

Genetic diversity and recruitment of the tropical palm, *Euterpe edulis* Mart., in a natural population from the Brazilian Atlantic Forest

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The genetic diversity and recruitment of plants of heart-of-palm tree (*Euterpe edulis* Mart.) were investigated in a natural population located in Southern Brazil. Five categories of plants, from seedlings to adults, were analysed using 16 allozymic loci. The results showed an average population level of genetic diversity ($H_e = 0.278$) greater than the average of plant species already studied. The recruitment process of *E. edulis* is related to its genetic characteristics. A significant increase in the heterozygote frequency towards the adult stages was observed at three loci (*Pgdh-2*, *G6pdh-1* and *Mdh-1*). This suggests the possible action of natural selection in promoting such heterozygote increase. In the

same way, a linear increase in allele frequencies was observed at four loci (*Prx-3*, *Prx-4*, *Pgdh-2* and *G6pdh-1*), indicating that recruitment is also related to a greater survival of individuals that are carriers of certain alleles. The maintenance of high diversity levels, as well as the increase in the heterozygote frequency, are positive aspects for *in situ* conservation. Furthermore, an increase in heterozygote frequency is favourable to the management of the species, since the maintenance of a stock of reproductive individuals with high heterozygosity levels favours the maintenance of the population dynamic and structure.

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Introduction

Heart-of-palm tree (*Euterpe edulis* Mart.; Arecaceae) is a native understore palm of the Brazilian Atlantic Forest, and is economically valuable because it is the main species used for palm heart extraction. This feature has caused intense exploitation since the end of 1960s, and has promoted an alteration of its natural populations. However, several studies have shown the possibility of management of this species in its natural ecosystem (Conte *et al.*, 2000a; Reis *et al.*, 2000a,b).

Knowledge of regeneration dynamics in natural populations and an understanding of the factors involved in recruitment are important in management systems. Such knowledge allows forecasts of the impact caused by the intervention in the forest, especially in reference to the possibility of replacement of the extracted stocks. In the case of *E. edulis*, replacement is dependent on the number of fruit-producing palms, as well as the process of recruitment of plants towards the subsequent stages (Conte *et al.*, 2000b; Reis *et al.*, 2000b).

The recruitment process is associated with different biological and nonbiological factors (Hutchings, 1997), and in the last decade some workers have also tried to relate the recruitment process to plant genetics (Eguiarte *et al.*, 1992; Murawski and Hamrick, 1992; Tonsor *et al.*, 1993; Alvarez-Buylla and Garay, 1994; Hossaert-McKey *et al.*, 1996; Doligez and Joly, 1997; Lee *et al.*, 2000). Using

allozyme markers, such studies have demonstrated a heterozygote increase towards the adult stages. Furthermore, positive associations between allozyme heterozygosity and fitness have been reported (Bush and Smouse, 1991; Aravanopoulos and Zsuffa, 1998).

Allozyme markers have been considered as neutral genes reflecting evolutionary processes affecting the entire genome. However, Mitton (1994) postulates that the environment may occasionally select for allozyme markers. Moreover, classical works (Clegg and Allard, 1972; Hamrick and Allard, 1972) have shown the existence of associations among environmental factors and allele frequencies at allozyme markers. Such behaviour has also been reported by Tonsor *et al.* (1993) and Cabin (1996), studying different life-history stages in plants. Thus, these examples appear to indicate that the recruitment process in natural populations can promote changes not only in genotype frequencies but also in allele frequencies.

In this paper, we analyse genetically the recruitment of plants of *E. edulis*, using allozyme markers, in a natural population from the Southern Brazilian Atlantic Tropical Forest.

Materials and methods

Study site

The study was performed in six 50 m × 50 m permanent plots, in a natural population of *E. edulis* located in the experimental area of the São Pedro de Alcântara District, Santa Catarina (Brazil). The climate of the region is warm temperate with hot summers. According to data of

CLIMERH/EPAGRI-SC (Government Agricultural Research Organisation for the State of Santa Catarina), the mean temperature of the study area is 20.6°C, with a mean annual rainfall of 1565 mm. The topography of the area is hilly, with an altitude around 300 m above sea level. The vegetation of the area is evergreen Atlantic Tropical Forest, and has suffered exploitation 30–40 years ago but today it is in a stage of forest succession between intermediate and advanced.

Characteristics of the species and population

E. edulis is one of the most abundant species of the Atlantic Tropical Forest domain in Brazil. It is a monoecious species with insect-pollinated flowers (Mantovani and Morellato, 2000). Outcrossing rate estimates (t_m), based on allozyme markers, showed values approaching 1.00 (range = 0.94–1.04; SE = 0.02–0.04) in seven populations (Reis et al, 1998). It has high annual production of animal dispersed fruits (Reis et al, 1996; Mantovani and Morellato, 2000; Reis and Kageyama, 2000). Natural regeneration occurs from a seedling bank, which is responsible for the species dynamism in the forest (Reis et al, 1996; Conte et al, 2000b).

Data from the population studied were collected inside each plot during a period of 10 years, between 1991 and 2000. Plants of *E. edulis* were classified into five categories (Reis et al, 1999; Conte et al, 2000b): I – insertion height of the youngest leaf less than 10 cm; II – insertion height from 11 to 50 cm; III – insertion height greater than 50 cm and the height of exposed stem less than 1.3 m; IV – greater than 1.3 m of exposed stem and nonreproductive; and V – reproductive plants. The demographic structure based on the five categories is represented in Figure 1.

Allozyme electrophoresis

Samples of leaf tissue were collected for allozyme analysis from approximately 70–100 individuals in each category of plants.

In total 10 enzymatic systems were used: α -esterase (α -EST, EC 3.1.1.1), shikimic dehydrogenase (SKDH, EC 1.1.1.25), peroxidase (PRX, EC 1.11.1.7), 6-phosphogluconate dehydrogenase (PGDH, EC 1.1.1.44), nicotinamide adenine dinucleotide dehydrogenase (NADHDH, EC 1.6.99.3), malate dehydrogenase (MDH, EC 1.1.1.37), phosphoglucosomerase (PGI, EC 5.3.1.9), isocitrate dehydrogenase (IDH, EC 1.1.1.42), phosphoglucosomutase (PGM, EC 5.4.2.2), and glucose-6-phosphate dehydrogenase (G6PDH, EC 1.1.1.49). Among the 10 systems employed, 16 zones with enzymatic activity were observed, revealing 11 presumed polymorphic loci. Each zone that showed a behaviour apparently independent

of the others and with Mendelian segregation was considered an allozyme locus, taking into account the possible quaternary structure of each enzyme in question (Kephart, 1990).

Statistical analysis

Banding patterns (phenotypes) were scored as genotypes and transformed into allele frequencies. Levels of genetic diversity within each category were described in terms of average number of alleles per locus (A), percentage of polymorphic loci (P ; 99% criterion), observed heterozygosity (H_o), Nei's (1978) expected gene diversity (H_e), and fixation index (F). All of these parameters, except F , were calculated using BIOSYS-1 software (Swofford and Selander, 1989).

Allele frequencies for the different loci were compared among the categories of plants by the method of linear regression in $r \times 2$ tables (Cochran, 1954). The coefficient of regression (b) was tested using χ^2 test, with one degree of freedom (Steel and Torrie, 1980). This approach allowed us to analyse changes in allele frequencies related to the process of recruitment towards the adult individuals.

Differences in the proportions between the observed number of heterozygous and homozygous individuals, among the categories of plants, were compared using a χ^2 test for each locus (Beiguelman, 1996). In this way, it was possible to evaluate differences in the amount of observed heterozygosity among the different categories studied. Data from all loci were aggregated by summing individual χ^2 values and their respective degrees of freedom for each locus (Workman and Niswander, 1970).

To test whether F -values of each category differed significantly from zero, two-tailed χ^2 values were calculated as $\chi^2 = F^2 N (k-1)$, for $[k(k-1)]/2$ degrees of freedom, where k is the number of alleles and N is the number of individuals sampled in each category (Li and Horvitz, 1953). Furthermore, the F -values were compared among the categories to evaluate the existence of deficiency or excess of heterozygotes.

Results

Allele frequencies

Among the 16 analysed loci, five were monomorphic (α -Est-2, Pgdh-1, Nadhdh-1, Mdh-2, Idh-1) and 11 were polymorphic (α -Est-1, Skdh-1, Prx-2, Prx-3, Prx-4, Prx-5, Pgdh-2, Mdh-1, Pgi-2, Pgm-1, G6pdh-1). Two loci (α -Est-1 and Prx-5) showed a very low level of polymorphism, with the most frequent allele close to fixation in each category (Table 1). However, several loci showed an expressive polymorphism and similar frequencies of the most common alleles (Prx-3, Prx-4, Pgm-1, with four alleles each, and Pgdh-2, with five alleles).

By the analysis of linear regression (Steel and Torrie, 1980), we observed significant variations in the allelic frequencies of some loci among the five categories of plants studied (Table 1). There was a significant increase in the frequency of Prx-3a, Prx-3b, Prx-4b, Pgdh-2c and G6pdh-1b, towards the adult stages. On the other hand, there was a significant reduction in the frequency of the alleles Prx-3d, Prx-4a and Pgdh-2a. Allelic variation at other loci was observed, but such variation did not present a defined trend among the plant categories.

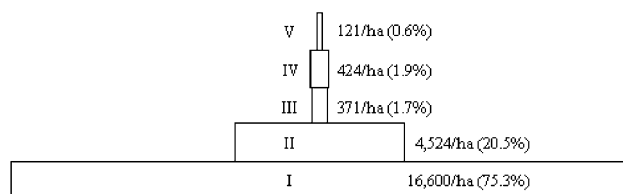


Figure 1 Demographic structure of *Euterpe edulis* in São Pedro de Alcântara, showing number and percentage of individuals in each category.

Table 1 Allelic frequencies by categories of plants for 11 polymorphic allozyme loci

Locus	Alleles	Categories of plants					χ^2 values	Mean of population
		I	II	III	IV	V		
α -Est 1	a	1.000	0.988	1.000	1.000	0.995	0.01 NS	0.997
	b	0.000	0.012	0.000	0.000	0.005	0.01 NS	0.003
Skdh-1	a	0.753	0.713	0.686	0.695	0.715	0.80 NS	0.713
	b	0.247	0.287	0.314	0.305	0.285	0.80 NS	0.287
Prx-2	a	0.844	0.820	0.814	0.845	0.820	0.07 NS	0.830
	b	0.091	0.058	0.114	0.065	0.080	0.08 NS	0.080
	c	0.065	0.122	0.071	0.090	0.100	0.39 NS	0.090
Prx-3	a	0.446	0.366	0.450	0.505	0.495	4.21 *	0.455
	b	0.022	0.023	0.029	0.075	0.070	9.99 *	0.046
	c	0.301	0.378	0.364	0.245	0.335	0.34 NS	0.321
	d	0.231	0.233	0.157	0.175	0.100	13.22 *	0.178
Prx-4	a	0.457	0.459	0.321	0.370	0.285	15.00 *	0.379
	b	0.280	0.221	0.329	0.390	0.390	12.97 *	0.325
	c	0.032	0.081	0.043	0.060	0.060	0.49 NS	0.056
	d	0.231	0.238	0.307	0.180	0.265	0.01 NS	0.241
Prx-5	a	0.968	0.971	0.936	0.985	0.985	1.57 NS	0.971
	b	0.005	0.023	0.057	0.015	0.005	0.09 NS	0.019
	c	0.027	0.006	0.007	0.000	0.010	3.08 NS	0.010
Pgdh-2	a	0.575	0.564	0.536	0.500	0.470	5.78 *	0.527
	b	0.091	0.099	0.100	0.060	0.105	0.02 NS	0.090
	c	0.048	0.122	0.143	0.130	0.120	4.38 *	0.111
	d	0.274	0.203	0.214	0.285	0.290	1.31 NS	0.257
	e	0.011	0.012	0.007	0.025	0.015	0.61 NS	0.014
Mdh-1	a	0.826	0.732	0.761	0.742	0.750	2.16 NS	0.762
	b	0.092	0.161	0.116	0.136	0.110	0.03 NS	0.123
	c	0.082	0.107	0.123	0.121	0.140	3.16 NS	0.115
Pgi-2	a	0.640	0.610	0.664	0.545	0.585	2.52 NS	0.605
	b	0.355	0.384	0.329	0.450	0.395	1.76 NS	0.386
	c	0.005	0.006	0.007	0.005	0.020	1.93 NS	0.009
Pgm-1	a	0.424	0.390	0.393	0.409	0.505	2.65 NS	0.427
	b	0.234	0.267	0.286	0.278	0.185	0.84 NS	0.247
	c	0.326	0.337	0.307	0.283	0.305	0.79 NS	0.311
	d	0.016	0.006	0.014	0.030	0.005	0.00 NS	0.015
G6pdh-1	a	0.852	0.894	0.936	0.895	0.880	0.59 NS	0.910
	b	0.048	0.100	0.057	0.105	0.110	4.31 *	0.086
	c	0.000	0.006	0.007	0.000	0.010	0.85 NS	0.004

* $P < 0.05$; NS – nonsignificant.

χ^2 values refer to the regression analysis of allelic frequencies among the five categories of plants. Allele frequencies for the population as a whole are given in the last column.

Diversity indices

From the 16 allozyme loci surveyed, 41 alleles were scored, giving an average of 2.6 (SE = 0.3) alleles per locus, with a percentage of 62.5% of polymorphic loci (Table 2). The mean observed heterozygosity was 0.264 (SE = 0.067) and the expected heterozygosity was estimated as 0.278 (SE = 0.070). Although these results indicate a certain heterozygote deficit in the population, the mean value of the fixation index ($F = 0.05$) showed nonsignificant deviation from zero ($P > 0.05$).

At the level of categories, diversity indices from the 16 loci presented little variation (Table 2). The average number of alleles per locus ranged from 2.4 to 2.6 and the percentage of polymorphic loci ranged from 62.5 to

68.7%. The observed heterozygosity ranged from 0.242 to 0.279 and the expected heterozygosity ranged from 0.259 to 0.284. Higher values of H_e than H_o were observed among the categories, especially in the first categories, although the F -values did not differ from zero.

A closer examination of the polymorphic loci at the population level (Table 2) showed quite similar results to other populations of *E. edulis* investigated by Reis *et al* (1998). The average number of alleles per polymorphic locus was 3.4 (SE = 0.3), the mean observed heterozygosity was 0.423 (SE = 0.067), and the expected heterozygosity was estimated as 0.445 (SE = 0.070), with a fixation index of 0.049 (not significantly different from zero). By analysis at the category level, the average

Table 2 Summary of the diversity indices for all loci (a) and polymorphic loci (b)

Categories of plants		N ^a	A ^b	P ^c	H _o ^d	H _e ^e	F ^f
I	a	92.9 (0.1)	2.4 (0.3)	62.5	0.242 (0.063)	0.259 (0.068)	0.066 NS ^g
	b	92.8 (0.1)	3.3 (0.3)	100.0	0.387 (0.067)	0.415 (0.072)	0.067 NS
II	a	85.6 (0.3)	2.6 (0.3)	68.75	0.270 (0.067)	0.284 (0.070)	0.049 NS
	b	85.3 (0.4)	3.4 (0.3)	100.0	0.432 (0.065)	0.452 (0.068)	0.044 NS
III	a	69.9 (0.1)	2.5 (0.3)	62.5	0.257 (0.065)	0.282 (0.070)	0.089 NS
	b	69.9 (0.1)	3.4 (0.3)	100.0	0.411 (0.064)	0.451 (0.068)	0.088 NS
IV	a	99.9 (0.1)	2.4 (0.3)	62.5	0.271 (0.071)	0.281 (0.071)	0.036 NS
	b	99.8 (0.1)	3.2 (0.3)	100.0	0.434 (0.075)	0.450 (0.072)	0.035 NS
V	a	100.0 (0.0)	2.6 (0.3)	62.5	0.279 (0.072)	0.282 (0.070)	0.011 NS
	b	100.0 (0.0)	3.4 (0.3)	100.0	0.445 (0.074)	0.450 (0.069)	0.011 NS
Mean of population	a	448.3 (0.4)	2.6 (0.3)	62.5	0.264 (0.067)	0.278 (0.070)	0.050 NS
	b	447.8 (0.6)	3.4 (0.3)	100.0	0.423 (0.067)	0.445 (0.070)	0.049 NS

^aN = mean sample size per locus. ^bA = average number of alleles per locus. ^cP = percentage of polymorphic loci; 99% criterion. ^dH_o = observed heterozygosity. ^eH_e = expected heterozygosity (Nei, 1978). ^fF = fixation index. ^gNS = $P > 0.05$. Values in parentheses are SE.

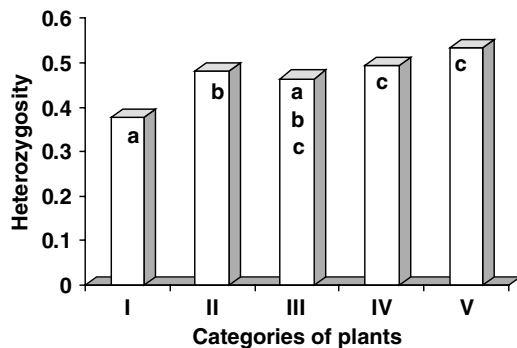


Figure 2 Mean observed heterozygosity for loci *Pgdh-2*, *G6pdh* and *Mdh-1*. Different letters indicate significant differences among the categories ($P < 0.05$; based on χ^2 test).

number of alleles per locus ranged from 3.2 to 3.4. The observed heterozygosity ranged from 0.387 to 0.445 and the expected heterozygosity ranged from 0.415 to 0.452, among the categories, while the *F*-values did not differ from zero.

An analysis of the amount of heterozygotes observed among the five categories of plants showed significant differences. Four loci were responsible for the appearance of such differences: *Prx-5* ($\chi^2 = 9.400$, $P < 0.05$), *Pgdh-2* ($\chi^2 = 19.985$, $P < 0.01$), *Mdh-1* ($\chi^2 = 14.148$, $P < 0.01$) and *G6pdh* ($\chi^2 = 9.553$, $P < 0.05$). With the exception of locus *Prx-5*, the other three loci showed significant differences between category I and most of the subsequent categories. When data from the loci *Pgdh-2*, *Mdh-1* and *G6pdh* were aggregated (Figure 2), they showed a clear gradient of heterozygote increase towards Category V. The greatest heterozygosity values were found in the Categories IV and V. Although the intermediary categories did not demonstrate a defined tendency of heterozygote increase, the results suggest that the largest changes in terms of genotype frequencies must take place with the recruitment of plants in Category I, because it showed the lowest heterozygosity rate among the five categories studied.

Discussion

Sources of changes in the allelic frequencies

Results indicated that a number of polymorphic loci showed oscillations in the allelic frequencies without a defined direction among the categories. This behaviour could be related to factors such as: (i) sampling effects in the field; (ii) differences due to differential reproduction that produced the older cohorts; or (iii) genetic drift. We believe that drift is the main cause because of the high mortality rate found among the younger individuals of this species (Reis *et al*, 1996, 2000a; Conte *et al*, 2000b).

However, four loci showed significant linear alterations in the allelic frequencies among the categories of plants (Table 1). At locus *Prx-3*, alleles *a* and *b* were favoured by the recruitment process, while the frequency of allele *d* was reduced towards the adult stage. In the same way, alleles *Prx-4b*, *Pgdh-2c* and *G6pdh-1b* were favoured, while the frequencies of alleles *Prx-4a* and *Pgdh-2a* were reduced. There are two main hypotheses to explain the observed changes in the allelic frequencies. The first is that natural selection acts directly on the allozymic loci in such a way as to favour certain alleles in the recruitment process. The second is that linkage disequilibrium occurs, in which some allozymic loci might be linked to other loci that are under the action of natural selection. However, considering the sparse evidence of linkage disequilibrium for the allozyme markers in natural populations (Woodwark *et al*, 1992), the first hypothesis seems to be more appropriate to explain such a phenomenon. If it is true, it implies that some allozyme loci are not completely neutral (Bergmann and Ruetz, 1991; Mitton, 1994; Eanes, 1999; Thelen and Allendorf, 2001).

Genetic diversity

In general, a great amount of genetic diversity at both the category and the population level was observed for *E. edulis* (Table 2). In fact, this study revealed that the *H_e* value would rank this species within the top group of

plant species already studied. An analysis of a group of 655 plant species belonging to 220 genera demonstrated an average heterozygosity of 0.150, with 51% of polymorphic loci (Hamrick *et al*, 1992). For a group including only tropical tree species (38 species), Hamrick *et al* (1992) obtained an average heterozygosity of 0.191, with 58% of polymorphic loci. Data compiled from 12 Brazilian Atlantic Tropical Forest tree species revealed an average heterozygosity of 0.206, with 53% of polymorphic loci (information from the authors of this paper).

An examination of the genetic diversity values obtained in the population studied also revealed a great capacity of this species to restore the levels of diversity. In fact, in spite of having been subjected to exploitation in the past, this population presents diversity levels compatible with undisturbed populations (Reis *et al*, 1998). The maintenance of this level of genetic diversity should allow this species to maintain its ability to adapt to novel environmental changes, mainly because of the possibility of the appearance of new recombinants in the next generations. Finally, the great homogeneity of the diversity indices among the five categories of plants suggests that the amount of adult individuals in this species is sufficient to oppose the natural loss of genetic variability by drift.

Heterozygosity and plant recruitment

As observed in the present work, many studies have reported an increase in heterozygosity towards the adult stages, as well as positive associations between heterozygosity and fitness for allozyme markers. As discussed above, allozyme markers are not completely neutral and effects of dominance and overdominance have been described (Eanes, 1999). In this aspect, inbreeding depression has been pointed out as the main cause to explain the low adaptive value of the homozygous individuals, since it can occur both in the presence of dominance or overdominance (Bush and Smouse, 1992; David, 1998; Lee *et al*, 2000).

The observed increase in heterozygote frequencies from small classes to adults could be generated by increased survival of the more heterozygous individuals (Eguiarte *et al*, 1992; Tonsor *et al*, 1993; Hossaert-McKey *et al*, 1996; Reis *et al*, 1998). However, heterozygote advantage constitutes only one of the possibilities to explain the increase of heterozygotes towards the adult stages (Kärkkäinen *et al*, 1999). In a given generation, an increase in heterozygote frequency may also be the result of selection only against one of the homozygotes. Moreover, an excess of heterozygotes can be the result of an unequal gene frequency among the parents of the population.

Linkage disequilibrium is another cause that could be used to explain heterozygote increases, in the same way as already discussed to explain changes in allelic frequencies. Such disequilibrium could generate associative overdominance between markers and background loci (Pamilo and Pálsson, 1998; Pogson and Fevolden, 1998). However, using allozyme and DNA markers, some correlation studies between growth rates and heterozygosity have shown negative evidence for the associative overdominance in natural populations (Pogson and Zouros, 1994; Thelen and Allendorf, 2001).

'Wahlund's effect' (Crow and Kimura, 1970) or the effects on observed genotype frequencies when pooling multiple, spatially differentiated subunits, could also lead to a deficiency of heterozygotes in the smaller size classes. However, this does not appear to be the case for *E. edulis*, due to the: (i) existence of overlapping generations within each category of plants studied; (ii) amount of homozygous individuals in the smaller classes was not significant; and (iii) lack of genetic structure among the six plots based on F_{ST} values calculated for each category of plants (F_{ST} -values did not differ from zero by bootstrap analysis). Moreover, the 'Wahlund's effect' was not observed in seven other *E. edulis* populations studied by Reis *et al* (1998).

Our results suggest that the 'bottleneck' for the recruitment process of *E. edulis* can be concentrated in Category I: more than 70% of the individuals that form the demographic structure of *E. edulis* are found in Category I (Figure 1). The mortality rate for this stage is greater than 80%, suggesting that selection for adaptive traits could act in the recruitment process of those individuals. Category I of *E. edulis*, which represents those individuals with insertion height of the youngest leaf less than 10 cm, corresponds to the stage with the greatest vulnerability to the factors involved in plant mortality. Thus, those individuals with a higher growth rate would have a greater opportunity to reach the adult stage. In this way, we believe that this process could be responsible for such heterozygote increases observed at some loci.

From this study, we can conclude that *E. edulis* possesses a great capability of restoring the levels of diversity, even after a process of exploitation. We detected levels of genetic diversity comparable with undisturbed populations of the species.

Our results provide support for the important prediction that the recruitment process of *E. edulis* is related to the genetic aspects of the plants. The increase in heterozygosity towards the adult stages is more concentrated in Category I. Furthermore, the linear increase in frequency of several alleles towards the adult stages appears to indicate that the recruitment process is also related to a greater survival, when the individuals are carriers of such alleles. In both cases, the results suggest that natural selection acts directly or indirectly with greater intensity on a limited number of allozyme loci.

This study also provides support for management and conservation strategies of the species. The observed genetic changes in the recruitment process, such as the heterozygote increase and the corresponding reduction of the F -values, are positive for *in situ* conservation of the species. Likewise, the increase in heterozygote frequency is favourable for management, since the maintenance of a stock of reproductive individuals with high heterozygosity levels can generate offspring with desirable genetic variability, thus conserving the dynamics and the structures of the populations.

Acknowledgements

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