

GENOME SIZE AND NUMERICAL POLYMORPHISM FOR THE B CHROMOSOME IN RACES OF MAIZE (*ZEA MAYS* SSP. *MAYS*, POACEAE)¹

MARCELA ROSATO,^{2,3} AMILCAR M. CHIAVARINO,^{2,3}
CARLOS A. NARANJO,² JULIAN CAMARA HERNANDEZ,⁴ AND
LIDIA POGGIO^{2,3,5}

²Instituto Fitotécnico de Santa Catalina (FCAF, UNLP)-Centro de Investigaciones Genéticas (UNLP-CONICET-CIC),
C.C. 4, 1836 Llavallol, Buenos Aires, Argentina;

³Departamento de Biología, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires,
1428 Buenos Aires, Argentina; and

⁴Cátedra de Botánica, Facultad de Agronomía, UBA, Buenos Aires, Argentina

Twenty-one native populations (1120 individuals) of maize from Northern Argentina were studied. These populations, which belong to 13 native races, were cultivated at different altitudes (80–3620 m). Nineteen of the populations analyzed showed B chromosome (Bs) numerical polymorphism. The frequency of individuals with Bs varied from 0 to 94%. The number of Bs per plant varied from 0 to 8 Bs, with the predominant doses being 0, 1, 2, and 3. Those populations with varying number of Bs showed a positive and statistically significant correlation of mean number of Bs with altitude. The DNA content, in plants without Bs (A-DNA)($2n = 20$), of 17 populations of the 21 studied was determined. A 36% variation (5.0–6.8 pg) in A-DNA content was found. A significant negative correlation between A-DNA content and altitude of cultivation and between A-DNA content and mean number of Bs was found. This indicates that there is a close interrelationship between the DNA content of A chromosomes and doses of Bs. These results suggest that there is a maximum limit to the mass of nuclear DNA so that Bs are tolerated as long as this maximum limit is not exceeded.

Key words: B chromosome; DNA content; genome size; maize; maize native races; Poaceae; *Zea mays* ssp. *mays*.

The supernumeraries or B chromosomes (Bs) are extra chromosomes that are added to the normal complement (A chromosome set; As), which is invariable in number in all ordinary plants. Bs are widely distributed in maize and are found in several lines, including commercial varieties, and at high frequencies in native populations (Longley, 1927, 1938; Randolph, 1928, Avdulow, 1933; Carlson, 1978; McClintock, Kato-Y, and Blumenschein, 1981). Although no obvious phenotypic effects can be attributed to the presence of Bs, they could have a role in the evolution of maize native populations, because of their high frequencies and wide distribution (Jones, 1995). In most organisms carrying Bs, accumulation mechanisms have been found (Jones and Rees, 1982). In maize these mechanisms are: (a) directed nondisjunction in the second pollen grain mitosis (Roman, 1947; Carlson and Chou, 1981), (b) preferential fertilization by male gametes carrying Bs (Roman, 1948), (c) reduction of meiotic loss of Bs (Carlson and Roseman, 1992). According to Carlson and Roseman (1992) these accumulation mechanisms are sufficient to account for the maintenance of B polymorphism in maize populations. These

mechanisms cannot, however, account for the differences of B frequencies in different populations (Chiavarino et al., 1995; Naranjo et al., 1995). Recently, the genetic control of B-chromosome transmission rate in a native population of maize was determined (Rosato et al., 1996a). These authors postulated that different frequencies of alleles positively controlling B transmission rate could be the explanation for the variation of B frequency in different populations.

The genus *Zea* illustrates the variation of DNA content among species, subspecies, populations, inbred lines, and open pollination lines that is possible in plants (Laurie and Bennett, 1985; Rayburn et al., 1985; Tito, Poggio, and Naranjo, 1991). Differences in the amount of heterochromatin and/or occurrence of B chromosomes contribute to the genome size variation of the genus (Laurie and Bennett, 1985; Rayburn et al., 1985; Porter and Rayburn, 1990; Tito, Poggio, and Naranjo, 1991). Heterochromatic C bands are the mitotic equivalent of the meiotic pachytene knobs of heterochromatin (Hadlaczký and Kálmán, 1975; Ward, 1980; Aguiar-Perecin and Vosa, 1985). Knob number varies both among plants and populations, and it has been useful in elucidating relationships among races of maize (Longley, 1938; Longley and Kato-Y, 1965; McClintock, Kato-Y, and Blumenschein, 1981). Many studies on the distribution and frequency of knobs, C bands, and B chromosomes in many organisms including maize have shown that these karyotypic features are often closely correlated with environmental variables (Bennett and Leitch, 1995; Jones, 1995).

Bretting and Goodman (1989) noted a generally negative correlation between B chromosomes and altitude in

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⁵ Author for correspondence.

the data of McClintock, Kato-Y, and Blumenschein (1981). However, these authors analyzed no more than two plants per population (McClintock, Kato-Y, and Blumenschein, 1981; Cuadros 8, 10, and 12). Porter and Rayburn (1990) found that the number of B chromosomes was not significantly correlated with altitude, C-band number, or nuclear DNA amount, when 12 Arizona Indian maize populations were studied.

Longley (1938) analyzed the association between the number of knobs and the occurrence of B chromosomes in indigenous populations of North America, he found a negative correlation between the number of heterochromatic knobs on the As and the presence of B chromosomes. A similar correlation was reported by Bianchi, Ghatnekar, and Ghidoni (1963).

Mangelsdorf and Cameron (1942) observed a negative correlation between knob number and altitude in Guatemala races of maize; Longley and Kato-Y (1965) and Bennett (1976, re-evaluating the data of Wellhausen et al., 1952) observed a similar correlation in other Latin American races. Rayburn et al. (1985) found a similar relationship while studying the C bands in maize lines adapted to various latitudes, and they also reported a positive correlation between DNA content and knob number and a negative one between DNA content and altitude. On the other hand, Porter and Rayburn (1990) found that the number of C bands was positively correlated with altitude and DNA content.

Rayburn and Auger (1990a) found a significant negative correlation between genome size and altitude (52–2670 m) in four Mexican maize races. Rayburn (1990) found a negative correlation among the same variables in 12 New Mexico maize populations at 1510–2135 m. However, Rayburn and Auger (1990b) studying 12 Arizona maize populations growing at 30 up to 1617 m, found a significant positive correlation between genome size and altitude, in the same materials studied by Porter and Rayburn (1990).

These examples point out that the results of investigations regarding relationships among genome size (total DNA content), number of B chromosomes, C bands (knobs, heterochromatin), and altitude of cultivation in populations of maize of USA and Mexico are apparently contradictory. Interpretation is difficult. In a previous report made in six indigenous Argentine races of maize (Rosato et al., 1993) it was found that the presence of Bs is not always detected when measuring total DNA content. This situation could be explained if Bs were masked as a result of polymorphisms for repetitive DNA in the A chromosomes, as was postulated by Porter and Rayburn (1990).

Numerical polymorphism for B chromosomes is widespread in maize. Yet, little information is available based on detailed populational studies that could elucidate the relationships among numerical polymorphism of Bs, A-DNA content, and geographical distribution. In view of this, the aim of this paper was to analyze a large number of plants belonging to 21 native populations from 13 races collected in Northern Argentina. These samples range over all possible altitudes of cultivation of native maize in this region. The numerical polymorphism for Bs, A-DNA content, and their relationships with altitude of cultivation were analyzed.

MATERIALS AND METHODS

Plant materials—In Fig. 1 the distribution of material studied in the northern region of Argentina is shown. The sampling was made by the authors from original indigenous populations in 1994–1995. Part of the material was deposited in the seedbanks of Vavilov Laboratory (Facultad de Agronomía, UBA) and of IFSC (UNLP). The name and provenance are listed in the Appendix. The original populations are isolated, with no input of other populations and are maintained by an open pollination scheme. Samples were obtained from a mixture of all individuals available in each population.

Chromosome determinations—For each population 29–184 plants were scored for chromosome analysis. The criteria used to decide on the number of plants scored per population were the number of ears collected and they reflect the size of the populations. Seeds were germinated in petri dishes. Roots 0.5–1 cm long were treated with 0.002 mol/L 8-hydroxyquinolin for 3 h, fixed in 3:1 (ethanol:acetic acid), and stained with 2% hematoxylin and ferric citrate as mordant.

Determination of DNA content—With the aim of studying the variation in DNA content of A chromosomes (A-DNA) independently from the variation supplied by the Bs, this estimation was performed in plants without Bs ($2n = 20$). DNA content was measured in 20 telophase nuclei (2C) of the root tips of germinating seedlings; 3–18 plants per population were studied. The criteria used to decide on the number of plant scored for DNA determination was based in the available individuals with $2n = 20$, which was low in several populations. Roots 0.5–1 cm long were fixed in 3:1 (ethanol:acetic acid). The staining method was performed as described in Tito, Poggio, and Naranjo (1991). After fixation, the roots were rinsed for 30 min in distilled water. Hydrolysis was carried out with 5 mol/L HCl at 20°C for 30 min. The roots were then washed three times in distilled water for 15 min, and stained for 2 h in Schiff's reagents at pH 2.2 (Teoh and Rees, 1976). The material was then rinsed three times in SO₂ water for 10 min each, kept in distilled water, and squashed in 45% acetic acid. The coverslip was removed after freezing with CO₂ and the slide was dehydrated in absolute alcohol and then mounted in Euparal. The amount of Feulgen staining per nucleus, expressed in arbitrary units, was measured at a wavelength of 570 nm, using the scanning method with a Zeiss Universal Microspectrophotometer (UMSP 30). The DNA content per basic genome, expressed in picograms was calculated using an *opaque 2* line (raised by M. Aulicino) as the standard (2C = 6.658 pg) calibrated according to Bennett and Smith (1976) using *Allium cepa* var. Ailsa Craig (2C = 33.55 pg).

Statistical analyses—Simple correlations among mean number of Bs per plant per population and altitude, A-DNA content and altitude, and A-DNA content and mean number of Bs, were calculated using the Statgraphics Plus (7.1) program.

RESULTS

The morphology of B chromosomes seems to be similar in all populations. The B chromosome is telocentric, and it is the smallest of the complement, representing ~4% of the total chromosome volume. At pachytene the B chromosomes in the Argentine populations show a very similar structure to that described by Carlson and Chou (1981).

Numerical polymorphism for B chromosomes—The geographical distributions of the samples analyzed are described in Fig. 1. We studied 21 native populations, corresponding to 13 races of maize cultivated at different altitudes (80–3620 m) (Fig. 1). The Bs were mitotically

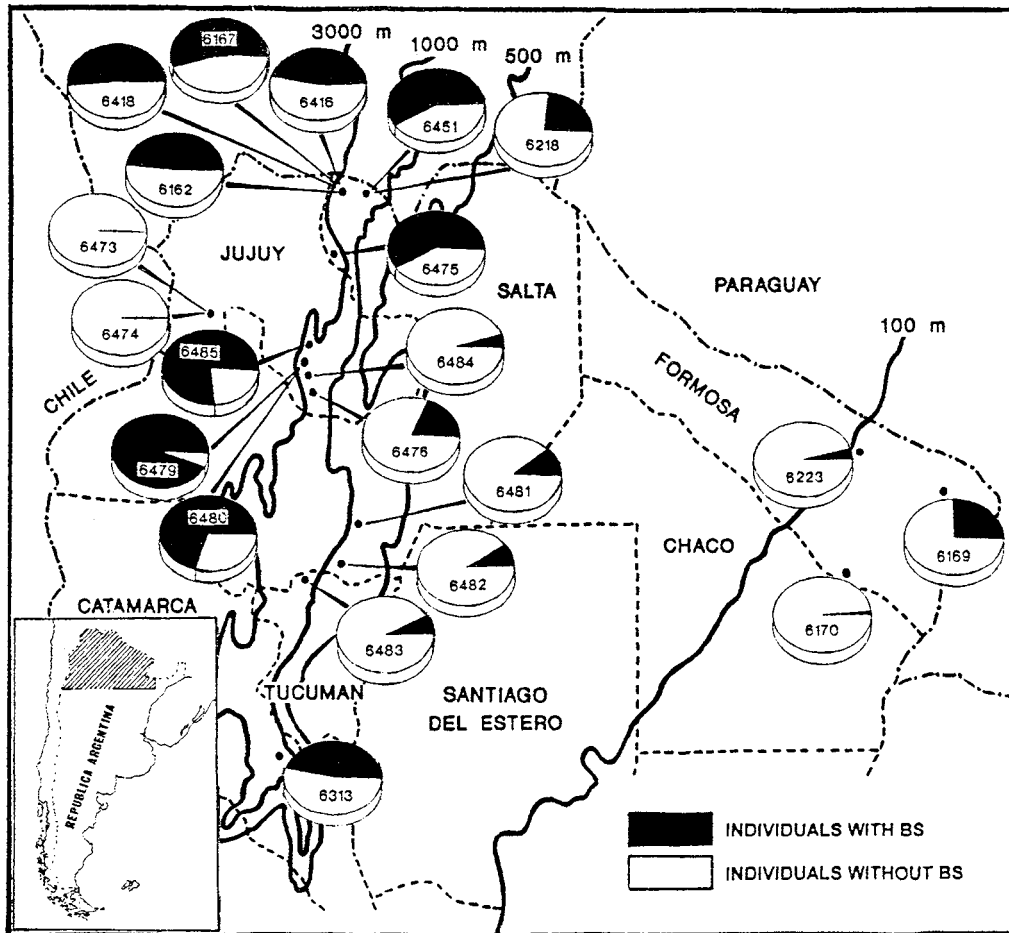


Fig. 1. Distribution of material studied from northern Argentina (inset map). The frequency of plants with B chromosomes is represented by the size of the black sector.

stable and present in at least one population of each race studied. Numerical polymorphism for Bs was found in 19 populations, while it was absent in the remaining two (VAV 6473 and 6474) (Table 1). The number of Bs per plant ranged from 0 to 8, with 0, 1, 2, and 3 being the more frequent doses. The variation in the percentage of plants with Bs among populations was very wide (0–94%) (Table 1). A highly significant positive correlation between the mean number of Bs per plant per population and altitude of cultivation was demonstrated ($r = 0.6355$, $P = 0.0035$) (Fig. 2), when the populations with numerical polymorphism for Bs were considered. The populations without Bs (VAV 6474 and 6473), which grow at 3520 and 3620 m, respectively, occur in a marginal area in the Andean region of Jujuy Province under extreme environmental conditions for this crop. When these populations were included in the statistical analysis the correlation was not significant ($r = 0.3698$, $P = 0.099$).

DNA content—The A-DNA content of 17 populations (107 individuals) was determined (Table 2). The range of variation was 36% (5.007–6.756 pg) among the 17 populations studied. It was found that A-DNA content (performed in plants without Bs; $2n = 20$) is significantly negatively correlated with altitude of cultivation ($r =$

-0.3134 , $P = 0.0021$), considering polymorphic populations for B chromosomes (Fig. 3). When the two non-polymorphic populations (VAV 6473 and 6474) were included in the analysis, the correlation was not significant ($r = -0.0953$, $P = 0.33$); both VAV 6473 and 6474 have a high A-DNA content.

The DNA content, determined in plants without Bs (A-DNA), was also negatively correlated with the mean number of Bs of the 17 populations ($r = -0.3392$, $P = 0.00035$) (Fig. 4). Interestingly, populations belonging to the same race also showed the same tendency. For instance, populations VAV 6484 and 6451, belonging to the “Amarillo chico” race, with frequency of Bs of 0.20 and 0.9 had decreasing values of A-DNA content (6.353 and 5.665 pg, respectively). The same happened when populations VAV 6474, 6473, and 6167 (all from Altiplano race) were compared. The first two, cultivated at ~3520 and ~3620 m, without Bs, had an A-DNA content of 6.5 and 6.49 pg, respectively, whereas the VAV 6167, with a frequency of Bs of 1.29 showed a lower DNA content in the A genome (5.0 pg) (Table 2).

DISCUSSION

Populational frequencies of Bs—In the indigenous populations of maize studied here, a very high frequency

TABLE 1. B chromosome frequencies and collection data.

Race	Population	Altitude (m)	Number of plants with different doses of Bs (0-8Bs)									Total	Plants with Bs (%)	Mean no. of Bs per plant
			0	1	2	3	4	5	6	7	8			
Blanco	VAV 6479	2180	3	13	9	14	6	5	1		1	52	94.2	2.615
Blanco	VAV 6485	2670	10	10	11	9	2	1		1		44	77.3	1.795
Amarillo grande	VAV 6480	2420	15	12	13	7	2	2	1			52	71.2	1.596
Altiplano	VAV 6167	3000	15	4	9	2	4					34	55.9	1.294
Harinoso	VAV 6475	3240	20	15	8	4	3					50	60.0	1.100
Capia blanco	VAV 6418	2600	24	8	11	1	4					48	50.0	1.020
Amarillo chico	VAV 6451	2000	45	44	9	11	1					110	59.1	0.900
Pisingallo	VAV 6416	2600	20	13	3	2	2	1				41	51.2	0.927
Pisingallo	VAV 6313	1600	100	59	10	13	2					184	45.6	0.685
Capia rosado	VAV 6162	2900	19	14	3					1		37	48.6	0.730
Colorado	VAV 6169	80	25	7	2							34	26.5	0.323
Chiriguano	VAV 6218	2000	22	6	1							29	24.1	0.276
Amarillo chico	VAV 6476	1690	41	7	3							51	19.6	0.255
Blanco y ocho rayas	VAV 6481	750	48	1	5	1						55	12.7	0.255
Amarillo chico	VAV 6484	2010	45		2	2						49	8.2	0.204
Orgullo cuarentón	VAV 6482	910	44	4	1							49	10.2	0.122
Blanco y ocho rayas	VAV 6483	1250	34		2							36	5.5	0.111
Colorado	VAV 6223	80	37	2								39	5.1	0.051
Pichingá	VAV 6170	80	42	1								43	2.3	0.023
Altiplano	VAV 6474	3520	40									40	0.0	0.000
Altiplano	VAV 6473	3620	43									43	0.0	0.000
Total			692	220	102	66	26	9	2	2	1	1120	38.2	

of plants with Bs was found. Of a total of 1120 plants, 428 had 1–8 Bs (38.2%). Nineteen populations out of the 21 studied presented a numerical polymorphism, reaching a maximum of 94% in B frequency for a Blanco population (Table 1). Longley (1938), analyzing the frequency of Bs in 431 plants found 66 with Bs (15.31%). Longley and Kato-Y (1965: Table 2d) studying Latin American races of maize found 95 plants with Bs from a total of 1023 plants (9.3%). Kato (1976: Table 12) found that 46 out of 94 populations of 9 Mexican races of maize exhibited numerical polymorphism for Bs; 86 out 531 plants (16.2%) had Bs with mean population frequencies

varying from 0 to 33%. The frequencies recorded in the present study would be the highest ones if compared with the previous few populational studies carried out on B frequencies in native races of maize.

Relationship between populational frequency of Bs and altitude—The mean number of Bs is positively correlated with altitude of cultivation, when populations with numerical polymorphism for Bs are considered (Fig. 2). Populations cultivated between 1600 and 3240 m have, in general, the higher frequency of plants with Bs (19.6–94.2%), while those cultivated at altitudes lower than 1600 m have the lower frequencies (2–26%) (Table 1, Fig. 1). Porter and Rayburn (1990) did not find this kind of correlation; this could reflect the low number of individuals analyzed (3–5) per population.

In our study, the populations VAV 6473 and 6474 constitute an interesting exception to the correlation found, perhaps because they are cultivated in marginal areas for the common distribution of maize. In *Crepis capillaris*, *Myrmeleotettix maculatus*, and *Trimerotropis pallidipennis* Bs are frequent in those areas “where the species thrive and disappear in circumstances where the burden on fitness is too heavy to bear,” i.e., in marginal environments (Confalonieri, 1995). Perhaps Bs are only tolerated in populations that are not under severe selective stress (Hewitt, 1973; Parker et al., 1991; Confalonieri, 1995). Our results also indicate that the maize B chromosome is tolerated in populations without severe selective pressure.

DNA content of A chromosomes (A-DNA) and altitude—In the 17 populations reported (Table 2) a 36% variation (5.0–6.8 pg) in DNA content of the members of the regular complement (A-DNA) was demonstrated. This range of variation is very high compared with the values of total DNA content reported for 32 populations

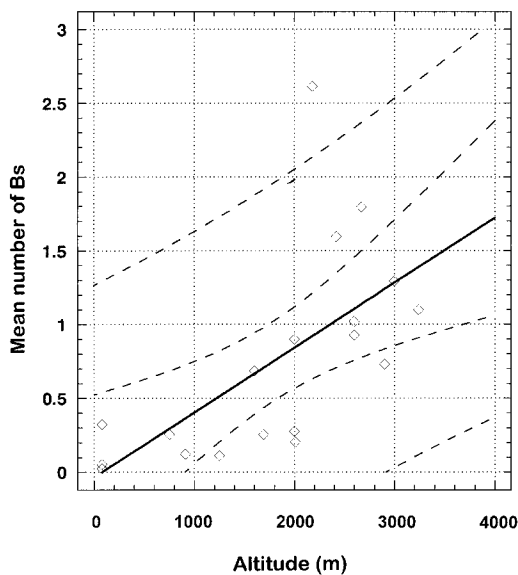


Fig. 2. Correlation of mean number of Bs per plant with altitude in populations polymorphic for B chromosomes ($r = 0.6355$; $P = 0.0035$).

TABLE 2. Individual and mean A-DNA content of plants without B chromosomes.

Race	Population	A-DNA content (pg) (107 individuals)	A-DNA content $\bar{X} \pm SE$ (pg) (total no. of measured nuclei)
Blanco	VAV 6479	6.500; 6.400; 6.240	6.380 \pm 0.076 (60)
Blanco	VAV 6485	5.790; 5.550; 6.050; 6.050 5.840; 5.520	5.800 \pm 0.094 (120)
Amarillo grande	VAV 6480	5.840; 6.050; 5.970; 5.910 6.340; 5.790; 6.600; 6.340	6.105 \pm 0.102 (160)
Altiplano	VAV 6167	4.310; 5.000; 5.440; 5.280	5.008 \pm 0.250 (80)
Harinoso	VAV 6475	6.820; 6.450; 6.510; 6.800 6.280; 5.920; 6.710; 6.440	6.491 \pm 0.106 (160)
Capia blanco	VAV 6418	5.500; 5.710; 5.710; 5.730 5.510	5.632 \pm 0.052 (100)
Amarillo chico	VAV 6451	5.180; 5.230; 5.620; 5.640 5.650; 6.670	5.665 \pm 0.219 (120)
Pisingallo	VAV 6313	5.630; 5.680; 6.510; 5.770 6.060; 5.940; 6.060; 6.380 5.850; 6.350; 6.400; 6.500 6.090; 5.180; 6.130; 6.720 6.790; 6.640	6.149 \pm 0.101 (360)
Capia rosado	VAV 6162	5.430; 5.610; 6.180	5.740 \pm 0.226 (60)
Amarillo chico	VAV 6476	6.090; 6.520; 5.710; 6.850 6.560; 5.960	6.282 \pm 0.176 (120)
Blanco y ocho rayas	VAV 6481	6.520; 6.790; 6.730; 6.860 6.780; 6.860	6.757 \pm 0.052 (120)
Amarillo chico	VAV 6484	6.090; 6.120; 6.880; 6.400 6.570; 6.220; 6.180	6.351 \pm 0.109 (140)
Orgullo cuarentón	VAV 6482	6.290; 6.130; 6.280; 6.270 5.760; 6.160	6.148 \pm 0.082 (120)
Blanco y ocho rayas	VAV 6483	6.446; 6.420; 6.958; 6.580	6.601 \pm 0.124 (80)
Pichingá	VAV 6170	6.000; 6.188; 6.048; 6.450	6.172 \pm 0.101 (80)
Altiplano	VAV 6474	6.250; 6.490; 6.640; 6.500 6.600; 6.460; 6.660	6.514 \pm 0.053 (140)
Altiplano	VAV 6473	6.510; 5.880; 6.160; 7.050 7.050; 6.280	6.488 \pm 0.196 (120)

of maize from USA and Mexico (Laurie and Bennett, 1985; Rayburn, 1990; Rayburn and Auger, 1990a, b; Porter and Rayburn, 1990).

Mangelsdorf and Cameron (1942), Longley and Kato-Y (1965), and Bennett (1976, re-evaluating the data of

Wellhausen et al., 1952) reported a negative correlation between knob content (noncentromeric heterochromatin) and altitude. Our results with populations growing up to 3200 m are in agreement with the negative correlation between knob number and altitude; the knob heterochro-

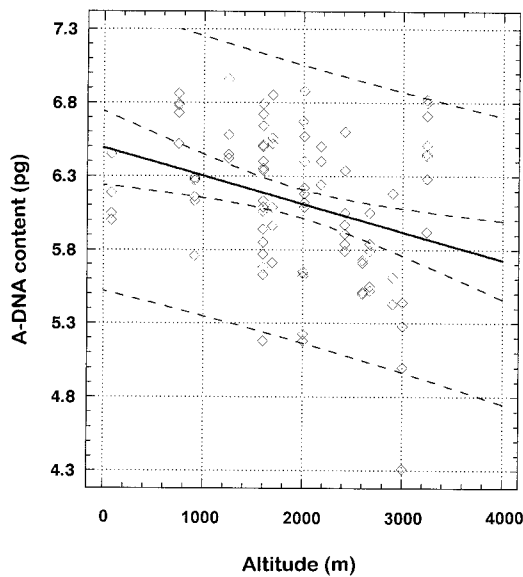


Fig. 3. Correlation of A-DNA content with altitude ($r = -0.3134$; $P = 0.0021$), using the A-DNA values of all individual determinations; VAV 6473 and 6474 were not included (Table 2).

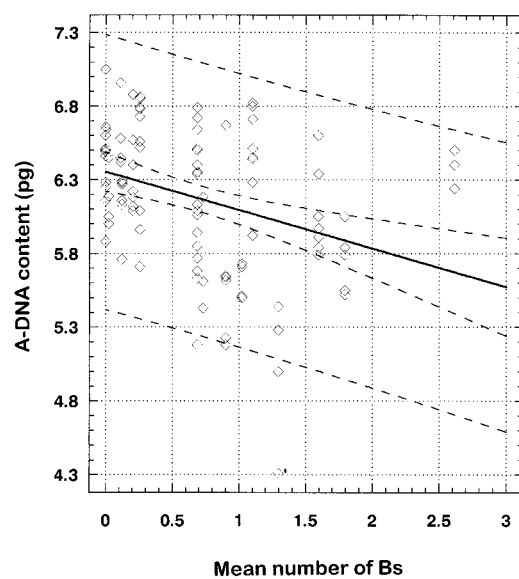


Fig. 4. Correlation of A-DNA content with number of Bs per plant in each population ($r = -0.3392$; $P = 0.00035$), using the A-DNA values of all (107) individual determinations (Table 2).

matin could be the portion of the genome that accounts for part of the conspicuous variation in A-DNA content found in the present study (Tito, Poggio, and Naranjo, 1991). Indeed, we found an increment of heterochromatic content in samples from lower altitudes compared with those of higher altitude (Rosato et al., 1996b).

Several previous studies have analyzed the total DNA content of populations of maize adapted to various altitudes. Rayburn and Auger (1990a) found a negative correlation between total DNA content and altitude (52–2670 m) in four ancient indigenous races of Mexico, while Rayburn and Auger (1990b) found an inverse relationship in 12 Arizona Indian populations, collected from 30 to 1617 m. Rayburn (1990) analyzed the genome size of 12 populations collected in New Mexico. These populations ranged in altitude from 1510–2135 m. A significant negative correlation was observed between genome size and altitude. This author concluded that low genome size appears to be a characteristic of maize from elevations above 1983 m. It is significant that these prior studies considered total DNA content (i.e., DNA of A chromosomes plus DNA of Bs, if they are present). For that reason our results may not be strictly comparable, because we described the DNA content of A chromosomes exclusively.

A-DNA content and populational frequency of Bs—

A significant negative correlation between A-DNA content (measured in 0B individuals) and the mean number of Bs per plant was found (Table 2, Fig. 4). These results suggest that in each race, Bs are tolerated at high frequencies in populations with low A-DNA content.

A similar phenomenon was found by Longley (1938) when analyzing the association between the number of knobs and the occurrence of Bs. He found that Bs are more frequent in plants with fewer than seven knobs in their A chromosomes. Moreover, this negative correlation was found by Bianchi, Ghatnekar, and Ghidoni (1963). Rhoades (1955) suggested that knobs and Bs are two heterochromatic entities that could be playing a similar subvital role.

Conclusions—All populations growing at elevations <3300 m had numerical polymorphism for B chromosomes, and the mean number of Bs was positively correlated with altitude. The negative correlation between A-DNA content and frequency of plants with Bs indicates that Bs are better tolerated in populations with lower A-DNA values. The results indicate that there may be a maximum limit to the mass of nuclear DNA or nucleotype (Bennett, 1987) so that Bs are tolerated as long as this maximum limit is not exceeded. Therefore, higher B frequency is correlated with lower A-DNA content. The clinal variation of A-DNA content and the consequent inverse correlation of B frequencies over an altitudinal gradient could have an adaptative significance for two reasons. (1) The populations analyzed were not distributed over a transect (Fig. 1). They were cultivated by indigenous people and hardly interbreed with each other. Therefore, historical isolation of populations with high and low A-DNA content by genetic drift at both extremes of an altitudinal gradient and subsequent gene flow between them do not constitute a very plausible explana-

tion. (2) Similar patterns of variation were found in several independent groups of populations distributed over distinct geographic areas: Central America, Mexico, and the USA (Mangelsdorf and Cameron, 1942; Longley and Kato-Y, 1965; Rayburn et al., 1985; Rayburn, 1990; Rayburn and Auger, 1990a). These similar types of clinal variation are unlikely to result from stochastic processes.

LITERATURE CITED

- AGUIAR-PERECIN, M. L. R., AND C. G. VOSA. 1985. C-banding in maize II. Identification of somatic chromosomes. *Heredity* 54: 37–42.
- AVDULOW, N. 1933. On the additional chromosomes in maize. *Bulletin of Applied Botany Serie*, 2: 120–130.
- BENNETT, M. D. 1976. DNA amount, latitude and crop plant distribution. In K. Jones and P. E. Brandham, editors. *Current Chromosome Research*, 151–158. North Holland, Amsterdam.
- . 1987. Variation in genomic form in plants and its ecological implications. *New Phytologist* 106 (Supplement): 177–200.
- , AND L. J. LEITCH. 1995. Nuclear DNA amounts in angiosperms. *Annals of Botany* 76: 113–176.
- , AND J. B. SMITH. 1976. Nuclear DNA amounts in angiosperms. *Philosophical Transactions of the Royal Society of London B* 274: 227–274.
- BIANCHI, A., M. V. GHATNEKAR, AND A. GHIDONI. 1963. Knobs in Italian maize. *Chromosoma* 14: 601–617.
- BRETTING, P. K., AND M. M. GOODMAN. 1989. Karyotypic variation in Mesoamerican races of maize and its systematic significance. *Economy Botany* 43: 107–124.
- CARLSON, W. R. 1978. The B chromosome of corn. *Annual Review of Genetics* 12: 5–23.
- , AND R. R. ROSEMAN. 1992. A new property of the maize B chromosome. *Genetics* 131: 211–223.
- , AND T. S. CHOU. 1981. B chromosome nondisjunction in corn: control by factors near the centromere. *Genetics* 97: 379–389.
- CHIAVARINO, A. M., M. ROSATO, C. A. NARANJO, J. CÁMARA-HERNÁNDEZ, AND L. POGGIO. 1995. B chromosome polymorphism in N. Argentine populations of maize. *Maize Genetics Cooperation Newsletter (USA)* 69: 94.
- CONFALONIERI, V. A. 1995. Macrogeographic patterns in B-chromosome and inversion polymorphisms of the grasshopper *Trimerotropis pallidipennis*. *Genetics, Selection and Evolution* 27: 305–311.
- HADLACZKY, G. Y., AND L. KÁLMÁN. 1975. Discrimination of homologous chromosomes of maize with Giemsa staining. *Heredity* 35: 371–374.
- HEWITT, G. M. 1973. Evolution and maintenance of B chromosomes. *Chromosome Today* 3: 208–222.
- JONES, R. N. 1995. Tansley Review Number 85. B chromosome in plants. *New Phytology* 131: 411–434.
- , AND H. REES. 1982. B chromosomes. Academic Press, New York NY.
- KATO-Y, T. A. 1976. Cytological studies of maize (*Zea mays* L.) and Teosinte (*Zea mexicana* Schradе Kuntze) in relation to their origin and evolution. *Massachusetts Agricultural Experiment Station, Bulletin* Number 635.
- LAURIE, D. A., AND M. D. BENNETT. 1985. Nuclear DNA content in the genera *Zea* and *Sorghum*. Intergeneric, interspecific and intraspecific variation. *Heredity* 55: 307–313.
- LONGLEY, A. E. 1927. Supernumerary chromosomes in *Zea mays*. *Journal of Agricultural Research* 35: 769–784.
- . 1938. Chromosomes of maize from North American Indians. *Journal of Agricultural Research* 56: 177–195.
- , AND T. A. KATO-Y. 1965. Chromosome morphology of certain races of maize in Latin American. *International Center for the Improvement of Maize and Wheat (CIMMYT). Chapingo, Mexico, Research Bulletin* 1: 112.
- MANGELSDORF, P. C., AND J. W. CAMERON. 1942. Western Guatemala a secondary center of origin of cultivated maize varieties. *Botanical Museum Leaflet of Harvard University* 10: 217–252.
- MCCLINTOCK, B., T. A. KATO-Y, AND A. BLUMENSCHNEIN. 1981. Constitución cromosómica de las razas de maíz. Su significado en la

- interpretación de relaciones entre las razas y variedades en las Américas. Colegio de Postgraduados. Chapingo, México.
- NARANJO, C. A., A. M. CHIAVARINO, M. ROSATO, E. QUINTELA FERNÁNDEZ, AND L. POGGIO. 1995. Tamaño del genoma y polimorfismo para cromosomas B en razas nativas Argentinas y Bolivianas de maíz. *Proceeding of III Latin American and XVI Anden Zone of Maize Researches Meeting* (Bolivia) Tomo II: 969–980.
- PARKER, J. S., G. H. JONES, L. A. EDGAR, AND C. WHITEHOUSE. 1991. The population cytogenetics of *Crepis capilaris*. IV. The distribution of B-chromosomes in British populations. *Heredity* 66: 211–218.
- PORTER, H. L., AND A. L. RAYBURN. 1990. B-chromosome and C-band heterochromatin variation in Arizona maize populations adapted to different altitudes. *Genome* 33: 659–662.
- RANDOLPH, L. F. 1928. Types of supernumerary chromosomes in maize. *Anatomy Research* 41: 102.
- RAYBURN, A. L. 1990. Genome size variation in Southern United States indian maize adapted to various altitudes. *Evolutionary Trends in Plants* 4: 53–57.
- , AND J. A. AUGER. 1990a. Nuclear DNA content variation in the ancient indigenous races of Mexican maize. *Acta Botanica Neerlandica* 39: 197–202.
- , AND J. A. AUGER. 1990b. Genome size variation in *Zea mays* ssp. *mays* adapted to different altitudes. *Theoretical and Applied Genetics* 79: 470–474.
- , H. J. PRICE, J. D. SMITH, AND J. R. GOLD. 1985. C-band heterochromatin and DNA content in *Zea mays*. *American Journal of Botany* 72: 1610–1617.
- RHOADES, M. M. 1955. History and origin of corn. II. Cytogenetic aspects of the origin and evolutionary history of corn. *In* Corn and improvement, ch. 4. Academic Press, New York, NY.
- ROMAN, H. 1947. Mitotic nondisjunction in the case of interchanges involving the B type chromosome in maize. *Genetics* 32: 391–409.
- . 1948. Directed fertilization in maize. *Proceedings of the National Academy of Sciences, USA*. 34: 36–42.
- ROSATO, M., L. POGGIO, C. A. NARANJO, AND J. CÁMARA HERNÁNDEZ. 1993. Genome size in six races from northwestern Argentina. *Maize Genetics Cooperation Newsletter (USA)* 67: 67–68.
- , A. M. CHIAVARINO, C. A. NARANJO, M. J. PUERTAS, AND L. POGGIO. 1996a. Genetic control of B chromosome transmission rate in *Zea mays* ssp. *mays* (Poaceae). *American Journal of Botany* 83: 1107–1112.
- , J. CÁMARA HERNÁNDEZ, C. A. NARANJO, AND L. POGGIO. 1996b. Relaciones entre el tamaño del genoma, polimorfismo numérico para cromosomas B y altura de cultivo en razas nativas de maíz. *II Jornadas Argentino-Chilena de Genética, Not. Biología (Chile)* 4(3):185.
- TEOH, S. B., AND H. REES. 1976. Nuclear DNA amount in populations of *Picea* and *Pinus* species. *Heredity* 36: 123–137.
- TITO, C. M., L. POGGIO, AND C. A. NARANJO. 1991. Cytogenetic studies in the genus *Zea*. 3. DNA content and heterochromatin in species and hybrids. *Theoretical and Applied Genetics* 83: 58–64.
- WARD, F. J. 1980. Banding patterns in maize mitotic chromosomes. *Canadian Journal of Genetics and Cytology* 22: 61–67.
- WELLHAUSEN, E. J., L. M. ROBERTS, X. HERNANDEZ, AND P. C. MANGELSDORF. 1952. Races of maize in Mexico: their origin, characteristics and distribution. Bussey Institution, Harvard University, Cambridge, MA.

APPENDIX.

ALTIPLANO. Collection material: Salta Province, Santa Victoria Department, from El Puesto, at ~3000 m above sea level, VAV-6167; Jujuy Province, Susques Department, from Susques, at ~3620 m above sea level, VAV-6473; from Mal Paso of Susques, at ~3520 m above sea level, VAV-6474.

AMARILLO CHICO. Collection material: Salta Province, Santa Victoria Department, from El Condado, at ~2000 m above sea level VAV-6451; Jujuy Province, Capital Department, from Termas de Reyes, at ~1690 m above sea level, VAV-6476; Jujuy Province, Tumbaya Department, from Tumbaya, VAV-6484.

AMARILLO GRANDE. Collection material: Jujuy Province, Tumbaya Department, from La Ciénaga of Purmamarca, at ~2420 m above sea level, VAV-6480.

BLANCO. Grain collection: Jujuy Province, Tumbaya Department, from Purmamarca at ~2180 m above sea level, VAV-6479 and Tilcara Department, from Colonia San José, at ~2670 m above sea level, VAV-6485.

CAPIA BLANCO. Collection material: Salta Province, Santa Victoria Department, from Acoyte, at ~2600 m above sea level, VAV-6418.

CAPIA ROSADO. Collection material: Salta Province, San Victoria Department, from Rodeo Pampa, at ~2900 m above sea level, VAV-6162.

CHIRIGUANO. Collection material: Salta Province, Santa Victoria Department, from El Condado, at ~2000 m above sea level, VAV-

6218. Observations: Race **Chiriguano** is only distributed within-Santa Victoria Department, province of Salta. It does not have the ample distribution of other races of the highlands in the provinces of Jujuy and Salta.

COLORADO. Collection material: Formosa Province, Pilcomayo Department, from Frontera and Pilagás Department, from Misión Tacaaglé, both at <100 m above sea level, VAV-6169 and 6223, respectively.

HARINOSO. Collection material: Salta Province, Iruya Department, from Iruya, at ~3400 m above sea level, VAV-6475.

PICHINGA. Collection material: Formosa Province, Pirané Department, from Villa Dos Trece, at <100 m above sea level, VAV-6170.

PISINGALLO. Collection material: Salta Province, Santa Victoria Department, from Acoyte, at ~2600 m above sea level and Catamarca Province, Ambato Department, from Piedras Blancas, Los Tordillos, at ~1600 m above sea level, VAV-6416 and 6313, respectively.

BLANCO Y OCHO RAYAS. Collection material: Salta Province, Metán Department, from Metán Viejo, at ~750 m above sea level, VAV-6481; Tucuman Province, Trancas Department, from Las Arcas, at ~1250 m above sea level, VAV-6483.

ORGULLO CUARENTON. Collection material: Salta Province, Candelaria Department, from La Candelaria, at ~910 m above sea level, VAV-6482.