

Genetics of Rubber Tree (*Hevea brasiliensis* (Willd. ex ADR. de Juss.) Müll. Arg.)

2. Mating System*)

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Summary

Using electrophoresis data on 17 alleles in 4 loci of 2 natural rubber tree (*Hevea brasiliensis*) populations, analyses of variance were used to estimate variance components from which the parameters \hat{F} , \hat{I} , $\hat{\theta}_1$, $\hat{\theta}_2$ were estimated. The estimates demonstrated that the major part of the genetic variability is concentrated within populations. The co-ancestry coefficient of the plants within families was close to that expected for half-sib families ($\hat{\theta}_1 = 0.127$). The genetic diversity values between populations ($\hat{\theta}_2 = 0.0025$) was low. The mean outcrossing rate for rubber trees in natural populations was 64.46 %, while the inbreeding coefficient was 21.81 %. The biological importance of these parameters in the equilibrium of natural populations is discussed.

Key words: Natural population, rubber tree, isozyme, outcrossing rate and inbreeding.

FDC: 165.5; 228.8; 176.1 *Hevea brasiliensis*.

Zusammenfassung

Mittels elektrophoretischer Daten wurden Varianzanalysen nach dem "unbalanced hierarchy model" an 2 natürlichen Kautschuk-Baum-Populationen (*Hevea brasiliensis*) 17 Allelen aus 4 Standorten vorgenommen. Durch die Bestimmung der Varianzkomponenten wurden die Parameter \hat{F} , \hat{I} , $\hat{\theta}_1$, $\hat{\theta}_2$ und \hat{t} ermittelt. Die Varianzen zeigen, daß der überwiegende Teil der genetischen Variabilität innerhalb der Population zu finden ist. Der "co-ancestry"-Koeffizient der Pflanzen innerhalb der Gruppen (Familien) ergab einen Wert ähnlich dem für die half-sib Gruppen (Familien) ($\hat{\theta}_1 = 0,127$). Der genetische Diversitätsfaktor war unter Populationen klein ($\hat{\theta}_2 = 0,0025$). Die mittlere Rate für Fremdkreuzungen der Kautschukbäume aus den natürlichen Populationen betrug 64,46%, die für die Inzucht 21,81 %. Die biologische Signifikanz der natürlichen Populationen wird diskutiert.

Introduction

The mating system is an important determinant in the composition of the genetic structure of plant populations (CLEGG, 1980).

For breeders, knowledge of the mating system permits a better appraisal of the maintenance of inbred lines, formulation of strategies for hybridization, recombination and assessment of methods for genetic sampling and preservation of wild relatives of cultivated species (JAIN, 1975).

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As the consequences of inbreeding are frequently deleterious in many cultivated plants, adequate estimates of their occurrence are needed for better evaluations of agronomic characteristics.

Several methods have been used to estimate the outcrossing rate of plants. In general this involves the use of the method of maximum likelihood which normally requires numerous calculations. WEIR (1990) proposes the utilization of a methodology that estimates the outcrossing rate, the inbreeding coefficient and the genetic distance between plants by breaking down the variance components obtained from the analysis of variance of data originated from electrophoresis.

The objective of this study is to estimate the natural outcrossing rate and the inbreeding existing in 2 natural rubber tree populations by analysing data obtained by electrophoresis.

Material and Methods

The material used in this study consisted of plants originating from rubber tree seeds collected in 2 natural populations located in the State of Acre, in native rubber tree populations existing in the Reserva Florestal do Catuaba (Catuaba Forest Reserve), situated alongside Highway BR 364 (km 22), belonging to the Federal University of Acre (UFAC) and in an area belonging to EMBRAPA/UEPAE-Rio Branco, located alongside Highway BR 364 (km 14) (Figure 1 ⁴⁾).

The electrophoretic analyses on starch gels used fresh extract of young rubber tree leaves in the foliar stage "B" (drooping leaves, anthocyanin coloration, with about 1.0 cm to 2.0 cm), according to LEBRUN and CHEVALLIER'S (1988) recommendation. The enzymatic systems were malate dehydrogenase (MDH) = EC 1.1.1.37, shikimic dehydrogenase (SKDH) — EC — 1.1.1.25, and leucine aminopeptidase (LAP) — EC — 3.4.11.1 were studied (Table 1).

One leaflet from each of 20 different plants per family were collected for each run. A total of 26 and 27 open-pollinated families for population 1 and 2, respectively, with variable number of 13 to 22 plants per progeny were analysed.

An analysis of variance was made for each allele identified, as proposed by WEIR (1990), according to the unbalanced hierarchy model, and with 3 levels of hierarchy.

The estimates of the variance components were obtained by breaking down the mean squares, where the variances among genes/individual/family/population ($\hat{\sigma}_G^2 = QM_G$), among individuals/family/population ($\hat{\sigma}_I^2 = (QM_I - QM_G)/2$), among families/population ($(QM_F - QM_I)/K_1$) and among populations ($\hat{\sigma}_P^2 = [QM_P - (QM_I - K_2\hat{\sigma}_F^2)]/K_3$) were estimated.

4) For figures 1, 2, 3, 4, 5 and table 1 see part 1 (Genetics of Rubber Tree (*Hevea brasiliensis* (WILD. ex ADR. de JUSS.) MÜLL. ARG.). 1. Genetic Variation in Natural Populations) in this issue.

The mean coefficients of inbreeding of all plants in both population (\hat{F}) and of inbreeding within populations (\hat{f}) were estimated using the following expressions: $\hat{F} = (\hat{\sigma}_T^2 - \hat{\sigma}_C^2)/\hat{\sigma}_T^2$ and $\hat{f} = (\hat{F} - \hat{\theta}_2)/(1 - \hat{\theta}_2)$.

The outcrossing rate of the species was estimated for each allele by utilizing the following expression: $\hat{t} = (1 - \hat{f})/(1 + \hat{f})$.

The mean estimates of the parameters \hat{F} , $\hat{\theta}_1$, $\hat{\theta}_2$, \hat{f} and \hat{t} , considering all alleles of each locus separately and all loci simultaneously, were obtained by the average of the individual mean squares, weighted by the number of degrees of freedom.

Results and Discussion

Two loci (LAP-1 and LAP-2) were identified in the leucine aminopeptidase (LAP) system. Five alleles were identified in LAP-1; by convention they were denoted: allele 1, the most common; alleles 2 and 3 those showing RM's (relative migration) higher than 1, respectively, and alleles 4 and 5, those showing RM's lower than 1 (Figure 2). Four alleles were identified in locus LAP-2, of slower migration, where allele 2 presented RM higher than 1 and the others values lower than 1 (Figure 3).

In the shikimic dehydrogenase (SKDH) system only 1 locus with 5 alleles was identified. Allele 2 presented RM higher than 1 (Figure 4).

The interpretation of the band pattern of all loci in the malate dehydrogenase (MDH) system proved to be difficult. In this system, the most rapid locus, presenting 3 alleles, was identified and analysed. Allele 3, the

Table 2. — Mean squares between populations, among families/population, among individuals/family/population, between genes/individual/family/population in the unbalanced hierarchy model for 17 alleles from 4 loci in 2 rubber tree populations.

LOCI	ALLELES	MEAN SQUARES			
		POPULATIONS	FAMILIES	INDIVIDUALS	GENES
LAP-1	1	1,5902	1,1989	0,1160	0,1170
	2	0,0337	0,3747	0,0374	0,0329
	3	0,0111	0,3028	0,0410	0,0369
	4	0,5058	0,1357	0,0321	0,0369
	5	0,2227	0,2427	0,0342	0,0433
	G. L. *	1	51	966	1017
LAP-2	1	0,6034	0,7322	0,0953	0,0876
	2	2,01.10 ⁻³	9,54.10 ⁻⁴	1,04.10 ⁻³	1,04.10 ⁻³
	3	0,0012	0,0499	0,0192	0,0109
	4	0,5876	0,5840	0,0884	0,0756
		G. L. *	1	51	908
SKDH	1	1,0299	1,0869	0,2600	0,1872
	2	0,0268	0,6277	0,2231	0,1379
	3	0,2354	0,5097	0,1066	0,0898
	4	0,9155	0,3540	0,0548	0,0440
	5	0,1440	0,0597	0,0144	0,0106
	G. L. *	1	51	799	852
MDH-1	1	2,2227	0,1053	0,0319	0,0238
	2	0,1814	0,0357	0,0116	0,0051
	3	1,1340	0,0566	0,0229	0,0187
	G. L. *	1	51	936	987

* Degrees of freedom

Table 3. — Estimates of variances between populations ($\hat{\sigma}_P^2$), among families/population ($\hat{\sigma}_F^2$), among individuals/family/population ($\hat{\sigma}_I^2$), between genes/individual/family/population ($\hat{\sigma}_G^2$), of total variance ($\hat{\sigma}_T^2$) for 17 alleles in 4 loci of 2 natural rubber tree populations.

LOCI	ALLELES	$\hat{\sigma}_P^2$	$\hat{\sigma}_F^2$	$\hat{\sigma}_I^2$	$\hat{\sigma}_G^2$	$\hat{\sigma}_T^2$
LAP-1	1	3,7.10 ⁻⁴	0,0282	-5,0.10 ⁻⁴	0,1170	0,1451
	2	-3,4.10 ⁻⁴	8,8.10 ⁻⁵	2,2.10 ⁻⁵	0,0329	0,0436
	3	-2,9.10 ⁻⁴	6,8.10 ⁻⁵	5,2.10 ⁻⁵	0,0305	0,0423
	4	3,6.10 ⁻⁴	2,7.10 ⁻⁵	-2,4.10 ⁻⁵	0,0369	0,0376
	5	-2,3.10 ⁻⁵	5,4.10 ⁻⁵	-4,5.10 ⁻⁵	0,0433	0,0442
	\bar{M}	2,3.10 ⁻⁵	0,0104	0,0000	0,0521	0,0625
LAP-2	1	0,1089	0,0176	0,0038	0,0876	0,1089
	2	9,2.10 ⁻⁷	-2,5.10 ⁻⁶	2,5.10 ⁻⁷	1,1.10 ⁻⁵	1,1.10 ⁻⁵
	3	-5,1.10 ⁻⁵	8,5.10 ⁻⁴	4,1.10 ⁻⁵	0,0109	0,0158
	4	-6,3.10 ⁻⁶	0,0137	0,0064	0,0756	0,0957
	\bar{M}	-4,0.10 ⁻⁵	6,4.10 ⁻⁵	2,9.10 ⁻⁵	0,0350	0,0443
SKDH	1	-1,0.10 ⁻⁴	0,0257	0,0364	0,0187	0,2492
	2	-7,2.10 ⁻⁴	0,0126	0,0426	0,0138	0,1924
	3	-3,4.10 ⁻⁴	0,0125	0,0084	0,0898	0,1104
	4	6,5.10 ⁻⁴	0,0093	0,0054	0,0440	0,0594
	5	9,7.10 ⁻⁵	0,0014	0,0019	0,0106	0,0140
	\bar{M}	-8,3.10 ⁻⁵	0,0123	0,0189	0,0939	0,1250
MDH-1	1	2,2.10 ⁻³	2,0.10 ⁻³	4,1.10 ⁻³	0,0238	0,0320
	2	1,5.10 ⁻⁴	6,5.10 ⁻⁴	3,3.10 ⁻³	0,0051	9,1.10 ⁻³
	3	1,1.10 ⁻³	9,0.10 ⁻⁴	2,1.10 ⁻³	0,0187	0,0228
	\bar{M}	1,1.10 ⁻³	1,2.10 ⁻³	3,1.10 ⁻³	0,0159	0,0213
GENERAL MEAN		1,8.10 ⁻⁴	8,7.10 ⁻⁵	6,4.10 ⁻⁵	0,0545	0,0697

slowest, overlapped the most rapid allele of another possible locus (Figure 5).

The estimates of variance between populations ($\hat{\sigma}_P^2$), calculated from the analyses of variance of the frequencies of the alleles in the populations (Table 2), represented about 0.25% of the total variation estimated for the average of all alleles (Table 3), whereas the variation between families/populations ($\hat{\sigma}_F^2$) represented 12.48 % of total variation. The highest percentage of variation was for the estimate of variance between genes/individual

Table 4. — Estimates of the inbreeding coefficients of plants in populations (\hat{F}) and within populations (\hat{f}), of the coancestry within families ($\hat{\theta}_1$), of the genetic distance between populations ($\hat{\theta}_2$) and of the outcrossing rate (\hat{t}) for 17 alleles in 4 loci of 2 natural rubber tree populations.

LOCI	ALLELES	\hat{F}	\hat{f}	$\hat{\theta}_1$	$\hat{\theta}_2$	\hat{t}
LAP-1	1	0,1937	0,1914	0,1971	0,0028	0,6787
	2	0,2454	0,2512	0,1938	-0,0078	0,5985
	3	0,2790	0,2835	0,1549	-0,0063	0,5582
	4	0,0186	0,0081	0,0824	0,0106	0,9839
	5	0,0205	0,0210	0,1223	-0,0005	0,9589
	\bar{M}	0,1664	0,1664	0,1664	0,0000	0,7147
LAP-2	1	0,1956	0,1967	0,1602	-0,0014	0,6713
	2	-0,0026	-0,0022	0,0024	0,0048	1,0044
	3	0,3122	0,3151	0,0495	-0,0042	0,5208
	4	0,2099	0,2099	0,1430	-0,0001	0,6530
	\bar{M}	0,2099	0,2099	0,1444	-0,0001	0,6530
SKDH	1	0,2489	0,2492	0,1029	-0,0004	0,6010
	2	0,2832	0,2859	0,0617	-0,0037	0,5553
	3	0,1867	0,1892	0,1106	-0,0031	0,6818
	4	0,2588	0,2507	0,1678	0,0109	0,5991
	5	0,2433	0,2380	0,1076	0,0069	0,6155
	\bar{M}	0,2488	0,2494	0,0976	-0,0008	0,6008
MDH-1	1	0,2555	0,2018	0,1288	0,0672	0,6641
	2	0,4422	0,3998	0,0868	0,0707	0,4287
	3	0,1798	0,1364	0,0876	0,0480	0,7569
	\bar{M}	0,2535	0,2116	0,1080	0,0531	0,6502
GENERAL MEAN		0,2181	0,2161	0,1270	0,0025	0,6446

/family/population ($\hat{\sigma}_G^2$), which represented 78.19 % of total variation. The variation between individuals/family/population ($\hat{\sigma}_I^2$) was 9.18% over total variation.

These results indicate that the major part of the genetic variability is concentrated within the rubber tree populations studied. PAIVA et al. (1994), using the same material, employed NEI's (1973) methodology to estimate the variability between and within populations and also found a greater proportion of genetic variability within the population.

The value of the coancestry coefficient of the plants within families ($\hat{\theta}_1$) for the mean of the 17 alleles for the 4 loci was 0.1270 (Table 4), which was close to the value expected for half sib families (0.1250). It should be mentioned that a high value of $\hat{\theta}_1$ was expected, considering that the outcrossing rate was lower than 100 % in the populations studied.

Another parameter which assesses genetic diversity between populations is COCKERHAM'S coefficient of genetic distance ($\hat{\theta}_2$), estimated from the analysis of variance of the frequencies of the alleles in the population. The value of $\hat{\theta}_2$ estimated for each allele was variable, but relatively low for all alleles. Some coefficients showed negative estimates, probably indicating that the real value is zero. The mean coefficient for the 17 alleles was 0.0025 (Table 4). Low values for NEI's (1972), WRIGHT'S (1965) and NEI'S (1977) coefficient of genetic diversity between the 2 populations, 0.003, 0.006, and 0.0003, respectively, were found by PAIVA et al. (1994), when they analysed the same material.

The traditional methods for assessing the mating system of a species are based on the observation of crossings, on the behavior of pollinating agents, on the examination of the flower morphology of the plants, or on the results of experiments with controlled pollinations. Even though these methods provide indications on the mating system of the species, they do not provide a direct measurement of the reproductive success in the populations and become inadequate for an analysis at the populational level.

The determination of the crossing rate in natural populations has always shown limitations, such as: irregular distance between plants, mainly in tree species, the natural barriers between plants, the identification of a good genetic marker, and the expression of dominance exhibited, in most cases, by these markers. RITLAND and JAIN (1981) stress the power and the versatility of the estimation processes when electrophoresis data are used, considering that many segregant loci with codominant alleles may, frequently, be found in the populations.

The estimates obtained for the outcrossing rates in rubber trees calculated from the analysis of variance of the frequencies of the alleles in the populations demonstrate that they are quite variable when estimated for each allele. These estimates show lesser variation for the mean between the loci 60.08 % (SKDH) to 71.47% (LAP-1). The mean rate for the 17 alleles studied in the 4 loci presented a value of 64.46 % of outcrossing for the species (Table 4).

FERWERDA and WIT (1969) report that rubber trees have not shown preference for cross pollination over self pollination, although the fruit set percentage obtained in artificial pollinations tends to be slightly lower after self pollination than after cross pollination. On the other hand, BOUHARMONT (1962) found significant differences in the development process after fertilization and in the percentage of

fruit set in both forms of pollination. The authors also stresses that most seeds from a certain tree are probably derived from selfing because the transfer of pollen within an individual probably occurs more promptly than that between plants.

The estimates obtained for the inbreeding coefficients within the population (\hat{f}_I), at the level of rubber tree populations, and of the mean inbreeding coefficient of plants in the populations (\bar{F}), at the level of the species, estimated from the analysis of variance of the frequencies of the alleles in the 2 populations, presented similar values for the mean of the 17 alleles analysed (21.61 % and 21.81 %, respectively) (Table 4).

As shown, the mean inbreeding rate for rubber trees, in natural populations, was always higher than 20 %. In view of this result, it cannot be stated that the inbreeding was due only to selfing. Since the outcrossing rate is approximately 64 %, the selfing rate would be 36 %, and therefore the inbreeding may also have originated from crossing of related plants.

SIMMONDS (1989) reports that the studies on cross pollination in rubber tree plantings apparently have not been well understood, due to the fact of the occurrence of dwarf plants possibly caused by selfing of plants in seed gardens of good origin. The cited author also reports that the selfing rate varies around 16 % to 28 %; he also reports that the selfing rate estimated for clone PB 5/51, in Prang Besar (Malaysia) was 22 %.

O'MALLEY et al. (1988), using multilocus methodology, estimated a crossing rate of $\hat{t} = 0.85 \pm 0.03$ for Brazil nut and stressed that outcrossing is predominant in this species: however, they do not discard the possibility of low levels of inbreeding.

Tropical ecosystems undoubtedly present a greater diversity of species and a greater complexity in the inter-relationships between organisms. The diversity results from the sum of various interacting factors in the ecosystem. Consequently, the individuals of one species, in a certain way, are isolated from other individuals of other species. This has implications in the dynamics of the forest in terms of plant x animal interaction, which are interdependent and well coadapted, thus conferring integration and stability upon the ecosystem (PIANKA, 1983).

Based on these arguments, it may be inferred that each species in tropical forest developed its own strategies of adaptation in dynamic equilibrium with the heterogeneity of the ecosystem. What may be inferred is that the strategies utilized by 1 species may not serve as reference for other species.

Thus, it is reasonable to suggest that the natural outcrossing rate estimated for rubber trees, although low for the patterns of a species believed to be allogamous, as well as the degree of inbreeding of the species, is a biological strategy developed by the species that allows it to maintain an equilibrium in the tropical ecosystem. The reproductive system may contribute to the fact that rubber trees cultivated in a tropical environment are decimated by the pathogen (*Microcyclus ulei*), but coexist harmoniously in equilibrium in natural populations.

The degree of inbreeding estimated for rubber trees in natural populations, be it due to selfing or to crossing between related plants, may present adaptive advantages. One possibility would be to promote homozygosis of the deleterious genes and, due to natural selection, eliminate plants not adapted to the natural environment.

Another hypothesis which may explain the low outcrossing rate estimates is that inbreeding may already exist in the population. By the methodology utilized, the outcrossing rate is estimated based on the inbreeding coefficient of the population and the inbreeding coefficient estimated in the offspring generation is increased as a result of the crossing between partially related plants. In this case, the outcrossing rate would be underestimated.

The inbreeding depression phenomenon in rubber trees has been observed for some time (SHARP, 1940 and 1951; ROSS and BROOKSON, 1960). TAN and SUBRAMANIAN (1976) showed that self progenies are inferior to outcrossed progenies in relation to vigor and rubber yield. Presumably, the inbreeding effect is quite common in rubber trees, however, according to BOUYCHOU (1969) its intensity may be variable in different clones. HO (1976), in analysing the rubber tree improvement program of the RRIM (Rubber Research Institute of Malaysia) and of Prang Besar, reports that inbreeding has adverse effect on the yield and vigor of the plants, reducing the success of pollination and increasing the proportion of weak plants.

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