The Taxonomy and Evolution of *Tripsacum* and Teosinte, the Closest Relatives of Maize

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ABSTRACT


Together the genera *Tripsacum* and *Zea* form the subtribe Tripsacinae of the tribe Andropogoneae of the family Gramineae. These genera share in common a number of morphological features, including the highly specialized cupulate fruitcase. *Tripsacum* contains 13 or more perennial species which can be divided into sections *Tripsacum* and *Fasciculata*. Section *Tripsacum* has a larger number of more distinct species which have a much broader geographic range. *Zea* contains two perennial and two annual species which divide into two different groups, sections *Luxuriantes* and *Zea*. Section *Luxuriantes* is the more primitive section with two perennial and one annual species, all of which show considerable similarity to some tripsacums. Section *Zea* contains a single species with three subspecies: a) *Z. mays* spp. *mays* (maize or Indian corn); b) *Z. mays* spp. *parviglumis* (a small-spikeleted annual teosinte of middle elevation in southwestern Mexico and western Guatemala); and c) *Z. mays* spp. *mexicana* (a large-spikeleted annual teosinte of high elevation in central and northern Mexico). The morphological, biochemical, and genetic evidence suggests that one of these two wild subspecies is the direct ancestor of cultivated maize.

The genus *Zea* contains the cultivar, maize (*Z. mays* L. spp. *mays*), and its wild relatives of Mexico and Central America, the teosintes. The genus *Tripsacum* contains 18 or more species of wild grasses which occur from temperate North America (Massachusetts) to Paraguay in South America. Together these two genera form the subtribe Tripsacinae of the tribe Andropogoneae of the family Gramineae (Clayton, 1973). The Tripsacinae, like other members of the Andropogoneae (such as sorghum), have their spikelets arranged in pairs, with one member of the pair being sessile and the other borne on a slender pedicel. The spikelet pairs are distichously arranged along the branches of the inflorescence. The Tripsacinae are distinguished from the other Andropogoneae by the following: a) Their male and female spikelets are born in separate inflorescences (as in *Zea*) or separate parts of the same inflorescence (as in *Tripsacum*); b) In the female inflorescence, the pedicellate member of the spikelet pair is completely suppressed (Figs. 1 and 2). [Maize is an exception to this rule, as the pedicellate spikelets of its female inflorescence (ear) are fertile and produce grains.]. c) The grain is invested by a cupulate fruitcase which is composed of the deeply excavated rachis internode and the outer glume of the sessile spikelet (Figs. 1 and 2). (Again, maize is an exception in that its grains are not enclosed in cupulate fruitcases but are instead naked.)

*Tripsacum* has been recognized as closely related to *Zea* because of the morphological features described above and because it is known to cross with maize and produce viable but mostly infertile hybrids (Galvin, 1961, 1962; Mangelsdorf and Reeves, 1981, 1939). Further, biochemical data have shown that these two genera are more closely related to one another than to other members of the Andropogoneae (Khavkin et al., 1979; Smith and Lester, 1980). The fact that both taxa are native to the New World with their centers of diversity in southern Mexico supports the conclusion that they are closely related (Figs. 3-6).

Because of their affinity to maize, *Tripsacum* and teosinte have been the subjects of numerous biosystematic and evolutionary studies. Much of the work on *Tripsacum* was stimulated by Mangelsdorf and Reeves (1989), who suggested that introgression of *Tripsacum* germplasm into *Zea mays* was responsible for some of the present-day variation in the cultivar. However, it was not until 1967 with the publication of Wilkes' thesis (Teosinte: the closest relative to maize) and the resurrection of the hypothesis that teosinte was the direct ancestor of maize by Beadle (1972), deWet and Harlan (1972), Galinat (1971), and Ilits (1971) that the teosintes were subjected to careful taxonomic study.

In this paper I will summarize much of the taxonomic and evolutionary information available for both
Fig. 1. Inflorescence structure of *Tripsacum dactyloides* (Weatherwax, 1935: Fig. 7).

Fig. 2. Pistillate inflorescences of maize and teosinte (Weatherwax, 1935: Fig. 9). On the left, a cluster of female teosinte spikes as commonly found within the leaf sheaths of the main stem of plants grown in dense competition; thus, the cluster is lateral with respect to this mainstem.
*Tripsacum* and the teosintes. Understanding the taxonomy and evolution of the teosintes is of obvious importance. The teosintes belong to the same genus as maize (some even to the same species) and one of the teosintes is the direct ancestor of maize. Further, they all cross with maize to produce fertile hybrids, making them potentially useful sources of germplasm for maize improvement. Understanding the taxonomy and evolution of *Tripsacum* is of less agronomic interest. *Tripsacum* was not directly or even indirectly involved in the origin of maize and there is no evidence that it has contributed substantially to maize diversity (cf. deWet and Harlan, 1978; Galinat, 1977). Further, *Tripsacum*-maize hybrids are essentially sterile, making it difficult to use them in maize improvement. However, insect pests and a virus disease associated with *Tripsacum* have become problems on maize, and a thorough understanding of these diseases and insects requires some basic knowledge of *Tripsacum* (Nault and DeLong, 1980; Nault et al., 1980).

**THE GENUS TRIPSACUM**

Despite the relatively small number of species in this genus and that several botanists have studied it in varying depths over the past 50 yr, *Tripsacum* remains a taxonomically difficult group. The reasons for this include the following. First, the genus contains diploids, triploids, tetraploids, and even higher ploidy levels (N=18); some species have several of these. Second, some species of *Tripsacum* are apparently facultative apomicts which can give rise to minutely but consistently differentiated forms (deWet et al., 1981; Farquharson, 1955). Finally, natural hybridization between species may have produced intermediates which blur species boundaries (Randolph, 1970). Nevertheless, because of the efforts of Hitchcock (1906), Cutler and Anderson (1941), Randolph (1970), and deWet, Harlan and their associates (deWet et al., 1976; deWet et al., 1981), all of whom have studied aspects of *Tripsacum* taxonomy, a reasonably clear picture of the genus can be drawn.

All species of *Tripsacum* are perennial and all but one (*T. zopilotense* Hernandez and Randolph) produce stout rhizomes. They are vegetatively robust plants ranging from 1-5 m in height with leaves 1-10 cm wide. Their inflorescences are terminal on the stems and branches. When the branches of the main stems fail to elongate, their inflorescences remain partially enclosed by the leaf sheaths. The inflorescence is composed of 1 to 100 spikelike branches bearing pistillate spikelets below and staminate ones above (Fig. 1). Each pistillate spikelet contains both a fertile floret (flower) and a suppressed one; these are enclosed together in the cupulate fruitcase. The indurate fruitcases are either rectangular or trapezoidal in outline, and the horizontal abscission layers between them allow the inflorescence to disarticulate so the fruitcases can be dispersed. The

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*Fig. 3. Distribution of Tripsacum dactyloides and T. floridanum in the United States and the Caribbean.*
Fig. 4A. Distribution of *Tripsacum* in Mexico and Central America. Section *Tripsacum*.

Fig. 4B. Distribution of *Tripsacum* in Mexico and Central America. Section *Fasiculata*. 
staminate spikelet contains two fertile florets, each with three fully functional anthers. The outer glumes of the male spikelets generally have 10 to 20 nerves; the two major lateral nerves are elaborated into wings near the apex of the spikelet.

*Tripsacum* chromosomes are frequently marked by terminal heterochromatic regions called knobs, although some species apparently lack these structures (Chaganti, 1965; Longley, 1941; Ting, 1960). Chromosome knobs are found in other genera of the Andropogoneae; however, they are most common in *Tripsacum* and *Zea* (Galinat, 1977).

In 1906, Hitchcock divided the genus into sections *Dactyloides* and *Fasciculata*. Changes in the rules of nomenclature now require that section *Dactyloides* be called section *Tripsacum*; however, the taxonomy of the plants has not changed and this sectional division remains useful today.

**Section *Tripsacum***. The key taxonomic traits of this section are: a) the pedicellate spikelet of the spikelet pair sessile or nearly so; b) outer glume of staminate spikelets coriaceous; and c) branches of inflorescences few in number (usually 1 to 10), digitately arranged, stiff and straight, and ascending or weakly arched.

This section contains nine species which cover the entire geographic range of the genus.

**Tripsacum dactyloides** L. As applied by most workers, this name refers to an extremely diverse group of plants ranging from Massachusetts in North America to Colombia and Venezuela in South America, as well as the Caribbean Islands (deWet et al., 1981). The plants range from small to robust, being from 1-3.5 m tall and having leaves from 0.5-5.0 cm wide. The inflorescence may have from 1 to 10 branches and the male spikelets vary from 5-9 cm in length. The species includes diploids, triploids, and tetraploids, as well as higher

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**Fig. 5.** Distribution of *Tripsacum* in South America.
ploidy levels. Some members of this species are facultative amomicts (Farquharson, 1955). Newell and de Wet (1974) studied cytological and morphological variation in T. dactyloides of the United States, but found no way in which this portion of the species could be divided taxonomically. Further, taxonomic research will undoubtedly result in splitting this "species" into several smaller, more reasonably defined groups.

Both the diploid and tetraploid forms of T. dactyloides have been crossed to maize. The morphology, cytology, and potential agronomic uses of these hybrids and their derivatives have been studied extensively (Cohen, 1982; de Wet et al., 1978; Stalker, et al., 1977).

_Tripsacum floridanum_ Porter ex Vasey. This is a slender plant with culms rarely more than 1 m tall and leaf blades less than 1 cm in width. The inflorescence is composed of one to three branches and has male spikelets similar to those of _T. dactyloides_. The two species appear to be closely related both morphologically and cytologically (Tantravahi, 1968). The species is diploid and occurs in the Pinelands of southern Florida and in Cuba. It is of interest that this species crosses relatively easily with maize as compared to some other _Tripsacum_ (Galatin, 1961, 1962).

_Tripsacum zopilotense_ Hernandez and Randolph. This slender, diploid species, unlike other tripasacms, lacks rhizomes. Its leaves are at most 2 cm wide and its culms rarely exceed 1.5 m in height. The inflorescence is composed of a single spike which bears relatively small male spikelets (5-7 mm long). This species was described from specimens collected in the Zopilote Canyon in Guerrero, Mexico (Hernandez and Randolph, 1950). Similar narrow-leaved, rhizomeless tripasacms from localities in Guerrero, Jalisco, and Chiapas have also been classified as _T. zopilotense_ (Randolph, 1970).

_Tripsacum bravum_ Gray. This moderately robust species has culms from 1-2 m in height and leaves from 3-5 cm in width. Like _T. australre_ Cutler and Anderson, its basal leaf sheaths are tomentose, especially along the midrib. Each of its numerous inflorescences consists of a single (rarely two or three) spike. It is unique among the tripasacms in having few (three to six) nerves on the outer glume of its male spikelets. The species is diploid and known only from the moist woods and shady roadside escarpments of Valle de Bravo, Mexico, Mexico (de Wet et al., 1976).

_Tripsacum andersonii_ Gray. This species, generally known as "Guatemala grass", is cultivated and occurs ferally in both Meso and South America. It is the most robust of all _Tripsacum_ species, with culms up to 5 m tall and leaves up to 10 cm wide. It forms dense clumps and spreads by means of its robust stolons. Its fruitcases (4-6 mm wide and 7-8 mm long) and male spikelets (7-9 mm long) are among the largest in the genus. Unlike male spikelets of other species of _Tripsacum_, one member of its pairs is borne on a short pedicel (1-3 mm). It grows throughout much of Latin America from Peru to Guatemala.

_Tripsacum andersonii_ is unique within the genus in two respects. First, it is sterile, reproducing only by vegetative means. Second, its chromosome number (2N = 64) is unknown among other tripasacms (Levings et al., 1976). [Curiously, a specimen from Costa Rica (Pohl and Davidee 11411) of this species was determined to have 2N = 72, the unusual tetraploid number in the genus.] Because of this unusual chromosome number, the species has been interpreted as a _Zea_Tripsacum hybrid with three sets of _Tripsacum_ chromosomes (5 x 18) plus one set of _Zea_ chromosomes (N = 10) (de Wet and Harlan, 1978; de Wet et al., 1981).

_Tripsacum latifolium_ Hitchcock. This species is particularly robust, forming large clumps and having culms up to 5 m tall and leaves up to 7 cm wide. In habit, it resembles _T. andersonii_ and at times these two species have been confused. This similarity led de Wet and Harlan (1978) to hypothesize that _T. latifolium_ is the _Tripsacum_ parent of _T. andersonii_ (the supposed _Zea-Triapsacum_ hybrid). _T. latifolium_ is distinguished from _T. andersonii_ and most other tripasacms by its unusually small male spikelets (4-6 mm long). In some specimens, the spikelets are nearly as broad as long and superficially resemble those of the genus _Paspalum_. The species is tetraploid, and it occurs in the mesic woods of Guatemala, Belize, and Honduras. A specimen from Costa Rica has also been identified as _T. latifolium_; however, as illustrated by Pohl (1980), it has a distinctly pedicelled spikelet, a character not found in _T. latifolium_.

_Tripsacum australre_ Cutler and Anderson. This robust species has culms up to 4 m in height and leaves up to 6 cm in width. It is distinguished by its densely tomentose basal leaf sheaths. The species is diploid and reproduces sexually. It grows in the moist open woodlands of Venezuela, Colombia, Brazil, Bolivia, and Paraguay (Cutler and Anderson, 1941; cf. de Wet et al., 1981).

_Tripsacum peruvianum_ de Wet and Timothy. This is an erect (1-2.5 m tall), moderately robust species with leaves 3-4.5 cm wide. It is distinguished by its strongly hirsute leaf sheaths. The inflorescence has three to five branches. The species occurs along shady stream banks in Peru and Ecuador. It is a gametophytic amomict (2N = 72, 90, 108) (de Wet et al., 1981).

_Tripsacum cundinamarce_ de Wet and Timothy. This robust species has culms 3-4 m tall and leaves 4-6 cm wide. The inflorescence is composed of three to nine spikes having small spikelets (6-7 mm long). The species is distinguished by its glabrous, glaucous leaf sheaths and blades. This diploid species is found on river banks of the Department of Cundinamarca, Colombia (de Wet et al., 1981).

Section _Fasciculata_ Hitchcock. The key taxonomic traits of this section are: a) inflorescences with 10-100 or more lax spikelike branches, with the lower ones fascicled; b) one member of each spikelet pair borne on a slender pedicel; and c) outer glume of the staminate spikelet membranaceous.

This section contains four species which are restricted to Mexico and Central America.

_Tripsacum maisar_ Hernandez and Randolph. This is a particularly robust species with thick culms (4 cm in diam) up to 4.5 m in height and leaves which range
from 7-10 cm in width. Its basal leaf sheaths are densely hirsute, while its coriaceous leaf blades are essentially glabrous. The terminal inflorescence has from 18-50 or more spikelike branches, with spikelets from 5-8 mm long. The species is diploid and occurs from Costa Rica (?) to Guatemala to Nayarit, Mexico. Except for differences in general robustness, ploidy, and pubescence, T. maizari is remarkably similar to T. pilosum.

_Tripsacum pilosum_ Scribner and Merrill. This is a robust tetraploid with culms up to 3 m tall and leaves from 3-6 cm wide. The lower leaf sheaths are densely hispid and the blades are pilose. The inflorescence has 2 to 15 spikelike branches which have relatively large spikelets (7-9 mm long). This species is broadly distributed, ranging from Honduras to Zacatecas, Mexico.

_Tripsacum lanceolatum_ Rupr. ex Fourn. This is a narrow-leaved (1-3 cm wide), small to moderately robust species (1-2 m tall), with hispid lower leaf sheaths. The inflorescence has relatively few (one to nine) spikelike branches, the lowest number for section _Fasciculata_. The species occurs on the moist escarpments and stream banks of western Mexico (Jalisco) north to Arizona (deWet and Harlan, 1978). The species is tetraploid.

_Tripsacum laxum_ Nash. This is a robust species up to 3.5 m tall with leaves up to 8 cm wide. Its inflorescence has 5 to 20 long and slender spikelike branches. It is distinguished from other tripsacums of section _Fasciculata_ by its usually glabrous leaf sheaths and blades. The species is diploid and occurs from southern Mexico to Guatemala.

Fig. 7. Branched and unbranched plants of _Zea luxurians_ (Weatherwax, 1935: Fig. 6).
THE GENUS ZEA

Zea contains only four species and the relationships among these are well understood. The genus lacks the cytological complexities of Tripsacum; three of its species are diploid (N = 10) and one is tetraploid. Although each of the wild species hybridizes in nature with cultivated maize, backcrosses are infrequent, and there is no evidence of introgression into the wild taxa by the cultigen (Doebly, 1980; cf. Wilkes, 1972).

Zea contains both annuals and perennials, but only the annuals are robust maize-like plants. While most maize varieties are strictly monopodial, the teosinte when grown in the open or in cultivation tend to produce a lateral branch at each node as well as 1 to 10 (or more) basal tillers. However, in Mexico and Guatemala, the teosinte generally grow in strong competition with the surrounding vegetation; thus tillering is rare and branches are either absent or produced only along the upper third of the main stem. In teosinte a tassel crowns the apex of both the culms and their branches (Fig. 7), while the female spikes are produced either singly or in clusters within the leaf sheaths. Thus, the female spikes are lateral in position with respect to the main stem and its primary branches (Fig. 2). In maize the female spike (ear) is usually terminal on a highly shortened, primary, lateral branch, a position usually occupied by a tassel in an open grown teosinte (cf. Itis, 1979, 1981). Also in maize, tassels are restricted to the apex of the main stem and do not occur on lateral branches as in teosinte.

In teosinte each individual female spike is surrounded by a spathe (a modified leaf sheath) that protects it from being damaged before it matures. The spikes are composed of 4 to 12 or rarely more distichously arranged cupulate fruitcases which are exceedingly indurate and polished on the exterior. Abscission layers between the fruitcases allow them to separate from one another at maturity so they can be individually dispersed.

The male inflorescence (tassel) has up to 100 or more spikelike branches along which the spikelet pairs are distichously arranged. The central spike of the maize tassel is an exception to this rule of distichy in that its spikelet pairs, like those of the maize ear, are polystichously arranged (Fig. 8).

Like Tripsacum, Zea can be divided into two natural sections.

Section Luxuriantes Doebly and Itis. The key taxonomic traits of this section are: a) tassels with few branches, usually less than 15; b) male spikelets with stiff, firm glumes, the outer one flat on the back and having two strong lateral nerves which elaborate into wings apically; c) fruitcases trapezoidal; and d) chromosome knobs strictly terminal.

This section contains two perennial and one annual species.

Zea diploperennis Itis, Doebly and Guzman. This is a robust, clump-forming, perennial species that forms both short, tuberous and cordlike rhizomes with short internodes. The plants are from 1-2.5 m tall with leaves up to 5 cm wide. The male inflorescence has 2 to

Fig. 8. Staminate inflorescence of maize (Weatherwax, 1995; Fig. 10).
18 branches and the outer glumes of its spikelets possess well-developed lateral wings. The species is rare, restricted to the Sierra de Manantlan, Jalisco, Mexico (Ilitis et al., 1979).

**Zea perennis** (Hitchcock) Reeves and Manglesdorf. This species closely resembles *Z. diploperennis* but differs in several key characters. Notably, the plants are less robust, about 1.5 m tall with leaves from 1-3 cm wide. It lacks the short, thick, tuberous rhizomes of *Z. diploperennis*, but produces an abundance of longer, cordlike rhizomes with much longer internodes. These rhizomes spread aggressively so that the species grows in thick, dense mats. The morphology of the inflorescence is very nearly identical to *Z. diploperennis*, although *Z. perennis* has fewer (one to eight) tassel branches. *Z. perennis* is the only tetraploid in the genus. It has a narrow distribution and is known only from the vicinity of Ciudad Guzman, Jalisco, Mexico.

**Zea luxurians** (Durieu and Ascherson) Bird. This is a robust annual species that grows up to 3.5 m tall. It resembles the perennials in many respects, including its trapezoidal fruitcases, terminal chromosome knobs, and few tassel branches. It resembles the other annual teosintes in its almost strictly monopodial habit. It is distinguished from all *Zea* species by the numerous (15 to 25) closely spaced nerves on the outer glume of its male spikelet. The species is essentially restricted to southeastern Guatemala, with one additional population known from Honduras. A single collection made in 1842 is known from Oaxaca, Mexico, but the species has never been re-collected at this locality (cf. Doebly and Ilitis, 1980).

**Section Zea.** The key taxonomic traits of this section are: a) tassels with up to 100 or more (236) branches; b) male spikelets with flexible, papery glumes, the outer one rounded on the back, its major lateral nerves less strongly differentiated from the intermediate ones than in section **Luxuriantes** and without wings; c) fruitcases triangular in teosinte and represented by indurate invaginations (cupules) in the rachis (cob) in maize; and d) chromosome knobs both terminal and internal in position.

This section contains one species with three subspecies. One of the subspecies has two recognized varieties.

**Zea mays** L. spp. *parviglumis* Ilitis and Doebly var. *parviglumis*. Race Balsas of Wilkes (1967). In the wild, this is a robust (up to 3.5 m tall), untillered, but much branched plant with a strong root system. Its tassel has up to 236 branches which bear the smallest [5-7(8) mm long] spikelets known in the genus. The fruitcases are also small, varying from 31 to 60 mg in weight. The leaf sheaths lack the dark red anthocyanaceous coloration and dense pubescence typical of *Z. mays* spp. *mexicana*. The leaf blades vary from sparsely to moderately pubescent, the most pubescent forms occurring in southwestern Jalisco. This teosinte grows in Mexico at medium elevations (400 to 1600 m) in the states of Guerrero, Michoacan, and Mexico (the Balsas River drainage), as well as southwestern Jalisco.

**Zea mays** L. spp. *parviglumis* var. *huehuetenangensis* Ilitis and Doebly. Race Huehuetenango of Wilkes (1967). This variety is morphologically very similar to var. *parviglumis*, but differs in that it is adapted to a wetter habitat with a longer growing season. Thus, the plants tend to be much taller (up to 5 m), have larger, glabrous leaves, and are much later in flowering. This teosinte is known only from the province of Huehuetenango in western Guatemala.

The similarity in tassel morphology between vars. *huehuetenangensis* and *parviglumis* is not entirely reflected in their biochemistry and cytology. Isoenzymatically, there are larger differences between these two varieties than one would predict based on morphology (Doebly, M. M. Goodman, and C. W. Stuber, unpublished). The same is true for their chromosome knobs (Kato, 1976). However, these two varieties are quite similar in their cytoplasm DNA's (Timothy et al., 1979) and seed proteins (Mastenbroek et al., 1981). These varieties might best be recognized as separate subspecies, if it were not for their similar inflorescence morphologies, cytoplasm genomes, and seed proteins.

**Zea mays** L. ssp. *mexicana* (Schrad) Ilitis. In the wild, this is a robust (up to 3.5 m tall), usually unilliered plant with a weak root system. Its tassel has relatively few (1 to 30) branches which bear large spikelets (6.5-10.5 mm long). The fruitcases are generally large, ranging from 56-104 mg in weight. The leaf sheaths are often dark red in color and densely pubescent. It grows at relatively high elevations (1750-2500 m), mostly in central and, to a much lesser extent, in northern Mexico.

The subspecies is divided into three weakly differentiated races. Race *Chalco* has the reddest, most pubescent leaf sheaths and is restricted to the Valley of Mexico and its slopes. The plants of race *Nobogame* are generally somewhat depauperate and flower earlier than others of *Z. mays* ssp. *mexicana*. This race, the most northern of all teosintes, is restricted to the Nobogame Valley of Chihuahua. Race *Central Plateau* has some depauperate populations which resemble race *Nobogame* and other robust populations indistinguishable from race *Chalco* (Wilkes, 1967). Race *Central Plateau* occurs in Michoacan, Guanajuato, eastern Jalisco, and Durango.

**Zea mays** L. ssp. *mays*. The essential botanical difference between maize and the annual teosintes of Mexico are confined to the inflorescences. While the central spike of the teosinte tassel is slender and distichous, the central spike of the maize tassel is substantially thickened and polystichous (Fig. 8). The female inflorescences of maize and teosinte are especially dissimilar. As mentioned previously, the teosinte female spike is composed of 4 to 12 distichously arranged, highly indurate cupulate fruitcases, each containing a single fertile spikelet. These spikes, which disarticulate at maturity, are lateral to the mainstem and its primary branches. The maize female spike (ear) is polystichous, with from 8 to 26 or more rows of grain, these firmly attached to a massive central axis (cob) and thus incapable of dispersing. The equivalents of the teosinte cupulate fruitcases in the maize ear are the hidden, indurate invaginations in the cobs known as cupules.
The entire maize spike is completely surrounded by a series of enlarged leaf sheaths (husks) which originate on the telescoped primary branch (shank) and protect the developing ear from pests and predators. The ear is terminal on a lateral branch (Fig. 2).

**THE PHYLOGENY OF THE TRIPSSACINAE**

In this section, I will discuss the evolutionary relationships among the tripssacums and teosintes. To begin, one can safely conclude that of the two genera, *Tripssacum* is the older and more primitive. Support of this statement comes from several independent lines of investigation.

First, in considering the inflorescence, one must recall that the inflorescences of most Andropogoneae contain at least some bisexual spikelets. This is the primitive condition. In *Tripssacum*, the spikelets are not bisexual but rather may be either female proximally or male distally; these two types of spikelets occur together in the same inflorescence. In this sexual dimorphism, one witnesses an advancement over the typical Andropogonaceous pattern. In *Zea* there is further evolutionary change in that not only are the spikelets unisexual but the male and female spikelets are segregated into separate inflorescences. In this sense then, *Tripssacum*, with its male and female spikelets in the same inflorescence, more closely resembles other Andropogoneae, suggesting that it is less specialized than *Zea*.

Similarly, if the structure of the cupulate fructicase is considered, it will be recognized that the *Tripssacum* fructicase much more closely resembles the rachis internode (the structure from which it evolved) than does the fructicase of teosinte. The *Tripssacum* fructicase is often rectangular in outline (cylindric in shape), the same as the rachis internode. Although it shows considerable induration, it never approaches the extreme induration of the teosinte fructicase. In this sense then, the fructicase of *Tripssacum* more closely resembles the rectangular, non-indurate rachis internode, its precursor.

In seasonal growth form, *Zea* also appears more specialized. Although the overwhelming majority of Andropogoneae are perennial (suggesting this to be the primitive condition), a few genera include some annual species. In this regard, *Zea*, which includes two annuals, must be judged more specialized than *Tripssacum*, which has only perennials.

The biogeography of *Tripssacum* and *Zea* also hints that *Tripssacum*, with its much broader, natural distribution, is the older genus. Similarly, the larger number of species in *Tripssacum* suggests a longer evolutionary history for this genus.

Except for the basic division of *Tripssacum* into sections *Fasciculata* and *Tripssacum*, little is known of the evolutionary relationships within the genus. Both of these sections have a combination of specialized and primitive characteristics. Morphologically, the stiff, ascending inflorescence branches and the brittle, chartaceous, and flattened outer glumes of section *Tripssacum* resemble quite closely certain species of other genera of the Andropogoneae, including *Andropogon* and *Rottboellia*. However, one apparently advanced morphological trait found in section *Tripssacum* is that the pedicellate male spikelet of each pair is essentially sessile. The male spikelet pairs in section *Fasciculata*, on the other hand, are clearly one pedicellate-one sessile; this is the usual pattern in the Andropogoneae.

In *Zea*, the morphological and other evidence suggests that the teosintes of section *Luxuriantes* are the most primitive taxa in the genus. These teosintes, especially the perennials, hold many morphological features in common with *Tripssacum*, including: a) typically many-nerved, flattened outer male glumes with two prominent lateral nerves developed into wings; b) short, flattened internodes in the male portion of the inflorescence; c) trapezoidal fructicases; and d) perennials rhizomatous root system and in the perennials, a weakly monopodial habit. Cytologically, the chromosomes of section *Luxuriantes*, like those of *Tripssacum*, have many terminal chromosome knobs and no internal ones. Section *Zea*, on the other hand, has internal chromosome knobs which probably represent an evolutionary advancement.

After the initial divergence of sections *Luxuriantes* and *Zea*, diversification continued within each of these two taxa. Within section *Luxuriantes*, *Z. luxurians* probably separated quite early from the perennials. It might have abandoned the perennial habit as an adaptation to disturbed conditions in the dry and highly seasonal environments of southeastern Guatemala and acquired the monopodial form typical of annual pioneers. The divergence between *Z. diploperennis* and *Z. perennis* apparently came somewhat later by means of autopolyploidy (Shaver, 1962; Galinat, 1971).

Section *Zea* probably diverged from section *Luxuriantes* by developing the annual habit as an adaptation to disturbed conditions and to highly seasonal, arid habitats. It can be observed that perennial species commonly assume the annual habit in adapting to dry, seasonal environments. At some point, section *Zea* underwent diversification, producing the two wild subspecies of *Z. mays*. One of these, *Z. mays* spp. *mexicana*, colonized the higher, colder, drier sites with a shorter growing season and is characterized by large seeds, red hairy sheaths, large male spikelets, and fewer tassel branches as an adaptation to this environment (Doebly, 1980). The other, *Z. mays* spp. *parviglumis*, colonized the lower, warmer, seasonally moister sites with a longer growing season and is characterized by small seeds, glabrous green or dilute red sheaths, small male spikelets, and many tassel branches (Doebly, 1980).

**THE ORIGIN OF MAIZE**

The origin of maize has beguiled botanists for well over a century. During this time most authors have supported either the hypothesis that maize evolved from a polystichous wild maize (Manglesdorf, 1974; Randolph, 1976; Wilkes, 1979) or that teosinte is the ancestor of maize (Beadle, 1972; deWet and Harlan, 1972; Galinat, 1971; Iltis, 1971; Iltis and Doebly, 1980; Kato Yamakake, 1976). Since the early 1970's, the tide of opinion has moved in favor of the latter theory; however, the subject remains controversial.
In my own view, the most parsimonious interpretation of the facts is to consider the anomalous polystichy of maize, which is found only in the cultigen and in no other Andropogoneae, as the utilitarian artifact of domestication (Doebly and Itis, 1980). Specifically, maize appears to be a domesticated form of one of the teosintes of section Zea, differing from these teosintes in none of its essential botanical characteristics. Other available data support this interpretation of morphology. Beadle (1972) has indicated that the number of critical gene differences between maize and teosinte are very small, perhaps only four or five. Timothy et al. (1979) have shown that certain maize lines and Z. mays ssp. mexicana and ssp. parviglumis were not distinguished by either their chloroplast or mitochondrial genomes. A study of isoenzymatic variation of maize and teosinte showed no substantial differences between maize and Z. mays ssp. parviglumis var. parviglumis (Doebly, M. M. Goodman, and C. W. Stuber, unpublished). Cytological studies of certain maize races and teosinte showed no substantial differences between Z. mays ssp. parviglumis var. parviglumis and Z. mays ssp. mays (Kato Yamakake, 1976). Indeed, when size and position of chromosome knobs, presence of B chromosomes, and an abnormal form of the tenth chromosome are all considered, this teosinte and many Mexican maize races are astounding similar (McClintock et al., 1981). Finally, and perhaps most importantly, maize and the teosintes of section Zea belong to the same species, crossing with complete freedom and producing fully fertile hybrids in most cases (Darlington, 1956; Itis, 1972).

While many authors have recognized that the biosystematic data point to teosinte as the ancestor of maize, the archaeological evidence apparently does not. The oldest archaeological maize recovered from Tehuacan possesses long, soft glumes, a narrow flexible rachis, and shallow non-indurate cupules (Mangelsdorf, 1974). These are all characteristics which would be difficult to derive from the female teosinte spike. For this reason and others, Mangelsdorf and his colleagues have remained staunchly committed to their theory that maize evolved from a "wild maize" and not from teosinte. Recently, Itis (1979, 1981) proposed a new theory called the Catastrophic Sexual Transmutation Theory which tries to explain both the biosystematic and archaeological evidence. Itis suggests that the central spike of the teosinte tassel, which normally terminates a lateral branch in teosinte (and not the teosinte female spike), gave rise to the familiar maize ear. This idea is related to earlier theories of Kellerman (1895), Montgomery (1906), and Weatherwax (1995) in which the maize ear is derived from a male inflorescence but not the male inflorescence of teosinte.

This theory makes good sense morphologically because the maize ear is terminal on a lateral branch, a position that in teosinte is usually occupied by a tassel. Thus, the initial step in the domestication of maize would have been a sex change from male to female of the central spike of the tassel terminating the lateral branch. Itis believes this change and the subsequent (or concurrent) condensation of the central spike into the maize ear happened rapidly; thus, we have the "Catastrophic Sexual Transmutation Theory."

One of the most intriguing aspects of this theory is its implication for the archaeological specimens from Tehuacan. As described above, they do not appear intermediate between the teosinte female spike and the maize ear. However, under Itis' theory, they are precisely the intermediates expected. The central spike of the teosinte tassel has a flexible rachis, shallow non-indurate cupules, and spikelets with long, soft glumes, the same as the Tehuacan specimens (cf. Mangelsdorf, 1974). Further, the central tassel spike of teosinte has two functional spikelets per node (cupule), the same as the maize ear but unlike the teosinte ear. So by following Itis' theory, one need no longer be concerned with the reactivation of a suppressed female spikelet (cf. Beadle, 1972).

Itis' theory on the origin of the maize ear must now be assessed in relationship to the older theory that the maize ear evolved from the female spike of teosinte (Galatin, 1971). The need for this reassessment provides an opportunity to restudy in detail the developmental morphology of the inflorescences of Zea. The future for research on the ancestry of maize promises to be full of new discoveries and revelations.

THE USE OF TRIPSACUM AND TEOSINTE IN MAIZE BREEDING

Neither Tripsacum nor teosinte have been of any importance in improving maize or in broadening its genetic base. They have not generally been used by commercial maize breeders simply because any positive traits they possess are drastically overshadowed by other deleterious traits, including reduction in yield, loss of stalk strength, and undesirable changes in plant architecture such as increases in tiller and ear number. Indeed, with rare exceptions, practicing maize breeders are not only reluctant to work with these wild relatives of maize, but have generally portrayed a reluctance to incorporate even tropical maize races in their breeding programs. For this reason, the chase of tapping these genetic resources has fallen largely on the shoulders of the basic research community. The accomplishments of these scientists demonstrate a certain degree of promise in some areas, most notably in the area of disease and insect resistance. There have been several accomplishments to date.

Bergquist (1981), starting with a maize-T. dactyloides hybrid, obtained agronomically useful inbred lines that were resistant to the common rust, Puccinia sorghi Schw. Similarly, resistance to northern leaf blight was obtained from T. floridanum by Hooker and Perkins (1980). Nault and Findley (1981) are in the process of developing maize resistant to maize chlorotic dwarf virus using Z. diploperennis as the source for this resistance.

The wild relatives of maize may be useful in breeding for resistance to other diseases and insects. Branson (1971) and Branson and Guss (1972) have shown that T. dactyloides, T. laxum, and T. floridanum are highly
resistant to western corn rootworm (Diabrotica virgifera LeConte). Branson (1972) found these same three species to show considerable resistance to the corn leaf aphid [Rhopalosiphum maidis (Fitch)]. Nault et al. (1982) report the perennial teosinte to be resistant or immune to a number of maize viral diseases, including maize chlorotic dwarf, maize chlorotic mottle, maize streak, and maize stripe.

The fact that the perennial species of the Tripsacinae show greater resistance to diseases and insects is of some interest. In general, perennials maintain higher disease and insect resistance because their sedentary and long-lived lifestyle makes them easily locatable by pests which accumulate on them. Annuals, which can evade diseases by migrating more regularly from place to place, are not under as strong selection to develop resistance, and thus tend to show greater susceptibility to diseases and predation (Feeny, 1976).

The ability of researchers to transfer disease resistance from *Tripsacum* and teosinte to maize resides in part in the genetic nature of these traits. If polygenic, the chances of successfully transferring the trait are small and get progressively smaller as the number of genes increases. This is especially true with *Tripsacum* because its chromosomes exhibit a low degree of homology with those of maize, making it difficult to transfer a single gene, let alone several genes, simultaneously. At the other extreme, there exists considerable hope that *Z. diploperennis* can make an important contribution to maize improvement, because it is both genetically similar to maize and a disease resistant perennial.

**LITERATURE CITED**


