

TRIPSACUM-MAIZE INTERACTION: A NOVEL CYTOGENETIC SYSTEM¹

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ABSTRACT

The genera *Zea* and *Tripsacum* cross readily when they are not isolated by gametophytic barriers, and it has been postulated that intergeneric introgression played a role in the evolution of maize. The basic $x = 9$ *Tripsacum* and $x = 10$ *Zea* genomes have little cytological affinity for each other in hybrids that combine 10 *Zea* with 18 *Tripsacum* chromosomes. However, one to four *Tripsacum* chromosomes sometimes associate with *Zea* chromosomes in hybrids between *Z. mays* ($2n = 20$) and *T. dactyloides* ($2n = 72$). These hybrids with 10 *Zea* and 36 *Tripsacum* chromosomes frequently produce functional female gametes with 36 *Tripsacum* chromosomes only. When they are pollinated with maize, their offspring again have 36 *Tripsacum* and 10 maize chromosomes, but the *Tripsacum* genome is contaminated with maize genetic material. In these individuals, intergenome pairing is the rule, and when they are pollinated with maize, their offspring have 36 *Tripsacum* and 10, 12, 14, 16, 18, or 20 *Zea* chromosomes. Plants with 36 *Tripsacum* and 20 *Zea* chromosomes behave cytologically as allopolyploids, although the *Tripsacum* genome is contaminated with maize, and one basic maize genome is contaminated with *Tripsacum* genetic material. When they are pollinated with maize, offspring with 18 *Tripsacum* and 20 *Zea* chromosome are obtained. Further successive backcrosses with maize selectively eliminate *Tripsacum* chromosomes, and eventually plants with $2n = 20$ *Zea* chromosomes are recovered. Many of these maize plants are highly "tripsacoid." Strong gametophytic selection for essentially pure *Zea* gametes, however, eliminates all obvious traces of *Tripsacum* morphology within a relatively few generations.

Cultivated maize (*Zea mays* L.) is an unusual grass. Its female inflorescence has no morphological counterpart anywhere in the family Gramineae. ASCHERSON (1875) proposed that maize is domesticated teosinte (*Z. mays* ssp. *mexicana* (Schrad.) Iltes), a wild grass of Mesoamerica with which it crosses to produce fertile hybrids (cf. also BEADLE 1939; GALINAT 1971; de WET and HARLAN 1972; BEADLE 1972). MANGELSDORF and REEVES (1939) concluded, however, that no evolutionary force is known that could change a teosinte spike into a complex maize ear, and postulated that domesticated maize must have been derived from a wild grass that resembled a modern maize in female inflorescence structure. This conclusion is supported by available archeological evidence (MANGELSDORF, MACNEISH and GALINAT 1964); at least, the oldest known archeological race of maize from Tehuacan is morphologically maize and not teosinte.

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MANGELSDORF and REEVES (1939) postulated that teosinte probably originated as a byproduct of hybridization between early domesticated maize and a species of the widely distributed American Maydinae genus *Tripsacum*. REEVES and MANGELSDORF (1959) proposed that this interaction could have taken place much earlier when wild maize was more fertile with *Tripsacum* than is modern maize. However, GALINAT (1970), and DE WET, HARLAN and GRANT (1971) demonstrated experimentally that such a hybrid origin for teosinte is highly unlikely. Be that as it may, MANGELSDORF (1961, 1968) concluded that although not conclusive, evidence at least is extensive 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*". SEHGAL and BROWN (1965), and JOHNSTON (1966) demonstrated the presence of teosintoid traits in corn belt maize of the United States, and WILKES (1967, 1970) indicated that maize still introgresses with teosinte in Mexico. Evidence that *Tripsacum* played a role in the evolution of modern maize, however, is less conclusive. Disregarding the postulate of MANGELSDORF (1961) that hybridization between maize and teosinte is actually "secondary introgression from *Tripsacum*", stated evidence of natural gene exchange between *Zea* and *Tripsacum* is of doubtful significance. Introgression of teosinte into maize is recognized by an increase in induration of glume and rachis tissues (cf. MANGELSDORF 1961). Several races of South American maize are highly teosintoid (ROBERTS *et al.* 1957). Since teosinte is absent from South America, and since these races are not closely related to teosintoid Mesoamerican maize, MANGELSDORF (1968) postulated that they must have received their teosintoid characteristics through direct introgression with local races of *Tripsacum*.

Attempts by MANGELSDORF and REEVES (1939) to transfer *Tripsacum* genes to modern maize met with little success. They crossed tetraploid ($2n = 36$) *T. dactyloides* (L.) L. and *T. floridanum* Porter and Vasey with maize ($2n = 20$). These hybrids were female fertile, and when backcrossed with maize, the cytologically unreduced female gamete functioned sexually to produce offspring with 20 maize and 18 *Tripsacum* chromosomes. In these offspring the maize chromosomes formed mostly 10 bivalents during meiotic prophase, with the *Tripsacum* chromosomes present as univalents. Only rarely was association of maize and *Tripsacum* chromosomes observed. In any case, *Tripsacum* chromosomes were rapidly eliminated in later backcrosses, and plants with $2n = 20$ maize chromosomes were eventually recovered. Except for "a perceptible trace of *Tripsacum* influence" in a few plants, recovered maize were "normal corn plants differing in no way from ordinary corn plants, although half of their parentage was contributed by *Zea* chromosomes from the triploid hybrid" (REEVES and MANGELSDORF 1939). Later, MAGUIRE (1961) demonstrated that a piece of *Tripsacum* chromosome can be transferred to the maize genome, and REEVES and BOCKHOLD (1964) claimed to have modified a maize inbred through experimental introgression with *Tripsacum*.

Hybrids between octaploid *T. dactyloides* ($2n = 72$) and maize, produced by MANGELSDORF and REEVES (1939), were completely sterile. Attempts by RANDOLPH (1952) to cross other species of *Tripsacum* with maize failed. We have

now succeeded in crossing *T. floridanum* ($2n = 36$), *T. dactyloides* ($2n = 36, 72$), *T. pilosum* Scribn. and Merr. ($2n = 72$), and *T. lanceolatum* Rupr. and Fourn. ($2n = 72$) with maize, using either genus as the female parent. The major barrier to crossing between *Zea* and *Tripsacum* seems to be gametophytic in nature, and by selecting compatible parents all taxa of these genera can probably be crossed with each other.

BREEDING BEHAVIOR OF MAIZE-TRIPSACUM HYBRIDS

Genus *Zea* includes *Z. mays* (cultivated maize) and *Z. mays* ssp. *mexicana* (teosinte), both diploids with $2n = 20$, and *Z. perennis* (Hitchc.) REEVES and MANGELSDORF ($2n = 40$). Teosinte is widely distributed in Mesoamerica (WILKES 1967), and *Z. perennis* is known from the type locality near *ciudad Guzman* only (COLLINS 1921). Genus *Tripsacum* includes some nine species (CUTLER and ANDERSON 1941; HERNANDEZ and RANDOLPH 1950; RANDOLPH 1970) with chromosome numbers of $2n = 18, 36, 54, 64$, and 72 . *Zea* is characterized by male terminal inflorescences, and lateral inflorescences that are either female, or with a male section above each female branch. In *Tripsacum* both terminal and lateral inflorescences are bisexual, with male spikelets arranged above the female ones on each inflorescence branch. Wild species of *Zea*, and all species of *Tripsacum*, are further characterized by solitary fertile pistillate spikelets that are alternately arranged in sunken cavities of hardened rachis joints, with each cavity covered by the indurated lower glume. Rachis joints articulate at maturity with the caryopsis tightly enclosed in the fruit case. Female inflorescences of cultivated maize are modified into ears consisting of four or more pairs of fertile pistillate spikelets arranged in shallow cupules around, and along, a central core (cf. GALINAT 1970).

Hybrids combining 10 *Zea mays* (*Zm*) chromosomes with 18, 36 and 72 *T. dactyloides* (*Td*) chromosomes, and hybrids combining 20 *Zm* with 36 *Td* chromosomes were studied cytogenetically (DE WET *et al.* 1972a, DE WET *et al.* 1972b). All hybrids resemble *Tripsacum* more than *Zea* with respect to gross inflorescence morphology, no matter how many haploid *Zea* and *Tripsacum* genomes are involved (NEWELL and DE WET, 1973).

The basic genomes of *Tripsacum* ($x = 9$) and *Zea* ($x = 10$) have little cytological affinity for each other in hybrids that combine 18 *Td* + 10 *Zm* chromosomes. However, one, or at most two, *Zm* chromosomes can form loose bivalents with *Td* chromosomes during meiotic prophase, and segmental interchange occasionally takes place between a *Td* chromosome and chromosome 2 of maize (cf. also MAGUIRE 1961, 1965).

The *Tripsacum* chromosomes in most hybrids with 36 *Td* and 10 *Zm* chromosomes associate into bivalents during meiotic prophase, with the *Zm* chromosomes present as univalents. In some hybrids, however, the 10 *Zm* chromosomes also form bivalents (HARLAN *et al.* 1970), and in others 1-4 *Zm* chromosomes occasionally associate with *Td* chromosomes to form intergenomic bivalents and trivalents. Cytologically it would appear as if four different *Tripsacum* chromosomes can associate with maize chromosomes 2, 4, 7 and 9 respectively. These *Td*

chromosomes have as yet not been positively identified. However, it is significant to note that GALINAT (1971) lists several genes in common, respectively, between *T. dactyloides* chromosomes 4, 5 and an unidentified chromosome, and maize chromosomes 2, 9 and 7.

Hybrids with 72 Td + 10 Zm chromosomes are characterized mostly by maize univalents during meiotic prophase, with the Td chromosomes behaving essentially as they did in the *Tripsacum* parent. Occasionally, however, as many as eight Zm chromosomes associate with Td chromosomes, forming bivalent or multivalent configurations. Hybrids with 36 Td + 20 Zm chromosomes behave cytologically as allopolyploids. The 36 Td chromosomes form 18 bivalents and the 20 Zm chromosomes form 10 bivalents during meiotic prophase, and later cytological stages of sporogenesis are completely regular.

Hybrids produced by us are male sterile but are female fertile when backcrossed with maize. Depending on the genetic constitution of the *T. dactyloides* parent, hybrids range from pseudogamous obligate gametophytic apomicts to fully sexual. Hybrids with 72 Td + 10 Zm chromosomes are essentially obligate apomicts, while hybrids combining 18 or 36 Td with 10 or 20 Zm chromosomes are usually at least partially sexual.

Hybrids with 18 Td + 10 Zm chromosomes behave cytogenetically as described by MANGELSDORF and REEVES (1939) and CHAGANTI (1965). When they are pollinated with maize, offspring having 18 Td + 20 Zm chromosomes are obtained. When these are again backcrossed with maize, Td chromosomes are selectively eliminated and most offspring have 0-4 Td and 20 maize chromosomes. Two or more successive further backcrosses give rise to plant with only maize chromosomes. These recovered maize populations are phenotypically pure maize. We could induce no obvious introgression from *Tripsacum* into maize through hybridization with tetraploid *T. dactyloides*. At least, induration of glume and rachis tissues, as is characteristic of teosinte introgression, did not increase through these hybridization and backcross procedures. It is possible, however, that more subtle gene exchanges did take place.

Hybrids with 36 Td + 10 Zm chromosomes are cytologically the most interesting. When they are pollinated with maize, about 95% of the offspring again have 36 Td + 10 Zm chromosomes, while the remaining 5% have 36 Td + 20 Zm chromosomes. Individuals with 36 Td + 20 Zm probably originate when apomictic embryo sacs function sexually, and get fertilized by a maize male gamete. At first it was thought that the cytologically maternal-like offspring all originated from seed that developed apomictically. However, it soon became obvious that some 67% of them carry genetic characteristics of the new pollen parent, indicating that they must have originated sexually. Functional female gametes with 36 Td chromosomes and no maize chromosomes are produced when the Zm univalents are excluded from the telophase nuclei during the first meiotic division, and cytokinesis fails to take place during the second meiotic division of megaspore formation (DE WET *et al.* 1970; DE WET *et al.* 1973). These gametes apparently never develop apomictically but give rise to offspring which again

have 36 Td + 10 Zm chromosomes when they are fertilized by a male gamete of the new maize pollen parent.

Backcross individuals with 36 Td + 10 Zm chromosomes that originated apomictically again produce offspring with 36 Td + 10 Zm and 36 Td + 20 Zm chromosomes when they are pollinated with maize. Those that originated sexually, produce offspring with $2n = 46, 48, 50, 52, 54$ and 56 chromosomes. Female gametes with 36 Td + 2, 4, 6 or 8 Zm chromosomes are produced when 1, 2, 3 or 4 Zm chromosomes are included in a telophase nucleus at meiosis I, and cytokinesis fails to take place during the second division of macrosporegenesis (DE WET *et al.* 1972a). This comes about when Td and Zm chromosomes associate and the resulting one to four 2 Td-1 Zm trivalents fall apart at metaphase I in such a way that a Td-Zm bivalent moves as a unit to a pole. Intergenome pairing is rare in 36 Td + 10 Zm hybrids, but becomes the rule in later backcross generations as the Td genome becomes contaminated with Zm genetic material. Backcross individuals with 36 Td + 12, 14, 16 or 18 Zm chromosomes are male sterile but usually produce an abundance of morphologically variable offspring when pollinated with maize.

Backcross individuals with 36 Td + 20 Zm chromosomes produce maternal offspring (36 Td + 20 Zm), dihaploids (18 Td + 10 Zm) and an abundance of offspring with 18 Td + 20 Zm chromosomes when they are pollinated with maize. One such individual also gave rise to offspring with $2n = 66, 70$ and 72 chromosomes. These plants combine 36 Td + 30, 34 or 36 Zm chromosomes respectively. The dihaploids differ morphologically and cytogenetically from first generation hybrids with 18 Td + 10 Zm chromosomes (NEWELL and DE WET 1973). They are characterized by more frequent intergenome pairing than are first generation hybrids with a similar genome constitution. Dihaploids are highly apomictic, but usually produce some offspring with 18 Td + 20 Zm chromosomes when pollinated with maize. Plants with $2n = 38$ chromosomes derived from allopolyploids (36 Td + 20 Zm) as well as dihaploids (18 Td + 10 Zm) are male sterile but female fertile. When backcrossed with maize, Td chromosomes are selectively eliminated and offspring with $2n = 20$ maize chromosomes are recovered after two successive backcrosses. Individuals with $2n = 20$ maize chromosomes were also recovered from plants with 36 Td + 30 or 34 Zm chromosomes after four successive backcrosses with maize. Recovered individuals with $2n = 20$ are maize-like cytologically, but some carry a substantial amount of *Tripsacum* genetic material. The more tripsacoid ones have the following characteristics: they are weak perennials, tiller profusely, have branched lateral inflorescences with several small ears topped by a male spike; their branched terminal inflorescence is bisexual as in *Tripsacum*, they are male sterile, and usually produce only a few seeds when pollinated with maize. Some individuals are more maize-like in gross morphology and self-fertile, while others are weak and completely sterile. Selfing or backcrossing rapidly increases fertility, and obvious tripsacoid characteristics are gradually eliminated until essentially pure maize is recovered. However, the amount of genetic material that can permanently be transferred from

Tripsacum to maize appears to be substantial. But, among hundreds of recovered maize plants so far studied, increased induration of glume and rachis tissues, of the kind readily transferable from teosinte to maize, has never been observed.

THE ROLE OF TRIPSACUM IN THE EVOLUTION OF ZEA

The genera *Zea* and *Tripsacum* cross readily when they are not isolated by gametophytic barriers. Their basic genomes are sufficiently allied for as many as four chromosomes of octaploid *T. dactyloides* ($2n = 72$) to form loose associations with four chromosomes, probably 2,4,7 and 9, of maize. GALINAT (1970) has shown that each one of these maize chromosomes has at least one, and may have as many as eight, loci in common with chromosomes of the basic $x = 9$ *Tripsacum* genome. Natural introgression between *Zea* and *Tripsacum* is possible, and probably was always feasible. However, natural genetic interaction between these genera does not appear to be on the order of magnitude as postulated by MANGELSDORF and REEVES (1939), REEVES and MANGELSDORF (1959) or MANGELSDORF (1961).

The probability that teosinte could have originated as a byproduct of hybridization between maize and *Tripsacum* is infinitesimally small (DE WET, HARLAN and GRANT 1971). Cytogenetic evidence cited by REEVES and MANGELSDORF (1959) in support of this postulate is at best circumstantial. Furthermore, GALINAT (1971) failed in an attempt to defeat assemblages of genes in the *Tripsacum* genome that would be capable of producing a teosinte-like fruitcase when introduced into maize. Similarly, we failed to produce a teosinte-like plant through experimental genetic introgression from *Tripsacum* into maize, even though a substantial amount of intergeneric gene exchange does take place.

The postulate that modern maize is a complex hybrid, involving not only teosinte but also *Tripsacum* (MANGELSDORF 1961), has little experimental support. MANGELSDORF (1968) himself demonstrated that the so-called genes for "tripsacoid" traits extracted from South American races of maize induce phenotypic changes in a maize inbred that are similar to those that can be introduced from teosinte rather than *Tripsacum*. Some primitive races of maize probably do cross in nature with *Tripsacum*. When *Tripsacum* is the female parent hybrid seeds are usually well developed, hybrids are vigorous, and those involving octaploid *Tripsacum* are perennial. When these hybrids backcross with *Tripsacum*, successive generations can be expected to become increasingly better adapted to the *Tripsacum* habitat, and introgression from *Zea* into *Tripsacum* is quite feasible. Successful introgression from *Tripsacum* into *Zea* is, however, doubtful. Gene exchange is made difficult by natural selection as well as the activities of man. Successive generations of backcrosses with maize will become increasingly dependent on cultivated fields for survival, and recovered tripsacoid maize will be as dependent on man for survival as is pure maize. Throughout the several generations required for recovery of maize-like offspring, hybrid derivatives are recognizable morphologically. Even in traditional agricultural systems, it seems highly unlikely that such obviously different plants with poor yield will be selected as

seed stock. With a change in selection pressures, however, tripsacoid plants may have selective advantages over pure maize. The highly "tripsacoid" Chococeño maize, which is grown in the Choco region of Western Columbia with a minimum of tillage, deserves further study (ROBERTS *et al.* 1957). However, even this race may have acquired its "tripsacoid" phenotype and habitat adaptation from teosinte rather than *Tripsacum* during an earlier period of its phylogenetic history (DE WET *et al.* 1972b).

MANGELSDORF (1947, 1958) proposed that wild maize must have been maize-like rather than teosinte-like in female inflorescence morphology. This conclusion is supported by the available archaeological record of maize domestication. The picture that emerges from archaeological studies in the Tehuacan Valley of Mexico is of a nomadic hunting food-gathering people who learned Barranca horticulture sometime between 7000 and 5000 B.C., when they started to grow squash, amaranth, chile, beans and eventually also a very primitive maize (MACNEISH 1971).

The oldest indisputable maize remains in Tehuacan are dated between 5000 and 2400 B.C. These tiny cobs are from 19 to 25 mm long, have usually eight rows of kernels, with 6–9 kernels per row, and an average of 55 kernels per cob. Female spikelets are uniformly paired and located in shallow cupules as is characteristic of modern maize, and the glumes are long and soft and probably covered the individual grains as in modern pod corn. These cobs were probably part of a branched female inflorescence, and each cob had male spikelets on an extension of the female ear. MANGELSDORF, MACNEISH and GALINAT (1967a) concluded that this Coxcatlan race of maize must have been wild. They point out that (1) the cobs are uniform in size and shape as one would expect from a wild grass; (2) the cobs have fragile rachises and thus could disperse their seeds naturally; (3) the glumes are long and must have covered the kernels as is common in wild grasses; (4) there are habitats in Tehuacan Valley where wild maize could have grown; (5) firm evidence of agriculture, as judged from the absence of other cultivated plants during the early stages of its use, is lacking; and (6) the predominant maize during later culture phases when agriculture was well established is larger and much more variable. The domesticated Abejas race which developed between 3400 and 2300 B.C. resembles Coxcatlan maize in detail except for size. Cobs now are between 28 and 61 mm long, have 8–10 rows per cob, 8–19 spikelets per row, and an average of some 114 kernels per cob.

The evidence presented by MANGELSDORF, MACNEISH and GALINAT (1967a), however, does not rule out the possibility that Coxcatlan maize was introduced into Tehuacan Valley as a domesticated horticultural crop (DE WET and HARLAN 1972). Long soft glumes do not necessarily indicate a wild grass; all cereals including maize are characterized by genes that produce oversized glumes. Many of the oldest cobs were recovered intact, indicating tough rachises, a primary characteristic of domesticated cereals. Maize is absent from among the debris left behind by food gatherers prior to the Coxcatlan culture phase, suggesting that this assumed wild maize either did not attract nomadic hunters as an important source of food, or probably was not available in Tehuacan before 5000 B.C. Morpho-

logically similar maize was grown by 2300 B.C. as far away as Tamaulipas in northeastern Mexico (cf. MANGELSDORF, MACNEISH and GALINAT 1967b), and New Mexico (cf. MANGELSDORF, DICK and CAMARA-HERNANDEZ 1967), suggesting to us that it was domesticated. Finally, evidence that *Zea* pollen antedating the advent of agriculture in Mesoamerica resembles that of modern maize rather than teosinte (IRWIN and BARGHOORN 1965), has been refuted by comparative studies of pollen morphology (GRANT 1973).

It is becoming apparent as additional evidence accumulates that teosinte is in fact wild maize (COLIN 1966; BEADLE 1972). MANGELSDORF (1947) suggested that the differences between teosinte and maize are so great that no genetic or evolutionary mechanism is known by which teosinte can be changed into maize. GALINAT (1971) lists the fourth chromosome complex, single versus paired pistillate spikelets, two-ranked versus four-ranked, and sessile versus pedicellate pistillate spikelets as the basic differences determining maize and teosinte female inflorescences. These contrasting characters do not all behave as simple genetic alternatives of each other; perhaps because some are not controlled by alternative allelic complexes. More basic to an understanding of maize evolution are the character differences studied by COLLINS (1919). These are (1) a change from brittle to tough rachis joints; (2) a change from hard indurated glume and rachis tissue to softer glumes and rachises; (3) restoring fertility in the second spikelet of each pair in a cupule; (4) yoking of alternate pistillate spikelet pairs; and (5) cross yoking of two-yoked spikelet complexes. Each one of these traits can be introduced into teosinte from maize. These traits probably will not be found in natural populations of teosinte. They will have selective value only under conditions of domestication.

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