

that they are not only active chromosomal structures but also that they have highly developed selective values.

There is experimental evidence that the knobs in maize are closely linked to genes controlling the development of different morphological or physiological characteristics. There is also evidence that the presence of knobs reduces recombination in the chromosome segments where they are located, at least when they are present in a heterozygous condition, and that this reduction in recombination is inversely related to the knob size. Consequently, it seems clear that the selective value of a given knob depends on the kind of genes that the knob is closely linked with. The knob itself might be one of the important factors in developing a specific linked gene complex (supergene) since the reduction of recombination, in concert with natural selection, favors the development of gene complexes better co-adapted to the particular sets of factors imposed upon the population by different selective pressures.

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Maize-teosinte introgression — The basic problem is how these two sympatric species intercross freely and yet maintain their specific identities. This study shows how chromosome structures including the knobs can account for this anomalous situation.

It has been found that some knob types present in relatively high frequencies in teosinte populations are absent or nearly so from maize populations that usually grow in close sympatry; however, the knobs in these same positions have been found in relatively high frequencies in the races of maize Zapalote Chico and Zapalote Grande in regions of Oaxaca and Chiapas of southern Mexico, where no teosinte populations have yet been found. This is the case for the knobs at the 4S2, 5S1 and 7S positions in populations of maize and teosinte from Chalco in southeastern state of Mexico and from the Mazatlán area in central Guerrero (Table 1). The single medium knob on 4S2 and the large one on 7S found in maize from Mazatlán are interpreted as having their origin from the Zapalote of Oaxaca rather than from teosinte. There are two main reasons for this conclusion: (1) there is no indication of introgression of these knobs in the Chalco region where it is known that hybridization occurs at a higher frequency than in Guerrero, and (2) the large knobs on 7S were found to be absent in teosinte from the Mazatlán region. These results seem to indicate that at least these knobs are not introgressing between maize and teosinte populations.

On the other hand, the knobs at 1L1 and 3S1 are present in both the maize and the teosinte populations from the Chalco region, but absent in maize and present

Table 1. Knob frequencies for the indicated positions on several chromosomes of maize and teosinte populations from two Mexican regions, Chalco in the southeastern part of the state of Mexico and Mazatlán in central Guerrero, where both plant species grow in close sympatry. The knob frequencies of maize populations from another region are included for comparative purposes.

Species/ region	Collec- tions	Knob position and size																Total chrom
		1L1				3S1				4S2				5S1				
		1	m	s	o	1	m	s	o	1	m	s	o	1	m	s	o	
MAIZE																		
Chalco, Mex.	10	4	5	3	114	3	8	0	115	0	0	0	126	0	0	0	126	126
Mazatlán, Gro.	4	0	0	0	124	0	0	0	124	0	1	0	123	0	0	0	124	124
Oaxaca-Chiapas	13*	0	5	8	135	18	22	7	101	4	29	16	99	17	13	0	118	148
TEOSINTE																		
Chalco, Mex.	14	131	8	2	25	1	21	0	144	31	9	2	124	61	20	1	84	166
Mazatlán, Gro.	5	9	5	1	37	18	1	0	33	12	9	2	29	7	7	0	45	52
		6L2				6L3				7S				7L1				
		1	m	s	o	1	m	s	o	1	m	s	o	1	m	s	o	
MAIZE																		
Chalco, Mex.	10	0	0	4	122	0	1	15	110	0	0	0	126	72	9	1	44	126
Mazatlán, Gro.	4	0	2	28	94	1	28	23	72	1	0	0	123	51	24	4	45	124
Oaxaca-Chiapas	13*	4	49	70	25	0	21	91	36	69	24	7	48	118	19	4	7	148
TEOSINTE																		
Chalco, Mex.	14	0	0	31	135	0	0	20	146	42	27	6	91	131	20	0	15	166
Mazatlán, Gro.	5	0	0	21	31	40	4	0	8	0	2	1	49	45	0	0	7	52

* Collections of the races Zapalote Chico and Zapalote Grande (from unpublished data of McClintock, Blumenschein and Kato)

in teosinte from Mazatlán. It is also known that all 1L1 knob types are frequently found in the Palomero Toluqueño race of maize and that those at the 3S1 position occur in populations from western Mexico, the Bajío region and the Central Mesa where Chalco is located and in the Zapalotes of Oaxaca. Teosinte populations of other regions also possess relatively high frequencies of these knobs; it is therefore difficult to be certain whether the knobs present in maize from Chalco represent introgression from teosinte or not. The fact that these knobs were absent in maize from Mazatlán seems to suggest that the knobs present in Chalco maize are not the result of introgression unless it is argued that in Mazatlán conditions of temporal and spacial isolation exist that prevent hybridization.

The 6L2 and 6L3 positions show knobs suggesting probable introgression in both directions (see the small knobs of 6L2 and the large and medium knobs of 6L3 in Mazatlán material). However, the small knobs of 6L3 in maize from Mazatlán most probably come not from teosinte but from some maize source, such as the Pepitilla race from northern Guerrero or the Zapalote from Oaxaca; considering these knobs introgressive also conflicts with the argument that introgression does not occur in Mazatlán due to differential flowering and/or fertilization.

The knobs at the 7L1 position show that the large size knobs are present in maize (including the Zapalotes) in frequencies similar to those found in teosintes from the two regions considered here; however, data on the smaller knobs indicate that introgression might be occurring in the Chalco region but (again) not in Mazatlán.

It is well known (and confirmed in these studies) that the Guatemalan teosintes have knobs only at the terminal positions of the long and the short arms of their chromosomes. With the exception of the 4S2, 7S and 9S knobs, none are known to occur at the other 14 positions in maize populations from Guatemala or in any other maize populations so far examined. It is also known that maize and teosinte hybridize with some frequency in Guatemala, generally producing highly fertile hybrids, but it seems clear, in spite of this, that no common introgression (of at least 14 chromosomal segments) occurs.

The results given above could be interpreted in at least two ways: (1) No introgression occurs at all between teosinte and maize populations, in spite of the constant formation of fertile hybrids; if so, the isolating mechanism is probably a complex of different components. (2) Different maize and teosinte populations and chromosomal segments behave differently so that populations

growing in one region introgress some chromosomal segments and those of other regions may introgress other segments.

The fact is that the available data show that at least several chromosome segments are not introgressing in populations of maize and teosinte; whether other segments are introgressing or not is a question that is not possible to answer at the present time and further more critical investigations are needed in order to discriminate among different possibilities.

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Abnormal chromosome 10 — Two types of abnormal chromosome 10 are known in teosinte, but only one of these types has been found in maize populations. In the type that is common to both species chromosome 10 has an extra distal segment of chromatin which possesses a large subterminal knob. The second type, which is found only in teosinte populations, differs from the first type only in that the extra segment having the subterminal knob also has a small or medium terminal knob. In order to facilitate the discussion of these two types of abnormal chromosome 10, the first is designated type I and the second, type II.

The geographical distribution and frequencies of the two different types of abnormal chromosome 10 in populations of maize and teosinte from regions of central Mexico are given in Table 1. The frequency with which the abnormal chromosome 10 appears in populations of maize and teosinte is very low; however, the type I abnormal chromosome 10 is scattered in maize populations throughout the whole region concerned. These data also show not only that the type I abnormal chromosome 10 is found in both species and the type II only in teosinte, but also indicates that the two types occur separately in populations of teosinte from different regions. Type I was found only in teosinte plants from eastern and southeastern Michoacan and the western part of the state of Mexico, while type II was found in one collection from southern Guanajuato, in collections from Guerrero and in the Chalco region in southeastern Mexico state. This differential distribution of these chromosome types in teosinte might indicate that they possess genetic constitutions which make each of them become better co-adapted to gene complexes of different populations growing under different environments.

When the data from maize and teosinte are compared, especially those from Chalco in the state of Mexico and from Mazatlán in central Guerrero, it becomes clear that these chromosomal segments are not introgressing from maize to teosinte or vice versa. Therefore, the fact that both types of abnormal