CRYPTIC GENES FOR "TRIPSACOID" CHARACTERISTICS IN *MAÍZ AMARGO* OF ARGENTINA AND OTHER LATIN-AMERICAN VARIETIES

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The evidence that modern cultivated maize is a complex hybrid, the product not only of repeated racial crossing within the species but also with teosinte and *Tripsacum*, if not conclusive it at least extensive. The evidence for this, derived not from one source but from several: archaeology, morphology, genetics, cytology, and systematics, was summarized several years ago (Mangelsdorf, 1961). Since then additional data bearing on the problem have been presented. The prehistoric wild corn, uncovered in archaeological sites in once-inhabited caves in the Valley of Tehuacán in México, appears to be ''pure'' maize. This early maize lacks the ''tripsacoid'' characteristics, especially induration of the tissues of the rachis and lower glumes, which are introduced into maize when it hybridizes with its relatives, teosinte and *Tripsacum*. Maize with these characteristics began to make its appearance in the Tehuacán sites sometime between 2300 and 1500 B.C. Soon thereafter an explosive evolution occurred which may have involved not only genetic recombination but also the mutagenic effects induced by the introduction of foreign germ plasm (Mangelsdorf *et al.*, 1964). Galinat (1963) and Sehgal (1963) have studied the morphological effects of extracted teosinte and ''*Tripsacum*'' chromosomes introduced into the inbred strain A158. Sehgal and Brown (1965) and Johnston (1966) have shown that a number of the inbred strains employed in the production of hybrid corn in the Corn Belt of the United States have characteristics of the rachis and spikelets, revealed by anatomical studies of sections of the cobs, which are similar to those found in modified inbred strains in which chromosomes or parts of chromosomes have been replaced by corres-

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ponding chromosomes or parts of chromosomes of teosinte. Wilkes (in press) in an extensive study of teosinte in México, Guatemala, and Honduras has found that natural hybridization between maize and teosinte occurs even more frequently than had previously been supposed. That there has been and still is extensive introgression of teosinte into maize is no longer to be seriously doubted.

Less conclusive is the evidence of introgression of *Tripsacum* into maize. Chromosomes having effects similar to those of teosinte can be extracted from Latin-American varieties including those of South America. Since teosinte does not occur in South America, we concluded (Mangelsdorf and Reeves, 1959) that such chromosomes are the product of introgression of *Tripsacum* which occurs over a considerable range in South America.

The experiments reported in this paper are concerned with an attempt to determine whether chromosomes extracted from modern Latin-American varieties, which induration of the tissues of the rachis and lower glumes, also carry genes for other characteristics such as distichous spikes and solitary pistillate spikelets which were derived from *Tripsacum* but whose effects are ordinarily concealed because they cannot be phenotypically expressed in genotypes which consist predominately of maize germ-plasm. The experiments are based on an observation made some years ago (Mangelsdorf, 1952) of hybrids of teosinte and the unmodified inbred strain, 4R3, and hybrids of teosinte and a modified strain of 4R3 in which a chromosome of maize had been replaced by a chromosome of teosinte. The F_1 hybrid ears of these two crosses differed strikingly in several characteristics. The hybrid involving the original 4R3 had four-ranked ears and paired spikelets while the one involving the modified strain of 4R3 had two-ranked ears and single spikelets. This simple experiment demonstrated that the strain which had been modified by teosinte introgression carried concealed genes for these two teosinte characteristics although it did not itself exhibit them. This suggested that perhaps cryptic genes governing two of the principal botanical characteristics which distinguish *Tripsacum* and teosinte from maize, distichous spikes and solitary pistillate spikelets, might be detected in crosses of teosinte with inbred strains modified by the introduction of extracted chromosomes from Latin-American varieties.

In 1964 we crossed a number of inbred strains of corn by a variety of teosinte from Guerrero, México. A single plant of teosinte provided the pollen for all of the crosses. The inbred strains of maize comprised four distinct groups: (1) A158, the control; (2) strains of A158 modified by the introduction of chromosomes or parts of chromosomes from Florida, Durango, and Nobogame teosinte; (3) strains of A158 modified by the introduction of chromosomes, affecting the induration of the tissues of the rachis and glumes, from modern Latin-American varieties; (4) Strains of A158 modified by chromosomes from two different Latin-American varieties, affecting the induration of the tissues of the rachis and glumes, introduced into one strain.

SOURCES OF THE CHROMOSOMES MODIFYING THE STRAINS

The chromosomes with tripsacoid effects which are involved in modifying the strains of A158 employed in these experiments were derived from nine different Latin-American varieties. Brief descriptions of each of these follow: They are arranged in sequence from north to south with respect to their place of origin.

México 1077. A yellow flint corn received in 1946 from Dr. E. J. Wellhausen designated as Chihuahua Nº 6; apparently related to the race, *Onaveña,* of Sonora, described by Wellhausen *et al.* (1952), who suggested that it is the product of introgression of the race, *Raventador,* into the race, *Maíz Blando.*

Cuba 394. Received from David Sturrock, Cienfuegos, Cuba, in 1941. A typical Cuban flint with orange-yellow endosperm related to the race, *Argentino,* described by Hatheway (1957).

Honduras 1639. Received in 1949 from Dr. Loring Jones under the name, *Maíz Negro;* collected from an altitude of *ca* 200 feet near Marcovia, Department of Choluteca. This is a maize with purple aleurone color related to the race *Maíz Negro de Tierra Caliente* of Guatemala described by Wellhausen *et al.* (1957).

Nicaragua 501. Received in 1941 from Masatepe, Department of Carazo. Like Honduras 1639, this is a maize with aleurone color and is related to *Maíz Negro de Tierra Caliente* of Guatemala.

Venezuela 1536. Received in 1949 from Dr. D. G. Langham under the name, *Criollo,* from Merida. A yellow flint corn probably related to the race, *Costeño,* of Colombia and Venezuela described by Roberts *et al.,* (1957) and Grant *et al.,* (1963).

Bolivia 1157. Received in 1957 from Dr. H. C. Cutler, collected near Reyes, Bolivia. A nine-rowed ear with bronze aleurone color related to the race, *"Interlocked Soft Corn"* of Brazil (Brieger *et al.,* 1958), *Piricinco* of Perú (Grobman *et al.,* 1961), and *Coroico* of Bolivia (Ramírez *et al.,* 1960).

Brazil 1691. Received in 1948 from Dr. F. G. Brieger. A fairly typical ear of the race *Southern Cateto,* described by Brieger *et al.* (1958).

Paraguay 333. Received from Dr. H. C. Cutler under the name *Mais tupi* collected near Concepción, Paraguay. A white seeded flint corn similar to the *Cristal Paraguay* described by Brieger *et al.* (1958).

Argentina 1807. Received in 1951 under the name, *Maíz Amargo,* from Ing. Urbana F. Rosbaco who described its culture in the province of Entre Ríos (1951).

The cobs of this maize are the most tripsacoid that we have encountered in a modern variety and are quite similar to certain segregates in our experimental maize-teosinte and maize-*Tripsacum* hybrids. A much larger number are shown in his own article. Brieger *et al.* regard all types of *Maíz Amargo* as "extracts" of *Calehaqui White Flint* and the two races may well be related. However, none of the ears illustrated by them of this and related races approach the *Maíz Amargo* of Entre Ríos in their extreme tripsacoid characteristics.

This maize is called "amargo" because it is somewhat resistant to the attacks of grasshoppers, presumably because it is unpalatable to them. Horowitz and Marchioni (1940) suggested some years ago that the resistance might be the result of previous hybridization with *Tripsacum*. The data from our experiments lend support to this suggestion.

It is significant in this connection that the cytoplasmic male sterility described by Gini (1939) was derived from *Maíz Amargo.* According to Lewis (1941) cytoplasmic male sterility is the most common cause of male sterility in species hybrids. Most of the cases of cytoplasmic male sterility described in Edwardson's review (1956) were derived from intergeneric, interspecific, or interracial crosses. Duvic (1965) considers it reasonable to hypothesize that the two types of cytoplasmic sterility found in corn may be evidence of interspecific or intergeneric crosses at some time in the past.

Also significant is the fact that four of the nine sources of tripsacoid chromosomes involved in these experiments are races from the lowlands of South America described by Brieger *et al.* Although these authors were skeptical of the existence of tripsacoid characters, they did recognize that some of these races have "very hard cobs which are highly sclerenchymatized including the rachis flaps and the horny parts of the glumes". These are exactly the characteristics which we have regarded as resulting from previous introgression and they are also the characteristics which we employed to identify the chromosomes of Latin-American varieties which we introduced into the inbred A158.

In the majority of first generation hybrids between A158 and "tripsacoid" races, half or more of the ears exhibit the tripsacoid characteristics of the parent but less than half show these characteristics to the same degree as the parents. This situation is repeated in subsequent generations. An obvious explanation is that plants in open-pollinated populations are usually heterozygous for tripsacoid chromosomes and that crossing over produces gametes transmitting only part of the chromosomes or blocks of genes involved. It is significant in this connection that of the nine modified strains of A158 involving chromosomes from Latin-American varieties six have white cobs although A158 itself has red cobs. This shows that the tripsacoid characteristics are borne on chromosome 1 on which the gene for white cob occurs.

The question which we now ask is whether these visible characteristics, induration of the rachis and glumes which we have introduced into A158, are associated with other characteristics of teosinte or *Tripsacum* which are ordinarily concealed but which might be detected in crosses with teosinte.

Ears representing the first three lots mentioned above are illustrated by Sehgal (1963) and the tripsacoid characters of the second and third groups are shown in the longitudinal sections of cobs illustrated in his Figs. 10 and 11.

The modified strains in group 4 were developed by intercrossing the strains in group 3 and selecting in the F_2 generation segregates which were more extreme in their characteristics than either of their two parental strains.

The F_1 hybrids of the crosses of these four groups with Guerrero teosinte were grown in hills of five plants each at the Waltham Field Station in 1965. Since previous experience had shown that such hybrids ordinarily do not flower until October and in some seasons are killed by frost before flowering, all plants were subjected to short-day traetment by covering them for 14 hours each day with large metal cans until floral development of the tassel had been induced. When the tassel was visible to the naked eye in a longitudinal section of a stalk which was sacrificed for the purpose of determining floral initiation the short-day treatment was stopped.

The data which are set forth in Table 1 are concerned with the characteristics of the lateral spikes and represent averages of five spikes from each cross. The length of the staminate and pistillate portions of the spikes are based on actual measurements. The remaining data represent arbitrary grades on the number of ranks, frequency of single spikelets, and fragility of the rachises. A score of 0 represents the most maize-like condition and a score of 4 the most tripsacoid. The final column represents the total tripsacoid score obtained by combining the separate scores.

TABLE I. — Characteristics of the lateral spikes of crosses of Guerrero teosinte with the inbred strain A158 and modified strains with substituted chromosomes from teosinte and from Latin-American varieties.

Pistillare Parrot	*Length of spike, cm.*			*Grades of "Tripsacum" Influence*			
	♀	♂	*Percent ♂*	*Rank*	*Pairing*	*Fragility*	*Total*
A158	9.8	8.6	47	2.2	0.6	0.6	3.4
Florida 3	8.8	9.6	52	4.0	2.2	1.2	7.4
Florida 1, 3, 9	9.4	12.2	68	2.2	1.4	0.2	3.8
Florida 4	7.4	13.0	64	4.0	2.6	3.0	9.6
Durango 1, 7, 9	6.0	12.8	68	3.0	2.4	3.2	8.6
Nobogame 4A	7.6	4.4	37	2.8	1.8	3.6	8.2
Nobogame 4B	1.2	2.6	68	2.4	2.8	3.8	9.0
Average	6.7	9.1	58	3.1	2.2	2.5	7.8
Mexico 1077	7.8	11.4	59	1.6	1.2	2.0	4.8
Mexico 1077	7.8	10.1	56	2.8	1.8	3.8	8.4
Honduras 1639	8.2	20.6	72	4.0	3.0	2.0	9.0
Nicaragua 501	6.8	13.6	67	2.2	3.6	2.0	7.8
Cuba 394	8.6	10.0	54	2.8	2.4	2.0	7.2
Brazil 1691	2.4	11.4	83	4.0	3.0	3.0	10.0
Paraguay 333	6.0	12.4	67	4.0	2.6	2.4	9.0
Argentina 1807	8.0	14.4	64	3.0	3.0	2.0	8.0
Bolivia 1157	9.6	9.2	49	2.6	2.0	3.0	7.6
Average	7.2	12.6	63	3.0	2.5	2.5	8.0
Mex. - Ven.	9.4	6.6	42	2.0	1.8	2.2	6.0
Hond. - Nic.	7.4	19.2	72	4.0	3.2	2.4	9.6
Nic. - Braz.	7.2	10.0	58	3.6	3.0	3.8	10.4
Bol. - Arg.	7.2	15.2	68	4.0	3.2	2.4	9.6
Average	7.8	12.8	60	3.4	2.8	2.7	8.9

An examination of the data in Table 1 reveals the following facts:

(1) There is strong correlation between the objective data based on actual measurements of the staminate and pistillate portions of the spike and the arbitrary grades. This indicates that the latter, although to some degree subjective, are also to some degree valid.

(2) Every hybrid involving a modified strain of A158 is more tripsacoid in one or more characteristics than the control. Seventeen of the 19 crosses are more tripsacoid in both measurements and grade.

(3) The chromosomes from Latin American varieties are on

the whole about as strong in their effects as the chromosomes introduced into A158 directly from teosinte.

(4) The chromosomes from South American varieties: Bolivia, Argentina, Brazil, and Paraguay are on the average slightly stronger in their tripsacoid effects than those from México. The difference, however, is of doubtful significance.

(5) The crosses involving modified strains of A158 in which chromosomes or parts of chromosomes had been introduced from two Latin-American varieties were slightly more tripsacoid on the average than those involving only one variety.

Comparing the lateral spikes of the crosses A158 Guerrero teosinte with a comparable cross of a modified strain of A158 involving a chromosome from the *Maíz Amargo* of Argentina, the latter differs from the control in having a larger proportion of its length bearing staminate spikelets, in being two instead of four ranked, and in bearing solitary instead of paired spikelets. Indeed this spike might well be mistaken for a spike of *Tripsacum* itself. Considered with the data presented in Table 1 it provides rather convincing evidence that chromosomes with tripsacoid effects extracted from *Maíz Amargo* and other South American races also carry cryptic genes for some of the principal botanical characteristics which distinguish maize from its relatives, teosinte and *Tripsacum*.

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