Gene Flow from White into Negro Populations in Brazil

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GLASS AND LI (1953) have introduced a statistical model that allows calculations to be made, not only of the intermixture between two base populations but also of the dynamic pattern of the gene flow from one population to another, during a known period of intermixture. The formula derived from Glass and Li is:

$$(1 - m)^k = \frac{q_k - Q}{q_0 - Q}$$

To use this formula it is necessary to know: a) the gene frequencies, q_0 and Q, of the base populations; b) the gene frequency, q_k, of the hybrid population; and c) the number of generations, k, of contact between the base populations. The average rates of gene flow (m) from one population to another varies according to the assumed value of k and to the amount of accumulated admixture in the hybrid population. Some limitations of this method have been stressed by Glass and Li.

It should be of interest to compare the process of hybridization between Negro and White populations in Brazil to that in the United States, since the social conditions in the two countries have been and still are different. This is a first attempt to do so.

THE BRAZILIAN NEGRO

An important problem, which is not yet completely settled, is the African origin of Brazilian Negroes. The comparative ethnography of the Brazilian Negro was worked out, in its fundamental aspects, by the pioneer work of Nina Rodrigues (1932) and the later work of Ramos (1951a). The data on the relations between African and Brazilian cultural groups of Negroes shown in Table 1 result from these studies.

Table 1 shows that the Negroes who arrived in Brazil belonged to two main groups:

Bantu stock. This group is spread throughout Brazil. It is represented chiefly by the "Angola-Congolês" group from Angola and Congo, and to a lesser extent, by the "Contra-Costa" group from Moçambique. The Bantus settled in several places: in the States of Maranhão and Pará, from where they migrated to the inner part of Pará; in the States of Pernambuco and Alagoas, from which they migrated to the State of Ceará; and in the States of Rio de Janeiro, São Paulo and Minas Gerais, from where they migrated to the State of Goiás.

Sudanese stock. This group settled in the State of Bahia. The bulk of it is represented by the Ashanti from the Gold Coast, the Ewe from Dahomey, and chiefly

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TABLE 1. RELATIONS BETWEEN THE CULTURAL GROUPS OF AFRICAN AND BRAZILIAN NEGROES (BASED ON DATA BY RAMOS, 1951a)

African Cultural Group		Geographical Distribution in Africa	Culture Group Related in Brazil	Early Geographical Distribution in Brazil	Probable Time of First Arrival in Brazil	Remarks
Major groups	Subgroups					
I—Guinean-Sudanese Culture	Fulah Mandinga Houssah	Northern Sudan Senegal Guinea, Western and Central Sudan	"malê"	mainly in Bahia	beginning of the 17th century	Mahometan Negroes under Semitic and Hamitic influence. Small traffic to Brazil
II—Sudanese Culture	Fanti-Ashanti Ewe Yoruba	Gold Coast Dahomey Nigeria (mainly Southern)	Mina Gegê Nagô	Bahia	beginning of the 17th century beginning of the 19th century	Intense traffic bounded upon small area in Brazil. Mainly represented by Yoruba
III—Bantu Culture	Western group Eastern group	Congo, Angola Moçambique, Tanganika, Lakes' region, etc.	"Angola-Congolês" "Contra-Costa"	Rio de Janeiro, S. Paulo, Maranhão, Pernambuco, Alagoas	In the middle of 16th century	Culture group but linguistic. Heterogeneous stock under Hamitic influence. Intense traffic

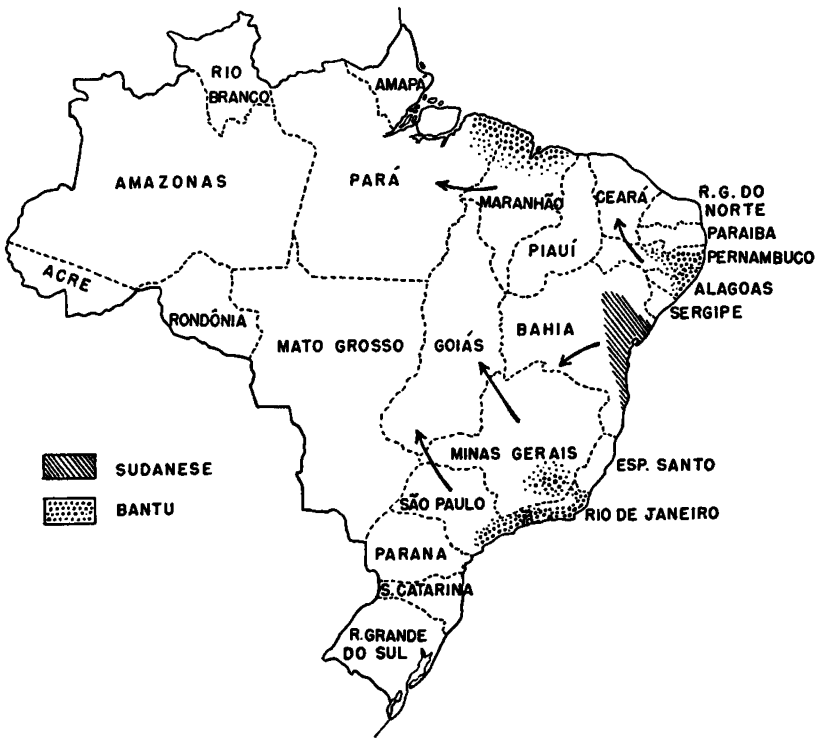

FIG. 1. Early settlements of African Negroes in Brazil and their further migrations (after Ramos 1951b, modif.)

the Yoruba from Nigeria (especially southern Nigeria). The Sudanese came in smaller numbers than the Bantus. The geographical distribution of the Bantus and the Sudanese overlaps to some extent in Brazil.

The above data, although somewhat inaccurate, may still be used for determining the present race admixture in Brazil. Figure 1 shows the places of early settlements of Negro slaves in Brazil and their subsequent migrations.

Another problem of interest is the determination of the ratio of Negro to White people in Brazil. The relative number of Negroes has changed in time. Before considering this change it is necessary to point out that in the Brazilian census a distinction is made between the full Negroes (called Negroes) and the lighter Negroes (Mulattoes). The total number of slaves introduced in Brazil is calculated to be about 18 million, which amounts to five to six million per century. The relative ethnic composition at three periods in Brazil, according to the censuses of 1798 (unofficial; cf. Ramos, 1951a), 1872 and 1950 are:

Year	Total population	Whites (%)	Negroes (%)	Mulattoes (%)
1798	3,250,000	39.0	54.0	7.0
1872	9,930,479	38.1	19.7	38.3
1950	51,944,397	61.6	10.9	22.5

TABLE 2. GENE FREQUENCIES OF RH TYPES AMONG AFRICAN NEGROES, BRAZILIAN NEGROES AND BRAZILIAN WHITES

	No.	$R^0(cDe)$	$R^1(CDe)$	$r(cde)$	Reference
			African Negroes		
Sudan Group					
Ewe	161	.480	.086	.235	Armattoe, Ikin & Mourant, 1953
Ashanti	113	.558	.120	.230	Armattoe, Ikin & Mourant, 1953
S. E. Nigeria	106	.563	.046	.238	Chalmers, Ikin & Mourant, 1953
S. W. Nigeria	145	.602	.058	.184	Chalmers, Ikin & Mourant, 1953
N. Nigeria	165	.539	.099	.136	Chalmers, Ikin & Mourant, 1953
Jos Plateau	124	.568	.007	.243	Chalmers, Ikin & Mourant, 1953
N. Sudanese	133	.461	.016	.237	Brooks, Garner, Ikin & Mourant, 1952
Average	947	.539	.062	.215	—
Bantu Group					
S. Afr. Bantu	644	.649	.027	.118	Shapiro, 1953
			Brazilian Negroes		
Bahia	326	.398	.160	.257	Pedreira, 1954
S. Paulo	277	.281	.242	.325	Ottensooser, Lacaz, Ferreira & Mellone, 1948
Rio de Janeiro	153	.399	.332	.318	Lopes & Junqueira, 1952
			Brazilian Whites		
Bahia	174	.068	.424	.347	Pedreira, 1954
S. Paulo	138	.068	.406	.390	Ottensooser, Lacaz, Ferreira & Mellone, 1948
Rio de Janeiro	605	.064	.420	.414	Lopes & Junqueira, 1952

In the southern states of Brazil, Negro-White intermixture should have occurred intensely until about 1872. By this time the migration of several European peoples other than Portuguese had begun, especially to the southern part of the country. These migrants have shown a greater resistance to crossing with the Negroes than have the Portuguese. The European migratory movements in the last century have contributed to the increase of the relative number of Whites in the census of 1950.

ESTIMATION OF GENE FLOW

The number of generations of Negro-White contact. According to Ramos (1951a), the date on which the first slaves arrived in Brazil is uncertain. There are some indications that slave trade in Brazil began in 1538, with the arrival of a small group of Negroes at Rio de Janeiro. The most intense traffic was from the 16th up to the 19th century (Taunnay, 1941). It is reasonable to postulate that the period of Negro-White contact in Brazil is about 350 years.

In order to ascertain the number of generations of intermixture (k) it is necessary to know the average length of a generation at the present time. According to the Brazilian Census (Mortara, 1947), the average age of mothers (including Negro

TABLE 3. GENE FREQUENCIES OF THE SENSITIVITY TO PHENYLTHIOUREA AMONG AFRICAN NEGROES BRAZILIAN NEGROES AND BRAZILIAN WHITES

Sample	Number	Taste Gene Freq.	Reference
African Negroes (W. Africa)	57	.813	Barnicot, 1950
Brazilian Negroes (S. Paulo)	115	.687	Saldanha (unpublished)
Brazilian Whites (Rio de Janeiro)	164	.448	Saldanha & Guinsburg, 1954

TABLE 4. GENE FREQUENCIES OF ABO BLOOD GROUPS AMONG AFRICAN NEGROES, BRAZILIAN NEGROES AND BRAZILIAN WHITES

	No.	I^A	I^B	i	Reference
African Negroes					
Sudan Group					
Ewe	161	.151	.169	.680	Armattoe, Ikin & Mourant, 1953
Ashanti	113	.148	.138	.714	Armattoe, Ikin & Mourant, 1953
S. E. Nigeria	106	.071	.079	.779	Chalmers, Ikin & Mourant, 1953
S. W. Nigeria	145	.064	.128	.744	Chalmers, Ikin & Mourant, 1953
N. Nigeria	167	.080	.157	.683	Chalmers, Ikin & Mourant, 1953
Jos Plateau	124	.069	.148	.714	Chalmers, Ikin & Mourant, 1953
N. Sudanese	133	.172	.145	.683	Brooks, Garner, Ikin & Mourant, 1952
Yoruba	325	.133	.143	.724	Cf. Glass & Li, 1953; table 4
Senegalese	238	.140	.192	.680	Cf. Glass & Li, 1953; table 4
Average	1512	.114	.144	.733	—
Bantu Group					
S. Afr. Bantu	6020	.190	.130	.680	Shapiro, 1951
Bas Congo	357	.153	.120	.727	Lambotte-Legrand & Lambotte-Legrand, 1950
Angola	2246	.157	.140	.703	David, 1949
Average	8623	.167	.130	.703	—
Brazilian Negroes					
Bahia I	7967	.165	.100	.735	Novais, 1953
Bahia II	326	.178	.063	.759	Pedreira, 1954
Average	8293	.172	.082	.747	—
S. Paulo I	277	.181	.115	.703	Faria & Ottensooser, 1951
S. Paulo II	3429	.172	.114	.712	Mellone, Ludovici, Maluf & Macruz, 1952
Average	3706	.177	.115	.708	—
Brazilian Whites					
Bahia I	4248	.223	.067	.708	Novais, 1953
Bahia II	174	.285	.026	.687	Pedreira, 1954
Average	4422	.254	.047	.698	—
S. Paulo I	3978	.241	.069	.689	Faria & Ottensooser, 1951
S. Paulo II	12494	.230	.071	.698	Mellone, Ludovici, Maluf & Macruz, 1952
Average	16472	.236	.070	.694	—

TABLE 5. FREQUENCIES OF GENES OF THE NEGRO AND WHITE BASE POPULATIONS, PERCENTAGE OF WHITE ADMIXTURE AND AVERAGE RATES OF GENE FLOW FROM WHITE INTO NEGRO POPULATIONS, CONSIDERING THE TWO EARLY MAIN GROUPS OF NEGROES IN BRAZIL: BANTU AND SUDANESE (ASSUMING K = 12).

Gene	African Negroes (q_0)		Brazilian Negroes (q_k)		Brazilian Whites (Q)		Difference ($q_0 - Q$)	White Admixture (%)	Average Gene Flow (m)
R^0	Bantu Group (1)	.649	S. Paulo	.281	S. Paulo	.068	.581	63.34	.0803
(*cDe*)	Sudan Group (2)	.539	Bahia	.398	Bahia	.068	.471	29.94	.0292
R^1	Bantu Group (1)	.027	S. Paulo	.242	S. Paulo	.406	.379	56.73	.0676
(*CDe*)	Sudan Group (2)	.062	Bahia	.160	Bahia	.424	.362	27.08	.0261
Taste gene	W. Africa	.813	S. Paulo	.687	Rio Jan.	.448	.365	34.53	.0354
r (*cde*)	Bantu Group (1)	.118	S. Paulo	.325	S. Paulo	.390	.272	76.11	.1126
	Sudan Group (2)	.215	Bahia	.257	Bahia	.347	.132	31.82	.0314
I^A	Bantu Group (2)	.167	S. Paulo	.177	S. Paulo	.236	.069	14.48	.0121
	Sudan Group (2)	.114	Bahia	.172	Bahia	.254	.140	40.15	.0419
I^B	Bantu Group (2)	.130	S. Paulo	.115	S. Paulo	.070	.060	25.00	.0238
	Sudan Group (2)	.144	Bahia	.082	Bahia	.047	.097	65.05	.0839

1. S. Africa Bantu 2. Average frequency

and White) at the birth of their children during the year of 1940, is 28.6 years. The corresponding figure for fathers is not available, but must be greater than that for the mothers, since men marry later than women. The length of a generation has, therefore, to be taken as somewhat higher than 28.6 years, a convenient estimate being 30 years.

The gene frequencies of the base populations. It is necessary to know the gene frequencies of the base and the hybrid populations in order to calculate the average gene flow from White into Negro populations. The studies on gene frequencies of Brazilian Negro populations are few. We used data on genes for the Rh types, R^0 (*cDe*), R^1 (*CDe*) and *r* (*cde*), for sensitivity to phenylthiourea (taste gene *T*), and for ABO blood groups (I^A and I^B). The corresponding frequencies appear in table 5 in order of decreasing value of their differences in the base populations. Other genes, whose frequencies in the base populations differed by less than 10 per cent were not used. Since Brazilian Negroes seem to originate from two different African stocks, Bantu and Sudanese, separate calculations were made for each of them. For the Rh gene frequencies (table 2) and for the average of the frequencies of the ABO genes (table 4), data found by several investigators were used as representing the frequencies for each group. For the taste gene (table 3) only one sample (Barnicot, 1950), from West Africa, was available. The data available on gene frequencies of Brazilian Negroes discriminate between full Negroes and Mulattoes. Since these people belong to the same populations, their average gene frequencies were used as representing the Brazilian Negro.

In the Rh system, the frequencies of the D^u gene were not considered, since this gene may be classified as *d* and its frequency among Whites is negligible (Mourant, 1954). The *r* (*cde*) gene frequencies for the Mulattoes of the State of Rio de Janeiro has been used instead of that for Mulattoes plus Negroes because the number of individuals in the Negro sample classified as Rh negative *rr* (*cde/cde*) is too small and the

corresponding gene frequency is lower than that of the African Negro. This is probably due to the small number of full Negroes tested.

The taste thresholds for phenylthiourea sensitivity (table 3) were determined for a sample of Brazilian Whites (Saldanha and Guinsburg, 1954) and for a sample of Brazilian Negroes by the author (unpublished). In both cases the thresholds were measured according to the technique described by Harris and Kalmus (1949). Calculations based on phenylthiourea sensitivity were possible only for the State of São Paulo.

The gene frequencies of ABO blood groups were recalculated by Fisher's new method (cf. Race and Sanger, 1950) since the calculations by Bernstein's method

TABLE 6. PERCENTAGE OF WHITE ADMIXTURE AND AVERAGE RATES OF GENE FLOW PER GENERATION FROM WHITE INTO NEGRO POPULATIONS, CALCULATED FROM THE FREQUENCIES OF GENES OF THE RH BLOOD SYSTEM IN DIFFERENT AFRICAN SAMPLES (ASSUMING K = 12)

African Samples	Brazilian Samples					
	Bahia		S. Paulo		Rio de Janeiro	
	White admixture (%)	Gene flow	White admixture (%)	Gene flow	White admixture (%)	Gene flow
			R^0 (*cDe*)			
Ewe	19.91	.0184	48.31	.0535	19.48	.0180
Ashanti	32.66	.0326	54.90	.0643	32.19	.0317
S. E. Nigeria	33.34	.0332	56.97	.0680	25.39	.0243
S. W. Nigeria	38.20	.0394	60.12	.0738	37.74	.0388
N. Nigeria	29.96	.0292	54.78	.0641	29.48	.0288
Jos Plateau	34.00	.0341	57.40	.0686	33.54	.0335
N. Sudanese	16.04	.0146	45.78	.0498	15.62	.0141
S. Afr. Bantu	43.21	.0461	63.34	.0803	42.57	.0452
			R^1 (*CDe*)			
Ewe	21.87	.0205	60.96	.0791	73.66	.1052
Ashanti	13.16	.0119	42.66	.0454	73.00	.1033
S. E. Nigeria	30.43	.0299	54.45	.0635	76.48	.1136
S. W. Nigeria	27.87	.0270	52.86	.0609	75.70	.1112
N. Nigeria	18.77	.0177	46.58	.0509	72.59	.1023
Jos Plateau	36.70	.0375	58.90	.0714	78.70	.1209
N. Sudanese	35.30	.0357	57.95	.0697	78.22	.1193
S. Afr. Bantu	33.51	.0335	56.73	.0676	77.61	.1173
			r (*cde*)			
Ewe	19.65	.0182	58.07	.0699	46.37	.0507
Ashanti	23.08	.0216	59.38	.0725	47.81	.0528
S. E. Nigeria	17.44	.0159	57.24	.0684	45.46	.0493
S. W. Nigeria	44.79	.0483	68.45	.0917	58.27	.0703
N. Nigeria	57.35	.0686	74.41	.1075	65.47	.0848
Jos Plateau	13.47	.0121	55.79	.0658	43.86	.0469
N. Sudanese	18.19	.0166	57.53	.0688	45.77	.0498
S. Afr. Bantu	60.74	.0750	76.11	.1126	70.38	.0975

are not suitable for studies of race admixture (Boyd, 1950). The frequencies of the ABO genes in the base populations are not very suitable for calculating the gene flow because their difference in these populations is small (table 5).

The average values of gene flow. The estimations of gene flow were calculated for the States of Bahia, São Paulo and Rio de Janeiro. It was postulated that the direction of the gene flow is from White into Negro populations only. This is not completely true, as is stressed by Glass and Li (1953) in the study of the American Negro.

The gene flow was calculated first by using the gene frequencies of the Sudanese Negroes for the State of Bahia and those of the Bantu Negroes for the States of São Paulo and Rio de Janeiro (table 5). However, as both African stocks have, in part, spread throughout Brazil, calculations were also made for each of the three States based on the frequencies of the Bantu sample and various Sudanese samples.

The results presented in this paper are only tentative because further studies on the origins of the Brazilian Negro may change the present views, upon which our calculations are based.

Table 6 gives various estimates of the accumulated White admixture in Brazilian Negro as well as the gene flow from White into Negro populations in three States of Brazil. The figures are higher for the States in which Negroes have a Bantu ancestry (São Paulo and Rio de Janeiro) than for the State in which they have a Sudanese ancestry (Bahia).

The modal values of percentage of White admixture and average gene flow from White into Negro populations are:

Place	White admixture (%)	Gene flow (m)
Bahia	ca. 35	.035–.040
São Paulo Rio de Janeiro	ca. 55	.060–.065
Brazil	ca. 40	.045–.050

DISCUSSION

The gene flow to the Negro population of Bantu origin (in São Paulo and Rio de Janeiro) is roughly twice as great as that calculated for the Negroes of Sudanese origin (in Bahia). However, there is some indication that the Negroes introduced into Bahia were not exclusively of Sudanese ancestry.

Sudanese Negroes who settled in Bahia are mainly represented by people of Yoruba culture (see table 1) from South Nigeria (Ramos, 1951a). It is believed they have arrived at Bahia during the beginning of 19th century. Therefore, the time of intermixture with Whites is for this Negro group decreased to about 150 years, that is, 5 generations. The intermixture which occurred before that time must have taken place between the White and Bantu groups which were introduced in Brazil at the beginning of the 16th century. By recalculating the amount of White admixture and average gene flow from the White into the Negro populations in the State of Bahia, using the R° (*cDe*) gene frequencies of Yoruba (S. W. Nigeria) and South Africa Bantu independently, we get the figures: 39 per cent, $m = .094$ and 47 per cent, $m = .051$, assuming $k = 5$ and $k = 12$ respectively. Probably the correct figures should be intermediate between these.

The values of accumulated admixture and average gene flow are in general higher for Brazil than for the United States (Roberts, 1955). This difference is not difficult to explain. In Brazil hybridization is increasing more and more in recent times, following the slave freedom law. In the United States the situation has not changed much since the time of slavery as evidenced by the small number of Negro-White official marriages. In Brazil these cases are very numerous, especially in the Northern States of Bahia and Maranhão. However, the frequency of hybridization is probably variable in Brazil, according to the States, as a consequence of the different attitude towards intermixture of the European immigrants settling in different places. Portuguese, in contrast to most Europeans, are very fond of crossbreeding.

It is probably that the Brazilian Negroes are subjected to ecological and social forces which differ from those acting upon the Negroes in the United States. This can lead to selective forces of different intensity in the two countries. Unfortunately, it is difficult to discriminate between the frequency oscillation caused by gene flow and that caused by natural selection. An influence exerted by natural selection must be found by comparing gene flow for different gene loci in the same population. There is an indication of the action of selective forces if two estimates based on different genes differ appreciably.

Haldane (1942) and Wiener (1942) have noticed that the intrauterine selection against the heterozygotes (*Dd*) of the Rh system due to erythroblastosis fetalis must decrease the frequency of the rarer gene in the population. This selective process becomes apparent when a decrease of the *r* (*cde*) allele in Negro hybrid populations is detected. Glass (1950), however, found that this allele is becoming commoner among the United States Negroes. This has been explained as being caused by a compensatory increase of fertility in families with mother-fetus incompatibility. The estimates for Brazil of average gene flow derived from *r* (*cde*) allele do not differ from those derived from other genes. However, in the State of Bahia, the Mulattoes show a relatively lower frequency of this allele than is found among the full Negroes and Whites (these frequencies in Bahia are .390 for Whites, .273 for Negroes, and .242 for Mulattoes, according to Pedreira, 1954).

In the present paper no consideration has been given to the Negro-Amerindian intermixture. Glass (1955) has shown that Indians have not contributed appreciably to the gene frequencies of the United States Negroes. This conclusion probably does not apply for every Brazilian State. Intermixture between Negroes and Indians probably occurred to a considerable extent in the Northern States, mainly in Ceará and Maranhão. In Maranhão, for example, the ABO gene frequencies found among Mulattoes differ from the expected values calculated by considering only Negro-White crosses (see Silva, 1948). This discrepancy might be explained by taking into account the Indian contribution to the intermixture. In the Southern States, however, the Indian contribution was negligible and probably does not influence the accuracy of the data calculated in this paper.

SUMMARY

The average gene flow per generation from White into Negro populations in Brazil was calculated by Glass and Li's method. The modal values are .045–.050, assuming 12

generations of intermixture, and the White admixture accumulated in the Negro population is about 40%. Data from Sudanese and Bantu African Negroes, from which the Brazilian slaves originated, were used, for calculating gene flow and White admixture for three different States, according to the African origin of the early settlements of Negroes in Brazil. Variable estimates were found that must be due to the different number of generations of contact between Sudanese and Bantu Negro groups with the Whites in different states.

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