Relationships Within the Dichanthium annulatum complex

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Dichanthium annulatum (Forssk.) Stapf of the tribe Andropogoneae is widely distributed in the tropics and subtropics of the Old World and extends from Australia and nearby Pacific Islands to Northwestern Africa and southward to South Africa. Cytotaxonomic studies by Celarier and Harlan (1955), Celarier *et al.* (1958), Harlan *et al.* (1958), Mehra and Celarier (1958), and Mehra (1960) 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 the agamic complex (Harlan *et al.* 1958, 1961). Morphological and cytological studies of the few hybrids involving the Tropical and Mediterranean types have indicated that they are very closely related (Mehra, 1960). The study reported here describes the mechanisms of variation and probable origin of the morphological types within the complex as a whole.

MATERIALS AND METHODS

Hybrids between different morphological types were produced by Richardson following his emasculation technique (1958) as well as with-

out emasculation where a synthetic sexual plant was used as a female parent. Cytological studies of the microsporocytes were made using the standard aceto-carmine squash technique. Morphological studies are based on field observations as well as on the herbarium specimens filed with the Department of Botany and Plant Pathology, Oklahoma State University.

Results and Discussions

The most conspicuous differences between the four morphological types are summarized in Table I. The type we have called 'Tropical' is usually moderately robust, decumbent with thick racemes; the glumes are broad, blunt and conspicuously covered with long bulbous-based hairs. This type is most common in India and eastward in humid to wet regions. Both diploid (2n=20) and tetraploid (2n=40) forms occur, the former being much smaller than the latter but otherwise very similar.

The South African type in our collection is a large, erect, robust plant with very broad racemes. The glumes are blunt and equipped with a conspicuous fringe of long, bulbous-based hairs. Our accessions are all hexaploid (2n=60) and came from South and East Africa.

The Mediterranean type is erect and fine stemmed with narrow racemes. The glumes are more pointed than the Tropical type and the bulbous-based hairs are rather sparse. It seems to be adapted to desert conditions ranging from the eastern edge of the Indian desert in Rajasthan westward across Pakistan, Afghanistan, Iran, Iraq, Saudi Arabia, Egypt, Tunisia, and Algeria to Morocco. All accessions so far obtained are tetraploids.

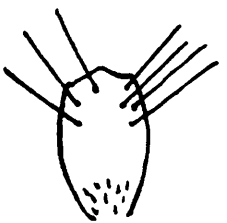
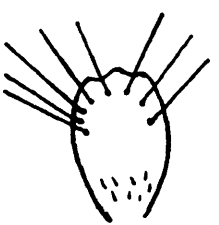
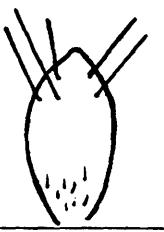
The type called Senegal in Harlan *et al.* (1958) is an extreme form of the desert type with very slender racemes and almost glabrous glumes. The original collections obtained from Bambey, Senegal were tetraploid, but recently very similar, but diploid, forms have been obtained from Kutch and Ajmer, India. It may be, therefore, that the characters of slender racemes and glabrous, pointed glumes may have adaptive value, or may be linked to characters of adaptive value, in very dry regions.

Morphologically, the Mediterranean type differs from the Tropical type in the direction of *Bothriochloa intermedia,* gangetica type. The slender racemes, pointed glumes, reduction of glume hairs and erect growth habit all suggest that the Mediterranean type is an introgression product involving the Tropical type and *B. intermedia,* gangetica type. These forms are sympatric in the gangetic plains of India and the upper Indic plains of West Pakistan. Field observations in 1960 and analyses of field collected populations in 1961 indicate that such introgression does indeed occur in some localities.

Artificial hybrids between several of the possible combinations were made, and cytological data are presented in Table II. In three of the $4n \times 4n$ hybrids hexaploid F_1's were obtained. The fact that unreduced female gametes are functional has previously been reported (Harlan *et al.* 1958, 1961). The hybrid 57-×-1171-1 apparently received 40 chromosomes from the Tropical type female parent and 20 from the Mediterranean type male parent. Morphologically, it is an almost exact synthesis of the South African type and differs from the latter only in being much more sexual than a typical South African type. It is supposed, therefore, that the South African type was produced in nature by this means (Figure 1).

The pairing relationships of chromosomes of hybrids involving various types indicate that clear-cut genomic constitutions are not to be found in the species. Even though hybrid 57-×-1171-1 received a complete set of

TABLE I. CHARACTERISTIC DIFFERENCES BETWEEN MORPHOLOGICAL TYPES WITHIN THE D. ANNULATUM COMPLEX.

Characteristic Differences	Tropical	South African	Mediterranean	Senegal
Chromosome No. (2n=)	20 (A-3242) 40 (A-4099)	60 (A-4080)	40 (A-4830)	20 (A-8452) 40 (A-5430)
Growth Habit	Decumbent	Erect	Erect	Erect
Size	Moderate	Robust	Fine stemmed	Fine stemmed
Width of Raceme	Broad	Very broad	Narrow	Very narrow
Length of Infl. Axis (Average mm.)	10.2 16.5	23.4	21.8	16.0 20.1
Length Longest Raceme (Average mm.)	36.8 58.0	84.0	69.6	59.4 66.2
Glume shape and Hair Pattern				

Wet | Dry condition

Adaptations

40 chromosomes from one parent; the triploid hybrid 59-×-932-1 shows up to 14 bivalents and rather few trivalents. Bivalent formation appears to be genetically controlled and preferential pairing is common in the group.

TABLE II. CHROMOSOME ASSOCIATION IN THE HYBRIDS BETWEEN THE DIFFERENT MORPHOLOGICAL TYPES OF D. ANNULATUM AT METAPHASE I.

Hybrids and Parents (collection No.)	2n	Chromosome Configuration (average and range) I	II	III	IV
Tetraploid Tropical × Mediterranean					
		1.56	22.68	0.47	0.60
57-×-1171-1	60	0-4	22-26	0-2	0-2
(×-98) × 4390					
57-×-1172-1	40	1.34	17.50	0.08	0.64
		0-4	14-20	0-1	0-3
Mediterranean × Tetraploid Tropical					
		6.23	15.53	0.05	0.59
56-×-147-1 4391 × 5296	40	0-14	11-20	0-1	0-2
56-×-188-1 4830 × 5398	60	1.44	27.02	0.02	0.71
		0-4	24-30	0-1	0-3
Tetraploid Tropical × Senegal					
57-×-711-1 (×-98) × 5430	40	1.30	18.05	0	0.65
		0-6	12-20	0	0-4
Senegal × Tetraploid Tropical					
57-×-947-1 5430 × (×-98)	60	3.48	26.15	0	1.0
		2-6	19-28	0	0-4
Tetraploid Tropical × S. African					
57-×-698-1 (×-98) × 4080	50	6.50	16.34	0.65	2.41
		4-8	13-20	0-2	0-4
S. African × Tetraploid Tropical					
57-×-816-1 4083 × (×-98)	50	6.53	18.06	0.66	1.0
		3-10	14-22	0-2	0-3
Tetraploid Tropical × Diploid Tropical					
59-×-932-1 (×-98) × 3242	30	8.74	10.86	0.53	0
		2-11	8-14	0-3	0
Diploid Tropical × Tetraploid Tropical					
56-×-60-1 3242 × 5399	40	2.21	18.05	0	0.42
		0-4	16-20	0	0-2

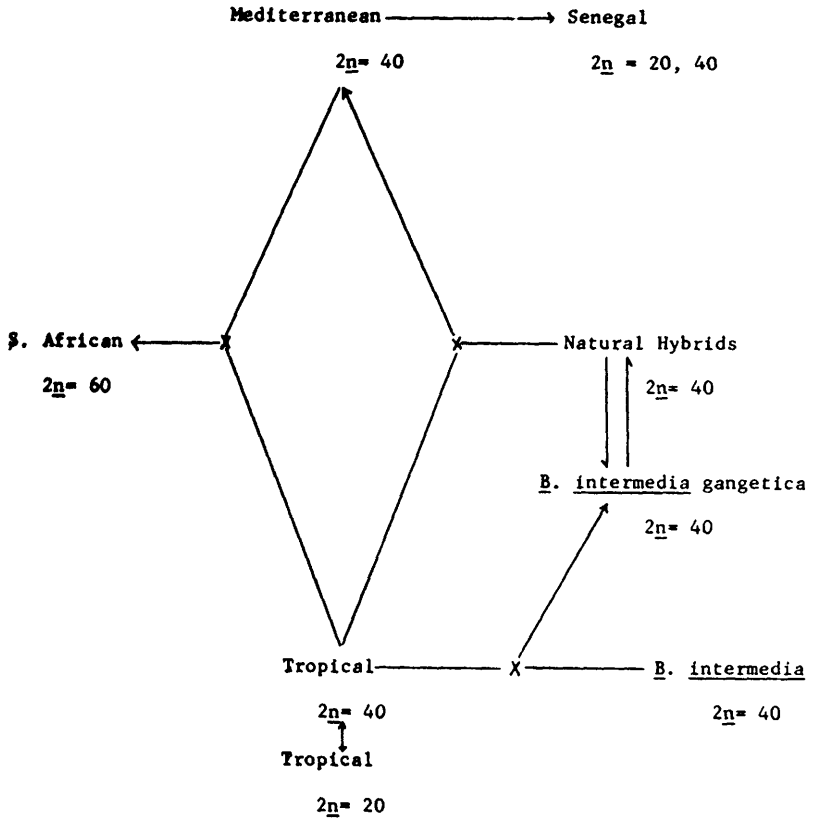


Figure 1. A diagramatic scheme for the origin of morphological types within the *D. annulatum* complex.

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