CYTOTAXONOMIC STUDY OF THE

Dichanthium annulatum

COMPLEX

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DEDICATION

To the memory of the Late Dr. Robert Paul Celarier

whose researches have contributed so much

to our knowledge of the difficult genera of the

Andropogoneae

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INTRODUCTION

Most of the forage crops grown in the United States are introductions from Europe, Asia, and Africa. Only a relatively small number of native grasses and practically no native legumes are used as cultivated forage plants. In many cases these introductions have been far superior to native species in productivity, persistence under use, aggressiveness, and in some cases, forage quality (Celarier and Harlan, 1955).

The introduction of materials has not been very systematic until recent years, and some of the better adapted species, or ecotypes within a species, perhaps have not yet been evaluated. Furthermore, only a few of these introduced species have been collected throughout their geographical range of distribution, even though at least some of them have been known for some time to be of considerable agronomic importance.

It has been recognized that several members of the grass tribe Andropogoneae have forms with considerable potential as pasture and range forage (Celarier and Harlan, 1955; Harlan et al., 1958). Of the genera that have been studied, Dichanthium, Bothriochloa, and Capillipedium are among those which have forms with certain desirable agronomic characters. Although, the group as a whole has much potential, no single collection has all of the desirable agronomic qualities. It will be necessary to develop plant breeding methods to utilize selected members of these grasses in the development of altogether new combinations of forms with desirable agronomic qualities. It has been suggested that if the vigor, productivity, and high quality of some collections

of Dichanthium could be combined with the winter hardiness of some collections of Bothriochloa, strains of great value to the Great Plains might be obtained (Harlan et al., 1958). A systematic survey of the morphological and cytological variation prevalent within different species of these genera would be helpful in selecting the desirable collections to be used in the breeding program. Although, these genera are of considerable importance in the Old World and seem to have much promise for the New World, they are poorly understood cytologically and taxonomically. Only an analysis of Bothriochloa ischaemum Keng has been more or less completed (Celarier, 1957; Celarier and Harlan, 1958) and a similar survey is needed for the other species of these genera.

The objective of this study was to grow together, in an experimental garden, several introduced accessions of the Dichanthium annulatum complex collected throughout its geographical range of distribution, and to conduct both a taxonomical and cytological survey of them. The carrying out of such an objective should provide information from which to draw conclusions concerning the pattern of variation prevalent in this complex, and also about its origin and evolutionary mechanics.

Preliminary cytological and taxonomic studies (Celarier and Harlan, 1956; Celarier et al., 1958; Mehra and Celarier, 1958; Harlan et al., 1958) have pointed out the presence of a polyploid series within the Dichanthium annulatum complex with somatic chromosome numbers of 20, 40, and 60. Four morphological types (Tropical, Mediterranean, Senegal, and South African) were recognized within this complex. Furthermore, these studies have pointed out the correlation between chromosome number, geographical distribution, and morphological types within some accessions belonging to this complex. Several accessions were not included in

these studies. Also, more information is needed for some of these reported accessions. Cytological studies (Celarier et al., 1958; Sikka and Mehra, 1956) have revealed the presence of multivalents during microsporogenesis in the tetraploid and the hexaploid accessions belonging to this complex. It would be of interest to study whether such polyploid types have originated by segmental allopolyploidy or by autoalloploidy or autopolyploidy, followed by a long period of chromosome and genetic differentiation. Also, it would be desirable to understand the relationship between different morphological types within the same ploidy level. Mehra and Celarier (1958) suggested the presence of introgression between the Tropical and the Mediterranean tetraploid type . Celarier and Harlan (1957) have shown that apomixis is the predominant method of reproduction in the tetraploids and the hexaploids, and that the diploids are completely sexual. Although, the hexaploids may be obligate apomicts, the tetraploids are thought to be facultative apomicts (Celarier and Harlan, 1957; Celarier et al., 1958). In view of the presence of facultative apomixis and introgression between the Tropical and the Mediterranean tetraploid type , it would be desirable to produce artificial hybrids involving these two types and to grow their selfed progenies. A detailed morphological and cytological study of these (F_1 and F_2 plants) populations should provide information about the extent to which the characters of these two taxa recombine, and therefore might make it possible to draw conclusions about their relationships.

The origin and evolution of the hexaploid South African type is not yet known. Celarier et al. (1958) have suggested that the South African type might be the product of the fertilization of an unreduced

gamete of the tropical type of D. annulatum by a normal gamete of D. aristatum, another South African species. In order to understand the origin of the South African type, controlled crosses should be attempted to check the validity of their suggestion.

The investigation now to be discussed constitutes, then, a detailed analysis of morphological, taxonomical, and cytological studies of the Dichanthium annulatum complex; a correlation, if any, between the chromosome number, the geographical distribution and the morphological type within several accessions of this complex; a study of the relationship between the Tropical and the Mediterranean type; and a study of the origin of the South African type (D. papillosum Stapf).

REVIEW OF LITERATURE

Taxonomy

Historical taxonomy.

The *Dichanthium annulatum* complex belongs to the tribe *Andropogoneae* of the grass family. This taxon was first described as *Andropogon annulatus* by Forskal in 1775. In subsequent years this taxon was described as *Andropogon Bladhii* (Retz, 1785), *A. camosus* (Link, 1827), *A. obtusus* (Nees, 1841), *A. scandens* (Roxburgh, 1820), *Lipeocereis annulata* (Nees, 1841), *A. geripensis* (Stend, 1855), and *A. papillosus* (Hochst, 1835-43). Hackel (1889) in his treatment of the genus *Andropogon* included this taxon under the subgenus *Dichanthium*. Also, Hackel (1889) recognized five varieties (*monostachyus*, *genuinus*, *decalvatus*, *Bladhii*, and *humilis*) within *A. annulatus* Forsk. Hooker (1897) in his treatment followed Hackel (1889) and added another variety i.e., *Andropogon annulatus* var. *papillosus*. Randle (1899) presented a detailed description of the variety *papillosus* of *Andropogon annulatus* Forsk.

Hackel's (1889) treatment of this taxon was followed by several workers (Hooker, 1897; Cooke, 1908; Durand and Schinz, 1892-1894; and Prain, 1903). Since the subgenus *Dichanthium* of Hackel (1889) was earlier recognized as a separate genus by Willemet (1796), Stapf (1917) cleared the confusion in the synonymy of this taxon and presented a detailed description of it under two separate epithets i.e., *Dichanthium annulatum* (Forsk) Stapf and *Dichanthium papillosum* (Hochst) Stapf.

Stapf's (1917-1919) treatment was followed by several workers (Haines, 1924; Blatter & McCann, 1928; Bor, 1947; Gardner, 1952; Chippindall, 1955; and Pandeya, 1953).

Celarier and Harlan (1955) in their treatment included D. annulatum Stapf and D. papillosum Stapf under the Dichanthium annulatum complex and recognized three distinct morphological types (Tropical, Mediterranean, and South African types). Harlan et al. (1958) recognized, in addition the Senegal type from Senegal, French West Africa.

Descriptive taxonomy.

Hackel (1889), in his noteworthy monograph of the tribe, included in the genus Andropogon a number of taxa now generally recognized as distinct genera. In general, Hackel's system was followed by several workers (Hooker, 1897; Trimen, 1900; Cooke, 1908) until the work of Stapf (1919) on the grasses of tropical Africa. Stapf (1919), in his treatment of the tribe, disagreed with Hackel in assigning generic rank to several of the subgenera of the genus Andropogon. Since Stapf's work, most taxonomists working on the tropical materials have, for the most part, accepted his treatment (Camus and Camus, 1922; Hubbard, 1934; Blatter and McCann, 1935; Keng, 1939; Henard, 1940; Bor, 1940; Blake, 1944; Rhind, 1945; and Gardner, 1952). On the other hand taxonomists working on the temperate materials have largely followed the tradition of Hackel (1889) or its modification by Kumarov (1934-1945), Hitchcock (1950).

The Dichanthium annulatum complex is characterized by the presence of pedicelled spikelets, which are male or neuter, unpitted first glume, racemes pedunclate without long dense silky hairs, pedicellate spikelets being equal to or shorter than sessile, lower glume of the sessile

spikelet a simple awn, and racemes digitate (Celarier, unpublished).

Synonyms, geographical distribution, and the distinguishing characters of the varieties described by Hackel (1889) are outlined below:

(a) A. annulatus var. monostachyus.

Racemes solitary or two, inflorescence rachis 4-5 mm long, racemes 3-3.5 cm long; perfect spikelet articulate, 5 mm long, oblong more than twice as much shorter, less densely hairy; first glume very smooth except cilia of keel. Pedicellate spikelets often without fourth glume putting forth a short straight awn, and which also hinges the unfolding pistil.

Distribution: Australia.

(b) A. annulatus var. genuinus.

Racemes 3-10 (very often 5), 4-6 cm long; common rachis 1.5-2.5 cm long, 3-5 nodes inserted, the lower peduncles 5-8 mm long; first glume of fertile spikelets, except cilia of keels, covered over with rigid hairs, with tubercled base, little longer and somewhat equalling the glume; papillose moreover on lower back, first glume of the pedicellate spikelet with tuberculate hairs scattered over almost all the back.

Synonyms: A. annulatus Forsk, A. Bladhii Roxb, A. camosus Link, Lipeocercis annulata Nees and A. geripensis Stend.

Distribution: Northern Africa, Morocco, Algeria, Tunisia, Egypt, Arabia, Iran, India, China, Australia, and Pacific Islands.

(c) A. annulatus var. decalvatus.

The first glume of the perfect spikelet glabrous except the minutely ciliolate keels, pedicellate often papillose, other characters like var. genuinus.

Synonyms: A. scandens Roxb, has slightly glabrous spikelets, with culms somewhat ascending.

Distribution: It appears along with var. genuinus in Egypt, Afghanistan, and India.

(d) A. annulatus var. Bladhii.

Racemes 8-15, common rachis 4 cm long, 5-6 nodes inserted, lower peduncles 10 mm long, first glume of the perfect spikelet smooth except the setulose ciliate keels, or scattered with sparse hair.

Synonyms: A. Bladhii Retz, A. obtusus Nees. According to Hackel (1889) the plant of Retz is too little separated from the variety genuinus, from which it departs through intermediate forms.

Distribution: India and China.

(e) A. annulatus var. humilis.

Plants small, racemes 4-6 only, without definite arc of tubercle hair.

Distribution: Australia.

This variety was given a species status by Black (1936) as Dichanthium humilius.

Hooker (1897) in his treatment followed Hackel (1889) and described four varieties from India. These varieties were var. genuinus, var. decalvatus, var. Bladhii, and var. papillosus.

Hackel's (1889) treatment of this taxon into different varieties was followed by several workers (Durand and Schinz, 1892-94; Prain, 1903; Cooke, 1908; Camus and Camus, 1922). Since the subgenus Dichanthium of Hackel (1889) was earlier recognized as a separate genus by Willemet (1796), Stapf (1917) cleared the confusion in the synonymy of

this taxon. Stapf (1917) presented a detailed description of the taxon under two epithets Dichanthium annulatum (Forsk) Stapf and Dichanthium papillosum (Hochst) Stapf. The synonyms and the distinguishing features of these two species are outlined below (Stapf, 1917):

(a) Dichanthium annulatum Stapf.

Lower glume of sessile spikelets without a semilunar row of long tubercle-based hair below the hyaline tip, and blade margins not revolute.

Under this species Stapf (1917) included all the material listed by Hackel (1889) as A. annulatus Forsk varieties i.e., genuinus, decalvatus, Bladhii, and the var. papillosus of Hooker (1897).

(b) Dichanthium papillosum (Hochst) Stapf.

Lower glume of the sessile spikelets with a semilunar row of long tubercle-based hair below the hyaline tip; blade margins at length revolute.

Under this species Stapf included the material described as A. annulatus var. papillosus Randle or Andropogon papillosus Hochst.

Stapf's (1917-19) treatment was followed by several workers (Haines, 1924; Blatter and McCann, 1928; Bor, 1947; Gardner, 1952; Chippindall, 1955; and Pandeya, 1953).

Celarier and Harlan (1955) in their treatment included D. annulatum Stapf and D. papillosum Stapf under the Dichanthium annulatum complex and recognized three distinct morphological types i.e., Tropical, Mediterranean, and South African. Harlan et al. (1958) recognized besides these three types the Senegal type from Senegal, French West Africa. The distinguishing features of these four types are outlined

below (Celarier and Harlan, 1955; Harlan et al., 1958):

(a) Tropical type.

Rachis and pedicel without a groove, peduncle usually glabrous, joints and pedicels with very few hairs. Primary axis of the inflorescence very short, racemes short, stubby in a subdigitate arrangement. Glumes of the sessile spikelets broad, truncate at tip, often obovate, densely covered with long hair, mostly tubercle-based. Plants erect, decumbent or prostrate, and nodes with a conspicuous ring of long hair.

(b) Mediterranean type.

Similar to above with the following exceptions: glumes of the sessile spikelets more narrow and pointed at the tip, racemes longer than Tropical type, slender and often arranged in a more open windmill pattern. Plants relatively tall, erect or slightly decumbent, leaves more numerous than the Tropical type.

(c) South African type.

This type is referred to D. papillosum Stapf. This taxon is similar to above with the following exceptions: glumes of the sessile spikelets considerably more hairy than others, with a semilunar ring of long hair at the apex usually tubercle-based. Racemes of the Tropical type, but usually more numerous. Plants erect or semidecumbent and robust.

(d) French West African type.

This type is similar to the Mediterranean type of D. annulatum except that the spikelets are nearly glabrous.

Geographical Distribution

Because of the weedy nature of the Dichanthium annulatum complex, it is difficult to determine with certainty what constitutes its natural geographical distribution. However, it is widespread throughout the tropics and subtropics of the Old World. It is found throughout Africa (Durand and Schinz, 1892-94; Hutchinson and Dalziel, 1927; Stapf, 1917), and has been reported from Senegal (Trochain, 1940), Morocco (Ball, 1877), Tunisia (Battandier and Trabut, 1902; Cuenod, 1954), Algeria (Battandier and Trabut, 1895, 1902), northern and central Sudan (Andrews, 1956; Broun and Massey, 1929; Crowfort, 1928), Ethiopia (Durand and Schinz, 1892-94; Stapf, 1917), northeastern tropical Africa (Hutchinson and Dalziel, 1931-36), Portuguese East Africa, Zambesi Delta, Expedition Islands, Mozambique, Nyasaland (Stapf, 1917), Angola (Hutchinson and Dalziel, 1931-36), Lower Guinea, Mouhino, Loanda (Stapf, 1917), Southern Rhodesia (Sturgeon, 1954), Union of South Africa (Chippindall, 1955; Marloth, 1915; Stapf, 1917), Mauritius (Hubbard and Vaughan, 1940; Hutchinson and Dalziel, 1931-36), and from Rodriguez (Hubbard and Vaughan, 1940).

The D. annulatum complex is found abundantly in Israel (Dinsmore, 1911), Syria, Palestine, and Sinai (Post, 1933), Iraq (Zohary, 1950), Arabia (Blatter, 1936), Egypt (Ascherson and Schweenfurth, 1887; Forskal, 1775; Muschler, 1912; Vivi Tackholm and M. Drari, 1941), Iran (Parsa, 1952), Baluchistan (Burkill, 1909), and Afghanistan (Boissier, 1884).

This complex extends into West Pakistan and India (Hooker, 1897), and it occurs abundantly in South India (Rangachariyar, 1921; Rangachariyar and Mudalier, 1921), Madras (Gamble, 1934), Mysore (Govindu

and Thirumalachar, 1952), Bombay (Cooke, 1908; Blatter and McCann, 1935), Uttar Pradesh (Bor, 1947), Madya Pradesh (Pandeya, 1953), Bihar and Orissa (Haines, 1924), Bengal (Prain, 1903) and in Punjab (Collett, 1902). D. annulatum is not reported from Ceylon, but it has been collected in Burma (Rhind, 1945) and Indo China (Camus and Camus, 1922). Although the distribution of this complex in China is not well known, it probably is common in the southern part of the country. This complex has been reported from Kwangtung, Nainan, Yunan (Handel-Muzzetti, 1936; Keng, 1933), Canton (Hitchcock, 1929; Randle, 1906; Sauer, 1947), Ischang, and from Hong Kong (Randle, 1906). It is also common in Malaya and Indonesia (present report), and is seen occasionally in Australia (Ewart, 1917; Gardner, 1952), several Polynesian Islands, and Fiji Islands (Summerhayes and Hubbard, 1927).

Cytology

Cytogeography.

Cytological studies in the Dichanthium annulatum complex have, until recently, been confined to the determination of the chromosome numbers. Karper and Chisholm (1936) were the first to determine the chromosome number of this species and they reported 2n = 40. This number was soon confirmed by several workers (Hubbard and Vaughan, 1940; Krishnaswamy, 1941; Janaki-Ammal, 1945; Oke, 1950). Celarier and Harlan (1955) reported the presence of a polyploid series in this complex with somatic chromosome numbers of 20, 40, and 60 and the 2n = 20 type was confirmed by Mehra (1955) and Gould (1956). Also, de Wet and Anderson (1956) have reported 2n = 30 in the South African type D. papillosum.

Sikka and Mehra (1956) reported one diploid and eight tetraploid accessions from India. Celarier et al. (1958) studied fifty-eight accessions of the D. annulatum complex, representing entries from almost all of its geographical range of distribution. In this study they reported four diploids, seven hexaploids, and the remaining forty-seven tetraploids. Also, Harlan et al. (1958) reported four diploid , forty-five tetraploid , and seven hexaploid accessions. Celarier et al. (1958) compiled the previous records (Oke, 1950; Sikka and Mehra, 1956; and Gould, 1956) of the chromosome numbers and geographical locations, and plotted these along with the accessions studied by them on a geographical map. Their data showed that the tetraploids are found throughout the range of distribution of the complex, whereas both the diploids and the hexaploids have a more restricted distribution. The diploids have been reported from the Gangetic plains of India. The hexaploids may be restricted to South Africa (Celarier et al., 1958).

Meiotic behavior.

Meiotic behavior of the Dichanthium annulatum complex was studied by several workers (Celarier et al., 1958; Sikka and Mehra, 1956; Karper and Chisholm, 1936). The findings of these investigators are briefly as follows: During meiosis the diploids were observed to be completely regular, the hexaploids extremely irregular, and the tetraploids represented almost all intermediate degrees of irregularities. The meiotic irregularities encountered were essentially of the same kind in all accessions, and differed only in their relative frequencies. These meiotic irregularities were the presence of multivalents and univalents at diakinesis and metaphase I; lagging chromosomes,

dividing and non-dividing univalents, chromosome bridges and fragments at anaphase I; lagging chromosomes at anaphase II; and varying number of micronuclei at both the dyad and the tetrad spore stages. Pollen fertility was also observed to be variable in different accessions.

Celarier and Mehra (1959) reported on the meiotic behavior of a desynaptic plant of D. annulatum Stapf. This accession was obtained from South China. The meiotic irregularities encountered in this desynaptic plant were of the same kind as found in other tetraploids, but were in much higher frequencies.

Cytotaxonomy

Cytological studies (Celarier et al, 1958; Harlan et al., 1958) and morphological studies (Harlan et al., 1958; Mehra and Celarier, 1958) have shown that the diploids were all of the Tropical type, and found only in northern and eastern India, the hexaploids were all of the South African type, and found only in South Africa, but the tetraploids were of several morphological types, and were distributed throughout the tropics and the subtropics from French West Africa to Fiji Islands.

MATERIALS AND METHODS

Accessions.

The plant materials reported in this investigation were grown in the Experimental Garden of the Oklahoma Agricultural Experiment Station according to the procedure outlined by Celarier and Harlan (1956). Forty, one hundred, and sixty-four accessions of the Dichanthium annulatum complex comprising samples from both western (French West Africa) and eastern (Australia) extremes of its range were grown in 1956, 1957, and 1958 respectively. There was, however, a deficiency of collections from Southeast Asian countries. Although it is likely that several significant types are missing from this collection, it does seem probable that most of the major types are represented in the material sampled. Appendix A (Table I) shows the accession number, origin and collector for all the accessions used in the present investigation.

Herbarium specimens.

Herbarium specimens were taken for all accessions, and after study has been completed, they will be deposited in the following herbaria: Herbarium of Oklahoma State University, Stillwater, Oklahoma; United States National Herbarium, Washington, D. C.; Royal Botanical Gardens Herbarium, Kew, England; Missouri Botanical Gardens, St. Louis, Missouri; University of California Herbarium, Berkeley, California; University of Pretoria Herbarium, Pretoria, South Africa. In general, nine herbarium specimens were prepared from each accession such that

five were taken from the plant used for cytological study, while the rest were prepared from the other plants of the same accession.

Cytological studies.

Bud material for cytological studies was collected between 8 and 11:30 a.m. during the flowering season, fixed in Carnoy's solution (6 parts ethyl alcohol: 3 parts acetic acid: 1 part chloroform), stored in a refrigerator and studied as time permitted. The anthers were smeared in acetocarmine, the slides were sealed and occasionally made permanent according to the procedure outlined by Celarier (1956). Materials of some entries showed no ill effects after 24 months of storage, and none appears to have deteriorated appreciably during the first nine months. Although no attempt was made to use exactly the same number of cells to analyse the chromosome conditions, certain minimum numbers were required. At diakinesis and metaphase I no fewer than 20 (or maximum of 50) cells were scored for any accession, and in the irregular materials an attempt was made to study 50 cells. At anaphase I and telophase I an attempt was made to analyze 50 cells and no fewer than 30 cells were used. For dyads and tetrads a minimum of 50 cells were analyzed. For pollen analysis a minimum of 500 cells were studied.

Several accessions were studied in two different seasons, some in three, and occasionally an accession was studied under greenhouse conditions as well as from the field. Since there was no obvious difference in chromosome behavior in these two environments, the data were combined.

Morphological studies.

Morphological data for most of the accessions were recorded in the field. Five plants were studied for each accession if the accession was uniform, otherwise five plants of each type were studied separately. For inflorescence characters five inflorescences were subjectively chosen in an attempt to represent the variation present in an accession. No attempt was made to find extremes, but large, small, and intermediate inflorescences were included in the sample.

Several accessions were studied in two different years, some in three, and occasionally an accession was studied from herbarium specimens as well as from the field. Since there was no obvious difference in the average values of the morphological characters studied under these different conditions, the data were combined (for details see Mehra et al., 1959).

In order to study the patterns of association of the morphological characters, the pictorialized scatter diagram method (Anderson, 1949, 1957) was used, and the morphological indices were prepared according to the hybrid index method (Anderson, 1936, 1949, 1957).

Hybridization between the Tropical and the Mediterranean type.

In order to understand the relationship between the Tropical and the Mediterranean type of the Dichanthium annulatum complex, controlled crosses (Table I) involving these taxa were attempted according to the technique outlined by Richardson (1958). F_1 hybrids were grown in 1957, and studied both morphologically and cytologically in the manner outlined for the accessions.

F_2 plants were raised from a cross involving D. annulatum X-98 X D. annulatum A-4390. Since this cross produced two hybrids one

tetraploid and the other hexaploid, the two F_2 populations were grown separately. Morphological data for these populations were recorded in the field in the same manner as for their parents. Preliminary cytological study was conducted in a few selected F_2 plants from the tetraploid population.

TABLE I

ARTIFICIAL AND NATURAL HYBRIDS BETWEEN THE TROPICAL AND MEDITERRANEAN TYPES OF THE D. annulatum COMPLEX

Hybrid Number	Female Parent Accession Number	Female Parent Location	Male Parent Accession Number	Male Parent Location	Somatic Chromosome Number
		Artificial Hybrids			
1. 56-X-22-1	3182	Israel	5296	Dharwar, India	40
2. 56-X-112-1	"	"	4393	Dehradun, India	40
3. 56-X-116-1	4099	Punjab, India	4830	Saudi Arabia	40
4. 56-X-116-2	"	"	"	"	40
5. 57-X-1171-1	X-98*		4390	Tunisia	60
6. 57-X-1172-1	"		"	"	40
		Natural Hybrids**			
7. 55-X-98-1-0.P.1	X-98*		Unknown		40
8. 55-X-98-1-0.P.2	"		"		40
9. 55-X-98-1-0.P.3	"		"		40
10. 55-X-98-1-0.P.5	"		"		40
11. 55-X-98-1-0.P.6	"		"		40
12. 55-X-98-1-0.P.7	"		"		40

* X-98, a Tropical tetraploid, was obtained from a cross involving A3242 X A5411 (for details see Harlan et al., 1958)

** 55-X-98-1.0.P(1 to 3 and 5 to 7) were raised from open pollinated seeds produced on X-98.

RESULTS

Cytology

Cytogeography.

The chromosome number of ninty-seven accessions has been determined during the course of the present investigation and diploids* (8), tetraploids (82), and hexaploids (7) were found. Out of these accessions, eighteen were early introductions into the United States and the West Indies and their origins are no longer known. Seventy-nine accessions were from native collections, and these are plotted on a geographical map (Fig. 1). Also, on this map are ten sites that were taken from the literature (Oke, 1950; Gould, 1956; Sikka and Mehra, 1957; Celarier, 1959). The degree of ploidy of each accession is also indicated in Figure 1.

From this map it is seen that the tetraploids are found almost throughout the range of distribution of the complex, whereas both the diploids and the hexaploids have a more restricted distribution. The diploids have been found only in the Gangetic plain of India and in adjacent Burma, and the hexaploids may be restricted to southern Africa

*Although five has been proposed as the basic chromosome number for the tribe (Celarier, 1956, 1957), it is nevertheless felt that in some groups ten is the basic building material and should be considered as functional diploids (Celarier and Harlan, 1957; Celarier et al., 1958).

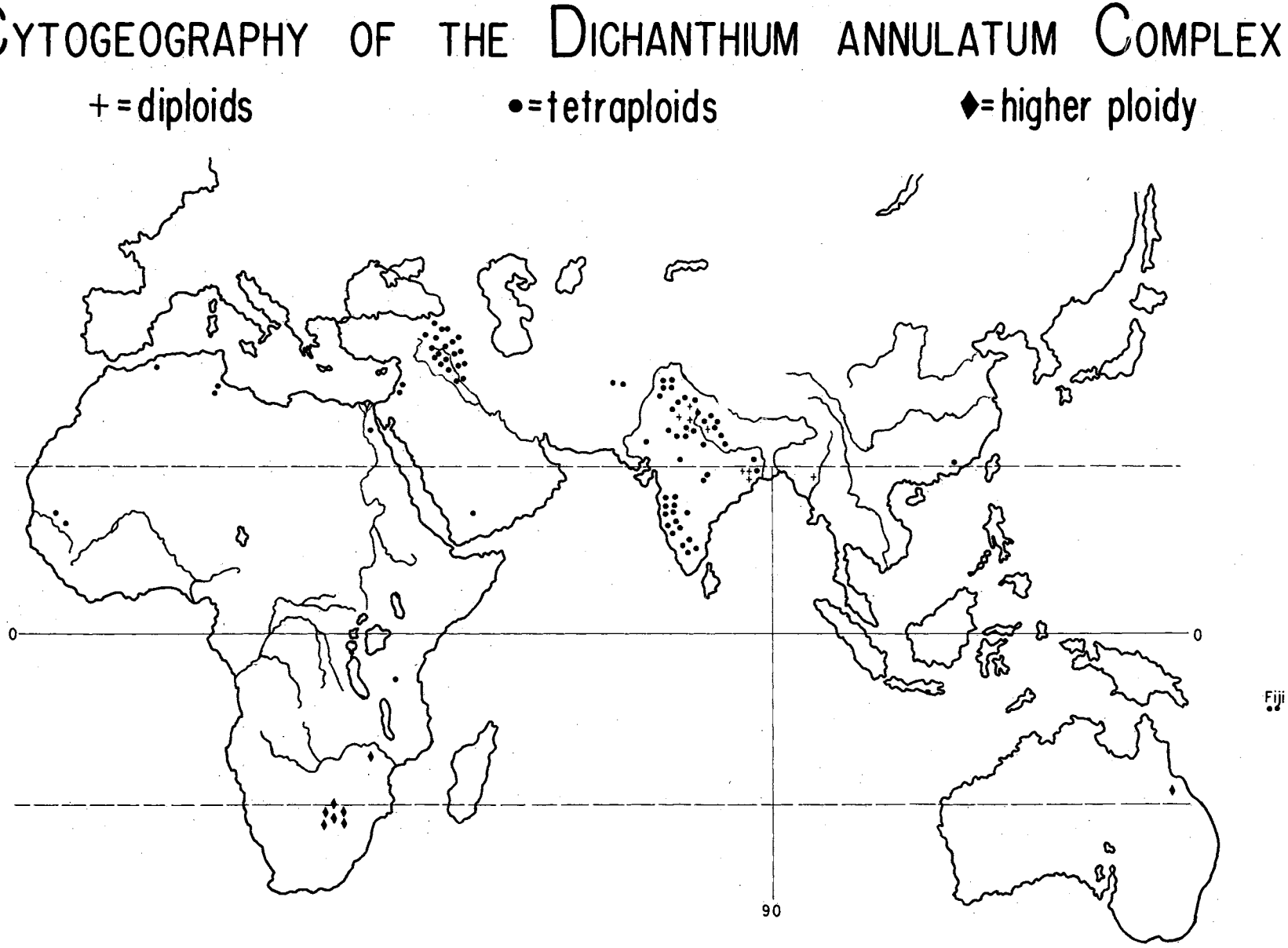


Fig. 1. Geographical distribution of ninety-three collections of the Dichanthium annulatum complex.

(the hexaploid found in Australia may very likely be a synthetic plant, for details see Discussion).

Diploids

Meiotic behavior.

Six out of the eight diploids studied were of Indian origin, the seventh was from Burma, and the eighth was an early introduction that had escaped and become naturalized in South Texas. This Texas accession (A-1526b) was a single plant found in an otherwise tetraploid population (A-1526a).

At diakinesis and metaphase I, ten bivalents were seen (Plate I; 1) and at anaphase I there was a normal 10:10 distribution of the chromosomes to the daughter cells (Plate I; 2). The second division was also observed to be completely regular.

Except for the occasional precocious disjunction of one bivalent in A-5396 from Belatal, India, all accessions were normal.

Tetraploids

Meiotic behavior.

Meiotic behavior was studied during microsporogenesis in eighty-two accessions (for details see Appendix A). All accessions showed some irregularities during the process of meiosis. The irregularities encountered were essentially of the same kind, but their frequencies were dissimilar in different accessions. These irregularities were the presence of univalents and multivalents at metaphase I; lagging chromosomes and bridges with fragments at anaphase I; laggards at anaphase II;

Legend for Plate I

Fig. 1-15. Meiosis in D. annulatum X 1180.

Fig. 1. Metaphase I in A-3242 from Calcutta, India, with ten bivalents.

Fig. 2. Anaphase I in A-3242 with 10:10 distribution of the chromosomes to the daughter cells.

Fig. 3. Metaphase I in A-2566 a South Texas introduction with 18 bivalents and one quadrivalent.

Fig. 4. Anaphase I in A-3182 from Israel with three lagging chromosomes.

Fig. 5. Anaphase I in A-2566 with two lagging chromosomes.

Fig. 6. Anaphase I in A-2568 from Coimbatore, India, showing a bridge and fragment.

Fig. 7. Telophase I in A-2566 with a bridge and fragment.

Fig. 8. Telophase II in A-1526a from South India, showing numerous univalents.

Fig. 10. Metaphase I in A-3789 from Giza, Egypt, with 14 bivalents and three quadrivalents.

Fig. 11. Metaphase I in A-3789 with 20 bivalents (two bivalents in the center are lying together).

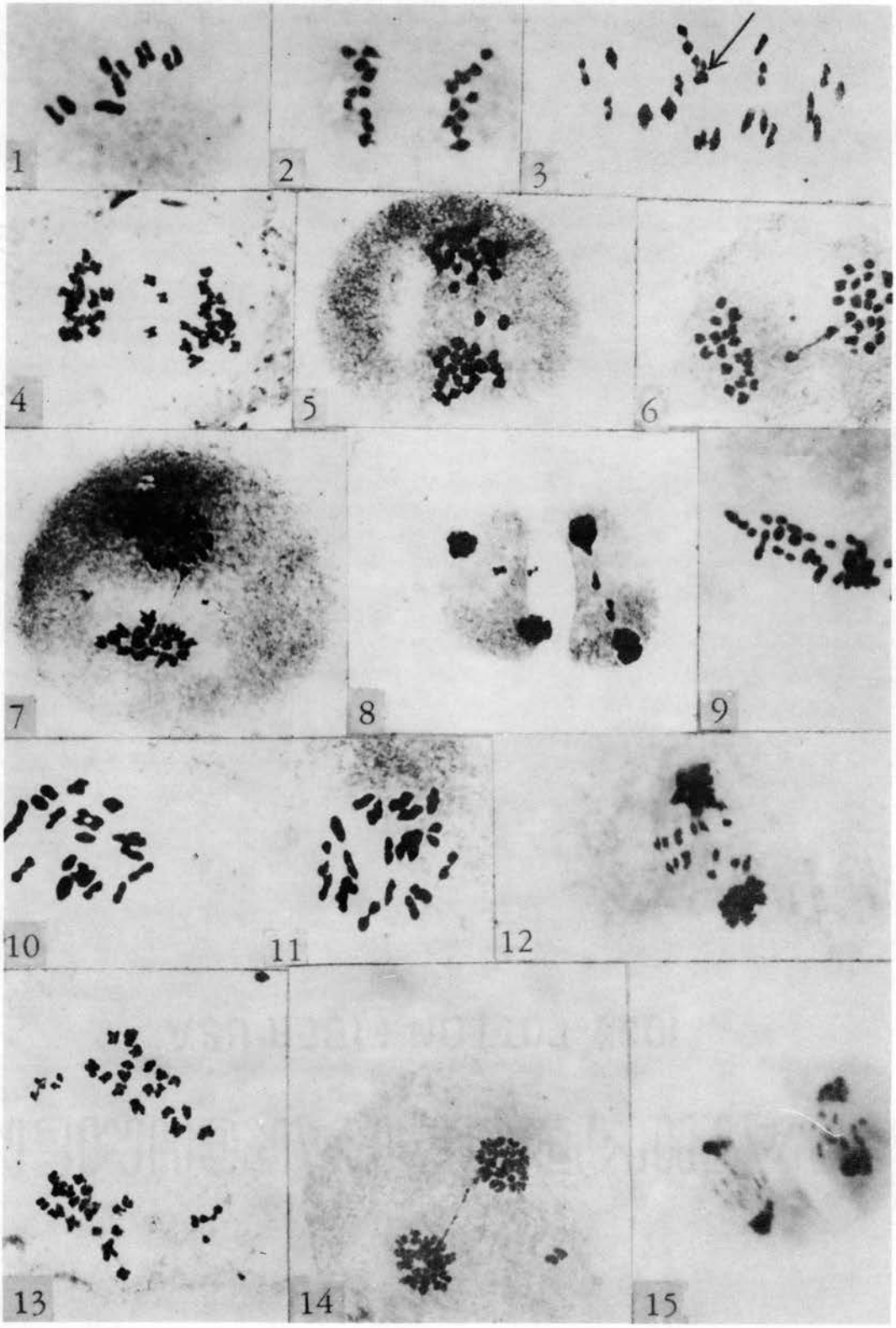
Fig. 12. Anaphase I in A-5397 from Mathura with numerous lagging chromosomes.

Fig. 13. Anaphase I in A-3789 from Egypt with dividing laggards and a lagging fragment.

Fig. 14. Telophase I in A-3789 showing a bridge but no obvious fragment and an excluded chromosome.

Fig. 15. Anaphase II in A-5397 from Mathura with many lagging chromosomes, both dividing and non-dividing.

PLATE I



and numerous micronuclei at both the dyad and tetrad spore stages (Plate I; 3-15).

Patterns of chromosome behavior.

A comparative study of the chromosome behavior during meiosis was conducted in forty accessions of the Dichanthium annulatum complex. Five cytological features of meiosis: the average frequencies of univalents, bivalents, trivalents, and quadrivalents (per cell) at metaphase I, and chromosome bridges at anaphase I were analyzed in three grades in all these accessions (Table II). The variation patterns (Fig. 2) of these cytological features were analysed by using the pictorialized scatter diagram method. Two additional cytological features the percentage of cells with lagging chromosomes (univalents) and the average number of lagging chromosomes at anaphase I were used as ordinate and abscissa of the pictorialized scatter diagram (Fig. 3). Cytological indices (Fig. 4) were prepared for all accessions by using the hybrid index method.

It appears from the Figure 3, that most of the accessions have different patterns of associations of the cytological features. In general, most of the accessions have low frequencies of trivalents at metaphase I and chromosome bridges at anaphase I, while others have none at all. Furthermore, for the most part, low frequency of bivalents seem to be associated with, firstly a high frequency of either univalents or quadrivalents (sometimes both) at metaphase I, and secondly with a high frequency of cells with number of lagging chromosomes at anaphase I.

Although different accessions have varying degrees of cytological

TABLE II

CLASS INTERVALS OF THE CYTOLOGICAL FEATURES

IN THE Dichanthium annulatum COMPLEX

Cytological Features	INDEX VALUES 0	1	2
Metaphase I			
Univalents	0.0-0.9	1.0-1.9	2.0 or more
Bivalents	18.5-19.5	18.1-18.4	18.0 or less
Trivalents	0.0-0.09	0.1-0.2	2.1 or more
Quadrivalents	0.0-0.50	0.51-0.79	0.80-1.2
Anaphase I			
Chromosome Bridges	0.0	0.01-0.09	0.10-0.15
Lagging Chromosomes (per cell)	0.0-0.3	0.31-0.70	0.71 or more
% Cells with Lagging Chromosomes	0-25	26-45	46-60

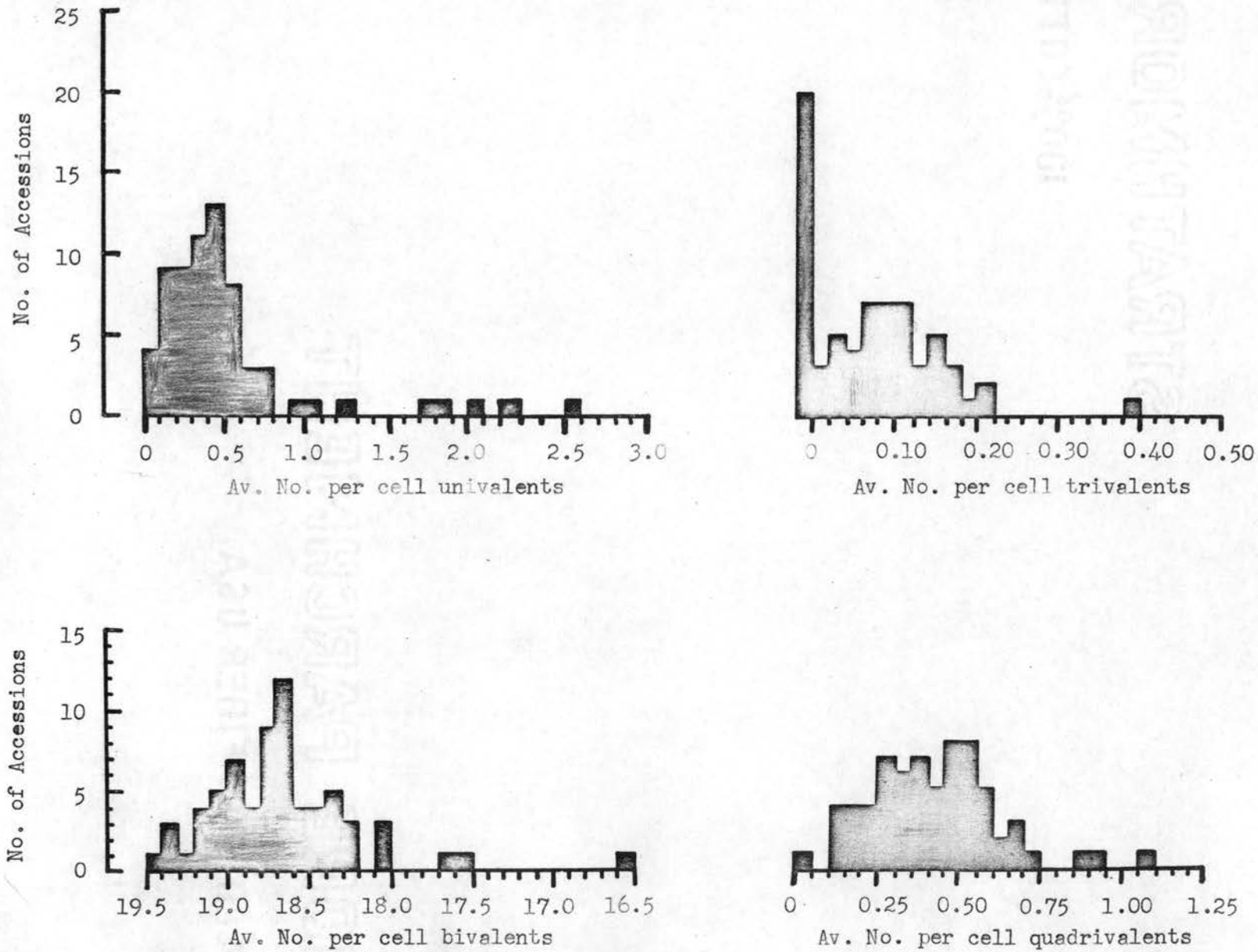


Fig. 2. Frequency histograms showing cytological variation in the D. annulatum complex.

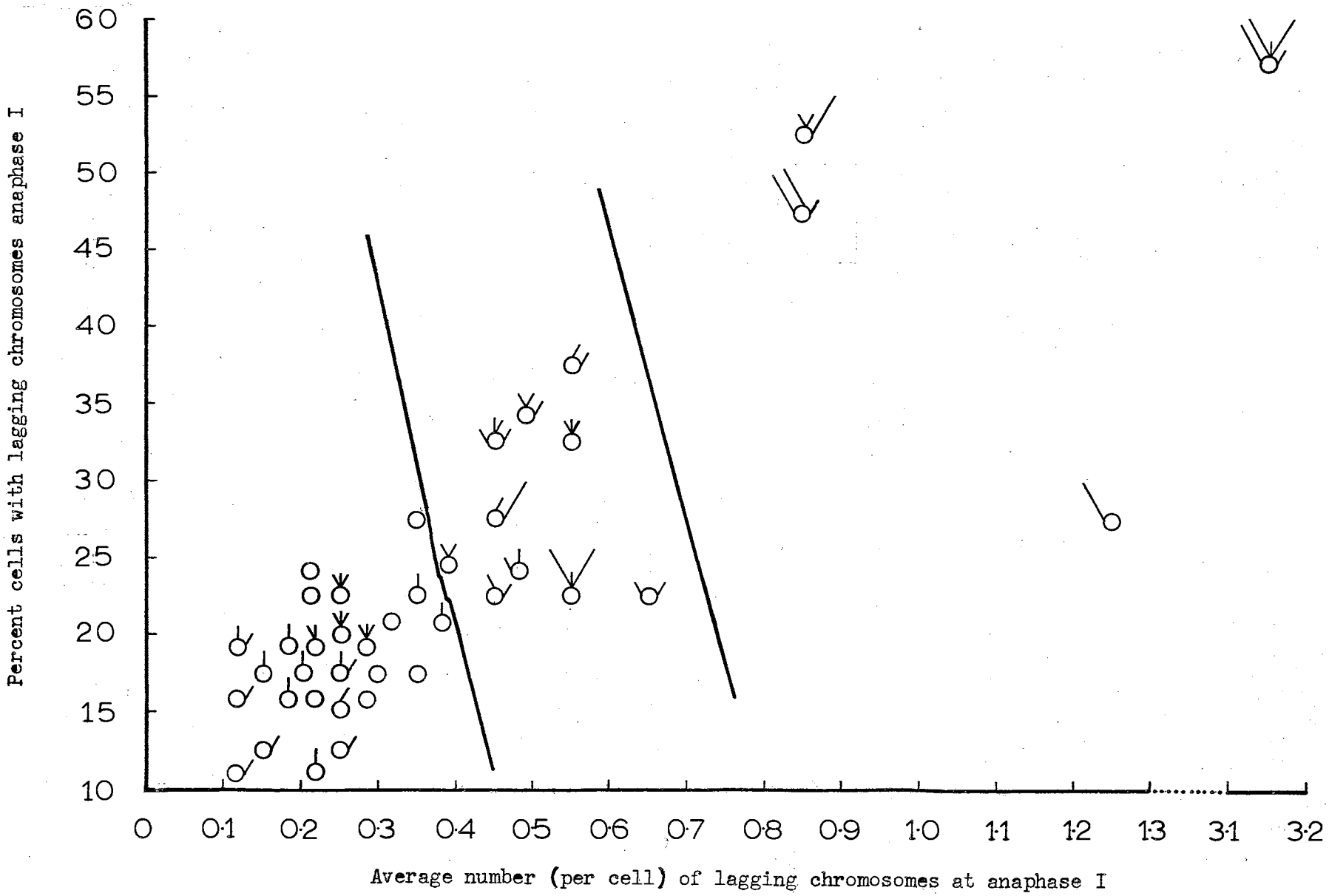


Fig. 3. Pictorialized scatter diagram showing the cytological variation in forty tetraploid accessions of the D. annulatum complex.

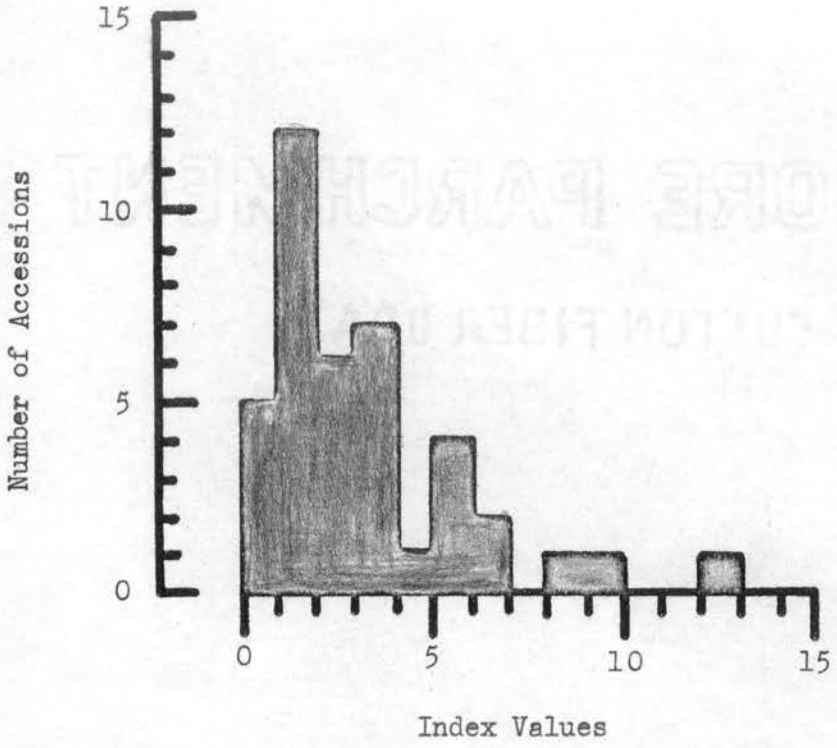


Fig. 4. Histogram illustrating the frequency distribution of cytological index values in forty tetraploid accessions of the D. annulatum complex.

irregularities during meiosis, the bulk of the material falls into three fairly recognizable groups which seem to be associated with the degree of chromosomal irregularities at anaphase I (Fig. 3). These three groups are i.e., slightly irregular, medium irregular and highly irregular.

(a) Slightly irregular.

This group located towards the left in Figure 3 is composed of such accessions which show an association of the following cytological features: low average frequencies (per cell) of univalents (0.0 to 0.9), trivalents (0.0 to 0.2), and quadrivalents (0.0 to 0.6) at metaphase I, low percentage of cells (10 to 26) with lagging chromosomes (0.0 to 0.4) at anaphase I, and a high average frequency (per cell) of bivalents (18.4 to 19.5) at metaphase I. The cytological index ranged from 0 to 3 for this group (Fig. 4).

(b) Medium irregular.

The second group occupies the central position in Figure 3. This group is composed of such accessions which have varying combinations of the cytological features studied. Lagging chromosomes (0.4 to 0.7 per cell) were observed in 20 to 60% of the cells at anaphase I. In general, the average (per cell) frequencies of univalents (0.0 to 1.8) and trivalents (0.0 to 0.2) were low, while those of bivalents (18.0 to 18.5) and quadrivalents (0.4 to 0.9) at metaphase I were medium. The cytological index ranged from 3 to 6 for this group (Fig. 4).

(c) Highly irregular.

Four accessions belong to this group, and the cytological index ranged from 8 to 12. Since these accessions showed different

patterns of associations of the cytological features studied, the data are presented separately as follows: (a) One (A-5326) of the four accessions, located near the lower corner on the right side, is characterized by the association of high frequencies (per cell) of univalents (2.0) and bivalents (18.60), low frequencies (per cell) of trivalents (0.06) and quadrivalents (0.16) at metaphase I, absence of chromosome bridges at anaphase I, and a high frequency of lagging chromosomes (1.24) in medium number (26%) of cells at anaphase I. It seems that chromosomal irregularities in this accession are because of the presence of a high frequency of univalents. The cytological index was observed to be 5 in this accession (A-5326). (b) The second accession (A-3182) is characterized by the association of medium frequencies (per cell) of bivalents (18.20) and quadrivalents (0.68), low frequency of univalents (0.88 per cell) and no trivalents at metaphase I. Also, lagging chromosomes (0.89 per cell) were observed in 53% of the cells at anaphase I. The cytological index was observed to be 8 in this accession. (c) The third (A-3789), located near the second accession (A-3182), is characterized by the association of a very high frequency (per cell) of univalents (2.20), low frequencies (per cell) of bivalents (18.00) and quadrivalents (0.45), and no trivalent at metaphase I, and high frequency of cells (50%) with high frequency of lagging chromosomes (0.87 per cell). The cytological index was observed to be 9 for this accession. (d) The fourth accession (A-5397) is located near the upper corner on the right side of Figure 3. This accession was extremely irregular, and its cytological index was 12. This accession is characterized by the presence of high frequencies

(per cell) of univalents (2.60), trivalents (0.16), and quadrivalents (0.98), very low frequency of bivalents (16.50 per cell) at metaphase I, and a very high frequency of cells (58%) with lagging chromosomes (3.16 per cell) at anaphase I.

Meiotic behavior.

Seven accessions have been found to be hexaploids. All these are of the South African type (D. papillosum Stapf). Five of these were from South Africa, one from Southern Rhodesia and the seventh was a mixture in an accession of Capillipedium parviflorum Stapf from Australia (Appendix A). Of these seven accessions only five were studied in detail.

The meiotic behavior was extremely irregular in all accessions, consisting principally of univalents and multivalents at diakinesis and metaphase I; bridges, fragments, and lagging chromosomes at anaphases (I and II), and micronuclei at the dyad and tetrad spore stages (Plate II; 16-23).

There was considerable variation in the number of univalents in individual cells of all accessions, but the averages showed some real differences between accessions. The Australian accession (A-4788b) had a very low frequency (0.40 per cell), while one of the South African accessions (A-2567) had considerably more (5.04). The maximum number (ten in a cell) of univalents were observed in A-2567.

Trivalents were observed in low frequencies in all accessions except the Southern Rhodesian accession (A-3716), while the highest frequency (0.52 per cell) was found in A-4080.

Quadrivalents were present in all accessions and their frequencies were similar to those observed in the tetraploids except for the

Legend for Plate II

Figs. 16-23.

Fig. 16. Metaphase I in A-3716 from Southern Rhodesia with univalents, bivalents and quadrivalents and possibly trivalents (at arrow).

Fig. 17. Metaphase I in A-4788b from Australia with hexavalent at arrow.

Fig. 18. Metaphase I in A-4788b with hexavalent at arrow.

Fig. 19. Anaphase I in A-3716 with lagging chromosomes and a bridge / fragment.

Fig. 20. Anaphase I in A-2567 from South Africa with seven lagging chromosomes.

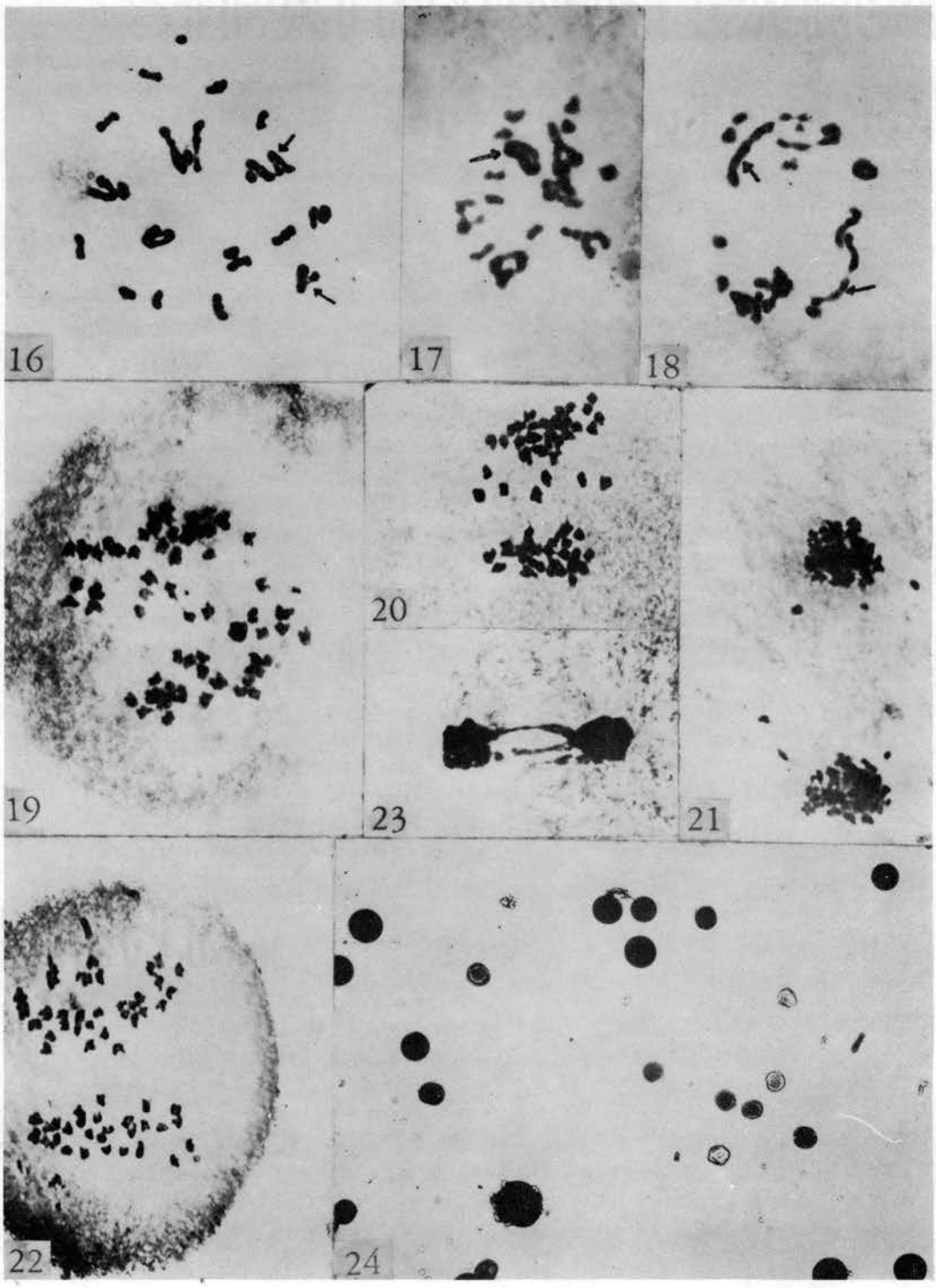
Fig. 21. Telophase I in A-3716 with several excluded chromosomes and chromatids.

Fig. 22. Anaphase I in A-3716 with no obvious disturbances except unequal distribution of the chromosomes to the daughter cells.

Fig. 23. Telophase I in A-2567 with chromosome bridges that appear to be due to stickiness.

Fig. 24. Pollen in A-3182 from Israel with both empty and full pollen grains; note the extreme variation in size of the apparently functional grains.

PLATE II



Australian entry (A-4788b), which had considerably more (1.65 per cell). No configurations greater than quadrivalents were observed in all accessions except the one from Australia, which had a rather high frequency of hexavalents (Plate II; 16-18). In a few cells as many as three hexavalents were seen.

At anaphase and telophase I chromosome bridges and fragments were found in rather low frequencies (Plate II; 23) in all accessions and although lagging chromosomes (Plate II; 19-21) were also observed in all accessions, their frequencies were dissimilar (0.46 to 1.92 per cell). Unequal distribution of chromosomes to daughter cells was also common.

In the second division the frequencies of lagging chromosomes were observed to be variable (0.18 to 0.78 per cell).

Micronuclei were observed at both the dyad and tetrad spore stages in all accessions. The pollen grains were observed to be variable in size (Plate II; 24).

Patterns of chromosome behavior.

Patterns of chromosome behavior were analyzed in these five hexaploid plants. Two rather distinct cytological groups were recognized as follows:

Group I.

This group is characterized, at metaphase I by having many univalents (as many as ten in some cells) with an average per cell frequency between 1.52 to 5.0, few quadrivalents (less than one per cell), and no greater configurations. Anaphase I and telophase I had approximately 50 per cent cells with lagging chromosomes (between one and two per cell). Included in this group are the four African accessions.

Group II.

This group includes only the Australian accession, and is characterized by few univalents (0.40 per cell), a considerable number of quadrivalents (1.65 per cell), and frequent hexavalents (0.60 per cell). At anaphase and telophase I eighty per cent of the cells were normal and the frequency of lagging chromosomes was only 0.60 per cell. Only nine per cent cells had lagging chromosomes in the second division.

External Morphology

A comparative morphological investigation was conducted on fifty-three accessions in the Dichanthium annulatum complex.

Seven morphological characters were analyzed in each accession. The average values of these characters are given in Appendix B. The variation of the average values of each character is presented in Figure 5. It is seen from Figure 5 that considerable variation occurs in most of the characters studied. The ranges of the mean values of these characters were compared among the diploid, tetraploid, and hexaploid accessions (Table III). It is seen from Table III that, although the ranges for five of these characters overlapped in the diploid, tetraploid, and hexaploid accessions, these different polyploid types could be distinguished from each other with fair reliability on the basis of the remaining two characters i.e., the average length of the primary axis and the average length of the longest raceme.

Five morphological characters were used on the metroglyphs, and the pictorialized scatter diagrams were prepared by using the number of racemes and the length of the longest raceme as ordinate and

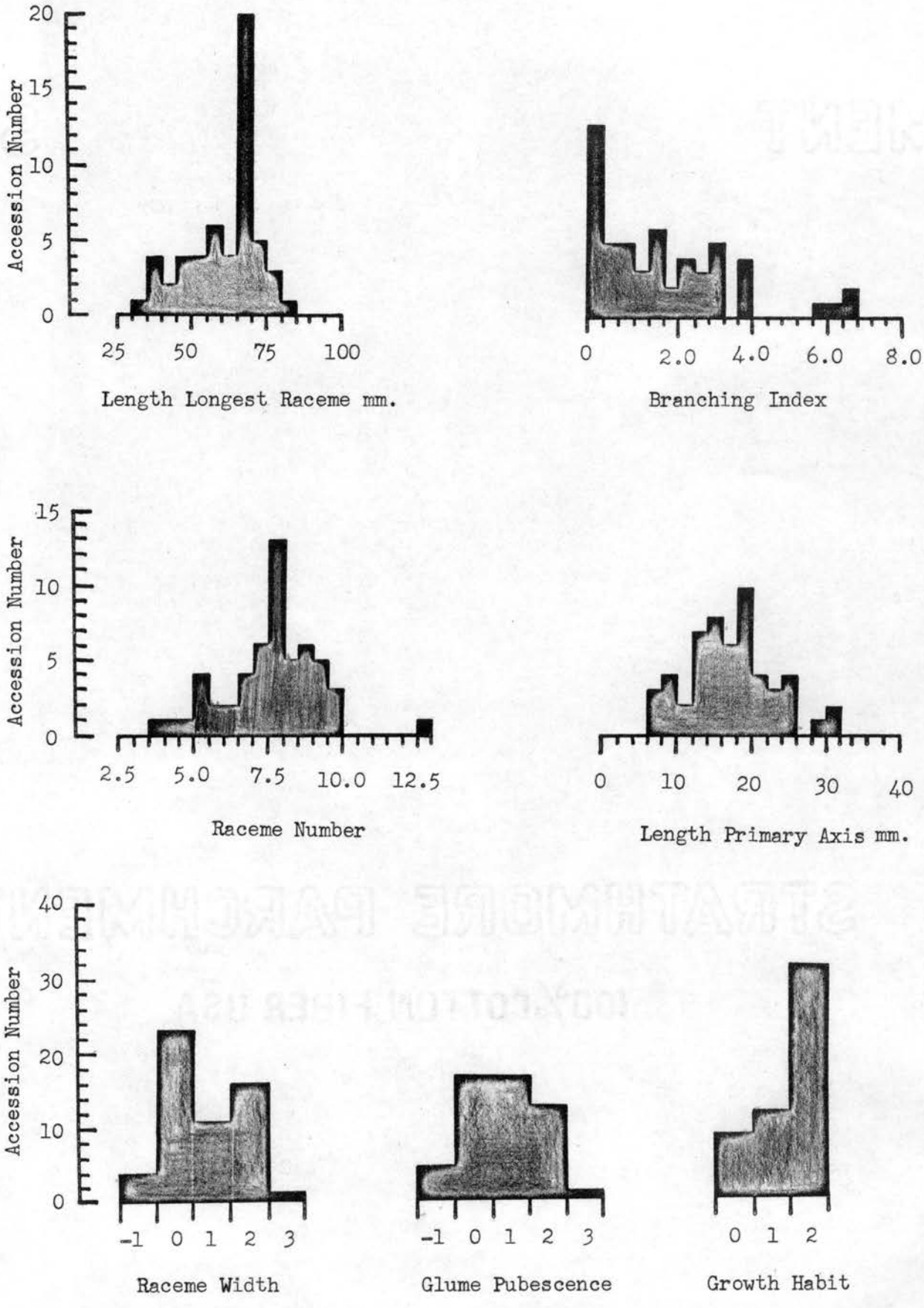


Fig. 5. Frequency Histograms Showing Morphological Variation in the D. annulatum Complex.

TABLE III

COMPARISON OF THE RANGE OF MORPHOLOGICAL VARIATION IN THE DIPLOID, TETRAPLOID, AND HEXAPLOID ACCESSIONS OF THE *D. annulatum* COMPLEX

	Diploids	Tetraploids	Hexaploids
1. Length Primary Axis (mm)	8.4-12.1	12.0-24.6 (32.8 in A-5397)	23.4-33.0 (19.0 in A4788(b))
2. Raceme Number	4.0-6.0	5.2-9.4 (12.6 in A5397)	7.0-9.6
3. Inflorescence Branching Index	0.00-0.02	0.0-6.8	2.4-6.0 (0.70 in A4788(b))
4. Length Longest Raceme (mm)	30.2-40.2	47.6-70.0	71.8-84.0
5. Raceme Width	thick	thick, intermediate or thin	thick
6. Glume Pubescence	hairy	hairy, intermediate or glabrous	very hairy
7. Growth Habit	prostrate sometimes decumbent	prostrate, decumbent or erect	erect

abscissa respectively (Fig. 6). Each character was measured in five classes and was plotted separately on the scatter diagrams according to the manner outlined in Table IV.

It appears from Figure 6 that the bulk of the accessions fall into three well marked groups that are associated with the polyploid levels.

Diploids.

The first group consists of the diploid accessions. These plants are of the Tropical type, characterized by the presence of the prostrate or sometimes decumbent forms. These plants have short inflorescences bearing racemes which are without secondary branches, mostly thick, sometimes medium thick as in 3965 (b), but are shorter in length and fewer in number than most of the tetraploid accessions of the Tropical type. The first glumes of the sessile spikelets in these diploids are either highly pubescent like X-98 or medium pubescent, but are never glabrous.

Tetraploids.

The second, the tetraploid group, to which belongs the bulk of the accessions, occupies the central position in Figure 6. The morphological variation exhibits a suggestive pattern. On one side, adjacent to the diploids, are typical Tropical tetraploids. These plants are prostrate or decumbent, and have medium size inflorescences bearing racemes which are without secondary branches, mostly thick, but of medium length and number. The first glumes of the sessile spikelets are highly pubescent in most of these plants. On the other side are grouped a few distinct Mediterranean tetraploids which are generally erect plants possessing somewhat longer and more lax inflorescences with longer, and

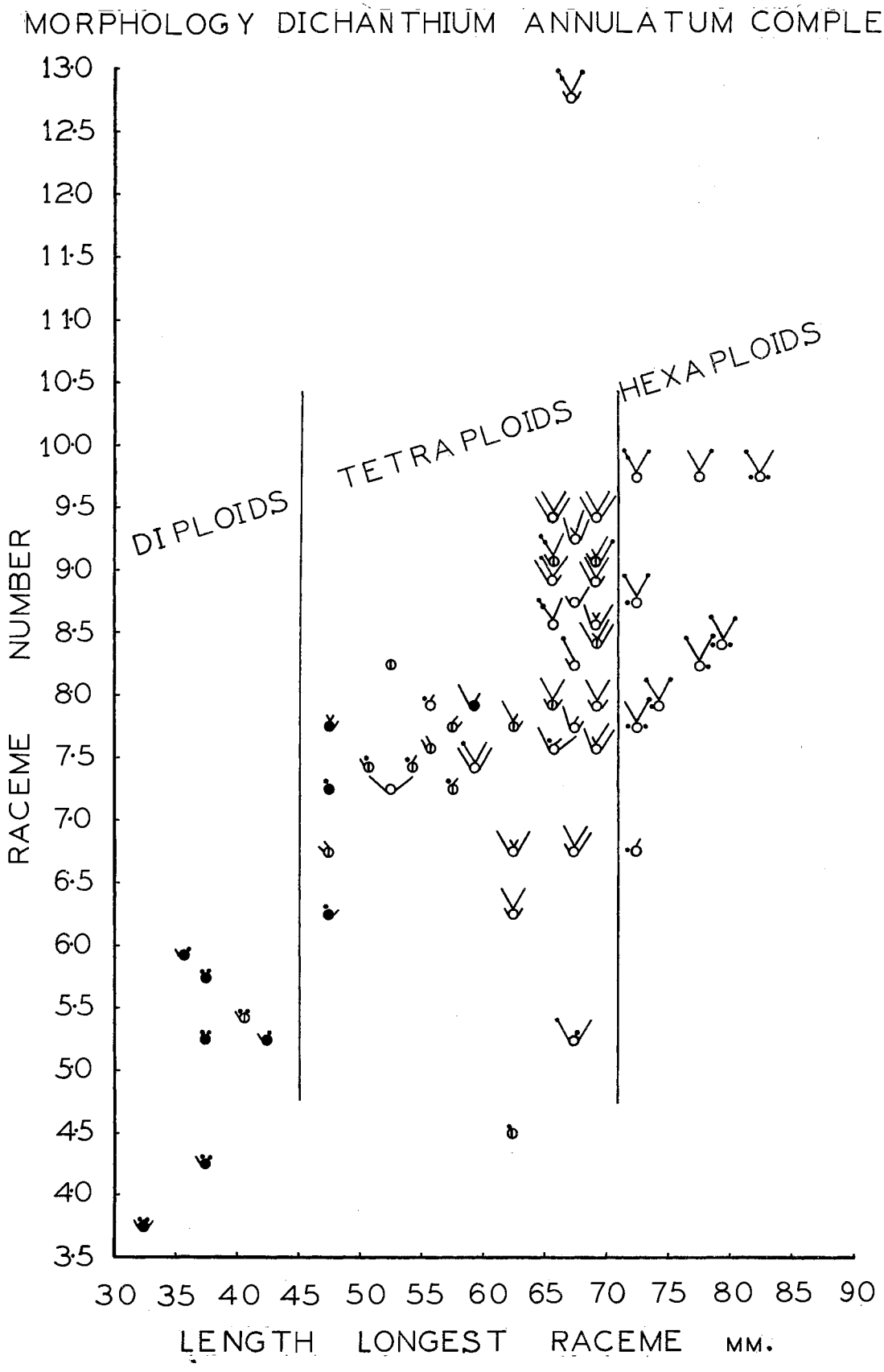


Fig. 6. Pictorialized scatter diagram illustrating the morphological variation in the Dichanthium annulatum complex.

TABLE IV

CLASS INTERVALS OF THE MORPHOLOGICAL CHARACTERS STUDIED IN THE D. annulatum COMPLEX

	Index Value						
	-1	0	1	2	3	4	5
Length Primary Axis (mm)	0-12	13-16	17-19	20-24	25-39	40-60	66 or more
Raceme Number	1.0-3.5	3.6-6.0	6.1-8.0	8.1-9.5	9.6-12.5	12.5-20.0	21 or more
Inflorescence Branching Index	0.0	0.2-0.9	1.0-1.7	1.8-3.1	3.2-6.0	6.1-6.9	7.0 or more
Length Longest Raceme (mm)	5-30	31-45	46-60	61-70	71 or more		
Raceme Width	very thick	thick	medium	thin	very thin		
Glume Pubescence	very hairy	hairy	medium	slightly hairy	glabrous		
Growth Habit		prostrate	decumbent	erect			

more slender racemes bearing more secondary branches than those of the Tropical type. Besides these two distinct types there are present some morphologically variant types which possess most of the characters of one type and one or two characters of the other type. Fairly decumbent types with thick racemes and highly pubescent glumes on the sessile spikelets are recognized among the Mediterranean types, and also Tropical types are recognized possessing certain features (erect habit, slightly hairy glumes on sessile spikelets, and medium thick racemes) of the Mediterranean type.

At a low central position in Figure 6 an accession which represents the Senegal type from French West Africa can be recognized. This type has most of the characteristics of the Mediterranean type, but differs from it because of the presence of almost glabrous glumes on the sessile spikelets. This type differs from the typical Mediterranean type in having shorter inflorescences with fewer and more slender racemes, and no secondary branching.

A group of accessions, located in the upper center of Figure 6, seem to be separable into two distinct types. One of these types is composed of erect plants which have somewhat longer and more lax inflorescences than those of the Tropical type. These plants have longer racemes bearing more secondary branches than those of the Tropical type. These plants resemble the typical Tropical type, because of the presence of medium thick racemes and pubescent glumes on the sessile spikelets. The other type within this group resembles the Mediterranean type, but it has somewhat longer inflorescences possessing racemes which are more slender, longer in length, and with more secondary branches than those of the typical Mediterranean types.

One odd accession, located in the upper center of Figure 6, occupies an isolated position. This accession is erect growing, and has longer and more lax inflorescences than those of the other tetraploid types described above. The inflorescences in this accession (A-5397) have many racemes (average 12.6 per inflorescence) of medium thickness, bearing more secondary branches than those of the other tetraploid types, but possessing medium pubescent glumes on the sessile spikelets.

The presence of such morphological characters as erect habit, an increase in the length of the primary axis, in the secondary branching, number and length of the racemes, and in the pubescence on the first glumes of the sessile spikelets, in several accessions of the tetraploid types seems to suggest possible introgression with certain species of the genus Bothriochloa (Fig. 7).

The third group comprises erect growing South African types which are all hexaploids. These plants are characterized by their inflorescences having a much longer primary axis with longer, but thicker and more branched racemes than those of the tetraploid (Tropical, Mediterranean, and Senegal types) types. The glumes on the sessile spikelets in these plants are more pubescent than those of the Tropical type.

A morphological index was prepared for the seven characters studied in fifty-three accessions of the Dichanthium annulatum complex, and the data are presented in Figure 8. It is seen in Figure 8 that the morphological indices ranged from -2 to 0 in the diploid Tropical types, 1 to 4 for the typical tetraploid Tropical types, 11 to 13 for the typical tetraploid Mediterranean types, and 11 to 14 for the typical South African types. The plants, possessing index values other

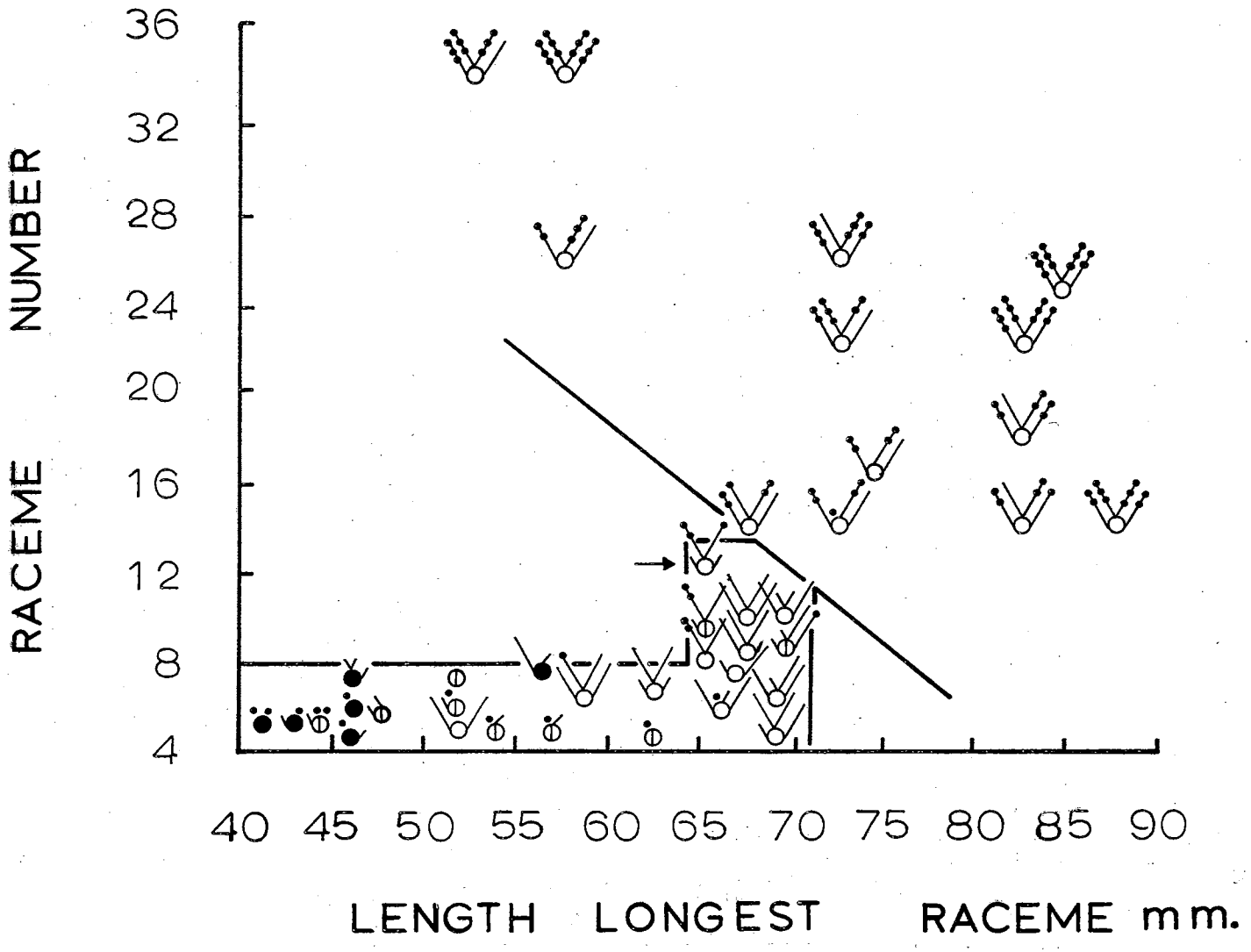


Fig. 7. Pictorialized scatter diagram showing introgression between the D. annulatum complex and the B. intermedia complex.

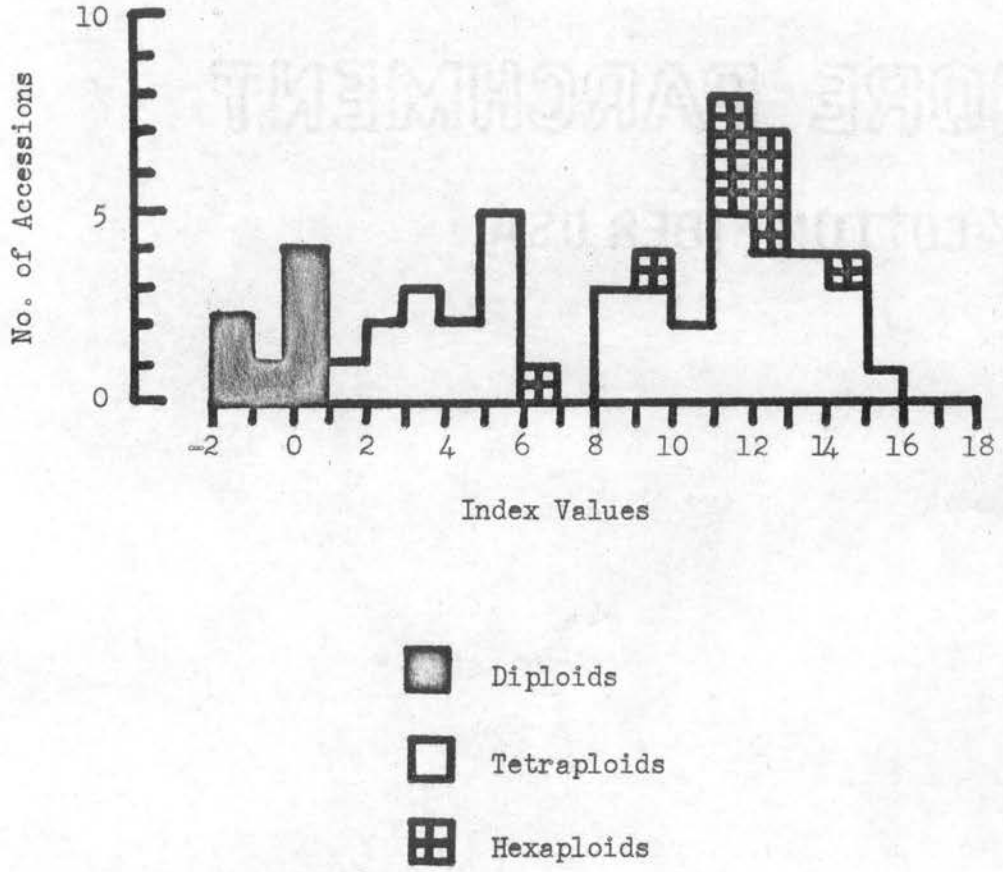


Fig. 8. Histogram illustrating the frequency distribution of morphological index values in fifty-three accessions of the D. annulatum complex.

than those of the typical types, seem to be the product of introgression between the Tropical and Mediterranean types or between these two types and certain species of the genus Bothriochloa.

Cytogeography and Morphological Variation

A cytological and morphological survey was conducted in forty-four accessions of the Dichanthium annulatum complex, and the data are plotted on a geographical map (Fig. 9). The degree of ploidy, meiotic behavior, and the morphological appearance of each accession is indicated in Figure 9.

From the map (Fig. 9) it is seen that all the diploids are of the Tropical type, and seem to be restricted to the Gangetic plain of northern India and adjacent Burma. All plants show regular meiotic behavior.

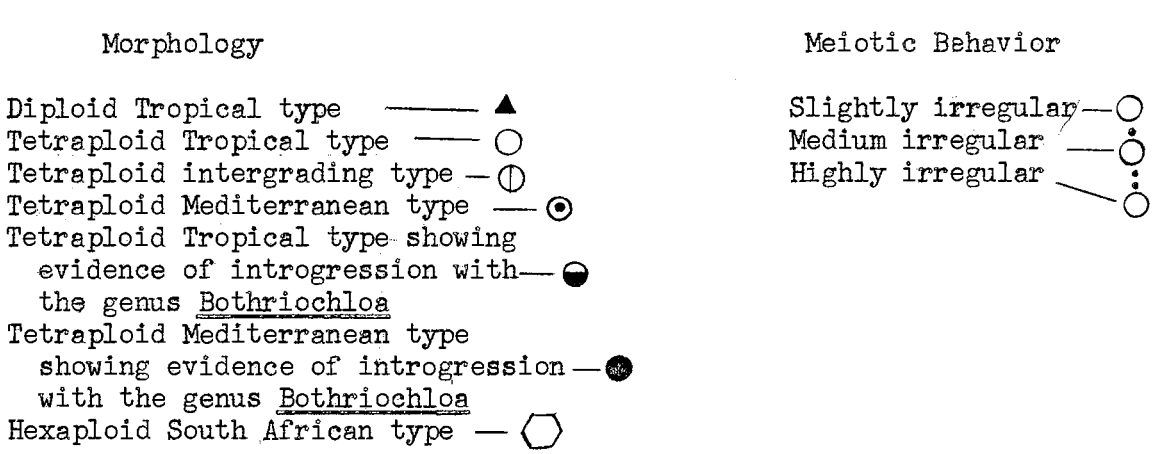
The hexaploids are all of the South African type (D. papillosum Stapf), restricted perhaps to southern Africa. All are extremely irregular in meiotic behavior.

The tetraploids, distributed almost throughout the range of the geographical distribution of the complex, show at least five recognizable types, as follows:

1. Tropical type
2. Tropical type, showing evidence of introgression with Bothriochloa
3. Intergrading types between the Tropical and the Mediterranean type
4. Mediterranean type
5. Mediterranean type, showing evidence of introgression from Bothriochloa

Legend for Figure 9

Figure 9. Cytogeography and morphological variation in the *D. annulatum* complex.



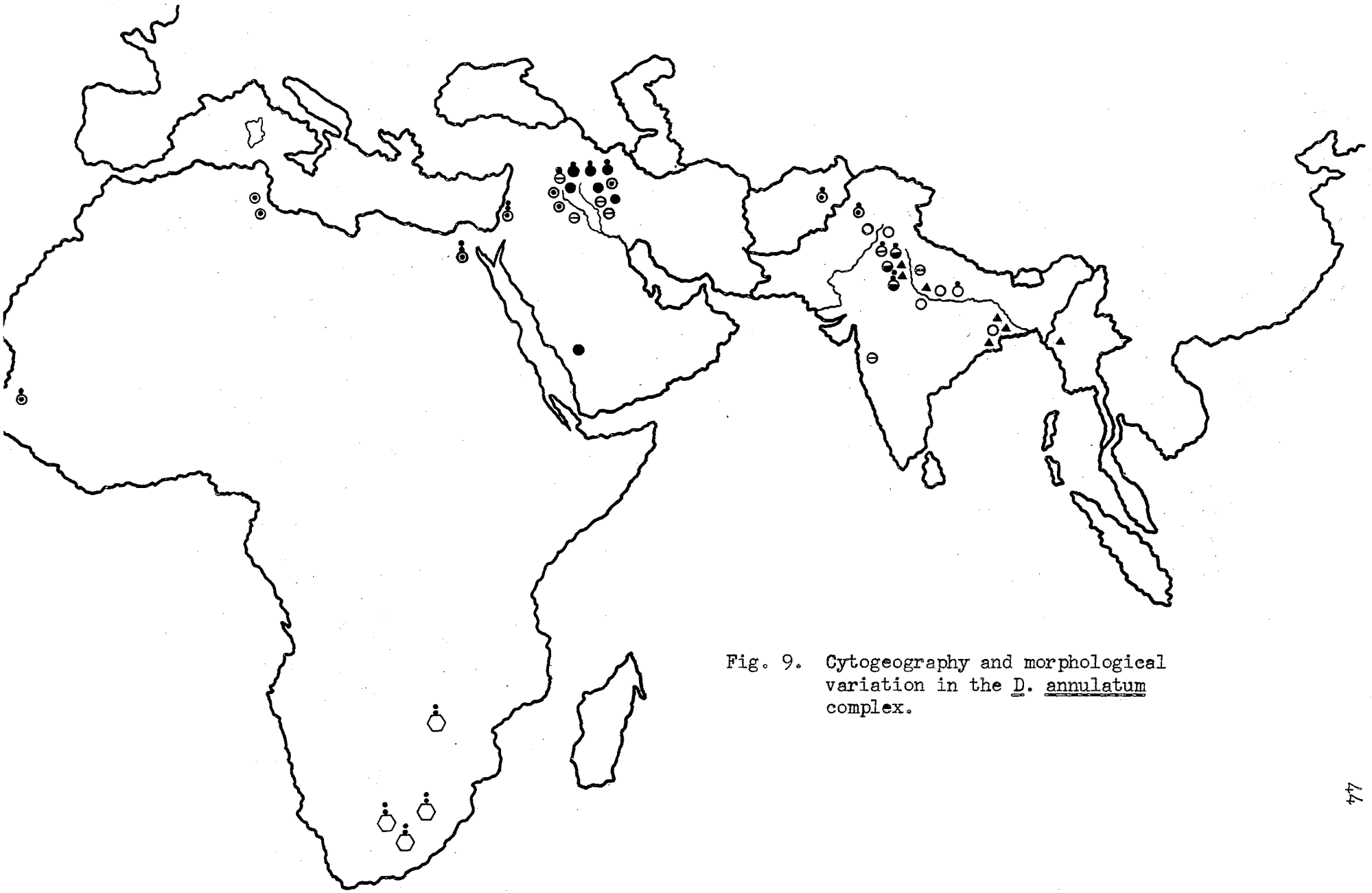


Fig. 9. Cytogeography and morphological variation in the D. annulatum complex.

The Tropical type, distributed in India and West Pakistan, shows medium or slightly irregular meiotic behavior. Also, in India and West Pakistan there are types which seem to suggest evidence of introgression from the Mediterranean type and from Bothriochloa intermedia O. Kuntze, and are medium or extremely irregular during meiosis.

The Mediterranean type seems to be distributed from French West Africa through Tunisia, Egypt, Iraq, Saudi Arabia to Afghanistan, and northwestern West Pakistan. These plants are medium irregular during meiosis. Certain types from Iraq show evidence of introgression from the Tropical type and from the genus Bothriochloa. These types, showing introgression with the genus Bothriochloa, are more irregular during meiosis than typical types. In general, the tetraploids show both cytological and morphological differentiation characteristic of polyploids and closely related species hybrids.

Relationships of the Tropical and Mediterranean Types

F_1 Hybrids

A preliminary cytological and morphological study was conducted in twelve hybrids involving the Tropical and Mediterranean tetraploid types. Of these twelve hybrids one is a hexaploid and the rest are tetraploids. The hexaploid hybrid looks morphologically like Dichanthium papillosum, and it shall be discussed separately. The details on the tetraploid hybrids are given, as follows:

The tetraploid hybrids were intermediate between the Tropical and Mediterranean types with respect to several morphological and cytological features (Appendix A, Table I; Appendix B). All these

hybrids were slightly irregular in meiosis. Cytological irregularities in these hybrids were of the same kind as those of their respective parents, but were in low frequencies. At metaphase I univalents, bivalents, trivalents, and quadrivalents were observed in all these hybrids. Successive stages of meiosis were observed to show lagging chromosomes at anaphase I and II and micronuclei at both the dyad and tetrad spore stages. In general, these tetraploid F_1 hybrids were either slightly irregular or medium irregular, but were never extremely irregular.

F_2 Population

Out of the eleven F_1 hybrids only one was selfed, involving X-98 (female) X A-4390 (male), and 144 F_2 plants were obtained. Detailed morphological notes were recorded for all of these, and cytological studies were conducted on 13 plants.

Cytology.

The chromosome numbers were determined for thirteen plants, belonging to this population (Appendix A, Table I). Of these thirteen plants six have a somatic chromosome number $2n = 20$, and seem to be polyhaploids. The rest of the seven plants are tetraploids. Meiotic behavior was studied in all these plants, and the results were as follows:

Polyhaploids.

At diakinesis and metaphase I ten bivalents were observed, and at anaphase I there was a normal 10:10 distribution of the chromosomes to the daughter cells. The second division was also observed to be regular.

In general, except for occasional precocious disjunction of one bivalent in a few cells, all polyhaploids seem to be fairly normal (for details see Appendix A; Table I).

Tetraploids.

A preliminary cytological study was conducted on seven tetraploid plants. The meiotic behavior seemed to be intermediate between the parents. The cytological irregularities were like the parents and F_1 hybrids. In general, these plants were either medium irregular or slightly irregular during meiosis, but never extremely irregular (at least in the F_2 plants, studied to date (for details see Appendix A, Table I).

Morphology.

The morphology of one hundred and forty-four F_2 plants was studied in detail. Seven morphological characters were analyzed and the data were recorded in five classes (Table IV). The range of variation of the average values of these characters is presented in Figure 10, and the data are compared with those obtained from the parents and the F_1 hybrid (Table V).

It is seen from Figure 10 that considerable variation occurs in all of the characters studied. The average values for most of these characters ranged from very low values (lower in comparison to the lower parent) to very high values (higher than those of the higher parent).

Patterns of morphological variation were analyzed in these F_2 plants by using the pictorialized scatter diagram method. The data are presented in Figure 11A. Seven morphological characters used in this study are the same as those used for the analysis of the morphological variation of the accessions (for details see Table IV). Also, in the

Lengend for Figure 10

Frequency Histograms Showing Morphological Variation in the F_2 Plants Obtained by Selfing the 4n F_1 Hybrid between the Tropical and the Mediterranean Type

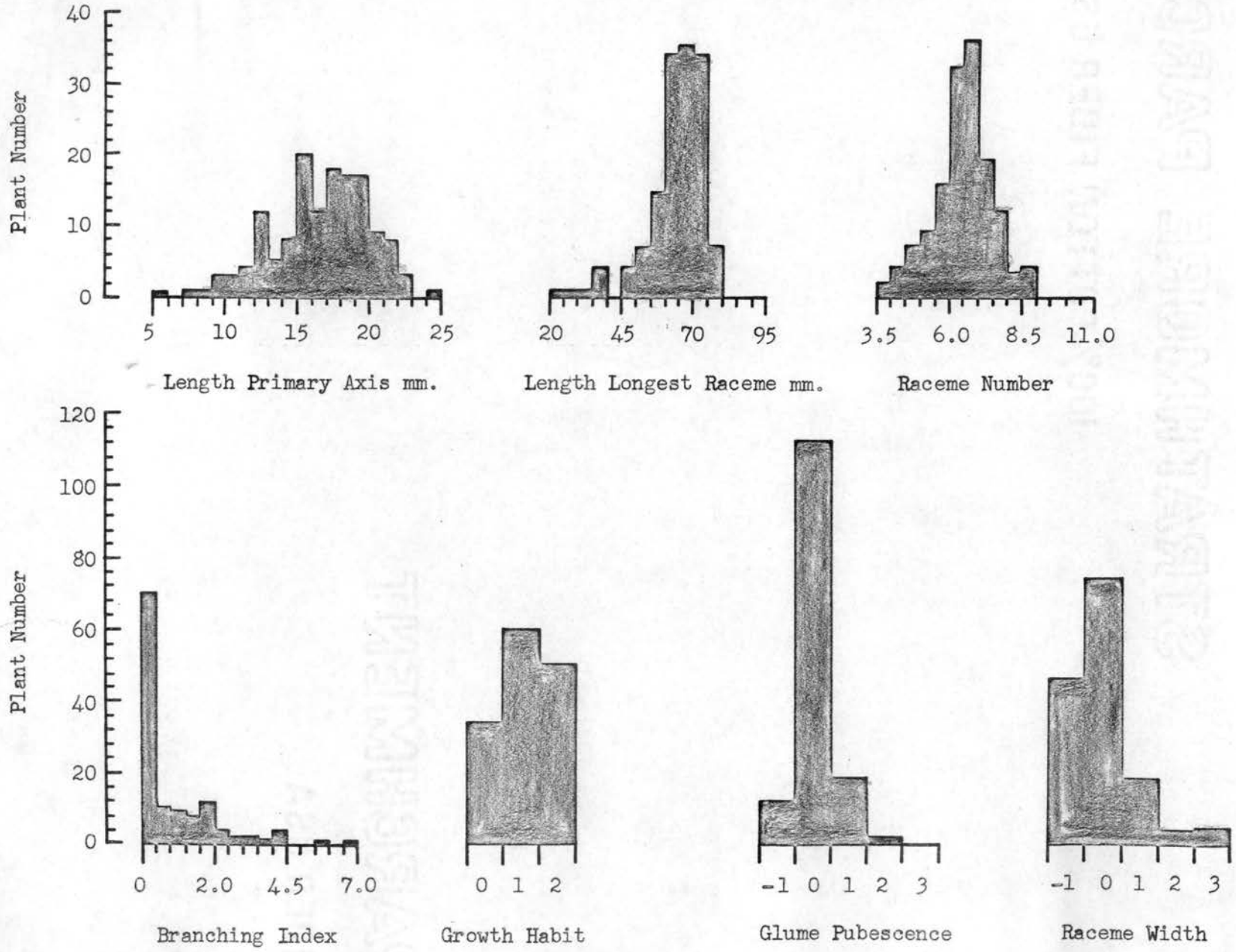

Plant Number
40
30
20
10
0
5 10 15 20 25
Length Primary Axis mm.
20 45 70 95
Length Longest Raceme mm.
3.5 6.0 8.5 11.0
Raceme Number
Plant Number
120
100
80
60
40
20
0
0 2.0 4.5 7.0
Branching Index
0 1 2
Growth Habit
-1 0 1 2 3
Glume Pubescence
-1 0 1 2 3
Raceme Width

Fig. 10.

TABLE V

COMPARISON OF THE MORPHOLOGICAL CHARACTERS IN THE PARENTS,

F_1 HYBRIDS, AND F_2 POPULATIONS OF

THE *D. annulatum* COMPLEX

Accession or Hybrid Number	Material	Length Primary Axis (mm)	Raceme Number	Inflorescence Branching Index	Length Longest Raceme	Raceme Width	Glume Pubescence	Growth Habit
X-98	Tropical Type	15.0	4.8	0.0	64.8	≠	≠	D*
A-4390	Mediterranean Type	20.4	6.6	2.0	69.6	≠≠	≠≠	E
57-X-1171-1	X-98 X 4390, 2n = 60 (South African Type)	25.2	8.2	2.0	89.4	≠	-	E
57-X-1172-1	X-98 X 4390, 2n = 40	19.6	7.2	0.4	70.6	≠	≠≠	E
57-X-1171-1-≠	Selfed Plants from 57-X-1171-1	3.0-25.0**	3.5-12.2	0.0-9.0	20.0-90.0	-,≠,≠≠	- - ≠≠≠≠	P,D,E
57-X-1172-1-≠	Selfed Plants from 57-X-1172-1	5.0-24.0	3.5-8.8	0.0-7.0	20.0-78.8	- - ≠≠≠≠	- - ≠≠≠≠	P,D,E

* Decumbent (D), Prostrate (P) and Erect (E).

** The data for the F_2 population represent the ranges of the mean values of these characters.

Legend for Figure 11.

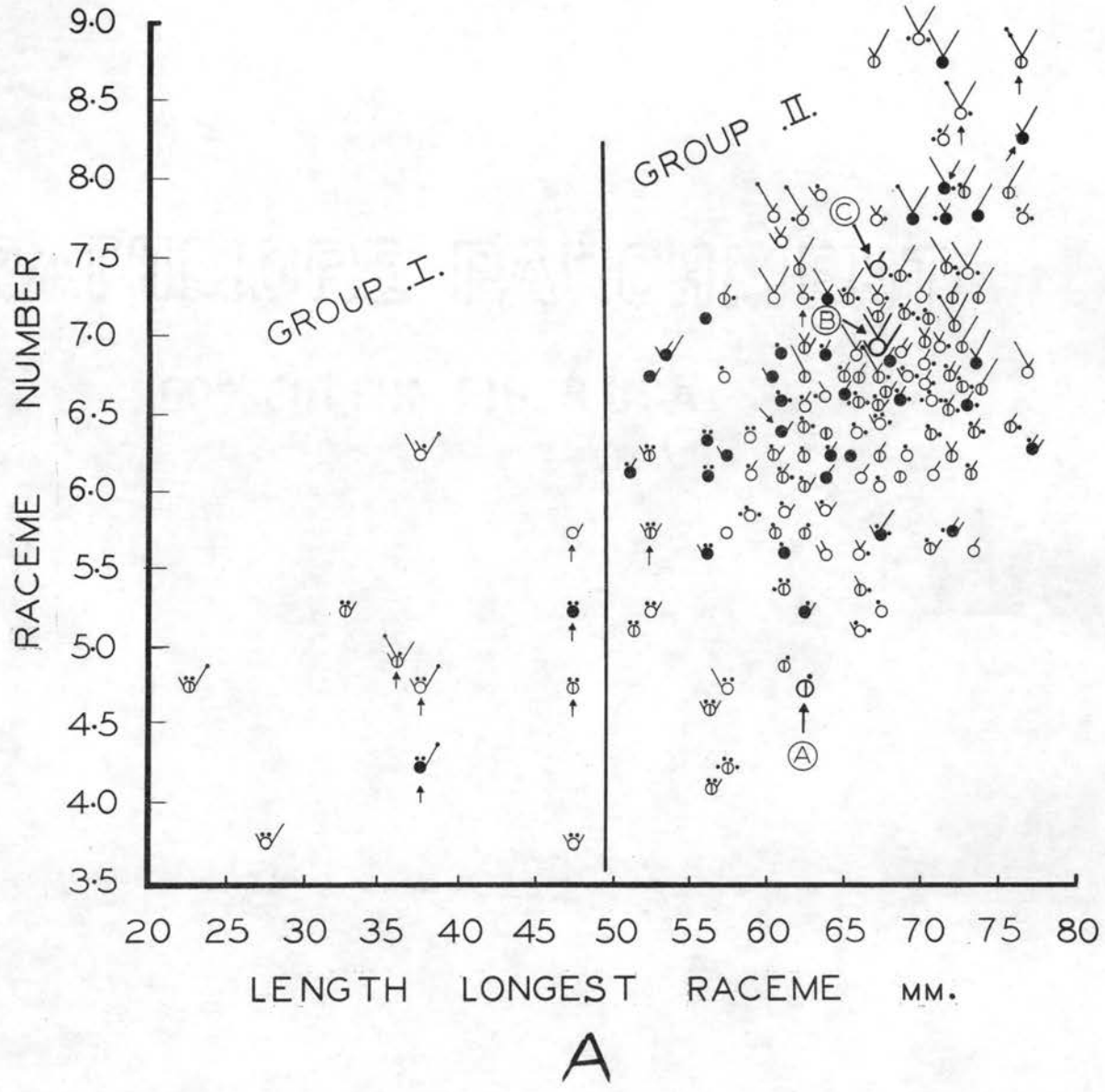
Morphological analysis of the F2 population, obtained by selfing the 4n F1 hybrid between the Tropical and Mediterranean types of the Dichanthium annulatum complex.

A Pictorialized scatter diagram.

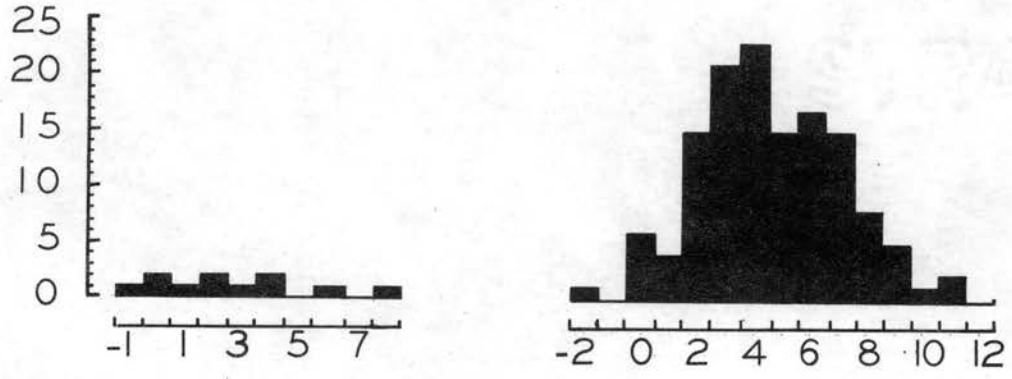
The plants shown near the arrows are polyhaploids (Group I), and tetraploids (Group II) respectively.

Ⓐ = x-98, Ⓑ = A-4390, and Ⓒ = F_1 hybrid (x-98 x A-4390).

B and C Frequency histograms of the morphological indices for the plants in Group I and Group II of the scatter diagram respectively.



A



B C

Figure 11.

Figure 11A the metroglyphs are plotted for the parents and the F_1 hybrid.

Although considerable variation exists in the patterns of association of these morphological characters, the population seems to fall into two well marked groups, as follows:

Group I.

This group consists of eleven dwarf plants. All these plants have short inflorescences, bearing few racemes (3.5 to 6.5 per inflorescence) which are also short in length (20 to 50 mm). Chromosome numbers were determined for six of these plants. All these were polyhaploids ($2n = 20$), and it is likely that the rest are also polyhaploids. Character association analysis revealed the presence of three distinct types within this group, as follows:

Type I.

Two plants, located near the separation line, belong to this type, and are polyhaploids. These two plants show the association of the following morphological characters: Prostrate or decumbent growth, short primary axis, few racemes, little or no secondary branching of the racemes, short racemes, thick racemes, and highly pubescent glumes of the sessile spikelets. The morphological indices of these plants are either -1 or 0 (Fig. 11B). These plants look like the Tropical type accessions, but are usually weaker in comparison to the naturally occurring diploid Tropical type plants.

Type II.

One plant belongs to this type. This plant is shown higher up on the chart, but in the center of the Group I.

Character association analysis revealed the presence of the following characters: erect habit, short primary axis, medium number of short racemes with secondary branches, thin racemes, and almost glabrous first glumes of the sessile spikelets. This plant resembles the Mediterranean type with respect to four morphological characters i.e., erect habit, thin racemes (thinner than the typical Mediterranean type) bearing secondary branches, and almost glabrous first glumes of the sessile spikelets. Although no diploid Mediterranean types are reported in the literature, it seems likely that this plant would resemble a diploid Mediterranean type. The morphological index is eight for this plant (Fig. 11B).

Type III.

This type is composed of eight plants. These plants show varying combinations of the characteristics of the Tropical and Mediterranean types. Character association analysis revealed the presence of the following features: prostrate, decumbent or erect growth, short primary axis, few racemes, with or without secondary branches, thin or medium thick, but short racemes, and medium or highly pubescent first glumes of the sessile spikelets. The morphological indices range from 1 to 6 (Fig. 11B). Three out of these eight plants are polyhaploids, and it seems likely that the same chromosome number may also be present in the rest of the plants.

Group II.

One hundred and thirty-three plants belong to this group. It is seen from Figure 11A that considerable morphological variation occurs in these plants. Morphological analysis shows that most of these F_2 plants have thick racemes and pubescent glumes on the sessile spikelets. Morphological survey shows that different plants represent varying degrees of recombination of the characteristics of each parent. Most of the possible recombinant types are seen in Figure 11A.

In the lower one third of Figure 11A there are a number of plants which have the same class intervals for most of the characters as those of the Tropical type, but possess one or more characters of the Mediterranean type. Similarly, there are a number of plants in the population which have the same class intervals for most of the characters as those of the Mediterranean type, but possess one or more characters of the Tropical type. In the center of Figure 11A there are a number of plants in the population which possess varying recombinations of different characters (or of different class intervals of these characters) of each parent. In the upper part of Figure 11A there are a number of plants which have an association of the following morphological characters: long primary axis, many racemes which are longer, and have more secondary branches than those of the Mediterranean type (A-4390), and thick racemes, the glumes of which possess more hair than those of the Tropical type. These plants are all tetraploids, and a few of them resemble D. papillosum Stapf.

The morphological indices of these tetraploid plants range from -2 to 11, but most of them had index values between those of the parents (Fig. 11C).

Origin of Dichanthium papillosum Stapf

F_1 Hybrids

One of the hybrids involving the Tropical type and the Mediterranean type was hexaploid, and it resembled the South African type (D. papillosum Stapf) both cytologically and morphologically (Table V, for details see Appendix A and B). Nine accessions of the South African type used in the morphological study are obligate apomicts or at least very strongly apomictic, but this hybrid is sexual.

F_2 Population

The morphology of one hundred and twenty-five F_2 plants was studied in detail. Seven morphological characters were analyzed, and the data were recorded in five class intervals (Table IV). The range of variation of the average values of these characters is presented in Figure 12, and the data are compared with those obtained from the parents and the F_1 hybrid (Table V).

It is seen from Figure 12 that considerable variation occurs in all of the characters studied. The average values for most of the characters ranged from very low values (lower than the lower parent or hybrid) to very high values (higher than those of the higher parent or hybrid).

Patterns of morphological variation of the parents, F_1 hybrid, and F_2 population were analyzed by using the pictorialized scatter diagram

Legend for Figure 12

Frequency Histograms Showing Morphological Variation in the F_2 Plants Obtained by Selfing the 6n F_1 Hybrid between the Tropical and the Mediterranean Type

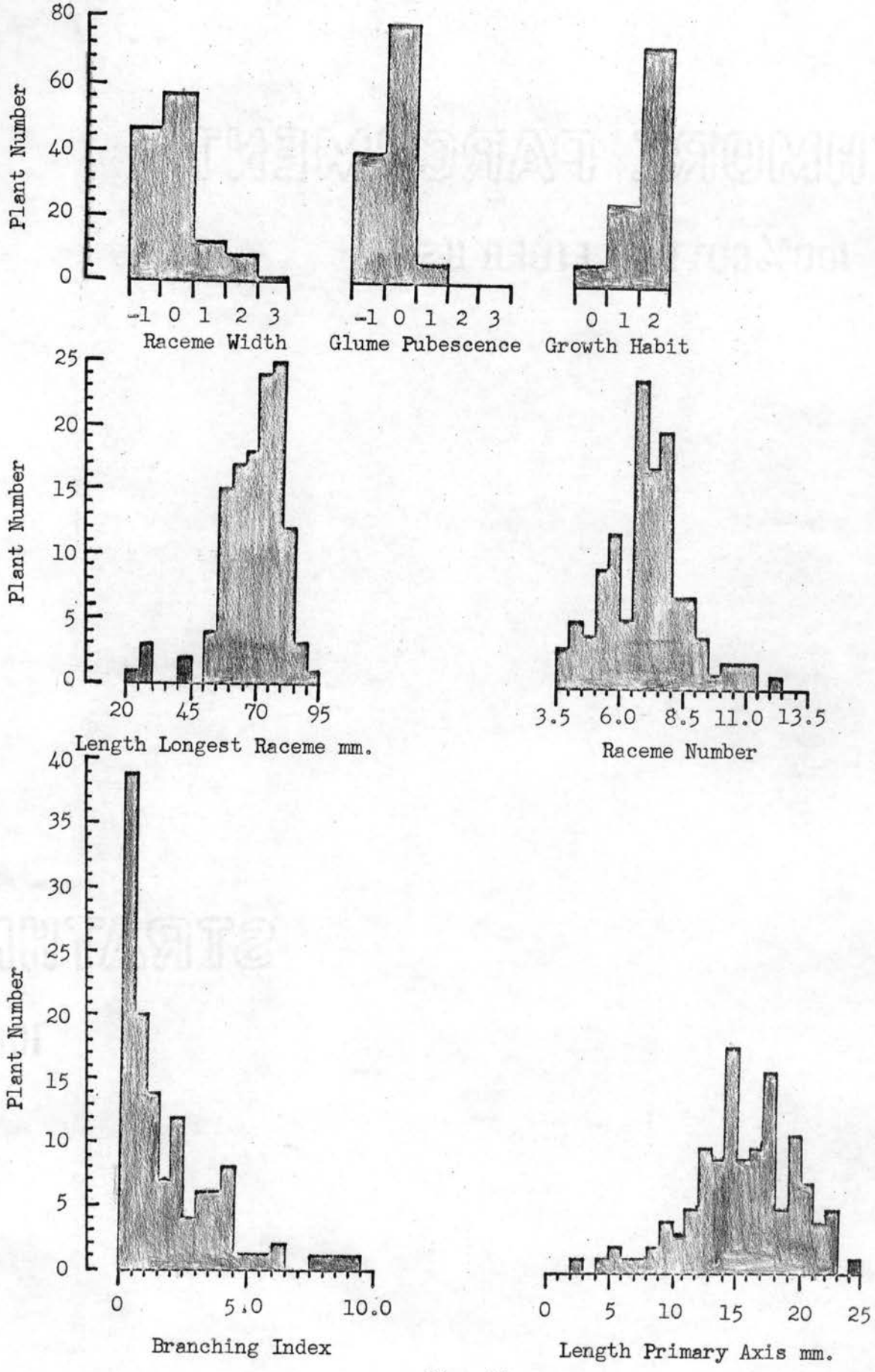

Plant Number
80
60
40
20
0
-1 0 1 2 3
Raceme Width
-1 0 1 2 3
Glume Pubescence
0 1 2
Growth Habit
Plant Number
25
20
15
10
5
0
20 45 70 95
Length Longest Raceme mm.
3.5 6.0 8.5 11.0 13.5
Raceme Number
Plant Number
40
35
30
25
20
15
10
5
0
0 5.0 10.0
Branching Index
0 5 10 15 20 25
Length Primary Axis mm.

Fig. 12.

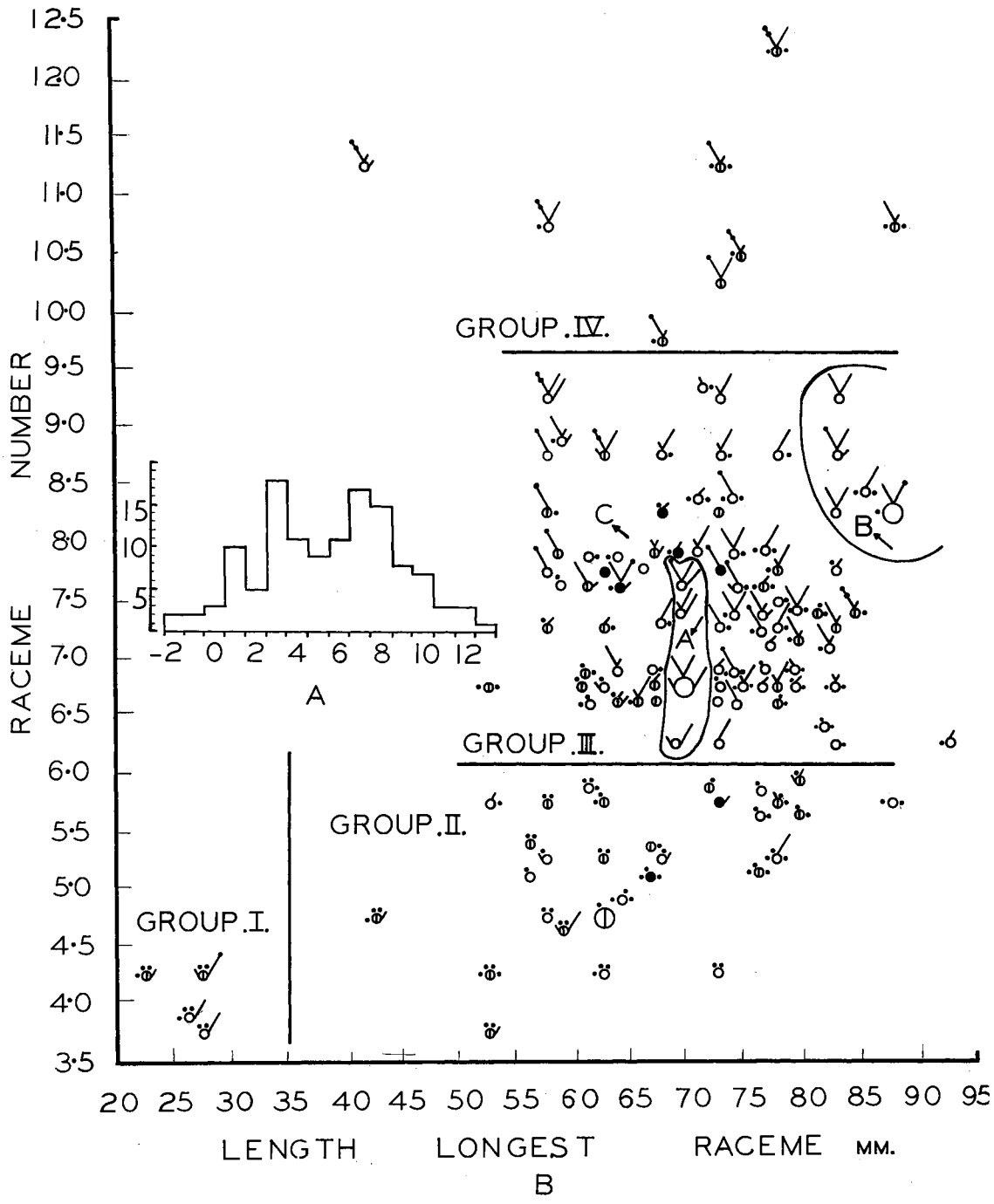


Fig. 13. Morphological analysis of the F2 population, obtained by selfing the 6n F1 hybrid between the Tropical and Mediterranean types of the Dichanthium annulatum complex.

A. Frequency histogram for the morphological indices.
B. Pictorialized scatter diagram.

method, and the data are presented in Figure 13B. Morphological indices were prepared for these plants according to the hybrid index method (Fig. 13A).

Character association analysis of this population seems to suggest that there are four fairly recognizable groups, as follows:

Group I.

This group is composed of two erect plants and two decumbent plants. All these plants are short, bearing short inflorescences with few racemes which are short in length. Furthermore, three of these plants have thin racemes, while the fourth has medium thick racemes. The presence of erect habit and thin racemes in two of these plants seems to indicate a resemblance to the Mediterranean type. One of these plants has medium thick, unbranched, and short racemes which are fewer in number, and it looks like the diploid Tropical type. The fourth plant is decumbent, and it has very thin racemes (thinner than the Mediterranean type) which have medium pubescent glumes on its sessile spikelets. This plant seems to have a combination of the characters of the Tropical and Mediterranean types. The morphological indices of these four plants show a range from -2 to 2.

Group II.

The second group, located at the lower side of the Figure 13B is composed of thirty plants. Most of these plants have few unbranched racemes on a short primary axis. These plants show variation in growth habit (prostrate, decumbent, or erect), the width and the length of the racemes, and the amount of hair on the first glumes of the sessile spikelets. Different plants seem to

have varying combinations of these characters (or their class intervals). One of these plants is decumbent, and it has thin racemes, the glumes of which are medium pubescent. In general, several plants belonging to this group seem to have the same class intervals of several characters studied as those of X-98. The morphological indices show a range from -1 to 4.

Group III.

The bulk of the plants belong to this group. The following morphological types were recognized as follows:

Type A.

This type is composed of three plants which seem to have the same class intervals of several morphological characters as those of A-4390 (Mediterranean type). All these plants are erect and have thin racemes. The morphological indices range from 8 to 12.

Type B.

This type is composed of four plants which seem to have the same class intervals of several characters as those of the F_1 hybrid. All these plants have the following characters: erect habit, long primary axis, long racemes which are thick, bearing secondary branches (except in one) and more in number than A-4390, and very pubescent glumes of the sessile spikelets.

Type C.

This type is composed of several plants which possess varying combinations of the characters (or class intervals of characters) of the parents and the F_1 hybrid. In

general, many intergrading types are seen, and their respective morphological indices show a wide range (3-11) of variation.

Group IV.

Eight plants belong to this group. These plants have, in general, the following characters: many racemes which are thick and have many secondary branches.

Morphological analysis reveals that these plants seem to have an association (or a tendency of association) of the following characters: very long inflorescences with many secondary branches, thick racemes, and pubescent glumes of the sessile spikelets. All these characters show higher index values in these plants than those in the F_1 hybrid and the naturally occurring D. papillosum Stapf. The morphological indices range from 10 to 12.

In general, it seems that several combinations of the characters of the Tropical, Mediterranean, and South African types are represented in this population.

DISCUSSION

The problem of the origin and evolutionary mechanics of the Dichanthium annulatum complex has been approached from the point of view of experimental taxonomy, including comparative morphology and geographic distribution, as well as from the points of view of genetics and cytology. It is, therefore, appropriate to examine the findings from this complex in the light of the entire series of investigations.

The Dichanthium annulatum complex consists of a polyploid series with the basic building material of $n = 10$. As mentioned previously, although five may be the basic number for the tribe, ten is probably the basic building material in some groups, and those with $2n = 20$ should be considered as functional diploids (Celarier, 1957; Celarier and Harlan, 1957; Celarier et al., 1958). Cytological investigation has revealed that diploids, tetraploids, and hexaploids are common, triploids, and probably others may occur occasionally, but there is no indication of aneuploidy in nature. The diploids and hexaploids seem to be fairly well correlated with geographical distribution and morphological appearance, but the tetraploids show no such obvious correlation.

Detailed studies of meiosis in the tetraploid and hexaploid types have shown that some of the chromosomes in them can associate together to form multivalents. This would indicate that some of the chromosomes (or segments of chromosomes) are homologous. The question arises whether such polyploid types would have arisen by segmental

allopolyploidy or by auto-allopolyploidy or by autopolyploidy followed by a long period of chromosome and genetic differentiation. Stebbins (1947, 1950) has described in great detail the occurance and characteristics of polyploids, and has also pointed out the difficulties in classifying them. Chromosome associations at the first division of meiosis are the usual source of information concerning type of polyploidy in a given plant. The presence of multivalents is considered as an indication of autopolyploidy and their absence allopolyploidy (Stebbins, 1950). However, Muntzing and Prakken (1940) and Giles and Randolph (1951) have proposed, for two different reasons, that the absence of multivalents should not be treated as an evidence of allopolyploidy. The former authors found a genotypically controlled tendency to form only bivalents in an autopolyploid Phleum. The latter authors conducted a detailed study of the frequency of quadrivalents in a strain of autotetraploid maize at the beginning and end of a ten year period. They found that there were fewer quadrivalents and more bivalents at the end of the period than those at the beginning. The meiotic behavior of the chromosomes in most of the tetraploids is slightly irregular, with low frequencies of univalents and quadrivalents at metaphase I, a condition which suggests that they are segmental allopolyploids. The presence of chromosome bridges and fragments suggests structural hybridity, but it does not, however, prevent synapsis. Some of these quadrivalents may be the result of translocation. Besides, some accessions were characterized by the presence of a high frequency of univalents (sometimes also multivalents), a low frequency of bivalents, and a high frequency of lagging chromosomes at anaphase I. Such a condition may be due to polyploidy and hybridization.

Harlan and Celarier (1957) have shown that apomixis is the predominant method of reproduction in the tetraploids and hexaploids, and that the diploids are apparently completely sexual. Although the hexaploids may be obligate apomicts, the tetraploids are facultative with the percent sexuality ranging from possibly 10 down to less than one.

Pollen fertility studies have demonstrated the presence of a high percentage of stainable (with acetocarmine) pollen even in the cytologically irregular types of D. annulatum. (Celarier et al., 1958). It has been shown previously that the pollen is needed to stimulate seed production even though the materials are apomicts and the pollen does not function in the fertilization of the egg (Celarier and Harlan, 1957).

All of the available evidence suggests that the D. annulatum complex is primarily agamic. This situation is somewhat similar to the polyploid complex as described by Babcock and Stebbins (1938) in Crepis. The diploids studied are all of one morphological type, but because of the limited collections available for study, it seems likely that diploids may also be found in the other morphological types. There is another possibility that diploids were in abundance in the long past, but now they occur as polyhaploids among the otherwise tetraploid populations where they are not easily distinguishable from the tetraploids. Polyhaploids ($2n \cong 20$) have been recovered among the segregating populations of hybrids involving the Tropical and Mediterranean tetraploids. Diploids seem to form the foundation for the genome building processes, since it has been demonstrated that diploids occasionally produce sexual tetraploids, and these in turn can be crossed readily with other tetraploids. The tetraploid compliment of this complex is in several respects the most unstable, and is

likely to be still in a very active state of evolution. Hexaploids studied in the present investigation were all of one morphological type, the South African type, and were very similar with respect to several morphological characters.

In the light of the present investigation a working hypothesis (Fig. 15) concerning the origin of the various types and their present activities is proposed, as follows:

The Tropical tetraploids having the same morphological appearance as the diploids, they probably arose as a result of crossing between two genetically somewhat different Tropical diploids followed by chromosome doubling. This would, therefore, be a segmental allotetraploid, and it is also assumed that it would still be sexual. As explained by Stebbins (1950) such a polyploid has the ability for genetic segregation, in respect to both the morphological differences between the parental types and the chromosomal differences which formed the sterility barriers between the parents.

Natural selection would be continually operating in such polyploids, especially in relation to fertility. Although the direction of evolutionary trend would depend on the constitution of the individual chromosomes, it is likely that reproductive isolating mechanisms shall eventually develop among the different ecotypes. Some isolation could be expected because of self fertilization or apomixis. In any event, during this period an extremely polymorphic population would be expected and it might well have covered the major portion of the range of the geographical distribution of the complex, even though the parental types may have

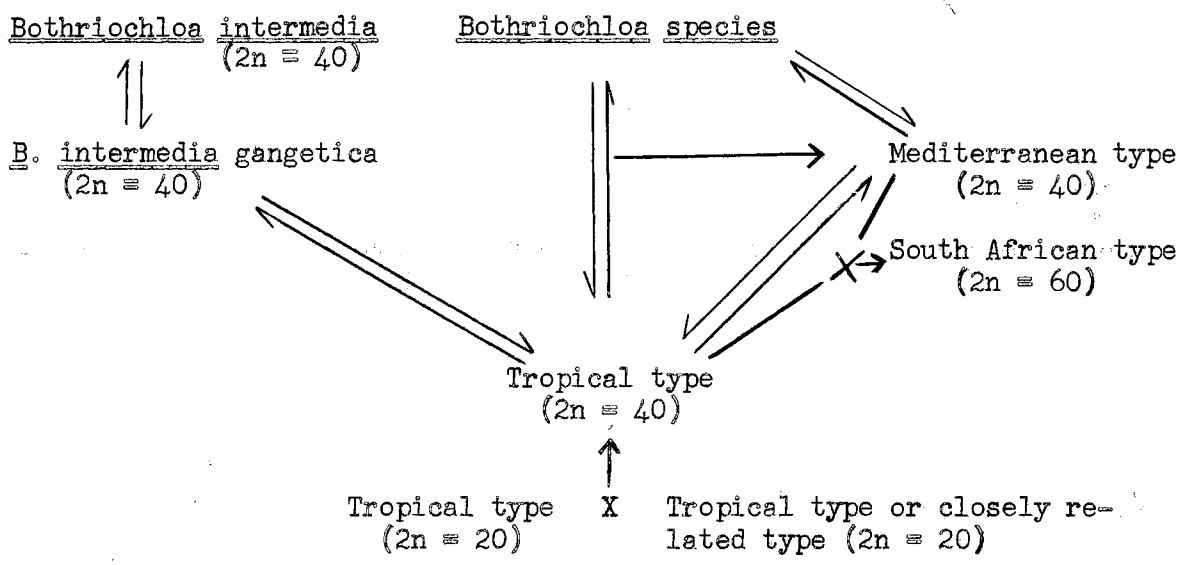


Fig. 15. The origin and evolution of the Dichanthium annulatum complex. (⇅ = Introgression between the two taxa)

been distinct morphological units with restricted ranges. It is further to be expected that if at this stage the genetic mechanism for facultative apomixis was developed, it would be easy to visualize how swarms of quite heterozygous clones might have become established in nature. It is also known that facultative apomixis can still exhibit some amount of crossing and recombinations (Clausen, 1954; Celarier and Harlan, 1957). The observed morphological variation in the tetraploids appears to be very similar to what would be expected if such a condition existed in them.

The morphological differences between the Mediterranean and Tropical types are slight and somewhat obscured by a few accessions which are intermediate between the two. Nevertheless the Mediterranean type seems to be slightly more irregular cytologically and most of the differences found in the Mediterranean type (the thinness of the racemes, less pubescence on the glumes, long racemes with secondary branches, and erect habit) are in the direction of the closely related genus Bothriochloa. It is likely that the Mediterranean type may be the product of the introgression of genes from one or more Bothriochloa species into the Tropical type.

It is also noted that one accession of this complex that did not easily fit into either the Tropical or Mediterranean types was extremely irregular cytologically. Harlan (1960 in press) has pointed out the morphological evidence of introgression between Bothriochloa intermedia and D. annulatum through B. intermedia gangetica type. This accession is intermediate between the gangetica type B. intermedia and D. annulatum with respect to

several morphological characters, and it may represent further evidence of introgression between Dichanthium annulatum and Bothriochloa intermedia. Such introgression is probably occurring at the present time, especially in those areas where several species of Dichanthium and of closely related genera occur side by side, and where there is considerable environmental variation.

Relationships of the Tropical and Mediterranean Types

Cytological studies of the F_1 hybrids involving these types revealed that most of the chromosomes (36 to 40) pair as bivalents. The average chromosome configurations were analyzed in all hybrids separately, and these were observed to be similar to those of their respective parents. The question arises as to whether the pairing was between the compliments of the two parents or whether it was partially or completely by autosyndesis i.e., pairing within each of the parental compliments. Since these plants are tetraploids and their chromosomes are extremely similar in their morphology, no direct distinction is possible, therefore only indirect evidence may be used in determining the nature of pairing. The possibility cannot be overlooked, nevertheless that the two genomes in a particular species might have some homology, which due to differential affinity between the chromosomes (Darlington, 1937), is not expressed in the multivalent formation. Also, the formation of bivalents in the parents may be genotypically controlled as in Phleum (Muntzing and Prakken, 1940).

It does not seem to be likely that autosyndesis occurs in the F_1 hybrids, since firstly the quadrivalents were observed to have very low frequencies, and these were simple rings or chains, characteristic of

configurations resulting from structural hybridity, and secondly a considerable amount of recombinations between parental characters was observed in the F_2 populations, indicating segregation and crossing over between some of the chromosomes of the two parental types. Furthermore, although back cross progeny of this hybrid was not obtained, a back cross progeny involving the same female parent (recurrent parent), but D. fecundum S. T. Blake as a male parent was analyzed cytologically (Borgaonkar, unpublished). All of the plants analyzed in this cross were observed to be slightly irregular with a lack of high frequencies of trivalents, but a regular formation of 18-20 bivalents at metaphase I. Thus, it seems more likely that these two morphological types (Tropical and Mediterranean) are very closely related, and that the chromosome pairing observed was due to allosyndesis.

Morphological analysis of the F_2 population has revealed the presence of a considerable amount of segregation and almost all possible recombinations of the characteristics of these types. Some plants were observed to be dwarf, and these were polyhaploids ($2n \cong 20$). These polyhaploids were of the Tropical type, Mediterranean type, and intermediates between these two types. Also, some plants were recovered in this population which showed a close resemblance to D. papillosum with respect to most of the morphological characters studied, while some other plants seemed to have a tendency to vary more towards the direction of the genus Bothriochloa than either of the parental types. Some of the F_2 plants showed hybrid vigor and transgressive segregation with respect to several morphological characters. Nothing is known about the mode of reproduction of these F_2 plants, but the fact to be emphasized about such an F_2 population is that segregation in it is very complex

due first to the large number of gene pairs which are segregating simultaneously; second to the degree of sexuality; and third to the presence of probable introgression from Bothriochloa. As a result a genotype exactly like the parents shall be recovered rarely, but a considerable number of new gene recombinations will be formed. The observed morphological variation of the plants from this F_2 population seems to be similar to what has been demonstrated experimentally in the progeny of artificial hybrids between the subspecies of plants (Clausen and Hiesey, 1958).

The Origin of D. papillosum Stapf

Although all of the hexaploids studied were of one morphological type i.e., South African type, they seem to have two cytological types. One group, including the entries from South Africa, is characterized by the presence of many univalents and few quadrivalents at metaphase I. There is a noticeable increase in univalents and a decrease in quadrivalents as compared to the tetraploids. This condition might be explained as the result of increased differentiation in the chromosomes of the hexaploids in comparison to those of the tetraploids. These cytological results are similar to those obtained from hexaploid X hexaploid hybrids in which four genomes are involved (Brown and Menzel, 1952). It is assumed that in this hexaploid type two genomes are represented twice and that their chromosomes pair with fair regularity, whereas the other two genomes are represented only once and pairing between them is poor. It might be represented as follows:

$$AA\ A_1A_1\ A_2A_2 \times AA\ A_1A_1\ A_3A_3$$

$$AA\ A_1A_1\ A_2A_3$$

The other hexaploid type, including the Australian accession, is characterized by the presence of few univalents, a considerable number of quadrivalents, and frequent hexavalents at metaphase I. This accession seems to have lesser differentation of chromosomes than the South African accessions. Fertilization of an unreduced gamete of one tetraploid type by a reduced gamete of a closely related tetraploid type would be expected to produce something similar to this type. The genomes involved might well be $AAAAA_1A_1$. It seems likely that the genomes involved in both cases are closely related, but probably differ in the degree of differentiation of their respective chromosomes.

Morphological studies of these hexaploids revealed that they have a combination of the characters of the Tropical (thick racemes and pubescent glumes) and Mediterranean types (long primary axis, long racemes with secondary branches, and erect habit). In many respects they seem to represent extreme values of the characters of the Tropical and Mediterranean types.

Celarier et al. (1958) proposed that the South African type might be the product of the fertilization of an unreduced egg of the Tropical type of D. annulatum by a normal gamete of a closely related South African species D. aristatum or vice versa.

In a personal communication to Dr. R. P. Celarier, the Chief Division of Botany, Department of Agriculture, Pretoria, South Africa has expressed his suggestions and criticisms about the proposed (Celarier et al., 1958) mode of origin of the South African type, i.e., D. papillosum (for details see Appendix D). Part of the letter reads, as follows:

> ...I also noticed that you have considered the possibility of the D. annulatum hexaploid originating as a result of hybridization of the latter with D. aristatum C. E. Hubbard. This, however, is highly unlikely since D. aristatum is, as far as I know, an Australian species and its occurance in South Africa is of a local nature. In my opinion, it is certainly introduced and occurs /except for one other locality/ only at Onderstepoort just North of Pretoria, where it maintains itself, being common in some years and probably absent in others. It does not seem to have spread in ten years, I have observed it. One other record is known from Natal, but again the plant was growing not very far from an agricultural research station. I am sending you this information to clear up the wrong impression that might have been created when these specimens of D. aristatum were sent to you. I suppose that no note to say that it was introduced accompanied the specimens.....

One of the F_1 hybrids involving the Tropical and Mediterranean types turned out to be $2n = 60$. It is very likely that an unreduced egg of the Tropical type was fertilized by the reduced gamete of the Mediterranean type. This hybrid was sexual, and it was observed to be very similar in morphological appearance and meiotic behavior to the African D. papillosum (South African type) used in the present investigation.

Harlan et al. (1958) have pointed out that the faculty for the production of functional unreduced eggs is probably widespread in the Bothriochloeae, especially among the 4n X 4n crosses. They have shown that in the cross involving B. intermedia gangetica 2655 X D. annulatum 4099 a number of hybrids were obtained, about two thirds of which had the 6n number of chromosomes. Also, Celarier (unpublished) obtained a similar situation in crosses involving D. caricosum X D. aristatum.

An analysis of the F_2 plants obtained by selfing the synthesized D. papillosum showed that considerable variation exists in them with respect to the morphological character studied. In general, several combinations of the characters of the Tropical, Mediterranean, and

South African types were represented in this population.

Cytological studies are still to be conducted in this population, and it does seem likely that types with less than $2n \cong 60$ (also more than $2n \cong 60$), may be recovered in this population.

As mentioned already, a few individuals from the F_2 population obtained by selfing 4n F_1 hybrids showed transgressive variation which in some characters exceeded the limits of both parents. Some of these plants showed much resemblance to the South African type, and it is likely that this might be a beginning of something like the South African type. Furthermore, it seems that a double dosage of the Tropical type may be required to produce the hexaploid South African type. It should also be pointed out that the Australian hexaploid with a high frequency of quadrivalents and hexavalents might be the product of the fertilization of an unreduced gamete of the Tropical type by a normal gamete of another type of the D. annulatum complex which is more closely related to the Tropical type than the Mediterranean type.

SUMMARY

The problem of the origin and evolutionary mechanics of the Dichanthium annulatum complex has been approached from the point of view of experimental taxonomy.

A detailed cytological and morphological study of the D. annulatum complex was conducted from samples collected from almost all of its range of geographical distribution. In this study ninty-seven accessions were analyzed cytologically and fifty-three morphologically.

Assuming ten to be the basic number, eight diploids, eighty-two tetraploids, and seven hexaploids were examined.

In general four morphological types could be recognized (Tropical, Mediterranean, French West African, and South African), but there were a few accessions that did not fit very well into any of these categories. Some of these types seem to show evidence of introgression from the genus Bothriochloa.

The diploids were all of the Tropical type and found only in the Gangetic plain of northern India, the hexaploids were all of the South African type and seemed to be restricted in southern Africa, but the tetraploids were of several morphological types and distributed throughout the tropics from French West Africa to the Fiji Islands.

During meiosis the diploids were completely regular, and the hexaploids were extremely irregular. The tetraploids showed almost all intermediate degrees of irregularities.

The irregularities commonly observed were the presence of univalents and multivalents besides bivalents at metaphase I, lagging chromosomes and chromosome bridges with fragments at anaphase I and telophase I, lagging chromosomes at anaphase II, and micronuclei at both the dyad and tetrad spore stages. These irregularities were the same in all accessions which differed from one another only in the frequencies of these irregularities.

For the most part, the chromosomal irregularities encountered are those commonly associated with polyploidy and hybridization, and both of these have evidently played a part in the evolution of the complex.

Morphological evidence seemed to suggest possible introgression of this complex with species of the genus Bothriochloa. Also, further evidence was obtained for the possible introgression between the Tropical and Mediterranean types.

Morphological and cytological studies of the F_1 hybrids involving the Tropical and Mediterranean types revealed that the pairing of the chromosomes in them was normal, and that these hybrids were intermediate between the parents with respect to several morphological characters. The morphological analysis of the F_2 progeny showed considerable amount of recombinations between the parental characters, thus indicating that these types are very closely related.

In one of the hybrids an unreduced egg of the Tropical type appears to have been fertilized by a reduced gamete of the Mediterranean type. This hybrid looked very much like the South African type, and its F_2 progeny showed considerable variation in the direction of the South African type, Tropical type, and to some extent the Mediterranean type.

Taking all these factors into account a working hypothesis of the origin of the various components of the complex and their respective present activities was proposed.

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APPENDIXES

APPENDIX A

TABLE I

CHROMOSOME CONFIGURATIONS OF *D. annulatum* COMPLEX AT DIAKINESIS AND METAPHASE I

A No.	Collector	Location	2n	Range	Average per cell I	II	III	IV	No. of Cells Studied
				Diploids					
3242	K. Biswas	Calcutta, India	20	10II		10			50
3965(b)	K. Biswas	Calcutta, India	20	10II		10			50
6180	K. L. Mehra	Calcutta, India	20	10II		10			25
5396	K. L. Mehra	Belatal, India	20	0-2I,9-10II	0.32	9.84			50
6224	F. W. Gould	New Delhi, India	20	10II		10			25
6577	Crop Res. Br.	Delhi, India	20	10II		10			25
6192	K. L. Mehra	Burma	20	10II		10			25
1526(b)	J. Smith	South Texas	20	10II		10			50
				Tetraploids					
3182	A. Kamm	N. Gallilea, Israel	40	0-4I,15-20II,0-2IV	0.88	18.20		0.68	38
3789	H. Said	Giza, Egypt	40	0-7I,10-20II,0-3IV	2.20	18.00		0.45	50
94		Morocco	40	0-4I,14-20II,0-1III,0-3IV	0.64	18.44	0.08	0.56	50

TABLE I (Cont'd)

A No.	Collector	Location	2n	Range	Average per Cell I	II	III	IV	No. of Cells Studied
7419	Abu Hamadi	Morocco	40	0-4I,16-20II,0-1III 0-2IV	0.76	19.07	0.10	0.20	30
4390	Crops Res. Br.	Zerkine, Tunisia	40	0-2I,16-20II,0-1III 0-2IV	0.52	18.74	0.08	0.44	50
4391	Crops Res. Br.	Thyna, Tunisia	40	0-2I,16-20II,0-2IV	0.32	18.60		0.62	50
4830	Sam Logan	Saudi Arabia	40	0-2I,16-20II,0-1III 0-2IV	0.22	18.92	0.14	0.38	50
5429	L. Sauger	Senegal, Fr. West Africa	40	0-4I,16-20II,0-1III 0-2IV	0.41	18.64	0.08	0.52	50
5430	L. Sauger	Senegal, Fr. West Africa	40	0-4I,16-20II,0-1III 0-3IV	0.26	18.32	0.10	0.70	40
4804	H. J. Van Rensburg	Tanganyika, East Africa	40						
3903	H. W. Springfield	Abu Ghraib, Iraq	40	0-3I,14-20II,0-2III 0-3IV	0.38	18.44	0.20	0.52	50
5113	" " "	Baghdad, Iraq	40	0-4I,16-20II,0-1III 0-2IV	0.50	19.23	0.04	0.23	30
5114	" " "	" "	40						15
5115	" " "	" "	40						15
5116	" " "	" "	40	0-2,15-20II,0-1IV 0-2IV	0.52	18.70	0.04	0.52	50
5119	" " "	" "	40	0-4I,16-20II,0-1III 0-1IV	1.00	18.80	0.20	0.20	20
5120	" " "	" "	40						10
5123	" " "	" "	40	0-2I,16-20II,0-1III 0-1IV	0.42	19.08	0.10	0.28	50
5126	" " "	" "	40	0-4I,16-20II,0-2IV	0.70	18.55		0.55	20

TABLE I (Cont'd)

A No.	Collector	Location	2n	Range	Average per Cell I	II	III	IV	No. of Cells Studied
5128	H. W. Springfield	Baghdad, Iraq	40	0-2I,17-20II,0-1I 0-1IV	0.45	18.70	0.05	0.50	20
5131	" " "	" "	40	0-4I,17-20II,0-1III 0-1IV	0.68	19.12	0.12	0.18	50
5134	" " "	" "	40	0-3I,16-20II,0-1III 0-2IV	0.52	18.60	0.12	0.48	25
5136	" " "	" "	40	0-4I,15-20II,0-1III 0-2IV	1.10	18.20	0.10	0.55	20
5139	" " "	" "	40	0-2I,16-20II,0-1III 0-2IV	0.42	18.98	0.06	0.36	50
5143	" " "	" "	40	0-2I,16-20II,0-1III 0-2IV	0.32	18.60	0.16	0.50	60
5145	" " "	" "	40	0-2I,15-20II,0-1III 0-2IV	0.68	18.72	0.04	0.44	25
5146	" " "	" "	40						10
4099	J. E. Smith	Punjab, India	40	0-2I,16-20II,0-1III 0-2IV	0.24	19.08	0.08	0.34	50
4636	Fodder Res. Sta.	Sargodah, West Pakistan	40	0-2I,16-20II,0-1III 0-2IV	0.80	18.52	0.16	0.42	50
6575	Crops Res. Br.	Bannu, Pakistan	40	0-4I,16-20II,0-1III 0-2IV	0.58	18.36	0.10	0.60	35
6073	J. J. Norris	Tando Jam, West Pakistan	40	0-2I,16-20II,0-2III 0-1IV	0.50	19.0	0.10	0.30	30
6225	Gould	Kandahar, Afghanistan	40	0-7I,15-20II,0-1III 0-1IV	1.78	18.72	0.18	0.06	50
6573	Gould	"	40	0-4I,16-20II,0-2III 0-2IV	0.74	18.30	0.22	0.50	50
2564	B. P. Pal	New Delhi, India	40	0-4I,16-20II,0-2IV	0.52	19.00		0.37	50

TABLE I (Cont'd)

A No.	Collector	Location	2n	Range	I	II	III	IV	No. of Cells Studied
2568	C. R. Mudaliar	Madras, India	40	0-4I,14-20II,0-1III 0-3IV	0.30	18.20	0.06	0.78	48
2654	" " "	Coimbatore, India	40	0-4I,14-20II,0-1III 0-3IV	0.52	18.62	0.16	0.44	50
3227	T. A. Koshy	Allahbad, India	40	0-2I,16-20II,0-2IV	0.12	18.90		0.52	50
3713	" " "	Allahbad, India	40	0-3I,12-20II,0-1III 0-4IV	0.50	17.64	0.18	0.92	50
4019	M. S. Pawar	Hydrabad, India	40	0-2I,16-20II,0-2IV	0.82	18.96		0.32	25
4393	M. B. Raizada	Dehradun, India	40						10
4565	S. K. Mukherjee	Nadia, West Bengal India	40	0-4I,16-20II,0-1III 0-2IV	0.64	18.90	0.12	0.30	50
4600	D. Harper	Lucknow, India	40	0-4I,14-20II,0-1III 0-3IV	0.58	18.34	0.14	0.58	50
5288	K. L. Mehra	Delhi, India	40	0-4I,16-20II,0-1III 0-2IV	0.64	18.86	0.12	0.32	50
5295	" " "	Coimbatore, India	40	0-4I,14-20II,0-3IV	0.40	18.56		0.62	50
5296	" " "	Dharwar, India	40	0-2I,13-20II,0-3IV					
5302	S. M. Sikka	Karnal, India	40	0-3I,16-20II,0-1III 0-2IV	0.36	18.74	0.08	0.48	50
5326	Bhola Nath	Indore, India	40	0-6I,15-20II,0-2III 0-1IV	2.0	18.60	0.06	0.16	50
5397	K. L. Mehra	Mathura, India	40	0-6I,13-20II,0-2III 0-3IV	2.60	16.50	0.15	0.98	50
5398	" " "	Karnal, India	40	0-4I,12-20II,0-1III 0-3IV	0.46	18.34	0.18	0.58	50

TABLE I (Cont'd)

A-No.	Collector	Location	2n	Range	I	II	III	IV	No. of Cells Studied
5399	K. L. Mehra	Rohtak, India	40	0-2I,16-20II,0-1III 0-1IV	0.46	18.64	0.14	0.46	50
5400	" " "	Hempur, India	40						10
5405	" " "	New Delhi, India	40	0-4I,16-20II,0-1III 0-2IV	0.56	18.80	0.08	0.40	50
5408	" " "	Bareilly, India	40	0-4I,16-20II,0-2IV	0.60	18.86		0.42	50
5411	" " "	Delhi, India	40	0-4I,16-20II,0-1III 0-2IV	0.36	18.64	0.04	0.56	50
5437	" " "	Lucknow, India	40	0-3I,14-20II,0-1III 0-3IV	0.56	18.06	0.12	0.74	50
5438	" " "	Poona, India	40	0-2I,16-20II,0-1III 0-2IV	0.48	19.08	0.08	0.28	25
6090	L. G. Kulkarni	Hydrabad, India	40	0-6I,16-20II,0-1III 0-1IV	1.30	18.64	0.02	0.34	25
6837	S. M. Sikka	New Delhi, India	40	0-5I,16-20II,0-2III	2.08	18.04	0.40	0.16	25
				0-1IV	2.08	18.04	0.40	0.16	25
6866	T. N. Knoshoo	Amritsar, India	40	0-2I,16-20II,0-1III 0-2IV	0.25	18.95	0.15	0.35	20
7026	J. C. Sen Gupta	Poona, India	40						10
7133	R. D. Misya	Benares, India	40	0-2I,17-20II,0-1IV	0.24	19.16		0.36	25
7183	L. S. S. Kumar	Thana, India	40						10
6844		Java, Indonesia	40	0-4I,16-20II,0-2III 0-2IV	0.62	18.71	0.12	0.40	35
6154(b)		South China	40						

TABLE I (Cont'd)

A No.	Collector	Location	2n	Range	Average per Cell I	II	III	IV	No. of Cells Studied
4395		Cuba	40	0-2I,17-20II,0-1IV	0.28	19.10		0.38	50
6263	J. L. Spencer	Puerto Rico	40						10
5798	" " "	" "	40	0-2I,16-20II,0-2IV	0.32	19.16		0.34	50
5602	L. W. Parham	Suva, Fiji Islands	40						10
5593	" " "	" " "	40	0-2I,16-20II,0-1III 0-2IV	0.38	18.42	0.10	0.62	50
1526(a)	J. Smith	South Texas	40	0-2I,15-20II,0-2IV	0.24	18.44		0.72	50
2566	Trew	South Texas	40	0-2I,16-20II,0-2IV	0.48	18.60		0.58	20
6373	F. W. Gould	College Station, Texas	40	0-2I,18-20II,0-1IV	0.20	19.38		0.26	50
6375	" " "	" "	40	0-4I,14-20II,0-1III 0-2IV	0.68	18.60	0.04	0.50	50
6574	Crops Res. Br.		40	0-2I,18-20II,0-1III 0-1IV	0.18	19.32	0.02	0.28	50
6576	" " "		40		0.56	18.62	0.12	0.46	
6896	" " "		40						
6981	" " "		40						
7034	" " "		40	0-2I,15-20II,0-2IV	0.20	18.54		0.66	50
7035	" " "		40	0-4I,17-20II,0-1III 0-1IV	0.43	19.32	0.07	0.18	32
7036	" " "		40	0-2I,18-20II,0-1IV	0.36	19.40		0.21	32

TABLE I (Cont'd)

A No.	Collector	Location	2n	Range	I	II	III	IV	No. of Cells Studied
7037	Crops Res. Br.		40	0-1I,16-20II,0-2IV	0.08	18.76		0.60	25
7039	" " "		40	0-2I,16-20II,0-2IV	0.16	18.76		0.58	50
				Hexaploids					
2567	J. Smith	South Africa	60	0-10I,22-30II,	5.04	26.10	0.20	0.54	22
				0-1III,0-2IV	5.04	26.10	0.20	0.54	22
4080	J. E. Smith	South Africa	60	0-5I,23-30II,0-2III 0-3IV	1.52	27.26	0.52	0.60	50
4081	J. E. Smith	South Africa	60						
4083	J. E. Smith	South Africa	60	0-6I,24-30II,0-2III 0-2IV	2.05	27.25	0.35	0.60	40
4106	J. E. Smith	South Africa	60						
3716	K. E. Sturgeon	Southern Rhodesia	60	0-8I,21-30II,0-4IV	1.68	27.60		0.78	50
4788(b)	W. Hartley	Rodds Bay, Australia	60	0-3I,19-28II,0-1III 0-3IV,0-3VI	0.40	24.55	0.10	1.65	50

TABLE I (Cont'd)

A No.	2n	Range	Average per cell I	II	III	IV
		Synthetic Tetraploid				
X-98	40	0-6I,15-20II,0-1III,0-3IV	1.24	17.08	0.12	1.06
		Tropical Type X Mediterranean Type				
		F_1 Hybrids				
		Artificial Hybrids				
56-X-22-1	40	0-4I,16-20II,0-1III,0-2IV				
56-X-112-1	40	0-2I,16-20II,0-2IV				
56-X-116-1	40	0-2I,18-20II,0-1III,0-1IV				
56-X-116-2	40	0-4I,16-20II,0-1III,0-2IV				
57-X-1171-1	60	0-4I,22-26II,0-2III,0-2IV				
57-X-1172-1	40	0-4I,14-20II,0-1III,0-3IV				
		Natural Hybrids				
55-X-98-1-0.P.-1	40	0-4I,13-20II,0-1III,0-3IV	1.46	17.08	0.02	1.08
55-X-98-1-0.P.-2	40	0-4I,13-20II,0-1I,0-3IV	1.08	18.57	0.18	0.31
55-X-98-1-0.P.-3	40	0-4I,12-20II,0-1I,0-2IV	1.18	17.60	0.22	0.74

TABLE I (Cont'd)

A-No.	2n	Range	Average per cell I	II	III	IV
55-X-98-1-0.P.-5	40	0-7I,14-20II,0-1III,0-3IV	1.94	17.42	0.14	0.70
55-X-98-1-0.P.-6	40	0-4I,16-20II,0-2IV	1.60	17.80		0.70
55-X-98-1-0.P.-7	40	0-6I,15-20II,0-1III,0-2IV	1.70	17.88	0.02	0.62
		F_2 Progeny of 57-X-1172-1				
		Polyhaploids				
Six Plants*	20	0-2I,9-10II				
		Tetraploids				
Seven Plants*	40	0-4I,16-20II,0-1III,0-2IV				

* These plants are shown near the arrows in Figure 11. Group I (polyhaploids), Group II (tetraploids).

APPENDIX A

TABLE II

CHROMOSOME BEHAVIOR AT ANAPHASE AND TELOPHASE IN THE D. annulatum COMPLEX

Accession Number	AI – TI Average per Cell						AII – TII Average per Cell			
	% Normal	Lag. Chr. ÷ Lag.		n. ÷ Lag.	Bridges	Frag.	% Normal	Laggers – lag.		n. – Lag.
Diploids										
3242	100						100			
3965(b)	100						100			
5396	100						100			
1526(b)	100						100			
Tetraploids										
3182	47	0.89	0.37	0.54	0.14	0.05	52	0.61	0.06	0.55
3789	50	0.87	0.15	0.72	0.04	0.03	37	0.88	0.06	0.82
94	74	0.50	0.38	0.12			81	0.44	0.06	0.38
4390	80	0.28	0.18	0.10			84	0.18	0.05	0.13
4391	81	0.24	0.18	0.06			90	0.11	0.02	0.09
4830	82	0.20	0.14	0.06			89	0.18	0.02	0.16
5430	65	0.55	0.35	0.20			83	0.15	0.11	0.04
3903	80	0.26	0.24	0.02			88	0.17	0.03	0.14
5123	78	0.32	0.26	0.06			81	0.27	0.13	0.14
5143	80	0.20	0.16	0.04	0.04	0.04	89	0.13	0.01	0.12
5145	86	0.14	0.08	0.06	0.04	0.04				
4099	75	0.27	0.26	0.01			84	0.17	0.03	0.14
4636	91	0.22	0.20	0.02			90	0.15	0.03	0.12
6225	76	0.46	0.40	0.06			85	0.41	0.03	0.38

TABLE II (Cont'd)

Accession Number	AI - TI Average per Cell						AII - TII Average per Cell			
	% Normal	Lag. Chr.	÷ Lag.	n.÷Lag.	Bridges	Frag.	% Normal	Laggers	- Lag.	n. - Lag.
2568	65	0.41	0.21	0.20	0.04	0.02	95	0.03	0.01	0.02
2654	80	0.19	0.16	0.03			89	0.12	0.01	0.11
3713	76	0.52	0.36	0.16			91	0.19	0.07	0.12
							95	0.27	0.09	0.18
4600	82	0.22	0.10	0.12			90	0.11	0.03	0.08
5288	80	0.22	0.14	0.08	0.02	0.02	75	0.38	0.08	0.30
5295	72	0.45	0.40	0.05	0.16	0.16	84	0.34	0.04	0.30
5302	70	0.36	0.24	0.12			85	0.19	0.04	0.15
5326	74	1.24	1.14	0.08			84	0.52	0.05	0.47
5397	42	3.16	2.56	0.60	0.04	0.04	56	1.52	0.48	1.04
5399	76	0.36	0.30	0.06			88	0.19	0.01	0.18
5408	80	0.20	0.16	0.04	0.04	0.04	87	0.13	0.02	0.11
5411	78	0.28	0.20	0.08	0.04		90	0.15	0.05	0.10
5437	80	0.26	0.14	0.12			90	0.15	0.05	0.10
6090	78	0.64	0.58	0.06	0.02	0.02	73	0.28	0.02	0.26
4395	85	0.26	0.17	0.09	0.01	0.01	91	0.19	0.04	0.15
5593	78	0.30	0.26	0.04			89	0.18	0.03	0.15
1526(a)	80	0.36	0.24	0.12			89	0.13	0.03	0.10
2566	62	0.59	0.21	0.38	0.05	0.03	85	0.14		0.14
6375	84	0.30	0.22	0.08			76	0.50	0.06	0.44
6574	76	0.40	0.34	0.06			82	0.18	0.02	0.16

TABLE II (Cont'd)

Accession Number	AI – TI Average per Cell % Normal	Lag. Chr. ÷ Lag.	n. ÷ Lag.	Bridges	Frag.	AII – TII Average per Cell % Normal	Laggers – Lag.	n. – Lag.
6576	82	0.20	0.20			85	0.19	0.19
6896	74	0.48	0.44	0.04		80	0.21	0.04	0.17
6981	80	0.36	0.24	0.12		88	0.16	0.04	0.12
7035	84	0.28	0.28			89	0.14	0.01	0.13
7036	82	0.26	0.26						
				Hexaploids					
2567	30	1.92	0.45	1.47	0.12	0.03	83	0.16	0.01	0.16
4080	70	0.46	0.28	0.18	0.06	0.01	84	0.25	0.05	0.20
4083	52	1.88	1.54	0.34	0.02	0.02	70	0.48	0.08	0.40
3716	28	1.12	0.16	0.96	0.03	0.02	46	0.49	0.07	0.42
4788(b)	80	0.60	0.44	0.16	0.02	0.02	91	0.18	0.07	0.11

APPENDIX A

TABLE III

CHROMOSOME BEHAVIOR AT THE DYAD AND TETRAD SPORE STAGES IN THE *D. annulatum* COMPLEX

Accession Number	Dyad Spore Stage: Percent Normal Cells	Dyad Spore Stage: Micronuclei per Cell	Tetrad Spore Stage: Percent Normal Cells	Tetrad Spore Stage: Micronuclei per Cell
		Diploids		
3242	100		100	
3965	100		100	
5396	100		100	
1526(b)	100		100	
		Tetraploids		
3182	80	0.25	73	0.11
3789	92	0.11	86	0.04
94	86	0.10	84	0.06
4390	82	0.11	86	0.04
4391	80	0.13	85	0.05
4830	90	0.05	86	0.04
3903	74	0.16	76	0.08
5123	80	0.12	82	0.06
5143	92	0.04	88	0.03
4099	92	0.04	88	0.02
4636	82	0.11	86	0.04
6225	84	0.11	80	0.07
2568	97	0.02	98	0.02
2654	84	0.06	76	0.09
3713	88	0.06	92	0.02
4600	90	0.06	94	0.02
5288	76	0.23	70	0.11
5302	82	0.11	80	0.07
5399	90	0.05	86	0.04
5411	90	0.05	88	0.03
5437	80	0.13	79	0.08
6090	80	0.12	74	0.05
5593	88	0.08	84	0.06
1526(a)	88	0.10	84	0.06
2566	93	0.06	92	0.02

TABLE III (Cont'd)

Accession Number	Dyad Spore Stage: Percent Normal Cells	Dyad Spore Stage: Micronuclei per Cell	Tetrad Spore Stage: Percent Normal Cells	Tetrad Spore Stage: Micronuclei per Cell
6375	80	0.13	82	0.26
6574	84	0.11	78	0.07
6576	84	0.10	82	0.06
6896	82	0.12	78	0.07
6981	78	0.15	80	0.06
7035	82	0.10	84	0.06
		Hexaploids		
2567	77	0.17	67	0.12
4080	76	0.19	74	0.10
3716	61	0.30	79	0.09

APPENDIX B

TABLE I

MORPHOLOGICAL ANALYSIS OF THE D. annulatum COMPLEX

Accession Number	Length Primary Axis (mm)	Raceme Number	Inflorescence Branching Index	Length Longest Raceme	Raceme Width	Pubescence First Glume	Growth Habit
			Diploids				
1. 3242	10.2	5.6	0.00	36.8	/	/	P*
2. 3965(b)	10.0	4.0	0.00	30.2	//	//	P
3. 6180	10.1	5.4	0.02	40.2	/	//	P
4. 5396	12.1	6.0	0.02	38.0	/	//	P
5. 6224	9.2	5.1	0.00	40.2	/	//	D
6. 6577	8.5	4.2	0.00	38.6	/	//	P
7. 6192	9.6	5.2	0.00	38.0	/	/	P
			Tetraploids				
8. 3182	20.8	7.2	4.0	56.0	///	///	E
9. 3789	18.0	6.6	1.2	62.8	///	///	E
10. 4390	20.4	6.6	2.0	69.6	///	//	E
11. 4391	20.2	6.5	3.0	65.0	//	//	E
12. 4830	21.8	7.8	1.6	69.6	///	///	E
13. 5430	11.8	5.2	0.4	66.2	///	////	E
14. 3903	21.2	8.2	1.2	68.2	///	///	D
15. 5114	20.4	8.0	2.0	65.6	//	//	E
16. 5116	19.8	8.6	1.6	67.0	///	///	E
17. 5119	18.8	7.8	0.8	70.0	//	///	E
18. 5120	21.6	7.8	2.8	69.8	//	//	D
19. 5123	23.8	9.4	1.6	70.0	///	//	D
20. 5125	24.0	8.8	2.0	68.8	///	//	E

* Prostrate (P), decumbent (D), and erect (E)

TABLE I (Cont'd)

Accession Number	Length Primary Axis (mm)	Raceme Number	Inflorescence Branching Index	Length Longest Raceme	Raceme Width	Pubescence First Glume	Growth Habit
21. 5131	20.6	9.2	1.2	66.8	///	///	E*
22. 5136	20.4	9.4	2.0	68.0	///	///	E
23. 5137	21.0	8.8	2.4	66.8	///	///	E
24. 5139	18.6	7.6	0.0	67.4	///	///	E
25. 5145	16.0	8.6	0.8	69.6	///	//	E
26. 5146	24.6	8.6	4.0	69.2	//	///	E
27. 3227	14.2	7.8	1.6	56.6	/	//	D
28. 3713	15.6	8.2	0.8	54.4	/	/	D
29. 4565	18.2	7.6	1.6	47.6	//	/	P
30. 5302	22.2	9.0	6.8	67.8	/	//	D
31. 5397	32.8	12.6	6.4	70.0	/	//	E
32. 5398	22.4	9.0	6.8	66.2	/	/	E
33. 5399	17.4	7.8	2.8	62.4	/	/	E
34. 5438	18.2	8.0	0.8	57.2	//	/	D
35. 6866	16.0	6.8	1.6	49.6	/	//	D
36. 7133	17.0	7.2	0.0	57.4	/	/	D
37. 4099	13.0	6.4	0.0	49.2	/	/	P
38. 4636	16.2	8.4	3.2	65.6	/	//	E
39. 6573	15.0	7.2	0.4	51.4	///	///	E
40. 4395	14.0	7.2	0.0	53.4	/	//	D
41. 6263	16.0	7.4	0.0	49.4	/	/	P
42. 5602	17.4	7.2	0.0	55.0	/	/	D
43. 1526(a)	17.8	7.8	0.0	56.8	/	/	E
44. X-98	15.0	4.8	0.0	64.8	/	/	D

* Prostrate (P), decumbent (D), and erect (E)

TABLE I (Cont'd)

Accession Number	Length Primary Axis (mm)	Raceme Number	Inflorescence Branching Index	Length Longest Raceme	Raceme Width	Pubescence First Glume	Growth Habit
			Hexaploids				
45. 2567	33.0	9.0	4.00	73.6	≠	-	E*
46. 4080	23.4	9.6	3.20	84.0	-	-	E
47. 4083	27.4	8.5	3.20	76.8	-	≠	E
48. 4105	27.0	8.2	3.20	71.3	≠	-	E
49. 4106	26.0	8.0	2.40	73.0	-	-	E
50. 3716	26.2	9.6	2.80	76.0	≠	≠	E
51. 5429(b)	30.6	9.6	6.00	71.8	≠	≠	E
52. 4788(b)	19.0	7.0	0.70	72.5	≠	-	E
53. 5112	25.0	8.2	4.05	78.0	-	-	E

* Prostrate (P), decumbent (D), and erect (E).

APPENDIX C

Taxonomic description of the genus Dichanthium according to Stapf (1917) Gramineae. In Prain, D. Flora of Tropical Africa. Vol. 9: 177-180. London.

. . . 36. DICHANTHIUM, Willemet in Usteri, Ann. xviii. (1796), 11.

Spikelets 2-nate, one sessile, the other pedicelled, similar in shape, different in sex, except the lowermost 1 or 2 pairs of each raceme which are (with occasional exceptions in D. annulatum) homogamous (♂ or neuter), in many-jointed shortly peduncled subdigitate, rarely subpanicled or racemosely arranged, racemes; joints and pedicels filiform, solid, disarticulating subhorizontally except the lowest barren pairs; fertile sessile and pedicelled spikelets deciduous, the former with the adjacent joint and pedicel. Florets 2 in the fertile sessile spikelets (lower reduced to an empty valve, upper ☿), 1 in the barren sessile and all the pedicelled spikelets, or neuter, or suppressed. Sessile spikelet dorsally compressed, awned (except the basal homogamous ones); callus small, shortly bearded. Glumes equal, thinly chartaceous; lower usually very obtuse, 2-keeled with narrow sharply inflexed margins; upper boat-shaped, 3-nerved, acutely keeled. Valve of lower floret hyaline, nerveless, of upper floret reduced to a hyaline upwards firmer linear stipe, passing into a slender awn (very rarely finely 2-toothed with the awn from the sinus in a doubtful or aberrant Indian species). Valvule 0 or minute. Lodicules 2, minute, glabrous. Stamens 3. Stigmas exserted laterally at or above the middle or near the tips. Grain oblong, obtuse, dorsally compressed; embryo rather more than half the length of the grain. Pedicelled spikelet awnless; valve if present hyaline, nerveless.--Perennial, very rarely annual, grasses with simple or branches usually many-noded culms, bearded or beardless at the nodes. Panicles usually subdigitate with a short or very short primary axis, rarely the latter elongated; racemes always shortly peduncled. Spikelets small, rarely the male somewhat larger.

Species 8, in the tropical and warm-temperate regions of the Old World.

Lower glume of sessile ☿ spikelets without a semilunar row of long tubercle-based cilia below the hyaline tip; blade margins not revolute ... ... 1. D. annulatum.

Lower glume of sessile ☿ spikelets with a semilunar row of long tubercle-based cilia below the hyaline tip; blade margins at length revolute ... ... 2. D. papillosum.

APPENDIX C (Cont'd)

1. D. annulatum, Stapf. Perennial, densely caespitose, innovations extra- and intra-vaginal. Culms up to over 3 ft. high, sub-erect or geniculate-ascending, usually slender, terete, grooved on alternate sides of internodes, simple or very frequently branched, smooth. Leaf-sheaths terete, tight, striate, glabrous, mostly bearded at the nodes; ligules firmly scarious, oblong, obtuse, up to over 1 lin. long; blades linear, tapering to a fine point, slightly contracted at the base, up to 1 ft. (usually much less) by 1½-2 (rarely 3) lin., glaucous, more or less rigidly glabrous or sparingly hairy often from tubercles, smooth below, more or less rough above, margins cartilaginous and scaberulous upwards, midrib whitish above; lateral nerves 3-4 on each side, firm. Inflorescence subdigitate, erect; common rhachis filiform, 3-8 (rarely 12) lin. long, shortly bearded at the branch axils; branches solitary, usually simple, naked up to 3 (rarely 4) lin., quite glabrous. Racemes 3-9, rarely only 1 or more than 12 (up to over 20), slender, smoewhat flaccid, up to over 2 in. long, pale or flushed with purple; joints and pedicels finely filiform, solid, ½ to almost 1 lin. long, ciliate (sometimes on one side only) or the lowest almost glabrous, uppermost cilia often as long as the joint. Sessile spikelets subimbricate, oblong, obtuse, 1½-2 lin. long, usually that of the lowest pair ♂ or neuter and awnless; callus very small, shortly bearded. Lower glume thinly chartaceous, often with purplish tips, slightly concave, at least above the middle, sharply ciliolate from the middle upwards, otherwise with (rarely without in the African specimens) some long very fine spreading hairs from near the keels, particularly in the upper part, glabrous or sparingly pubescent on the back; upper glume acute, minutely ciliate, glabrous. Valve of lower floret linear to oblong, hyaline, glabrous or ciliolate; awn of upper floret 8-10 lin. long, very fine. Anthers ½ lin. long. Grain oblong, 1 lin. long, dorsally compressed; scutellum over ½ lin. long. Pedicelled spikelet about as long as the sessile, ♂ or neuter, usually darker. Lower glume semiconvolute, up to 13-nerved; lower glume and value as in the sessile or more or less reduced.

2. D. papillosum, Stapf. Perennial, innovations extra- and intravaginal. Culms up to over 3 ft. high, erect or slightly geniculate-ascending, somewhat robust, terete, more or less wiry below, 7-9-noded, sparingly branched, branches suberect. Leaf-sheaths terete, tight, strongly striate, bearded at the nodes, and sometimes ciliate towards the mouth, otherwise glabrous; ligules up to 1 lin. long, truncate or rounded, ciliate; blades linear, tapering to a long fine point, scarcely contracted at the base, up to over 6 in. by 1½-2½ lin.,

APPENDIX C (Cont'd)

rather rigid, glaucous, flat, at length revolute, somewhat rough on the upper side from minute tubercle-based hairs, margins cartilaginous, scaberulous upwards, midrib slender, lateral nerves 3-4 on each side, fine. Inflorescence subdigitate, erect; common rhachis filiform, about 9 lin. long, shortly bearded at the branch axils; branches solitary, simple, naked up to 4 lin., quite glabrous. Racemes 3-5 (or 7 according to Hackel), rather stout, more or less flexuous, about 2 in. long, purplish-grey; joints and pedicels finely filiform, solid, 3/4-1 lin. long, ciliate on both or only on one side, upper cilia longer than the joint or pedicel. Sessile spikelets imbricate, broad-oblong, very obtuse, 2-2½ lin. long; callus very small, shortly bearded. Lower glume thinly chartaceous with tips hyaline and whitish between the keel ends, obscurely concave on the back, minutely asperulous on the keels, long-ciliate from small tubercles placed along the margins and in a semilunar row across the glume just below the hyaline tip, hairy on the back, intracarinal nerves above 5, more marked upwards, upper glume minutely truncate, glabrous. Valve of lower floret linear to oblong, hyaline, glabrous or ciliolate; awn of upper floret up to 9 lin. long, column puberulous. Anthers 1 lin. long. Stigmas exserted terminally or subterminally. Pedicelled spikelet ♂, very similar to the sessile. Lower glume long-hairy all over, up to 13-nerved, upper 3- to sub-5-nerved, ciliolate upwards. Valve oblong, ciliate at the obtuse top . . .

U.A.D. 156a.

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In reply please quote this number.
In antwoord gelieve na hierdie nommer te verwys.
REF. B 11/

DEPARTMENT OF AGRICULTURE,
DEPARTEMENT VAN LANDBOU,
Division of Botany,
Afdeling Plantkunde,
590 Vermeulen Street,
Vermeulenstraat 590,
PRETORIA.

28th September, 1959.

Dr. Robert P. Celarier,
Botany Department,
Oklahoma State University,
Stillwater,
Oklahoma,
UNITED STATES OF AMERICA.

Dear Dr. Celarier,

I must thank you very much for the reprints of the reports of the work done on Old Word Bluestems by you and your co-workers. I have found them most interesting. I must also apologise for not acknowledging some of the other pamphlets received in the past, but I can assure you that they have all been appreciated.

I notice that in your studies you do not mention Bothriochloa glabra or B. radicans. Would you like to receive seed of these as well? If you want more collections of the other species and of Dichantium annulatum I will try to get it for you.

I also noticed that you have considered the possibility of the D. annulatum hexaphloid origenating as a result of hybridisation of the latter with D. aristatum C.E. Hubb. This however is highly unlikely since D. aristatum is, as far as I know, an Australian species and its occurence in S. Africa of a very local nature. In my opinion it is certainly introduced and occurs (except for one other locality) only at Onderstepoort just North of Pretoria, where it just maintains itself, being common in some years and practically absent in others. It does not seem to have spreading much in the 10 years I have observed it. One other record is known from Natal, but again the plant was growing not very far from an agricultural research station. I am sending you this information to clear up the wrong impression that might have been created when these specimens of D. aristatum were sent to you. I suppose that no note to say that it was introduced accompanied the specimens.

I am very interested in the method of detecting polyploids in complex species by measuring pollen grains and stomata. Do you think that there is a possibility that it will also be useful in the investigation of closely allied species? I realise that it is to be used with great caution however.

Yours very sincerely,

CHIEF: DIVISION OF BOTANY.

VITA

Kharaiti Lal Mehra

Candidate for the Degree of

Doctor of Philosophy

Thesis: CYTOTAXONOMIC STUDY OF THE *Dichanthium annulatum* COMPLEX

Major Field: Plant Breeding and Genetics

Biographical:

Personal data: Born in Lahore, West Pakistan, April 15, 1930, the son of the Late Mani Ram Mehra and Nand Rani Mehra.

Education: Graduated from S. D. High School, Lahore, W. Pakistan in 1946; received the Bachelor of Science (Hons.) degree from Delhi University, Delhi, India, with a major in Botany in 1952; received the Master of Science degree from Delhi University with a special paper in Economic Botany in 1954; attended graduate school at Washington University in St. Louis, Missouri, spring, 1958; completed requirements for the Doctor of Philosophy degree in May, 1960.

Professional experience: Research assistant in the Botany Division, Indian Agricultural Research Institute, New Delhi, India, 1955-56; research assistant to Dr. Edgar Anderson, St. Louis, Missouri, spring, 1958; research assistant to Dr. W. L. Brown, Pioneer Hibred Corn Co., Johnston, Iowa, summer, 1959; research assistant in the Agronomy Department, Oklahoma State University, Stillwater, Oklahoma, 1956-59; research assistant to Dr. B. B. Hyde, Oklahoma University, Norman, Oklahoma, fall, 1959.

Professional organizations:

Member: Oklahoma Academy of Sciences, Sigma Xi, Indian Society of Genetics and Plant Breeding, International Society of Plant Morphologists.

Ordinary associate: The Linnean Society of London.