Mating system parameters in species of genus *Prosopis* (Leguminosae)

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The section Algarobia of genus *Prosopis* involves important natural resources in arid and semiarid regions of the world. Their rationale use requires a better knowledge of their biology, genetics and mating system. There are contradictory information about their mating system. Some authors claim they are protogynous and obligate outcrosser. However, some evidence have been shown indicating that they might not be protogynous and that they might be somewhat self-fertile. The current paper analyses genetic structure and mating system parameters in populations of seven species of this section from South and North America based on isozyme data. In all species a significant homozygote excess was found in the offspring population but not in mother plant genotypes. Multilocus and mean single locus outcrossing rates (*tm*, *ts*) indicated that about 15 % selfing can occur in the studied populations. The heterogeneity between pollen and ovule allele frequencies was low suggesting population structuration, in agreement with the estimates of correlation of *tm* within progeny (*rt*) and correlation of outcrossed paternity (*rp*). The difference of F_{IS} estimates between offspring and mother plants suggest some selection favouring heterozygotes between seedling and adult stages.

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Some species of the section Algarobia of genus *Prosopis* constitute important natural resources in arid and semiarid regions of the world. They are promising multipurpose species for reforestation, production of wood, charcoal, forage, and human food. Their breeding and improvement have been recommended by several authors (BURKART 1976; FELKER 1979; LEAKEY and LAST 1980; GALINDO-ALMANZA 1983; GALINDO-ALMANZA and GARCIA 1986a,b). To reach this goal it is paramount to know the biology, genetic variability and differentiation, mating system, genetic structure, and adaptive strategies of these species.

The species so far studied of this section exhibit high variability in morphological characters such as production, size and shape of fruits, life form, growth rate, adaptability to extreme temperature and salinity (FELKER 1979; GALINDO-ALMANZA 1983; ROIG 1993). Important intraspecific genetic variability was also detected by means of isoenzyme electrophoresis (SAIDMAN 1985, 1986, 1988, 1990, 1993; SAIDMAN and VILARDI 1987, 1993; SAIDMAN et al. 1997, 1998a) and random amplified polymorphic DNA segments (SAIDMAN et al. 1998b; Bessega submitted).

There are strong evidence of frequent hybridization among several species, coming from morphological, biochemical and isoenzymatic studies (PALACIOS and BRAVO 1981; NARANJO et al. 1984; HUNZIKER et al. 1986; SAIDMAN 1990; VERGA 1995). The virtual lack of clear reproductive barriers as well as the high genetic similarity between "good taxonomic species" has led to the assumption that several sympatric species of this section inhabiting the Chaqueña Biogeographical Region in Argentina would constitute a syngameon (PALACIOS and BRAVO 1981; SAIDMAN 1985; GRANT 1989).

Both facts, high intraspecific variability and interspecific hybridization rate have been related with floral biology. For a long time these species were assumed to be protogynous (BURKART 1937, 1952, 1976) and this property together with lack of clear reproductive barriers was considered as responsible of an outcrossing mating system which, in time, might explain the high intraspecific variability and the occurrence of interspecific hybridization (SOLBRIG and BAWA 1975; SOLBRIG and CANTINO 1975; NEFF et al. 1977; SIMPSON, 1977; SIMPSON et al. 1977; HUNZIKER et al. 1986). However, according to more recent results this assumption should be revised. Studies of maturation of flowers and nectar produc-

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tion in three Southamerican species of this section (*P. flexuosa*, *P. chilensis* and *P. pugionata*) made by GENISSE et al. (1990) do not support this point. They concluded that flowers are not protogynous and suggested that the high variability in some species of Algarobia would be maintained by an autoincompatibility system independent of protogyny. Besides, GALINDO-ALMANZA et al. (1992) observed through pollination studies that Mexican populations of *P. glandulosa* var. *torreyana* and *P. laevigata* are at least partially autocompatible. KEYS and SMITH (1994) studying the mating system in three populations of *P. velutina* from U.S.A. (using isoenzymatic markers) concluded that the outcrossing rate is about 90 % and that selfing can occur at a low rate. Finally, studies of population structure based on isozyme electrophoresis using WRIGHT's (1951) *F* statistics (KEYS and SMITH 1994; SAIDMAN et al. 1998a) show a general trend to homozygote excess in seedlings collected from natural populations, which might be compatible with a certain degree of selfing. However, *Prosopis* species populations are expected to be structured because pollen and seed dispersals are limited. The endozoic seed dispersal determines that seeds from the same mother plant are eaten by herbivores and transported away jointly. They are then deposited in dung and full or half sib seeds tend to germinate together in a narrow area. Besides, the pollination is entomophilous (GENISSE et al. 1990) favouring crosses among near neighbour plants. Therefore, the homozygote excess might also be consequence of population substructure.

Taking into account the contradictory data available on the mating system of these species our objectives were to estimate mating system and population structure parameters of seven species of the section Algarobia of genus *Prosopis*. During the analysis of our data we also tested the first genetic interpretation (based on indirect evidence) of the isozyme bands described in previous works (SAIDMAN 1985, 1986, 1988, 1990, 1993; SAIDMAN and VILARDI 1987, 1993; SAIDMAN et al. 1997, 1998a) by analyzing family data.

MATERIALS AND METHODS

Sampling description

The sampling involved one population of each of seven species of section Algarobia that occur in semiarid regions of the Chaqueña Biogeographic Region in Argentina, and Texas and Arizona in USA (Table 1). Each population is a fairly continuous forest of several square kilometres wide. The populations sampled are isolated from each other and apparently are made up from pure stands, with no evidence of interspecific hybridization. Six of the studied species, *P. glandulosa*, *P. velutina*, *P. chilensis*, *P. nigra*, *P. alba*, and *P. flexuosa* belong to the series Chilenses, and the remaining one, *P. ruscifolia*, to the series Ruscifoliae.

At least 10 mother plants were sampled in each population from Argentina. The samples from populations from United States were kindly donated by Dr. C. J. De Loach (Grassland Research Station-USDA/ARS). They included 5 mother plants. In all cases the trees were separated at least 50 m. from each other. This distance between sampled mothers plants reduce the probability that they interbreed, because enthomophilic pollination is related with limited pollen dispersal. About 50 pods were collected from each mother plant. All seeds from each tree were stored in single bags. From each of these bags seeds were randomly sampled for the isozymal analysis of each progeny array. The number of seeds analyzed per mother plant (family array size) was about 10 in Argentinean species and 15 in species for USA.

Genetic characterization

A total of 7 isoenzymatic system which were shown to reveal polymorphic and codominant loci (SAIDMAN 1985, 1986, 1988, 1990, 1993; SAIDMAN and VILARDI 1987, 1993; SAIDMAN et al. 1997, 1998a) were used in the current study: alcohol dehydrogenase (ADH), esterase (EST), glutamate oxalacetate transaminase (GOT), amino peptidase (AMP), 6-phosphogluconate dehydrogenase (6PGD), isocitrate

Table 1. *Geographic location of population analyzed*

Serie	Species	Population	Latitude	Longitude
Chilenses	*P. alba*	Burruyacu	26°30′	64°43′
	P. nigra	Huilla Catina	27°32′	64°06′
	P. chilensis	Patquia	30°02′	66°52′
	P. flexuosa	Quilmes	26°22′	65°58′
	P. velutina	Santa Rita	31°35′	110°53′
	P. glandulosa	Weslaco	26°09′	97°59′
Ruscifoliae	*P. ruscifolia*	Rivadavia	24°11′	62°53′

Table 2. *Enzyme structure of the analyzed systems*

Enzyme system	Gene symbol	EC	Structure	No of loci detected	Max. No of alleles detected
Alcohol dehydrogenase	*Adh*	1.1.1.1	Dimeric	2	4/3
Aminopeptidase	*Amp*	3.4.11.1	Monomeric	1	3
Esterase	*Est*	3.1.1	Monomeric	1	4
Glutamate dehydrogenase	*Got*	2.6.1.1	Dimeric	2	5/5
Isocitrate dehydrogenase	*Idh*	1.1.1.42	Dimeric	2	2/4
6-phosppgluconic dehydrogenase	*6-Pgd*	1.1.1.43	Dimeric	2	2/3
Shikimic dehydrogenase	*Skd*	1.1.1.25	Monomeric	1	3

dehydrogenase (IDH) and shikimic dehydrogenase (SKD). The technique employed was horizontal electrophoresis on polyacrylamide gels. The methods employed for the former five systems are described in SAIDMAN (1985, 1986). For IDH and SKD the method was modified from VERGA (1995). The homogenates for ADH were made from 24 h soaked seeds; for the remaining systems 5–7 day old cotyledons were used.

Controlled crosses in *Prosopis* species have not been successful so far. In cases like this one, the genetic interpretation of the isozyme data is usually based on (1) the presence of banding patterns typical for specific isozymes; (2) biochemical and developmental allelism tests (SAIDMAN 1985, 1986); (3) the possibility of a maternal genotype that could have generate the progeny array; and (4) the fit of the progeny array data to the expected Mendelian segregation ratios for a diploid organism (KEYS and SMITH 1994; VERGA 1995). In species of the section Algarobia additional support to the genetic interpretation was obtained from the analysis of segregating patterns of natural hybrids (SAIDMAN 1985, 1986, 1990). In the present study the analysis of segregation in progeny arrays was used to support previous hypotheses on the genetic determination of isozyme bands.

Loci were numbered consecutively, with the most anodal being designated locus 1. Alleles within loci were designated by a number referring to their relative mobility on the gel respect to bromophenol.

Data analysis

Genetic structuration

Allelic and genotypic frequencies of the whole seed population sample was estimated including all available loci. Similar numbers of seeds from different mother plants were analyzed. The bias from Hardy–Weinberg expectations were evaluated by means of the F_{IS} fixation index (WRIGHT 1951) estimated by the method of NEI (1977) using the program Biosys 1.7 (SWOFFORD and SELANDER 1981).

Mating system parameters

Estimates of multilocus (t_m) and mean single locus (t_s) outcrossing rates, correlation of *tm* within progeny arrays (*rt*), the correlation of outcrossed paternity (*rp*), and fixation index of maternal parents (F_{ISM}) were calculated using the MLTR program (K. Ritland, Department of Forest Science, University of British Columbia), an improved version of the MLT (RITLAND 1990a) computer program. This program is based on the multilocus mixed-mating model and the estimation procedure of RITLAND and JAIN (1981) which assumes that progeny are derived from either random mating (outcrossing) or self-fertilization. The maternal genotypes for each family is inferred by the method of BROWN and ALLARD (1970). The estimation of mating system parameters was made by the Expectation-Maximization method to assure convergence.

The analysis of mating system parameters was limited to those loci which could be simultaneously studied in each individual. The mixed-mating model assumes independent segregation of alleles at the different marker loci. In order to support this assumption with the available data we tested the null hypothesis of no association between genotypes at different loci. The absence of such associations can be considered as evidence for independent segregation (see DOLIGUEZ and JOLY 1997). Possible genotypic associations among these loci were tested using the program GENEPOP (RAYMOND and ROUSSET 1995). The method creates contingency tables for all pairs of loci in each population and then performs a probability test (or Fisher exact test) for each table using a Markov chain.

Estimated pollen and ovule allele frequencies were compared by means of a contingency table using the Pearson Chi-square test.

RESULTS

Genetic interpretation

The analysis of segregation within progeny arrays allowed to confirm previous (SAIDMAN 1985, 1986, 1990) interpretation of the genetic determination of isozyme bands. In all families the maternal genotype could be inferred from progeny genotypes. The subunit structure (monomeric or dimeric) could be determined on the basis of the number of bands observed in heterozygous individuals. Table 2 summarizes the isozyme structure and the number of alleles detected for each locus.

Genetic structure

Allelic frequencies and fixation indices for the whole seed (offspring) sample are listed in Table 3. In all cases F_{IS} in this sample (F_{ISO}) was positive, varying

Table 3. *Allelic frequencies and fixation index (F_{ISO}) estimated in the offspring populations. N: sample size, SE: standard error of F_{ISO}*

		P. alb	*P. nig*	*P. chi*	*P. fle*	*P. rus*	*P. vel*	*P. gla*
Adh-1	1^{30}	0.000	0.579	0.120	0.490	1.000	0.780	0.936
	1^{28}	1.000	0.412	0.880	0.388	0.000	0.220	0.064
	1^{24}	0.000	0.009	0.000	0.122	0.000	0.000	0.000
Adh-2	2^{20}	0.000	0.000	0.000	0.000	0.058	0.000	0.000
	2^{17}	1.000	1.000	1.000	1.000	0.926	1.000	1.000
	2^{14}	0.000	0.000	0.000	0.000	0.016	0.000	0.000
Amp-2	2^{88}	0.406	0.127	0.256	0.455	0.387	0.794	0.417
	2^{76}	0.594	0.461	0.565	0.545	0.411	0.206	0.466
	2^{70}	0.000	0.412	0.179	0.000	0.202	0.000	0.117
Est-1	1^{93}	0.000	0.289	0.000	0.000	0.000	0.000	0.000
	1^{92}	0.889	0.579	0.125	0.833	0.886	0.097	0.094
	1^{91}	0.111	0.132	0.634	0.161	0.114	0.742	0.469
	1^{90}	0.000	0.000	0.241	0.006	0.000	0.161	0.438
Got-1	1^{72}	0.012	0.006	0.163	0.516	0.051	0.116	0.077
	1^{71}	0.000	0.000	0.000	0.000	0.000	0.802	0.055
	1^{70}	0.000	0.000	0.000	0.000	0.000	0.000	0.440
	1^{69}	0.988	0.570	0.837	0.437	0.949	0.081	0.363
	1^{61}	0.000	0.424	0.000	0.047	0.000	0.000	0.066
Got-2	2^{54}	0.000	0.000	0.000	0.000	0.000	1.000	0.000
	2^{48}	0.034	0.280	0.134	0.314	0.591	0.000	0.608
	2^{40}	0.966	0.699	0.866	0.637	0.409	0.000	0.315
	2^{34}	0.000	0.021	0.000	0.049	0.000	0.000	0.000
	2^{27}	0.000	0.000	0.000	0.000	0.000	0.000	0.077
Idh-1	1^{100}	0.093	0.013	0.258	0.005	0.000	0.250	0.054
	1^{70}	0.886	0.176	0.677	0.116	0.391	0.750	0.920
	1^{63}	0.021	0.782	0.065	0.858	0.609	0.000	0.026
	1^{60}	0.000	0.029	0.000	0.021	0.000	0.000	0.000
Idh-2	2^{43}	1.000	0.000	0.000	1.000	0.000	0.000	0.000
	2^{30}	0.000	0.000	0.632	0.000	0.000	0.000	0.000
	2^{26}	0.000	1.000	0.368	0.000	1.000	1.000	1.000
6-Pgd-1	1^{30}	0.000	0.431	0.531	0.010	0.628	0.000	0.000
	1^{26}	1.000	0.569	0.250	0.990	0.372	1.000	1.000
	1^{0}	0.000	0.000	0.219	0.000	0.000	0.000	0.000
6-Pgd-2	2^{23}	0.230	0.067	0.625	0.118	0.256	0.000	0.000
	2^{21}	0.098	0.008	0.062	0.198	0.161	0.000	0.000
	2^{0}	0.672	0.925	0.313	0.684	0.583	1.000	1.000
Skd-1	1^{24}	0.144	0.353	0.750	0.587	0.076	0.531	0.093
	1^{22}	0.561	0.549	0.031	0.207	0.924	0.469	0.651
	1^{19}	0.295	0.098	0.219	0.206	0.000	0.000	0.256
N		90	100	85	90	84	74	91
F_{ISO}		0.389	0.242	0.175	0.391	0.295	0.312	0.383
SE		0.107	0.161	0.086	0.139	0.085	0.175	0.103

Table 4. *Significance levels for chi-square tests of independence of genotypes between loci (Fisher exact test). NS: $p > 0.05$; *: $p < 0.05$; **: $p < 0.01$. In no case the association was significant at matrix level*

	Amp-1	*Est-1*	*Got-1*	*Got-2*	*6Pgd-1*	*6Pgd-2*	*Idh-1*	*Idh-2*
Est-1	NS							
Got-1	NS	NS						
Got-2	NS	NS	NS					
6Pgd-1	NS	NS	NS	*				
6Pgd-2	—	NS	NS	*	NS			
Idh-1	**	NS	NS	*	NS	NS		
Idh-2	—	—	—	—	NS	NS	NS	
Skd-1	NS	NS	NS	*	NS	NS	NS	*

from 0.175 to 0.391, indicating a general trend towards homozygote excess within populations.

Mating system parameters

Since the mixed mating model assumes independence among loci, possible genotypic associations were tested within each species and across species. The trends observed were similar in all populations and the results are summarised in Table 4. Only 6 of a total of 31 locus pairs showed significant association, but in no case the disequilibrium was significant at matrix level applying the Bonferroni sequential test. Since genotypes for most pairs of loci were independent the bias in the results due to physical linkage between loci were considered negligible.

Ovule and pollen allele frequencies (Table 5) were compared through contingency table analysis. Out of 44 comparisons only 8 yielded significant differences. These result suggests low heterogeneity between pollen and ovule frequencies.

Multilocus (*tm*) and average single locus (*ts*) outcrossing rates were similar to each other (Student test: $T_6 = 0.98$, $P = 0.36$). Multilocus outcrossing rate estimates in the studied species varied from 0.718 in *P. alba* to 1 in *P. nigra* (Table 6), indicating that these species are mostly outcrossing but selfing can occur at least in some populations. The correlation of *tm* within progeny arrays (*rt*) in most cases was high, suggesting that outcrossing rates differ among mother plants. The correlation of outcrossed paternity (*rp*) was also high, indicating that many individuals within a progeny array are full sibs.

The estimates of fixation indices for maternal genotypes (F_{ISM}) were in almost all cases lower than the corresponding values for their offspring's (F_{ISO}) (see Tables 3 and 5), and in some species the confidence interval of F_{ISM} includes zero. The comparison of F_{IS} between maternal and offspring genotypes yielded highly significant differences (Student test: $T_6 = 7.87$, $P = 0.0002$).

DISCUSSION

Classical studies in species of the Section Algarobia (SIMPSON 1977) pointed that these species are protogynous and obligate outcrosser. This view contrasts with more recent studies of floral biology by GENISSE et al. (1990) that indicate that species of Algarobia are not protogynous. However, this authors were yet prone to accept that these species are obligate outcrosser and hypothesise that this condition would be consequence of some autoincompatibility system.

However, results of isozyme analysis showed significant excess of homozygotes in all populations so far studied of species of this section (SAIDMAN 1985, 1986, 1988, 1990, 1993; SAIDMAN and VILARDI 1987, 1993; SAIDMAN et al. 1997, 1998a, VERGA 1995, KEYS and SMITH, 1994), which suggests high levels of inbreeding. Such inbreeding would be expected if there is family structure within populations, but it might also be caused by some degree of selfing.

The last possibility seem to be supported by different pollination studies showing that *P. glandulosa*, *P. laevigata* (GALINDO-ALMANZA et al. 1992) and *P. velutina* (KEYS 1993; KEYS and SMITH 1994) are at least partially selfcompatible. Solving the question about the relation between mating system and homozygote excess in species of section Algarobia requires testing the genetic interpretation of isozyme bands, and analysing mating system parameters and population structure.

In the current study the genetics of the loci were inferred from single-tree progeny arrays. The number of loci considered to control the isozyme systems studied here were similar to the results of previous studies (SOLBRIG and BAWA 1975; SAIDMAN 1985, 1986, 1988, 1990, 1993; SAIDMAN and VILARDI 1987, 1993; SAIDMAN et al. 1997, 1998a; VERGA 1995). In agreement with other studies in species of Algarobia all populations analyzed here showed high homozygote excess for the seed population ($F_{ISO} > 0$).

Table 5. *Pollen and ovule allele frequencies and fixation index (F_{ISM}) estimated from populations of Prosopis. Significant values are underlined*

		P. alb		*P. nig*		*P. chi*		*P. fle*		*P. rus*		*P. vel*		*P. gla*	
		p	o	p	o	p	o	p	o	p	o	p	o	p	o
Amp-2	2^{88}	—	—	—	—	—	—	0.45	0.40	—	—	0.79	0.87	0.43	0.40
	2^{76}	—	—	—	—	—	—	0.54	0.60	—	—	0.21	0.13	0.43	0.50
	2^{70}	—	—	—	—	—	—	—	—	—	—	—	—	0.14	0.10
Est-1	1^{93}	0.02	0.06	0.30	0.28	—	—	0.01	0.04	0.03	0.05	0.13	0.11	0.07	0.10
	1^{92}	0.94	0.78	0.51	0.61	—	—	0.85	0.73	0.86	0.90	0.69	0.78	0.52	0.50
	1^{91}	0.04	0.17	0.18	0.11	—	—	0.13	0.18	0.11	0.05	0.18	0.11	0.42	0.40
	1^{90}	—	—	—	—	—	—	0.01	0.04	—	—	—	—	—	—
Got-1	1^{72}	0.05	0.05	0.01	0.05	—	—	0.56	0.50	0.06	0.10	**0.03**	**0.30**	**0.17**	**0.08**
	1^{71}	—	—	—	—	—	—	—	—	—	—	**0.73**	**0.50**	**0.01**	**0.08**
	1^{70}	—	—	—	—	—	—	—	—	—	—	—	—	**0.59**	**0.46**
	1^{69}	0.94	0.95	0.62	0.53	—	—	0.44	0.50	0.94	0.90	**0.21**	**0.10**	**0.22**	**0.30**
	1^{61}	—	—	0.37	0.42	—	—	—	—	—	—	**0.03**	**0.10**	**0.01**	**0.08**
Got-2	2^{54}	—	—	—	—	—	—	—	—	—	—	0.88	0.68	—	—
	2^{48}	0.09	0.05	0.33	0.17	—	—	0.20	0.40	**0.45**	**0.81**	0.03	0.08	0.61	0.70
	2^{40}	0.91	0.95	0.65	0.78	—	—	0.65	0.55	**0.52**	**0.14**	0.03	0.08	0.39	0.30
	2^{34}	—	—	0.01	0.06	—	—	0.15	0.05	**0.03**	**0.05**	0.03	0.08	—	—
	2^{27}	—	—	—	—	—	—	—	—	—	—	0.03	0.08	—	—
Idh-1	1^{100}	—	—	—	—	0.30	0.43	0.01	0.05	—	—	0.47	0.11	0.06	0.09
	1^{70}	—	—	—	—	0.66	0.50	0.19	0.09	—	—	0.53	0.89	0.89	0.82
	1^{63}	—	—	—	—	0.04	0.07	0.78	0.81	—	—	—	—	0.05	0.09
	1^{60}	—	—	—	—	—	—	0.01	0.05	—	—	—	—	—	—
Idh-2	2^{43}	—	—	—	—	0.04	0.07	0.99	0.95	—	—	0.03	0.11	0.02	0.09
	2^{30}	—	—	—	—	0.29	0.47	—	—	—	—	—	—	—	—
	2^{26}	—	—	—	—	0.67	0.47	0.01	0.05	—	—	0.97	0.89	0.98	0.91
6pgd-1	1^{30}	—	—	—	—	**0.24**	**0.27**	**0.35**	**0.55**	—	—	0.96	0.89	0.98	0.91
	1^{26}	—	—	—	—	**0.23**	**0.67**	**0.6**	**0.45**	—	—	0.04	0.11	0.02	0.09
	1^{0}	—	—	—	—	**0.53**	**0.07**	—	—	—	—	—	—	—	—
6pgd-2	2^{23}	—	—	—	—	0.10	0.07	0.09	0.15	—	—	0.04	0.10	0.02	0.08
	2^{21}	—	—	—	—	0.80	0.71	0.29	0.35	—	—	0.04	0.10	0.02	0.08
	2^{0}	—	—	—	—	0.10	0.21	0.62	0.50	—	—	0.92	0.80	0.96	0.84
Skd-1	1^{24}	**0.23**	**0.06**	**0.36**	**0.06**	**0.12**	**0.87**	0.57	0.60	0.03	0.10	0.67	0.63	0.19	0.09
	1^{22}	**0.58**	**0.61**	**0.46**	**0.67**	**0.57**	**0.06**	0.24	0.15	0.97	0.90	0.33	0.37	0.49	0.64
	1^{19}	**0.19**	**0.33**	**0.18**	**0.28**	**0.31**	**0.06**	0.19	0.25	—	—	—	—	0.32	0.27
# families		10		10		10		10		10		5		5	
# prog/family		10		10		8		10		9		13		15	
F_{ISM}		0.008		0.000		0.225		0.000		0.022		0.098		0.022	
SE		0.001		0.000		0.116		0.000		0.003		0.032		0.000	

Table 6. *Estimates of mating system parameters in species of Prosopis. Standard error in parenthesis. tm and ts denote multilocus and single locus outcrossing rates respectively. rt and rp denote correlation of tm within progeny arrays and correlation of outcrossed paternity*

	P. alba Burruyacu	*P. nigra* Huilla Catina	*P. chilensis* Patquia	*P. flexuosa* Quilmes	*P. ruscifolia* Rivadavia	*P.velutina* Santa Rita	*P. glandulosa* Weslaco
tm	0.718 (0.174)	1.000 (0.014)	0.809 (0.111)	0.882 (0.055)	0.782 (0.114)	0.741 (0.099)	0.976 (0.092)
ts	0.864 (0.118)	0.928 (0.029)	0.687 (0.115)	0.876 (0.027)	0.811 (0.051)	0.779 (0.060)	0.880 (0.055)
tm-ts	−0.046 (0.062)	0.071 (0.032)	0.122 (0.049)	0.006 (0.036)	−0.028 (0.073)	−0.038 (0.042)	0.096 (0.045)
rt	0.866 (0.139)	0.870 (0.030)	0.398 (0.184)	0.942 (0.025)	0.854 (0.095)	0.851 (0.040)	0.925 (0.028)
rp	0.805 (0.086)	0.620 (0.167)	0.964 (0.114)	0.990 (0.001)	0.990 (0.001)	0.990 (0.001)	0.990 (0.001)

The relative importance of biparental endogamy (family structure) and selfing for this bias from Hardy-Weinberg was weighed by estimating mating system parameters. Multilocus outcrossing rate estimate range in these species was rather narrow in spite of the fact that the number of families sampled in the North American populations was relatively low. The current estimates were also similar to the values obtained by KEYS and SMITH (1994) for populations of *P. velutina*. The range of values for *Prosopis* species is similar to the estimates recorded for shrub and tree species (PREMOLI 1996; DOLIGUEZ and JOLY 1997) and other entomophilous legumes (MORAN et al. 1989; SURLES et al. 1990; GODT and HAMRICK 1991; KRUEGER and KNAPP 1991; YOUNG and BROWN 1998). Taking together the estimates obtained in the current paper with those of KEYS and SMITH (1994), the averaged *tm* for populations of species of Section Algarobia is 0.81. This value means that about 19 % of selfing can occur in these species, a value compatible with the homozygote excess and the results obtained by GALINDO-ALMANZA et al. (1992) and KEYS and SMITH (1994). The similarity between *tm* and *ts* also suggest selfing instead of biparental endogamy to explain homozygote excess.

The joint analysis of outcrossing rates, correlation of outcrossed paternity within progeny arrays (*rp*) and correlation of outcrossing rate within progeny arrays (*rt*) yielded two main conclusions. 1) Many individuals within progeny array are full rather than half sibs. This may be consequence of partial selfing and limited pollen dispersal favouring crosses among near neighbours, resulting in an important family structure. The lack of differentiation between pollen and ovule allelic frequencies is also compatible with the hypothesis of limited pollen dispersal. 2) The outcrossing rate varies among mother plants, probably due to micro-spatial variation in population density and/or ecological factors. More isolated plants might have higher selfing rates than those situated in more dense patches.

Self compatibility coupled with limited pollen dispersal is expected to lead to increasing inbreeding in natural conditions. The entomophilic condition of *Prosopis* species (GENISSE et al., 1990) determines that pollen is usually unable to migrate large distances. An additional factor increasing inbreeding in *Prosopis* species would be their endozoic dispersal seed system. Before the colonization of America and the introduction of livestock by Europeans the main vectors for seed dispersal of *Prosopis* species would have been small herbivorous mammals (MARES et al. 1977), which are not able to transport seed over large distances. Merriam kangaroo rat was shown to disperse velvet mesquite (*P. velutina*) seeds between 15 and 50 m (REYNOLDS 1954). With these antecedents it is difficult to understand how the high variability is maintained in the species so far studied of section Algarobia and why genetic distances between species are as low as those observed between conspecific populations of other genus (SAIDMAN 1985, 1986, 1988, 1990, 1993; SAIDMAN and VILARDI 1987, 1993; SAIDMAN et al. 1997, 1998a).

A first hypothesis advanced to explain the low genetic differentiation and high genetic variability in species of Algarobia was related to the high interspecific hybridisation rate in natural populations (SAIDMAN 1985; SAIDMAN and VILARDI 1987). However, SAIDMAN et al. (1998a) observed that estimates of effective gene flow were insignificant ($Nm < 1$) among populations of different species, even for sympatric or neighbouring ones. This result indicates that hybridisation and introgression do not by themselves explain the high similarity among species of Algarobia.

The differences between adult (F_{ISM}) and offspring (F_{ISO}) inbreeding coefficients suggest an alternative explanation for the maintenance of variability in species of Algarobia. In all species studied here F_{ISM} values were much lower than the corresponding F_{ISO}. This means that there is a genotypic frequency change from one stage to the other which might be selectively determined. Changes in inbreeding coefficient estimates between seed and adult samples have been related to inbreeding depression (see RITLAND 1989, 1990b). Assuming equilibrium of adult F RITLAND (1989) estimated relative selfing viability (that is, the fitness of selfed individuals relative to outcrossed ones) for 10 populations across three genera of herbaceous plants. These estimates ranged from 0 to 0.84. In *Mimulus guttatus* and *M. nasutus* populations RITLAND (1990b) estimated that relative fitness of selfed individuals was significantly lower than 0.5, the threshold needed to favour genes for selfing. Selective forces favouring heterozygous seeds and reducing the proportion of selfed individuals in the adult population have also been suggested by KEYS and SMITH (1994) in one population of *P. velutina*. Substantial evidence on the causes of variability maintenance in *Prosopis* might be obtained from deep selection component analyses based on larger samples. If selection actually favours outcrossed individuals in species of section Algarobia an equilibrium condition may be reached that allows keeping variability despite selfing and population substruration.

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