PHYLOGENETICS OF APOMICTIC COMMON DALLISGRASS (PASPALUM DILATATUM)

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ABSTRACT
Common dallisgrass, *Paspalum dilatatum* Poir., an important warm season forage grass, is an obligate apomict with 50 chromosomes which associate as 20 bivalents and 10 univalents during meiosis. Because efforts to improve the grass have not been successful, a phylogenetic investigation was initiated to identify the progenitors of common dallisgrass in an effort to circumvent the apomictic barrier to improvement. The genomic composition has been determined for four dallisgrass biotypes: yellow-anthered (2n=4x=40) IIJJ; common (2n=5x=50) IIJJX; Uruguayan (2n=6x=60) IIJJXX; and Uruguaiana (2n=6x=60) IIJJXX. While the source of the X genome is unknown, the genes controlling apomixis are on at least one of the X chromosomes because biotypes with 10 or more X chromosomes are apomictic. However, when four or five of the X chromosomes are missing, apomixis is not expressed. This suggests that apomixis is controlled by more than one gene and at least one of the X chromosomes must be present for apomixis to be expressed.

KEYWORDS:
Apomixis, genome relationships, dallisgrass, chromosomes

INTRODUCTION
The taxon *Paspalum dilatatum* Poir. consists of several different biotypes with common–dallisgrass being the most prevalent and important. This apomictic biotype is native to southern Brazil, Uruguay and northeastern Argentina, and is an important forage grass throughout many warmer regions of the world. Even though common dallisgrass is an excellent forage grass, it is susceptible to ergot, *Claviceps paspali* , which often leads to low seed set and livestoc poisoning. Because apomixis is a barrier to improvement, efforts to improve this biotype by conventional breeding methods have not been successful. Since common dallisgrass is a natural hybrid, a phylogenetic investigation was initiated to identify its progenitors for the purpose of resynthesizing improved forms of the grass and learning more about the genetic control of apomixis. This paper reports the progress of this program.

RESULTS AND DISCUSSION
The pivotal member of the phylogenetic program is a yellow-anthered biotype from Uruguay. It is known as yellow-anthered dallisgrass and is a sexual tetraploid with 40 chromosomes which pair as 20 bivalents during meiosis (Bashaw and Holt, 1958; Bashaw and Forbes, 1958). Since this biotype is sexual and meiotically stable, it has been used extensively in the hybridization program. Its 40 chromosomes consist of two different genomes which were identified as the I and J genomes. Thus, the yellow-anthered biotype has the genomic formula IIJJ (Burson, et al., 1973; Burson, 1981).

Common dallisgrass is a natural hybrid with 2n=5x=50 chromosomes which associate as 20 bivalents and 10 univalents during meiosis (Bashaw and Forbes, 1958) and reproduces by aposporous apomixis (Bashaw and Holt, 1958). A single yellow-anthered x common hybrid was produced that had 45 chromosomes which associated as 20 bivalents and 5 univalents during meiosis (Bennett, et al., 1969). Thus, common dallisgrass has the genome formula IIJJX where X represents the 10 univalents and is a genome of unknown origin (Burson, 1983).

Another biotype, Uruguayan dallisgrass, is a hexaploid that was introduced into the US from Uruguay. It reproduces by apomixis and has 60 chromosomes that pair as 30 bivalents (Burson, *et al*., 1991). Hybrids between the yellow-anthered and Uruguayan biotypes had 50 chromosomes which associated as 20 bivalents and 10 univalents. Since yellow-anthered has the genome composition IIJJ, this indicates the Uruguayan biotype also has the I and J genomes plus an unknown third genome. This genome was arbitrarily assigned the letter X resulting in genome formulas of IIJJX and IIJJXX for the hybrids and the Uruguayan biotype, respectively (Burson, 1991a). It was hypothesized that the yellow-anthered and Uruguayan biotypes are the direct progenitors of common dallisgrass. It was proposed that a sexual tetraploid plant with the genome formula IIJJ, similar to the yellow-anthered biotype was pollinated by the apomictic hexaploid Uruguayan biotype with the genome composition IIJJXX producing hybrids with the genomic composition IIJJX. Even though these 50-chromosome hybrids would be meiotically unstable, they would be sufficiently fertile to reproduce and propagate themselves because of apomixis. Apomixis also would provide a means of maintaining the 50 chromosomes even though meiosis was irregular. This hybrid is what we know today as common dallisgrass and demonstrates the importance of apomixis in the origin and preservation of germplasm. This hypothesis was recently strengthened when it was determined that all three members of the X genome in the Uruguayan biotype were homologous with three of the X chromosomes in common dallisgrass. This indicates that the X genomes in the common and Uruguayan biotypes are similar and it opens new avenues for determining the source of this genome using the Uruguayan biotype rather than common (Burson, 1991b).

Another apomictic hexaploid dallisgrass type, known as Uruguaiana dallisgrass, was recently introduced from Brazil. This biotype is not as meiotically stable as the Uruguayan biotype in that its 60 chromosomes associate as 24 bivalents and 12 univalents (Burson, *et al*., 1991). Hybrids between the yellow-anthered and Uruguaiana biotypes had 50 chromosomes which associated as 20 bivalents and 10 univalents indicating a genome composition of IIJJX. The univalents in the Uruguaiana biotype resulted from incomplete pairing of members of the X genome. This biotype apparently has different forms of the X genome and has been assigned the genomic formula IIJJXX.

The genes controlling apomixis in dallisgrass appear to be associated with one or more chromosomes of the X genome. All three apomictic biotypes investigated have the X genome, whereas the sexual type lacked this genome. In 1969, a hybrid was recovered from crosses between yellow-anthered and common dallisgrasses. This hybrid was sexual and had 45 chromosomes of which 40 were members of the I and J genomes and five the X genome. From this, it was hypothesized that the gene(s) controlling apomixis may be on one or more of the missing X chromosomes (Bennett, *et al*., 1969). However, since only one hybrid was investigated, this was highly speculative. Recently five additional yellow-anthered x common hybrids were recovered. Three had 45 chromosomes and the remaining two had 46 chromosomes. These 45- and 46-chromosome hybrids were missing five and four X chromosomes, respectively. All five hybrids were sexual; however, there was evidence of limited aposporous

development in that of 456 young ovules examined cytologically, active nucellar initials along with a functional megaspore were observed in six ovules. Apparently these enlarged nucellar cells are incapable of differentiating into aposporous sacs because all of the mature ovules examined contained sexual embryo sacs. These findings provide support for the hypothesis that the gene(s) controlling apomixis is associated with one or more of the X chromosomes. Another possibility is that apomixis is controlled by two or more genes located not only on a member of the X genome but also on one or more members of the I and/or J genomes. However, a gene on at least one of the X chromosomes has to be present for apomixis to be expressed. Crosses are presently being made to produce additional yellow-anthered x common hybrids to further test these hypotheses.

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