

The non-shattering rachis becomes semi-lethal in teosinte because it inhibits seed dispersal. But the reciprocal condition, partial abscission layers in the corn cob, may be tolerated because a comparatively high level of condensation in corn prevents complete rind abscission through a fusion of the apex of the cupule to the glume cushion above. Pith abscission is ineffectual in the absence of complete rind abscission, so modern corn can cope with some gene flow from teosinte for these two abscission factors because of their usual neutral effect on the corn cob.

The reduction in crossing over between Su and G13 in this segregation from the usual 34 percent to 20 percent is interpreted as being due to interference from a small heterozygous inversion.

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Adaptiveness of knobs in teosinte — The chromosome knob constitutions of 310 plants from 54 collections of Mexican teosinte and 88 plants from 7 collections of Guatemalan teosinte have been determined. The analysis of the regional distribution of knob types showed that they occur in combinations that are characteristic for each population.

There are two general knob categories in Mexico: (1) knobs that are widely distributed in almost all local populations, and (2) knobs that have a more specific regional distribution; furthermore, within each of these groups the knobs of different size generally do not show the same frequencies within and between regions. Some of the data illustrating these points are given in Tables 1 and 2 in terms of the relative frequencies found in each of the geographical regions.

The knobs found at the 3L1, 5L1 and 9S positions are representative of the first group. The 5L1 position is predominated by the large knobs in all regions except Nobogame in northern Mexico; the medium knobs and the knobless positions are always present but in relatively lower frequencies than the large knobs. On the other hand, although all the regional populations have knobs in the 3L1 and the 9S positions, their frequency varies according to the region. The 3L1 position is predominated by large knobs in the Chalco region; in the regions of Guerrero-S.E. Michoacan-W. Mexico, this position is predominantly knobless. There are higher knob frequencies in the Guanajuato-N. Michoacan region than in the regions farther south where the large and medium knobs and the knobless

Table 1. Relative frequencies (percent of the total number of chromosomes examined) for the different knob types found at the indicated positions in teosinte populations from various Mexican regions. The number of collections used from each region is given in the last column.

Region	Knob position and size												Total	Coll.
	3L1				5L1				9S					
	l	m	s	o	l	m	s	o	l	m	s	o		
Nobogame	3.1			96.9	15.6		6.2	78.1	6.2		3.1	90.6	32	2
Gto.-N.Mich.	40.7	23.7	0.8	34.7	73.7	11.8		14.4	13.5	10.1	8.4	67.8	118	12
N.E.Mich.	71.4	3.6		25.0	85.7	7.1		7.1	10.7	7.1	14.3	67.8	28	3
E.Mich.-W.Mex.	5.1	10.2		84.7	63.2	7.1		29.6	62.2	10.2	5.1	22.4	98	9
Huetamo, Mich.	2.0	10.0	2.0	86.0	90.0	4.0		6.0	80.0	6.0	2.0	12.0	50	4
N. Guerrero	31.6	14.5	1.3	52.6	75.0	13.1		11.8	50.0	13.1	10.5	26.3	76	5
Central Gro.	9.6	3.8		86.5	71.1	1.9		26.9	51.9	13.4	3.8	30.8	52	5
Chalco, Mex.	79.5	6.0	1.8	12.6	80.1	9.6		10.8	51.8	7.8	3.0	37.3	166	14
	4S2				5S1				9L2					
	l	m	s	o	l	m	s	o	l	m	s	o		
Nobogame				100.0				100.0				100.0	32	2
Gto.-N.Mich.	0.8			99.1				100.0	13.5	16.1	7.6	62.7	118	12
N.E.Mich.			3.6	96.4	25.0			75.0	7.1		10.7	82.1	28	3
E.Mich.-W.Mex.		2.0	7.1	90.8		2.0		97.9		4.1	3.0	92.8	98	9
Huetamo, Mich.	14.0	30.0	16.0	40.0	2.0			98.0			4.0	96.0	50	4
N. Guerrero	9.2	18.4	3.9	68.4	2.6			97.3	7.9	15.8		76.3	76	5
Central Gro.	23.1	17.3	3.8	55.8	13.4			86.5	3.8			96.1	52	5
Chalco, Mex.	18.7	5.4	1.2	74.7	36.7	12.0	0.6	50.6				100.0	166	14
	1L1				6L1									
	l	m	s	o	l	m	s	o						
Nobogame			46.9	53.1				100.0					32	2
Gto.-N.Mich.	47.4	16.9	5.1	30.5	18.6	8.5		72.9					118	12
N.E.Mich.	57.1	14.3		28.6	10.7	7.1		82.1					28	3
E.Mich.-W.Mex.				100.0				100.0					98	9
Huetamo, Mich.	4.0	4.0	6.0	86.0				100.0					50	4
N. Guerrero		11.8	11.8	76.3				100.0					76	5
Central Gro.	17.3	9.6	1.9	71.1			1.9	98.1					52	5
Chalco, Mex.	78.9	4.8	1.2	15.0	76.5	6.6	1.2	15.7					166	14

Table 2. Relative frequencies (percent of the total number of chromosomes examined) for the different knob types found at the 2L2, 5S2 and 8S terminal positions in teosinte populations from northern and southern Guatemalan regions. The number of collections from each region is given in the last column.

Region	Knob position and size												Total Coll.	
	2L2				5S2				8S					
	l	m	s	o	l	m	s	o	l	m	s	o		
Northern Guatemala	1.9	15.4	36.5	46.1	71.1	11.5	1.9	15.4	61.5	21.1	5.8	11.5	52	3
Southern Guatemala	47.2	13.9	11.1	27.8	69.4	5.5	2.8	22.2				100.0	36	4

positions are present in similar frequencies. In Chalco, large knobs occur at relatively high frequencies in the 3L1, 5L1 and to a lesser extent in the 9S position. In the Guanajuato-N. Michoacan region the large knobs are even lower in frequency in the 9S position but remain high in the 3L1 and 5L1 positions. In the S.E. Michoacan-Mexico-Guerrero region the reverse situation occurs, with a high frequency of large knobs in the 9S position and a low frequency in the 3L1 position. Nobogame teosinte is almost knobless in all positions.

Three positions are given illustrating the second group of knobs. The 4S2 and 5S1 positions illustrate the case where teosinte from the Chalco region has shown knobs at these positions, while the Guanajuato-N. Michoacan populations are usually knobless in these positions. In the Guerrero-S.E. Michoacan-W. Mexico region knobs were present at 4S2 in rather low frequencies and almost entirely lacking at the 5S1 position. In this regard the 9L2 position seems to show a reverse situation with relation to the knob distribution at the 4S2 and 5S1 positions. The knobs are present in Guanajuato-N. Michoacan and also (in an irregular fashion) throughout the Guerrero-S.E. Michoacan-W. Mexico region but are completely absent in populations from the Chalco region.

The 1L1 and 6L1 positions illustrate another pattern. Teosinte populations from both the Chalco region and the Guanajuato-N. Michoacan region exhibit a high frequency of knobs, especially the large knobs, while the plants from other regions either have completely knobless chromosome segments (as for 6L1) or carry a mixture of knobbed and knobless segments (as in the 1L1 position).

Three general knob distribution patterns were found in northern and southern Guatemala (Table 2). One of the patterns is exemplified by the terminal knobs in the 2L2 position. In the northern teosintes the knobless condition predominates, and the frequencies go down as the knob size increases; whereas in the south the situation is reversed, with a predominance of the large knobs. The second pattern is illustrated by the knobs at the 5S2 position; teosinte populations from both regions show similar tendencies in the relative frequencies of their knobs. The third pattern is illustrated by the knob data from the 8S position; in the northern region the large knobs usually predominate with variable but always lower frequencies for other knob types, while in the southern populations the knobs are absent.

These results seem to show quite clearly that the knobs found at different positions on the chromosomes are not distributed at random among the teosinte populations of different regions. This non-randomness would seem to indicate

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