Eastern Gamagrass Breeding in New York and Oklahoma

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Introduction

There has been increased interest in breeding eastern gamagrass [*Tripsacum, dactyloides* (L.) L.] in recent years due to the discovery of gynomonoecious variants with their increased seed production potential, and the inherent superior forage quality and production potential of this species over other warm season grasses. This paper reviews the reproductive biology and breeding systems of eastern gamagrass and reviews the breeding efforts conducted at the USDA-NRCS Big Flats Plant Materials Center (PMC) in Big Flats New York and the USDA-ARS Southern Plains Range Research Station (SPRRS) in Woodward Oklahoma.

Eastern gamagrass is a tall, highly productive, long-lived, perennial, warm-season native grass. Eastern gamagrass is palatable and highly digestible to all classes of livestock. It can be used for hay, silage, and intensively managed pastures. It produces forage earlier in the spring than most other warm-season grasses and later than most cool season grasses and legumes. The perennial nature of gamagrass offers advantages over annual forages including lower fuel, labor, and production costs.

Taxonomy

Eastern gamagrass is in the family Poaceae, tribe Andropogoneae, and subtribe Tripsacinae. It shares the same subtribe as corn [*Zea mays L*.]. It is now accepted that teosinte [*Zea mays L.* subsp*. mexicana*] is the progenitor of corn and it hybridizes freely with corn in the wild. Eastern gamagrass hybridizes with corn under experimental conditions and frequently their chromosomes pair during meiosis.

Tripsacum comprises 15 species in 2 sections and is native only to the Western Hemisphere (Brink and de Wet 1983). *Tripsacum dactyloides* is the most widespread and morphologically variable of the species.

Distribution

Eastern gamagrass is widely distributed from Connecticut to Nebraska south to Texas and Florida in the United States and south to Paraguay and Brazil in South America. There are forms of *Tripsacum* adapted to North American

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prairies and eastern coastal plains, deep sandy soils, semi arid regions, rocky out-crops, river banks and tropical rain forests (Harlan and de Wet 1977).

Cytology

Eastern gamagrass occurs predominately at the diploid (2n=2x=36), triploid (2n=3x=54), and tetraploid (2n=4x=72) levels although pentaploids (2n=5x=90) and hexaploids (2n=6x=108) have been reported (Farquharson 1955).

Mode of Reproduction

The reproduction process in *Tripsacum* is by both sexual and facultative apomixis. Apomixis is a form of reproduction in which seeds are produced asexually. An unreduced egg cell in the embryo sac develops into a zygote without the union of the egg and sperm. Since the egg cell has developed from mitotic rather than meiotic cell division and fertilization is absent the zygote is genetically identical to the maternal plant from which it originated. Embryological analysis demonstrated diploids to be exclusively sexual while the polyploid cytotypes reproduced as facultative apomicts (Burson et al. 1990 and Sherman et. al. 1991). The predominant form of apomictic reproduction in *Tripsacum* is characterized as being diplosporous pseudogamy of the *Antennaria* or mitotic type. In diplosporous apomixis, the megaspore mother cells tend to elongate prior to nuclear division. The absence of a linear tetrad and the presence of a single elongated cell with the nucleus closer to the micropyle is characteristic of diplosporous apomixis. The nucleus then divides mitotically to form the 8 nucleate embryo sac. In pseudogamy, pollination is required for endosperm development. It has been found that 2-4% of the time apomixis occurs by the *Taraxacum* type of diplosporous apomixis where a partial meiosis allows for some pairing and crossing over to occur (Leblanc et. al. 1995; Kindiger and Dewald 1996). This creates some genetic variability in the offspring without a change in chromosome number. In the *Taxaracum* type of diplospory, a megaspore mother cell differentiates from the nucleus and begins meiosis, but meiosis is inhibited at a particular stage by unknown mechanisms and the nucleus is restored to a form that enables mitosis to occur (Kultunow 1993). This is called first division restitution.

Monoecious and Gynomonoecious Inflorescence

Inflorescences of gamagrass typically have a female section below and a male section above on the same raceme (monoecious). The female portion is composed of a few (1-12) solitary spikelets that normally contain a single fertile floret each. Male spikelets are born in pairs at each node of the rachis and contain two functional florets each with three anthers. There is a mean of 65 times more anthers than pistils (Dewald and Jackson 1988). The inflorescence exhibits protogyny in which the female portion flowers before the male. The flowering in eastern gamagrass is indeterminate flowering from June to September in New York.

In 1981 a gynomonoecious sex form GSF-I, (PI 483447) *T. dactyloides* (L.) L. forma *prolificum* was discovered in an evaluation at the USDA-NRCS Manhattan Kansas Plant Materials Center from a seed collection made in Ottawa County, Kansas. GSF-II (PI 483448) was found in 1982 at the collection site of GSF-I. These plants exhibit gynomonoecy with pistillate spikelets below and perfect spikelets above on the same raceme. The lowermost pistillate spikelets and the thick rachis form a cupulate fruitcase structure similar to that of the monoecious form (MSF). The basal solitary spikelets have two fertile pistillate florets instead of one. Each of the paired spikelets, which are normally male, contains two functional female florets and rudimentary stamens. At the extreme apex of the inflorescence a few paired spikelets contain two functional perfect (male and female) florets. The cupules in the basal portion of the GSF racemes are generally well developed but become progressively more shallow and eventually disappear in the apical portion of the raceme (Dewald and Dayton 1985). The GSF variant averaged 22 times more pistils than the MSF inflorescence indicating a seed increase potential of 20 fold. The anthers on the GSF inflorescence is only 22% of those of the MSF type resulting in unsatisfactory seed set (Dewald and Jackson 1988). The size and weight of the caryopses originating in the region of paired spikelets on the GSF raceme are about 25% less than the size and weight of those originating on the lower solitary spikelets of the MSF plants. Seed produced by GSF plants have good germination (Jackson 1992).

The GSF trait is governed by a recessive gene. The progeny of selfed and intermated F_1 hybrids segregated 3 MSF to 1 GSF indicating the gynomonoecious condition is under recessive monogenic control. There was sufficient deviation to suspect the presence of structural modifiers in certain cross combinations. (Dewald et. al. 1987).

BREEDING

Purpose

The characteristics of gamagrass which have limited its development and cultivation have been low seed production, inferior seed quality, and establishment difficulties. Breeding efforts have increased since the discovery of the gynomonoecious form with the hope to solve some of these problems. Eastern gamagrass has a wide geographic range and is adapted to many soils and climate conditions. There is a vast amount of genetic diversity within eastern gamagrass and between *Tripsacum* species which can be tapped for increased yield, seed production, and disease and insect resistance. The inherent forage quality is very good and should be maintained or improved during the breeding process. Its area of adaptation may be moved northward with improvements in winter hardiness and frost heaving resistance. Variability has been observed in the leaf width, stem heights and width, disease resistance, forage quality, maturity date, yield, plant architecture, degree of center persistence, and seed head shatter resistance.

History of Present Varieties

'Pete' eastern gamagrass (PI 421612), formerly designated PMK-24, originated from seed collections made in 1958 from native stands in Kansas and Oklahoma. In 1960, seventy original seed lots were bulked to establish the first generation of a composite strain. The strain was advanced through three generations via combine harvesting and replanting of open-pollinated seed. The first generation varied considerably in maturity; some selection for uniformity of maturity is presumed to have occurred during this process. The third generation of the composite was both the breeders seed field and the foundation field. The strain was released on a germplasm basis in 1974. A formal release of foundation 'Pete' was made to certified growers in 1989 by the USDA-SCS, USDA-ARS and Kansas and Oklahoma Agricultural Experiment Stations (Fine et. al. 1990).

'Iuka' is based on a collection of over 500 accessions from Oklahoma, Texas, Kansas, and Arkansas. In 1979 a 21-plant selection based on apparent forage value was made from the original collection. A one-acre block was vegetatively established then advanced two generations.

Breeding at the Diploid Level Using GSF Germplasm

Considerable work has been done breeding eastern gamagrass at the USDA-ARS Southern Plains Range Research Station (SPRRS) at Woodward Oklahoma. Many initial hybrids were made from crosses using a wide array of MSF accessions onto the GSF-I and GSF-II variants as well as backcrossing and intercrossing with GSF hybrids to come up with unique and vigorous germplasm.

In 1983-84 over 450 northern accessions from collections located at the USDA-ARS SPRRS and the USDA-NRCS Manhattan Kansas Plant Materials Center were divided and brought to the Big Flats Plant Materials Center. After several years of over-wintering in this climate superior accessions were selected and used as pollinators onto GSF-I. After intercrossing the F1 generation, 320 GSF genotypes were produced. 25 genotypes were selected for further evaluation based on good agronomic and seed production characteristics.

At the USDA-ARS SPRRS shatter resistance, a primary goal, has not been achieved in the breeding program. Some progress has been made in identifying and selecting for reduced rachis internodes for shatter resistance. Accessions have been identified in which seeds mature prior to disarticulation of rachis internodes which would allow harvest before shattering. More determinate flowering, which occurs in material with branched lateral inflorescences, would make timing of harvest easier to pinpoint.

The lack of an adequate amount of pollen in the GSF inflorescence has always been acknowledged as a problem for seed production. A solution to this problem was to use heterozygous MSF plants in pollinator rows similar to corn seed production (Salon et. al. 1990). An alternative is the use of intermediate sex forms that are a product of the vast number of hybrids being produced in Oklahoma. They are characterized by having solitary, sometimes paired, female spikelets on the basal portion of the racemes with paired female fertile florets extending upwards for one-fourth to one-half the length of the tassel section. Spikelets of the intermediate type have two fertile florets instead of one, and seed production potential is increased by 10-15 fold compared to the MSF type. There is a sufficient increase in pollen production over the GSF type to insure adequate pollination. In certain genetic backgrounds, partial sex reversal (feminization of ¼ to ¾ of the male-paired spikelets in the tassel) occurs in diploids, which are heterozygous for the gsf1 gene, i.e. gsf1/GSF1 genotypes. When intermediate sex form plants are selfed the normal ratio of progeny is 1 gynomonoecious: 2 intermediate: 1 MSF sex form.

Selection at the Tetraploid Level

A 450-accession evaluation nursery was established at Big Flats, other collections were made including five from near Beltsville Maryland. These plants exhibited growth characteristics and maturity dates much different than the bulk of the collection, with wider lighter green leaves upright growth habit and later flowering. Divisions of these plants were made and a seed increase block was formed (PI 591483). Flow cytometry data showed that these were tetraploid. They flowered about 2 weeks later than 'Pete' and yielded about 25% more biomass. There have been no molecular studies done to differentiate between the initial clones and their progeny to determine if they are genetically different. Progeny from this composite are very uniform. Observations at Big Flats indicate problems with winter hardiness during establishment in some years; therefore this composite will be targeted for use in southern Pennsylvania and the Mid-Atlantic region.

Breeding for Forage Quality

A study was conducted at the USDA-NRCS Big Flats Plant Materials Center and Cornell University looking at the forage quality of eastern gamagrass as measured by crude protein (CP), neutral detergent fiber (NDF), acid digestible fiber (ADF), lignin, in vitro true digestibility (IVTD) and digestible NDF. The reproductive and vegetative tillers of six gamagrass accessions plus the cultivar (cv) 'Pete' were evaluated for three first cutting dates in 1997 and 1998. There were significant differences between genotypes for vegetative tillers for all variables measured, except for ADF in 1997 and for lignin in 1998. For reproductive tillers, there were significant differences except for NDF and lignin in 1998. It seems that variability exists between eastern gamagrass accessions that could be used in a breeding program. Only minor forage quality differences, which varied by year and tiller type, were found between reproductive and vegetative tillers when averaged across accessions and cutting dates.

Breeding for Frost Heaving Resistance

Frost heaving is a major problem in some years reducing the successful establishment of eastern gamagrass in the Northeast. Many of the poorly drained soils that gamagrass could grow on due to its aerenchyma cells in the roots are prone to frost heaving. A field of ‘Pete’ gamagrass, which exhibited good spring establishment in 1996, had severe frost heaving over the winter with over 75% of the plants killed. Four hundred of the surviving plants were dug up in 1998 when dormant and immediately replanted into a crossing block at the Big Flats PMC. Seed was harvested in 1999 and will be replanted into a frost heaving prone soil in the year 2000 for a second cycle of selection.

Incorporation of the GSF Trait in Polyploids to Stabilize with Apomixis and the Production of Sexual Tetraploids

The GSF trait increases the seed production potential of eastern gamagrass several fold and is being utilized in several breeding programs. It occurs in nature at the diploid level. The GSF trait is governed by a recessive gene. Tetraploids are apomictic and many are found to be more robust and productive than the diploids with later maturity dates but have the MSF seed head. The GSF inflorescence does not produce enough pollen for adequate seed set or for the production of true breeding lines in seed production fields. The transfer of the GSF trait from the diploid level to the tetraploid level, therefore, has several advantages. It will allow, by crossing apomictic plants as pollen parents and intermating progeny, the ability to fix the GSF trait with apomixis. Eastern gamagrass shows a high degree of shattering. Breeding apomixis into the genotypes used in seed production fields would practically eliminate the production of “off” types from the shattered seed and would reduce genetic drift. This would increase the length of time seed production fields can be maintained. The stabilization of other traits as well as the potential to maintain hybrid vigor may be possible with the use of apomixis in eastern gamagrass breeding programs.

On the other hand, sexually reproducing tetraploid eastern gamagrass will permit recombination and conventional breeding at the tetraploid level. The tetraploid gamagrass plants found along the Northeast and Mid-Atlantic coastal areas are larger, more robust, and flower around 2 weeks later than the diploids obtained from the Midwest. The tetraploids are less winter-hardy and appear to decline with center dieback more quickly than the diploids. It would be beneficial to be able to improve winter hardiness and longevity in these tetraploids by conventional breeding methods. Sexual tetraploids will also be useful for future genetic studies of the inheritance of apomixis and for study of the inheritance of the GSF trait at the tetraploid level (Salon and Earle 1998).

Chromosome Doubling of GSF Eastern Gamagrass in Tissue Culture

Tissue culture techniques were used to double the chromosome number of eastern gamagrass at the Big Flats Plant Materials Center and Cornell University. Shoots of diploid (2n=2x=36) GSF-I (PI-483447) plants were derived from callus initiated from immature inflorescences and embryos. These shoots were induced to microtiller in the presence of 3 mg l^{-1} benzyladenine. Amiprophosmethyl and colchicine were used to induce chromosome doubling to rapidly dividing microtillers. These plants were tetraploid (2n=4x=72) as determined by flow cytometry and root tip chromosome counts. These plants were morphologically normal and produced seed with the GSF inflorescence. Test crosses were made with a known diploid. Flow cytometry and chromosome counts showed that the progeny were triploid, proving that the induced tetraploids reproduced sexually. (Salon and Earle 1998). The induced sexual GSF tetraploid (PI-591482) was released as germplasm by the USDA-NRCS and Cornell University and registered as SG4X-1 (Salon and Pardee 1996).

Genome Accumulation

A method to transfer genes from the diploid level to the tetraploid level and from polyploids down to the diploid level is being used by the USDA-ARS SPRRS in Woodward Oklahoma. It is referred to as genome accumulation. In this method fertile apomictic triploids are formed by 2x X 4x crosses. Triploid hybrids of eastern gamagrass are largely sterile, but a few 1-10% are partially female fertile due to apomictic reproduction. Four of these released by the USDA-ARS SPRRS, were selected out of 832 triploids from four hybrid combinations evaluated for seed set, pollen fertility, and agronomic attributes (Dewald et al. 1992). Fertile triploids can be used to provide an intermediate step for the creation of new and genetically unique tetraploid germplasm. These triploids are crossed using diploids as the pollen parent and due to the formation of unreduced gametes by the triploids, tetraploid progeny are formed. Fertile triploid eastern gamagrass hybrids often produce tetraploid progeny at a frequency of 10-30% (Dewald and Kindiger 1994 a&b). These tetraploids carry three genomes (54 chromosomes) from the triploid maternal parent and one genome (18 chromosomes) from the reduced gamete of the diploid parent. They are called B_{III} hybrids resulting from a 2n + n mating (Bashaw and Hignight 1990; Bashaw et al. 1992). These tetraploids are apomictic but now carry genes from their diploid parent. The introgression of diploid germplasm into apomictic tetraploid germplasm provides for the enrichment of the genetic diversity at the tetraploid level.

Hexaploids can also be formed by genome accumulation. Using tetraploid apomictic germplasm as the maternal parent crossed with other apomictic tetraploids, B_{III} hybrids are formed 5-8% of the time. An experimental hybrid, WW-2190 selected for high fertility, was reported to produce B_{III} hybrid offspring 50% of the time. These hybrids receive 72 chromosomes from the maternal parent from unreduced embryos and 36 chromosomes from the reduced pollen parent resulting in a (2n=6x=108) hexaploid. These hexaploids have proven useful as a bridge for moving apomictic tetraploid germplasm to the sexual diploid level. When crosses are made between diploids as the maternal parent and hexaploids as pollen parents, 99% of the resulting progeny are diploids. It is suspected that hexaploids produce pollen of many ploidy levels and that the pollen carrying the haploid number is far more competitive resulting in diploid progeny. Diploids generated from this 2x X 6x cross are highly variable and possess a wide diversity of alleles contributed from the apomictic polyploid genotypes (Kindiger and Dewald 1997).

This method has been successfully used to move the GSF trait from the diploid level to the triploid level where it was stabilized by apomixis. FGT-1 a fertile gynomonoecious apomictic triploid, was released by the USDA-ARS SPRRS in Woodward, Oklahoma (Dewald and Kindiger 1996). FGT-1 was developed by combining recessive genes for gynomonoecy from diploids (2n=2x=36) with genes for apomixis from polyploids in three generations of interploidy matings. A first generation fertile triploid hybrid was produced from a GSF plant as the maternal parent. This triploid was crossed with a mixture of pollen from 7 heterozygous diploids for the gsf trait creating a B_{III} tetraploid. This tetraploid was crossed onto a GSF diploid; out of 90 triploid progeny recovered three were gynomonoecious and one was relatively fertile (35-55% seed set) exhibiting both gynomonoecy and apomictic reproduction.

Interspecific Hybridization in *Tripsacum*

Crosses between *Tripsacum dactyloides* and all other *Tripsacum* species (Cutler and Anderson 1941) are readily accomplished, regardless of ploidy or the taxonomic section a species had been assigned (Brink and de Wet 1983). No interspecific crossing barriers have been observed by work conducted at the USDA-ARS in Woodward Oklahoma on *T. dactyloides, T. andersonii* J.R. Gray, *T. floridanum* Porter ex Vasey, *T. maizar* Hern.-Xol. & Randolph, and *T. zopilotense* Hern.-Xol. & Randolph. Various interspecific hybrids have identical reproductive characteristics with the production of B_{III} hybrids. Most *Tripsacum* species can be crossed to yield viable hybrids. *T. floridanum* crosses with *T. dactyloides* to yield viable sexually fertile hybrids and the two species should probably be considered one. Sexual diploids crossed with apomictic tetraploids of a different species will yield allotriploids, some of which will be seed fertile due to apomixis. These can then be crossed by diploids to yield allotetraploids by genome accumulation. Interspecific crosses provide an opportunity to expand the genetic diversity across the species (Kindiger and Dewald 1997).

Hybridization of Tripsacum and Maize

Corn was crossed with gamagrass as early as 1931 (Manglesdorf and Reeves 1931). Many workers have since made similar crosses using corn as the female parent and these hybrids are female fertile. Further backcrossing to corn results in recovery of pure corn with slight to no introgression of gamagrass germplasm after 4 to 8 backcrosses with corn. Recent work has been conducted at the USDA-ARS SPRRS crossing *Tripsacum* onto corn for the purpose of transferring genes for apomixis from eastern gamagrass into corn.

Until recently, attempts to use gamagrass as a female parent in crosses with corn have resulted in only a few sterile hybrids. In 1995, the first fertile hybrid produced by crossing gamagrass as the female parent with corn was achieved at the USDA-ARS SPRRS. This hybrid had 18 chromosomes of gamagrass and 10 from corn. When the hybrid was backcrossed to corn, plants with thirty-eight chromosomes (18 gamagrass + 20 corn) resulted. In further backcrossing to corn, all gamagrass chromosomes were eliminated leaving only corn chromosomes in a gamagrass cytoplasm. It is expected that the cytoplasmic gene pool of gamagrass will interact with the nuclear genes of corn to result in an improved product. Test on disease, insect, and stress tolerance, nutritive value, yield and adaptation are in progress (Dewald et al. 1999).

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