

information losses to stimulate the biasing effect of "extant" records.

Finally, a new range chart was constructed from what was left after the information removals. The diversity curves computed from this are also shown in Fig. 5. Species diversity increases sharply toward the Recent whereas generic diversity shows a maximum, offset to the right of the original maximum. When genera are grouped into hypothetical families (not shown), the diversity maximum is offset to the right but not as far.

The simulation demonstrates that diversity patterns such as are observed in the fossil record can be produced by the application of known biases to quite different diversity data. The simulation does not, of course, prove the alternative model for Phanerozoic diversity because of our present ignorance of the actual impact of the biases. The simulation does suggest, however, that the model proposed in Fig. 5 is a plausible one for the Phanerozoic record of marine invertebrates.

The alternative model cannot be applied literally to land-dwelling forms because the exploitation of terrestrial habitats started much later in geologic time and may be still going on. The fossil record of terrestrial organisms is subject to the same biases, however, and so should be read with caution.

Summary

Apparent taxonomic diversity in the fossil record is influenced by several time-dependent biases. The effects of the biases are most significant at low taxonomic levels and in the younger rocks. It is likely that the apparent rise in numbers of families, genera, and species after the Paleozoic is due to these biases. For well-skeletonized marine invertebrates as a group, the observed diversity patterns are compatible with the proposition that taxonomic diversity was highest in the Paleozoic. There are undoubtedly other plausible models as well, depending on the weight given to each of the biases. Future research should therefore be concentrated on a quantitative assessment of the biases so that a corrected diversity pattern can be calculated from the fossil data. In the meantime, it would seem prudent to attach considerable uncertainty to the traditional view of Phanerozoic diversity.

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Maize and Its Wild Relatives

Teosinte and *Tripsacum*, wild relatives of maize, figured prominently in the origin of maize.

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The close relatives of maize, teosinte and the genus *Tripsacum*, have assumed increasing importance in the understanding of the evolution under domestication of the New World's most important plant food. *Tripsacum* hybridizes with maize under experimental conditions, and teosinte crosses with maize in its native habitat, Mexico and

Central America. Much of the heterotic vigor of maize is attributed to introgressive hybridization from its closest relative, teosinte. Today, the maize crop is the single largest harvest in the United States and is the staple food for most of the inhabitants of Latin America.

Considering the importance of the hybridization of maize (*Zea mays* L.) with its wild relatives (Fig. 1) teosinte [*Z. mexicana* (Schrad.) O. Ktze.] (1),

an annual grass looking very much like maize, and *Tripsacum* (2), perennial grasses quite distinct from maize in appearance, it is startling to realize how little is known about this phenomenon in the wild. Maize and teosinte are genetically compatible and hybridize freely with each other in places where the isolating mechanisms between the two have broken down, as in the Sierra Madre Occidental of northern Mexico, the Central Plateau and Valley of Mexico in central Mexico, and in Hehuatenango of northern Guatemala. *Tripsacum* does not hybridize readily with maize in the field, but hybrids can be produced under experimental conditions. There is reason to be alarmed by the rapid extinction of these wild relatives in and around maize fields where teosinte is known to have hybridized with maize for at least three millennia. This extinction of the native populations of teosinte is disastrous from the standpoint of future introgression, since it

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will end the introduction of foreign germ plasm into the native races of maize, a plant very dependent on heterotic vigor for its yields.

Where Maize Originated

Maize, because of its long association with man and with his conscious and unconscious alteration of its genetic architecture, is no longer capable of reproducing itself without being cultivated. Since maize is an obligate cultigen with no clearly discernable wild form still extant, it is not surprising that an aura of intrigue surrounds its origin.

The Indians' earliest concept of the origin of maize recognized that the plant did not grow wild in the countryside. In the Nahuatl oral tradition, maize came from the red ants (3): "Once again the gods asked, Oh you gods, what is man to eat? And a search was begun high and low for a food. It was then that the red ant brought back corn seed from the land of plenty [underworld]. . . ."

In examining the lines of evidence presented by Swiss botanist Alphonse

de Candolle (4) in his *Origin of Cultivated Plants* (1882)—botanical, archeological, historical, and linguistic evidence—Harshberger (5) came to the conclusion that maize originated in Mexico and, more specifically, that it had once been a wild plant in central Mexico, at elevations above 4500 feet (1371.6 meters), in a semiarid region with rains during the growing season (summer) of approximately 15 inches (38.1 centimeters). Unknown to Harshberger was the fact that the region he specified exactly parallels those areas of Mexico where teosinte and *Tripsacum* are found and where maize and teosinte hybridize naturally (Fig. 2).

Between 1920 and 1940, the Russian geneticist and plant breeder N. I. Vavilov gathered and maintained a tremendous genetic wealth at the Institute of Plant Industry in Leningrad (6). In his expeditions to the New World, Vavilov collected seed from over 2800 specimens of maize alone. Vavilov recognized that specific areas of the world were centers of diversity for cultivated plants and, based on the maize collections, the greatest single center of overall diversity was found to be Mexico. In addition, teosinte,

the closest wild relative of maize, was native to Mexico. Vavilov considered teosinte to be the progenitor of maize, and he attached considerable significance to the fact that teosinte was fully fertile with maize and that naturally occurring hybrids between the two could be found in Mexico.

The Closest Relative: Teosinte

The Russians were able to locate only very restricted populations of teosinte and therefore came to the conclusion that it had been more widely distributed in the past, but was in the 1920's a very constricted, "dying-out weed" (6, p. 144). Teosinte was far from dying, but since its appearance is quite similar to that of maize, its presence in Mexican maize fields was seldom detected by the Russian or later investigators. To the casual observer, maize and teosinte are so similar in appearance, with nearly identical staminate flowers borne in tassels (Fig. 1A) and pistillate flowers enclosed in a system of husks in a lateral position on the stem, that the most reliable characteristic separating the two is the



Fig. 1. The wild relatives of maize. (A) The maize-mimetic teosinte typical of cultivated corn fields in the Valley of Mexico (Chalco) and the Central Plateau. (B) Teosinte growing as a part of the native flora in competition with other plants, notably composites, in Guerrero, Mexico. (C) The tall flowering cane of *T. maizar* (Guerrero, Mexico), with its broad leaves and multi-branched tassel, is the most maize-like in appearance of all the *Tripsacum* species.

pistillate fruit—a distichous spike in teosinte (Fig. 3) and a polystichous structure (the familiar ear) in maize. Teosinte is further distinguished from maize in that the seeds are dispersed as individual rachis segments from the disarticulating spike, and this ability to disperse seed, an ability maize does not possess, distinguishes teosinte as a wild plant (7).

Today the natural distribution of teosinte is well known and recognized to be limited to the seasonally dry, subtropical zone with summer rain (Köppen Cw) along the western escarpment of Mexico and Guatemala and the Central Plateau of Mexico. This distribution fits very well within the cultural area of the ancient Mexican and Mayan civilizations referred to by anthropologists as Mesoamerica.

The natural distribution of teosinte falls within some of the best agricultural land in Mexico. In Jalisco, Guanajuato, and Michoacan, teosinte is found mostly along stone fences bordering maize fields—not because it has invaded the maize field as a weed,

but because it is making a last stand on this narrow strip of untilled soil. In a few localities, such as Chalco, it has successfully invaded the maize field proper; but at several sites on the Central Plateau where teosinte used to grow, a fact documented by specimens collected before the turn of the century, it has died out in recent times because of farming and pasturage (Fig. 2). The largest population, and the one least likely to disappear in the near future, is that which occupies hundreds of square miles in the mountains of the Rio de las Balsas. The teosinte of this region along the western escarpment (at elevations of 800 to 1950 meters) is the least maize-like of all the teosintes found in Mexico; only the teosinte from southern Guatemala is less maize-like.

There are six recognized races of teosinte, four of which occur in Mexico (8). Both teosinte ($2n = 20$) and maize ($2n = 20$) are highly variable, outcrossing, wind-pollinated species, and the two hybridize readily with each other. The F_1 hybrid is both robust and fertile, and its backcrossing to maize and the

subsequent introgression of teosinte is recognized in at least 17 of the 25 races of maize in Mexico (8). This introgression of genes from teosinte and the resulting heterotic effects on maize has renewed interest in other wild relatives and their possible role in the origin of maize.

The Genus *Tripsacum*

The genus *Tripsacum* has assumed increasing importance for research into the origin of maize ever since the hybridization of maize with *Tripsacum* was first reported by Mangelsdorf and Reeves in 1931 (9). Seven of the nine recognized species are native to Mexico and Guatemala, an eighth, *T. floridanum*, is native to Florida and Gulf Coast Texas, and the ninth, *T. australe* (and possibly other, as yet undescribed species) is native to South America. The center of variation for *Tripsacum* is the western escarpment of central Mexico. This is almost exactly the same region in which the largest single

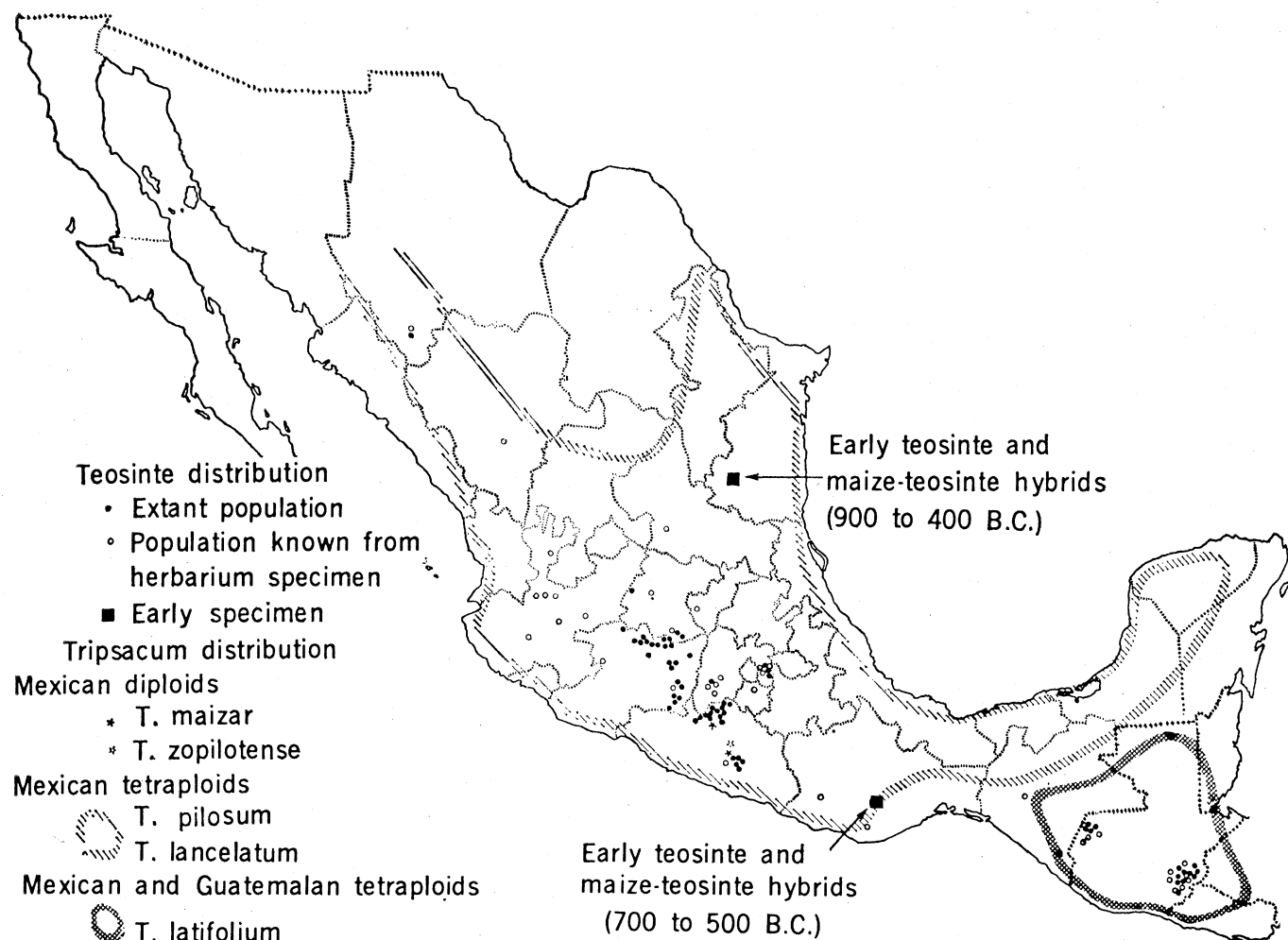


Fig. 2. Distribution of the wild relatives of maize in Mexico and Guatemala.

population of teosinte is found. The habitat preferences of *Tripsacum* spp. in Mexico are nearly identical to those of teosinte: seasonally dry, summer rains, an elevation of about 1500 meters, and limestone soils (10).

Tripsacum is usually placed in the tribe Maydeae along with *Zea* (maize and teosinte), but the genus does show certain morphological resemblances to members of the tribe Andropogoneae, particularly to the genus *Manisuris*. In fact, the only significant difference between *Tripsacum* and *Manisuris* is that *Manisuris* has perfect flowers, while *Tripsacum* has both male and female spikelets which are borne distinctly, but which, unlike those of maize and teosinte, are on the same inflorescence.

Polyploidy has been very important in the evolution of *Tripsacum* (11–15). The diploid forms are all morpho-

logically distinct and allopatric in their distribution. The polyploid forms are not always easily distinguishable on either a morphological or a geographical basis.

There are four diploid ($n=18$) species of *Tripsacum* (16): *T. floridanum* Porter ex Vassey, *T. australe* Cutler and Anderson (17), *T. maizar* Hernandez-X and Randolph (Fig. 1C), and *T. zopilotense* Hernandez-X and Randolph (18). Both *T. zopilotense* and *T. maizar* appear to be relict species that once occupied a much wider range. The habitats of these two species, although very different, are less than 100 kilometers apart (Fig. 2).

One species, *T. dactyloides* L., has both diploid ($n=18$) and tetraploid ($n=36$) forms. Besides *T. dactyloides*, there are four other tetraploid forms: *T. laxum* Wash., *T. lanceolatum* Ropr.

ex Fourn., *T. latifolium* Hitch., and *T. pilosum* Scrib. & Merr. Recent evidence indicates that these tetraploids are segmental, allotetraploid derivatives of *T. maizar*- and *T. zopilotense*-like diploids (14).

The differences in habitat and the ecological barriers suggest that the diploid species of *Tripsacum* have diverged significantly from each other since their suspected amphidiploid origin from $n=9$. The diploid species with a chromosome number of $2n=36$ have a regular meiosis with 18 bivalents, a characteristic of genomic allopolyploids in which the homologous chromosomes between the genomes are so distinct that they fail to pair. Some of the diploid species are well on their way to developing barriers to gene exchange, as shown by the sterility in the crosses of *T. dactyloides* ($2n=36$) with *T. zopilotense* ($2n=36$) and *T. floridanum* with *T. zopilotense*. Crosses of *T. dactyloides* with *T. floridanum* and *T. maizar* with *T. zopilotense* are fertile and readily accomplished. At the present time, it is difficult to distinguish between primitive and evolved diploid species.

The tetraploid species ($2n=72$) of *Tripsacum*, on the other hand, form a continuous range of variation, and field studies indicate that they hybridize readily. Morphologically, it is often extremely difficult to separate *T. lanceolatum* from *T. pilosum* in central Mexico and *T. laxum* from *T. lanceolatum* and *T. pilosum* in southern Mexico. *T. latifolium* is in many respects very similar to *T. lanceolatum*, the two being distinguished by their allopatric distribution. The three tetraploids (*T. lanceolatum*, *T. laxum*, and *T. pilosum*) all have a decided preference for limestone soils and a seasonally dry habitat at elevations of 1250 to 1850 meters.

Polyploidy in *Tripsacum*

The nature of the polyploidy in the tetraploid species of *Tripsacum* is not known. Anderson (11) has suggested that the tetraploid forms originated by hybridization and chromosome doubling between related diploids, while Randolph (12) has suggested that the tetraploids of Mexico and Central America originated from the hybridization of the two most morphologically distinct and possibly most primitive diploids, *T. zopilotense* and

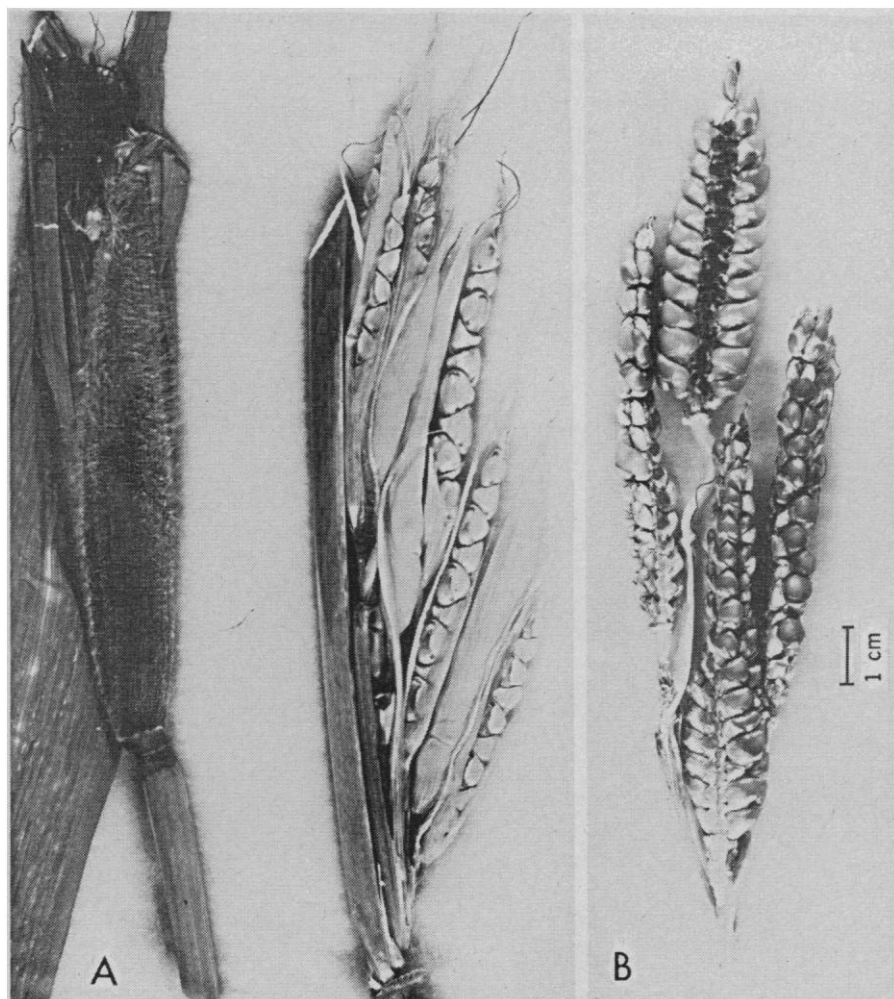


Fig. 3. The fruit of teosinte and F_1 hybrid with maize. (A) Teosinte and maize are so similar in appearance, with nearly identical husk systems enclosing the fruit, that the most reliable differentiating characteristic is the distichous spike of teosinte, which consists of from 7 to 12 disarticulating rachis segments, each completely enclosing a single seed. (B) The familiar polystichous ear of maize is expressed as the four-rowed ear in the F_1 hybrid. The ear of the F_1 is more maize-like in appearance because each seed is borne naked, free of the enclosing rachis tissue.

T. maizar. The tetraploids in which meiosis has been observed (13, 14) have shown a low quadrivalent and a high bivalent formation. These tetraploids are all reasonably fertile and thus appear to be segmental allopolyploids.

It is quite possible that the *T. pilosum*-*T. lanceolatum* complex of central Mexico originated from chromosome doubling following the hybridization of *T. zopilotense* and *T. maizar*. Tantravahi (14) has shown by multiple character analysis (19) and meiotic irregularities that *T. pilosum* and *T. lanceolatum* are two extremes of a relatively young and segregating polyploid complex. Part of this variation is preserved in the tendency of perennial *Tripsacum* clones to reproduce vegetatively by means of their rhizomes.

The polyploid nature of *T. laxum* and *T. latifolium* has been studied by Randolph (13) and Tantravahi (14); both agree that *T. maizar* was a possible parent, but disagree as to the second possible parent. Tantravahi has used qualitative extrapolation to suggest that a diploid very similar to *T. australe* was the second putative parent.

At the present time, it is difficult to distinguish further evolutionary relations in the polyploid speciation of *Tripsacum*. It is hypothesized that, from the presumed center of origin and present center of diversity on the western escarpment of Mexico (at elevations of 1000 to 1500 meters), two divergent diploids moved northward into what is now the United States and that these diploids gave rise to *T. dactyloides* ($2n = 72$). Similarly, the tetraploid complex of the Central Plateau (*T. lanceolatum*-*T. pilosum*) is probably of hybrid origin, as are the supposed tetraploids of Guatemala (*T. laxum*-*T. latifolium*).

Experiments have established that exchanges can and do occur between maize and *Tripsacum* chromosomes (20), even though all evidence indicates that the recent evolution within the genus *Tripsacum* has been independent and distinct from that of maize. It was with *T. dactyloides* ($2n = 72$) that Mangelsdorf and Reeves first successfully hybridized maize with *Tripsacum*. Since then, *T. floridanum* and *T. dactyloides* ($2n = 36$) have been hybridized with maize. Studies of the hybrids have indicated that certain segments of *Tripsacum* chromosomes can be substituted for corresponding segments in maize chromosomes and the plants re-

main both viable and fertile. Galinat (21) has mapped more than 25 homologous loci on the chromosomes of these two genera. The accumulated information on maize-*Tripsacum* hybrids and their derivatives indicates that the respective genetic architectures of maize ($2n = 20$) and *Tripsacum* ($2n = 36$, $n = 72$), while quite different, are more similar than their karyotypes would suggest.

The naturally occurring populations of *Tripsacum* in Mexico and Guatemala appear to be holding their own and are not threatened by possible extinction. The only exceptions might possibly be the two Mexican diploids, *T. zopilotense* and *T. maizar*, which have a very confined distribution. A perennial

garden of *Tripsacum* clones from Mexico and other Latin American countries has been established at the Fairchild Tropical Garden, Coral Gables, Florida. This living collection represents much of the variation in the genus and, as a *Tripsacum* gene bank, is available for future plant breeding.

Parallel Variation in Maize, Teosinte, and *Tripsacum*

Although maize-*Tripsacum* hybrids have not been observed in the field and *Tripsacum*-teosinte hybrids remain to be produced, my field studies in Mexico have indicated that there are several parallel variations in these three taxa



Fig. 4. Teosinte on the margin of a maize field.

that are suggestive of gene exchange, parallel variation, or possibly both. The most tassel-branched forms of teosinte (Balsas race) and the most tassel-branched species of *Tripsacum* (*T. maizar*) are found in the foothills of the Rio de las Balsas, in Guerrero. Those maize plants with the most vivid color are found on the Central Plateau. In this same region are found the most intensely colored races of teosinte (Central Plateau and Chalco races) and the *Tripsacum* species (*T. pilosum*, *T. lanceolatum*, and possibly a new species native to Ciudad Hidalgo, Michoacan) with the most well developed red color. There is also parallel distribution in central Mexico of some of the widest leaves and hairiest forms of maize, teosinte, and *Tripsacum*.

Introgression in Early Maize

The Tehuacán archeological sequence, from a prehistoric wild maize of 7000 years ago to the maize (22) that is now cultivated in central Mexico, has been an exciting discovery and confirms the evolution of a crop plant from a wild to a fully domesticated plant. The earliest cobs (5000 B.C.) are characterized by a uniformity of size and a bisexual condition, with the pistillate spikelets below and the staminate spikelet, usually found only in the tassel, at the tip of the ear. The cobs have relatively long protective glumes that would have enclosed, or partially enclosed, each kernel. The fragile rachis dispersed the seeds. These characteristics are all thought to be those of a wild plant, and, indeed, these are just the characteristics that maintain teosinte as a wild plant in Mexican maize fields.

The remains of later cobs are all larger and more varied. In all of its botanical characteristics except size, the early cultivated maize (3500 B.C. to 2300 B.C.) is virtually identical to the earliest remains. The increase in size is attributed to the improved growing conditions brought about by cultivation and irrigation.

Starting in about 1500 B.C., an explosive period of variation appears in the remains. Because the rachis and glumes of those cobs are highly indurated, Mangelsdorf *et al.* (22) have called the cobs early tripsacoid. In teosinte, as in *Tripsacum*, the tissue making up the rachis and lower glumes

of the fruit case are highly thickened and indurated. These characteristics also appear in the progeny of the teosinte-maize hybrid; therefore, early cobs exhibiting these characteristics are suspected of possessing germplasm from teosinte.

Where the introgressed maize at Tehuacán came from is not known, since neither *Tripsacum* nor teosinte is present in the vegetable remains. There is little doubt that the source of the variation in the maize cobs is hybridization with teosinte. There have been discovered remains of F_1 hybrids in Oaxaca (23) and beautifully preserved, entire teosinte spikes and cobs from F_1 hybrids in northern Mexico (24), both of which are of comparable age to the introgressed maize at Tehuacán.

It is evident from the findings at Tehuacán that the genes of wild maize were responsive to the improved environment provided by cultivation, but that it was the hybridization with teosinte which resulted in the explosive variation and increased productivity that characterize the modern maize of Mexico. Introgressive hybridization with teosinte is not just a phenomenon of the past (Fig. 4). It is still occurring at several places in both Mexico and Guatemala—with dramatic effects on the maize.

Teosinte in Maize Fields

Teosinte is found exclusively as a weed in maize fields throughout the Valley of Mexico. Hybridization between maize and teosinte is widespread, with the result that teosinte is becoming an even more effective maize-mimetic plant and is incorporating maize genes into its genome. This is especially evident in the case of the genes controlling plant color and leaf characteristics. Those teosinte plants that grow in the furrows of plowed fields are weeded out, but the maize-mimetic teosinte plants that grow in the rows cannot be distinguished from maize until the time of flowering. Usually these teosinte plants are not removed until after pollen has been shed. By that time, teosinte pollen has had ample opportunity to cross with maize, and mature seeds have formed in teosinte on the first pistillate spikelets that flowered. Farmers have made considerable efforts to weed teosinte

out of the fields, but almost invariably the plants are given to livestock as fodder, and the seeds, protected by their hard cases, are passed in the feces, which, in turn, is used to fertilize the field.

Although the number of F_1 hybrids found in a maize field at the end of a season does not indicate the full extent of hybridization of teosinte and maize during the previous year, it does provide a sampling of the hybridization of these two taxa. My field studies have indicated that a frequency of one F_1 hybrid for every 500 maize plants, or 2 to 5 percent of the teosinte population, is typical for the Chalco region of the Valley of Mexico and represents a significant gene exchange between a wild or, in this particular case, a "weedy" plant and a cultivated relative. That genetic exchange does not terminate in the F_1 hybrid has been documented in these fields by the recovery of a number of first- and second-generation backcross progeny both to maize and to teosinte.

The role of teosinte introgression in the evolution of maize is fully recognized and has been skillfully manipulated to increase yield. I have discovered that Mexican cultivators often select as seed ears two extremes from the variations within their fields, often a long, slender ear and a many-rowed, short ear, expecting in the following year a plant that yields an ear somewhere between the two extremes. Experimental inbreeding of some of my Mexican, field-collected F_1 hybrids backcrossed to maize have produced two distinct extremes—long, slender ears and many-rowed, stubby ears. These ears are morphologically comparable to those selected by native cultivators as seed ears.

My plant-by-plant mapping (25) of maize fields in central Mexico where teosinte is present indicates specific patterns from which I have constructed a model for the effectiveness of the maize-teosinte hybridization and resulting introgression into maize. When F_1 hybrids do occur, they are often bunched, which suggests that they have a common parent; this is true even in fields where the distribution of teosinte is reasonably uniform, and it indicates the effectiveness of the partial seasonal isolation between teosinte and maize. When teosinte is abundant, the frequency of F_1 hybrids increases proportionately, but the frequency of back-

crosses to maize does not appear to increase significantly. When the teosinte is present, but not abundant, and is distributed throughout the field, the absolute number of F_1 hybrids decreases, and the relative number of subsequent backcrosses to maize increases.

Apparently the most effective structure for introducing teosinte germ-plasm into maize is to have a low percentage of teosinte plants well distributed throughout the field and to have their seasonal isolation from maize be incomplete. The F_1 hybrids flower earlier in the season than teosinte, and they therefore hybridize with maize, resulting in a greater abundance of backcross progeny than of F_1 hybrids.

This is exactly the pattern that has been observed in the fields of Nobogame (26), the Bajío, and the Rio de las Balsas, where the introgression of teosinte is now being exploited to form new races of maize (Fig. 4).

The Extinction of

Teosinte Populations

The process by which the highly productive modern ear of maize has evolved is in grave danger of disappearing. This pattern of evolution, involving hybridization with teosinte, is being threatened by the rapid extinction of teosinte that is now taking place. The genetic wealth of maize can be stored in a seed bank, and the races of teosinte can also be stored, but the introgression of teosinte and the formation of new races in maize defy storage.

Teosinte populations are undergoing extinction because of (i) the elimination of the wild populations in the regions of maize fields (caused by the increased demands of grazing), with the subsequent genetic swamping of those few plants that do remain in there, and (ii) the replacement of the native races of maize by commercial hybrid seed or a cash crop such as strawberries.

Teosinte and the native races of maize in Mexico form a vital part of the genetic underpinnings of the world corn crop. The center of origin for maize and for naturally occurring populations of teosinte is shifting to maize fields with a considerably narrower range of variation and a limited genetic base. By the best estimates, the geographic distribution of teosinte in Mexico today is less than half what it was in 1900, and in the last 10 years I have watched the rate of extinction accelerate. We can ill afford the loss of such genetic wealth in this day of exploding population.

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16. Description of the diploid *Tripsacum* spp. of Mexico and adjoining regions: *T. floridanum* Porter ex Vasey, $2n = 36$, is a narrow-leaved perennial whose height seldom exceeds 1 meter. The terminal inflorescence is usually solitary, although two branched inflorescences may occur. This plant is usually limited to very moist soils in frost-free areas. Prior to its recent discovery in eastern Texas by Tantravahi and Wilkes, this species was thought to be limited to the southern tip of Florida. *Tripsacum zopilotense* (Hernandez-Xolocotzi and Randolph), $2n = 36$, is also a narrow-leaved perennial that seldom exceeds 1 meter in height. The terminal inflorescence is usually solitary. This species is distinguished from *T. floridanum* by its pendent leaves and relatively soft glumes in the flowering spikelets. Its distribution is confined to the canyon of the Zopilote in Guerrero, Mexico. This diploid is found in a scrub-thorn vegetation zone in an arid region on the western escarpment (at an elevation of 800 to 1000 meters) of central Mexico. *Tripsacum maizar* (Hernandez-X and Randolph), $2n = 36$, is the largest and most maize-like of all the *Tripsacum* species. The leaves are very broad (7 to 10 cm) and up to 3 meters long. The plant height exceeds 5 meters, and the terminal inflorescence is multibranched. This weakly perennial species is limited to two or three localities (at an elevation of 800 to 1400 meters) in Guerrero, Mexico, where there is sufficient moisture in the soil to support a luxuriant vegetative growth throughout the year. *Tripsacum dactyloides* (L.) L., $2n = 36$, $2n = 72$, is a robust perennial growing in clumps from well-developed rhizomes. Plant height seldom exceeds 3 meters. The terminal inflorescence usually has two or three branches. The diploids are difficult to distinguish from the tetraploids in the field, but the two can be separated by several criteria, such as pollen size and stomata size. The diploids are limited to the Mississippi Valley and the Great Plains. The tetraploids are found throughout the range and are the only form found along the eastern half of the United States, in moist habitats such as stream banks, as far north as central Illinois and southern New England.
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