SECTION A, BIOLOGICAL SCIENCES

Subsection Botany

A Cytogenetical Study of Hybrids between Dichanthium annulatum and D. fecundum—II.[1]

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A previous study (Borgaonkar and de Wet, 1960) of the hybrids between the two tetraploid species *Dichanthium annulatum* (Forssk.) Stapf and *D. fecundum* S. T. Blake, and of the back-cross population with *D. annulatum*, has indicated that the two species are rather closely related, and there is a possibility of gene exchange between them. It was pointed out that *D. fecundum* does not deserve a specific status since it differs from *D. annulatum* in only one major character, that of the bisexuality of the pedicellate spikelet. A follow-up study of the F_2 generation of the hybrid and two back-cross plants was undertaken and will be presented in this paper.

MATERIALS AND METHODS

During the summer of 1960 fourteen F_2 plants were grown from seeds collected from inflorescences which were not bagged, and in the winter of 1960-61 the F_1 hybrid was selfed by covering the inflorescences with paper bags in a plastic house. Eighteen plants were grown during the following summer of 1961. Two of the back-cross plants of *D. annulatum* × *(D. annulatum* × *D. fecundum)* were selfed. Seeds were collected from open inflorescences also, and twenty-three plants were grown. All the plants were grown in a uniform nursery as outlined by Celarier and Harlan (1956). Herbarium specimens have been deposited with the Department of Botany and Plant Pathology, Oklahoma State University, Stillwater.

Cytological studies were made by the standard acetocarmine squash technique. Microsporocytes were fixed in Carnoy's fluid (6:3:1) and stored in 70% alcohol at ±5°C.

EXPERIMENTAL STUDIES

The details of the morphological characters are given in Table I. The collection of *D. fecundum* (A-6525) from Queensland, Australia, is an apomict and *D. annulatum* (X-98) an artificial hybrid which is sexual and self-sterile. Morphological studies on the F_2 plants have shown that the segregation of characters, which would normally be expected in sexual species-hybrids, was not observed. The plants were uniformly decumbent with an average height of 3′ to 3½′. Characters such as hair at nodes, ratio of length of longest raceme/length of primary axis, number of nodes on the inflorescence, number of primary racemes, number of spikelets on a raceme, hair pattern on glume, and chromosome number did not show much variation as is evident from Tables I and II.

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TABLE I. DETAILED MORPHOLOGICAL OBSERVATIONS OF THE PARENTS, F₁ AND SELFED F₂ PLANTS

Culture No.	Fertility of pedicellate spikelet	Hair at nodes of the culm	Hair on leaf sheath	Hair on leaf blade	Hair at ligule	Length of primary axis	Length of longest raceme	Ratio Length of longest raceme. Length of primary axis	Number of nodes	Number of spikelets	Number of Primary racemes
D. annulatum (X-98)	MF	D+++	+	+++	+	11.6	68.5	5.90	3.5	32.2	5.5
D. fecundum (A-6525)	F	D+	+	+	+	10.9	94.1	8.63	2.1	42.7	3.7
F_1 Hybrid	F	D++	+	+	++	9.5	63.6	6.69	2.8	26.6	3.9
F_2 Plant No. -2	F	D++	+	+	++	9.0	65.5	7.28	2.5	29.0	3.5
" -3	F	D++	+	+	++	13.9	68.3	4.91	3.5	27.6	5.0
" -4	MF?	D++	+	+	++	6.0	65.5	10.91	2.0	24.0	3.0
" -5	F	D++	+	+	++	12.9	63.2	4.90	3.3	27.4	4.6
" -6	F	D++	+	+	++	12.4	67.7	5.46	3.3	27.1	4.3
" -7	F	D++	+	+	++	9.4	62.7	6.67	3.0	25.1	4.2
" -8	F	D++	+	+	++	12.1	65.7	5.34	3.3	27.0	4.6
" -9	F	D++	+	+	++	8.3	65.4	7.88	2.6	26.0	3.8
" -10	F	D++	+	+	++	14.5	63.3	4.36	3.5	25.4	4.7
" -11	F	D++	+	+	++	11.8	65.1	5.52	3.1	26.0	4.4
" -12	F	D++	+	+	++	11.3	64.5	5.71	3.2	26.3	4.3
" -13	F	D++	+	+	++	9.0	62.3	6.49	2.9	25.5	4.1
" -14	F	D++	+	+	++	13.3	62.2	4.68	3.8	26.4	4.9
" -15	F	D++	+	+	++	13.9	63.4	4.56	3.6	27.4	4.8
" -16	F	D++	+	+	++	11.9	64.9	5.45	3.2	27.1	4.5
" -17	F	D++	+	+	++	12.6	64.3	5.10	3.0	26.6	4.4
" -18	F	D++	+	+	++	10.2	60.4	5.92	3.2	25.8	4.2
" -19	F	D++	+	+	++	13.5	63.7	4.72	3.4	26.2	4.7

TABLE II. CHROMOSOME BEHAVIOR AT I METAPHASE

Accession or hybrid number	$2n$ =	Chromosome range and average per cell			
		I	II	III	IV
D. annulatum (X-98)	40	0-4	12-18	0-1	1-4
		0.75	15.50	0.08	2.16
D. fecundum (A-6525)	40	0-3	15-20	0-1	0-2
		0.46	18.42	0.03	0.65
F_1 Hybrid	40	0-4	17-20		0-1
		0.73	19.50		0.07
F_2 Plant No. -3	40	0-3	17-20	0-1	0-1
		0.81	19.40	0.18	0.18
" -14	40	0-2	18-20	0-1	0-1
		0.25	19.58	0.08	0.08
" -17	40	0-2	18-20	0-1	0-1
		0.50	19.50	0.07	0.07

De Wet, Mehra and Borgaonkar (1961) have shown from a study of chromosome association in *Dichanthium* hybrids that autosyndetic pairing of chromosomes occurs in this genus. Cytologically there is no indication of any variation from the back-cross population and the chromosome number of the few plants studied was $2n=40$. Details of cytological observations are given in Table II. The association of chromosomes during metaphase I was similar to the parents and the hybrid and a few trivalents and quadrivalents were observed.

DISCUSSION AND CONCLUSIONS

Free gene exchange between apomicts is prevented by the very nature of the reproductive behavior. It is generally accepted that apomixis is genetically controlled (Muntzing, 1940; Gustafsson, 1946-47; Stebbins, 1950; Clausen, 1954). A number of hypotheses have been suggested as to the possible number of genes controlling the exact mechanism (Powers, 1945). In the present study it appears that the apomictic mode of reproduction is dominant to sexual behavior. The latter would have given us a segregating F_2 population which would have shown morphological variation and possibly some chromosomal variation as was observed in some *Bothriochloa* hybrids (Borgaonkar and de Wet, 1961). Morphological observations on the F_2 plants, from F_1 selfed as well as from F_1 open pollinated seeds, have not shown segregation of characters which would normally be expected. The two species are readily distinguishable as *D. fecundum* which has bisexual pedicellate spikelets and *D. annulatum* which has male-fertile pedicellate spikelets. In the F_1 hybrid the character of bisexuality was dominant and in the back-cross with *D. annulatum* it segregated in the ratio of 1:1 indicating its control by a single pair of genes (Borgaonkar and de Wet, 1960). In the F_2 generation it should have segregated in 3:1 ratio. Instead all the plants were found to possess bisexual pedicellate spikelets. Even in various other characters studied, variation, other than due to environmental or non-genetical factors, was not observed (Table I). In the back-cross study considerable variation was found in about ten characters (Borgaonkar and de Wet, 1960).

The two back-cross plants, both possessing bisexual pedicellate spikelets gave, from selfed and open pollinated seeds, ten plants possessing bisexual pedicellate spikelets and 13 plants possessing male-fertile pedicellate spikelets. This segregation could be explained as follows. Let us assume *D. annulatum* (X-98) to possess *ss* genes for sexuality and *ff* genes for male fertility of the pedicellate spikelet recessive to *SS* genes for apomictic behavior in *D. fecundum* and *FF* genes for bisexuality of the pedicellate spikelet. Then these two species on crossing will give, and have given, F_1 hybrids which are *Ss Ff,* i.e., they possess bisexual pedicellate spikelet and are apomictic as observed in this study. Such F_1 hybrids, *SsFf* on back-crossing with *D. annulatum ssff* will give four possible types of plants *FfSs, Ffss, ffSs,* and *ffss.* The two back-cross plants involved in this study had bisexual pedicellate spikelets and segregated upon selfing, indicating that they had possibly an *Ffss* constitution. The above explanation is the simplest based on present evidence, but it may be that the mechanisms are more complex. Plants where apomixis is dominant have also been reported in the literature (Stebbins, 1950).

In conclusion it may be observed that the apomictic mode of reproduction seems to be dominant in the cross *D. annulatum* × *D. fecundum* and there is no segregation in the F_2 of the character of bisexuality of pedicellate spikelet and other morphological characters. No cytological variation was noticed. A study of selfed and open progeny of two back-cross plants has indicated that apomixis may be simply inherited.

LITERATURE CITED

Borgaonkar, D. S. and J. M. J. de Wet. 1960. A cytogenetical study of hybrids between *Dichanthium annulatum* and *Dichanthium fecundum.* Phyton (Argentina) 15: 137-144.

.... 1961. Segregation among partial apomictic *Bothriochloa* hybrids. Am. J. Botany 48: 545 (Abstract).

Celarier, R. P. and J. R. Harlan. 1956. An Andropogoneae garden in Oklahoma. Taxon 5: 183-186.

Clausen, J. 1954. Partial apomixis as an equilibrium system in evolution. Caryologia 6: 469-479.

de Wet, J. M. J., K. L. Mehra and D. S. Borgaonkar. 1961. Chromosome Association in *Dichanthium* Hybrids. Cytologia 26: 78-82.

Gustafsson, A. 1946-47. Apomixis in higher plants. I, II, III. Lunds Univ. Arsskrift 42: 1-66, 43: 71-178, 43: 183-370.

Muntzing, A. 1940. Further studies on apomixis and sexuality in *Poa.* Hereditas 26: 115-190.

Powers, L. 1945. Fertilization without reduction in guayule *(Parthenium argentatum* Gray) and a hypothesis as to the evolution of apomixis and polyploidy. Genetics 30: 323-346.

Stebbins, G. L., Jr. 1950. Variation and evolution in plants. Columbia University press. New York. 643pp.