

SYSTEMATICS OF TRIPSACUM (GRAMINEAE)

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ABSTRACT

The genus Tripsacum L. (Gramineae) is New World in distribution. It crosses with Zea L. and together they form the Tripsacinae of the Andropogoneae. The genus was divided into species with pendulous inflorescence branches having the upper spikelet of each staminate pair pedicelled - T. fasciculatum Trin. ex Aschers., T. lanceolatum Rupr. ex Fourn., T. maizar Hern. and Randolph and T. pilosum Scribn. and Merr., and species with stiff inflorescence branches having both spikelets of a staminate pair essentially sessile - T. andersonii Gray, T. australe Cutler and Anderson. T. bravum Gray, T. dactyloides (L.) L. T. floridanum Porter ex Vasey, T. latifolium Hitchc. and T. zopilense Hern. and Randolph. Within groups species are distinguished on the basis of habit, size and pubescence.

TRIPSACUM L. is the only grass genus with which domesticated maize (Zea mays L. ssp. mays) is known to cross and produce viable hybrids. The genus was at one time implicated with the origin and evolution of North American maize (Mangelsdorf and Reeves, 1939), but has since been shown to be genetically independent from Zea (de Wet and Harlan, 1976). Nevertheless, Tripsacum is an important potential source of genetic variability in maize improvement. For this reason the behavior of Tripsacum chromosomes in a maize gametophyte has been studied in some detail (de Wet and Harlan, 1974). These studies, however, involve only T. dactyloides (L.) L., and T. floridanum Porter ex Vasey from north of the Mexican border. Collections of Mesoamerican and South American Tripsacum have been assembled and are being maintained by Fairchild Tropical Garden (Florida), CIMMYT (Mexico), and CIAT (Colombia). A preliminary survey of morphological variability within the genus was presented by Cutler and Anderson (1941), and Randolph (1970) suggested that the usually recognized Mesoamerican taxa often grade morphologically into one another. This paper illustrates the major morphological complexes of Tripsacum as recognized by their type specimens or specimens from type localities.

MATERIALS AND METHODS

This study is based on 1500 herbarium specimens, including types, on living plants grown in uniform nurseries at Urbana, (Illinois), Redlands (Florida), Tlaltizapan (Morelos, Mexico) and Medellin (Colombia), and naturally occurring populations across the range of Tripsacum in North and South America. Specimens were obtained on loan from the United States National Museum (US), Missouri Botanical Garden (MO), Gray Herbarium of Harvard University (GH), University of Michigan (MICH), Fairchild Tropical Garden (FTG), Chicago Natural History Museum (F)

Instituto de Botanica, Brazil (SP), Herbario Nacional del Instituto de Biologia, Univ. Nacional de Mexico (MEXU), Instituto Botanico, Venezuela (VEN), and The Herbarium, Kew (K). Specimens collected by the authors in their numerous travels across the range of the genus are filed in the herbarium of the Crop Evolution Laboratory (CEL).

RESULTS

Tripsacum is composed of two more or less well defined species complexes (Hitchcock, 1906). Typically T. fasciculatum Trin. ex Aschers., T. lanceolatum Rupr. ex Fourn., T. maizar Hern. and Randolph, and T. pilosum Scribn. and Merrill have the upper spikelet of each staminate pair supported by a slender pedicel, the staminate portion of each inflorescence branch is pendulous, the branches of terminal inflorescences are often numerous, and the lower primary branches are often divided to form fascicles arranged on a somewhat elongated primary axis. In contrast, T. andersonii Gray, T. australe Cutler and Anderson, T. bravum Gray, T. dactyloides (L.) L., T. floridanum Porter ex Vasey, T. latifolium Hitch. and T. zopilotense Hern. and Randolph have both staminate spikelets of each pair sessile or essentially so, the staminate portion of each inflorescence branch is at most curved, the branches of terminal inflorescences are relatively few in number, and they are more or less subdigitately arranged on a short primary axis. Within complexes species are primarily distinguished on the basis of spikelet size, number of inflorescence branches, absence or presence of rhizomes, size, and on pubescence of leaf blades and sheaths. A workable key to the species was presented by de Wet and Harlan (1976).

TRIPSACUM ANDERSONII Gray Sp. Nov. (Fig. 1).

Tripsacum guatemalensis Chitwood and Berger, Plt. Disease Rep. 846. 1960. Nomen nudem.

Gramen perenne rhizomatosum, 1-4 m altum. Culmis repentibus ad nodos radicanibus, glabris, foliorum vaginis glabris. Lamina plana, 6-8 cm lata, ad 120 cm longa, superne glabra vel pilosa, subter glabra. Inflorescentia terminalis ex 1-5 racemis composita. Una ex pari spicularum staminiferarum pedicellata, 7-9 mm longa. Spiculae femineae 4-5.5 mm diametro.

This species was described to include the widely cultivated tropical forage commonly known as "Guatemala" grass. It is a robust perennial with short rhizomes and decumbent culms that reach 4m in height. Leaf-sheaths are glabrous or nearly so, as are the up to 8 cm wide blades. Terminal inflorescences have 1-5 branches, each consisting of 4-12 fruitcases and a section of paired staminate spikelets above. One spikelet of each staminate pair is sessile and the other is supported by a stiff, 1-2 mm long pedicel that is almost as broad as it is long. Glumes of the staminate spikelets are coriaceous and 7-9 mm long. The species is largely female sterile and has $2n=64$ chromosomes (Levings, Timothy and Hu, nd).

This is primarily a cultivated species, but occurs spontaneously along streams in Tropical Mesoamerica and Tropical South America. Staminate spikelet glumes resemble those of hybrids between maize and Tripsacum discussed by Newell and de Wet (1973). Indeed the species behaves cytologically as if it combines 54 Tripsacum and 10 Zea chromosomes. The chromosomes associate into 12-21 I, 12-23 II, 0-8 III and 0-2 IV configurations during meiotic prophase, with at least 10 univalents moving precosiously to the equator during late diakinesis. Tripsacum taxa with $2n=54$ chromosomes are rare, but T. andersonii could have originated as a cross between diploid Tripsacum ($2n=36$) and maize ($2n=20$). When diploid Tripsacum is pollinated by maize, the resulting hybrids often have 36 Tripsacum + 10 Zea chromosomes. When these are backcrossed with the Tripsacum parent, offspring with 54 Tripsacum + 10 Zea chromosomes are obtained (de Wet et al., 1973). The Tripsacum species that may have been involved have as yet not been identified. The species probably originated in northwestern South America, an area from which Tripsacum is poorly collected, and the taxonomy of the genus is poorly understood.

Selected specimens: TYPE-E. Anderson 15576, San Francisco, El Paraiso, "Zacate de Guatemala", Honduras (Holotype, MO; Isotype, NY). P. H. Allen 2252, El Valle de Anton, Prov. Cocle, Panama (MO). CEL 4606 10 miles from Mexican border town of Ciudad Cuauhtemoc, Guatemala (CEL). CEL 4269, 24 km west of Barinitas along mountain stream on road from Barinas to Merida, Venezuela (CEL). E. Asplund 12381, Tingo Maria rivershore, Dept. Huanuco, Peru (US). V. P. Patino, Cultivado localidad Jauquincito, Rio Maya, Buena Ventura Valle, Colombia (MO). R. Klein 2702, Florianopolis, cultivado Santa Catarina, Brazil (US).

TRIPSACUM AUSTRALE Cutler and Anderson, Ann. Mo. Bot. Garden 28: 259. 1941 (Fig. 2).

This is a morphologically variable species with erect or decumbent culms up to 3 m tall. The leaf-sheaths typically have a lanulose tomentum, especially above the middle, while the 2-6 cm wide blades are essentially glabrous, except for the petiolate part of lower leaves which may be covered with a woolly tomentum. Terminal inflorescences have 1-5 branches that are erect or curved at maturity. The glumes of staminate spikelets are coriaceous and 5-9 mm long, with both spikelets of each pair sessile. The species is diploid with $2n=36$ chromosomes.

Tripsacum australe is widely distributed in South America. It is poorly understood taxonomically, and is recognized to include slender erect as well as robust erect to decumbent plants. Inflorescence morphology is similar to that of T. dactyloides, and T. australe can consistently be distinguished from this species only by the lanulose tomentum on the leaf-sheaths. The leaf-sheaths of T. dactyloides range from glabrous to densely pilose, and Thomas Morong 675 from Central Paraguay (NY,US) cited by Hitchcock (1906) under T. dactyloides ssp. hispidum actually belongs with T. australe. A wide range of

specimens are cited by Cutler and Anderson (1941), and only a few selected specimens will be listed here to indicate the range of morphological variability in the species.

Selected specimens: TYPE-O. E. White 2324, marshy edges of forest, Ixiamus, Amazon Basin, Bolivia (NY,US). H. C. Cutler 5635, 12 km south of Aquidauna, Mato Grosso, Brazil. N. C. Fasset 26001, Upper Rio Lebrija, northwest of Cucaramanga, Santander, Colombia (US). A. S. Hitchcock 20643, between Huigra and Naranjapa, Chimborazo, Ecuador (NY,US). D. H. Timothy 207 (66-14) 2 km east of Terpoto on road to Shapaja, San Martin Tarapoto, San Martin Prov., Peru (FTG). J. A. Steyermark 27875, between Sabana Grande and southeastern base of Cerro Duida, Amazonas, Venezuela (US).

TRIPSACUM BRAVUM Gray, Sp. Nov. (Fig. 3).

Gramen perenne, rhizomatosum 1.5-3m altum. Culmis erectis, foliorum vaginae lanulosae tomentosae. Lamina plana, 3-5 cm lata, ad 60 cm longa, superne sparse induta, subter glabra. Inflorescentia terminalis ex 1 raro 2 racemis composita. Spiculae staminiferae sessiles, 3-5 mm longa. Spiculae femineae 2-2.5 mm diametro.

This is an erect species with medium robust culms up to 3 m tall. Leaf-sheaths are essentially glabrous except along the midrib and near the insertion of the blade where they are tomentose. The 3-5 cm wide blades are tomentose below, and tomentose above near the base and along the midrib. Terminal inflorescences have one spike, with the male section stiffly erect. Glumes of staminate spikelets are membranaceous, 4-6 mm long, and both spikelets of a pair are sessile. The species is a diploid with $2n=36$.

Tripsacum bravum seems to be endemic to the Valley de Bravo where it occupies open woodland. It resembles T. dactyloides in spikelet morphology, except that the glumes are membranaceous rather than coriaceous. From T. australe it differs in having the sheaths tomentose primarily along the midrib rather than all over the outer surfaces.

Selected specimens: TYPE-J. R. Harlan and M. Gutierrez 93, 2.6 miles below Valle de Bravo Dam on road to Santo Tomas, State of Mexico (ILL, MEXU, CEL).

TRIPSACUM DACTYLOIDES (L.) L. Syst. Nat. ed. 10: 1261. 1759 (Fig. 4).

The synonymy of T. dactyloides is discussed by Cutler and Anderson (1941) and synonyms need not again be listed here. We include in T. dactyloides subspecies hispidum Hitchc. which they transferred to T. lanceolatum.

This is a medium robust species with essentially erect culms up to 3 m tall. Leaf-sheaths are glabrous to pilose, and the 0.5-4 cm wide blades are glabrous to pilose. Terminal inflorescences have 1-6 branches, rarely more, with the male section stiffly erect or curved

at maturity. Glumes of staminate spikelets are typically coriaceous and 5-10 mm long, and both spikelets of a pair are sessile or the upper one may be supported by a stiff pedicel usually not more than 1 mm long. Chromosome races of $2n=36,54$ and 72 occur across the range of the species (Newell and de Wet, 1974b).

Although extremely variable in inflorescence, vegetative and habitat characteristics, Newell and de Wet (1974b) demonstrated that T. dactyloides cannot readily be divided into distinct taxonomic units. The species is a facultative gametophytic apomict, and morphologically distinct complexes frequently have no ecogeographic unity. For this reason T. dactyloides var. occidentale Cutler and Anderson is not recognized as distinct from typical T. dactyloides. Similarly, T. dactyloides ssp. hispidum is included in typical T. dactyloides. Hitchcock (1906) recognized this subspecies to include plants with hispid leaf blades and glabrous or hispid sheaths. He further pointed out that the "staminate flowers are less chartaceous than is usual in T. dactyloides" and that in "some specimens the upper spikelet of the staminate pair is somewhat pedicelled". However, numerous specimens which are typically T. dactyloides in inflorescence morphology, have hispid or pilose blades and sheaths. These plants extend from the southcentral U.S. throughout Mexico, and resemble in this respect T. lanceolatum and T. pilosum. However, the upper staminate spikelet at each rachis node is at most shortly pedicelled, and the male section of the inflorescence branches is never pendulous. Both T. lanceolatum and T. pilosum are characterized by slender pedicels and slender, pendulous racemes.

The type of this species was not available for study. It is based on Coix dactyloides L. (Sp. Pl. 972.1753). Tripsacum dactyloides is widely distributed across the range of the species. Numerous specimens from the U.S. are cited by Cutler and Anderson (1941). Selected specimens from Mesoamerica and South America are cited here to indicate the range of the species.

Selected specimens: G. V. Nash and N. Taylor 1099, scrub, Blackville, Inagua, Bahamas (US). H. H. Rusby and F. W. Pennell 1127, Arroyo on foothills, Huila, east of Neiva, Cordiller Oriental, Colombia (NY). A. H. Liogier 12597, Limestone hill, west of El Cerado near town, Dominican Republic. M. A. Solis 21584, Naranjapata Prov., Chimborazo, Ecuador (NY). P. C. Standley 75520, Jutiapa, hills between Jutiapa and Plan de Unrulia, N. of Jutiapa (NY). L. F. Randolph and A. Molina R. H. 66-102, Morazan, Los Mesas east side of Yeguaré Valley (FTG). F. L. Wynd and C. H. Mueller 536, Coahuila, Canon de Sentenela, Hacienda Piedra Blanca, Sierra del Carmen, Villa Acuna, Mexico (MEXU). C. Patoni 266, Durango, Ciudad de Durango, Cerro de Mercado, Mexico (MEXU). P. Fryxwell 612, Guerrero, Pochote, 9 miles west of Teloloapan on rocky hillside, Mexico (MEXU). G. B. Hinton 15206, Michoacan, Rancho Viejo, Apatzingam, Mexico (NY). R. McVaugh 13392, Nayarit, 10 miles SE of Tepic Mexico (MEXU). Arsene 1328, Puebla, vicinity of Puebla, Mayorazgo, Mexico (ILL). C. G. Pringle 3811, San Luis Potosi, rocky hills, Las Canoas, Mexico (US). H. H. Bartlett 10310, Tamaulipas, Cerro Parrena, vicinity of San Jose, Sierra de San Carlos, Mexico (NY). V. M. Patino 109, Adjuntas Momboy-Motalan, carretera Valera-Merida, Edo Trujillo (VEN).

TRIPSACUM FASCICULATUM Trin. ex Aschers., Bot. Zeit. 33: 525. 1877
(Fig. 5).

Tripsacum fascilatum Trin. ex Steudel, Nomencl. Bot. ed. 2: 721. 1841.
Nomen nudum.

Dactyloides fasciculatum Kuntze, Rev. Gen. Pl. 2: 773, 1891.

Tripsacum laxum Nash, N. Amer. Fl. 17: 81. 1909.

The name Tripsacum fasciculatum was first used for an American grass by Steudel (1841). The name was accepted and validly described by Ascherson (1877). Two specimens are cited, a collection of Schiede from 'Hacienda de la Laguna', and one of Liebman from 'Mirador', both localities in the State of Veracruz, Mexico. Probably to avoid confusion with Andropogon fasciculatum L., which does not refer to an American grass (Hitchcock, 1908), Nash (1909) described T. laxum, based on T. fasciculatum Trin. ex Ascherson. Cutler and Anderson (1941) accepted T. fasciculatum, while Randolph (1970) preferred to use T. laxum. There is, however, no valid reason why the epithet fasciculatum should be discarded in favor of laxum in the genus Tripsacum.

The species as recognized by Cutler and Anderson (1941) and Randolph (1970) includes two morphologically distinct complexes, the cultivated 'Guatemala' grass, and spontaneous T. fasciculatum which conforms to the type. The cultivated complex was recently described as T. andersonii (de Wet and Harlan, 1976). A fragment of the type of T. fasciculatum, collected in 1836 by H. Schiede at the 'Hacienda de la Laguna', consisting of two inflorescence branches, is in the Smithsonian (US). Liebman 541, also cited by Ascherson, could not be located in the Berlin Museum. However, another Liebman specimen (549) from 'Mirador' is in the herbarium of the Missouri Botanical Garden (MO). Furthermore, Gallotti 5796 (NY) collected from the type locality was available for study.

This species is a robust perennial with short rhizomes and somewhat decumbent culms up to 3.5 m tall. The leaf sheaths are glabrous or sparsely pilose, and the glabrous blades are up to 8 cm wide. Terminal inflorescences consist of 5-14 branches, with the male sections typically pendulous. Staminate spikelet glumes are 5-8 mm long, with the upper one of each spikelet pair supported by a slender 2-5 mm long pedicel, and the other one sessile. The species is a diploid with $2n=36$ chromosome. It occupies mesic woodlands of central Mexico, along the coastal escarpments of both eastern and western mountain ranges.

Selected specimens: TYPE-H. Shiede 947, Hacienda de la Laguna, Veracruz, Mexico (Isotype US). Gallotti 5796, Veracruz, Hacienda de la Laguna, Mexico (NY). Liebman 549, Veracruz, Mirador, Mexico (MO). CEL 4872, Veracruz, 1/2 mile west of Fortin de Las Flores on highway 150, Mexico (CEL). CEL 4616, Colima, 7.6 miles south of Puerto Los Mazos pass on highway 80 to Baras de Navidad Mexico (CEL). A. S. Hitchcock 7103, Colima, rocky grassy hillside, Alzada, Mexico (US). CEL 4590, 18 miles from Ipala on road to Jalapa, Guatemala (CEL). CEL 4591, 11.2 miles from Jalapa on road to Progreso, Guatemala (CEL).

TRIPSACUM FLORIDANUM Porter ex Vasey, Contr. U. S. Nat. Herb. 3:6.
1892 (Fig. 6).

Tripsacum dactyloides var. floridanum Beal. Grasses N. Amer. 2: 19.
1896.

This is a small, slender perennial with culms up to 1 m tall. The leaf-sheaths are glabrous, as are the narrow, 0.4-0.8 cm wide blades. Terminal inflorescences are erect with one or two branches. Staminate spikelets are 5-6 mm long, and both spikelets of a pair are sessile. The species is diploid with $2n=36$ chromosomes. It is known from Cuba and southern Florida. Cutler and Anderson (1941) reported specimens from coastal eastern Texas. These plants have broader (0.9-1.3 cm), and more erect leaf-blades. They cross with T. floridanum, and although chromosome pairing is complete during meiotic prophase, the hybrids are sterile. They also cross readily with more typical representatives of T. dactyloides and these hybrids are generally fertile.

Selected specimens: TYPE-A.P. Garber 77, Miami, Florida (NY).
R. W. Pohl 7592, vacant lot, Homestead, Dade County, Florida (GH).
E. L. Ekman 14152, Oriente, Yara, road to Nagua, Cuba (US).

TRIPSACUM LANCEOLATUM Rupr. ex Fourn., Mex. Pl. 2: 68. 1886 (Fig. 7).

Tripsacum lanceolatum Rupr. in Benth., Pl. Hartw. 347. 1857. Nomen nudum.

Tripsacum acutiflorum Fourn., Bull. Soc. Roy. Bot. Belg. 15: 466. 1876.
Nomen nudum.

Tripsacum lemmoni Vasey, Contrib. US Nat. Herb. 3: 6. 1892.

Tripsacum dactyloides var. lemmoni (Vasey) Beal. Grasses N. Amer. 2:
19. 1896.

This is medium robust perennial with 1-2 m tall, erect culms from a well developed rhizome system. The leaf-sheaths are densely hispid at the base of the plant, while those near the top of the culms may become almost glabrous. Leaf-blades are glabrous to moderately pilose and 1-2.8 cm wide. Terminal inflorescences have 2-9 branches, with the lower ones sometimes fascicled, and with the male sections of all branches pendulous. Glumes of staminate spikelets are 5-8 mm long, and the upper spikelet of each pair is supported by a slender, 3-5 mm long pedicel. The species is a hexaploid with $2n=72$ chromosomes.

Plants from the northern limit of the species, the mountains of southern Arizona and of northern Sonora and Chihuahua, are characterized by leaf-blades that are scarcely more than 2 cm wide, and the leaf-sheaths are essentially glabrous except at the base of the plant where they are hispid. These plants belong with T. lemmoni Vasey. However, they grade so completely into the more robust and pilose plants of central Mexico that T. lemmoni cannot be recognized as a distinct species. The species cross with T. dactyloides, and their genomes are cytologically homologous. However, hybrids produced by us are either sterile or reproduce as gametophytic apomicts. Numerous specimens are

cited by Cutler and Anderson (1941). However, they included Mexican T. dactyloides in this species.

Selected specimens: TYPE-T. Hartweg 252, Mexico, In saxosis, Aguascalientes (K,GH). CEL 4181, 35 miles west of Bisbee in Coronado National Forest, Bear Canyon, Huachuca Mts., Arizona (CEL). J. G. Lemmon 2932, on high peak with southern slope, near moist rock, Huachuca Mts., Arizona (US, type of T. lemmoni). T. S. Brandegee 4, El Taste, Baja California, Mexico (NY). H. S. Gentry 2496, Sierra Camelo, Rio Mayo, Chihuahua, Mexico (GH). T. R. Soderstrom 757, 30 miles southeast of Durango on Durango-Zacatecas highway, Durango, Mexico (ILL). J. N. Rose 3570, road between Haegilla and Mesquitec, Jalisco, Mexico (GH). L. H. Harvey 1660, Canon de Huepari, North of Aribabi, Sonora, Mexico (GH). H. S. Gentry 6359. Ocurahui, Sierra Suratato, Sinaloa, Mexico (MO).

TRIPSACUM LATIFOLIUM Hitchc., Bot. Gaz. 41: 294. 1906 (Fig. 8).

This is a robust perennial with decumbent culms from well developed rhizomes forming large clumps up to 5 m tall. The leaf sheaths are glabrous or sparsely tomentose, particularly along the midrib, and the 4-7 cm wide blades are sparsely pubescent on the upper surface and glabrous below. Terminal inflorescences have 3-7 branches, with the male section of these branches erect or slightly curved. Staminate spikelet glumes are 4-7 mm long, rounded at the apex, and both spikelets of a pair are sessile or the upper one may be supported by a 1 mm long, stout pedicel. The species is diploid with $2n=36$ chromosomes. This species occupies mesic woodlands from Central Mexico to Costa Rica. From Nayarit south to Guatemala it frequently grows sympatrically with T. pilosum and T. dactyloides. Its sparsely pubescent leaves and curved inflorescence branches give the appearance of a hybrid between T. pilosum and T. dactyloides. The smaller staminate spikelets, and complete absence of introgression between these two species indicate that T. latifolium is a valid species. Tripsacum latifolium resembles T. fasciculatum in vegetative morphology. However, the staminate spikelets are consistently smaller in T. latifolium, and the upper spikelet of each staminate pair is never supported by a long and slender pedicel. Tripsacum fasciculatum can further be distinguished from T. latifolium by its typically pendulous inflorescence branches.

Selected specimens: TYPE-H. von Tuerckheim 8333, Cubiliqutz, Dept. Alta Verapaz, Guatemala (US). Hunt 315, Mango Creek, Stann Creek District, Honduras (US). R. Pohl 11624, Puntarenas, edge of forest, Costa Rica (ISU). W. E. Harmon and J. A. Fuentes 2183, between San Pedro Carcha and campus, Alta Verapaz, Guatemala (MO). A Molina 10593, Montana La Cumbre, caserío Las Pinitas, Dept. Cortes, Honduras (NY).

TRIPSACUM MAIZAR Hern. and Randolph, Sec. Ganad. (Mex.) Of. Est. Exp. Fol. Tecn. 4: 7.1950. (Fig. 9).

This is a robust perennial with erect culms, 2-4.5 m tall from well developed rhizomes. The leaf-sheaths are densely hirsute with coarse hairs, and the leathery, 6-10 cm wide blades are glabrous or sparsely pilose near the base. Terminal inflorescences are large, with the lower branches fascicled and arranged on a somewhat elongated primary axis. Inflorescence branches range from 18 to 50, with the male sections typically pendulous. Staminate spikelet glumes are 5-7 mm long, and the upper spikelet of each pair is supported by a slender 2-5 mm long pedicel. The species is diploid with $2n=36$ chromosomes. It resembles robust specimens of T. pilosum. However, the latter species is a tetraploid ($2n=72$), and the leaf blades are at least pilose near the base. Tripsacum maizar is a forest species and occurs from Nayarit and Veracruz south to Oaxaca.

Selected specimens: Type-E. Hernandez and L. F. Randolph 4431, Acahuizotla, Guerrero, Mexico (Herb. of Secr. de Agric. y Ganaderia, Mexico). A. S. Hitchcock 231, steep slope of ravine, Alzada, Colima, Mexico (NY). CEL 4638, 2.2 miles south of Puerto Los Mazos, near Atlán, Jalisco (CEL). L. F. Randolph and E. Hernandez 65-1238, 3.2-3.4 km north of intersection with road to Tequila, above Guadalajara-Tepic highway, Jalisco, Mexico (FTG). L. F. and F. R. Randolph 66-271, near la Herradura, 20-21 km north of Tepic (FTG). CEL 4640, 6.1 miles from Cahuatpec, Oaxaca, Mexico (CEL).

TRIPSACUM PILOSUM Scribner and Merrill, Div. Agrost. Bull. (USDA) 24: 6 1910 (Fig. 10).

This is a robust perennial with up to 3 m tall erect culms from well developed rhizomes. The leaf-sheaths are moderately to densely hirsute and the 3-6 cm wide blades are moderately pilose or rarely almost glabrous except near the base. Terminal inflorescences have 2-15 branches with the male sections pendulous. Glumes of the staminate spikelets are 6-9 mm long, and the upper spikelet of each pair is supported by a 2-4 mm long slender pedicel. The species is tetraploid with $2n=72$ chromosomes. This is a widely distributed and morphologically variable species. It occurs in various habitats from Central Mexico to Honduras. Robust specimens of T. pilosum resemble T. maizar, except that the leaf-blades are pilose, the stem below the inflorescence is usually pubescent, and terminal inflorescences usually have around eight branches in T. pilosum and 15 or more in T. maizar. Furthermore, T. maizar is a diploid while T. pilosum is tetraploid.

Selected specimens: TYPE-J. N. Rose 2841, between Colotlan and Bolanos, Jalisco, Mexico (US). CEL 4662, near Km 29 on road from Tuxtla Gutierrez to San Cristobal de las Casas, Chiapas, Mexico (CEL). CEL 4094 4 miles east of Taxco, Guerrero, Mexico (CEL). H. C. Cutler 1940, 5 km east of Tonilita (NY). C. Martinez-Calderon 353, Chiltepec and vicinity, Tuxtepec district, Oaxaca, Mexico (GH). H. C. Cutler 4306, Km 19.5 on Guatemala-Barberera road, Guatemala (NY). L. O. Williams and A. Molina 10346, Santa Clara creek, Rio Yeguare Valley, Honduras (GH).

TRIPSACUM ZOPILOTENSE Hern. and Randolph, Sec. Ganad. (Mex.) Of. Est.
Exp. Fol. Tecn. 4: 22. 1950 (Fig. 11).

This is a caespitose perennial without rhizomes. Culms are erect and up to 1.5 m tall. Leaf-sheaths are glabrous to moderately pilose particularly at the base of the plant, and the 0.5-1.6 cm wide blades are glabrous or sparsely pilose near the base. Terminal inflorescences consist of single spikes, with the male section stiffly erect. Staminate spikelet glumes are 5-7 mm long with both spikelets of a pair sessile. The species is diploid with $2n=36$ chromosomes. It is narrowly endemic in Querrero, and occupies the most xeric habit of all Tripsacum species.

Selected specimens: TYPE-E. Hernandez and L. F. Randolph 4413, Canada del Zopilote, km 262.5 carratera Mexico-Acapulco, Guerrero, Mexico (Isotype GH). H. E. Moore Jr. 5188, Canon del Zopilote, Guerrero, Mexico (GH).

DISCUSSION

Species limits in Tripsacum are relatively well defined. Drooping inflorescence branches, and staminate spikelet pairs of which the upper spikelet is supported by a slender, 2-6 mm long pedicel, characterize T. fasciculatum, T. lanceolatum, T. maizar and T. pilosum. Within this group, T. fasciculatum is distinguished from the other species by its essentially glabrous leaf-sheaths and blades. Tripsacum maizar and T. pilosum are robust as is T. fasciculatum, but they and the smaller T. lanceolatum have pilose to hirsute leaf-sheaths, at least at the base of the plant. Tripsacum lanceolatum is distinguished from the others by its narrow, 1-3 cm wide leaf-blades. Tripsacum maizar differs consistently from T. pilosum in having leathery, glabrous leaf-blades rather than pilose ones, and usually also by fewer (<15) inflorescence branches. Tripsacum pilosum can sometimes also be distinguished from T. maizar by having both spikelets of some staminate pairs sessile on the same rachis where the upper spikelet of most staminate pairs is distinctly pedicelled. The upper spikelet of each staminate pair is always pedicelled in T. maizar. Randolph (1970) lists two collections of T. pilosum-T. maizar intermediates. They have more inflorescence branches than is typical for T. pilosum (up to 17), but their pilose leaf-blades put them into this species. We have collected specimens in Jalisco with glabrous leaf-blades as in T. maizar, but with usually less than 15 inflorescence branches. Such individuals occur where T. maizar ($2n=36$) and T. pilosum ($2n=72$) occur together. They may represent hybrids between these two species, but the collections we studied all are tetraploid rather than triploid as could be expected from such hybridization. Tripsacum pilosum, however, is a facultative gametophytic apomict, and it may be that atypical biotypes became fixed as a result of this mode of asexual reproduction.

The inflorescence branches of T. andersonii, T. australe, T. bravum, T. dactyloides, T. floridanum, T. latifolium and T. zopilotense are stiff or at most curved, never slender and pendulous, and both spikelets of each staminate pair are sessile, or the upper one may be supported by a stiff pedicel that is usually almost as broad as it is long. Tripsacum zopilotense is easy to identify in the field, since it is the only species without well developed rhizomes. It resembles T. floridanum in having

curved leaves. The latter species, however, is from Florida and the Caribbean Islands, while T. zopilote is confined to Zopilote Canyon in Querrero. Randolph (1970) lists three atypical T. zopilote collections. We have collected tetraploid specimens from the entrance of Canada del Zopilote and Acahuizotla which we include in T. dactyloides. Morphologically similar specimens were also collected from northeast of Taxco. They are characterized by sparsely pilose leaf-sheaths, have broader leaves than T. zopilote, and resemble this species only in having single spikes terminating the flowering culms. They appear to represent a morphologically distinct, gametophytic apomictic complex of T. dactyloides adapted to rather arid habitats.

Tripsacum andersonii is the most robust of the species group with non-pendulous inflorescences. It can be confused with T. latifolium in the field before they flower. Both have broad leaves with the sheath usually somewhat tomentose particularly along the midrib. Both species also have 1-7 branches on terminal inflorescences, and both may have the upper spikelet of a staminate pair shortly pedicelled. However, the staminate spikelets of T. andersonii are much larger (7-9 mm) than those of T. latifolium (4-7 mm), and T. andersonii is sexually sterile with $2n=64$ chromosomes, while T. latifolium is a sexually reproducing diploid ($2n=36$). The T. latifolium-T. maizar intermediates which Randolph (1970) collected at Fortin and Sebastopol probably can be included in T. maizar. We have collected T. maizar and T. fasciculatum from around Fortin de Las Flores in Veracruz. All of our collections from this locality are diploid and reproduce sexually.

Tripsacum bravum is characterized by solitary, or rarely two spikes terminating the flowering branches and by leaf-sheaths that are tomentose along the mid-rib. This species differ from tomentose collections of T. zopilote, T. dactyloides and T. australe with solitary spikes by being more robust with broader (3-5 cm) and more glaucous leaf-blades.

Tripsacum dactyloides is morphologically variable, but no consistent patterns of morphological traits correlated with chromosome number, habitat or geographic distribution could be found. The Chiapas collection which Randolph (1970) classified with atypical T. zopilote fits more naturally with T. dactyloides. We have also collected this morphological type from near Tuxtla Gutierrez but did not count its chromosome number. Its slender habit suggests that this type deserve specific rank. Randolph (1970) recognizes T. dactyloides ssp. hispidum as a distinct taxon. The type (Fig. 12) is a typical T. dactyloides with hispid leaf-sheaths, of the kind that is widely distributed in more arid habitats from southern Arkansas through Tamaulipas south to Central Mexico. Hitchcock (1906) suggested that this subspecies connects T. dactyloides with T. lanceolatum, since one spikelet of a staminate pair may sometimes be shortly pedicelled. However, evidence of natural hybridization between these two species is absent. We have collected a robust T. dactyloides from Jalisco south into Guatemala, and also in

Venezuela with one spikelet of a staminate pair supported by a 1-2 mm long pedicel. Pilose as well as glabrous populations occur, in Mexico usually where T. pilosum and common T. dactyloides occur together. These Mexican populations are tetraploid gametophytic apomicts, and may represent derivatives of hybridization between these two species. Comparative morphological studies, however, were not conclusive.

Tripsacum australe is as variable morphologically as is T. dactyloides. Inflorescence morphology of these two species are alike and for the present tomentose specimens from South America are included in T. australe, and glabrous or pilose specimens in T. dactyloides. The species, however, ranges from 1 m to 4 m in height, and varies from erect and slender to robust and decumbent in growth habit. All the collections studied by us are diploid and reproduce sexually. Collections of T. dactyloides from South America studied by us are all tetraploids. A comparative morphological study of Tripsacum in South America may reveal that distinct species could be recognized within the present T. australe. Such a study is now underway.

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REFERENCES

- Ascherson, P. 1877. Kleine phytographische Bemerkungen (14. Euchlaena Schrad. und Tripsacum fasciculatum Trin.) Bot. Zeitung 33: 521-526.
- Cutler, H. C. and E. Anderson. 1941. A preliminary survey of the genus Tripsacum. Ann. Mo. Bot. Gard. 28: 249-269.
- de Wet, J. M. J. and J. R. Harlan. 1974. Tripsacum-maize interaction: A novel cytogenetic system. Genetics 78: 493-502.
- de Wet, J. M. J. and J. R. Harlan. 1976. Tripsacum and the origin of maize. In D. B. Walden (Ed.), Breeding and Genetics of maize. Wiley Interscience, in press.
- de Wet, J. M. J., J. R. Harlan, L. M. Engle and C. A. Grant. 1973. Breeding behavior of maize-Tripsacum hybrids. Crop Sci. 13: 254-256.
- Hitchcock, A. S. 1906. Notes on North American grasses. IV. Synopsis of Tripsacum. Bot. Gaz. 41: 294-298.
- Hitchcock, A. S. 1908. Types of North American grasses. Contr. U. S. Nat. Herb. 12: 113-158.

- Levings, C. S., D. H. Timothy and W. W. L. Lu. nd. Cytological characteristics and nuclear DNA buoyant densities in corn, teosinte, Tripsacum and corn-Tripsacum hybrids. Manuscript.
- Mangelsdorf, P. A. and R. G. Reeves. 1939. The origins of Indian corn and its relatives. Texas Agr. Exp. Sta. Bull. 574: 1-315.
- Newell, C. A. and J. M. J. de Wet. 1974a. Morphology of some maize-Tripsacum hybrids. Amer. J. Bot. 61: 45-63.
- Newell, C. A. and J. M. J. de Wet. 1974b. Morphological and cytological variability in Tripsacum dactyloides (Gramineae). Amer. J. Bot. 61: 652-664.
- Randolph, L. F. 1970. Variation among Tripsacum populations of Mexico and Guatemala. Brittonia 22: 305-337.

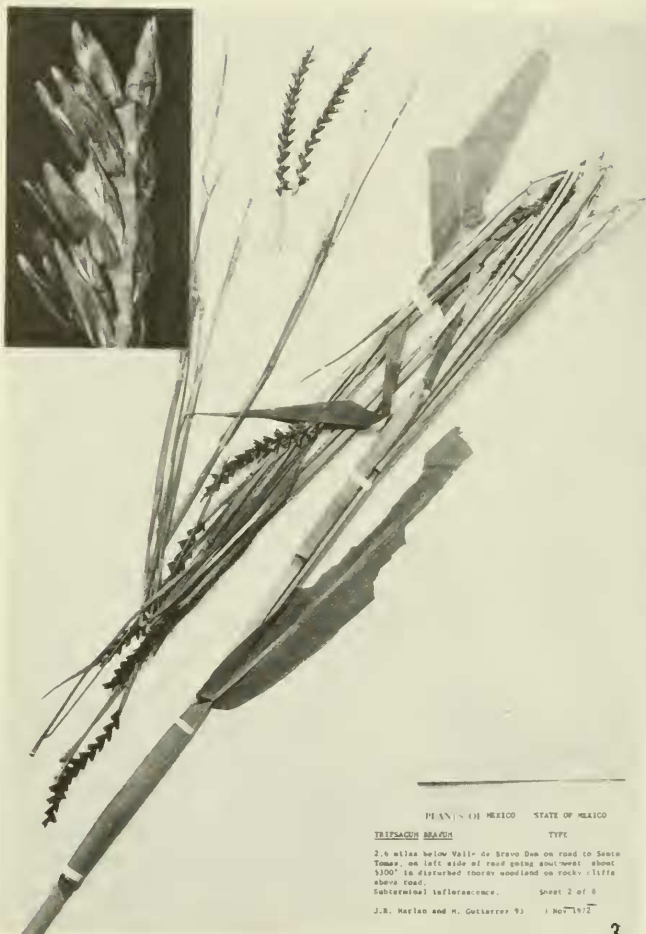
LEGEND TO FIGURES

- Figures 1-12. Morphology of Tripsacum taxa. Fig. 1. T. andersonii;
Fig. 2. T. australe; Fig. 3. T. bravum; Fig. 4. T. dactyloides;
Fig. 5. T. fasciculatum; Fig. 6. T. floridanum; Fig. 7.
T. lanceolatum; Fig. 8. T. latifolium; Fig. 9. T. maizar;
Fig. 10. T. pilosum; Fig. 11. T. zopilotense;
Fig. 12. T. dactyloides ssp. hispidum.



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TRIPACUM MAJUS

TYPE

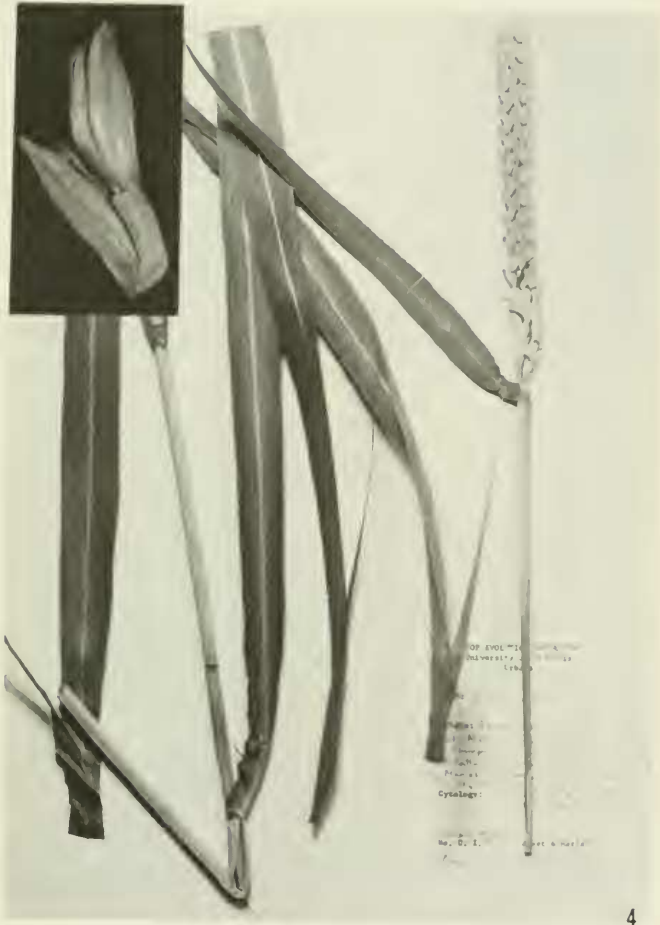
2.5 miles below Vallé de Bravo Dam on road to Santa
Teresa, on left side of road going southwest about
5300' in disturbed thorny woodland on rocky cliffs
above road.

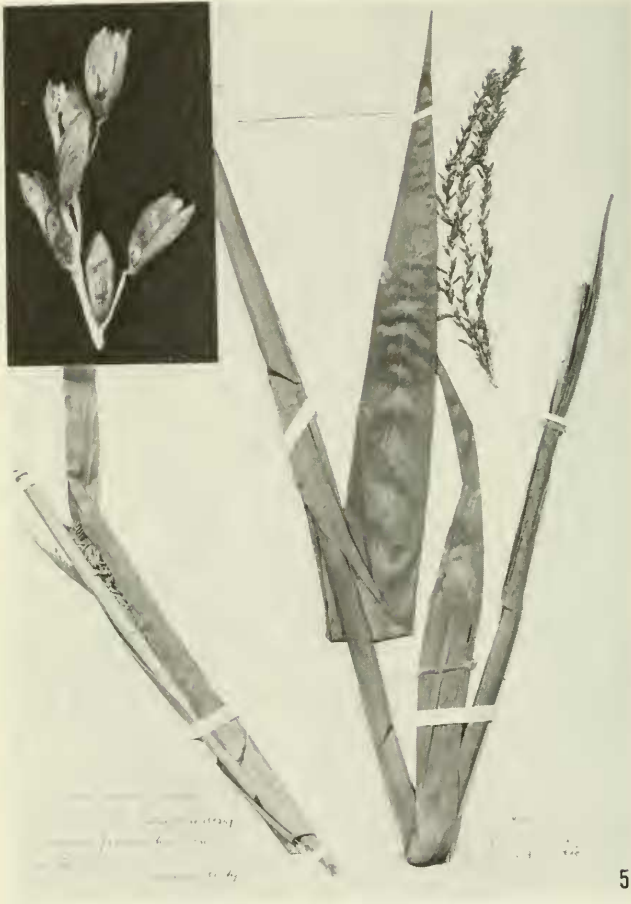
Subterminal inflorescence.

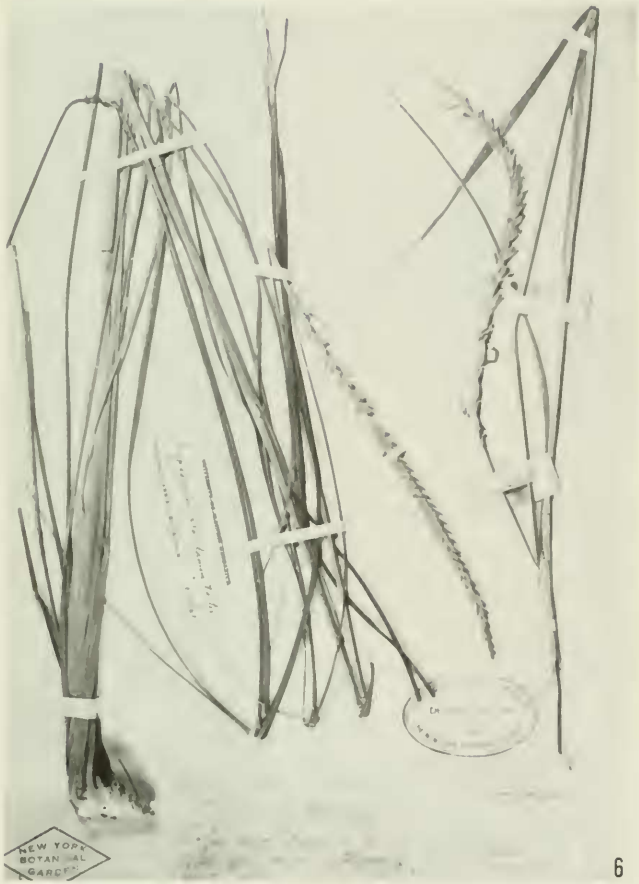
Sheet 2 of 8

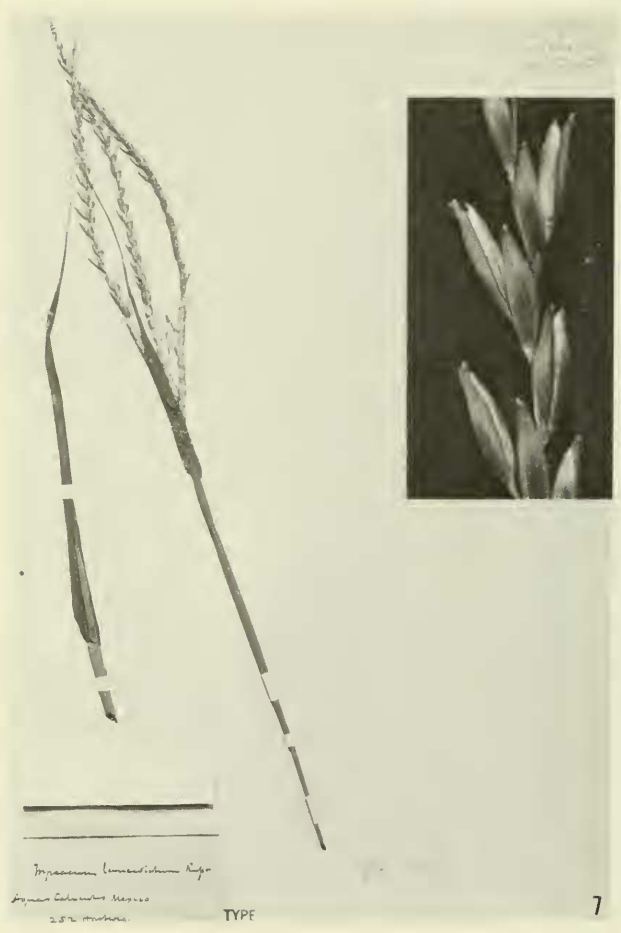
J.R. Harlan and H. Gutierrez 91 1807-1972

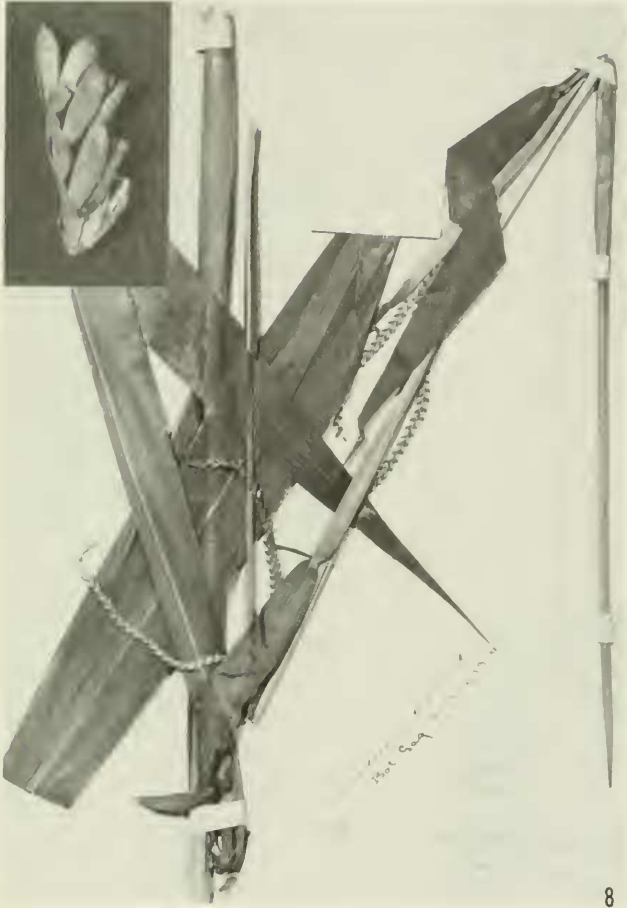
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our death
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Tripsacum daltan



