginning of November, when most genotypes started reproductive growth, at a height of 8–10 cm. The herbage mass harvested was dried in a forced air oven at 70 °C for 48 h for dry matter weight (t/ha) determinations. Prior to harvest leaf length (cm), panicle number (number of panicles per plant) and panicle length (cm) were determined. Leaf length was recorded as the distance from the ground surface to the tip of a sample in fully extended leaves, panicle number as the number of panicles of a sample of plants and panicle length as the distance from the ground level to the tip of a sample

of panicles. After harvest, the crown diameter (cm) was registered as the mean of two perpendicular readings of each plant. After each harvest, the plot was fertilized with 25 kg N/ha as urea, according to local recommendations for the locality.

Statistical analysis

Analysis of variance and covariance were conducted on the field data with ANOVA programmes and the MANOVA option using the Statistical Analysis System (SAS Institute 1990). A transformation of the data was found to be unnecessary because no significant association was found between hybrid mean values and variances. The variable panicle number did not show a normal distribution and was transformed by $\log(y+1)$ prior to performing the analysis. Data combined over a 2-year period in each locality were analysed separately using a split-plot in time analysis (Steel & Torrie 1980), except for leaf length, crown diameter, panicle number and panicle length, which in Río Cuarto were measured only during 1 year. Expected mean squares and mean products were based on a random effects model. Variance components and covariance were estimated by equating mean squares to their expectations and solving for each component. Standard errors for variance components were estimated according to Becker (1984). Genetic coefficients of variation, which provide a unitless measure of trait genetic variance relative to its mean, were calculated as

$$CVg = (\sigma_g/\mu)100$$

where σ_g is the square root of genetic variance and μ is the mean value for each trait. Broad-sense heritability estimates based on the variance components were calculated for each trait following Hanson (1963):

$$h^2 = (\sigma_g^2)/[(\sigma_g^2) + (\sigma_{gy}^2/y) + (\sigma_e^2/ry)]$$

where y and r denote the number of years and replicates, respectively. The subscript g indicates variance components associated with genotypes; gy, genotype × year and e, experimental error. Estimates of heritability for leaf length, crown diameter, panicle number and panicle length evaluated during only 1 year in Río Cuarto were calculated as

$$h^2 = (\sigma_g^2)/[(\sigma_g^2) + (\sigma_e^2/r)]$$

Heritability was estimated on a plot mean basis for the selection and the target localities. Two-side 90% confidence intervals were also computed to determine the accuracy of the heritability estimates. The lower 90% confidence limit for h^2 was defined as $1 - [F_{\alpha/2: df1, df2}/F]$ and the upper 90% confidence limit was defined as $1 - [1/F_{\alpha/2: df1, df2}(F)]$ where $F = 1/(1-h^2)$ (Knapp *et al.* 1985).

The merit of Río Cuarto as the selection locality for genotypes to be grown in Villa Mercedes and Bahía Blanca was estimated in terms of the relative efficiency (E) of indirect selection in Río Cuarto related to direct selection in Villa Mercedes and Bahía Blanca. The efficiency of indirect selection is derived from the selection response model (Falconer & Mackay 1996) using the formula for the ratio of correlation to direct response

$$E = r_g h_Y/h_X$$

where r_g is the genetic correlation for the same trait measured in the locality of selection Y (Río Cuarto) and in the localities of interest X (Villa Mercedes or Bahía Blanca), h_X and h_Y are square roots of the broad sense heritability of the trait in Y and in X localities, respectively. The efficiency model E is based on the assumption that selection intensities i of direct and indirect selection are the same. The equation of efficiency of indirect selection states that if $E > 1$, indirect selection is more efficient than direct selection, and if $E < 1$, direct selection in the target locality is more efficient.

RESULTS

Estimated mean values and variances for different traits of lovegrass hybrids growing in three localities are shown in Table 1. In Villa Mercedes, the dry matter weight was 74·60% of the same measurements made in Río Cuarto. The corresponding values for leaf length, crown diameter, panicle number and panicle length were 79·20%, 78·88%, 103·24% and 115% respectively. In Bahía Blanca the forage yield was 62·48%; leaf length 42·79%, crown diameter 63·54%, panicle number 100·79% and panicle length 76·86% of the values obtained in Río Cuarto. Thus, the highest mean value for each vegetative trait (yield, leaf length and crown diameter) was obtained for plants growing in Río Cuarto. For plants growing in Villa Mercedes the corresponding values were intermediate and the lowest ones were obtained in Bahía Blanca. This locality proved to be the least productive environment for vegetative growth. Río Cuarto was the most productive environment for this species, while Villa Mercedes had the highest mean values for all the reproductive traits considered.

The components of genetic variance were significant for both vegetative and reproductive traits (Table 1). A relationship between variation among genotypes and productivity in the different localities was found. The lowest values for genotypic variances except for crown diameter and panicle length were obtained in Bahía Blanca, the least productive environment. The highest values for dry matter yield, panicle number and panicle length were obtained in Río Cuarto, the most productive environment.

Because climatic conditions were different between 1996 and 1997 significant genotype × year interactions were also detected for all the traits considered,

Table 1. *Variance component estimates, mean values and standard errors for five agronomical traits of 18 hybrids of* Eragrostis curvula *growing in three localities in the semiarid region of Argentina*

Trait	Parameter	Río Cuarto	S.E.	P	Villa Mercedes	S.E.	P	Bahía Blanca	S.E.	P
Dry matter	Mean (t/ha)	76·91	27·28		57·38	15·93		48·05	18·40	
	σ_g^2*	87·02	60·12	≤0·01	83·25	42·86	≤0·01	38·77	27·86	≤0·01
	σ_{gy}^2*	47·43	27·30	≤0·01	26·77	10·88	≤0·01	10·90	20·95	
	σ_e^2*	100·01	22·94		19·38	4·45		135·57	31·10	
Leaf length	Mean (cm)	61·21	9·05		46·65	6·14		26·19	4·10	
	σ_g^2	7·52	5·70	≤0·05	27·82	10·03	≤0·01	6·20	2·56	≤0·01
	σ_{gy}^2	ne			2·19	1·11	≤0·01	0·36	0·83	
	σ_e^2	20·10	4·74		3·42	0·78		5·55	1·27	
Crown diameter	Mean (cm)	28·29	2·70		22·32	3·11		17·98	2·77	
	σ_g^2	7·42	5·69	≤0·05	15·46	8·02	≤0·01	10·58	5·02	≤0·01
	σ_{gy}^2	ne			4·46	2·27	≤0·01	−1·45	2·03	
	σ_e^2	20·17	4·75		6·97	1·60		18·10	4·15	
Panicle number	Mean (number/plant)	11·82	9·07		12·20	9·26		11·91	7·73	
	σ_g^2	0·84	0·63	≤0·05	0·75	0·29	≤0·01	0·57	0·23	≤0·01
	σ_{gy}^2	ne			0·14	0·06	≤0·01	0·15	0·09	≤0·05
	σ_e^2	0·22	0·05		0·14	0·03		0·33	0·08	
Panicle length	Mean (cm)	58·17	23·30		67·24	18·62		44·71	20·60	
	σ_g^2	27·83	23·83	≤0·05	21·55	7·97	≤0·01	23·46	8·98	≤0·01
	σ_{gy}^2	ne			−0·10	1·14		5·55	3·19	≤0·05
	σ_e^2	88·96	20·97		8·82	2·02		11·68	2·68	

Locality column spans Río Cuarto, Villa Mercedes, and Bahía Blanca.

* g: genetic; gy: genotype × year; and e: experimental error.
ne: not estimated when genotypes were evaluated 1 year.

Table 2. *The eight more productive hybrids of* Eragrostis curvula *during 1996 and 1997*

Rank	Year 1996	1997
	Hybrid number	
1	5	5
2	8	1
3	7	8
4	1	7
5	6	17
6	13	6
7	17	15
8	11	13

except for forage yield in Bahía Blanca and for panicle length in Villa Mercedes. The magnitude of variance components for hybrid × year interaction effects, however, was relatively small compared with their corresponding genetic variance component. The significant genotype × year interaction for dry matter in Río Cuarto and in Villa Mercedes suggests that the relative differences among hybrids were not consistent across the years. The inconsistency in dry matter yields across the years is poorly supported by the rankings of the hybrids in each year (Table 2). For example, seven out of the eight top hybrids in 1997 were represented in the top seven in 1996, suggesting a good year-to-year reproducibility.

The genetic coefficients of variation (Table 3), which give us a perspective of the potential usefulness of the variability for genetic gain, were different among localities and showed to be related to the magnitude of the heritability since, except for dry matter and panicle length, the coefficient of variation for the other lovegrass traits measured in Río Cuarto were the lowest ones.

Heritability estimates obtained are broad sense because the differences among apomictic genotypes reflect both additive and non-additive genetic differences. All estimates demonstrated moderate to high heritabilities, ranging from 0·48 to 0·94. The highest heritability for all the traits considered was found in Villa Mercedes, while the smallest values, except for dry matter yield, were found in Río Cuarto. The values obtained in Bahía Blanca were slightly lower than the estimates assessed in Villa Mercedes.

The precision among heritability estimates varied as was demonstrated by the differences in the confidence interval widths that ranged from 10 % to

Table 3. *Genetic coefficient of variation* (CVg) *and broad sense heritability* (h²) *in the target growing localities* (*Río Cuarto*) *and in the localities of interest* (*Villa Mercedes and Bahía Blanca*) *for five traits of hybrids of* Eragrostis curvula

			Locality	
Trait	Parameter	Río Cuarto	Villa Mercedes	Bahía Blanca
Dry matter	CVg (%)	12·13	15·90	12·96
	Heritability	0·68*	0·83*	0·58*
	90% CI on h^2	0·90–0·49	0·94–0·71	0·84–0·20
	Width (%)†	45·47	24·60	76·43
Leaf length	CVg (%)	4·48	11·31	9·51
	Heritability	0·53‡	0·94*	0·85*
	90% CI on h^2	0·78–0·09	0·98–0·88	0·94–0·68
	Width (%)†	88·58	10·13	27·75
Crown diameter	CVg (%)	9·63	17·62	18·09
	Heritability	0·52‡	0·82*	0·78*
	90% CI on h^2	0·78–0·08	0·94–0·69	0·93–0·66
	Width (%)†	89·59	27·04	29·72
Panicle number	CVg (%)	28·45	86·94	74·02
	Heritability	0·53‡	0·89*	0·81*
	90% CI on h^2	0·78–0·09	0·95–0·76	0·92–0·57
	Width (%)†	88·14	20·01	37·76
Panicle length	CVg (%)	9·07	6·90	10·83
	Heritability	0·48‡	0·94*	0·83*
	90% CI on h^2	0·76–0·00	0·97–0·87	0·92–0·61
	Width (%)†	99·64	10·91	34·37

* $h^2 = (\sigma_g^2)/[(\sigma_g^2) + (\sigma_{ge}^2/l) + (\sigma_e^2/lr)]$.
† Expressed as the ratio (%) of the confidence interval width relative to the heritability point estimate.
‡ $h^2 = (\sigma_g^2)/[(\sigma_g^2) + (\sigma_e^2/r)]$.

155 %. With the exception of dry matter in Bahía Blanca, confidence interval widths of heritability estimates, based on measurements taken in 2 years, ranged from 10 % to 60 %. When heritability estimates were based on only one year's measurements, such as those taken for leaf length, crown diameter, panicle number and panicle length in Río Cuarto, the corresponding values for the intervals ranged from 129 % to 150 %.

Genetic correlations for genotype values between Villa Mercedes and Río Cuarto and between Bahía Blanca and Río Cuarto, which are reported in Table 4, were high for all the traits considered. These high genetic correlations for different traits suggest that the selection of plants based on their performance in Río Cuarto, as the locality of selection, might improve the mean values in either Villa Mercedes or Bahía Blanca localities. Although the correlation cannot be higher than 1·0, the genetic correlations for leaf length, crown diameter and panicle length between Villa Mercedes and Río Cuarto and the genetic correlations for panicle number and panicle length between Bahía Blanca and Río Cuarto were found to be $r_g > 1$. Mathematically it is possible to have an

assessment exceeding 1·0 (Baker 1986), but for the calculations of the predicted efficiency of the indirect selection, these estimates were considered as 1·0.

For a given selection intensity (*i*) the expected correlated response in Villa Mercedes and Bahía Blanca to the indirect selection was compared with the expected gain with a direct response to selection for different traits in Río Cuarto (Table 4). For dry matter yield indirect selection in Bahía Blanca did not differ when selection was done in Río Cuarto (-3%). However, for performance, indirect selection in Villa Mercedes was estimated to be less efficient (-29%). For the other four traits indirect selection was distinctly less efficient, ranging from -18 to -34%.

DISCUSSION

It has been shown that it is possible to select with some efficiency in an environment different from one of interest, under certain conditions. This kind of selection is termed indirect selection. Considering the same selection intensity for the trait under consideration in both environments, it is possible to obtain practical results when there is high genetic

Table 4. *Genetic correlation* (r_g) *for vegetative and reproductive traits between selection locality* (*Río Cuarto*) *and target growing localities* (*Villa Mercedes and Bahía Blanca*), *and predicted efficiency* (E) *of indirect selection in Villa Mercedes and Bahía Blanca relative to direct selection in Río Cuarto*

Trait	Locality	r_g	S.E.*	E
Dry matter	Villa Mercedes	0·78	0·013	0·71
	Bahía Blanca	0·89	0·013	0·97
Leaf length	Villa Mercedes	1·08	ne	0·75
	Bahía Blanca	0·83	0·014	0·66
Crown diameter	Villa Mercedes	1·14	ne	0·80
	Bahía Blanca	1·34	ne	0·82
Panicle number	Villa Mercedes	0·90	0·007	0·69
	Bahía Blanca	0·87	0·005	0·70
Panicle length	Villa Mercedes	1·07	ne	0·72
	Bahía Blanca	1·10	ne	0·76

* Standard errors of the genetic correlations estimated with an approximate equation (Falconer & Mackay 1996). ne: Not estimated when genetic correlation was greater than 1·0.

correlation between the target and the selection localities with a high difference between the estimations of the heritability in the locality of selection and in the locality of interest, specifically when $h_Y > h_X$.

Genetic correlation for a given trait measured in two different localities can provide some evidence about the genetic mechanisms involved in the expression of the trait. A high genetic correlation between localities suggests that the trait is determined by the same set of genes (Falconer & Mackay 1996). According to the data obtained in the present research the genetic mechanisms involved in the expression of the considered traits are the same, or at least very similar, in Río Cuarto, Villa Mercedes and Bahía Blanca environments. This common genetic basis implies that differences obtained in the final products of selection in different localities should be small. However, for several different traits, the expected rate of advance from selection would be expected to decrease considerably when selection is carried out in Río Cuarto in comparison with target localities.

The analysis of variance components showed the important contributions of genotypic variance in determining the phenotypic variance of several traits in Villa Mercedes. The error variance was the largest source of variation in Río Cuarto and genotype × year interaction effects were generally not high in Villa Mercedes and in Bahía Blanca. The occurrence of interaction for dry matter yields did not affect the top-ranking genotypes during the 2 years, suggesting

that the selected material is stable across the years (Ibañez *et al.* 2001).

A high value of heritability indicates a high degree of genetic control for a given trait. In general, the higher heritability estimates in localities of interest (Villa Mercedes and Bahía Blanca) relative to the estimates in the selection locality (Río Cuarto) may have resulted from lower experimental error and not from high genotype × year interaction effects in the target localities. In addition, heritabilities are determined more precisely when estimates are based on 2-year measurements rather than one, such as for crown diameter, leaf length, panicle number and panicle length, calculated in Río Cuarto. The width of the confidence intervals indicates that the confidence interval values were closely and negatively associated with the size of the heritability estimates. This relationship confirms the value of repeated measurements in a certain time interval for a reliable evaluation of lovegrass germplasm.

The results discussed above show that the environment and repeated measures play a very important role in determining the efficiency of indirect selection. The efficiency of indirect selection is related to the heritability of the trait and to the genetic correlation between localities. In this set of lovegrass hybrids, even when estimates of genetic correlation are elevated, it does not predict the possibility that different genotypes selected in Río Cuarto may provide the best overall combination of traits in Villa Mercedes and/or in Bahía Blanca. Though heritability estimates are more conducive to genetic progress by indirect selection on individual traits than genetic correlation between localities, they cannot be assumed to be the best criteria for selection in a particular environment (Allen *et al.* 1978; Atlin & Frey 1990).

The current set of genotypes is not large and representative enough to provide definite indications on genetic parameters for the species. Nevertheless the estimated decrease in efficiency of selection for all traits when considering Río Cuarto as a locality of selection is high and suggests that indirect selection may not have good prospects. In general, these results suggest that genetic progress would be faster if selection is done at Villa Mercedes rather than at Río Cuarto environment. Villa Mercedes as a locality of selection is considered a good alternative in order to increase the efficiency of the selection process because of higher heritability estimates and more accurate assessment of heritabilities. Though measurement of different traits in Villa Mercedes are more costly and labour-demanding in comparison with Río Cuarto, it offers a good alternative for obtaining a reliable assessment and for increasing the efficiency of selection. Based on the results obtained with *E. curvula*, and for the range of environments included in the present study, it is possible to suggest that, at

least in the initial stages of a breeding programme, the approximate gain in precision achieved with a predicted efficiency provides a tool for choosing a locality of selection that improves realized progress from selection.

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