HYBRIDIZATION RANGE OF *DICHANTHIUM ANNULATUM* (FORSSK.) STAPF

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INTRODUCTION

Dichanthium annulatum (Forssk.) Stapf is a highly polymorphic species in the generic group Bothriochloininae, tribe Andropogoneae of the family Gramineae. Throughout its range of geographic distribution from the west coast of North Africa to Australia and the Fiji Islands, it is represented by a number of distinctly different morphological types at different ploidy levels.

In nature, D. annulatum is sympatric with other species of Dichanthium Willemet, as well as with representatives of Bothriochloa O. Kuntze and Capillipedium Stapf. Natural hybridization, between the morphological types of D. annulatum and of this species with related species of Dichanthium, as well as with B. intermedia (R. Br.) A. Camus, was suggested by Celarier et al. (1958), Harlan et al. (1958, 1961) and deWet (1963). To study the range of possible hybridization, attempts were made to cross D. annulatum with species of different genera included in the Bothriochloininae. The most common cytological race of D. annulatum is tetraploid ($2n = 40$), which is a facultative apomict in its breeding behavior (Brooks, 1958). However, in 1955, a sexual and self sterile plant designated "X-98" was produced artificially, and it represents an autotetraploid of the diploid Indian collection (3242) of D. annulatum. This plant was used as the female parent because self-sterility makes hybridization relatively easy.

Hybrids were studied both cytologically and morphologically. Studies of the relationships of different taxonomic units, based on hybridization data, will be of value in reclassifying the genus from an experimental systematic view point and aid in the establishment of phylogenetic affinities within the generic group Bothriochloininae.

Results of the research and discussion of the data are presented. The first of the following chapters represents a review of natural and artificial hybridization in the Gramineae. The remaining chapters, as they appear in this dissertation, are written in a style acceptable to the various biological journals to which they will be presented for publication.

CHAPTER II

HYBRIDIZATION IN THE GRAMINEAE - A REVIEW

The first systematic study of hybridization in plants was made by Koelreuter from 1761 to 1806. Since that time, there has been an increasing awareness of the extensive hybridization that exists in plants, and of its important role in evolution. Wide crosses, when successful, result in complex segregation, which provides extraordinarily rich genetic material on which natural selection operates. Lotsy (1916) demonstrated that recombination of genes can give rise to types entirely different from either of the original parents. Some may have new adaptive properties and even show transgressive variation with respect to either of the parents. Cugnac and Camus (1931) and Ullman (1936) indicated that natural hybrids are to be expected with greater frequency in the Gramineae than in other flowering families. During recent years, such interspecific and intergeneric hybrids, whether natural or artificial, have become prominent as areas for biosystematic studies. They provide evidence necessary for a better understanding of species concepts based on genetic relationships among the taxonomic units involved in the crosses.

In nature, many species of the Gramineae have wide ranges of geographic distribution and some of these are often sympatric. Consequently, due to predominant outcrossing as a mode of reproduction, new forms and even new species may originate by hybridization followed by allopolyploidy. Anderson (1961) and Clausen (1961) have recently discussed natural introgression in various members of the family Gramineae. Clausen et al. (1945) indicated that actual parentage of many natural hybrids are known, and that this demonstrated the role hybridization played in speciation. Stebbins (1952) pointed out that the presently accepted taxonomic treatment of grasses places undue emphasis on a few easily observed character differences.

The general concept among breeders and workers in areas of experimental taxonomy, is that only those individuals can produce hybrids which are phylogenetically related. Hybrids of unrelated species are, as a rule, sterile unless polyploidy and apomixis enhances their survival in nature (Stebbins, 1956, 1958). In sexually reproducing organisms, members of a species have more or less free interchange of genes, and are separated from other species by gaps of genetic discontinuity in morphological and physiological characteristics. Consequently, hybridization below the level of species is more probable than that above the species level.

In forage grasses, Myers (1947) reported about 225 interspecific and intergeneric hybrids. An additional 256 interspecific and 95 intergeneric hybrids are listed by Carnahan and Hill (1961). Recent reports on hybrids obtained in the family Gramineae are presented in Tables I and II. In the following pages an attempt has been made to review the hybrids from the standpoint of their cytogenetic behavior and to consider the taxonomic status of the members involved in the crosses.

A. INTERSPECIFIC AND INTRASPECIFIC HYBRIDIZATION - Hybrids at or below the species level are relatively easy to obtain, however, their fertility depends upon several genetically controlled mechanisms (Stebbins, 1950, 1958; Dobzhansky, 1941; and Müntzing, 1929, 1938).

One hundred and twenty-six interspecific and intraspecific hybrids involving 17 genera of the grass family are listed in Table I. The list is limited mainly to the forage grass species, with the exception of Hordeum, Oryza and Secale.

AGROPYRON - Hunziker (1959) observed 36 per cent fertility in interspecific hybrids between Agropyron "Tilcara" and A. scabriglume. It was demonstrated that hybrids had mostly haplontic chromosomal sterility, while the allopolyploids had diplontic genic sterility. He also indicated that A. agroelymoides is an allopatric cryptic species, and has arisen from A. scabriglume through rapid speciation involving chromosomal repatterning.

Connor (1962), on the basis of fertility of interspecific hybrids, concluded that A. enysii and A. tenue belong to one coenospecies. Agropyron scabrum and A. kirkii are ecospecies and together form one coenospecies.

DeWey (1961, 1962), on the basis of morphology, fertility and chromosome pairing, assigned the genomic formulas, BBBBCC and AAAA, for A. repens and A. desertorum, respectively. He conclusively demonstrated autosyndesis among chromosomes of the two parents and in a hybrid between them. F_2 plants of a backcross of this hybrid to A. desertorum were more fertile than equivalent backcrosses to A. repens.

BOTHRIOCHLOA - The genus Bothriochloa, together with Dichanthium and Capillipedium, form an agamic complex. Hybrid data of this group were presented by Harlan et al. (1961) and Harlan et al. (1962). Bothriochloa grahamii may be crossed with other species of this genus, as well as with representatives of Dichanthium and Capillipedium.

TABLE I

RECENT REPORTS ON INTERSPECIFIC AND INTRASPECIFIC HYBRIDS IN THE GRAMINEAE

Name	Authority
Agropyron	
A. *repens* x *A*. *desertorum*	DeWey (1962)
A. *scabrum* x *A*. *kirkii*	Connor (1962)
A."Tilcara" x *A*. *scabriglume*	Hunziker (1959)
Bothriochloa	
B. *ambigua* x *B*. *grahamii*	Harlan *et* *al*. (1961)
B. *ambigua* x *B*. *ischaemum* var. *ischaemum*	"
B. *grahamii* x *B*. *caucasica*	"
B. *grahamii* x *B*. *ewartiana*	"
B. *grahamii* x *B*. *glabra*	Harlan *et* *al*. (1962)
B. *grahamii* x *B*. *grahamii*	Harlan *et* *al*. (1961)
B. *grahamii* x *B*. *intermedia*	"
B. *grahamii* x *B*. *ischaemum* var. *ischaemum*	"
B. *grahamii* x *B*. *ischaemum* var. *songarica*	"
B. *grahamii* x *B*. *kuntzeana*	Harlan *et* *al*. (1962)
B. *grahamii* x *B*. *longifolia*	"
B. *grahamii* x *B*. *ordorata*	Harlan *et* *al*. (1961)
B. *grahamii* x *B*. *pertusa*	"
B. *grahamii* x *B*. *radicans*	"
B. *intermedia* x *B*. *grahamii*	"
B. *intermedia* x *B*. *ischaemum* var. *ischaemum*	"
B. *sacchariodes* var. *longifolia* x *B*. *decipiens*	"
B. *saccharoides* var. *longifolia* x *B*. *erianthoides*	"
B. *saccharoides* var. *torreyana* x *B*. *decipiens*	"
Bromus	
B. *inermis* x *B*. *tyttholepis*	Nielsen *et* *al*. (1962)
B. *tyttholepis* x *B*. *pumpellianus*	"
Cynodon	
C. *transvaalenis* x *C*. *dactylon*	Forbes and Burton (1963)
Dactylis	
D. *glomerata* ssp. *aschersoniana* x ssp. *lusitanica*	Jones (1962)
D. *glomerata* ssp. *glomerata* x ssp. *aschersoniana*	"
D. *glomerata* ssp. *glomerata* x ssp. *glomerata*	"
D. *glomerata* ssp. *glomerata* x ssp. *hispanica*	"

TABLE I (continued)

Name	Authority
D. *glomerata* ssp. *glomerata* x ssp. *judaica*	Jones and Borrill (1962)
D. *glomerata* ssp. *glomerata* x ssp. *santai*	"
D. *glomerata* ssp. *glomerata* x ssp. *woronowii*	"
D. *glomerata* ssp. *hispanica* x ssp. *aschersoniana*	"
D. *glomerata* ssp. *hispanica* x ssp. *hispanica*	Jones (1962)
D. *glomerata* ssp. *hispanica* x ssp. *judaica*	Jones and Borrill (1962)
D. *glomerata* ssp. *hispanica* x ssp. *lusitanica*	"
D. *glomerata* ssp. *hispanica* x ssp. *woronowii*	"
D. *glomerata* ssp. *judaica* x ssp. *glomerata*	"
D. *glomerata* ssp. *lusitanica* x ssp. *glomerata*	"
D. *marina* x *D*. *glomerata* ssp. *aschersoniana*	"
D. *marina* x *D*. *glomerata* ssp. *judaica*	"
D. *marina* x *D*. *glomerata* ssp. *lusitanica*	"
D. *glomerata* ssp. *woronowii* x ssp. *aschersoniana*	Jones (1962)
D. *glomerata* ssp. *woronowii* x ssp. *lusitanica*	"
D. *slovenica* x *D*. *glomerata*	Doroszewska (1962)
Danthonia	
D. *auriculata* x *D*. *linkii*	Brock and Brown (1961)
D. *auriculata* x *D*. *pilosa*	"
D. *caespitosa* x *D*. *auriculata*	"
D. *caespitosa* x *D*. *linkii*	"
D. *caespitosa* x *D*. *pilosa*	"
D. *caespitosa* x *D*. *purpurascens* and reciprocal	"
D. *caespitosa* x *D*. *richardsonii*	"
D. *eriantha* x *D*. *caespitosa*	"
D. *laevis* x *D*. *caespitosa*	"
D. *linkii* x *D*. *caespitosa*	"
D. *linkii* x *D*. *laevis*	"
D. *linkii* x *D*. *longifolia*	"
D. *linkii* x *D*. *penicillata*	"
D. *linkii* x *D*. *pilosa*	"
D. *linkii* x *D*. *racemosa*	"
D. *linkii* x *D*. *semiannualaris*	"
D. *linkii* x *D*. *setacea*	"
D. *pilosa* x *D*. *eriantha*	"
D. *purpurascens* x *D*. *linkii*	"
D. *purpurascens* x *D*. *purpurascens*	"
D. *racemosa* x *D*. *caespitosa*	"
D. *racemosa* x *D*. *linkii*	"
D. *racemosa* x *D*. *richardsonii*	"
D. *richardsonii* x *D*. *caespitosa*	"

TABLE I (continued)

Name	Authority
D. richardsonii x *D. eriantha*	Brock and Brown (1961)
D. richardsonii x *D. laevis*	"
Dichanthium	
D. annulatum x *D. annulatum*	Harlan *et al*. (1961)
D. annulatum x *D. caricosum*	"
D. annulatum x *D. fecundum*	"
D. annulatum x *D. papillosum*	"
D. aristatum x *D. annulatum*	"
D. aristatum x *D. caricosum* and reciprocal	"
D. caricosum x *D. annulatum*	"
Elymus	
E. virginicus x *E. candensis*	Brown and Pratt (1960)
E. virginicus x *E. interruptus*	"
E. canadensis x *E. interruptus*	"
Festuca	
F. pratensis x *F. arundinacea*	Hertzsch (1961)
Holcus	
H. mollis x *H. lanatus*	Jones and Carroll (1962)
Hordeum	
H. compressum x *H. pusillum*	Schooler (1960a,b)
H. murinum x *H. compressum*	"
Oryza	
O. australiensis x *O. alta*	Li *et al*. (1961)
O. balunga x *O. perennis* ssp. *cubensis*	Yeh and Henderson (1961)
O. breviligulata x *O. perennis*	Li *et al*. (1962)
O. breviligulata x *O. sativa*	Yeh and Henderson (1962)
O. glaberrima x *O. glaberrima* var. *stapfii*	"
O. glaberrima x *O. sativa*	"
O. glaberrima var. *stapfii* x *O. sativa*	"
O. malampuzhensis x *O. officinalis*	Gopalkrishnan (1962)
O. minuta x *O. officinalis*	Li *et al*. (1962)
O. paraguaiensis x *O. australiensis*	Li *et al*. (1961)
O. paraguaiensis x *O. brachyantha*	"
O. paraguaiensis x *O. latifolia*	Li *et al*. (1962)
O. paraguaiensis x *O. minuta*	"
O. paraguaiensis x *O. officinalis*	"
O. paraguaiensis x *O. sativa* var. *spontanea*	"
O. perennis ssp. *cubensis* x ssp. *barthii*	Yeh and Henderson (1961)
O. sativa x *O. balunga*	"
O. sativa x *O. breviligulata*	Li *et al*. (1962)
O. sativa x *O. officinalis*	"
O. sativa x *O. paraguaiensis*	"
O. sativa x *O. perennis* ssp. *barthii*	Yeh and Henderson (1961)

TABLE I (continued)

Name	Authority
O. sativa x *O. perennis* ssp. *cubensis*	Yeh and Henderson (1961)
O. sativa x *O. sativa* var. *fatua*	Yeh and Henderson (1961)
O. sativa x *O. sativa* var. *formosana*	"
O. sativa var. *formosana* x *O. perennis* ssp. *cubensis*	"
O. sativa var. *spontanea* x *O. alta*	Li *et al.* (1962)
O. sativa var. *spontanea* x *O. eichingeri*	"
O. sativa var. *spontanea* x *O. latifolia*	"
O. sativa var. *spontanea* x *O. paraguaiensis*	"
O. sativa var. *spontanea* x *O. perennis*	"
Paspalum	
P. dilatatum x *P. malacophyllum*	Bennett and Bashaw (1960)
Pennisetum	
P. typhoides x *P. dubium*	Gildenhuys and Brix (1961)
Phalaris	
P. arundinacea x *P. tuberosa* var. *stenophera*	Starling (1961)
P. tuberosa x *P. canariensis*	Cialzeta (1963)
Secale	
S. africanum x *S. silvestre*	Khush (1962)
S. montanum (B) x *S. silvestre*	"
S. montanum (I) x *S. africanum*	"
S. montanum (I) x *S. vavilovii*	"
S. vavilovii x *S. africanum* and reciprocal	"
S. vavilovii x *S. silvestre*	"
Sehima	
S. nervosum x *S. spathiflorum*	Joshi and Patil (1960)
S. nervosum x *S. sulcatum*	"

BROMUS - Nielsen et al. (1961) indicated that direction of hybridization has an influence on seed set, as noted in crosses between Bromus inermis, B. tyttholepis and B. pumpellianus. When B. inermis was crossed with B. tyttholepis, 50 per cent of the plants were hybrids, whereas with the latter species as female parent and B. pumpellianus as a pollen parent, only 20 per cent of the plants were hybrids. This difference in production of hybrids was attributed to marked genotypic difference in cross-compatibility among the species.

CYNODON - Forbes and Burton (1963), from a triploid hybrid ($2n = 27$) between Cynodon transvaalensis ($2n = 18$) x C. dactylon ($2n = 36$), reported the maximum possible number of 9 trivalents, which indicates that the genomes of the two parents are homologous.

DACTYLIS - The relative ease with which successful crosses can be produced is usually related to the ploidy levels of the parents. Borrill (1961) reported a considerable reduction in ability to exchange genes when crosses were made between the diploid parents of the genus Dactylis. However, when crosses were made between the tetraploid representatives, fertility increased slightly. In the latter case, ease of hybridization is in accordance with the taxonomic grouping of the tetraploid representatives of Dactylis. He also indicated that in tetraploids, differentiation between parental chromosomes leads to preferential pairing as bivalents, and a reduced quadrivalent frequency. On the other hand, Jones (1962) pointed out that the gross similarity of the chromosome sets in the diploid, provides the reason for quadrivalent formation in the tetraploids despite their strictly hybrid origin. Less severe reduction in fertility in tetraploids than in the diploids could be due to greater similarity of the constituent sets. It may be too, that the buffering effect of polyploidy is a controlling factor.

Müntzing (1937) reported naturally occuring triploids in Dactylis. Jones and Borrill (1962), in discussing the role of triploids in gene exchange, relative to the evolution of the genus Dactylis, indicated that on backcrossing, the triploids were partially female-sterile and gave rise to either triploids or tetraploids. The few diploids which were produced are not likely to compete with the natural diploids either in vigor or fertility. Normal chromosomal pairing, characteristic of the tetraploid progeny, makes further introgression possible and a natural tetraploid population can be enriched with genes from diploids without any detectable difference in morphology. Zohary and Nur (1959) had earlier indicated that any model for evolution of Dactylis must take these possibilities into account. The latter authors indicated that natural triploids occur in contact areas between the diploid and tetraploid populations of D. glomerata in Israel and that such triploids set seed in this natural habitat. According to these authors, the triploids apparently produce a large proportion of unreduced eggs. Fertilization of such eggs by haploid pollen (from the diploid parent) and diploid pollen (from the tetraploid parent) results in the formation of tetraploids and pentaploids, respectively. Thus, by producing a large population of vigrous tetraploid progeny, triploids can serve as an efficient bridge for one-way gene flow from the diploid level to the tetraploid level. Contrary to this, Jones and Borrill (1962) indicated that the average cross fertility of a diploid female and tetraploid male was low and that the pairing at meiosis was influenced by the genetic constitution of the parents and not by interspecific affinities, i.e., by the taxonomic position of the parents. More successful crosses were obtained when the female parent was a tetraploid.

Doroszewska (1962), in a comparative study on *D. slovenica* and *D. glomerata*, came to the conclusion that the two species differ only by their range of distribution and that *D. slovenica* can be classified as a sub-species of *D. glomerata*.

DANTHONIA - Brock and Brown (1961), in *Danthonia*, obtained diploid, triploid, tetraploid and pentaploid hybrids when 2*n*, 4*n* and 6*n* sub-species were intercrossed. On the basis of per cent pollen fertility and seed set data, they found that, except for the hybrids between the diploid parents, the rest were fertile. They believed that the greater genetic compatibility between polyploids reflects greater buffering of multiple gene dosages, and thus the increased tolerance of genetic unbalance in allopolyploids.

DICHANTHIUM - Harlan *et al.* (1961) reported hybrids within *Dichanthium* involving primarily five species, and in certain cases, the ecotypes and biotypes, also. Discussion of these hybrids, along with others produced more recently in this genus, is presented in later chapters of this dissertation.

ELYMUS - Brown and Pratt (1960) were able to produce artificial F_1 hybrids of *Elymus virginicus* with *E. canadensis* and *E. interruptus*, and also between the latter two species. They indicated that the greater variability of *E. virginicus* is due to introgression with *E. canadensis* and *E. interruptus*. Several ecotypes and biotypes in *Elymus* were reported by Bjorn (1962).

HOLCUS - Jones and Carroll (1962) indicated that in crosses between *Holcus lanatus* and *H. mollis*, the triploid hybrids looked more like the tetraploid parent (*H. mollis*), due to their genomic constitution (2 *mollis*: 1 *lanatus*). Wild natural hybrids may easily be confused with *H. mollis* and so only chromosome counts may conclusively establish identification. Morphologically, however, these triploids have sterile indehiscent anthers. They also noticed that in some species, 4*n*, 5*n* and 6*n* races exist, but the morphological differences are not large enough to allow taxonomic separation.

HORDEUM - Schooler (1960a,b) obtained *Hordeum compressum* x *H. pusillum*, and *H. marinum* x *H. compressum* hybrids with loose pairing of chromosomes in F_1 plants, but after colchicine treatment, the absence of tetrasomic segregation in the F_2 indicated allotetraploid formation.

ORYZA - Yeh and Henderson (1961, 1962) and Li *et al.* (1961, 1962) obtained several hybrids in *Oryza* (Table I) and suggested that all species could be intercrossed as readily as varieties within a species. These hybrids, however, behave differently during meiosis.

Yeh and Henderson (1961) further indicated that *O. sativa* originated directly from *O. balunga* but that in the process of domestication, intermediate forms occurred which could be classified as *O. sativa* var. *fatua*. The suggestion was made that most of the currently common forms of *O. sativa* var. *fatua* arose through natural hybridization between *O. sativa* and these earlier types of *O. sativa* var. *fatua*.

Gopalkrishnan (1962) crossed the tetraploid *O. malampuzhensis* with the morphologically similar diploid species of *O. officinalis*. From cytogenetic studies, he suggested that *O. malampuzhensis* could be considered a chromosomal race of *O. officinalis*. Alternatively, he considered it to be a segmental alloploid which originated from hybridization between geographic races of *O. officinalis* followed by chromosome doubling.

PASPALUM - Bennett and Bashaw (1960), in *Paspalum dilatatum* ($2n = 50$) x *P. malacophyllum* ($2n = 40$), obtained hybrids with $2n = 70$ chromosomes indicating aposporous development of the embryosac in *P. dilatatum*. They also noticed that the male parent was sexual and restored sexuality in the F_1 plants. The appearance of the F_2 progeny and their aneuploid nature indicated that the F_1 reproduced sexually.

PENNISETUM - Gildenhuys and Brix (1961) reported two hybrids, *Pennisetum typhoides* x *P. purpureum* and *P. typhoides* x *P. dubium*, both with 21 somatic chromosomes. When these hybrids were treated with colchicine, the former produced $2n = 21$ and 42 chromosome plants with normal mitosis. On the other hand, the second hybrid produced various mitotic abnormalities at the tetraploid level similar to abnormalities occurring in *P. dubium*. The abnormalities led to chromosome numbers varying from 14 to 42, even in the same root. The authors indicated that the irregular behavior was due to the action of genes inherited from its aneuploid *P. dubium* parent, which only express themselves when in double dosage. Through genic control it may, therefore, be impossible to permanently double the somatic chromosome complement of *P. typhoides* x *P. dubium*.

PHALARIS - Starling (1961), McWilliam (1962) and McWilliam and Neal-

Smith (1962), on the basis of hybridization, indicated a close relationship between Phalaris tuberosa and P. arundinacea. The hexaploid chromosomal race of P. arundinacea crosses freely with its tetraploid race, as well as with P. tuberosa, but is effectively isolated from both due to the sterility of the hybrids. The hexaploid was considered to have arisen through hybridization and subsequent introgression between these two species along the junction of their respective distributions in southern Europe. Allison (1962) indicated that when F_1 hybrids were backcrossed to both parents, only the cross to P. tuberosa var. stenophera was successful. Cialzeta (1963) observed only bivalent and univalent chromosomes in triploid hybrids between the tetraploid P. tuberosa and the diploid P. canariensis. Pollen fertility was less than 3 per cent, but after chromosome doubling by means of colchicine, was increased to 67.8 per cent.

POA - In a quadruple synthesized apomict, Poa scabrella - pratensis - ampla - alpigena, obtained from second generation apomicts of two primary hybrids, Clausen (1961) indicated that morphologically it should be classified as Poa pratensis although it had some characters of its great grandparents, P. scabrella and P. ampla.

SEHIMA - Joshi and Patil (1960) obtained triploid hybrids by crossing the male-sterile tetraploid Sehima nervosum with the diploids, S. sulcatum and S. spathiflorum.

SECALE - Khush (1962) studied one strain each of Secale silvestre, S. vavilovii and S. africanum, two strains of S. montanum, the six possible interspecific hybrids, and a reciprocal hybrid of S. vavilovii and S. africanum. On the basis of geographical distribution, breeding behavior, growth habit, morphology, crossability, cytology and genetic affinities, *S. silvestre* differs from the remaining species rather strikingly, while the other species seem to be more closely interrelated. It was, therefore, suggested that *S. silvestre* be placed in a section by itself and the other four species (including *S. cereale*) in a different section. Khush and Stebbins (1961), on the basis of cytological studies, indicated that *S. cereale* differs from all four wild species by two reciprocal translocations and that this species originated from *S. montanum* by the progressive fixation of two translocations. This translocation fixation was facilitated by the adaptive superiority of the translocation heterozygotes and rearrangement homozygotes.

B. INTERGENERIC HYBRIDIZATION - The genera, *Aegilops*, *Agropyron*, *Bothriochloa*, *Dichanthium*, *Elymus*, *Hordeum*, *Oryzopsis*, *Sitanion*, *Stipa* and *Triticum*, appear to have been used most commonly in biosystematic studies of the Gramineae at the generic level. Table II lists 23 intergeneric hybrids.

TRIBE ANDROPOGONEAE - In the generic group Bothriochloininae of the subtribe Andropogoninae, the genera, *Bothriochloa*, *Dichanthium* and *Capillipedium*, together form an agamic species-complex, as defined by Babcock and Stebbins (1938) and Stebbins (1950). The intergeneric hybrids produced in this complex were reviewed by Harlan *et al.* (1961) and Harlan *et al.* (1962). Artificial hybrids of *Bothriochloa* with *Capillipedium* and *Dichanthium* were produced, but between the latter two genera no evidence of successful crossing has been reported so far. Evidence of natural introgression between *Bothriochloa* and *Dichanthium*

TABLE II

RECENT REPORTS ON INTERGENERIC HYBRIDS IN THE GRAMINEAE

Name	Authority
ANDROPOGONEAE	
Bothriochloa grahamii x *Capillipedium assimile*	Harlan *et al*. (1962)
B. grahamii x *C. parviflorum*	Harlan *et al*. (1961)
B. grahamii x *C. spicigerum*	"
B. grahamii x *Dichanthium annulatum*	"
B. grahamii x *D. aristatum*	"
B. grahamii x *D. caricosum*	"
B. grahamii x *D. fecundum*	"
B. grahamii x *D. papillosum*	"
B. ischaemum var. *songarica* x *D. annulatum*	"
FESTUCEAE	
Festuca pratensis x *Lolium multiflorum* and reciprocal	Hertzsch (1961)
F. pratensis x *L. perenne*	"
L. multiflorum x *F. pratensis*	"
L. perenne x *F. pratensis*	"
HORDEAE	
Agropyron repens x *Hordeum secalinum*	Cauderon and Saigne (1961)
A. intermedium x *Triticum dicoccum*	Cauderon (1961a,b)
A. intermedium x *T. durum* var. *mahmoudi*	"
A. intermedium x *T. persicum* var. *rubiginosum*	"
A. intermedium x *T. timopheevi*	"
A. intermedium x *T. vulgare*	"
Elymus cinereus x *Sitanion hystrix*	DeWey and Holmgren (1962)
Sitanion hystrix x *A. trachycaulum*	Boyle (1963)
STIPEAE	
Oryzopsis hymenoides x *Stipa nevadensis*	Johnson (1962a,b)
O. hymenoides x *S. speciosa*	Johnson (1960)

on the one hand, and *Bothriochloa* and *Capillipedium* on the other, was suggested by Faruqi (1963). Thus, on the basis of both natural and artificial hybrids, it was suggested by Harlan *et al*. (1961) that the three genera might be merged into one genus, with *Dichanthium* receiving priority. In this large agamic complex, *B. intermedia* appears to be a connecting link and has been named as a "compilospecies" by Harlan and deWet (1963).

TRIBE FESTUCEAE - The oldest known and described natural hybrid in the Gramineae above the species level is *Festuca pratensis* x *Lolium perenne* (Curtis, 1777) which has been named as *F. loliacea*. Jenkin (1933) indicated it to be an intertribal cross between Festuceae (*Festuca*) and Hordeae (*Lolium*). Later on, Hubbard (1934) and Bor (1947) classified the two genera under one tribe (Festuceae). Stebbins (1952) indicated that hybrids between the species of *Festuca* and *Lolium*, in reality, represent crosses between the two genera which have been placed in different tribes.

Wit (1959) pollinated diploid, triploid and tetraploid plants of *L. perenne* and *L. multiflorum* with diploid and tetraploids of *F. pratensis* after emasculation. Only the combinations $2n$ x $4n$ and $3n$ x $4n$ produced hybrids, but, with non-emasculated spikes in the field, hybrids were also obtained in the crosses $2n$ x $2n$ and $2n$ x $3n$. The number of hybrids produced per inflorescence in the field was, on an average, nearly as high as in corresponding crosses in the glasshouse. Triploid hybrids were more productive in forage than either of the parents ($2n$ and $4n$).

Hertzsch (1961) indicated that the diploid hybrid *L. multiflorum* x *F. pratensis* had the same type of normal chromosome pairing at meiosis as the *L. perenne* x *F. pratensis* hybrid, but was sterile. The sterility occurred in both the male and female flowers. In the triploid, *L. multiflorum* 4*n* x *F. pratensis* 2*n*, the inflorescence was an ear; in the tetraploid, *F. pratensis* 4*n* x *L. multiflorum* 2*n*, it was a panicle, which indicated that the genomes present in greatest number exert an influence on the formation of the inflorescence.

TRIBE HORDEAE - *AGROPYRON* x *HORDEUM* - Cauderon and Saigne (1961) obtained hybrids between *Agropyron repens* ($2n = 42$) and *Hordeum secalinum* ($2n = 28$). They designated the *A. repens* genome as R_1, R_2, Z_1, but the two genomes of *H. secalinum* are not known. However, it was suggested that one of the *H. secalinum* genomes is closely related with the Z_1 genome.

AGROPYRON x *TRITICUM* - Cauderon (1961a) listed intergeneric hybrids of *A. intermedium* with five species of *Triticum*, *T. dicoccum*, *T. durum* var. *mahmoudi*, *T. persicum* var. *rubiginosum*, *T. timopheevi* and *T. vulgare*. In general, the amphiploids of *Agropyron* and *Triticum* show good agronomic performance. Cauderon (1961b) also obtained hybrids of *T. vulgare* and *T. dicoccum* with *A. intermedium*, *A. campestre*, and *A. elongatum*.

Stebbins and Pun (1953), in their review of hybrids in the tribe Hordeae, suggested that no sharp distinction can be made between the species of *Agropyron* which are closely related to *Triticum*, and those which are not.

AEGILOPS x *TRITICUM* - Artificial hybrids between some species of *Triticum* and some of *Aegilops* have been produced (McFadden and Sears, 1946; Kihara and Lilienfeld, 1949) and evidence of natural introgression between these two genera was presented recently by Eochard

(1961) and Zohary and Feldman (1962). The latter authors also discussed the evolution of polyploids in the Aegilops-Triticum group.

ELYMUS x SITANION - DeWey and Holmgren (1962) found several putative hybrids of Elymus cinereus x Sitanion hystrix growing near Shoshone, Idaho. Cytological and morphological analyses confirmed the suggestions that these plants were bonafide hybrids. Both species are strict allopolyploids and their genomic constitution was suggested to be AABB and CCDD, respectively. Chromosomes of the parents associated into 14 pairs but in the hybrids, no cell contained more than four bivalents. They also indicated that E. aristatus appears to be, in reality, an intergeneric hybrid between E. cinereus x S. hystrix or E. triticoides x S. hystrix. Also, that although such F_1 hybrids are sterile, they can produce seeds by backcrossing. This was demonstrated by Stebbins and Snyder (1956) in E. glaucus x S. jubatum.

SITANION x AGROPYRON - Boyle (1963) in a controlled hybrid between Sitanion hystrix and Agropyron trachycaulum indicated that, although it is not possible to distinguish between autosyndetic and allosyndetic pairing, these two species, unquestionably, are more closely related than their present taxonomic status indicates.

Considering the various possibilities of intergeneric hybrids in the tribe Hordeae, Stebbins and Pun (1953), in fact, proposed that the genera Aegilops, Agropyron, Elymus, Haynaldia, Secale, Sitanion and Triticum be merged into a single large genus. However, they suggested that such a radical taxonomic step is not proper until more information becomes available concerning the species relationships. Later on, Stebbins and Snyder (1956) suggested that, on the basis of natural and artificial hybrids, Agropyron, Hordeum and Elymus be placed in a single genus for a better understanding of phylogenetic relationships.

TRIBE MAYDEAE - A biosystematic problem, similar to those mentioned above in the tribes Andropogoneae and Hordeae, leading to the grouping of different genera of a tribe into a single genus or a few genera, seems to be present in the *Maydeae* too. *Zea mays* and *Euchlaena mexicana* cross easily (Mangelsdorf and Reeves, 1939); also, the two genera conform very well to closely related cogeneric species, according to the suggestions of Reeves and Mangelsdorf (1942). Recently, Mangelsdorf (1961) and Anderson (1961) presented evidence of natural introgression of *Tripsicum* and *Euchlaena* in several races of maize in South America. This evidence was based on archeology, morphology, genetics, cytology and systematics.

TRIBE STIPEAE - Johnson (1960) reported spontaneous sterile hybrids between *Oryzopsis hymenoides* and *Stipa speciosa*. This hybrid was recognized to be *O. bloomeri*. Chromosomes of both parents associated into regular bivalents at meiosis. Hybrids were characterized by occasional bivalents, and mostly asynchronous splitting or random distribution of univalents at metaphase I. Johnson (1962a, b) reported that *S. nevadensis* (an amphiploid) and one of its parents, *S. elmeri*, crosses with *O. hymenoides* in nature. These hybrids have the morphological characteristics of *Stipa* species, in each case, diluted by that of *O. hymenoides* and are less readily distinguishable from each other, than are the *Stipa* parents themselves. Thus, nearly identical sterile hybrids (*O. bloomeri*) are produced from each *Stipa* parent. It was suggested, based on the assumption of homology between different genomes of the amphiploid *S. nevadensis*, that bivalent formation in polyploid species of Stipa might be genetically controlled. Colchicine induced amphiploids from O. hymenoides x S. elmeri and O. hymenoides x S. nevadensis were also obtained.

Thus, from the taxonomic point of view, delimitation of grasses in different units or categories is intrinsically difficult, because interspecific boundaries have become obscured by hybridization, polyploidy and apomixis. In a tribe, like Andropogoneae, where both sexual and apomictic modes of reproduction are prevalent, species relationships based on range of hybridization and the breeding behavior of the species and their hybrids is complicated by several mechanisms, some of which are discussed in subsequent chapters under appropriate headings, in this dissertation.

CHAPTER III

ORIGIN, MORPHOLOGY AND CYTOLOGY OF DICHANTHIUM ANNULATUM (X-98)

Dichanthium annulatum (Forssk.) Stapf is a polymorphic species, widespread throughout the tropics and subtropics of the Old World (Celarier et al., 1958; and Mehra, 1962). The Tropical type is represented by diploid ($2\underline{n} = 20$) and tetraploid ($2\underline{n} = 40$) races, both of which are widely distributed in India. Celarier and Harlan (1957) indicated that diploids are sexual and tetraploids are facultative apomicts. In 1955, over 4,000 emasculated spikelets of the diploid (3242) were pollinated with the tetraploid (5411). Four seeds were obtained and one of these produced a mature plant. This plant was not a triploid, as expected, but a tetraploid and was assigned the number, 55-X-98.

Morphologically X-98 resembles the female diploid parent in most respects, but is more vigorous, more erect in growth habit and has larger panicles. Although it is probable that X-98 could have originated through fertilization of a cytologically unreduced egg of the diploid female parent (3242) by the normal male gamete of the tetraploid male parent, morphological data (Table III) suggest that it is an autotetraploid derived from the diploid collection (3242). Cytological studies of X-98 show that, though occasionally trivalents and tetravalents may be formed, chromosomes usually associate into 20 pairs (Table IV). Thus, cytologically balanced gametes

TABLE III

GROSS MORPHOLOGICAL DATA OF *D. ANNULATUM* 3242, 5411 AND X-98

Characteristics	3242	5411	X-98
Growth habit	semi-decumbent	decumbent	decumbent
Av. length primary axis (mm)	10.20	15.25	11.60
Av. length longest raceme (mm)	36.80	53.70	68.50
Av. raceme number	5.60	5.80	5.50
Av. number primary axis nodes	3.00	4.50	3.50
Av. number spikelet-pairs per raceme	21.00	36.00	32.20

TABLE IV

CYTOLOGY OF *D. ANNULATUM* 3242, 5411 AND X-98

		Chromosome Associations*			
Name	2n	I	II	III	IV
3242	20	0.00 --	10.00 10	0.00 --	0.00 --
5411	40	0.36 0-4	18.64 16-20	0.04 0-1	0.56 0-2
X-98	40	1.24 0-6	17.08 15-20	0.12 0-1	1.06 0-3

*Average number and range of various configurations are listed.
I = univalents; II = bivalent; III = trivalents; IV = quadrivalent

are produced. Essentially regular chromosome association, in *Dichanthium*, is explained by deWet *et al.* (1961) to be due, in part, to autosyndesis and that it is genetically controlled. Müntzing and Prakken (1940), in *Phleum*, Darlington (1937), in *Pyrus*, Rees (1961), in *Secale*, and Riley and Chapman (1958), in *Triticum*, indicated that under situations where chromosome association is genetically controlled, bivalents, rather than multivalents, may be the usual mode of chromosome pairing in autopolyploids.

Emasculated florets of this autotetraploid failed to set seed without pollination. Similarly, after self-pollination, seeds were only rarely produced. When pollinated by a morphologically distinct natural biotype of *D. annulatum*, however, seed set was high (100% in some cases) and most of the progeny obtained represent hybrids.

These data indicate that *D. annulatum* (X-98) reproduces sexually and is highly self-sterile. For these reasons, this plant was used extensively in the hybridization experiments in an effort to determine phylogenetic relationships within the genus *Dichanthium* Willemet.

CHAPTER IV

HYBRIDIZATION RANGE OF *DICHANTHIUM ANNULATUM* (FORSSK.) STAPF

The species *D. annulatum* (Forssk.) Stapf is widely distributed, extending from the west coast of northern Africa across India, and southeast Asia to Australia and the Fiji Islands. Along its range of distribution this species is sympatric with a number of other species of *Dichanthium* Willemet, as well as several species belonging to the two related genera *Bothriochloa* O. Kuntze and *Capillipedium* Stapf. Morphological data, presented by Harlan *et al.* (1958, 1961), suggested that this species hybridizes in nature with *B. intermedia* wherever their ranges of distribution overlap.

Dichanthium annulatum is characterized by sexually reproducing diploids and facultatively apomictic tetraploid races. The plants used as female parents represent comparatively sexual tetraploids collected in nature, and an artificially produced sexual tetraploid which is largely self-sterile. These were pollinated, using various members of the tribe Andropogoneae as male parents, in an effort to determine the phylogenetic affinities of *D. annulatum*.

MATERIALS AND METHODS

In all, 62 different collections were used as male parents. These involved 9 species of *Dichanthium* (21 collections), 16 species of *Bothriochloa* (36 collections), 3 species of *Capillipedium*

(4 collections) and one species of Eremopogon (1 collection). These represent plants with $2\underline{n} = 20$, 40, 50 and 60 chromosomes. The seeds obtained were germinated according to the technique described by Ahring and Harlan (1961) and Ahring (1963). The seedlings were later transplanted to a uniform nursery as outlined by Celarier and Harlan (1956). Bud materials for cytological studies were fixed in Carnoy's solution (6:3:1). Meiotic analyses were done by the standard acetocarmine squash technique. Morphological studies are based on field observations as well as herbarium specimens.

RESULTS

Range of hybridization of D. annulatum was obtained using an artificially produced sexual plant (X-98) as the female parent and various members of the tribe Andropogoneae as male parents. The data are presented in Table V and Plate I. On an average, 0.05 seed per panicle was obtained from 80 panicles of X-98 when selfed. Thus, theoretically, any increase in seed-set over this, when pollinated with pollen from other collections, should represent hybrids. In general, when emasculation was not practiced, pollen of X-98 seems to interfere with foreign pollen. Most hybrids, however, were produced without emasculation. Artificial hybrids of X-98 with other tetraploid races of D. annulatum were easy to produce. These races are the Tropical and Mediterranean ecotypes and the Senegal type which may be regarded as a biotype of the Mediterranean ecotype. Crosses between the $4\underline{n} \times 4\underline{n}$ parents resulted in hybrids with $2\underline{n} = 40$ and 60 chromosomes, indicating that both the cytologically

TABLE V

CROSSING DATA OF *D. ANNULATUM*

Female Parent - *Dichanthium annulatum* (X-98) 2n = 40

Male Parents Species	Acc. No.	2n	Original Source	Seeds		Hybrids	
				Normal	Poorly Developed	Obtained	2n
I. *Dichanthium*							
i. *D. annulatum*							
(a) Tropical	3242	20	Calcutta, India	91	8	yes	30
	4099	40	New Delhi, India	138	0	yes	40
	5398	40	Karnal, India	274	10	yes	40
(b) Mediterranean	4390	40	Zerkine, Tunisia	12	10	yes	40,60
(c) Senegal	5430	40	Bambey, Senegal	102	6	yes	40,60
ii. *D. aristatum*	7199	20	Sangli, India	75	3	yes	30
	3025	40	Pretoria, S. Africa	0	10	no	--
	4086	40	New Delhi, India	1	3	no	--
	6178	40	Bihar, India	0	0	no	--
	6406	60	Philippines	2	1	no	--
iii. *D. caricosum*	8452	20	Poona, India	10	41	yes	30
	4291	40	Trinidad	0	8	no	--
	5599	40	Fiji Islands, Intrd.#	38	12	yes	40,60
	7157	40	Delhi, India	1	8	no	--
iv. *D. fecundum*	6525	40	Queensland, Australia	13	13	yes	40
v. *D. humilius*	7567	20	Queensland, Australia	0	7	no	--
vi. *D. panchganiense*	8278	20	Panchgani, India	78	10	yes	30
vii. *D. papillosum*	3716	60	S. Rhodesia	130	4	yes	50
	4080	60	S. Africa	95	0	yes	50
	4083	60	S. Africa	94	3	yes	50
viii. *D. sericeum*	4610	20	Queensland, Australia	0	6	no	--
ix. *D. superciliatum*	5628	20	Australia	0	0	no	--

TABLE V (continued)

Female Parent - Dichanthium annulatum (X-98) 2n = 40

Male Parents Species	Acc. No.	2n	Original Source	Seeds		Hybrids	
				Normal	Poorly Developed	Obtained	2n
II. Bothriochloa							
i. B. ambigua	5643	60	Canberra, Australia	0	0	no	--
ii. B. ewartiana	4596	60	Galton, Australia	0	0	no	--
	6137	60	Australia	0	1	no	--
iii. B. glabra	6511	40	Australia	0	0	no	--
iv. B. grahamii	X-750	40	(Synthetic hybrid)	120	8	yes	40, 60
	2655	40	Br. Guiana, Intrd.#	54	0	yes	40, 60
	5450	40	New Delhi, India	72	2	yes	40
	9064	40	Nasik, India	6	14	no	--
	9110a	40	Mt. Abu, India	3	0	no	--
v. B. insculpta	3704	60	Natal, S. Africa	0	0	no	--
	5152	60	S. Africa	1	0	no	--
	5194	60	S. Africa	0	0	no	--
	6902	50	S. Africa	0	0	no	--
vi. B. intermedia	4088	40	Texas, Intrd.#	1	3	no	--
	4394	40	Dehra Dun, India	0	0	no	--
	5409	40	Bariely, India	0	0	no	--
	5410b	40	Punjab, India	8	0	no	--
	5470	40	Nairobi, Kenya	1	3	no	--
	5594	40	Fiji Islands	2	0	no	--
	6587	40	Pakistan	0	5	no	--
	7010	40	Palampur, India	0	11	no	--
	8898	40	Rawalpindi, Pakistan	0	0	no	--
	8900	40	Rawalpindi, Pakistan	0	0	no	--
vii. B. ischaemum	1369	40	Coruh, Turkey	0	0	no	--
	6982	40	Kenya, Intrd.#	0	0	no	--
	726	50	Amoy, China	28	6	no	--
	3958	50	Sicily, Italy	0	1	no	--
	6459	50	Hong Kong, China	0	6	no	-(70)*
	1347	60	Triangle City, China	0	0	no	--

TABLE V (continued)

Female Parent - *Dichanthium annulatum* (X-98) $2n = 40$

Male Parents Species	Acc. No.	$2n$	Original Source	Seeds		Hybrids	
				Normal	Poorly Developed	Obtained	$2n$
	2582	60	Koohsiung, Formosa	0	0	no	--
	4711	60	Greece	0	1	no	--
viii. *B. longifolia*	8301	20	Poona, India	1	6	no	--
ix. *B. pertusa*	8865	20	N. Sorgodha, Pakistan	3	3	no	--
	8299	40	Khandala, India	2	0	no	--
x. *B. radicans*	4518	40	Ethiopia	0	1	no	--
III. *Capillipedium*							
i. *C. huegelii*	5794	20	Bombay, India	0	0	no	--
ii. *C. spicigerum*	4104	40	Texas, Intrd. #	0	0	no	--
	4599	40	Queensland, Australia	0	0	no	--
iii. *C. parviflorum*	6458	40	Hong Kong, China	0	0	no	--
IV. *Eremopogon*							
i. *E. foveolatus*	4072	40	Ajmer, India	0	0	no	--

*Hybrids were obtained with X-98 as the male parent.

Introd. = Introduction

LEGEND TO PLATE I

Hybridization range of *Dichanthium annulatum*

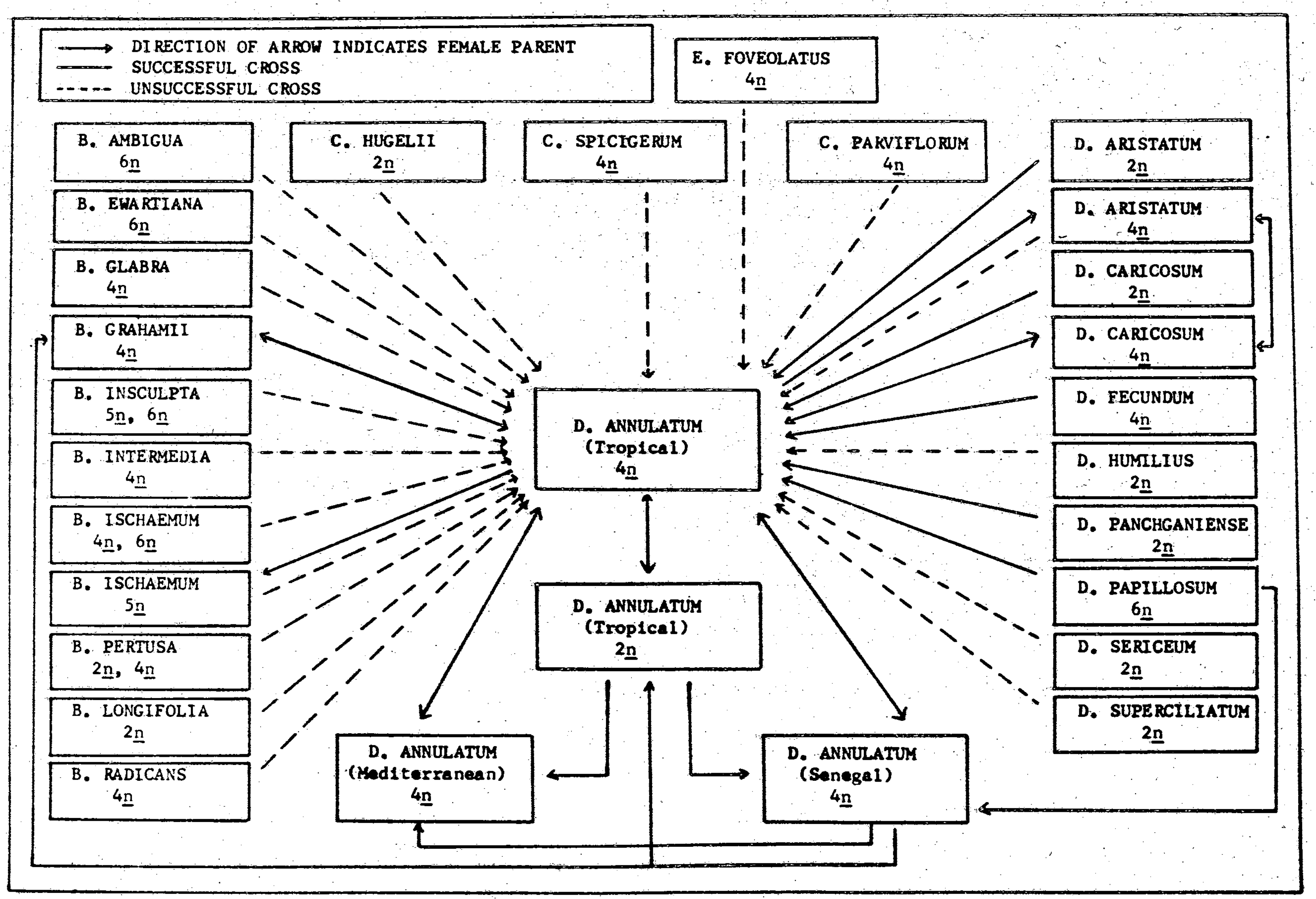

DIRECTION OF ARROW INDICATES FEMALE PARENT
SUCCESSFUL CROSS
UNSUCCESSFUL CROSS
E. FOVEOLATUS 4n
B. AMBIGUA 6n
C. HUGELII 2n
C. SPICIGERUM 4n
C. PARVIFLORUM 4n
D. ARISTATUM 2n
B. EWARTIANA 6n
D. ARISTATUM 4n
B. GLABRA 4n
D. CARICOSUM 2n
B. GRAHAMII 4n
D. CARICOSUM 4n
B. INSCULPTA 5n, 6n
D. FECUNDUM 4n
D. ANNULATUM (Tropical) 4n
B. INTERMEDIA 4n
D. HUMILIUS 2n
B. ISCHAEMUM 4n, 6n
D. PANCHGANIENSE 2n
B. ISCHAEMUM 5n
D. PAPILLOSUM 6n
D. ANNULATUM (Tropical) 2n
B. PERTUSA 2n, 4n
D. SERICEUM 2n
B. LONGIFOLIA 2n
D. SUPERCILIATUM 2n
B. RADICANS 4n
D. ANNULATUM (Mediterranean) 4n
D. ANNULATUM (Senegal) 4n

PLATE I

reduced as well as unreduced female gametes can function sexually. The apomictic female parents occasionally produced $2n = 20$ chromosome plants which represent polyhaploids.

Hybrids with $2n = 50$ chromosomes were produced with D. annulatum ($2n = 40$) as the female parent and the hexaploid D. papillosum ($2n = 60$) as the male parent. When X-98 was pollinated with pollen from D. fecundum ($2n = 40$), hybrids with $2n = 40$ chromosomes were produced.

Hybrids between D. annulatum and either D. caricosum or D. aristatum were obtained only with difficulty. At the tetraploid level, D. caricosum, when used as the pollen parent, produced hybrids with $2n = 40$ and 60 chromosomes. Dichanthium aristatum and D. annulatum produced hybrids with $2n = 40$ chromosomes, only when the first mentioned species was used as the female parent and D. annulatum as the pollen parent. Diploid races of both D. caricosum and D. aristatum gave rise to triploid hybrids when crossed with tetraploid D. annulatum as the female parent. Similarly, the diploid species, D. panchganiense, crossed readily with tetraploid D. annulatum.

Crosses with other diploid representatives of Dichanthium and tetraploid D. annulatum were not successful. With D. sericeum, a few poorly developed seeds were obtained but the seedlings died before they could be transplanted to the field. With D. superciliatum, no seed, whatsoever, was obtained.

Intergeneric crosses were attempted between D. annulatum and various species of Bothriochloa (Table V and Plate 1). Species of this genus which have so far been able to cross with D. annulatum are B. grahamii ($2n = 40$) and B. ischaemum ($2n = 50$). From crosses between the two tetraploid species, D. annulatum and B. grahamii, plants with $2n = 40$ and 60 chromosomes were obtained. These hybrids were of normal vigor and produced a large number of seeds. Hybrids of D. annulatum with B. ischaemum were obtained with difficulty, and only when the latter species was the female parent. The resulting plants ($2n = 70$) were weak and sterile. Morphological data indicates that the unreduced female gamete of B. ischaemum was fertilized by a normal male gamete of D. annulatum. With other species of Bothriochloa, except for occasional selfed seed, either poorly developed seeds were obtained which failed to germinate, or no seed was produced at all.

None of the attempted crosses of D. annulatum with the genera Capillipedium and Eremopogon were successful.

DISCUSSION

Hybrids between the biotypes and ecotypes of D. annulatum, as discussed by Celarier, et al. (1958), Mehra and Celarier (1958) and Mehra (1961, 1962), can be produced with relative ease. These, as indicated by Celarier and Harlan (1957) and Harlan et al. (1958, 1961), are facultative apomict tetraploids. Morphological variation is closely correlated with adaptation to either a tropical or desert habitat. For this reason the Tropical and Mediterranean types could be referred to as ecotypes, as described by Turesson (1922a, b), Stebbins (1950) and Baker (1959). In nature, the ecotypes of D. annulatum overlap in their geographic distribution. The ease with which artificial hybrids were produced, suggests very little or no genetic barriers between the various ecotypes, except for apomixis. This suggests that the ecotypes represent merely ecological variation of the same species.

Typical representatives of the genus Dichanthium are morphologically subdivided by deWet and Richardson (1963) into two tetraploid agamospecies and two diploid sexual species groups. Turesson (1929) defined agamospecies as an apomict-population, the constituents of which, for morphological, cytological or other reasons, have a common origin. Within the first agamospecies consisting of D. annulatum, D. andringitrense, D. fecundum, D. mucronulatum and D. papillosum, artificial hybrids, at least among the species available for study, are possible with relative ease. Borgaonkar and Singh (1962) suggested that D. papillosum originated from a cross between the Tropical and Mediterranean ecotypes of D. annulatum. The ability of the latter species to cross with D. papillosum could thus be expected. Hybrids between D. annulatum and D. fecundum were observed in nature (deWet, 1963) and were also produced artificially. The relative ease with which hybrids within this agamospecies could be produced indicates the close relationships between the species recognized taxonomically.

The second agamospecies includes D. aristatum, D. caricosum, D. tenue, D. pallidum and D. theinlwinii. Hybrids between members of this agamospecies and D. annulatum are produced with more difficulty. Crosses between D. annulatum (4n) and the diploid and tetraploid races of D. caricosum and D. aristatum are possible. Celarier et al. (1961b) indicated the existence of natural hybrids between D. annulatum and D. caricosum, and possibly also between D. annulatum and D. aristatum. Crossing data suggest that D. caricosum is more closely related to *D. annulatum* than is *D. aristatum*. A similar conclusion was previously reached by Celarier *et al.* (1961b). Attempted crosses of *D. annulatum* with other species or biotypes of this agamospecies were not successful. As expected, members of this group are more distantly related to *D. annulatum* than are those of the agamospecies to which the later species belongs.

Two diploid species groups are recognized in *Dichanthium*. The species, endemic to India, are *D. panchganiense*, *D. armatum* and *D. maccannii*. The only species available for study was *D. panchganiense*, and it crosses with *D. annulatum*. The other diploid species-group of *Dichanthium* is confined to Australia, and includes *D. sericeum*, *D. setosum*, *D. superciliatum* and *D. humilius*. The fact that no hybrid plant could be obtained between any one of these species and *D. annulatum* indicates that they are only distantly related to the *D. annulatum* species complex.

Hybrids between *D. annulatum* and *B. ischaemum* can be produced only when cytologically unreduced egg of the latter species is fertilized by normal male gamete of *D. annulatum*. This indicates some degree of genetic barrier and that the two species are phylogenetically widely separated. Weak and sterile hybrids could also suggest that in such wide crosses even apomixis could not salvage fertility. In the genus *Bothriochloa*, the only species with which successful artificial hybrids of *D. annulatum* were produced was *B. grahamii*. Harlan *et al.* (1961) and deWet (1963) suggested a hybrid origin of *B. grahamii* representing a cross between *D. annulatum* and *B. intermedia*. Hybrids between *D. annulatum* and *B. grahamii* would thus be expected. Crossing data presented by Harlan *et al.* (1962) indicated that barriers to gene flow are least between *B. grahamii* and *D. annulatum*. Indeed, on genetic grounds, *B. grahamii* could more naturally be included in *Dichanthium*. *Capillipedium* is able to cross with *B. grahamii* (Harlan *et al*., 1961) and thus, *B. grahamii* may be considered, systematically, as a connecting link between *D. annulatum* and species of *Capillipedium*. No direct relationship can, however, be established between the latter two taxa. The genus *Eremopogon* is completely isolated genetically from *D. annulatum*.

CONCLUSIONS

1. Hybrids between the morphological types of *D. annulatum* were easily produced.

2. *Dichanthium fecundum* and *D. papillosum* produced hybrids with *D. annulatum*, though with some difficulty.

3. Other species of *Dichanthium* with which *D. annulatum* could cross were: *D. caricosum* (2*n* = 20, 40), *D. aristatum* (2*n* = 20, 40) and *D. panchganiense* (2*n* = 20).

4. At the intergeneric level hybrids were obtained between *D. annulatum* (2*n* = 40) and *B. grahamii* (2*n* = 40) as well as *B. ischaemum* (2*n* = 50).

5. From the present study, on the basis of hybrid data, the genera *Capillipedium* and *Eremopogon* appear to be completely isolated genetically from *D. annulatum*.

CHAPTER V

BIOSYSTEMATIC STUDIES OF THE DICHANTHIUM ANNULATUM COMPLEX

The genus Dichanthium Willemet belongs to the generic group Bothriochloininae, tribe Andropogoneae of the family Gramineae (deWet, 1963). It includes several highly polymorphic species. Dichanthium annulatum (Forssk.) Stapf, throughout its range of distribution in the tropics and subtropics of the Old World, is represented by different ploidy levels and morphologically distinct types (Celarier and Harlan, 1955; Harlan et al., 1958; Mehra and Celarier, 1958; Celarier et al., 1958; Mehra, 1961, 1962; and Singh et al., 1962). Diploid representatives ($2n = 20$) of this species are sexual and the tetraploids ($2n = 40$) are facultative apomicts (Celarier and Harlan, 1957). In nature, D. papillosum (Hochst.) Stapf and the Mediterranean type of D. annulatum overlap in their geographic distribution (Plate II). Similarly, the Tropical type of D. annulatum and D. fecundum S. T. Blake overlap (deWet, 1963). Artificially produced hybrids, between the morphological types of D. annulatum, between D. annulatum and D. papillosum as well as D. fecundum, were studied in an effort to determine the relationships within this agamospecies.

MATERIALS AND METHODS

Artificially produced hybrids between the morphological types of D. annulatum as well as of D. annulatum with D. fecundum and D.

LEGEND TO PLATE II

Geographic distribution of the *D. annulatum* complex

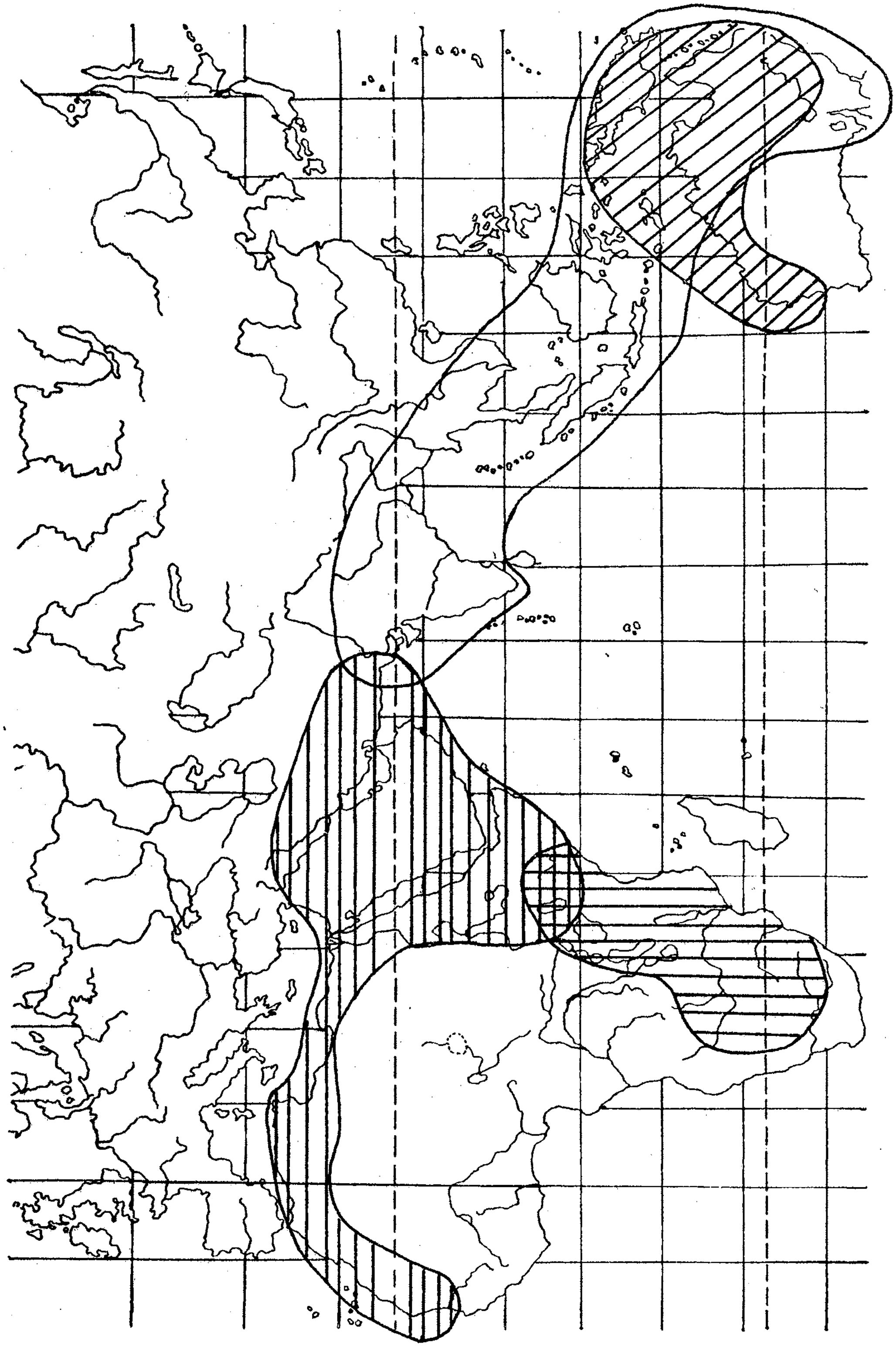
□ *D. annulatum* (Tropical type).

▤ *D. annulatum* (Mediterranean type).

▥ *D. papillosum* .

▧ *D. fecundum* .

PLATE II



papillosum were obtained by using the sexual plant, X-98, and also facultative apomict plants as the female parents. Hybrids with the apomict female parent of *D. annulatum* were produced by W. L. Richardson following the technique described by him (1958). Plants were grown in a uniform nursery as outlined by Celarier and Harlan (1956). Morphological studies are based on field observations correlated with herbarium studies.

RESULTS

Gross morphological characters of the Tropical and Mediterranean ecotypes, and the Senegal biotype of *D. annulatum*, along with those of *D. fecundum* and *D. papillosum*, are presented in Plates III and IV. Morphological data of the hybrids within *D. annulatum* and of the latter species with *D. fecundum* and *D. papillosum* are shown in pictorialized scattered diagrams (Plate IV), following Anderson's techniques (1949, 1957). Cytological studies are summarized in Table VI.

Mehra (1962) described, in detail, the morphology of the three types of *D. annulatum*. The following distinguishing characters of the different morphological types are the most significant. The Tropical ecotype is usually moderately robust, decumbent with thick racemes; the glumes are broad, obtuse, and have long bulbous-based hairs on the upper half of both the sessile and pedicellate spikelets. Both diploid ($2n = 20$) and tetraploid ($2n = 40$) races occur, the former being usually smaller than the latter but otherwise very similar. In India, both cytological races are widely distributed. The Mediterranean ecotype is more erect, and more slender with narrow racemes. The glumes are more pointed than that of the Tropical type, and the

LEGEND TO PLATE III

Inflorescences of the D. annulatum complex. - Showing variation in length of primary axis, and also number and length of racemes.

Figure 1. D. annulatum (Tropical type).

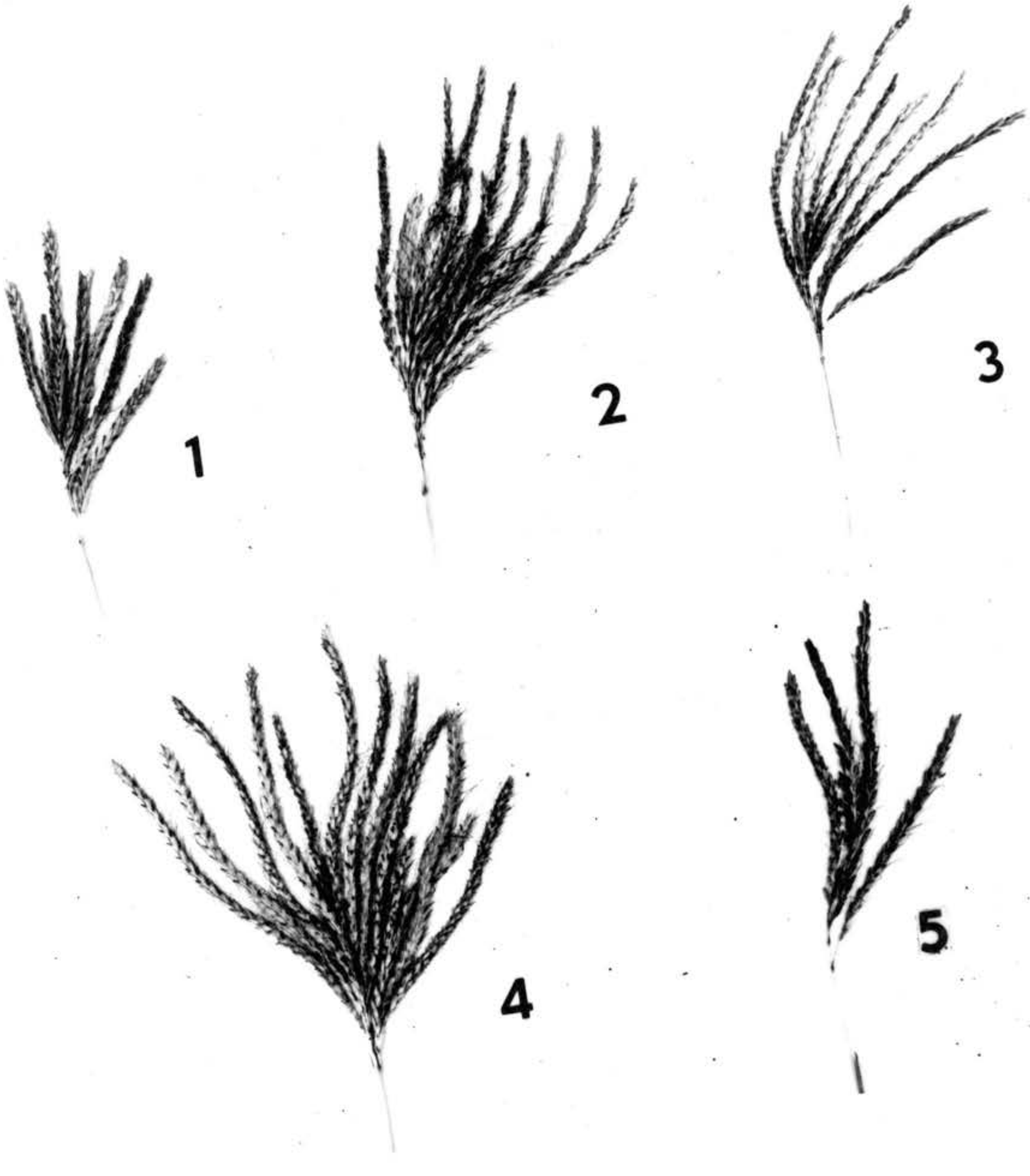
Figure 2. D. annulatum (Mediterranean type).

Figure 3. D. annulatum (Senegal type).

Figure 4. D. papillosum.

Figure 5. D. fecundum.

PLATE III



LEGEND TO PLATE IV

Morphological characteristics of the *D. annulatum* complex - parents and hybrids.

Chromosome No.: ○ = 20; ⫰ = 30; ⫰ = 40; ⫱ = 50; ⫱ = 60.

Total No. Racemes: ○ = <5; ⟍○ = 5-8; ⟍○ = >8.

No. Secondary Racemes: ○ = 0; ○⟋ = 0-1; ○⟋ = 1-3; ♂ = >3.

Figure 1. *D. annulatum* (Tropical) = ○ ; Hybrids = ●.

Figure 2. *D. annulatum* (Tropical) = ○ ; Mediterranean = ⦶ ;
Tropical x Mediterranean = ◐ ; Reciprocal = ◑.

Figure 3. *D. annulatum* (Tropical) = ○ ; Senegal = ⦶ ;
Tropical x Senegal = ◐ ; Reciprocal = ◑.

Figure 4. *D. annulatum* (Mediterranean) = ○ ; Senegal = ⦶ ;
Mediterranean x Senegal = ◐.

Figure 5. *D. annulatum* (Tropical) = ○ ; *D. fecundum* = ⦶ ;
D. annulatum x *D. fecundum* = ◐.

Figure 6. *D. annulatum* (Tropical) = ○ ; Senegal = ⊗ ;
D. papillosum = ⊖ ; Tropical x *D. papillosum* = ◒ ;
Senegal x *D. papillosum* = ⨂.

PLATE IV

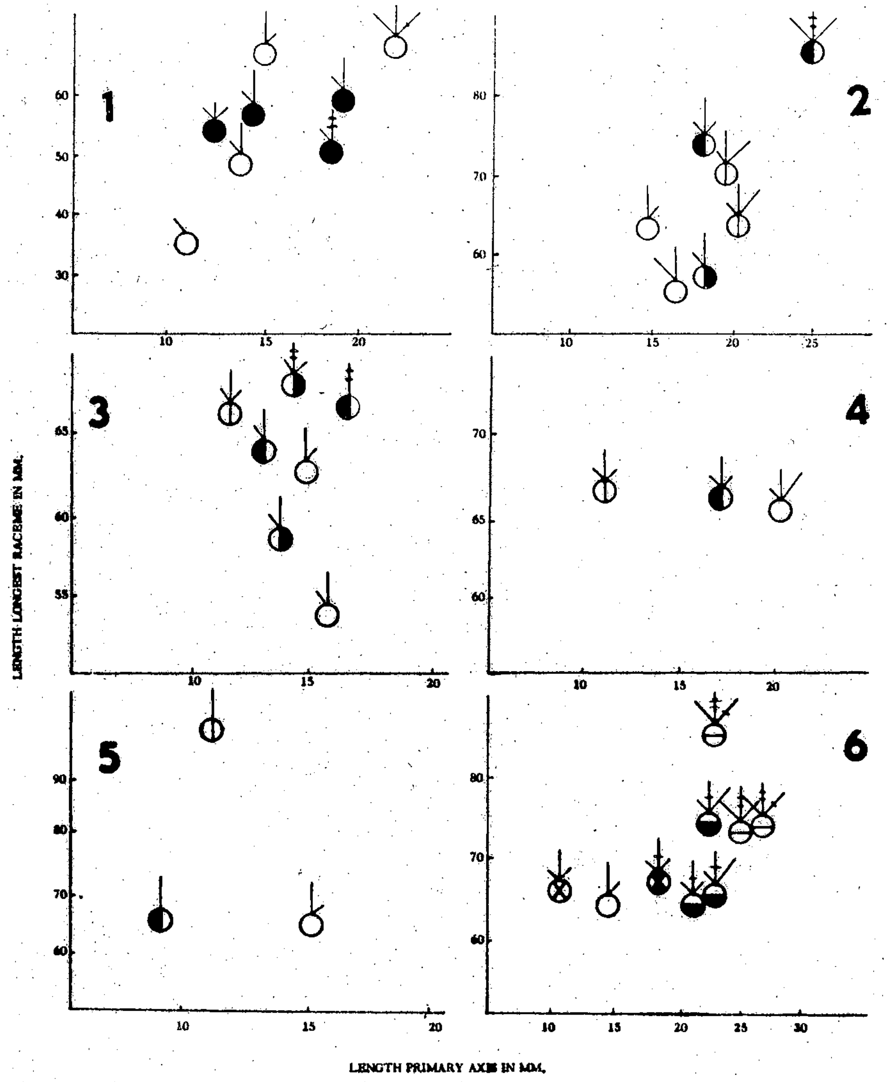

1
60
50
40
30
10
15
20
2
80
70
60
10
15
20
25
3
65
60
55
10
15
20
4
70
65
60
10
15
20
5
90
80
70
60
10
15
20
6
80
70
60
10
15
20
25
30
LENGTH LONGEST RACEME IN MM.
LENGTH PRIMARY AXIS IN MM.

TABLE VI

CYTOLOGY OF THE *D. ANNULATUM* COMPLEX

Name		2n	Chromosome Association*			
			I	II	III	IV
Dichanthium annulatum	Tropical	20	0.00 --	10.00 10	0.00 --	0.00 --
"	"	40	0.63 0-6	18.64 12-20	0.19 0-2	0.38 0-3
"	Mediterranean	40	0.49 0-4	19.22 16-20	0.05 0-1	0.23 0-2
"	Senegal	40	0.26 0-4	18.32 16-20	0.10 0-1	0.70 0-3
D. papillosum		60	1.75 0-8	27.37 21-30	0.29 0-2	0.66 0-4
D. fecundum		40	0.47 0-3	18.42 15-20	0.03 0-1	0.65 0-2
D. annulatum x *D. annulatum*	Trop. (20) x Trop. (20)**	20	0.00 --	10.00 10	0.00 --	0.00 --
" "	" (20) x " (40)	40	2.18 0-5	17.73 15-20	0.12 0-1	0.50 0-2
" "	" (40) x " (20)	20#	0.72 0-4	9.64 8-10	0.00 --	0.00 --
" "	" (40) x " (20)	30	6.64 2-8	11.68 11-14	0.00 --	0.00 --
" "	" (40) x " (40)	20#	1.00 0-2	9.50 9-10	0.00 --	0.00 --
" "	" (40) x " (40)	40	2.10 0-8	18.31 15-20	0.00 --	0.32 0-2
" "	" (40) x " (40)	60	2.94 0-6	28.27 26-30	0.00 --	0.13 0-1
" "	" (40) x Medit (40)	40	3.70 0-8	17.80 14-20	0.02 0-1	0.16 0-3

TABLE VI (continued)

Name		2n	Chromosome Association*			
			I	II	III	IV
D. annulatum x D. annulatum	Trop. (40) x Medit. (40)**	60	1.10	26.95	0.40	0.95
			0-6	22-26	0-2	0-2
" "	" (20) x Senegal(40)	40	2.10	18.27	0.00	0.34
			0-8	12-20	--	0-4
" "	" (40) x " (40)	60	4.92	26.28	0.12	0.54
			0-12	22-30	0-1	0-2
" "	Medit. (40) x Trop. (40)	40	4.15	17.26	0.03	0.31
			0-14	11-20	0-1	0-2
" "	" (40) x " (20)	20#	1.40	9.30	0.00	0.00
			0-4	8-10	--	--
" "	Senegal(40) x " (40)	40	2.10	17.95	0.00	0.50
			0-12	14-20	--	0-1
" "	" (40) x " (40)	60	3.30	27.09	0.00	0.63
			0-8	19-30	--	0-4
" "	Medit. (40) x Senegal(40)	40	5.70	17.15	0.00	0.00
			4-10	15-18	--	--
D. annulatum x D. papillosum	Trop. (40) x D. pap.(60)	50	4.14	19.91	0.68	1.00
			3-10	13-22	0-2	0-4
" "	" (40) x " (60)	20#	1.84	9.08	0.00	0.00
			0-4	8-10	--	--
" "	Senegal(40) x " (60)	50	3.40	22.30	0.00	0.50
			2-6	18-24	--	0-2
D. annulatum x D. fecundum	Trop. (40) x D. fec.(40)	40	0.72	19.50	0.00	0.07
			0-4	17-20	--	0-1

* Average number and range of chromosome association at Metaphase I; I = univalent; II = bivalent; III = trivalent; IV = quadrivalent

** 2n number of chromosomes.

\# Polyhaploid plants.

bulbous-based hairs are rather sparse. The Mediterranean ecotype is adapted to desert conditions ranging from the eastern edge of the Indian desert in Rajasthan westward across Iraq, North Africa to Morocco. All collections studied so far were tetraploids. The Senegal biotype, represented in this study by a single collection (5430) from northwestern Africa, is an extreme form of the Mediterranean ecotype and differs from the latter in having more slender racemes and almost glabrous spikelets.

HYBRIDS WITHIN AND BETWEEN THE MORPHOLOGICAL TYPES OF D. ANNULATUM

TROPICAL x TROPICAL. - Hybrids between the diploid and tetraploid races of the Tropical ecotypes are easy to produce at the same ploidy level, i.e., $2n$ x $2n$ or $4n$ x $4n$. With the tetraploid as female parent and the diploid as male, the triploid hybrids obtained were sterile due to extremely irregular meiosis. On the other hand, from an attempted reciprocal cross, with the diploid as female parent, tetraploid plants were obtained which were, possibly, autotetraploids. Cytologically the hybrids between tetraploids were characterized by $2n = 40$ and 60 chromosomes, indicating that the unreduced $4n$ egg can be fertilized by normal $2n$ pollen. Polyhaploid plants ($2n = 20$) were obtained from apomict tetraploid female parents. These plants originated from parthenogenetic development of the cytologically reduced female gametes. They resembled the natural diploids both morphologically and cytologically but these polyhaploids were sterile and weak.

TROPICAL x MEDITERRANEAN. — Hybrids with $2n = 40$ chromosomes, between the Tropical and Mediterranean ecotypes, could be recognized by a relatively larger panicle than the Tropical type. The hexaploid hybrids ($2\underline{n} = 60$) were more maternal in appearance than the tetraploid ones. Reciprocal crosses were also successful.

TROPICAL x SENEGAL. - Crosses between the Tropical ecotype and Senegal biotype produced plants with $2\underline{n} = 40$ and 60 chromosomes. Reciprocal crosses gave similar results. Hybrids were recognized mainly by a less pubescent glume of the sessile spikelets.

MEDITERRANEAN x SENEGAL. - Hybrids between these two morphological types had $2\underline{n} = 40$ chromosomes. No reciprocal crosses were attempted. Hybrids were recognized only by the glume pubescence which was even less than that of the hybrids between the Tropical and Senegal types.

DICHANTHIUM ANNULATUM x D. PAPILLOSUM

TROPICAL x D. PAPILLOSUM. - Hybrids between the Tropical ecotype and the hexaploid, D. papillosum, had $2\underline{n} = 50$ chromosomes. These hybrids were erect to decumbent in growth habit; racemes longer and more pubescent than D. annulatum (Tropical ecotype); hairs on the glume of the sessile spikelets sometimes arranged in rows along the subapical edges (characteristic of D. papillosum) as well as scattered (as in the Tropical ecotype). In breeding behavior, tetraploid D. annulatum is a facultative apomict while D. papillosum is essentially an obligate apomict. The hybrids reproduced apomictically and were cytologically irregular.

SENEGAL x D. PAPILLOSUM. - Hybrids between the Senegal biotype and D. papillosum were recognized primarily by $2\underline{n} = 50$ chromosomes, and the lower glume of the sessile spikelets had only a few scattered hairs. Cytology was essentially the same as that of Tropical x *D. papillosum*.

DICHANTHIUM ANNULATUM x *D. FECUNDUM*

Hybrids between the tetraploid *D. annulatum* and *D. fecundum* had $2n = 40$ chromosomes. Morphologically *D. fecundum* differs from *D. annulatum* primarily in having bisexual pedicellate spikelets, and this character was present in the F_1 hybrids as well. Except for the bisexual nature of the pedicellate spikelets, the hybrids were intermediate between the parents in most other morphological characters studied. Cytologically the hybrids were not much different from the parents. Hybrids between the sexual X-98 and the obligate apomict *D. fecundum* were apomictic in their breeding behavior.

DISCUSSION

Dichanthium annulatum was first described by Forsskal (1775) as *Andropogon annulatus*. Hackel (1889), in his treatment of the genus *Andropogon*, included it under the subgenus *Dichanthium*. This subgenus was earlier recognized as a separate genus by Willemet (1796), and when describing *D. nodosum*, he cited *Andropogon annulatum* Forssk., as a synonym. The latter species became the type for *D. annulatum* (Stapf, 1917) and the epithet "nodosum" is, therefore, illegitimate. Stapf's system of classification has been recognized by Haines (1924), Blatter and McCann (1935), Bor (1947, 1960), Chippindall (1955), Gardner (1952), Pandeya (1953) and Vickery (1961). Celarier and Harlan (1955), Harlan *et al.* (1958), Mehra and Celarier (1958), Singh *et al.* (1962) and Borgoankar and Singh (1962) indicated that

D. annulatum is closely related to D. papillosum.

Dichanthium annulatum is widely distributed in the tropics and subtropics of the Old World, extending from the West Coast of North Africa through Iraq and southeast Asia to Australia and the Fiji Islands. The Tropical ecotype includes both diploid and tetraploid races, while the Mediterranean ecotype and the Senegal biotype are strictly tetraploids. Tetraploids are the most common representatives of D. annulatum, and the three morphological types overlap in their natural ranges of distribution. Diploid collections of D. annulatum are fully compatible and may be crossed with tetraploids of the Tropical type. Harlan et al. (1961) suggested that these diploids may in reality represent polyhaploids. Such polyhaploids in D. annulatum are occasionally obtained from apomictic tetraploid plants as well as in the segregating F_2 population of the F_1 hybrid whose female parent was an apomict tetraploid.

RELATIONSHIPS BETWEEN THE MORPHOLOGICAL TYPES OF D. ANNULATUM.

Morphological variation within D. annulatum is represented by the Tropical, Mediterranean and Senegal types. The former two are the ecotypes, while the Senegal is a biotype of the Mediterranean ecotype which represents an introgression product involving the Tropical ecotype and the Gangetica biotype of B. intermedia (Celarier et al., 1958; Mehra, 1960; and Harlan et al., 1961). Although plants resembling the Mediterranean and Tropical ecotypes are found in western India and Pakistan, in general, representatives of D. annulatum occurring west of these areas are of the Mediterranean ecotype and those on the east, throughout the range of distribution, are of the Tropical ecotype. Celarier and Harlan (1957) indicated that tetraploids in Dichanthium are facultative apomicts. By this mode of reproduction, numerous distinct morphological types are expected to be produced and to become established in nature (Babcock and Stebbins, 1938; Gustafsson, 1946, 1947; Clausen et al., 1947; Clausen, 1954; and Baker, 1959). For this reason, variation between the distinct ecotypes of D. annulatum are greater than that found within one ecotype. A similar situation was reported in Potentilla glandulosa by Clausen et al. (1940) and Clausen (1948). Taxonomically, the distinct morphological types of D. annulatum can, therefore, be classified as D. annulatum var. annulatum ($2\underline{n}$ = 20, 40) and the three ecotypic races, Tropical ($2\underline{n}$ = 20, 40), Mediterranean ($2\underline{n}$ = 40) and Senegal ($2\underline{n}$ = 40), should be grouped under this variety.

RELATIONSHIP BETWEEN D. ANNULATUM AND D. PAPILLOSUM.

Borgaonkar and Singh (1962), on the basis of evidence available from an artificial hybrid with $2\underline{n}$ = 60 chromosomes, obtained by the incorporation of a complete chromosome-set of the Tropical ecotype and a haploid chromosome number of the Mediterranean ecotype, suggested that, in nature, D. papillosum ($2\underline{n}$ = 60) might have originated from a similar process. The two species overlap in their geographic distribution in northeastern Africa. The fact that D. papillosum produces artificial hybrids with the Tropical and Senegal types of D. annulatum, suggests a close relationship between these two taxa. Hybrid data indicate genetic isolation and D. papillosum may taxonomically be treated as D. annulatum var. papillosum, as was suggested by Pilger (1954).

RELATIONSHIP BETWEEN D. ANNULATUM AND D. FECUNDUM.

Morphologically the two tetraploids, D. annulatum and D. fecundum, resemble each other closely, except for the bisexuality of pedicellate spikelets in D. fecundum, a character controlled by a single dominant gene (Borgaonkar and deWet, 1960). Natural hybrids between D. annulatum and D. fecundum occur in Australia where the two species are sympatric (deWet, 1963). Artificial hybrids are produced with relatively little difficulty. On the basis of morphological and cytological similarity, D. fecundum may possibly be classified as D. annulatum var. fecundum, as was suggested by Hackel (1889).

Species relationships between D. annulatum, D. papillosum and D. fecundum, on the basis of chromosome association, is obscured by autosyndesis and gene controlled preferential pairing (deWet et al., 1961). Morphological evidence seems more reliable and suggests that the three species, together, form one agamospecies, as defined by Turesson (1929).

CONCLUSIONS

1. The Tropical (2n = 20, 40), Mediterranean (2n = 40) and Senegal (2n = 40) types are morphologically distinct races of D. annulatum.

2. In geographical distribution they overlap, and are not isolated genetically. Their morphological identity is maintained primarily by apomixis.

3. The three ecotypic races of D. annulatum may be grouped taxonomically under D. annulatum var. annulatum (2n = 20, 40).

4. Dichanthium papillosum and D. fecundum are isolated geographically but each overlaps with D. annulatum in their natural ranges of distribution.

5. Both *D. papillosum* and *D. fecundum* are closely related to *D. annulatum* and may be classified as *D. annulatum* var. *papillosum* ($2n = 60$) and *D. annulatum* var. *fecundum* ($2n = 40$), respectively.

6. On the basis of morphological and cytological studies of the artificial hybrids, *D. annulatum*, *D. papillosum* and *D. fecundum*, together, form one interrelated agamospecies.

CHAPTER VI

A STUDY ON THE ORIGIN OF DICHANTHIUM PAPILLOSUM (HOCHST.) STAPF

The hexaploid species Dichanthium papillosum (Hochst.) Stapf is widely distributed in Africa, south of the Sahara (deWet, 1963). Celarier and Harlan (1955), in their treatment, considered D. papillosum as a cytological race of D. annulatum (Forssk.) Stapf and referred to it as the South African type. Later, Celarier et al. (1958) proposed that the South African type might be the result of a cross between the Tropical type of D. annulatum and a closely related South African species, D. aristatum (Poir.) C. E. Hubbard. Pandeya (1953), Chippindall (1955) and deWet (1963) suggested that D. aristatum is not an African species and is probably a recent introduction from India. Morphologically, D. papillosum represents a combination of characters of the Tropical and Mediterranean ecotypes of D. annulatum. It differs from D. annulatum mainly in chromosome number, and it has the lower glume of the sessile spikelets more pilose, with the hairs forming a more or less transverse fringe near the apex. The morphological similarity, of an artificially produced hexaploid hybrid between these two ecotypes, and D. papillosum, suggested the possibility that the latter species might have originated from such hybridization (Mehra, 1960). To verify this conclusion, studies were made of the F_1 hybrids between the Tropical and Mediterranean ecotypes, the second generation population of these hybrids and backcross hybrids of D. papillosum with the ecotypes of D. annulatum.

MATERIALS AND METHODS

Plants studied were grown in a uniform nursery as outlined by Celarier and Harlan (1955). Morphological data are based on field observations correlated with herbarium studies. Developing microsporocytes were fixed in Carnoy's fluid and studied following the standard acetocarmine squash techniques. Hybrids were produced by Mr. W. L. Richardson, by using an apomict female parent of D. annulatum, as described by him (1958) and also by using the sexual plant, X-98, as the female parent.

RESULTS

Morphological characteristics of D. papillosum ($2n = 60$), D. annulatum ($2n = 40$) and an artificially produced hexaploid hybrid, are summarized in Table VII and shown in Plates V, VI, along with that of the F_2 population and backcross plants. Plate VI represents a pictorialized scattered diagram, using Anderson's technique (1949, 1957). Crossing data of D. annulatum and D. papillosum is presented in Table VIII. Cytological data are summarized in Table IX.

The collections of D. papillosum studied were characterized by plants with erect or moderately decumbent growth habit; the number of racemes, 8-12 per panicle (Plate V); the racemes 70-80 mm. long; and the lower glumes of the sessile spikelets always with long bulbous-based hairs along the edges near the apex. Cytologically all plants of D. papillosum studied, had $2n = 60$ chromosomes. The meiotic behavior was irregular with univalents and multivalents commonly

TABLE VII

MORPHOLOGY OF PARENTS AND HYBRIDS BETWEEN *D. ANNULATUM* AND *D. PAPILLOSUM*

Acc. & Plant No.	Name	$2\underline{n}$	Growth habit	Total No. racemes	Pubescence sessile glume	Average No. secondary racemes
3242	*D. annulatum* Tropical	20	P	5.6	T	0
X-98	" "	40	D	5.5	T	0.2
4099	" "	40	D	6.4	T	0
4390	" Mediterranean	40	E	6.0	T	0.2
5430	" Senegal	40	E	5.2	S	0.4
2567	*D. papillosum*	60	E	9.0	P	4.0
3716	"	60	E	9.6	P	2.8
4080	"	60	E	9.6	P	3.2
4083	"	60	E	8.5	P	3.2
4788b	"	60	E	7.0	P	0.7
56-X-112-1	*D. ann.* 4099 x *D. pap.* 4080	50	D	6.7	P	0.2
56-X-115b-1	*D. ann.* 4099 polyhaploid	20	D	6.1	P	1.0
56-X-288-1	*D. ann.* 5430 x *D. pap.* 4083	50	E	7.0	T	1.0
57-X-698-1	*D. ann.* X-98 x *D. pap.* 4080	50	D	6.6	P	0.5
57-X-816-1	*D. pap.* 4083 x *D. ann.* X-98	50	E	9.0	P	0.7
57-X-1171-1	*D. ann.* X-98 x *D. ann.* 4390	60	E	8.2	S	2.0
57-X-1171-1	Selfed 1	60	D	8.9	P	2.0
	" 2		D			
	" 3	60	E	8.0	P	2.0
	" 4	60	E	7.4	P	1.0
	" 5		E	6.0	T	0
	" 6	60	D	7.4	T	1.5
	" 7	60	E	5.6	T	0
	" 8		E	7.8	T	3.0
	" 9	60	E	6.8	P	2.5
	" 10		E	7.0	P	0

TABLE VII (continued)

Acc. & Plant No.	Name	2n	Growth habit	Total No. racemes	Pubescence sessile glume	Average No. secondary racemes
57-X-1171-1	Selfed 11		D	8.8	P	0
	" 12	60	D	4.0	P	0
	" 13	60	E	8.6	P	0
	" 14	30	D	7.1	P	2.0
	" 15	60	E	5.6	P	0
	" 16	30	E	4.2	P	0
	" 17		D	6.0	P	0
	" 18	60	E	8.1	P	1.0
	" 19		E	7.5	P	2.0
	" 20	60	E	6.6	T	0
	" 21		D	7.7	P	1.0
	" 22		D	6.9	T	0
	" 23		-	7.9	T	1.0
	" 24		D	7.5	T	0

Growth habit: P = Prostrate, D = Decumbent, E = Erect.
Pubescence sessile glume: T = Tropical type, P = *Papillosum* type, S = Senegal type.

TABLE VIII

CROSSING DATA OF *D.* *ANNULATUM* AND *D.* *PAPILLOSUM*

Parent		No.	Seed Set		No.
Female	Male	Emasc.	Well Developed	Poorly Developed	Hybrids
D. *annulatum* 4099	*D.* *papillosum* 4080	50	0	7	3
D. *annulatum* 5430	*D.* *papillosum* 4083	50	14	14	5
D. *annulatum* X-98	*D.* *papillosum* 4080	140	28	36	13
D. *papillosum* 4083	*D.* *annulatum* X-98	90	33	15	1

TABLE IX

CHROMOSOME CONFIGURATIONS OF HYBRIDS AND THEIR PARENTS AT METAPHASE I

Acc. & Plant No.	Name		2n	Chromsome Configuration*			
				I	II	III	IV
3242	*D. annulatum*	Tropical	20	0.00 --	10.00 10	0.00 --	0.00 --
X-98	"	"	40	1.24 0-6	17.08 15-20	0.12 0-1	1.06 0-3
4099	"	"	40	0.24 0-2	19.08 16-20	0.08 0-1	0.34 0-2
4390	"	Mediterranean	40	0.52 0-2	18.74 16-20	0.08 0-1	0.44 0-2
5430	"	Senegal	40	0.26 0-4	18.32 16-20	0.10 0-1	0.70 0-3
2567	*D. papillosum*		60	5.04 0-10	26.10 22-30	0.20 0-1	0.54 0-2
3716	"		60	1.68 0-8	27.60 21-30	0.00 --	0.78 0-4
4080	"		60	1.52 0-5	27.26 23-30	0.52 0-2	0.60 0-3
4083	"		60	2.05 0-6	27.25 24-30	0.35 0-2	0.60 0-2
4788b	"		60	0.40 0-3	26.35 19-28	0.10 0-1	1.65 0-3
57-X-1171-1	X-98 x 4390		60	3.10 0-4	24.25 22-26	0.40 0-2	1.80 0-2
"		Selfed	60	2.29 0-12	26.58 22-30	0.25 0-3	0.95 0-3
"		"	30	2.67 0-6	13.11 7-14	0.13 0-2	0.18 0-2
56-X-112-1	4099 x 4080		50	3.40 2-6	22.30 18-24	0.00 --	0.50 0-2

TABLE IX (continued)

Acc. & Plant No.	Name	2n	Chromosome Configuration*			
			I	II	III	IV
56-X-115b-1	4099 polyhaploid	20	1.84	9.08	0.00	0.00
			0-4	8-10	--	--
56-X-288-1	5430 x 4083	50	4.30	22.33	0.00	0.26
			0-10	20-25	--	0-1
57-X-698a-1	X-98 x 4080	50	5.86	17.45	0.68	1.80
			3-10	13-22	0-2	0-4
57-X-816-1	4083 x X-98	50	6.54	18.74	0.66	1.00
			3-10	14-22	0-2	0-3

*Average association as well as range of chromosome configurations are listed.
I = univalent; II = bivalent; III = trivalent; IV = quadrivalent

LEGEND TO PLATE V

Inflorescences of parents and hybrids between *D. annulatum* and *D. papillosum*.

Figure 1. *D. annulatum*.

Figure 2. Hybrid between *D. annulatum* and *D. papillosum*.

Figure 3. *D. papillosum*.

Figure 4. Artificial hexaploid hybrid (57-X-1171-1).

PLATE V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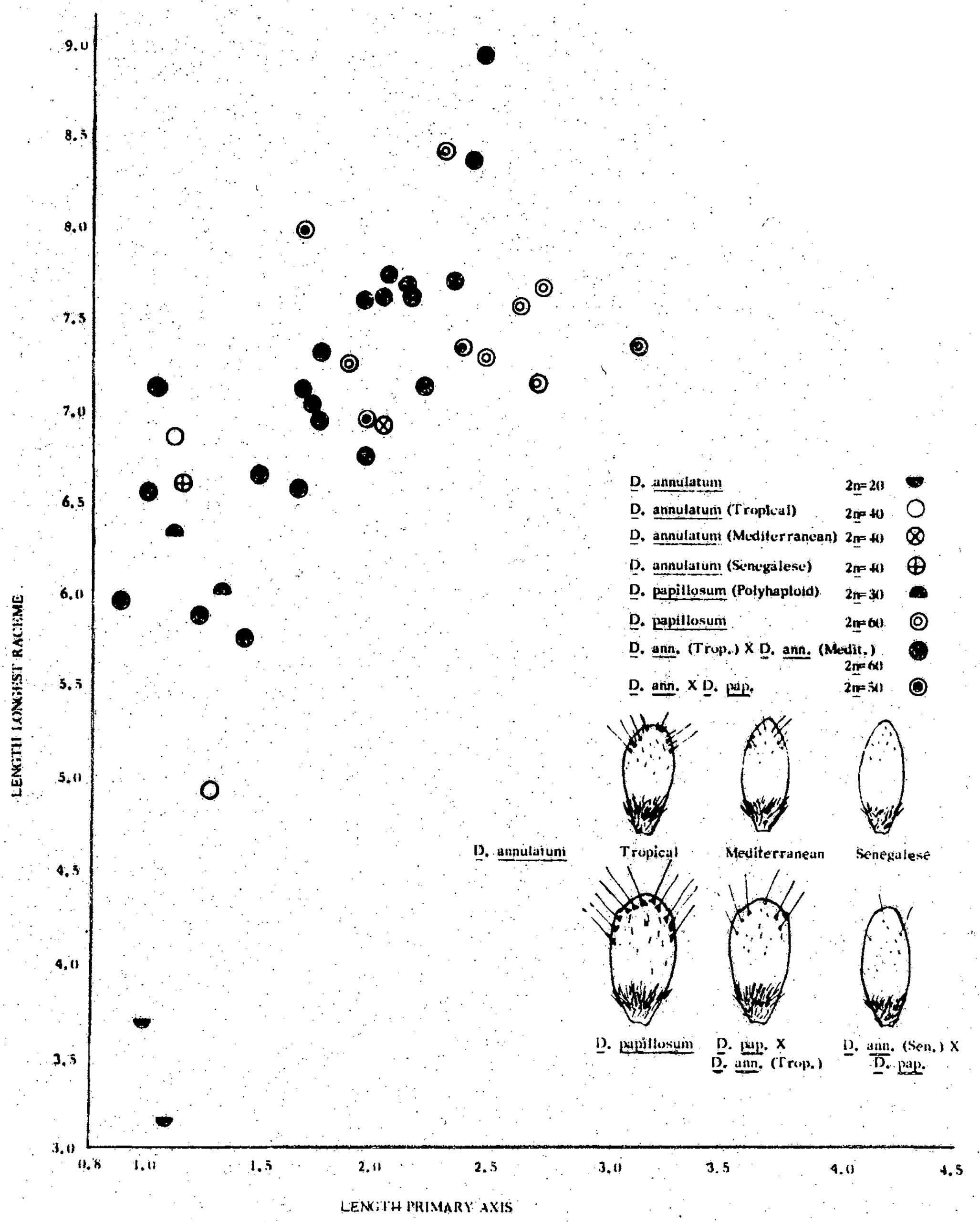
LEGEND TO PLATE VI

Glume characteristics and pictorialized scatter diagram of parents and hybrids.

PLATE VI


LENGTH LONGEST RACEME
9.0
8.5
8.0
7.5
7.0
6.5
6.0
5.5
5.0
4.5
4.0
3.5
3.0
0.8
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
LENGTH PRIMARY AXIS
D. annulatum 2n=20
D. annulatum (Tropical) 2n=40 ○
D. annulatum (Mediterranean) 2n=40 ⊗
D. annulatum (Senegalese) 2n=40 ⊕
D. papillosum (Polyhaploid) 2n=30
D. papillosum 2n=60 ◎
D. ann. (Trop.) X D. ann. (Medit.) 2n=60 ●
D. ann. X D. pap. 2n=50 ◉
D. annulatum
Tropical
Mediterranean
Senegalese
D. papillosum
D. pap. X D. ann. (Trop.)
D. ann. (Sen.) X D. pap.

encountered at metaphase I (Table IX). Bridges, fragments and lagging chromosomes were frequently observed at telophase I.

Celarier and Harlan (1955), Celarier *et al*. (1958) and Mehra (1962) recognized within *D. annulatum* three distinct races, the Tropical, Mediterranean and Senegal types. The first two are distinct ecologically, whereas, the Senegal type studied is represented by a single collection from Bambey, Senegal (northwestern Africa) and may be regarded as a biotype of the Mediterranean ecotype. The latter two types differ from each other mainly in the degree of glume pubescence.

The $2n = 60$ chromosome hybrid, 57-X-1171-1, obtained by using the tetraploid Tropical ecotype as the female parent and the Mediterranean ecotype of *D. annulatum* as the male parent, resulted through the fertilization of a cytologically unreduced female gamete by a normal male gamete. The hybrid had a combination of characters of the Tropical (thick raceme and strongly pubescent glumes) and Mediterranean (long primary axis of the panicle, long racemes with secondary branches and erect growth habit) ecotypes. Besides these morphological characters, the hexaploid F_1 plant was similar also in meiotic behavior to *D. papillosum* (Table IX). After selfing the F_1, plants with $2n = 30$ and 60 chromosomes were obtained (Mehra, 1960). Some of the $2n = 60$ chromosome plants, obtained artificially, resembled the natural *D. papillosum* in gross morphology (Plate V).

DISCUSSION

From the morphological and cytological data of *D. papillosum*, compared with similar studies of the artificially produced plants resembling *D. papillosum*, it would appear as if this species could have originated from hybridization between the two ecotypes of D. annulatum. Harlan et al. (1958) indicated that the ability to produce functional cytologically unreduced eggs is widespread among representatives of the Bothriochloininae. Recently, in reviewing the number of artificial hybrids produced between different members of the genera Bothriochloa O. Kuntz, Dichanthium Willemet and Capillipedium Stapf, Harlan et al. (1961) listed 98 4n x 4n crosses. Out of these, 25 hybrids had 2n = 60 chromosomes. Within the genus Dichanthium itself, out of 17 different hybrids listed as 4n x 4n, 5 were hexaploids. Normally it is expected that such hybrids (2n = 60) would resemble the female parent more closely than those with 2n = 40 chromosomes. However, morphologically the hexaploid plant obtained from the cross involving the Tropical and Mediterranean ecotypes of D. annulatum showed extreme characteristics of both parents. It resembled the natural D. papillosum in respect to growth habit, panicle size and pubescence of the glumes. Borgaonkar and Singh (1962) suggested that this could also have taken place in nature. Due to the prevalence of an apomictic mode of reproduction and genetic isolation, the hexaploid form could have become established in nature.

Polyhaploids with 2n = 30 chromosomes were obtained from the F_2 population. These plants were weak and sterile. DeWet and Anderson (1956) previously reported a race of D. papillosum with 2n = 30 chromosomes from South Africa. Clausen (1961) indicated that in Poa, from the F_2 population of crosses between two facultative apomicts, plants could be obtained that are vigrous and have sufficient apomictic fertility.

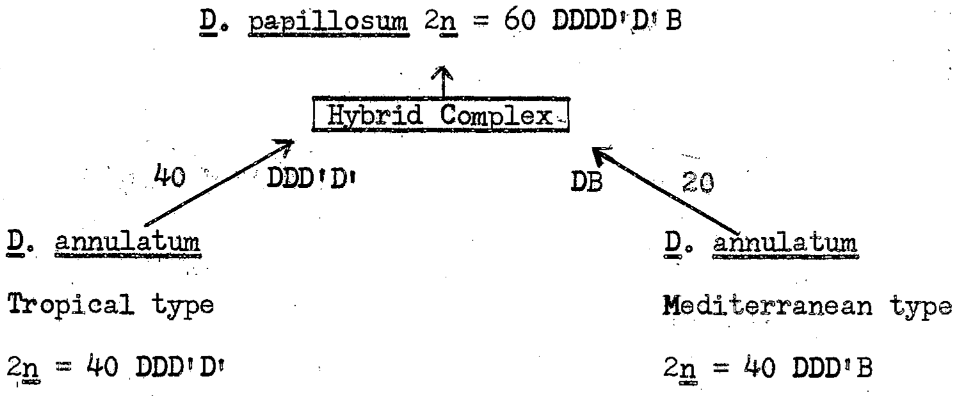
Celarier et al. (1958) hypothesized that there is a possibility that D. papillosum could have been the product of fertilization of a cytologically unreduced egg of the Tropical ecotype of D. annulatum by a normal male gamete of D. aristatum or vice-versa. This, however, is not likely. Pandeya (1953) and deWet (1963) indicated that D. aristatum is probably a recent introduction to Africa from India. On the basis of hybrid data available, it is believed that D. papillosum originated as a result of hybridization between the Tropical and Mediterranean ecotypes of D. annulatum.

Relationships between D. papillosum and the tetraploid ecotypes of D. annulatum were also studied. From the crossing data presented in Table VIII, it appears that, although attainment of artificial hybrids is difficult, due to pseudogamous apospory (Brooks, 1958), hybrids can be produced (Table VII, Plates V, VI). The fact that D. papillosum produced hybrids with the ecotypes of D. annulatum suggests a close relation between these two taxa (Singh et al., 1962). Cytological data of the hybrids is in conformity with the findings of deWet et al. (1961), that preferential autosyndetic pairing occurs in Dichanthium. Thus, interpretation of cytological data has to be made with caution. Similar difficulties were reported in recent papers by Johnson (1962, 1963) in natural hybrids between Oryzopsis and Stipa. Phylogenetic affinities of D. papillosum with the ecotypes of D. annulatum have, therefore, to be based primarily on morphological characteristics and crossing data.

Mehra and Celarier (1958) and Harlan et al. (1958, 1961) pointed out that hybridization between D. annulatum and B. intermedia resulted in the origin of B. grahamii of BBDD genomic constitution. The latter species when backcrossed to D. annulatum of the Tropical ecotype (DDD'D') apparently gave rise to the Mediterranean ecotype (DDD'B). The artificially produced hexaploid hybrid, since it was obtained as a result of fertilization of a cytologically unreduced egg of the Tropical ecotype with the normal male gamete of the Mediterranean ecotype, could, therefore, be of DDDD'D'B genomic constitution. Chromosome association into as many as 26 pairs, in this hexaploid hybrid, may be explained on the basis of autosyndesis and preferential pairing between D and D' genomes. Some multivalents are possible because of structural similarity between the chromosomes of the Tropical and Mediterranean ecotypes.

Considering *D. papillosum* to be of DDDD'D'B constitution and *D. annulatum* (Tropical ecotype) of DDD'D' constitution, artificial hybrids obtained could be of DDD'D'B genomic constitution. Presence of six univalents, on an average, suggests presence of the B genome (Table IX). Another hybrid between the Senegal biotype (DDD'B), having the same genomic constitution as the Mediterranean ecotype, and *D. papillosum* (DDDD'D'B) appears to be of DDD'BB genomic constitution. Presence of four univalents and absence of trivalents indicates that a few chromosomes of D' genome have associated into bivalents and some remain as univalents. Occasional quadrivalents may be due to association of D chromosomes (Table IX).

The phylogenetic relationships between *D. annulatum* ecotypes and *D. papillosum* are indicated as follows:



CONCLUSIONS

1. Plants resembling the hexaploid *D. papillosum* can be produced artificially.

2. Morphological and cytological data indicate that the artificially produced $2n = 60$ chromosome plant represents four genomes of the Tropical and two of the Mediterranean ecotypes of *D. annulatum*.

3. The hexaploid hybrid may, therefore, be of DDDD'D'B genomic constitution.

CHAPTER VII

RELATIONSHIP OF DICHANTHIUM ANNULATUM WITH THE D. CARICOSUM COMPLEX

Dichanthium caricosum (Linn.) A. Camus together with four other related species, D. aristatum (Poir) C. E. Hubbard, D. pallidum (Hock. f.) Stapf ex Fisher, D. tenue (R. Br.) A Camus and D. theinlwinii Bor, form one agamospecies (Celarier et al., 1961b). Morphological data suggest that natural hybridization occurs between D. caricosum and the related species D. annulatum (Forssk.) Stapf (Celarier et al., 1962).

The present paper deals with the relationship between D. annulatum and members of the D. caricosum complex.

MATERIALS AND METHODS

Crosses were made by using a sexual self-sterile plant (X-98), as well as facultatively apomictic representatives of D. annulatum, as the female parents. Some of the hybrids were produced by W. L. Richardson following his technique (1958) of emasculation. Plants were grown in an experimental garden as outlined by Celarier and Harlan (1956). Developing microsporocytes were fixed in Carnoy's solution (6:3:1) and cytological studies were made using the standard acetocarmine squash technique. Morphological data are based on field observations correlated with herbarium studies.

EXPERIMENTAL RESULTS

Selected morphological characteristics of D. annulatum, D. caricosum, D. aristatum and the artificially produced hybrids are illustrated in Plates VII, VIII, following the technique described by Anderson (1949, 1957). Cytological data are presented in Table X.

Morphologically D. annulatum differs from members of the D. caricosum complex mainly in glume shape and hair pattern. In D. annulatum, the lower glumes of the spikelets are obtuse to truncate while in the D. caricosum complex they are oblong or obovate. Furthermore, in contrast to D. annulatum, the lower glumes of the latter species complex are never long ciliate along the margins and they lack the bulbous-based hairs on the lower half. Experimental results presented here involve only D. caricosum and D. aristatum. These two species differ from each other mainly in that the latter has pilose rather than glabrous peduncles below the inflorescence.

Triploid, tetraploid and hexaploid hybrids were obtained when the tetraploid D. annulatum (X-98) was crossed with diploid and tetraploid races of D. caricosum. Hybrids were identified by their comparatively glabrous and somewhat obovate lower glume of the sessile spikelets. Morphological data indicated that the hexaploid hybrid ($2n = 60$) was obtained through fertilization of a cytologically unreduced egg of D. annulatum ($2n = 40$) by the normal male gamete of D. caricosum ($2n = 40$). Meiosis in the triploid hybrids was very irregular and in the hexaploid hybrid the chromosomes associated into as many as 28 pairs with univalents and multivalents frequently observed. In the tetraploid hybrids, 20 pairs of chromosomes were commonly observed at metaphase I, although univalents and multivalents

LEGEND TO PLATE VII

Inflorescences of parents and hybrids between the *D. caricosum* complex and *D. annulatum*. - Showing nature of variation with respect to length of the primary axis, length and number of racemes and thickness of the racemes.

Figure 1. *D. annulatum* (4*n*).
Figure 2. *D. aristatum* (2*n*).
Figure 3. *D. aristatum* (4*n*).
Figure 4. *D. caricosum* (2*n*).
Figure 5. *D. caricosum* (4*n*).
Figure 6. Hybrid between *D. annulatum* (4*n*) and *D. aristatum* (2*n*).
Figure 7. Hybrid between *D. aristatum* (4*n*) and *D. annulatum* (4*n*).
Figure 8. Hybrid between *D. annulatum* (4*n*) and *D. caricosum* (2*n*).
Figure 9. Hybrid between *D. annulatum* (4*n*) and *D. caricosum* (4*n*).

PLATE VII


1


2


3


4


5


6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8


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LEGEND TO PLATE VIII

Morphology of hybrids between the *D. caricosum* complex and *D. annulatum* on a pictorialized scatter diagram.

PLATE VIII

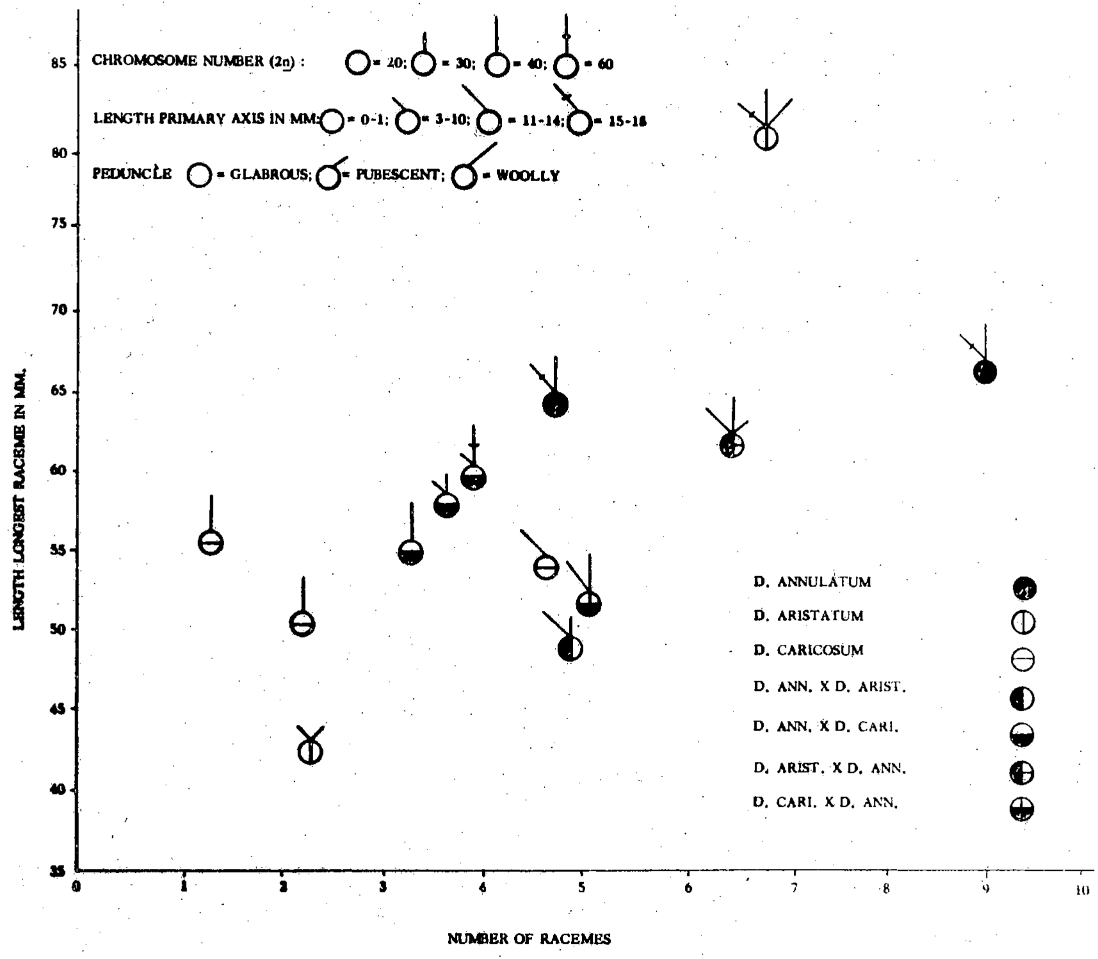

CHROMOSOME NUMBER (2n) : ○ = 20; ○ = 30; ○ = 40; ○ = 60
LENGTH PRIMARY AXIS IN MM: ○ = 0-1; ○ = 3-10; ○ = 11-14; ○ = 15-18
PEDUNCLE ○ = GLABROUS; ○ = PUBESCENT; ○ = WOOLLY
D. ANNULATUM
D. ARISTATUM
D. CARICOSUM
D. ANN. X D. ARIST.
D. ANN. X D. CARI.
D. ARIST. X D. ANN.
D. CARI. X D. ANN.
LENGTH LONGEST RACEME IN MM.
85
80
75
70
65
60
55
50
45
40
35
0
1
2
3
4
5
6
7
8
9
10
NUMBER OF RACEMES

TABLE X

CYTOLOGICAL DATA OF *D. ANNULATUM*, *D. CARICOSUM* COMPLEX AND THEIR HYBRIDS

Names	Collection Number	2*n*	Chromosome Association*			
			I	II	III	IV
Parents						
D. annulatum	X-98	40	1.24	17.08	0.12	1.06
			0-6	15-20	0-1	0-3
	5398	40	0.46	18.34	0.18	0.58
			0-4	12-20	0-1	0-3
D. aristatum	7199	20	0.00	10.00	0.00	0.00
			--	10	--	--
	2571	40	0.65	18.40	0.05	0.60
			0-2	16-20	0-1	0-2
D. caricosum	8452	20	0.00	10.00	0.00	0.00
			--	10	--	--
	2583	40	0.15	19.00	0.15	0.35
			0-4	16-20	0-1	0-2
	5599	40	0.24	18.80	0.12	0.45
			0-2	16-20	0-1	0-2
Hybrids						
X-98 x 7199		30	4.40	12.80	0.00	0.00
			2-6	12-14	--	--
2571 x X-98		40	2.09	16.31	0.23	1.15
			0-4	12-20	0-1	0-3
2571 x 5398		40	4.80	17.00	0.20	0.15
			4-8	16-18	0-1	0-1
X-98 x 8452		30	3.39	12.60	0.47	0.00
			2-10	10-14	0-1	--
X-98 x 5599		40	3.00	18.10	0.00	0.20
			0-6	16-20	--	0-1
		60	6.00	26.44	0.00	0.28
			4-10	23-28	--	0-2
2583 x 5398		40	1.40	19.00	0.00	0.15
			0-2	17-20	--	0-1

*Range and average number of various configurations at Metaphase I.
I = univalent; II = bivalent; III = trivalent; IV = quadrivalent.

may also be formed.

Dichanthium aristatum is represented by plants with 2*n* = 20, 40 and 60 chromosomes. The latter collection is probably a natural hybrid between *D. caricosum* and *D. aristatum* (Celarier *et al.*, 1962). Attempted crosses between *D. annulatum* (2*n* = 40) and *D. aristatum* (2*n* = 60) were unsuccessful. Crosses between the tetraploid *D. annulatum*, as the female parent, and *D. aristatum*, as the male parent, were successful only when the latter species was a diploid. The resulting triploid hybrid was sterile and cytologically very irregular during meiosis. Tetraploid hybrids between *D. annulatum* and *D. aristatum* could be produced by using *D. annulatum* as the male parent. In the tetraploid hybrids (2*n* = 40), the chromosomes associated mostly into 20 pairs but univalents and multivalents were occasionally present.

DISCUSSION

Variation within apomictic species results from mutation, occasional hybridization, genetic recombination and segregation, and each biotype becomes a fixed unit through apomixis. As indicated by Stebbins (1950), Clausen (1954), Baker (1959) and Ehrendorfer (1959), these apomictic biotypes may eventually be recognized as different taxonomic units. Celarier *et al.* (1962), in summarizing the phylogenetic relationships within the *D. caricosum* complex, indicated that ecotypes of different diploid species may have given rise to *D. caricosum* and *D. aristatum*. Biosystematics of this species complex was described in detail by deWet and Scott (1963).

Dichanthium caricosum and *D. aristatum* when crossed to *D. annulatum* behave differently. Crosses with *D. caricosum* were more easily produced than with *D. aristatum*. This would appear to indicate that *D. caricosum* is more closely related to *D. annulatum* than is *D. aristatum*. This was also demonstrated by deWet and Richardson (1963) on the basis of seed set studies.

Morphologically *D. caricosum* is closely related to *D. annulatum* differing from each other, mainly, in glume shape (Blatter and McCann, 1935). Plants resembling the artificially produced hybrids between the two species occur in nature (Celarier *et al.*, 1961b). Haines (1924) suggested that no single morphological character can be used consistently to separate these two species. This feature of blurred morphological boundaries in related species was described as early as 1928, by Zhukovsky in the genus *Aegilops*. He indicated that intermediate forms of overlaping variations occur, mainly, between tetraploid species sharing a common genome. Some of these forms can possibly be included in either species.

Natural introgression between *D. annulatum* and *D. caricosum* occurs in the Western Ghats of India and possibly other places. These introgression types cross more readily not only with *D. annulatum* and *D. caricosum* but also with *D. aristatum*. Also, the *D. caricosum* x *D. aristatum* type, represented in this study by 7199, crosses with *D. annulatum*, whereas other representatives of the *D. caricosum* complex do not. Both natural and artificial hybrids between *D. aristatum* and *D. caricosum* were reported by Celarier *et al.* (1962). Pandeya (1953) suggested that *D. aristatum* is an ecological race of *D. caricosum*. The whole relationship, therefore, suggests segmental alloploids in which one expects a rather high degree of chromosome pairing in addition to genic control (deWet et al., 1961).

Chromosome association in the hybrids of D. annulatum with D. caricosum and D. aristatum was essentially regular. The tetraploid hybrids formed 20 pairs of chromosomes although univalents and multivalents were sometimes observed. Similarly, the occurrence of as many as 28 bivalents in the hexaploid artificial hybrid, suggests preferential chromosome pairing and autosyndesis. Bivalent formation does not necessarily indicate close homology between the chromsomes of the species involved. Gene controlled bivalent formation was suggested by deWet et al. (1961) to be the common mode of chromosome association in Dichanthium.

CONCLUSIONS

1. Morphological and cytological data indicate that D. caricosum is more closely related to D. annulatum than is D. aristatum.

2. Members of the D. caricosum complex are more or less genetically isolated from D. annulatum.

3. Species relationships on the basis of chromosome association may not be satisfactorily established due to gene controlled preferential pairing and autosyndesis.

CHAPTER VIII

CHROMOSOME ASSOCIATION IN TRIPLOID *DICHANTHIUM* HYBRIDS

The genus *Dichanthium* Willemet includes a diverse group of species. The more typical representatives of this genus were sub-divided by deWet and Richardson (1963) into four species-groups. Two of these groups are diploid and reproduce sexually. The first diploid group is confined to Australia and includes *D. humilius* J. M. Black, *D. setosum* S. T. Blake, *D. sericeum* (R. Br.) A. Camus and *D. superciliatum* (Hack.) A. Camus. The other diploid group includes the Indian endemics, *D. armatum* (Hook. f.) Blatt. et McCann, *D. maccannii* Blatt. and *D. panchganiense* Blatt. et McCann. Morphologically the species within each group seem to be closely related. Genetically, however, these diploids appear to be isolated from each other, and no hybrid between any two diploid species has so far been produced. The two polyploid species-groups are characterized by species which reproduce apomicticly. Sexually reproducing diploid races of *D. annulatum* (Forssk.) Stapf, *D. aristatum* (Poir.) C. E. Hubb. and *D. caricosum* (Linn.) A. Camus are also known. To determine the phylogenetic affinities of the diploid species and races, named above, hybrids between them and the widely distributed tetraploid *D. annulatum* were attempted.

MATERIALS AND METHODS

Most of the hybrids were produced by using a sexual self-sterile plant (X-98) as the female parent. Some hybrids were obtained after emasculation, following the technique described by Richardson (1958), by using a facultative apomict of *D. annulatum* as the female parent.

Cytological data are based on studies of developing microsporocytes stained with acetocarmine. Morphological data are based on field observations correlated with herbarium studies.

RESULTS

Successful hybrids were obtained between the tetraploid *D. annulatum* and its diploid race, as well as between this tetraploid species and diploid races of *D. aristatum* and *D. caricosum*. Tetraploid *D. annulatum* can also cross with the diploid species *D. panchganiense*.

The distinguishing morphological characteristics of these species and their hybrids are summarized in Table XI. The diploid *D. annulatum* resembles the tetraploid female parent morphologically, except that it is less robust, and more prostrate in growth habit. The diploid *D. caricosum* differs from *D. annulatum* in the absence of bulbous-based hairs near the apex of the lower glumes of the spikelets. The diploid *D. aristatum* resembles *D. caricosum* in this respect, but the peduncle below the inflorescence is pubescent rather than glabrous. *Dichanthium panchganiense* differs conspicuously from the other species in having the lower 1-6 spikelet pairs homomorphous, while the sessile and pedicellate spikelets are distinctly different in the remaining spikelet pairs (Plate IX).

Cytologically the diploid species are characterized by strictly bivalent formation during meiosis. The tetraploid female parent is characterized mostly by bivalent formation, although some chromosomes

TABLE XI

GROSS MORPHOLOGY AND CHROMOSOME NUMBER OF TRIPLOID *DICHANTHIUM* HYBRIDS AND THEIR PARENTS

					Average		Pubescence		
Name	No.	2n	L.P.A.*	L.L.R.*	Raceme No.	Panicle Node No.	Leaf Sheath	Peduncle	Lower Glume Pitted
Parents									
Dichanthium annulatum	X-98	40	11.60	68.50	5.50	3.50	+	No	No
" "	3242	20	10.20	36.80	5.60	2.60	+	No	No
D. aristatum	7199	20	0.20	40.50	1.60	1.10	No	Yes	No
D. caricosum	8452	20	10.80	54.60	4.60	3.60	No	No	No
D. panchganiense	8278	20	0.15	25.00	1.20	1.30	+++	No	Yes
Hybrids									
D. ann. x *D. ann.*	X-98x3242	30	12.60	55.14	5.80	4.00	+	No	No
D. ann. x *D. arist.*	X-98x7199	30	7.25	44.37	4.75	3.00	+	No	No
D. ann. x *D. cari.*	X-98x8452	30	8.40	56.40	3.80	3.20	+	No	No
D. ann. x *D. panch.*	X-98x8278	30	8.04	42.60	3.70	2.46	++	No	Yes

*Length primary axis and longest raceme in mm. (average)
+ = sparsely hairy; ++ = pilose; +++ = densely pilose.

TABLE XII

CYTOLOGY OF TRIPLOID *DICHANTHIUM* HYBRIDS AND THEIR PARENTS

Name	No.	2n	Chromosome Association*			
			I	II	III	IV
Parents						
Dichanthium annulatum	X-98	40	1.24	17.08	0.12	1.06
			0-6	15-20	0-1	0-3
" "	3242	20	0.00	10.00	0.00	0.00
			--	10	--	--
D. aristatum	7199	20	0.00	10.00	0.00	0.00
			--	10	--	--
D. caricosum	8452	20	0.00	10.00	0.00	0.00
			--	10	--	--
D. panchganiense	8278	20	0.00	10.00	0.00	0.00
			--	10	--	--
Hybrids						
D. ann. x *D. ann.*	X-98 x 3242	30	3.15	13.20	0.15	0.00
			2-8	11-14	0-1	--
D. ann. x *D. arist.*	X-98 x 7199	30	4.40	12.80	0.00	0.00
			2-6	12-14	--	--
D. ann. x *D. caric.*	X-98 x 8452	30	3.86	12.95	0.08	0.00
			2-10	10-14	0-1	--
D. ann. x *D. panch.*	X-98 x 8278	30	11.40	9.30	0.00	0.00
			6-16	7-12	--	--

*Average and range of chromosome association at metaphase I.
I = univalent; II = bivalent; III = trivalent; IV = quadrivalent.

LEGEND TO PLATE IX

Hair pattern on glumes in *D. panchganiense*, *D. annulatum* and in the hybrids.

Figure 1. Lower glume of sessile spikelet (lower 1-6) in *D. panchganiense*.

Figure 2. Lower glume of pedicellate spikelet (lower 1-6) in *D. panchganiense*.

Figure 3. Lower glume of sessile spikelet (above 6th) in *D. panchganiense*.

Figure 4. Lower glume of sessile spikelet (lower 1-6) in hybrid between *D. annulatum* and *D. panchganiense*.

Figure 5. Lower glume of pedicellate spikelet (lower 1-6) in the hybrid.

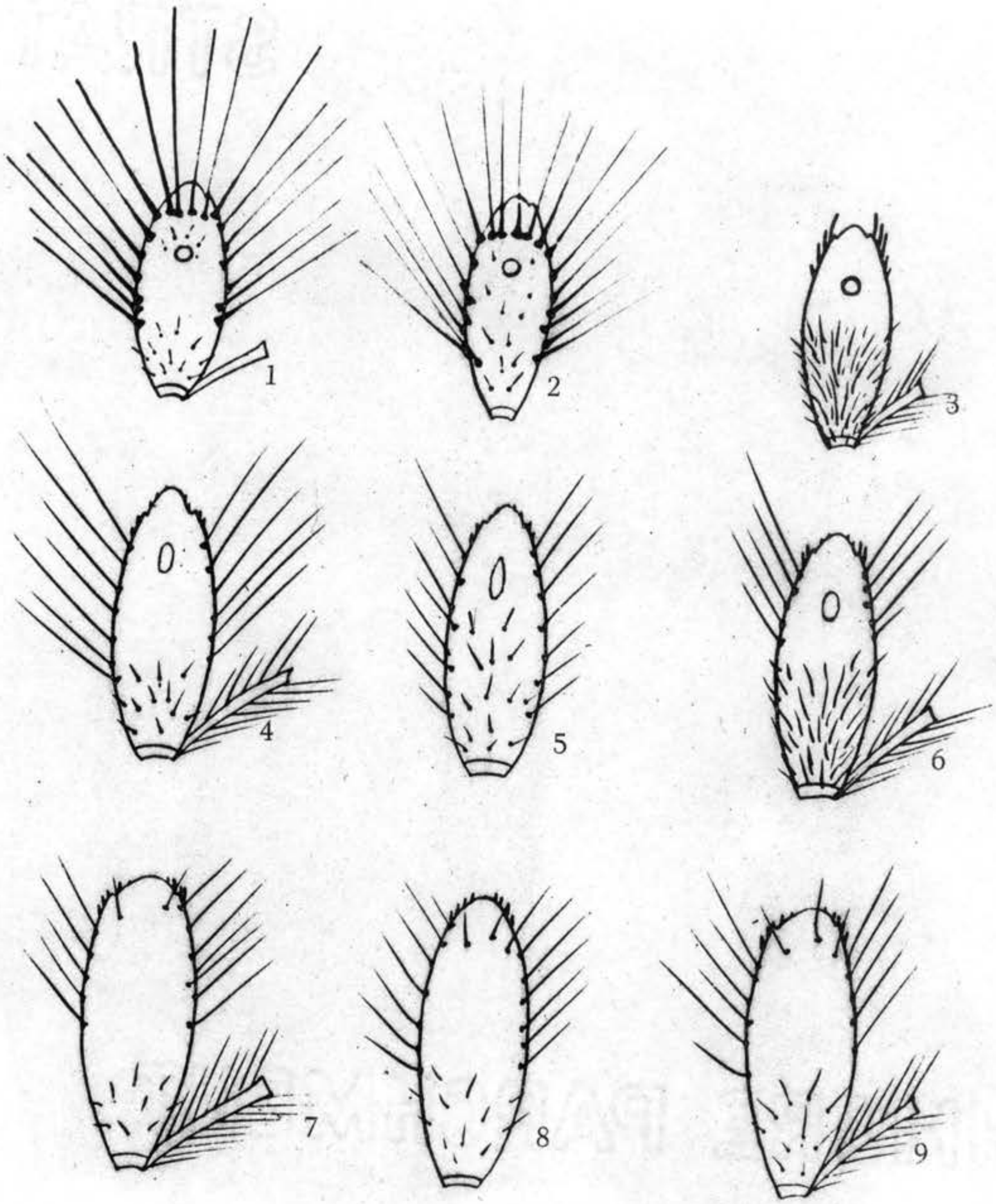
Figure 6. Lower glume of sessile spikelet (above 6th) in the hybrid.

Figure 7. Lower glume of sessile spikelet (lower half) in *D. annulatum*.

Figure 8. Lower glume of pedicellate spikelet in *D. annulatum*.

Figure 9. Lower glume of sessile spikelet (upper half) in *D. annulatum*.

PLATE IX



sometimes associate into multivalents or fail to pair at all (Table XII).

Artificially produced hybrids between the 2*n* = 20 and 40 chromosomal races of *D. annulatum* were recognized primarily by their chromosome number (2*n* = 30) and decumbent growth habit. These triploids, though sterile reproductively, were vigorous. Crosses between tetraploid *D. annulatum* and diploid *D. caricosum* were more difficult to produce. These triploid hybrids were characterized by a few long hairs at the apex of the obovate lower glume of the sessile spikelet, and by the very short primary axis of the inflorescence. Triploid hybrids, between *D. annulatum* and *D. aristatum*, were recognized by their 2*n* = 30 chromosomes, as well as by the shape and hair pattern on the glume of the sessile spikelet. The pubescent peduncle, a characteristic feature observed in the diploid *D. aristatum*, was absent in the hybrid. Celarier *et al.* (1962), in crosses between *B. intermedia* and *D. aristatum*, indicated a pubescent peduncle in some hybrids but a glabrous peduncle in others.

Triploid hybrids were also obtained after the emasculated florets of the tetraploid *D. annulatum* were pollinated with the diploid species, *D. panchganiense*. Morphologically, these hybrids had very conspicuous characteristics of *D. panchganiense*, such as, pubescent leaf-sheath and pitted glumes with long hairs on the sessile, as well as pedicellate spikelets (Plate IX). Individual hybrids were quite variable morphologically (Plates X, XI).

Cytologically, the triploid hybrids were characterized by irregular meiosis (Table XI, Plate XII). Hybrids between *D. annulatum* and *D. panchganiense* were very irregular (Plate XIII). The chromosomes associated into 7-12 bivalents and 6-16 univalents showing on an average 9.30 bivalents and 11.40 univalents at metaphase I, and a large number

LEGEND TO PLATE X

Inflorescences of *D. annulatum*, *D. panchganiense* and their hybrids. - Showing variation in length of primary axis, and also number and length of racemes.

Figure 1. *D. annulatum*.

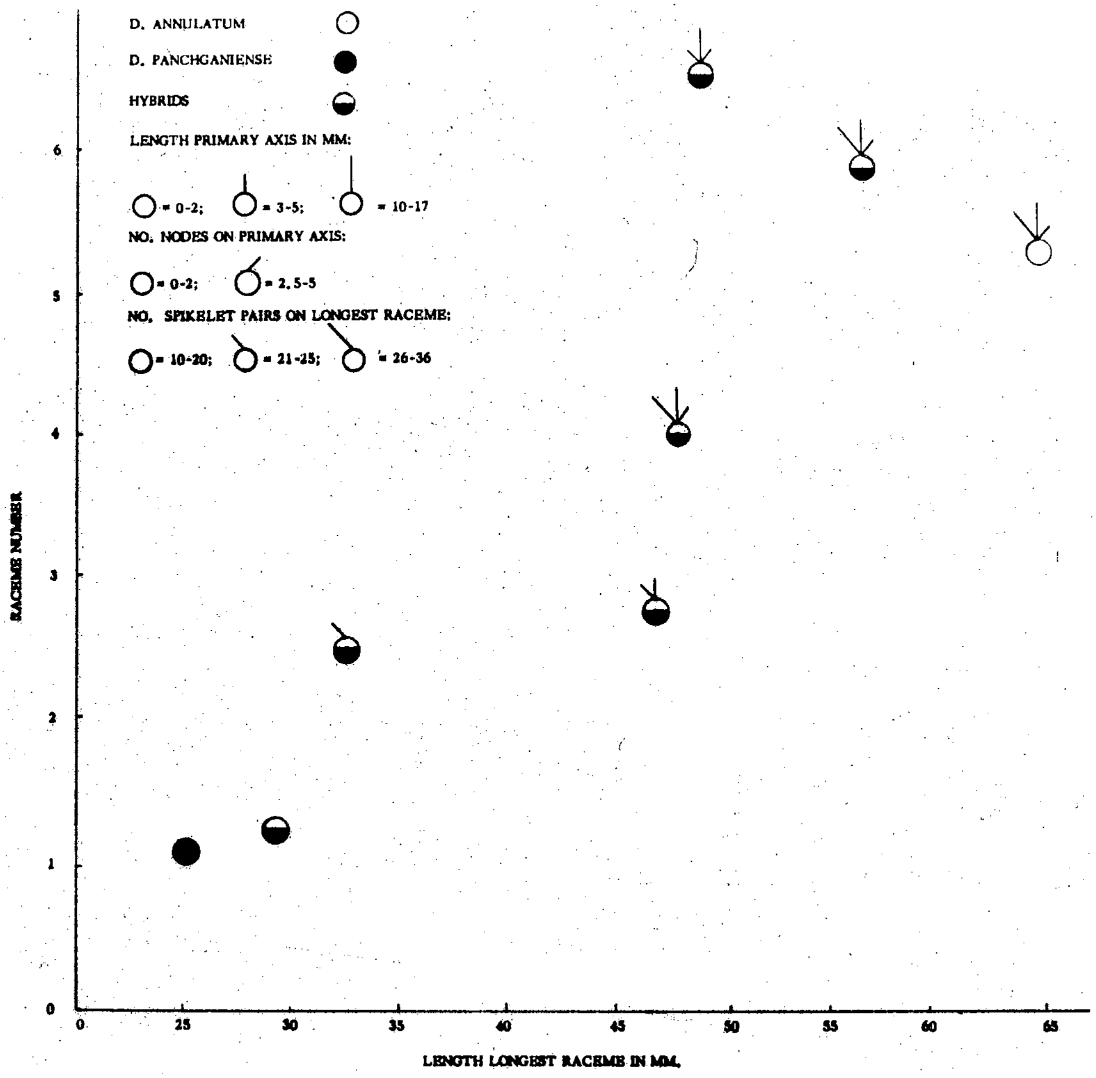
Figure 2. *D. panchganiense*.

Figure 3 - 8. Hybrids between *D. annulatum* and *D. panchganiense*.

LEGEND TO PLATE XI

Morphological variation in hybrids between *D. annulatum* and *D. panchganiense* on a pictorialized scatter diagram.

PLATE XI


D. ANNULATUM
D. PANCHGANIENSE
HYBRIDS
LENGTH PRIMARY AXIS IN MM:
= 0-2; = 3-5; = 10-17
NO. NODES ON PRIMARY AXIS:
= 0-2; = 2.5-5
NO. SPIKELET PAIRS ON LONGEST RACEME:
= 10-20; = 21-25; = 26-36
RACEME NUMBER
0
1
2
3
4
5
6
0
25
30
35
40
45
50
55
60
65
LENGTH LONGEST RACEME IN MM.

LEGEND TO PLATE XII

Cytology of triploid *Dichanthium* hybrids and their parents.

Figure 1. Metaphase I in *D. annulatum* (2n = 40) showing regular chromosome pairing.

Figure 2. Metaphase I in *D. annulatum* (2*n* = 40) showing 2 univalents, 15 bivalents, and 2 quadrivalents.

Figure 3. Anaphase I in D. annulatum (2n = 40).

Figure 4. Metaphase I in *D. annulatum* (2*n* = 20) showing regular pairing.

Figure 5. Anaphase I in *D. annulatum* (2*n* = 20).

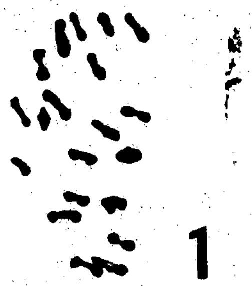
Figure 6. Anaphase I in a hybrid (2*n* = 30) between *D. annulatum* (2*n* = 40) and *D. caricosum* (2*n* = 20).

Figure 7. Metaphase I in a hybrid (2*n* = 30) between *D. annulatum* (2*n* = 40) and *D. panchganiense* (2*n* = 20) showing 14 univalents and 8 bivalents.

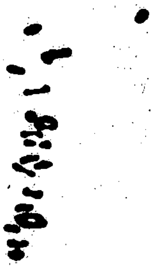
Figure 8. Metaphase I in a hybrid (2*n* = 30) between *D. annulatum* (2*n* = 40) and *D. aristatum* (2*n* = 20) showing 6 univalents and 12 bivalents.

Figure 9. Telophase I in a hybrid (2*n* = 30) between *D. annulatum* (2*n* = 40) and *D. panchganiense* (2*n* = 20) showing 6 dividing laggards.

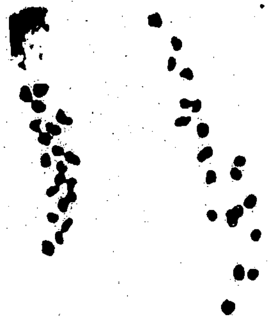
PLATE XII



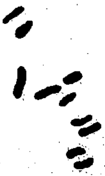
1



2



3



4

5

6

7

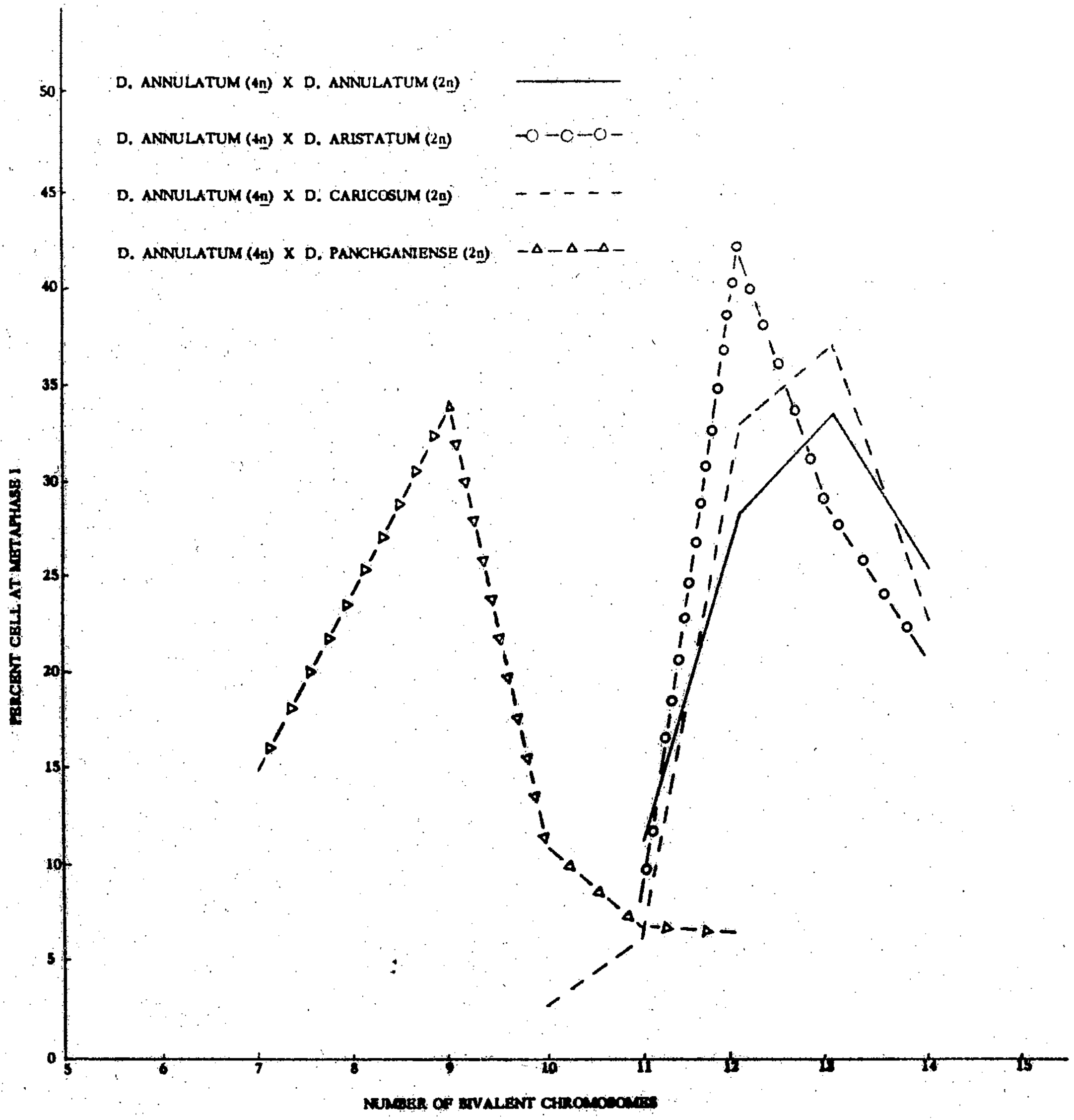
8

9

LEGEND TO PLATE XIII

Bivalent chromosome association in triploid *Dichanthium* hybrids.

PLATE XIII


D. ANNULATUM (4n) X D. ANNULATUM (2n)
D. ANNULATUM (4n) X D. ARISTATUM (2n)
D. ANNULATUM (4n) X D. CARICOSUM (2n)
D. ANNULATUM (4n) X D. PANCHGANIENSE (2n)
PERCENT CELL AT METAPHASE I
0
5
10
15
20
25
30
35
40
45
50
5
6
7
8
9
10
11
12
13
14
15
NUMBER OF BIVALENT CHROMOSOMES

of lagging chromosomes at telophase I (Plate XII). Some trivalents were occasionally observed in the hybrids between *D. annulatum* (4*n*) and the diploid races of *D. annulatum* and *D. caricosum*. After self-pollinating the triploid hybrids, no seeds were obtained, which suggested that these hybrids were completely sterile.

DISCUSSION

Diploid species and races in the genus *Dichanthium* reproduce sexually and are characterized by regular chromosome pairing. Polyhaploid plants (2*n* = 20) obtained from parthenogenetic development of cytologically reduced embryosacs of tetraploid parents were also regular in their cytological behavior. Harlan *et al.* (1961) suggested that the diploid races of *D. annulatum* may possibly represent a natural polyhaploid. However, artificial polyhaploids were, contrary to the natural ones, reproductively sterile.

In the triploid hybrids, obtained from crosses between tetraploid *D. annulatum* (DDD'D') and its diploid race (DD), the chromosomes associated mostly into bivalents. On an average 13.20 bivalents and 0.15 trivalents were formed. This may indicate that, either the chromosomes of the D genome belonging to the 4*n* parent, pair with the homologs in the D genome of the 2*n* parent, or they may pair preferentially with the chromosomes of the other basic genome, D', derived from the tetraploid parent. The presence of trivalents in some PMC's indicate some degree of homology between the three genomes in these triploid hybrids. Similarly, in hybrids obtained from crosses between 4*n* *D. annulatum* and both 2*n* *D. aristatum* (D_1D_1) and 2*n* *D. caricosum* (D_xD_x), the chromosomes commonly associated into bivalents.

The genomic symbols used here are the same as those suggested by Harlan *et al.* (1961). For convenience, the triploid hybrids between tetraploid *D. annulatum* and the diploid races of *D. aristatum* and *D. caricosum* may thus be represented by $DD'D_{'}$ and $DD'D_x$ genomes, respectively. Chromosome pairing in hybrids with $DD'D_{'}$ genomes may occur as $DD_{'}$, $D'D_{'}$ or DD'. Similarly, in the triploid hybrids with the genomes $DD'D_x$, the basic genome D_x may pair with D or D'. It is also possible to have DD' genomes involved in the bivalent formation. A few trivalents were formed in $DD'D_x$, and if sufficiently large number of PMC's are scored they may also be found in the triploid hybrids with $DD'D_{'}$ genomic consitution. However, the most common chromosome configuration observed in these triploid hybrids, at metaphase I, were bivalents and univalents. Cytologically, plants with $DD'D_{'}$ and $DD'D_x$ genomes behaved almost alike. Chromosomes may associate into 14 pairs, forming on an average 12.80 and 12.91 bivalents, respectively. The presence of more than 10 bivalents would suggest that at least some chromosomes are able to pair also within a genome.

Evidence available from the polyhaploid plants ($2n = 20$) indicates that the chromosomes of the D genome can pair preferentially with those of the basic genome D', both derived from the $4n$ parent. The chromosomes of such polyhaploid plants regularly form 10 bivalents during microsporogenesis. DeWet *et al.* (1961) suggested that autosyndesis and gene controlled preferential pairing is the common mode of chromosome association in *Dichanthium* hybrids. If we assume that genomes of the tetraploid and diploid parents can also pair in the triploid hybrids, a high frequency of trivalents should be formed. This, however, was never observed. The occasional presence of trivalents in these hybrids, may only suggest a partial homology between the chromosomes of the three genomes. This appears to rule out the possibility of allosyndesis between any one of the basic genomes of the tetraploid D. annulatum and the basic genomes, D_1 or D_x, of the diploid races of D. aristatum and D. caricosum, respectively. Pairing between D and D' genomes takes place preferentially. This could account for a maximum of only 10 chromosome pairs, and the remaining 4 bivalents must be a result of pairing within the basic genome ($n = 10$) of the diploid male parents. The latter mechanism seems to be genetically controlled, and induces some degree of pairing when true homologs are absent. A similar mode of chromosome association was reported in Bothriochloa hybrids (Chheda and Harlan, 1962).

Hybrids between tetraploid D. annulatum and the diploid species D. panchganiense were cytologically more irregular than the ones discussed above. Assuming D_2D_2 to be the genomic constitution of the diploid species, the triploid hybrid could be represented by $DD'D_2$ genomes. Meiosis in these hybrids is characterized by the presence of a large number of univalent chromosomes. If we assume chromosome homology between D. annulatum and D. panchganiense, bivalent formation in the triploid hybrid, $DD'D_2$, may be as DD_2 or $D'D_2$. It has already been indicated that D can pair with D', both derived from the tetraploid parent, when their close homologs are absent. In the triploid hybrid with $DD'D_2$ genomes, if D or D' pairs with D_2, 10 bivalents plus extra bivalents from pairing within the D or D' genome are expected. This may also be true if D pairs with D' and if chromosomes within D_2 also pair. This is what we proposed to be the case in other triploid hybrids. However, here in hybrids between D. annulatum

(4*n*) and *D. panchganiense* (2*n*) we have essentially 10 bivalents and 10 univalents.

We know from previous experience (deWet *et al.*, 1961) that pairing can take place within basic genomes, D and D'. Thus, if chromosomes of one of the two basic genomes of *D. annulatum* are homologous with those of the *D. panchganiense* basic genome, more than 10 bivalents would be expected. However, we got on an average only 9.30. This would suggest that there is preferential pairing of the DD' chromosomes and that those of the D_2 genome are not capable of pairing within themselves. This is what could be expected in a basic diploid species. Celarier *et al.* (1962) and deWet and Scott (1963) presented evidence of introgression with *D. annulatum* in the diploid race of *D. caricosum*, and introgression with *D. caricosum* in the diploid race of *D. aristatum*. The cytological data would suggest that *D. caricosum* is more closely related to *D. annulatum* than is *D. aristatum* or *D. panchganiense*; the latter species being more distantly related to *D. annulatum* than is *D. aristatum*.

CONCLUSIONS

1. Chromosome association in the triploid hybrids between the tetraploid *D. annulatum* and diploid races of the same species, as well as those of *D. aristatum* and *D. caricosum*, was essentially similar.

2. The most frequent chromosome configurations at metaphase I were bivalent, though a few univalents and an occasional trivalent may also be formed.

3. Mode of chromosome association in the triploid hybrids is genetically controlled which causes chromosomes to associate into

pairs, reducing the frequency of multivalent configuration and causing some degree of non-homologous pairing when true homologs are absent.

4. Cytological data suggest that there is little homology between the basic genomes of *D. panchganiense* and those of the tetraploid *D. annulatum*.

CHAPTER IX

INTERGENERIC HYBRIDS OF DICHANTHIUM ANNULATUM WITH BOTHRIOCHLOA GRAHAMII AND B. ISCHAEMUM

In the generic group Bothriochloininae, subtribe Andropogoninae, Harlan et al. (1958, 1961) and Harlan et al. (1962) reported several hybrids involving the genera Bothriochloa O. Kuntze, Dichanthium Willemet and Capillipedium Stapf. Artificial hybrids between Bothriochloa and both Dichanthium and Capillipedium can be produced, but the latter two genera seem to be isolated genetically.

Dichanthium annulatum (Forssk.) Stapf and Bothriochloa intermedia (R. Br.) A. Camus are sympatric throughout most of their range of geographic distribution. Harlan et al. (1961) and deWet (1963) suggested that B. grahamii (Haines) Bor represents a combination of characters from B. intermedia and D. annulatum. In the present paper the relationship of D. annulatum with the genus Bothriochloa, based on data from artificially produced hybrids, is discussed.

MATERIALS AND METHODS

Plants studied involved three collections of D. annulatum, five of B. grahamii and one of B. ischaemum. Hybrids were produced by using a sexual self-sterile plant (X-98) as well as facultative apomict representatives of D. annulatum as the female parents, following the technique described by Richardson (1958). Reciprocal intergeneric crosses were also attempted. Morphological studies are based on field observations correlated with herbarium studies. Chromosome associations were studied in developing microsporocytes stained with acetocarmine.

RESULTS

Intergeneric crosses of *D. annulatum* (2*n* = 40) with the genus *Bothriochloa* were successful only with *B. grahamii* (2*n* = 40) and *B. ischaemum* var. *songarica* (2*n* = 50). The latter hybrid was obtained when *D. annulatum* (X-98) was the male parent. The distinguishing morphological characteristics of *D. annulatum*, *B. grahamii*, *B. ischaemum* and their hybrids are presented in Plates XIV and XV. Cytological data are presented in Table XIII and Plate XVI.

Morphologically, the genus *Bothriochloa* differs from *Dichanthium* primarily in having the pedicels to the pedicellate spikelets long and with a translucent groove; hairs on the lower glume of the sessile spikelet confined to its lower half; and all spikelet pairs of a raceme heterogamous, rarely one pair homogamous (deWet, 1963). *Bothriochloa grahamii* differs from typical representatives of *Bothriochloa* in having the pedicels to the pedicellate spikelets solid or only slightly grooved, and the lower glume of the oblong-truncate spikelets with long cilia at the tip and along the margins. The latter type of hair pattern on the glume, characteristics of *B. grahamii*, resembles that of *D. annulatum*. However, *B. grahamii* differs from *D. annulatum* primarily in having the primary axis of the panicle as long as, or slightly longer than, the lower racemes, and in having the lower sessile spikelet on the raceme bisexual.

LEGEND TO PLATE XIV

Inflorescences of intergeneric hybrids and their parents. — Showing variation in length of primary axis, and also number and length of racemes.

Figure 1. *D. annulatum*.
Figure 2. *B. grahamii*.
Figure 3. *B. ischaemum*.
Figure 4. Hybrid between *D. annulatum* and *B. grahamii*.
Figure 5. Hybrid between *B. grahamii* and *D. annulatum*.
Figure 6. Hybrid between *B. ischaemum* and *D. annulatum*.

LEGEND TO PLATE XV

Morphology of intergeneric hybrids between *Dichanthium* and *Bothriochloa* on a pictorialized scatter diagram.

PLATE XV

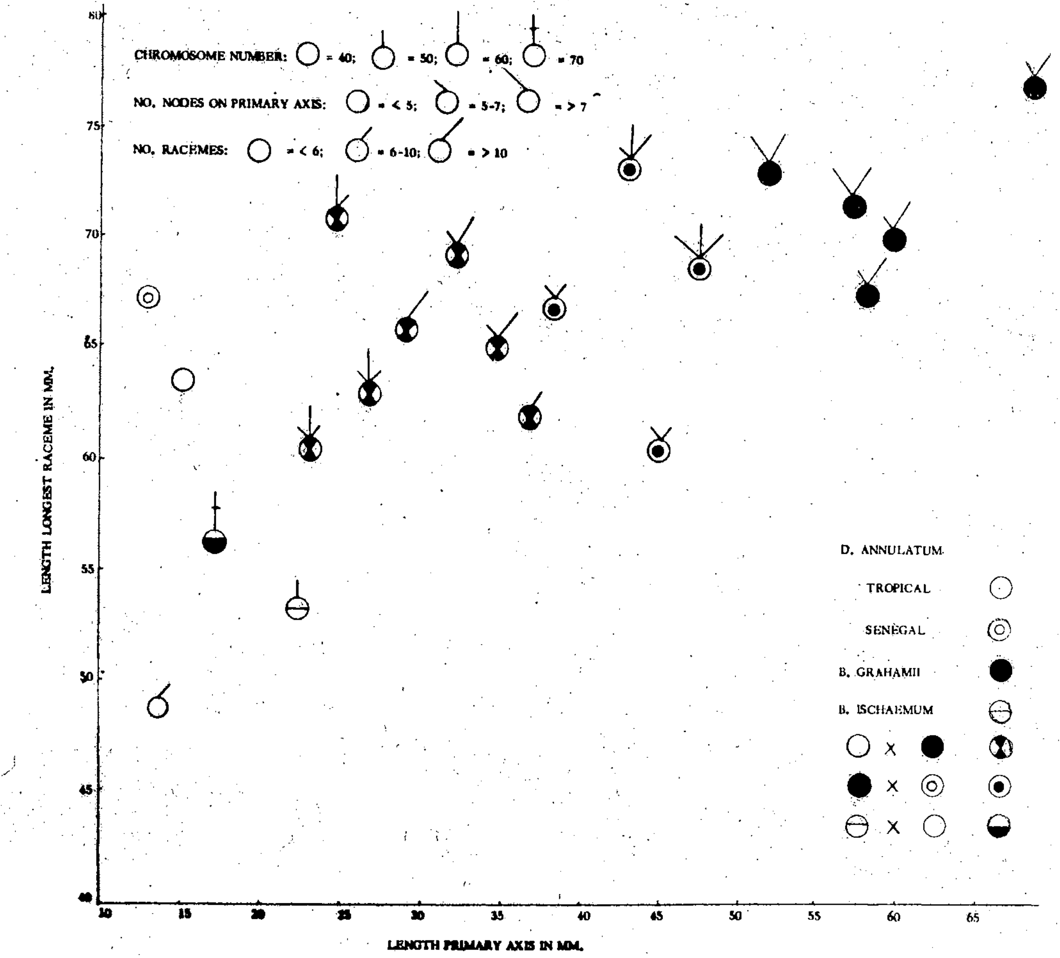

CHROMOSOME NUMBER: ○ = 40; ○ = 50; ○ = 60; ○ = 70
NO. NODES ON PRIMARY AXIS: ○ = < 5; ○ = 5-7; ○ = > 7
NO. RACEMES: ○ = < 6; ○ = 6-10; ○ = > 10
D. ANNULATUM
TROPICAL
SENEGAL
B. GRAHAMII
B. ISCHAEMUM
X
X
X
80
75
70
65
60
55
50
45
40
10
15
20
25
30
35
40
45
50
55
60
65
LENGTH LONGEST RACEME IN MM.
LENGTH PRIMARY AXIS IN MM.

TABLE XIII

CYTOLOGY OF INTERGENERIC HYBRIDS AND THEIR PARENTS

Name	No.	2n	I	II	III	IV*
Parents						
D. annulatum						
i. Tropical	X-98	40	1.24	17.08	4.12	1.06
			0-6	15-20	0-1	0-3
	4099	40	0.24	19.08	0.08	0.34
			0-2	16-20	0-1	0-2
ii. Senegal	5430	40	0.26	18.32	0.10	0.70
			0-4	16-20	0-1	0-3
B. grahamii	X-750	40	7.33	16.29	0.03	0.00
			0-16	12-20	0-1	--
	2655	40	1.21	19.30	0.01	0.04
			0-4	18-20	0-1	0-1
	4630I	40	3.20	18.40	0.00	0.00
			0-8	16-20	--	--
	5168(b)	40	2.37	18.43	0.07	0.14
			0-4	16-20	0-1	0-1
	5450	40	1.88	18-94	0.00	0.06
			0-6	17-20	--	0-1
B. ischaemum	6459	50	5.32	20.48	0.28	0.72
			2-10	18-23	0-1	0-2
Hybrids						
D. annulatum (2n = 40) x B. grahamii (2n = 40)						
	X-98 x X-750	40	6.23	16.07	0.01	0.40
			0-12	14-20	0-1	0-2
		60	8.74	25.21	0.00	0.21
			4-12	22-27	--	0-1
	X-98 x 2655	40	10.34	14.75	0.00	0.04
			0-28	6-20	--	0-2
		60	7.58	25.87	0.00	0.17
			4-12	24-28	--	0-1
	X-98 x 5450	40	5.18	16.87	0.04	0.24
			0-10	12-20	0-1	0-2
	4099 x 4630I	60	4.50	27.25	0.00	0.00
			4-8	26-28	--	--
	4099 x 5450	40	7.20	15.00	0.16	0.58
			6-10	12-17	0-1	0-2
		20	1.00	9.50	0.00	0.00
			0-2	9-10	--	--
B. grahamii (2n = 40) x D. annulatum (2n = 40)						
	2655 x 5430	40	7.34	16.33	0.00	0.00
			6-10	15-17	--	--
	5168(b) x 5430	60	6.93	25.87	0.27	0.13
			4-9	24-28	0-1	0-1

TABLE XIII (continued)

Name	No.	2n	I	II	III	IV*
	5450 x 5430	40	6.86 4-10	16.57 15-18	0.00 --	0.00 --
		60	9.53 6-14	24.37 23-27	0.07 0-1	0.38 0-2
B. ischaemum (2n = 50) x D. annulatum (2n = 40)						
	6459 x X-98	70	14.68 10-26	27.62 22-30	0.00 --	0.02 0-1

*I = univalent; II = bivalent; III = trivalent; IV = quadrivalent. Average number and range of chromosome association at Metaphase I.

LEGEND TO PLATE XVI

Cytology of intergeneric hybrids between *Dichanthium* and *Bothriochloa*.

Figure 1. Metaphase I in *D. annulatum* (2*n* = 40).

Figure 2. Metaphase I in *B. grahamii* (2*n* = 40).

Figure 3. Metaphase I in *B. ischaemum* (2*n* = 50).

Figure 4. Anaphase I in *B. ischaemum* (2*n* = 50).

Figure 5. Metaphase I in a hybrid (2*n* = 40) between *D. annulatum* and *B. grahamii*.

Figure 6. Metaphase I in a hybrid (2*n* = 60) between *D. annulatum* and *B. grahamii*.

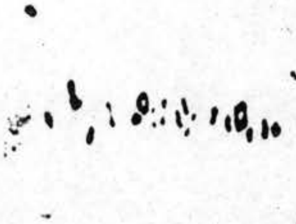
Figure 7. Anaphase I in a hybrid (2*n* = 60) between *D. annulatum* and *B. grahamii*.

Figure 8. Metaphase I in a hybrid (2*n* = 70) between *B. ischaemum* and *D. annulatum*.

Figure 9. Anaphase I in a hybrid (2*n* = 70) between *B. ischaemum* and *D. annulatum*.

Figure 10. Telophase I in a hybrid (2*n* = 70) between *B. ischaemum* and *D. annulatum* showing 2 dividing and 13 non-dividing laggards.

PLATE XVI



1

2

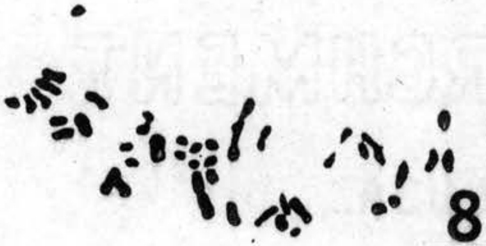
3

4

5

6

7



8

9

10

Harlan et al. (1961) referred to B. grahamii as the Gangetica type of B. intermedia. DeWet (1963), however, indicated that this species definitely represents a hybrid between B. intermedia and D. annulatum. Cytologically, B. grahamii is characterized by chromosomes which associate essentially into 20 pairs, although some chromosomes may either fail to pair or may form multivalents.

Bothriochloa ischaemum, as described by Celarier (1957) and Celarier and Harlan (1958), is distributed from China and Formosa through northern India to Turkey and Europe. The main distinguishing morphological characteristics of the species are: fairly well developed grooves in the pedicels; joints and pedicels with long silvery hairs; and upper portion of the lower glume of the sessile spikelet glabrous. Two varieties are recognized, the typical B. ischaemum var. ischaemum (2n = 40, 60) and B. ischaemum var. songarica (2n = 50, 60). The latter differs from the typical B. ischaemum in having a long primary axis of the panicle, with the ratio of the lower raceme over the axis, between 1.0 and 2.0; glumes not pitted but often strongly dished; plants decumbent and robust; and more densely hairy leaves. Gross morphology of the pentaploid B. ischaemum var. songarica, from Hong Kong, is presented in Plates XIV and XV. Cytologically the latter variety is characterized by irregular meiosis. Several univalents (2-10) and some multivalents at metaphase I, and lagging chromosomes at telophase I were always present.

Hybrids between D. annulatum and B. grahamii had 2n = 40 and 60 chromosomes. Morphological data suggest that the hexaploid hybrids were produced through fertilization of a cytologically unreduced egg of *D. annulatum* by the normal male gamete of *B. grahamii*. A similar phenomenon was also observed in the reciprocal crosses (Table XIII). The chromosomes of the $2n = 40$ and 60 chromosome hybrids associated into as many as 20 and 28 pairs, respectively, at metaphase I. Occurrence of trivalents and quadrivalents in the hybrids indicates some degree of segmental homology between the chromosomes of the two species. Bivalent formation may suggest autosyndesis or residual homeology based upon sets of 5 chromosomes each.

Attempted crosses between *B. ischaemum* ($2n = 50$) as a female parent and *D. annulatum* ($2n = 40$) as the male parent resulted in hybrids with $2n = 70$ chromosomes, which indicates that the cytologically unreduced egg was fertilized by a normal reduced male gamete. Morphologically the hybrids were recognized primarily by the presence of a few long hairs at the tip of the glume of the sessile spikelet. Other morphological characters are presented in Plates XIV and XV. Cytologically these hybrids were characterized by irregular meiosis. The chromosomes associated into as many as 30 pairs (Table XIII).

DISCUSSION

Natural hybridization seems to occur between representatives of the species *B. intermedia*, *B. grahamii* and *D. annulatum*, forming an agamic complex. Harlan *et al*. (1961) indicated that crosses between *B. intermedia* (Gangetica type) and *D. annulatum* are easier to obtain than between different biotypes of the Gangetica type, or often within *D. annulatum*. They further indicated that wherever sexuality can be found, genetic exchange also occurs between various kinds of *B. intermedia* and *B. ischaemum*.

Assuming the tetraploid *D. annulatum* and *B. grahamii* to be of DDD'D' and BBDD genomic constitution, respectively, as proposed by Harlan *et al.* (1961), the tetraploid hybrid could be represented by DD'BD genomes. From the cytological study it appears that in the absence of close homology, D' pairs with D preferentially, thus giving rise to 10 chromosome pairs. This assumption becomes evident from the studies of polyhaploid plants of *D. annulatum*, which are characterized by regular chromosome association. The additional 10 bivalents in the tetraploid hybrids are probably the result of pairing between or within the chromosomes of B and D genomes. Celarier *et al.* (1961a) and Chheda and Harlan (1962) suggested autosyndesis in B and D genomes, and also that there is segmental interchange between the chromosomes of the two genomes. The latter observation can account for the occurrence of trivalents and quadrivalents in the tetraploid hybrid between *D. annulatum* and *B. grahamii*. Chromosome association in the hexaploid hybrid DDD'D'BD may similarly be represented as follows:

$$DDD'D' \text{ x } BBDD \longrightarrow \underset{\smile}{DD}\quad \underset{\smile}{D'D'}\quad \underset{\circlearrowleft}{B}\underset{\circlearrowright}{D}$$

Mode of chromosome pairing in this hybrid may be explained on the basis of autosyndesis and by assuming a basic set of 5 chromosomes.

Cytological irregularities in the pentaploid ($2\underline{n} = 50$) *B. ischaemum* was suggested by Celarier (1957) to be the result of its hybrid origin. Assuming $B_xB_xB_xB'B'$ to be the genomic consitution of the allopentaploid as proposed by Harlan *et al.* (1961), the occurrence of 23 bivalents at metaphase I indicates pairing between B_xB_x and $B'B'$, and also that the chromosomes of the other B_x genome either remain as univalents or associate into bivalents. The genomic constitution of the $2n = 70$ chromosome hybrids may, for convenience, be represented as $B_xB_xB_xB'B'DD'$, since it has the full genomes of *B. ischaemum* and half of *D. annulatum*. In these hybrids 30 bivalents and 10 univalents were observed. This again suggests that the mode of chromosome association is B_xB_x, $B'B'$ and DD' and the remaining 10 univalents were probably from the other B_x genome. Cytological evidence is not clear enough to suggest homology between the chromosomes of the two species. However, the fact that a cytologically unreduced egg of *B. ischaemum* can be fertilized by a normal male gamete of *D. annulatum* suggests some relationship between the two species.

CONCLUSIONS

1. The cytologically reduced, as well as unreduced, female gametes of both tetraploid *D. annulatum* and *B. grahamii*, when crossed, can be fertilized to produce plants with $2n = 40$ and 60 chromosomes.

2. Intergeneric hybrids were produced between *D. annulatum* and both *B. grahamii* and *B. ischaemum*.

3. The chromosomes in the hybrids between these species pair preferentially between genomes derived from each parental species.

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